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Development time mediates the effect of larval diet on ageing and mating success of male antler flies in the wild

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High-quality developmental environments often improve individual performance into adulthood, but allocating toward early life traits, such as growth, development rate and reproduction, may lead to trade-offs with late-life performance. It is, therefore, uncertain how a rich developmental environment will affect the ageing process (senescence), particularly in wild insects. To investigate the effects of early life environmental quality on insect life-history traits, including senescence, we reared larval antler flies (*Protopiophila litigata*) on four diets of varying nutrient concentration, then recorded survival and mating success of adult males released in the wild. Declining diet quality was associated with slower development, but had no effect on other life-history traits once development time was accounted for. Fast-developing males were larger and lived longer, but experienced more rapid senescence in survival and lower average mating rate compared to slow developers. Ultimately, larval diet, development time and body size did not predict lifetime mating success. Thus, a rich environment led to a mixture of apparent benefits and costs, mediated by development time. Our results indicate that 'silver spoon' effects can be complex and that development time mediates the response of adult life-history traits to early life environmental quality.

1. Introduction

Early life resource availability can be a critical contributor to variation in individual performance. This is because organisms must make developmental 'decisions' in early life, such as the relative allocation of resources towards energy reserves (which can be mobilized later for metabolic processes) versus body structure (which cannot), which can have long-lasting fitness effects [1,2]. A high-quality developmental environment is generally predicted to confer lasting benefits on individual performance [3]; this is known as the 'silver spoon' effect [4]. For instance, high-quality environments in early life can lead to increased survival [5,6], fecundity [7], mating success [8–10], sperm quality and quantity [8,11,12], and immune function [13,14] in adulthood, compared to individuals from poor environments. However, late-life traits such as senescence—the progressive, intrinsic deterioration of organisms with age which leads to increased mortality and decreased reproductive performance—do not necessarily follow the same silver spoon pattern as life-history traits expressed during development and early adulthood.

In many cases, senescence rates are affected by energetic and physiological trade-offs with traits expressed in early life. Much of the research on trade-offs between early and late-life performance has focused on the costs of reproductive investment [15–19]. As future survival is uncertain, individuals with abundant access to resources may allocate highly to early life performance,

leading to more rapid declines with age [17,20–23]. Likewise, but less extensively studied, juvenile growth and development may also influence senescence, and are likely to depend on early life environmental quality. There is a long theoretical tradition linking rapid growth and development to earlier or faster senescence [24–26]. Faster growth also requires greater energy expenditure, leaving fewer resources available for subsequent somatic maintenance [2,27]. Some empirical studies have indeed found negative phenotypic [21] or genetic correlations [28] between development rate and lifespan, although not all show this pattern [8,29]. Conversely, individuals with high resource acquisition may experience relaxed trade-offs [30] and enjoy high physiological performance throughout their lifespan. Thus, the ultimate effect of early life environmental quality on senescence is unclear. Two recent meta-analyses failed to detect consistent silver spoon effects across taxa on longevity or actuarial senescence, and only a small effect on reproductive senescence [31,32]. Nevertheless, some studies have reported significant increases in lifespan and reduced senescence for individuals that experienced high-quality developmental environments [6,9,33].

While studies of insect life histories and senescence in captivity are common (e.g. [34–36]), studies of senescence in wild populations have focused mainly on vertebrates [37,38]. Patterns of survival and performance can differ markedly between wild and captive animals, including insects [39–41], and it is important to verify laboratory-based inferences under natural conditions. However, collecting longitudinal data on small, short-lived invertebrates poses significant logistical challenges, and studies of senescence in insects remain scarce, despite the abundance and diversity of these organisms [42]. A few field studies have detected trade-offs linking body size and reproductive effort to senescence rates in insects [18,43], but additional longitudinal studies are needed to understand the causes and fitness consequences of life-history variation in wild insects.

