

Does female resistance to mating select for live-fast-die-young strategies in males? A comparative analysis in the genus *Drosophila*

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Abstract

Female promiscuity is a pervasive selective force on male reproductive traits, and the strength of sexual selection is predicted to influence the trade-off between lifespan and reproduction. In species where sexual selection is intense, males are predicted to invest in sexual strategies that shorten their lifespan, potentially resulting in female-biased sexual dimorphism in longevity. However, comparative analyses have provided contrasting results, potentially due to the use of broad mating system categories or sexual size dimorphism as a proxy for sexual selection. Here, we used female remating rate (i.e. female promiscuity) as a more direct measure of sexual selection strength and conducted a phylogenetic comparative analysis of the relationship between female remating rate and sexual dimorphism in lifespan in 29 species of *Drosophila*. We did not find strong evidence that female remating rate was correlated with sexual dimorphism in lifespan. However, we found that male and female lifespans are positively correlated among species and that phylogeny and residual variance (i.e. variation in non-phylogenetic factors) are important in determining female remating rate, male and female lifespans separately, and the correlation between male and female lifespan. We suggest that variation in the nature of sexual competition and variation between studies could account for some of the unexplained variation among species in the relation between female remating rate and sexual dimorphism in lifespan.

KEYWORDS

ageing, disposable soma, female promiscuity, lifespan, longevity, phylogeny, remating rate, trade-off

1 | INTRODUCTION

Understanding how selection shapes the trade-off between lifespan and reproduction is a fundamental aim of evolutionary biology. Under the disposable soma hypothesis, individuals must allocate their limited energetic resources between somatic maintenance (ultimately affecting ageing and longevity) and reproduction (Kirkwood, 1977). Therefore, selection for increased investment in

reproduction should result in fewer resources available for investment in prolonged longevity. Much of the evidence for the disposable soma hypothesis comes from studies examining the effects of individual reproductive investment on ageing and lifespan (e.g. Hammers et al., 2013, 2019; Lemaitre et al., 2015), as well as studies of individual condition (i.e. the size of the resource pool available for investment in costly life-history traits) (e.g. Adler et al., 2016; Hooper et al., 2017; Hunt et al., 2004). For example, a recent study

on Seychelles warblers by Hammers et al. (2019) showed that females that received more help in cooperative breeding, thus expending less energy on parental care, aged at a slower rate compared with those that received less help during breeding, and an experimental study on field crickets showed that high condition males reared on a high protein diet invested more in sexual signalling (calling) but died sooner (Hunt et al., 2004). Comparative studies between species have also investigated how differences in selection pressures alter this trade-off (e.g. Clutton-Brock & Isvaran, 2007; Lemaitre & Gaillard, 2013; Liker & Székely, 2005; Tidière et al., 2015; Valcu et al., 2014). However, the relationship between reproductive investment and longevity is complex and remains poorly understood.

Sexual selection is a potent force that shapes investment in costly pre- and post-copulatory traits in males (e.g. Godwin et al., 2017; Kotiaho, 2000). By favouring elevated investment in reproductive traits at the expense of investment in somatic maintenance, intense sexual selection is predicted to drive the evolution of accelerated ageing and reduced lifespan in males (e.g. Bonduriansky et al., 2008; Lemaitre et al., 2020; Maklakov & Immler, 2016; Promislow, 1992; Promislow et al., 1992). Within species, observations have indeed shown that males that invest more in pre-copulatory traits such as courtship have earlier onset and more rapid progression of ageing compared with males that invest less in such traits (e.g. Cordts & Partridge, 1996; Hooper et al., 2017; Hunt et al., 2004; Papadopoulos et al., 2010; Wedell, 2010). However, studies examining the effects of post-copulatory investment on lifespan and ageing are limited (but see Chen et al., 2020; Gasparini et al., 2019; Lemaitre & Gaillard, 2013), and comparative studies between species have yielded contrasting results (see Tidière et al., 2015).

Comparative studies examining the relationship between male lifespan and sexual selection for elevated male reproductive investment might yield equivocal results because of differences in the traits used to assess the strength of sexual selection. For example, many comparative analyses use sexual size dimorphism (SSD) or broad categories of mating systems such as 'monogamous', 'promiscuous' and 'polygynous' as proxies for the strength of sexual selection (see Tidière et al., 2015). However, the use of broad categories can result in biases and may limit power by reducing degrees of freedom (Royston et al., 2006). Additionally, the use of SSD does not account for different selective pressures acting on the sexes. For example, sexual selection may act to increase male body size (e.g. Partridge & Farquhar, 1983; Shine et al. 2000), but fecundity selection can also act to increase female body size (Honěk, 1993), meaning that sexual selection is not the only force affecting SSD.

