

Fast females, slow males: accelerated ageing and reproductive senescence in *Drosophila melanogaster* females across diverse social environments

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Abstract

Females and males typically differ in lifespan, patterns of ageing, and reproduction. General explanations for variation in the magnitude of this sex-specificity remain elusive, and the role of the social environment in this context is under-explored. Sexual selection theory predicts that males should adopt a “live fast, die young” strategy, as their fitness is likely to be contingent on intense investment to achieve success in competing for potentially few matings. However, there is a growing realization that sexual selection can act on a much broader suite of “general performance” traits than only those directly related to mating competition. This, combined with frequently observed high costs of reproduction in females, makes an alternative prediction—that ageing and reproductive senescence can be high for females, and could potentially exceed what is seen in males. We tested these contrasting predictions in the fruit fly *Drosophila melanogaster*, using assays in which both sexes competed for reproductive opportunities over their lifetimes within varying socio-sexual environments. Females consistently exhibited “live fast, die young” life histories, whereas males had significantly longer lifespans and showed only limited declines in age-specific fitness and mating performance. We also identified new same-sex exposure effects—females housed with females exhibited faster reproductive ageing at a marginal lifespan cost, whereas corresponding males maintained higher courtship and activity with age, with no detectable effect on lifespan. The results highlight the crucial importance of social environments to the study of ageing and fitness. The possibility that rapid reproductive senescence is widespread in females is key to broadening our holistic understanding of the biology of sex differences in ageing and reproduction.

Keywords: *Drosophila*, life history, fitness, senescence, sex differences, sexual selection

Introduction

Females and males often have different lifespans, rates of ageing, and reproductive schedules (Bronikowski et al., 2022; Colchero et al., 2016; Lemaître et al., 2020b). Yet there remains a long-standing theoretical prediction that females should be the longer-lived sex because males are generally under stronger sexual selection (Bonduriansky et al., 2008; Trivers, 1972). Anisogamy underpins fundamental sex differences in life-history strategies of males and females (Schärer et al., 2012; Trivers, 1972), with males limited by the number of receptive females and the requirement to compete for mating opportunities or to fertilize eggs (Bateman, 1948). Following from this is the expectation that sex differences in lifespan, ageing, and reproductive success can result from sex differences in the allocation of limited resources that drive trade-offs between growth, reproduction, and survival (Lemaître et al., 2024; Stearns, 1989). Sexual selection should therefore favor greater investment into reproduction over maintenance in males, and the opposite pattern in females (Bregndahl et al., 2018). Consistent with this idea, males typically invest more heavily into the expression of sexually selected traits than do females, often at the cost of maintaining overall body condition (Harshman & Zera, 2007; Lemaître

et al., 2020a). Moreover, the pursuit of mating opportunities by males can increase mortality risks from environmental or extrinsic factors such as predation (Belwood & Morris, 1987; Godin, 2003; Tuttle & Ryan, 1981), parasitism (Cade, 1975), or intrasexual combat (Clutton-Brock & Isvaran, 2007; Lizé et al., 2014) over that of females (Bonduriansky et al., 2008). Consequently, at least outside a strongly kin-selected context, males are predicted to suffer from shorter lifespans, faster ageing, and sharper reproductive declines than are females (Harshman & Zera, 2007; Reznick, 1992).

The fundamental sex differences in gametes, mortality risks, lifespan, and reproductive costs outlined above are manifested as divergent life-history strategies, and they predict that males should generally adopt a “live fast, die young” life-history strategy in contrast to females (Reznick, 1992; Stearns, 1989). However, there are growing challenges to the generality of this view (Archer et al., 2012; Lemaître et al., 2020b; Travers et al., 2015). These stem from two main sources: an under-appreciation of the breadth of traits influenced by sexual selection, and of the importance of the social and sexual environment. For example, sex-specific selection may act on traits that are positively genetically correlated with lifespan in males, such as “general performance” traits (Lailvaux & Irschick, 2006), as well as traits di-

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rectly involved in mating competition. This is expected to potentially slow senescence in males (Bonduriansky et al., 2008). The intensity and frequency of male–female mating interactions is also important in this context as it can influence the magnitude of the costs of reproduction expressed (Chapman et al., 2003) and thus sex-specific ageing rates (Maklakov & Lummaa, 2013; Promislow, 2003). For example, male sexual traits can affect female lifespan directly, through effects on females of courtship receipt and mating attempts (Flintham et al., 2018), or indirectly through effects of pheromones or other cues (Booth et al., 2022; Maures et al., 2014). Furthermore, in realistic mixed sex environments, both sexes will have the opportunity to continuously influence the costs of reproduction experienced by the other. Indeed, continuous exposure to the opposite sex is expected to elevate costs of reproduction in females above those for males, and thus shorten female lifespan. Exposure to males can also elevate female ageing by shortening the age at which age-dependent mortality rates increase (Bonduriansky, 2014). Therefore, the existence of high costs of reproduction and elevated rates of ageing in females challenges the prevailing view and actually predicts that there should be more rapid ageing in females than males (Bonduriansky et al., 2008; Graves, 2007; Maklakov & Lummaa, 2013; Promislow, 2003). At present, direct experimental tests of these contrasting predictions are remarkably limited. In particular, we lack studies that also include effects due to social and environmental variation, both of which have significant, and under-appreciated, effects on sex differences in lifespan and ageing (Austad & Fischer, 2016; Kawasaki et al., 2008).

The broader sociosexual environment can influence the costs and benefits of reproductive investment in a sex-specific manner. For males, the presence of same sex rivals can increase investment into competitive traits, such as sperm number, ejaculate volume and composition, and mating duration, to combat perceived elevated sperm competition risk (Bretman et al., 2013; Cook & Wedell, 1996; Dore et al., 2021; Gage, 1991; Simmons et al., 1993; Wedell et al., 2002). Similarly, females exposed to other females can significantly alter their investment in egg production (Bailly et al., 2023; Borg et al., 2006, 2012; Fowler et al., 2022; Pilakouta et al., 2016). However, despite the potential importance of both same and opposite sex interactions on fitness, the effects of social environments are only rarely considered in studies of ageing (though see Rostant et al., 2023; Zajitschek et al., 2009). To date, we lack experimental studies that have simultaneously measured both lifespan, ageing rates, and overall fitness in both sexes under socially mixed competitive contexts.

In this study, we used the *Drosophila melanogaster* fruit fly system, which is a well-established, powerful model for studies of ageing and fitness (Bateman, 1948; Harrison et al., 2024; Piper & Partridge, 2018; Rose & Charlesworth, 1981). In this well-studied species, females are frequently suggested to live longer than males (e.g., Austad & Fischer, 2016). However, sex differences in lifespan can be modulated by environment and social factors, including diet (Chippindale et al., 1997; Magwere et al., 2004), mating status (Hoffman et al., 2021), and sex ratio (Rostant et al., 2020), such that males can outlive females. Our aim here was to test the competing predictions for which sex would show more rapid ageing and reproductive senescence under a range of socio-sexual environments. We compared, under ecologically relevant experimental designs, the fitness and ageing rates of both sexes kept alone, or exposed to same, mixed or opposite sex individuals. We predicted the emergence of sex differences across all key life-history traits—increased exposure to the opposite sex would decrease lifes-

pan and increase the rate of ageing for females, but not for males.