To determine the impact of early life environmental quality on senescence in survival and mating success of an insect under natural conditions, we manipulated the diet quality of antler fly larvae (*Protopiophila litigata*; Diptera: Piophilidae) raised in the laboratory. We then marked males individually, released them at antlers stationed in a natural forest environment, and monitored their survivorship and mating success in the wild. Antler flies are small (approx. 2 mm) necrophagous flies that oviposit exclusively on shed moose and deer antlers [44]. Males defend territories in large aggregations on the antler surface [45], and their high site fidelity and short adult lifespan make them well suited for studies of senescence in the wild because marked males can be released (in the absence of any enclosure) and their subsequent mating success and lifespan observed under entirely natural conditions. Previous studies have demonstrated significant increases in mortality rate (i.e. 'actuarial senescence') and decreases in mating rate (i.e. 'reproductive senescence') with age in wild male antler flies [39,43,46]. However, the effect of larval environment on such senescence remains unknown. In this study, we measured development time, body size, mating rate and longevity to determine the impact of early life resource availability on both early and late-life traits. This allowed us to assess whether a nutrient-rich early life environment causes a 'silver spoon' reduction in senescence, or whether it leads to an increase in senescence rates through physiological or energetic trade-offs with growth, development rate or reproduction.

2. Material and methods

(a) Experimental procedure

(i) Flies and culture techniques

An outbred laboratory stock population of *P. litigata* was created from a large sample (greater than 500) of adult flies collected in the spring and early summer of 2012 at Algonquin Wildlife Research Station, Algonquin Provincial Park, Ontario, Canada. The population was maintained at the University of Ottawa with non-overlapping generations at 23°C, 60% relative humidity and under a 17 L : 7 D photoperiod. The maintenance protocol is described in detail in reference [47]. In brief, adult flies are kept in acrylic cages, from which eggs are collected each generation via an oviposition dish placed in each cage. Oviposition dishes contain a layer of 2.5 g of ground beef covered by foam sponge moistened with variable amounts of a 20% w/v ground beef solution [38] up to three times a week to maintain moisture. Larvae feed and develop within these dishes, after which they emerge to pupate in a layer of coco peat (Nutri+, India).

(ii) Diet manipulation

Our experiment involved a manipulation of the larval diet to create four treatments (A, B, C, D) that differed in the ratio of ground beef to plant fibre within the oviposition dishes. The A diet used only regular ground beef, the same as the stock population, while diets B, C and D, consisted of 9 : 1, 8 : 1 and 7 : 1 mixtures of ground beef : powdered inulin fibre (Exact, Canada), respectively. All four diets were prepared by homogenizing the ground beef, with or without added fibre, using a standard household food blender. Preparations were stored in a freezer at −20°C prior to use. During larval development, all diets also received 1.5 ml of ground beef solution three times per week.

Our experiment used flies that had been reared for one generation on one of these four diets. To obtain these flies, we collected adults from the stock population and randomly placed them in five cages containing 125 individuals of each sex, with access to abundant sugar and water. We replaced dead flies daily to ensure constant sex ratio and density. An oviposition dish containing a sponge was added to each cage for 48 h, after which it was removed and replaced with a new one. Once the oviposition dishes were removed from the cage, each sponge was placed on 2.5 g of one of the four larval diets (ground beef with different levels of fibre or without fibre). Oviposition dishes were collected after each of nine consecutive 48 h laying periods beginning on 2 May 2013, creating nine temporal blocks of offspring. As there were five parental cages, one diet treatment within each block was applied to two oviposition dishes, and the treatments were rotated among cages across blocks. Larval diet treatments were not applied until after the oviposition dishes were removed, preventing females from adjusting their egg laying in relation to diet quality. After the application of the diet treatment, oviposition dishes were individually relocated to separate 250 ml mason jars with 10 g of dry coco peat layering the base and a mesh cap. These were incubated as described above for the stock population.