Female propensity to mate multiply (i.e. female 'promiscuity') is a pervasive selective pressure on male investment in both pre- and post-copulatory traits. For example, a comparative analysis within the *Drosophila* genus found that males from species with high female remating rates invested more in exaggerated post-copulatory traits such as sperm, and species with low female remating rates invested more in exaggerated pre-copulatory traits such as signals and weapons (Markow, 2002). This is likely because rapid female remating exposes males to sperm competition and thus selection for

post-copulatory traits that can enhance siring success (e.g. Godwin et al., 2017; Parker & Pizzari, 2010). Delayed female remating is expected to result in a male-biased operational sex ratio as the pool of sexually available females is reduced, generating greater pre-copulatory competition and selection for traits that enhance mating success (e.g. Kvarnemo & Ahnesjö, 1996; Minekawa et al., 2020). Because female remating rate is a continuous variable that does not require broad categories or measures that may be affected by different selective pressures, and because it is a trait that is known to be a pervasive selective force on male reproductive investment, we suggest that female remating rate could be a very useful measure of the strength of sexual selection in comparative studies of lifespan.

Using data on 29 species within the *Drosophila* genus, we investigated the relationship between female remating rate (reflecting female 'promiscuity') and the lifespan of males relative to females (hereafter 'relative lifespan'), as well as the average lifespan (days) of males and females separately (hereafter 'absolute lifespan'). We predicted a positive correlation between female remating rate and male lifespan relative to females, such that males live relatively longer in species where females remate more quickly. To better understand the factors driving this relationship, we also investigated the correlation between female remating rate and absolute female lifespan, the correlation between female remating rate and absolute male lifespan, and the correlation between absolute male and female lifespans. Given the non-independence of species-level comparative data (Felsenstein, 1985), we tested each of these correlations within a phylogenetic framework.

A positive correlation between absolute male and female lifespans is expected due to similarities in life histories within species, reflecting shared evolutionary history and shared ecologies. However, sex-specific deviations resulting in sexual dimorphism in lifespan are also expected and might be explained by variation in female remating rate. We predicted that species with slow female remating rates (expected to select for increased pre-copulatory investment due to a male-biased operational sex ratio) would exhibit shorter absolute and relative male lifespans compared with species with rapid female remating rate (expected to select for increased post-copulatory investment). This prediction is based on the assumption that the cost of investing in pre-copulatory traits outweighs the cost of investing in post-copulatory traits. Although investment in both types of traits can indeed be costly, greater costs of pre-copulatory traits relative to post-copulatory traits may be expected because, in holometabolous insects like *Drosophila* and many other animals, morphological traits are shaped during development (Boggs, 1981, 2009). In such species, the costs of investing in pre-copulatory traits are, therefore, paid by all males regardless of their realized mating success as adults. In contrast, post-copulatory investment tends to be flexible in its expression at the adult stage, with high costs of investment incurred only by males that mate often (Ferkau & Fischer, 2006; Kotiaho & Simmons, 2003). As a result, the mean costs of pre-copulatory investment might be expected to outweigh the mean costs of post-copulatory investment for males in many species—an expectation that is

consistent with the available evidence (e.g. Chung et al., 2021; Gasparini et al., 2019). Moreover, many pre-copulatory traits, such as prominent signals and weapons, can expose males to elevated risk of death from accidents and predation, which can directly reduce lifespan (albeit less so in a protected laboratory environment) as well as select for reduced investment in somatic maintenance (Kotiaho et al., 1998). Additionally, slower female remating rates may also result in lower direct costs to females (e.g. Chapman et al., 1995; Wigby & Chapman, 2005), and this could contribute to female-biased sexual dimorphism in lifespan in such species.