Methods

Experimental rationale

The experimental rationale was to expose individual “focal” males and females to varying social group treatments ($N = 40$ per sex: treatment combination; Figure 1) for 5 days out of every 7 days, then place all focal flies in a new vial on their own before giving them, on the next day, the opportunity to mate with a young virgin mating partner for 24 hr (to yield a standardized measure of age-specific reproductive output that could be compared across all treatments). Focal individuals were then returned to their 5 days social treatments and exposed to new, young competitors. This was repeated weekly until all focal individuals had died. A key distinction of our study over related previous work is that we followed mated individuals throughout their life to obtain individual-level measures of key life-history traits. The standardized weekly mating opportunity in our experimental design allowed for comparable fitness measures across the social treatments to estimate how lifetime reproductive effort might differ between the sexes and across different socio-sexual environments.

Social environments (Alone, Same Sex, Mixed Sex, Opposite Sex) were chosen to vary exposure to the same and the opposite sex. Therefore, some social environments also contained eggs and larvae. Males and females might also differentially alter the physical environment (e.g., microbiome) in a manner that could then impact male and female life-history traits. We considered each of these factors to be important parts of the broader social environment, and so included this variation to bring ecological relevance to our experiment.

Dahomey source population

Focal flies for the experiments were obtained from the outbred, laboratory-adapted wild type (WT) Dahomey population of *D. melanogaster*. This Dahomey population has been maintained at large population sizes on standard sugar yeast agar (SYA) medium (100 g brewer’s yeast, 50 g sugar, 15 g agar, 30 ml Nipagin, and 3 ml propionic acid per litre of medium) with overlapping generations to preserve high levels of naturally derived genetic variation. The use of a laboratory-adapted population that has reached genetic equilibrium is advantageous as it avoids the potential for differential gene-by-sex-by-environment interactions that could occur with flies sampled directly from the wild, which could confound social environment treatment effects. We note that the husbandry regimes of the population cages are unlikely to have exerted directional, sex-specific selection on life histories (Houle & Rowe, 2003; Magwere et al., 2004; Sgrò & Partridge, 2000, 2001).

Fly collection and maintenance

All flies used (experimental flies and competitors/mating partners) were maintained and raised using the same culturing procedures. All social treatment and mating assay competitors carried the recessive scarlet eye color mutation. This phenotypic marker had been backcrossed into the Dahomey WT population >4 times, and this population was maintained in cage cultures as per the standard Dahomey cages. All flies were raised and maintained on SYA medium. Flies were kept at 25 °C in ~50%–60% relative humidity and under 12h light:12h dark