(iii) Field relocation and observation

On 28 May 2013, all nine larval blocks were relocated to the Wildlife Research Station, Algonquin Provincial Park, Ontario, Canada. All containers sat on a bench in an uninsulated wood cabin with no environmental controls, and hence individuals were exposed to variable temperature, humidity and

photoperiod, similar to what would be experienced in the wild. Emerging males were removed daily and individually held in a vial to allow their cuticles to sclerotize. Each male was placed in a holding chamber [48] and photographed in dorsal view using a Canon A640 PowerShot digital camera mounted on a dissecting microscope with an ocular micrometre. From these images, wing length was measured from the tegula to the distal tip of the M vein using ImageJ v. 1.47 [49]. In this species, wing length is positively correlated with thorax length (electronic supplementary material, figure S1; Pearson correlation, $r = 0.645$; $p < 0.001$) and this measurement is highly repeatable ($R = 0.99$; [47]). An individual numeric code was painted on each male's thorax using enamel paint (The Testor Corporation, USA) and a paintbrush with a trimmed tip [48]. Males were immediately released within 1 m of one of two discarded moose antlers (A and B) that were set up on separate 0.8 m high wooden stands in the forest and separated by approximately 50 m distance. Antlers can only support flies for a few years after they are dropped, so supply is limited and subsequent monitoring is also labour-intensive; two antlers was, therefore, the most that was feasible. We released 179 males on the larger antler A and 41 males on the smaller antler B (electronic supplementary material, table S1). Dispersal among antlers is generally low in this species [50], and only 12 individuals were detected to have moved between antlers during the course of the study. Fewer than 10 marked males dispersed to a third antler within 50 m, monitored as part of a separate study, and these were returned to antler A or B.

Antlers were surveyed every 2 h from 9.00 to 19.00 for 42 consecutive days starting 11 June 2013. Only the 11.00 observation on 3 July was missed. During each observation, the identity and mating status (i.e. mating or not) of all marked males was recorded on each antler. The total number of flies and the total number of mating pairs (involving marked and/or unmarked males) was also recorded at each observation. Individuals were excluded from the analysis if they failed to survive at least 2 days after marking, as they may have been injured during the measuring and marking process [43]. Our analyses included 161 males tracked over 251 observation periods (7.04 ± 7.12 s.d. observations male^{-1} on average).

(b) Statistical analyses

All analyses were performed in R v. 3.6.3 [51].

(i) Effect of diet on development time and wing length

We first assessed the impact of our diet treatment on egg-to-adult development time and adult body size. To test for the effect of larval diet on development time, we used a linear model (LM) that included the effects of diet treatment and larval block as categorical variables. To test for the effects of larval diet treatment on wing length (our proxy for body size), we used a LM that included diet treatment and larval block, as well as a second LM containing diet treatment, development time (a continuous variable), their interaction and larval block. We performed type III *F*-tests using the R package *car* [52].

(ii) Adult performance and senescence

Development time (number of days between egg laying and adult emergence) varied among diet treatments (see Results), but there was also substantial independent variation within treatment levels such that we were able to discriminate the respective effects of diet and development time on male performance and actuarial and reproductive senescence. These analyses included additional confounding variables that could potentially affect male survival and mating success (see below for details). Continuous variables were scaled to mean of zero and standard deviation of one prior to analysis [53]. Model selection was carried out using a backward and forward stepwise likelihood ratio test (LRT) procedure, in which a global model was simplified (or a minimal model was complexified) until the model was not significantly improved by removing (or adding) any further terms, based on LRT [54]. If the two selected models differed, an LRT was used to compare them, and the significance of all terms was assessed using LRTs relative to the final model (i.e. the minimal adequate model, including block).

(iii) Actuarial senescence

The effects of diet treatment, development time and body size on male actuarial senescence were analysed using parametric survival models, implemented in the R packages *survival* [55] and *flexsurv* [56]. We chose this approach over semi-parametric Cox proportional hazards regression because Cox models only test for differences in overall mortality rate, but cannot detect differences in ageing rates among groups. We used an interval-censored survival model [57] in which we assumed death occurred between the age of last observation and the following day. To account for potential confounding effects, our model also included antler (coded as a continuous variable representing the proportion of observations for a given individual that occurred on antler A relative to antler B, to account for males that moved between antlers), average population density, average sex ratio and average mating rate (all as experienced over the lifetime of a given individual) as covariates. A fixed effect of larval block was included in all models (i.e. was not allowed to drop during model selection). To avoid overfitting given the modest size of this dataset ($n = 33$–47 individuals in each diet treatment), we did not test interactions.