2 | METHODS

2.1 | Literature search and data collection

First, we searched the database Scopus for literature that reported female remating rate in any species from the *Drosophila* genus using the search terms related to three categories: 'mating OR copulation,' 'rate OR frequency OR propensity OR latency' and 'drosophila.' This resulted in 71 estimates of female remating rate from 46 *Drosophila* species (see <https://osf.io/gpwyf/> for raw data including data sources). To standardize the time in which females remated, we used the per cent of females to remate 24 h after their first mating as this was the most common period reported in the data. However, four estimates of remating reported remating after a longer period in *D. santomea*, *D. yakuba*, *D. subobscura* and *D. malerkotliana*. For these measures, we estimated female remating rate at 24 h by assuming a linear increase in the number of rematings over time. The studies on these species reported very low remating rates, so our estimate resulted in remating rates close to zero at 24 h (<5%). Thus, a different function of increase in female remating would not substantially alter our estimated values.

Next, we conducted a targeted search for papers that reported both male and female lifespan for each species for which we had female remating rate data. This involved searching Google Scholar for published and unpublished data, including theses/dissertations, and contacting authors for additional information. Overall, we were able to obtain 132 measures of sex-specific lifespan from 29 out of the 46 species for which we had female remating rate data (see <https://osf.io/gpwyf/> for the raw lifespan data and the combined data from the 29 species for which data was available).

For all data collected, we used control/outbred individuals where possible. If this was not possible, data were taken from all treatments and genotypes and a mean value was calculated. Although we were only able to obtain single measures of female remating rate and/or lifespan for the less commonly studied species, we were able to obtain multiple measures for the other species; we obtained multiple measures of female remating rate for 55% of included species and multiple measures of lifespan for 80% of the included species <https://osf.io/gpwyf/>. Therefore, mean trait values were calculated for the species with multiple measures. Note that due to the vast

amount of research conducted on *Drosophila melanogaster*, we limited the papers to studies directly related to evolutionary ecology and studies that only used control/outbred flies reared within standard laboratory conditions for this species. This was to limit the large amount of variation likely caused by specific inbred strains and treatments.

All measures of lifespan and female remating rate were recorded in the laboratory, but different research groups used different laboratory conditions and experimental designs (see Discussion). Because few studies reported both female remating rate and lifespan, we were unable to account for such sources of variation between studies. Rather, for most species, mean values for lifespan and female remating rate were obtained from different studies.

2.2 | Statistical analyses

All analyses were conducted in R version 1.3.1073 using the package MCMCGLMM (Hadfield, 2010). Many comparative studies control for phylogeny in the response variable but not in the fixed-effect predictor. However, because both traits can be expected to have a phylogenetic signal, and the choice of 'fixed' effect is often arbitrary, we chose instead to use Bayesian multivariate models that account for phylogeny (see Hadfield & Nakagawa, 2010) in both female remating rate and sex-specific lifespan using an inverse variance-covariance matrix (VCV) of phylogenetic relatedness.

We created the phylogenetic tree of the species included in our analysis using the packages ROTL (Michonneau et al., 2016) and phytools (Revell, 2012). ROTL was used to search the Open Tree of Life (OpenTreeOfLife, 2019) for published molecular phylogenies and Phytools was used to create a phylogenetic tree with the ancestral parameter set to Brownian evolution. Four species were unable to be automatically added to the tree from the Open Tree of Life (*D. malerkotliana*, *D. pseudoobscura*, *D. bipunctinata* and *D. sulfurigaster*). These species were manually added to the tree based on published phenotypic phylogenies on Flybase.org. These species were added to the tree after resolving for polytomies, so the position of these species was inferred based on the phenotypic similarities to sister species and the resolved tree (see Figure 1). Species relatedness based on tree branch positions was then converted to an inverse VCV for inclusion as a random effect.

For all models, female remating rate was logit transformed using the car package (Fox et al., 2019). This function uses the formula $\log(p/(1-p))$ and automatically adjusts values of 0 and 1 to 0.025 and 0.975, respectively. Relative lifespan was calculated as a relative per cent difference, calculated using Equation 1. Thus, negative values indicate that males live shorter than females and positive values indicate that males live longer than females.

$$\text{Relative lifespan} = 100 \frac{(\text{Male lifespan} - \text{female lifespan})}{0.5(\text{Male lifespan} + \text{female lifespan})} \quad (1)$$