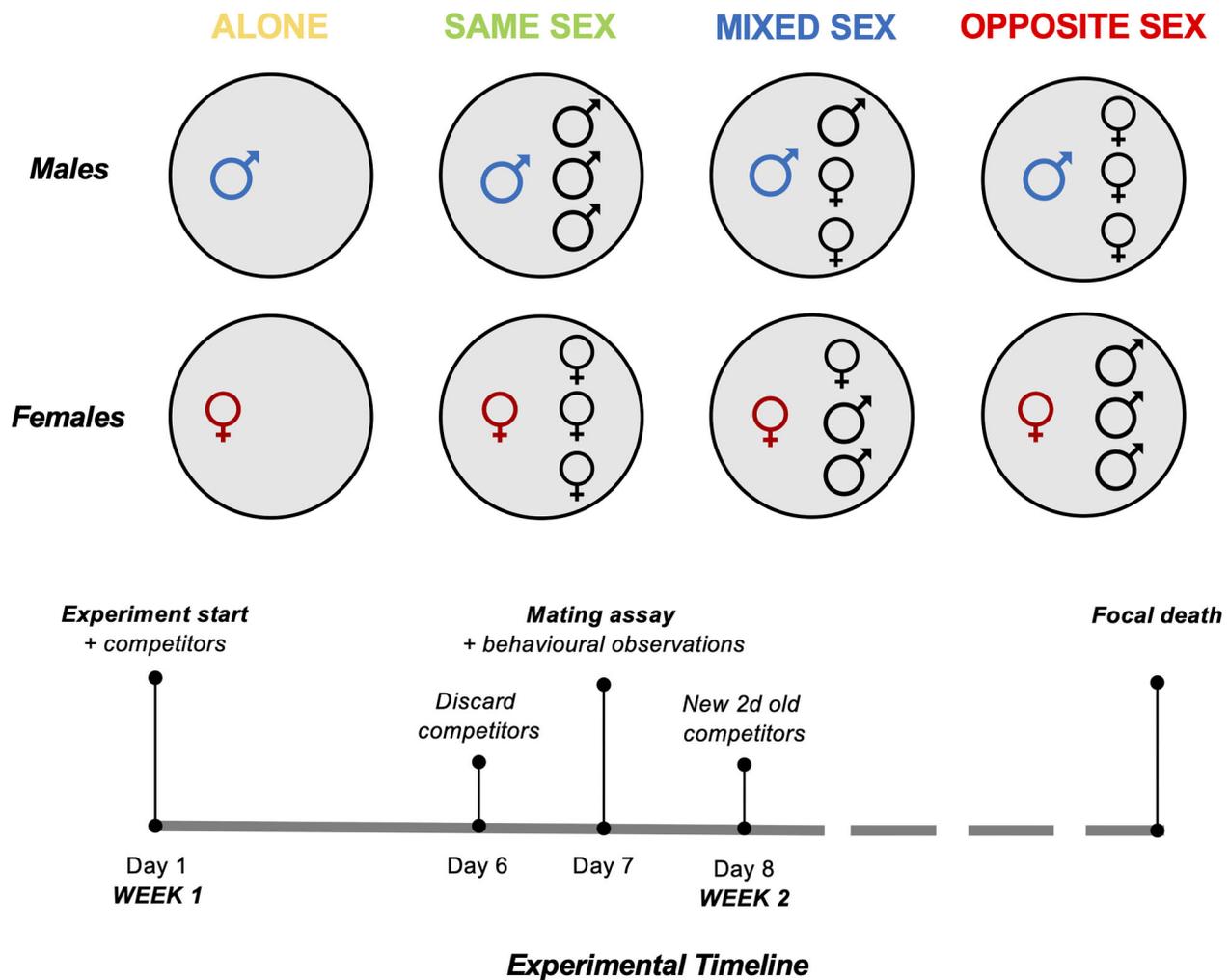


Figure 1. Experimental design to compare sex differences in lifespan, ageing, fitness, and behavior in response to exposure to same and opposite sex environments. Male and female *Drosophila melanogaster* were exposed to different social environments over their whole lifetimes in a 7-day repeating cycle: Alone (one focal per tube), Same Sex (one focal, three non-focals of the same sex per tube), Mixed Sex (one focal, one non-focal of the same sex, and two non-focals of the opposite sex), or Opposite Sex (one focal, three non-focals of the opposite sex). At the start of the experiment, we randomly assigned 2 days male and female flies ($N = 160$ males; $N = 160$ females; $N = 40$ flies per sex: treatment combination) to one of the four social exposure treatments (Day 1). After 5 days of social exposure, focal flies were isolated (Day 6) and then each given 24 hr of exposure in mating vials to a virgin scarlet-eyed partner of the opposite sex (one focal, two non-focal per vial) (Day 7). We observed and scored precopulatory behaviors in the first 2 hr following introduction in these mating vials and then left the pairs together for 24 hr. After 24 hr, focal flies were placed back into their respective social treatments with new, young non-focal flies (1–3 days at the start of each 7-day renewal) for another 5 days. Offspring from mating vials were counted after 12 days and used as a weekly indicator of individual fitness.

conditions. Eggs were collected from yeasted grape juice agar plates divided equally into four bottles with SYA for two generations, to standardize the rearing environment and thus minimize parental effects on offspring phenotypes. F2 flies (focal individuals used in this study) were collected into bottles containing SYA within 24 hr of emergence and left for 24 hr to freely interact/mate prior to the experimental setup. Experimental flies were reared at standardized densities to minimize any environmentally determined variation in body size that could confound social treatment effects.

Exposure of focal individuals to variation in same and opposite sex social environments

Following eclosion, 1 day old, mated focal flies were placed into individual glass vials (24×75 mm, containing 7 ml of SYA medium) and randomly assigned to one of the four social treatments: social isolation (Alone), with competitors of the same sex (Same Sex), in an equal sex ratio (Mixed Sex), or with competi-

tors of only the opposite sex (Opposite Sex). All competitors were three non-virgin scarlet flies 1–3 days post-emergence (Figure 1). Focal flies were kept in these social treatments for 5 out of every 7 days. On the sixth day, the scarlet competitors were discarded, and the focal fly was moved into a new SYA vial for 24 hr prior to the mating assay. During the 5 days social exposure periods, dead scarlet competitors were removed and replaced with a new scarlet from the same cohort (same age/sex). Deaths and censors of focal flies were recorded daily until all focal files were dead. At the end of each weekly social exposure period, old vials were kept for a further 12 days for all offspring to eclose and to allow the number of offspring produced by focal individuals to be determined by genotyping offspring based on their eye color.

Measurements of reproductive activity and fitness

Every 7 days, a virgin scarlet mating partner (1–3 days post-emergence) was placed into each mating vial via aspiration us-

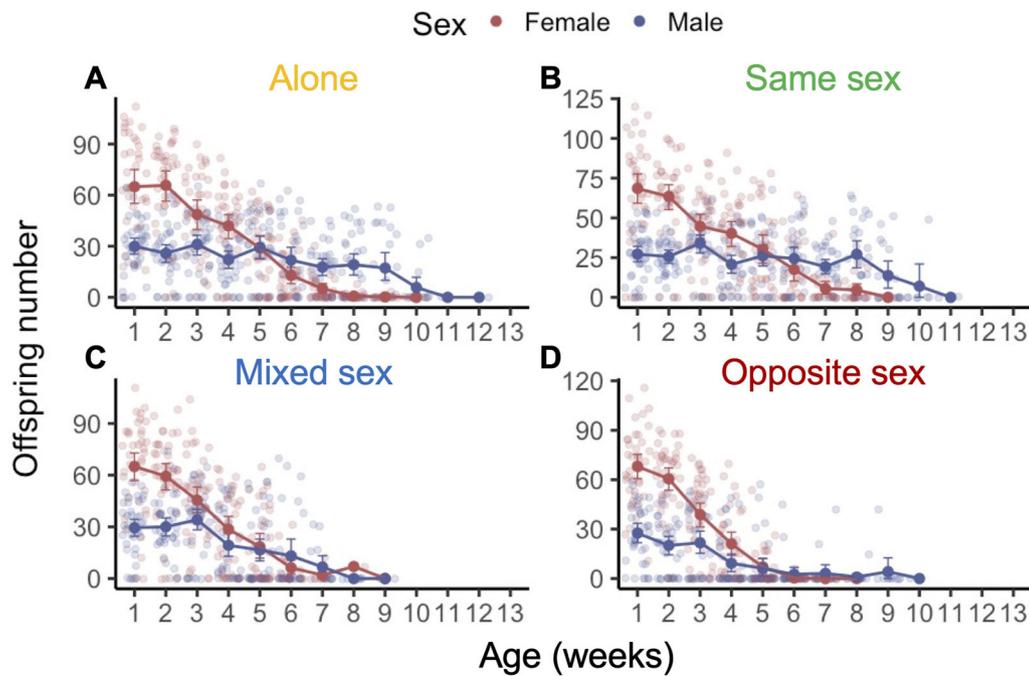


Figure 2. Overall reproductive senescence was greater in females in comparison to males. Comparison of female and male reproductive effort from the weekly mating exposure treatments for each of the four social exposure treatments (A–D). Plots depict the raw data, the mean, and the standard deviation for each week that we sampled reproductive output.

ing an electronic pooter. We then immediately observed and recorded the mating behavior of mating pairs for the first two hours of their pairing. Behavioral scans were scored anonymously with respect to social treatment. Scoring occurred at 5-min intervals using a “scanning” approach. We scored several key behaviors: (a) orientation of the male toward the female, (b) singing, (c) female chasing, (d) attempted mating, (e) mating, (f) activity that was unrelated to precopulatory behavior, and (g) inactivity. Due to logistical constraints, not all individuals were observed over the full course of their lifespan. However, all mating assays were conducted on a weekly basis even if the behavioral scoring did not take place. Mating pairs were left for 24 hr after which focal flies were moved into new social treatment SYA vials with novel, 1–3 days *scarlet* social competitors. Mating vials were kept for a further 12 days to quantify fitness from the number of emerged offspring (Figure 2).

Post hoc measurement of additional progeny

Two of the social treatments for each sex (Mixed and Opposite Sex treatments) comprised focal males and focal females maintained with the opposite sex for 5 out of every 7 days (in addition to the 24 hr mating windows). Therefore, individuals in these treatments could have additional mating opportunities. To post hoc test whether this resulted in flies from Mixed or Opposite Sex treatments producing significantly more offspring overall, and thus whether these additional reproductive opportunities altered life-history patterns, we also counted some of the progeny samples obtained from the 5 days social treatment periods: early-life (Weeks 1 and 3), mid-life (Weeks 6 and 7), and late-life (Week 10). Due to logistic constraints, we chose to sample 5 weeks spread across the lifespan to estimate fitness during the social exposure treatments. We genotyped the adult offspring sample (*scarlet* versus WT) to assign parentage to the focal individuals and give the total number of additional offspring

produced in all treatments over the 5 days social environment exposure periods. To calculate the number of extra offspring produced each day (to be comparable to the offspring counted from the 24 hr mating assay periods), we divided each of the total offspring counts by 5 (number of days in the treatment) to get a daily offspring value. For males, we then divided the daily offspring value by 2 (for males in Mixed Sex groups) or 3 (for males in Opposite Sex groups) to estimate the number of offspring produced per female per day during their social treatments. This gave us an average additional offspring count for each focal individual during their early-, mid-, and late-life periods. We chose to analyze the additional progeny in this way because the incomplete sampling across weeks, combined with some treatments having additional progeny versus no progeny, made it difficult to analyze offspring in a weekly age-specific reproduction model.