We performed survival model selection in three sequential steps. First, we used the R package *MuMIn* [58] to select the survival distribution that best fit the data based on the corrected Akaike information criterion (AICc; [59]). Second, we performed LRT model selection on the shape parameter, and then third, we performed stepwise LRT model selection on the scale parameter. For distribution selection (i.e. step 1), we used the *survival* package to fit models with exponential, Weibull, Gaussian, logistic, lognormal, log-logistic and extreme value distributions, and used the *flexsurv* package to fit the two-parameter Gompertz and three-parameter Weibull models (see the electronic supplementary material). The Weibull distribution consistently provided the best fit to our data effects on shape (electronic supplementary material, table S2). The scale parameter (λ) of the Weibull model represents the time at which approximately 63% of the individuals are dead, while the shape (α) describes the change in the age-specific mortality rate, which can remain constant ($\alpha = 1$) or can increase ($\alpha > 1$) or decrease ($\alpha < 1$) with age [60].

Next, we performed LRT model selection on the Weibull shape parameter (i.e. step 2). The *survival* package allows only a single factor to be fitted to the shape parameter, and any number of factors and covariates to be fitted to the scale parameter of the Weibull regression. Therefore, development time and wing length, being continuous variables of particular interest, were each binned into two levels corresponding to individuals above versus below the median value across the whole dataset, allowing us to test their effects, alongside diet treatment, as potential predictors of the shape of actuarial senescence. We then compared models that included either diet, binned development time, binned wing length effects or a single intercept (i.e. no effect), on the shape parameter (α) using LRT. Models included all single term effects described above (without interactions) on scale. As development time caused the greatest improvement in the model (see Results), we allowed shape values to vary between levels of binned development time for subsequent analyses. Finally, we performed forward and backward stepwise model selection on the scale

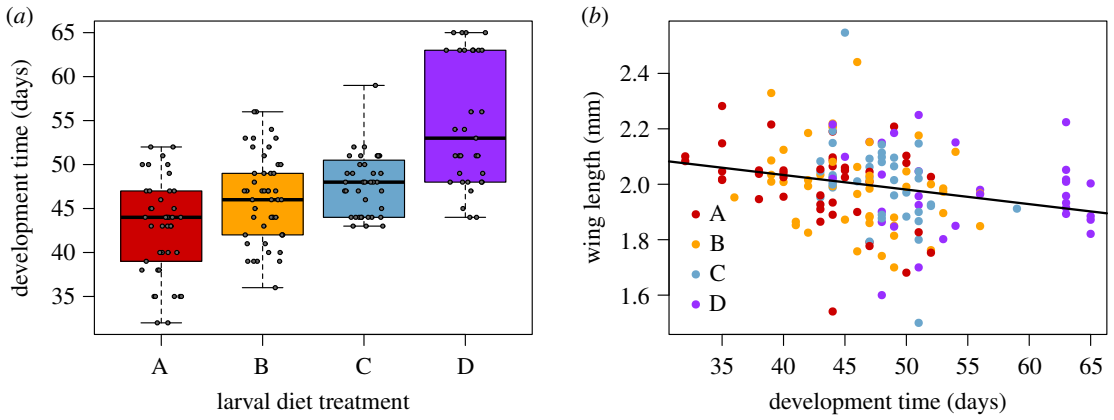

Figure 1. Variation in egg-to-adult development time and wing length within and among larval diet treatments. (*a*) Boxplot of development time in each diet. Thick horizontal lines denote the median, boxes demarcate the first and third quartiles and whiskers indicate the minimum and maximum values. (*b*) Wing size as a function of developmental time across all larval diet treatments. The regression was fitted on the pooled dataset ($F_{1,159} = 9.39$, $p = 0.003$ for this simplified regression), as there was no significant difference in intercept or slope among diets. Diet treatments: A (100% ground beef); B (9 : 1 ratio of ground beef : fibre); C (8 : 1 ratio of ground beef : fibre); D (7 : 1 ratio of ground beef : fibre). (Online version in colour.)

parameter, considering all variables described above (i.e. step 3). Both selection processes converged on the same minimal adequate model.