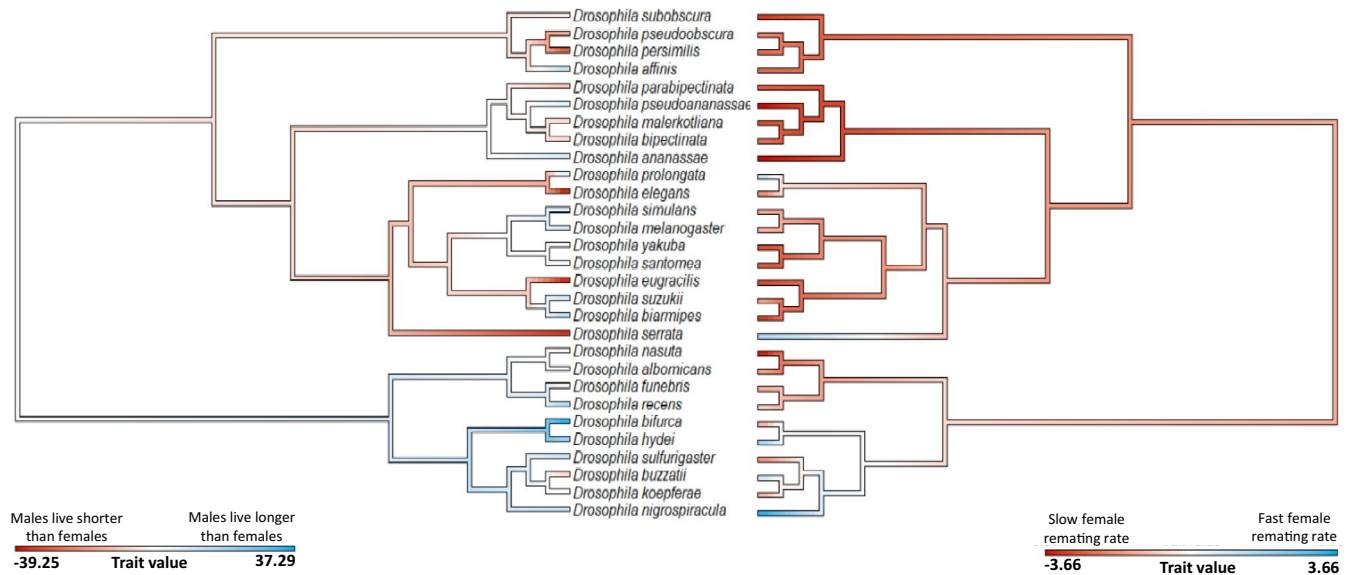


FIGURE 1 Constructed phylogenetic tree of the 29 *Drosophila* species with female remating rate and relative lifespan mapped onto the tree

Relative lifespan was not logit transformed as none of the values neared the margins so appeared unconstrained and approximated normality (i.e. all data were within -50 and 50) (see Supplementary Material S3 for an analysis on the raw difference in lifespan in days). Absolute lifespan (i.e. the average lifespan in days) was log transformed. We used two separate models to test for 1) a correlation between female remating rate and relative lifespan (i.e. a bivariate model) and 2) a correlation between female remating rate and absolute lifespan of males and females (i.e. a trivariate model). The latter model also tested for a correlation between absolute male and female lifespan. These models allowed us to estimate how each response variable and the correlation between response variables was influenced by phylogenetic variance (i.e. how closely related the species were) and residual variance (i.e. non-phylogenetic factors such as species ecology). Also, see Supplementary Material S3 for a repeat of model one, but with the 'raw' difference in lifespan rather than the relative difference in lifespan, and a univariate analysis with linear and quadratic terms of female remating rate as fixed effects and relative lifespan and the response.

The effects of phylogenetic and residual variance on the correlation between responses were calculated from the posterior distribution using Equation 2.

$$r = \frac{\text{cov}_{ab}}{\sqrt{(\sigma_a \times \sigma_b)}} \quad (2)$$

Where cov_{ab} is the posterior mean of the covariance between the two factors of interest, a and b (e.g. female remating and absolute/relative lifespan), σ_a is the variance of factor a (e.g. female remating) and σ_b is the variance of factor b (e.g. absolute/relative lifespan).

Lynch's Phylogenetic heritability (H^2) of female remating rate, and absolute and relative lifespan were calculated from the posterior distribution using Equation 3 (Hadfield & Nakagawa, 2010).

$$H^2 = \frac{\sigma_{a_{\text{phylo}}}}{(\sigma_{a_{\text{phylo}}} + \sigma_{a_{\text{residual}}})} \quad (3)$$

Where $\sigma_{a_{\text{phylo}}}$ is the variance of factor a that is due to phylogeny and $\sigma_{a_{\text{residual}}}$ is the residual variance of factor a .