Statistical analyses

All data analyses were conducted using R v 4.2.1 (R Development Core Team, 2020). For each of the trait and fitness models, we first fitted generalized linear mixed models (GLMMs) with different distributions and families using the *glmmTMB* (Brooks et al., 2017) package. Model fit was then assessed using the *DHARMA* (Hartig, 2020) package, and the best model was chosen from Akaike information criterion comparisons. We ran separate models for each sex. Models included treatment, week, and their interaction as fixed effects, and block was added as a random effect to account for any differences between the experimental blocks. Where there was significant zero-inflation, we ran zero-inflated models (for fitness) and hurdle models (for pre-copulatory traits). Courtship and age-specific reproduction models included quadratic age terms to account for nonlinear effects of age, and all age-related models included fly ID as a random effect to account for repeated individual measures. Pre-copulatory trait data were overdispersed, so we

included an observation-level random effect in these models (Harrison, 2014). There was significant zero-inflation present in the reproduction and behavioral models for both sexes. We ran negative binomial zero-inflated and hurdle models that included the interaction between treatment and week, and the quadratic age term, in the zero-inflation model. The two models did not significantly differ, so we chose to interpret the zero-inflated model, which treats some zeros as true zeros (i.e., loss of fertility rather than absolute failure to mate). Hence, we report the probability for each treatment group to produce zero or some offspring (zero-inflated model) and the conditional model (when offspring counts > 1). We ran analysis of variance (ANOVA) tests (type II for models with only fixed effects, type III for models with interaction terms) on the final models to obtain significance of fixed effects. An alpha of 0.05 was used to determine significance. Summary tables of the output for all models are provided in the [Supplementary Material \(Tables S1–S9\)](#).

Survival curves for each treatment and sex included censored individuals, and survival data were plotted by using Kaplan-Meier curves. We ran a Cox proportional hazards regression with sex, social treatment, and their interaction, as fixed factors in the full model. As sex was a significant predictor of mortality hazard, we ran separate models for males and females to test for effects of social treatment on mortality. Log-rank tests with a Bonferroni p -value adjustment were conducted to obtain pairwise comparisons for each sex-specific model. To test for sex-specific mortality and ageing patterns, we ran Bayesian trajectory analysis on the survival data separately for each sex, using the *BaSTA* (Colchero et al., 2012) package (v 1.9.5). We first used the *multibasta* function to fit several models with different mortality functions (exponential, Gompertz, Weibull, and logistic) and shapes (simple, Makeham, and bathtub). The model with the lowest deviation information criterion value was chosen as the final model. The best model for both males and females had a Gompertz mortality function and a Makeham shape parameter. Pairwise comparisons between treatments for each sex were obtained using the mean Kullback–Leibler discrepancy calibration, where values greater than 0.8 strongly indicate a true difference.

We then tested how reproductive effort might change as a function of age in both males and females across the weekly mating windows. Preliminary data visualization showed potential nonlinear age effects on reproduction, hence models included a quadratic term for age (time²) and its interaction with treatment. To account for greater early- than late-life reproduction, we calculated individual fitness (Λ_{ind}) from the lifetable of age-specific reproduction. We constructed a Leslie matrix of the offspring counts for each week for every individual until their death. Λ_{ind} is a rate-sensitive measure of fitness that weights early reproduction more heavily than later-life reproduction so that individuals who reproduce relatively more in early life have higher values of Λ_{ind} (Lind et al., 2021). The best-fitting models had a Conway–Maxwell–Poisson distribution and included treatment as a fixed effect and block number as a random effect.

We next investigated how pre-copulatory performance in males and females might change with age and treatment using the weekly behavioral score data. As there was significant zero-inflation, we included treatment, age, and age² as fixed effects (additive effects only, no interactions) in the zero-inflated component of a negative binomial hurdle model. The models were identical for males and females.

For mating effort, we counted the number of matings observed during each 2-hr behavioral assay. Mating generally occurs for 20 min; hence, multiple matings were recorded only if there was a “break” in scoring a mating between mating observations. For females, the best-fitting model had a Poisson distribution and included treatment and age, and their interaction, as fixed effects. For males, we also included treatment and age (additive effects only, no interaction) as terms in the zero-inflated component of a negative binomial hurdle model to account for significant zero-inflation.

For activity, the best-fitting model had a negative binomial distribution and included treatment and age, and their interaction, as fixed effects. For females, we also included age in the zero-inflated component of a negative binomial hurdle model to account for significant zero-inflation.

We conducted post hoc tests of whether additional progeny from the social treatments changed patterns of age-specific reproduction for males and females. We included the absolute progeny counts to the mating assay offspring counts and reran the age-specific reproduction models for males and females. The models combined counts for Weeks 1–3 (early), Weeks 4–6 (mid), and Weeks 7–12 (late).

Results

Overall reproductive senescence was greater in females in comparison to males

Among males that produced offspring, there was no effect of social treatment on offspring number, and no interaction between offspring number and age (ANOVA: treatment \times age: $\chi^2 = 0.26$, $df = 3$, $p = .97$; treatment \times age²: $\chi^2 = 0.33$, $df = 3$, $p = .95$; [Figure 2](#)). Thus, reproductively active males did not show evidence of reproductive senescence across any of the social environments tested. However, analyses of the data for all males showed that males from Mixed Sex and Opposite Sex treatments were significantly more likely to produce no offspring as they aged (mixed sex \times age: $z = 3.74$; $p < .001$; opposite sex \times age: $z = 4.08$; $p < .001$) in comparison to males held alone (alone \times age: $z = -0.13$; $p = .89$) or males from the Same Sex treatment (same sex \times age: $z = 0.07$; $p = .94$).

In contrast, across all social environments, females produced significantly fewer offspring as they aged, indicating the existence of widespread reproductive senescence (ANOVA: age: $\chi^2 = 1.76$, $df = 1$, $p < .001$; [Figure 2](#)). The likelihood of zero offspring production by Opposite Sex females (who experienced constant harassment from young males) also showed a significant increase with age (zero-inflated model: opposite sex \times age: $z = 3.76$; $p < .001$). There was a strong, nonlinear effect of age on offspring production for focal females from the Same Sex groups, with these females kept with other females producing significantly more offspring in early/mid-life than females from other social treatments (conditional model: same sex \times age²: $z = 2.84$, $p = .005$).