(iv) Mating rate and reproductive senescence

To test whether larval diet treatment affected male mating rate and/or reproductive senescence, we used generalized linear mixed-effects models (GLMM) using the R package *lme4* [61]. Mating rate, quantified as the probability of observing a male mating during an observation period, was analysed using a binomial error distribution with a logit link function. Mating in antler flies lasts 137 ± 52 min [62], and a given male was never observed mating in two consecutive observations (separated by 2 h). We tested for the effects of diet, development time and wing length on mating rate, as well as the effect of age and its interaction with each of these variables to test for effects on senescence. We also included potential confounding variables in all our models. Lifespan, antler fly density and sex ratio (the latter two estimated at the time of observation) were included as covariates, while antler, hour of day and larval block were included as categorical fixed effects (block was included in all models and not permitted to drop during model selection). We included observation (nested within day) and male identity as random effects in all models to account for non-independence among males during a particular observation and for repeated measures of the same male across observations, respectively. Observation periods with zero flies present on an antler were excluded from the analysis, as sex ratio cannot be calculated for these periods, but results were qualitatively similar when they were included (electronic supplementary material, tables S10 and S11). The initial model for backward selection contained all terms listed above. Forward selection from an initial model containing the two random effects (observation and male identity) and a fixed effect of block, converged on the same minimal adequate model.

(v) Lifetime mating success

Because males are generally mate-limited, lifetime mating success (LMS) is a major component of male fitness. LMS depends both on an individual's longevity and their mating rate throughout life. To investigate the effects of diet, development time and body size on male LMS (the total number of matings observed for each male), we used a generalized linear model with a negative binomial distribution and a log link function, implemented with the 'glm.nb' function in the R package *MASS* [51]. The initial model for backward selection contained the following terms: diet treatment, development time, wing length, antler, lifetime average density and lifetime average sex ratio, and larval block (as above, block was not permitted to drop during model selection). Forward selection from an initial model containing only a fixed effect of block converged on the same minimal adequate model.

(vi) Analyses of residual development time and residual wing length

Given collinearity among diet treatment, development time and wing length (see Results), we performed additional analyses using residual values as a conservative approach to inferring independent effects [63]. We calculated residual development time from a one-way ANOVA among diets—thereby representing only within-diet treatment variation in development time—and residual wing length from a regression against development time—representing the effect of body size independent of development time. We then performed model selection for survival, mating rate and LMS as above, using residual development time and residual wing length instead of the 'raw' variables. An effect of residual development time and/or residual wing length would infer the importance of that variable even when diet or development time, respectively, is allowed to account for all shared variation.

3. Results

(a) Effect of diet on development time and wing length

Egg-to-adult development time increased with decreasing diet quality ($F_{3,149} = 23.0$, $p < 0.001$; figure 1*a*), with a 28% increase in mean time between highest- and lowest-quality diets, but there was also substantial variation within each diet. Larval diet treatment did not significantly influence male wing length when considered alone ($F_{3,149} = 0.431$, $p = 0.731$). When considering development time and diet treatment together, wing length was negatively related to development time ($F_{1,145} = 13.4$, $p < 0.001$; figure 1*b*), diet quality still did not affect wing length ($F_{3,145} = 1.26$, $p = 0.289$) and there was no interaction between diet and development time on wing length ($F_{3,145} = 1.52$, $p = 0.212$).