All models used weakly informative priors, had low autocorrelation and had effective sample sizes >2000 . All models were intercept models with Gaussian distributions. All reported statistics are posterior means \pm 95% Credible Intervals (CI). See <https://osf.io/gpwyf/> for code, including prior structure and Supplementary Material S2 for posterior distributions for all correlations.

Additionally, we took advantage of the overlap of 10 *Drosophila* species between our dataset and the dataset of Markow (2002). Markow (2002) categorized males as having exaggerated pre-copulatory investment such as courtship tactics and/or exaggerated morphological traits, or as having exaggerated post-copulatory investment such as sperm length >6 mm and/or female incorporation of male ejaculate components into somatic tissues. Markow (2002) reported highly discrete investment categories, whereby species with exaggerated pre-copulatory traits lack exaggerated post-copulatory traits and vice versa. We conducted simple ANOVAs using the two categories of reproductive investment reported by Markow (2002) as predictors and our measures of remating rate and relative lifespan as response variables. An ANOVA was used to compare female remating rates between species with exaggerated pre- versus post-copulatory traits (based on Markow's categorization). A separate ANOVA was used to compare relative lifespans in species categorized as having either exaggerated pre- versus post-copulatory male traits. We did not include these categories as a covariate in our MCMCglmm's as this would significantly reduce our sample size and statistical power.

3 | RESULTS AND DISCUSSION

Female remating rates (per cent of females remating within 24 h after the first mating) ranged from 0% in *D. nasuta*, *D. ananassae* and *D. pseudoananassae* to 100% in *D. nigrospiracula* (mean = 22.41%, SD = 30.93). Relative lifespan ranged from -39.25% (i.e. strongly female-biased) in *Drosophila elegans* to +37.29% (i.e. strongly male-biased) in *D. bifurca* (mean = -1.17%, SD = 17.60), with the shortest absolute lifespan of 5.88 days in *D. koepferae* males and the longest absolute lifespan of 206.87 days in *Drosophila serrata* females.

Both phylogenetic and residual variance were important for female remating rate, relative lifespan (Table 1; Table S3) and absolute male and female lifespan (Table 2). All traits also had substantial phylogenetic heritability ($H^2_{\text{remating}} = 68.49$, 95% CI = 14.98, 96.50%; $H^2_{\text{relative lifespan}} = 10.01$, 95% CI = 0.15, 48.54%; $H^2_{\text{male lifespan}} = 64.90$, 95% CI = 35.12, 89.57%; $H^2_{\text{female lifespan}} = 65.48$, 95% CI = 36.29, 89.62%), but relative lifespan had the lowest phylogenetic heritability. This means that phylogenetic relatedness and variation not due to phylogeny (i.e. residual variance) were important for determining female remating rate and absolute and relative lifespans. The importance of phylogeny in these traits is not surprising as we can expect that more closely related species would have experienced more similar selection pressures on mating and lifespan. It would also be expected that non-phylogenetic factors such as species ecology would influence such traits (e.g. Burns & Strauss, 2011).

We also detected a positive correlation between absolute male and female lifespan that was significantly influenced by both phylogenetic and residual variance (Table 2). Such results indicate that both male and female lifespan have co-evolved and are influenced in a similar way by non-phylogenetic factors.

The estimated correlation between female remating rate and relative lifespan was positive as predicted, but this correlation failed to explain much of the variation among species and did not clearly differ from zero (Table 1; Figures 1 and 2). The lack of a clear relationship between female remating rate and relative lifespan is reflected in the weak effects of phylogeny and residual variance on the correlation (Table 1). This was also true for the correlations between female remating rate and absolute male and female lifespans, where we did not detect statistically clear relationships between female remating rate and absolute lifespans due to phylogenetic or residual variance (Table 2). Thus, our analysis does not provide strong evidence that

female remating rate and relative lifespan are positively correlated at the species level. Our results are consistent with other studies that failed to detect a relationship between sexual selection and sexual dimorphism in lifespan (e.g. Lemaitre & Gaillard, 2013; Owens & Bennett, 1994; Toïgo et al., 2013).