Reproductive effort was greatest in early life, which is the period that is key to determining an individual’s overall fitness. We calculated an individual fitness measure (Λ_{ind}), which accounts for the remaining lifespan of each individual and weights early life more heavily than late life reproduction (see the *Methods* section). For males and females that reproduced at least once ($\Lambda_{\text{ind}} > 0$), we found no effect of social treatment on Λ_{ind} (ANOVA males: treatment: $\chi^2 = 1.41$, $df = 3$, $p = .70$; females: treatment: $\chi^2 = 1.86$, $df = 3$, $p = .60$; [Supplementary Figures S1 and S2](#)). This

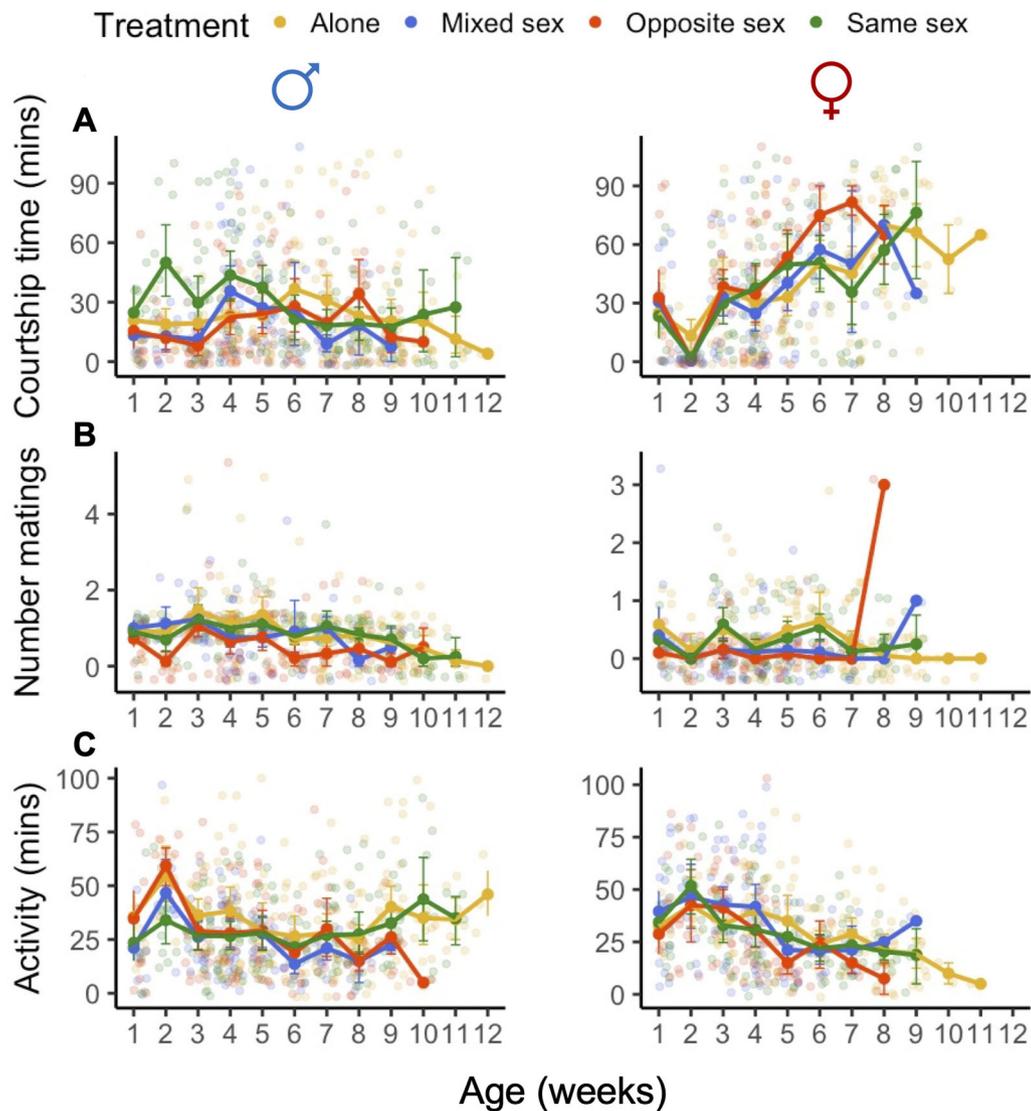


Figure 3. Pre-copulatory behavior and activity levels also declined significantly with age in females (right panels) but not males (left panels). (A–C) Behavioral observations made during a 2 hr observation period during the weekly mating exposure phase. Focal males and females were scored on their courtship effort (for males, male partner courtship effort for females) (A), the number of matings (B), and when focal flies were active in a manner unrelated to mating (C) (see the *Methods* section). Plots depict the raw data and the mean and standard deviation for each social exposure treatment for each week that we scored behavior during the mating assays.

surprising result suggests that reproductive effort was greatest during early life, across all social treatments, and for both sexes. Therefore, additional reproductive effort in later life did not significantly increase an individual's fitness.

Pre-copulatory behavior and activity levels also declined significantly with age in females but not males

We then tested whether pre-copulatory behavior also differed across the social treatments. This allowed us to examine whether males or females were adopting contrasting reproductive strategies, and whether any differences in behavior were age dependent. For courtship effort, we first combined counts for all pre-copulatory courtship behaviors (orientating, tapping/touching, singing, chasing, and attempting to mate) to obtain an index of total courtship effort during the weekly behavioral mating assays conducted across all treatments. Males

from the Opposite Sex treatments were significantly more likely to refrain from courting virgin females in the mating assays in comparison to males from the other social treatments (zero-inflated hurdle model: $z = 2.52$; $p = .01$; **Figure 3A**). Intriguingly, in these same assays, the likelihood that males were observed courting females increased significantly with age (zero-inflated hurdle model: age: $z = -2.73$; $p = .006$; **Figure 3A**). Analyzing only males observed to court females, we observed that the Same Sex treatment males showed lower courtship effort with age than did males from other social treatments (conditional model: same sex \times age: $z = -1.97$; $p = .05$; **Figure 3A**). In contrast, females showed no social experience- or age-related decline in attractiveness, and were courted by virgin males at similar levels in late- and early-life (ANOVA age: $\chi^2 = 1.93$, $df = 1$, $p = .16$; treatment: $\chi^2 = 3.81$, $df = 3$, $p = .28$; **Figure 3A**).