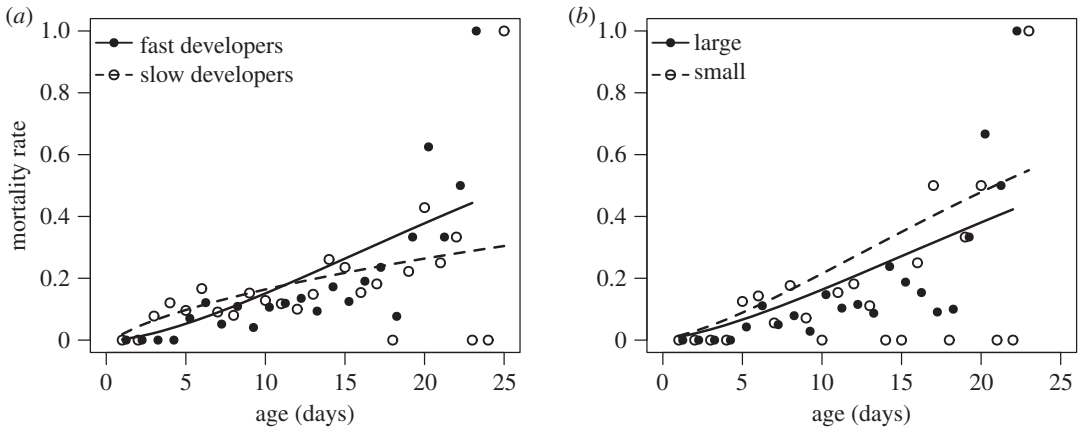

Figure 2. The effect of (*a*), egg-to-adult development time and (*b*), wing length (body size) on actuarial senescence (daily mortality rate) in male *P. litigata*. The effect of development time and wing length on the scale parameter were analysed as continuous variables, but are plotted as mortality curves for males above or below the median trait value. Symbols are observed daily mortality rates for the two groups, while the lines represent fitted mortality curves based on the best supported Weibull survival model (weighted means across blocks). Owing to the shape effect of development time, (*b*) shows mortality rates for fast developers only.

(b) Actuarial senescence

A Weibull survival distribution was a consistently best fit to the data (electronic supplementary material, table S2) and an effect of binned development time on the Weibull shape parameter (α) significantly improved the fit compared to an intercept-only model (LRT: $\chi^2_1 = 6.01$, $p = 0.014$). Effects on the shape parameter of diet (LRT: $\chi^2_3 = 0.733$, $p = 0.865$) and wing length (LRT: $\chi^2_1 = 2.92$, $p = 0.087$) did not improve fit (see also AICc values in the electronic supplementary material, table S2). We, therefore, included an effect of binned development time on shape in subsequent analyses of scale.

For the scale parameter (λ), both forward and backward model selection converged on a common model that included significant effects on scale of development time (LRT: $\chi^2_1 = 11.5$, $p < 0.001$) and wing length (LRT: $\chi^2_1 = 3.85$, $p = 0.0498$), but did not include diet treatment (LRT: $\chi^2_3 = 3.71$, $p = 0.294$). There was also no significant effect of antler, sex ratio, density or average mating rate on the scale of actuarial senescence (electronic supplementary material, table S3a). The development time effects reflected a higher initial mortality rate of slow compared to fast developers, and a steady increase in mortality rate with age for fast developers compared to a convex, decelerating mortality curve in slow developers (figure 2*a*; electronic supplementary material, table S4; shape parameter $\alpha = 2.47$ versus 1.75 for males with a development time below or above the median, respectively). The net outcome of these contrasting effects on shape and scale is that fast-developing males tended to live longer (median lifespan, pooling across diets: 11 days (95% confidence interval (CI): 4.0–20.3)) than slow developers (8 days (95% CI: 2.0–20.8)). There was also a small, but significant, trend for larger flies to experience lower mortality and increased lifespan (figure 2*b*).