It is possible that female remating rate drives the evolution of sex-specific aspects of ageing that do not have strong effects on longevity under benign laboratory conditions, such as the age of onset and rate of senescence (e.g. Gamelon et al., 2014; Hammers et al., 2013; Tidière et al., 2015). It would be interesting to assay male and female lifespans in more stressful environments, where the viability costs of male pre-copulatory traits might have stronger effects on male longevity. Furthermore, the relationship between female remating rates and sexual dimorphism in lifespan may be more apparent at the population level rather than the species level. Differences in environment experienced by different populations within species could lead to genetic differences with important effects on life-history strategies (Draye et al., 1994; Moczek, 2003; Puniamorthy et al., 2012). For example, a study of wild caught *D. melanogaster* from multiple populations found substantial differences in life-history strategies between populations, including fecundity and ageing (Draye et al., 1994). Variation among populations in female remating rates and male reproductive investment strategies could obscure evolutionary correlations at the species level. Alternatively, it is possible that the relative costs of investing in pre- versus post-copulatory traits are approximately equal and selection for heavy investment in either of these traits results in a similar trade-off with lifespan. If so, the relationship between female remating rate and sex-specific lifespan might be bell shaped because male sexually selected traits would impose substantial survival costs at both high and low female remating rates. However, we did not detect a quadratic effect of female remating rate on male relative lifespan (Table S4), indicating that there is no support for a bell-shaped relationship in our data.

The inclusion of other factors in the model is unlikely to change the relationship between female remating rates and relative lifespan, but it could explain some of the residual variation. We were unable to find enough data on other potentially relevant traits, such as the expression of exaggerated secondary sexual traits, for most of our focal *Drosophila* species. However, we utilized the overlap of 10 *Drosophila* species between our study and Markow (2002), who categorized species based on the presence of exaggerated pre- versus

TABLE 1 Posterior means and 95% Credible Intervals (CI) of the phylogenetic and residual variance in relative lifespan, female remating rate and the correlation between the two

	Phylogenetic variance			Residual variance		
	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior mean	Lower 95% CI	Upper 95% CI
Relative lifespan	61.07	0.12	243.22	314.89	151.43	518.27
Remating rate	5.93	0.13	18.09	2.06	0.30	3.92
Remating rate ~ relative lifespan correlation	0.16	-0.95	0.97	0.06	-0.36	0.53

Values in bold indicate that the 95% CI does not cross zero.

TABLE 2 Posterior means and 95% Credible Intervals (CI) of the phylogenetic signal and residual variance in absolute male and female lifespan, female remating rate and their correlations

	Phylogenetic variance			Residual variance		
	Posterior mean	Lower 95% CI	Upper 95% CI	Posterior mean	Lower 95% CI	Upper 95% CI
Male lifespan	0.93	0.13	2.21	0.39	0.14	0.70
Female lifespan	0.88	0.14	2.07	0.37	0.13	0.65
Remating rate	3.82	0.18	11.21	2.40	0.77	4.42
Male ~ Female lifespan correlation	0.58	0.05	0.90	0.65	0.37	0.84
Remating rate ~ Male lifespan correlation	-0.03	-0.72	0.73	0.19	-0.27	0.59
Remating rate ~ Female lifespan correlation	0.01	-0.71	0.73	0.18	-0.28	0.57

Values in bold indicate that the 95% CI does not cross zero.