Males from all social treatments maintained their mating effort as they aged (**Figure 3B**). The probability of not mating in

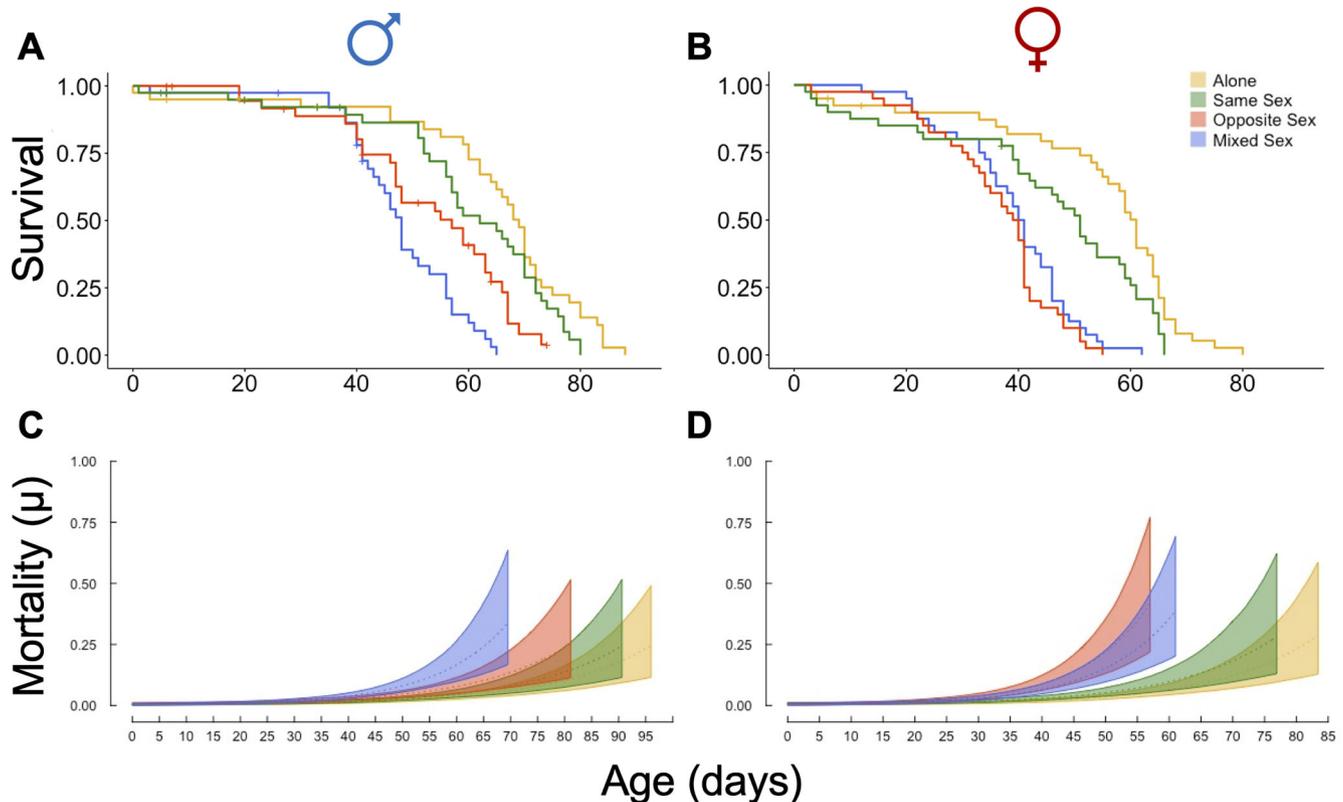


Figure 4. Males consistently outlived females and females aged rapidly when their social group contained males. (A, B) Survival probability for males (A) and females (B) in the different social exposure treatments. Censored individuals are indicated by a cross. (C, D) Mortality rate plots show the mean estimated mortality rate (dotted line) and 95% confidence interval (ribbon) for males (C) and females (D) for each social exposure treatment. Obtained from BASTa models (see the Methods section).

the weekly mating assays was significantly higher for Opposite Sex treatment males (zero-inflated hurdle model: $z = 6.09$; $p < .001$), and this increased significantly over time (zero-inflated hurdle model: $z = 7.74$; $p < .001$). However, among males from all social treatments that did mate, there was no significant decline in mating effort across time (ANOVA age \times treatment: $\chi^2 = 3.66$, $df = 3$, $p = .31$; Figure 3B). Females were reluctant to mate in the weekly mating assays across all social treatments, and this did not change with age (except for a single Opposite Sex group female that mated three times in her final mating assay; ANOVA age \times treatment: $\chi^2 = 8.57$, $df = 3$, $p = .04$; Figure 3B).

Finally, we tested whether there were age, sex, or social treatment effects on the general activity rates of flies, as a proxy for sexual and non-sexual performance/health. We first calculated a measure of activity rate by counting the number of activity scores and multiplying the total by 5 (for the 5 min period of each behavioral scan in the weekly mating assays). Only males that were kept with females (Opposite Sex treatments) showed significant age-related declines in activity rate (Figure 3C). Surprisingly, males kept with same sex rivals even slightly increased their activity levels as they aged, indicating potential positive effects of young rivals on a male's performance (Figure 3C). Conversely, females were significantly more likely to become inactive as they aged (zero-inflated hurdle model: age: $z = 2.05$; $p = .04$; Figure 3C). Females that were active also showed the greatest activity level declines in mid-life (conditional model: age²: $z = -2.93$; $p = .004$).

Males consistently outlived females and females aged rapidly when their social group contained males

Males outlived females across all social treatments. However, exactly how social group composition influenced lifespan was sex-specific (Figure 4A). As expected, both sexes had the longest lifespans when kept mostly on their own. Exposure to same sex rivals resulted in no detectable reduction in male lifespan (log-rank test: $p = .40$; Figure 4A), whereas exposure to females significantly shortened it (Opposite Sex: log-rank test: $p > .001$). Exposure to both rivals and females had the most marked effect and significantly reduced mean male lifespan further, to just 44 days (Mixed Sex: log-rank test: $p > .01$; Table S1). For females, the presence of any males (either in Mixed or Opposite Sex groups) significantly shortened lifespan (Mixed Sex: $p < .001$; Opposite Sex: $p < .001$) in comparison to females held mostly on their own. In contrast to the findings for males, exposure to same sex competitors also significantly reduced female lifespan ($p = .05$; Figure 4A).

To test whether there were effects of the social environments on underlying ageing patterns, we compared the mortality rates of males and females. There were no significant differences in the baseline mortality rates in the different social environments across males or females (Figure S3). However, males kept in Mixed Sex groups experienced faster ageing than did males in the other social treatments (Figure 4B). For females, those kept in social groups with males (Opposite or Mixed Sex) aged significantly more rapidly than did females kept alone or with other

females (Figure 4B). These results show that exposure to males accelerated senescence in females and increased the rate of ageing in males only in environments in which there was also competition for females.