(c) Mating rate and reproductive senescence

Males that developed more slowly had significantly higher mating rates (LRT: $\chi^2_1 = 11.5$, $p < 0.001$; figure 3; electronic supplementary material, table S5), but diet treatment did not significantly affect average mating rates (LRT: $\chi^2_3 = 2.65$, $p = 0.449$) when accounting for the effect of development time. In addition, the mating rate was higher at high density and on antler B, but there was no significant relationship between

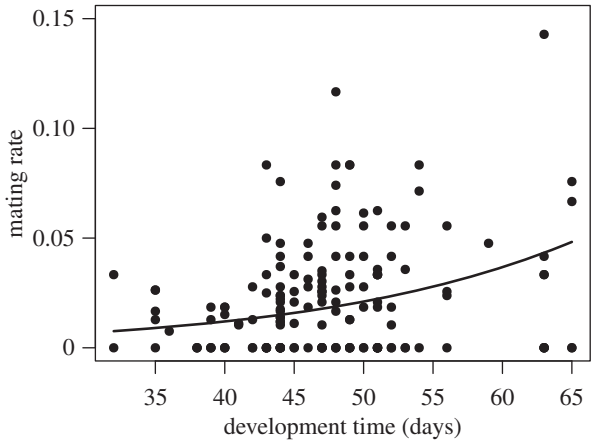

Figure 3. Relationship between egg-to-adult development time and average mating rate in male antler flies. Points represent the lifetime average mating rate for each male and the line represents predicted values from the minimal adequate GLMM (weighted mean across antlers and blocks).

mating rate and wing length, longevity, hour of day or block (electronic supplementary material, table S3b). The mating rate was not affected by age (LRT: $\chi^2_1 = 1.74$, $p = 0.187$), nor did age interact with either diet treatment, development time or wing length (all $p > 0.05$). Therefore, we do not detect reproductive senescence in our data. If an age term is added to the minimal adequate GLMM, the estimate of its effect on mating success is negative, as would be expected for reproductive senescence, but it is non-significant (minimal adequate model + age: β (logit scale) = -0.112 ± 0.086 s.e.).

(d) Lifetime mating success

Diet treatment did not affect LMS, nor did development time or wing length (all $p > 0.05$; electronic supplementary material, table S3c). LMS was significantly affected by the average fly density (LRT: $\chi^2_1 = 7.11$, $p = 0.008$) and the average sex ratio experienced over a male's life (LRT: $\chi^2_1 = 19.6$, $p < 0.001$), such that males which experienced higher density and less male-biased sex ratios tended to have higher LMS (electronic supplementary material, table S6). LMS did not differ among blocks or between antlers (electronic supplementary material, table S3c).

(e) Analyses of residual development time and residual wing length

Our supplementary analysis using residual development time and residual wing length allowed diet treatment to account for all shared variation with development time. Consequently, residual development time represented only development time variation within-diet treatment levels, and residual wing length reflected only size variation that was independent of development time. As expected, the previously non-significant effect of larval diet became significant when it was allowed to explain all shared variation with development time, with decreasing nutrient concentration being associated with both higher mortality (electronic supplementary material, tables S7a and S8) and greater average mating rate (electronic supplementary material, tables S7b and S9). However, the previously significant effects of development time persisted such that males with shorter residual development time had reduced mortality (electronic supplementary material, table S8) and had lower average mating rates (electronic supplementary material, table S9), consistent with the main analyses. Also consistent with the main analyses, residual wing length had a small effect on survival (electronic supplementary material, tables S7a and S8), but not mating success (electronic supplementary material, tables S7b and S9). There was again no effect of diet treatment on the shape of actuarial senescence; unlike in the main analysis, however, the effect of residual development time on shape was no longer significant, although it approached so ($p = 0.07$; electronic supplementary material, table S7a). Again, none of the variables of interest influenced LMS (electronic supplementary material, table S7c).