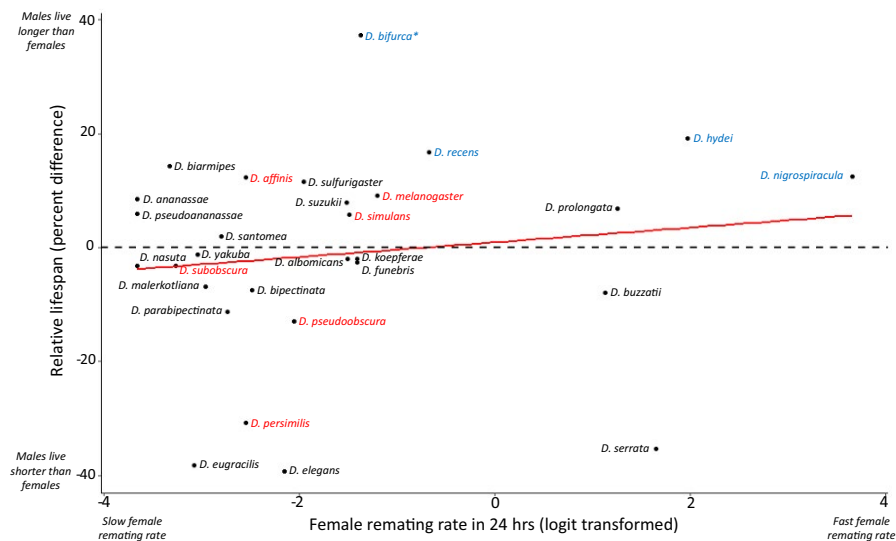


FIGURE 2 Scatterplot showing the correlation between female remating rate (logit transformed) and relative lifespan. The dotted line represents no difference in lifespan, whereas positive (negative) values indicate that males live longer (shorter) than females. Colours represent exaggerated investment in sexual traits based on Markow's (2002) categorization: blue = post-copulatory traits (sperm >6 mm and incorporation of male proteins by the female) and red = pre-copulatory traits (i.e. sexual dimorphism in courtship and pre-copulatory morphological traits), black = species included in our analysis that were not categorized by Markow (2002). *Indicates that sperm length is reported, but there are no data on pre-copulatory traits for *D. bifurca*

post-copulatory tactics in males. Using her male investment categories as predictors in an analysis of variance, we obtained results consistent with Markow (2002): Species with exaggerated pre-copulatory investment tended to have slower female remating rates compared with species with exaggerated post-copulatory investment (ANOVA: $F^1_8 = 10.18$, $p = 0.01$; Figure 2). We also found that males from species with exaggerated post-copulatory investment (both sperm gigantism and female incorporation of seminal fluid proteins) had longer relative lifespans compared with males from species with exaggerated pre-copulatory investment (ANOVA: $F^1_8 = 5.92$, $p = 0.04$; Figure 2). Interestingly, based on sperm lengths reported in Markow (2002), the species with the longest sperm (*D. bifurca*) also had the longest male lifespan relative to females and the species with the shortest sperm (*D. persimilis*) had one of the shortest male lifespans relative to females. However, female remating rates were

similar in these species (Figure 2), suggesting that sperm length may be correlated with male lifespan but not female remating rate.

In addition, methodological differences between studies are likely to have contributed to unexplained variation in our data. For example, the ambient (control-group) temperatures used in the lifespan dataset varied from 19 to 29.5°C (mean $23.6 \pm 2.46^\circ\text{C}$ SD), and 51% of lifespan measures came from virgin flies whereas 49% of lifespan measures came from mated flies. Both these factors are known to have considerable effects on lifespan (e.g. Mołotń et al., 2020; Travers et al., 2015). However, much of the variability in ambient temperatures likely reflects differences in species ecology and measures of lifespan under these temperatures may, therefore, be more reflective of natural conditions. Males and females were maintained in the same environments within all studies, and we have no *a priori* reasons to expect that differences in temperature between

studies would bias our measures of relative lifespan. However, such differences between studies undoubtedly added noise to our estimates and perhaps reduced our power to detect the predicted relationship between male relative lifespan and female remating rate.

In summary, our results suggest that independently, lifespan and remating rate are both affected by phylogenetic history and by non-phylogenetic sources of variance such as species-specific ecologies. We also show that male and female lifespan are correlated and that this correlation is determined by both phylogeny and residual variance. However, we did not find clear evidence of an evolutionary correlation between female remating rate and absolute or relative male lifespan. An evolutionary relationship between these traits might be detected with data on additional species, or on additional traits such as pre- and post-copulatory sexual traits (i.e. 'missing variables'; see Simmons et al., 2017). It would also be useful to repeat this analysis using estimates of male and female lifespans from more stressful environments compared with benign laboratory environments, where viability costs of male sexual strategies might be more apparent, and to examine the relationship between female remating and sex-specific lifespan at the population rather than the species level.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

ELM and RB conceived the idea. ELM conducted the data collection, analysis and wrote the manuscript. RB provided valuable advice during all stages of the project.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.13937>.

OPEN RESEARCH BADGES



This article has been awarded Open Data, Open Materials Badge. All materials and data are publicly accessible via the Open Science Framework at <https://osf.io/gpwyf/>.

DATA AVAILABILITY STATEMENT

Data and code are available on the Open Science Framework at <https://osf.io/gpwyf/>. See Supplementary Material S2 for a list all data sources used in this manuscript.

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