Sex-specific plasticity in reproductive strategies in response to same versus opposite sex exposure

Males that were exposed to females in their social treatments (i.e., males in Mixed or Opposite Sex treatments) had extra mating opportunities outside of the weekly mating assays. Hence, these males had the opportunity to produce significantly more offspring than the Alone or Same Sex treatment. We tested for this by counting the offspring produced in between the weekly mating assays by focal flies at five different time points: early-life (Weeks 1 and 3), mid-life (Weeks 6 and 7), and late-life (Week 10). As expected, the Mixed Sex and Opposite Sex treatment males produced significantly more additional offspring during early-life (Weeks 1 and 3) than did males that had no additional mating opportunities (Alone or Same Sex treatment males; Figure 5A). There was also a strong, additive effect of the number of non-focal females in the social treatment on the number of additional offspring produced. Males in the Opposite Sex treatment (exposed to three young females in the social treatments) produced significantly more offspring than did males in the Mixed Sex treatment (two young females and one rival male) and with Mixed Sex males producing double the offspring of males in the Alone or Same Sex treatments (exposed to a single female for only 24 hr each week). These findings showed that males could almost double their fitness in early life with each additional mating partner. In contrast, females did not significantly benefit from additional mating opportunities outside of the weekly mating assays (Figure 5A). Females from all social treatments produced similar numbers of offspring during their social exposure periods, regardless of the number of males to which they were exposed.

We then post hoc tested whether any additional offspring produced outside of the weekly mating assays significantly altered the pattern of life histories in males or females. To do this, we calculated the cumulative proportion of total offspring produced to determine, for each treatment, the average age by which $\geq 80\%$ of lifetime total offspring had been produced. This revealed that males in all social treatments were the same age, or older, than females when they achieved 80% of their total fitness (Figure 5B). Alone and Same Sex treatments were, on average, 7 weeks old when they achieved 80% of their total fitness (Figure 5B). However, Mixed and Opposite Sex treatment males achieved 80% of their total fitness much more rapidly, at around 3 weeks old, with their ~ 7 weeks of remaining lifespan resulting in no significant additional fitness gains (Figure 5B). Conversely, females in all social treatments consistently achieved 80% of their total fitness at 3–4 weeks of age (Figure 5B). These findings suggest that males exhibited a spectrum of plastic life-history strategies in response to their social environment—from “live fast, die young” (Mixed and Opposite Sex males) to “live slow, die old” (Alone and Same Sex males). Hence, when potential mating opportunities increased (i.e., more available females), males invested more heavily into maximizing their fitness during early life at the expense of reproduction later in life. Females, however, robustly adopted a consistent “live fast, die young” strategy that did not change with social environment nor additional mating opportunities.

Discussion

Our results challenge the prevailing view that strong sexual selection on males should lead to more rapid ageing and reproductive senescence in males than females. By using an experimental framework that employed a range of biologically relevant sociosexual environments, we showed that females experienced more rapid reproductive and actuarial senescence by mid-life than did males. The results highlighted a steep cost of early-life reproduction, elevated ageing, and rapid reproductive senescence in females across all social environments. In contrast, males consistently outlived females and maintained pre-copulatory performance and general activity levels well into old age. Taken together, our findings demonstrate that when both sexes can compete for reproductive opportunities over the course of their lifetime, females can exhibit a “live fast, die young” strategy. Our findings also support the idea that exposure to the same versus opposite sex can have strong and opposing consequences for actuarial ageing for males versus females (Rostant et al., 2023).

A major driver of the idea that males should show more rapid reproductive ageing than females is derived from evolutionary theories of ageing, which propose that increased rates of extrinsic mortality (assumed to be higher in males) should lead to accelerated rates of intrinsic mortality, which then reduces selection on late life performance (Bonduriansky et al., 2008; Williams, 1957; but see Caswell, 2007; Moorad et al., 2019). However, sexual selection can select for male traits that are positively genetically correlated with performance and lifespan. For example, sex-limited selection on mate search activity in male *Caenorhabditis remanei* nematodes resulted in the correlated evolution of longer lifespan in males only (Chen & Maklakov, 2014). Consequently, there was evolution of increased sexual dimorphism in lifespan, with males emerging as the longer living sex (Chen & Maklakov, 2014). Our findings that male *D. melanogaster* maintain their reproductive performance well into old age are consistent with the hypothesis that sex-specific selection maintains sexual dimorphism in age-specific life-history traits. Males in our study experienced no significant declines in their courtship effort, mating success, or general activity levels. The maintenance of male performance traits might increase the amount of harm inflicted on females during mating. Thus, if male general performance is maintained and extends lifespan, then male harassment should increase the costs of reproduction for females, thereby accelerating the demise of females. It is also possible that costly male harassment might be lessened in a more spatially complex environment where females can “escape” from mating interactions with males (e.g., Yun et al., 2017).

The fitness costs of exposure to the opposite sex were far greater in females than in males. Females kept with males had significantly shorter lifespans, aged more rapidly, and suffered sharp declines in reproductive output that were evident across all social environments. This is consistent with previous research reporting that negative phenotypic correlations between early-life reproductive effort and lifespan can produce sex differences in lifespan (Lemaître et al., 2015; Rice, 1996, 1998; Travers et al., 2015). Our unexpected finding of faster female than male reproductive senescence could be partly due to our population of flies being maintained under overlapping rather than discrete generations, which could, in theory, change sex-specific selection gradients compared to previous studies (e.g., Kimber & Chippindale, 2013). Overlapping generations are probably more ecologically relevant in this model organism.

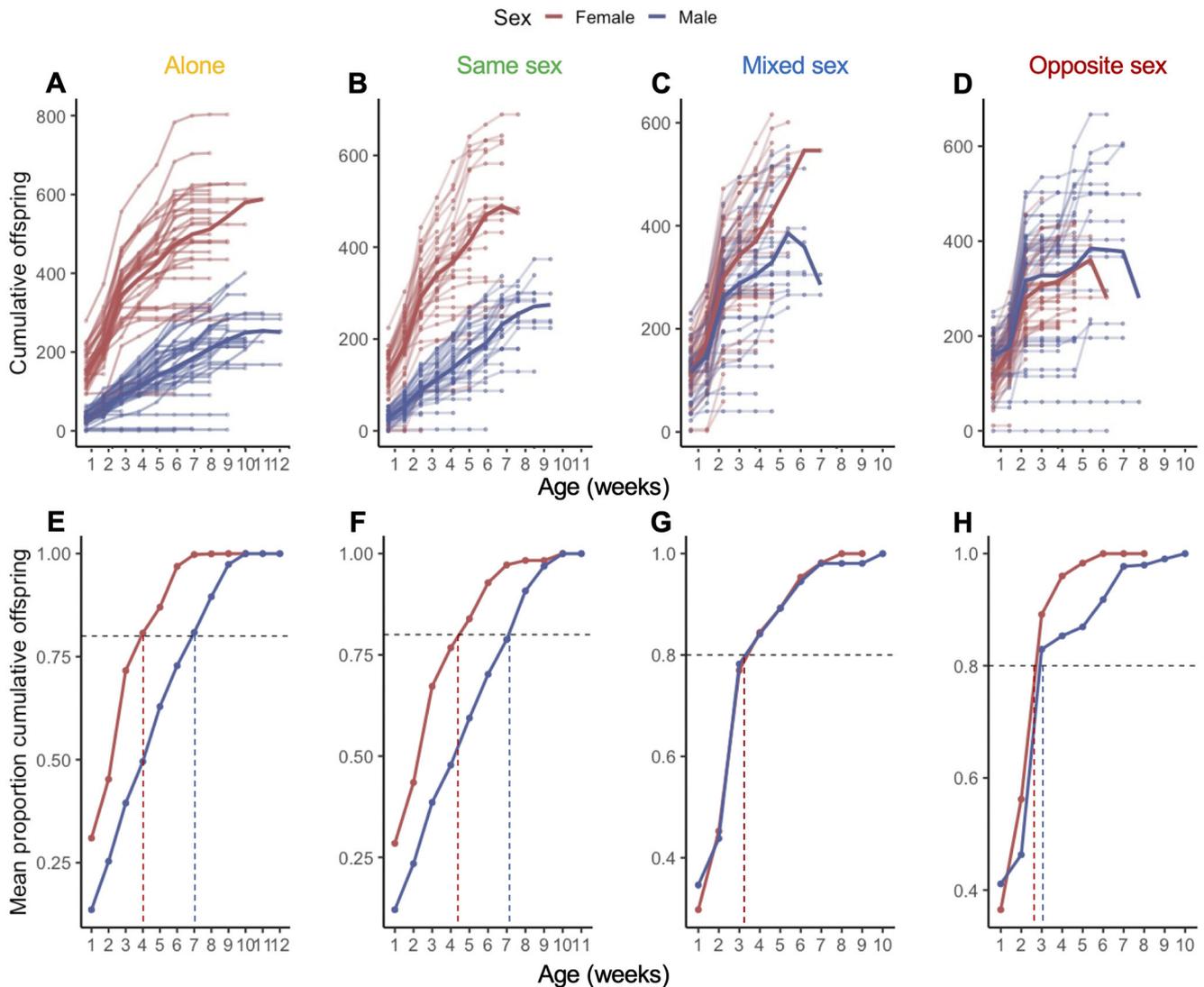


Figure 5. Males in all social treatments were the same age, or older, than females when they achieved almost all of their total lifetime fitness, suggesting that males can shift their reproductive effort to maximize reproductive output earlier in life in response to available mating opportunities. (A–D) Cumulative offspring for males and females produced during the weekly mating treatment phase when pooled with genotyped offspring from the social exposure phase at Weeks 1, 3, 6, 7, and 10. Individuals are plotted with the mean for males and females shown as a dark solid line for each social exposure treatment. (E–H) Comparison of the mean cumulative proportion of offspring produced by males and females. Vertical dotted lines indicate the average age at which females and males reached 80% of their total fitness (indicated by horizontal dotted line) within each of the social exposure treatments.

Sex differences in ageing rates could also be driven by widespread sexual conflict. Interlocus sexual conflict can contribute to the accumulation of alleles with deleterious effects in old age or select for alleles that enhance early life fitness at the cost of late life fitness (Bonduriansky et al., 2008; Maklakov & Chapman, 2019). This could then contribute to a “live fast, die young” strategy in females if negative effects of male seminal fluid proteins elevate rates of female mortality (Promislow, 2003). The optimal strategy promoted by natural selection in females might then be high rates of mating in early life because females would be unlikely to survive long enough in natural populations of flies to experience the fitness costs associated with deleterious alleles expressed in late life. In support of this hypothesis, removal of sexual selection can lead to the evolution of longer intrinsic lifespan in females (Archer et al., 2015; Maklakov et al., 2007). In our study, we provided focal individuals with young competitors and mating partners each week, po-

tentially magnifying the sex-specific effects of interlocus sexual conflict. However, our finding that rapid reproductive senescence was widespread across social treatments for females, including individuals that experienced minimal male contact (i.e., minimal interlocus sexual conflict), suggests that our experimental design was appropriate to resolve overall comparisons of male and female life history and ageing patterns.

An unexpected and striking result was the differences between males and females in the effects of same-sex competitors on several key life-history traits. For males, there was a beneficial effect of the presence of young, same sex rivals. Such males courted virgin females at a significantly higher rate, remained more active with age, and suffered no loss of lifespan when compared with males from the other social exposure treatments. In contrast, females from the same sex treatments had significantly higher fecundity, but also had significantly shorter lifespans, than females that were kept in isolation, but did not dif-

fer from the other social exposure treatments where males were present. Sex-specific effects of same-sex rival presence on lifespan have previously been reported for *D. melanogaster* (Bretman et al., 2013; Leech et al., 2019; Rostant et al., 2023), and the general observation is of negative effects of same sex competitors of the same age on male and not female lifespan. The detrimental effect of young same-sex competitors on female but not male lifespan that we observed here could partly be due to the effects of replacing non-focal competitors every week with novel, young individuals that could potentially provide older focal flies with lifespan-extending benefits (Cho et al., 2021). A key difference in our study over previous works is that all focal flies (even those spending most of their lives in social isolation) were provided with regular mating opportunities throughout their lives. Regularly mated females exposed to same sex competitors might experience additional costs associated with competition for oviposition sites (Fowler et al., 2022), which could contribute to more rapid ageing and loss of lifespan. Female lifespans are also much more sensitive to the nutritional environment than are males, with high-nutrition diets promoting higher fecundity but shorter lifespans (e.g., Chippindale et al., 1993). It is possible that, in the social environments containing more than one mated female, oviposition and subsequent larval activity changed the nutritional environment in a way that then reduced female lifespans. However, our results suggest that females exhibited higher reproductive senescence compared to males across all the social environments, including those where females were alone and, presumably, expressed reproductive costs at a lower level. Moreover, previous work using the Dahomey population has demonstrated that egg production per se has negligible effects on female lifespan (Barnes et al., 2008; Partridge et al., 1986). Further work is now required to understand the mechanisms underlying these intriguing and sex-specific plastic social effects and the full range of their potential impacts on male and female fitness.

Conclusion

In sum, our findings clearly show that female fruit flies are “living fast and dying young” compared to their male counterparts. Strikingly, this result applies both to reproductive ageing and to actuarial senescence, and most importantly is maintained across a range of social environments that encompass different forms of sociosexual interactions. Males showed little evidence of decline in their reproductive performance with age. These results challenge the view that sexual selection should lead to accelerated male ageing and suggest that high costs of mating and reproduction may result in faster female ageing. Future studies could usefully focus on evaluating sex-specific lifespan and ageing using different taxa in diverse sociosexual environments where both sexes are allowed to interact in a biologically relevant way.

Supplementary material

Supplementary material is available online at [Evolution Letters](#).

Data and code availability

All data and code used for analyses have been provided as supplementary material.

Author contributions

L.M.H., A.B., A.A.M., and T.C. conceived the experiment; L.M.H. and J.H. collected the data; L.M.H. analyzed the data and wrote the first draft of the manuscript; J.H., A.B., A.A.M., and T.C. edited the manuscript.

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Conflict of interest

The authors declare no competing interests.

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