4. Discussion

In this study, we manipulated the diet quality of larval antler flies, *P. litigata*, to investigate whether adult performance and lifespan would be improved by high larval diet quality under natural conditions, consistent with the silver spoon hypothesis [3,4], or whether they would decline owing to trade-offs with increased allocation towards growth, development rate or reproduction. Our results revealed complex effects of larval diet: males experiencing a richer diet developed faster, and fast-developing males tended to reach greater adult sizes and lived longer. However, fast developers also tended to have a lower average mating rate than slow developers such that the LMS of slow versus fast developers did not differ significantly. When accounting for the effect of development time, larval diet itself did not explain significant variation in adult body size, survival or mating rate. Furthermore, after accounting for development time, we found no significant effects of body size on mating rate, nor significant trade-offs between mating rate and longevity.

Early life diet did not have a consistent 'silver spoon' effect on all adult traits in male antler flies: fast development, caused at least in part by variation in diet quality among (and/or within) treatments, was associated with extended adult lifespan and larger size, but also more intense senescence and lower average mating rate. As a result, fast-developing males had similar LMS to slow developers, although they may ultimately have had somewhat higher fitness owing to potential differences in postcopulatory performance (see below). Other studies have similarly reported complex phenotypic effects of early life environmental quality: rich larval diets can lead to increased reproductive effort and a shortened lifespan and/or accelerated senescence [17,20,21,23], although we observed the opposite effect on lifespan and reproduction as previous studies. Given the complex influence of early life conditions reported in this and other studies, it is not surprising that two recent meta-analyses failed to detect consistent silver spoon effects on lifespan or actuarial senescence in laboratory or wild populations [31,32].

We did not detect strong evidence of trade-offs between early and late-life performance in our antler flies. Fast development was associated with longer lifespan, not shorter, and there was no significant relationship between longevity and average mating rate. Furthermore, body size, which depends on allocation towards growth in the larval stage, was not significantly associated with survival, mating success or senescence rate. This positive correlation of life-history traits suggests high variation in resource acquisition and/or genetic quality among individuals [30]. Nevertheless, development time had opposing effects on the average mating rate and survival, which could arise from an underlying survival–reproduction trade-off. This would be consistent with a previous study of this species that reported a significantly higher average mating rate in short-lived males [43]. Although it can be difficult to detect trade-offs in nature, studies of wild vertebrates have often identified trade-offs between early and late life [38]. However, wild field crickets (*Gryllus campestris*) experience no apparent trade-offs between early reproduction and survival, and only a modest effect of early reproduction on senescence in calling activity [18].

Decreasing diet quality tended to increase development time and decrease body size, but there was substantial variation in development time within each diet treatment, and in body size for a given development time, allowing the effects of these variables to be partitioned. Nevertheless, to ensure that the effect of development time in our analyses did not simply represent differences among diets, we also performed an alternative analysis using residual development time and residual wing length, representing the effects of these variables independent of larval diet and development time, respectively. Using this more conservative approach, development time remained a significant predictor of the scale of actuarial senescence, and of average mating rate, alongside larval diet which was now, unsurprisingly, also significant (electronic supplementary material, table S7a,b). Taken together, these results suggest that not only does intrinsic variation in development time covary with adult life-history traits, development time also mediates the plastic effects of larval diet quality on adult performance and ageing. Alternatively, an unmeasured variable highly correlated with development time could mediate the relationship between diet and life-history traits across life stages. Regardless, we find that development time is closely linked to variation in adult performance.

Development time had a complex effect on actuarial senescence. Rapid larval development was associated with a higher Weibull scale parameter, reflecting a lower initial mortality rate (figure 2; electronic supplementary material, table S4). However, as indicated by their higher Weibull shape parameter, males that developed quickly also senesced

more rapidly, while the age-specific mortality of slow developers plateaued at later ages (figure 2; electronic supplementary material, table S4). The co-occurrence of rapid development and rapid ageing is consistent with physiological trade-offs between early and late-life performance [24,25,28]. However, this did not translate into a survival cost, as the median lifespan of fast developers was greater than that of slow developers. Furthermore, only 37% of males survived beyond 12 days, the point at which age-specific mortality for fast developers exceeded that of slow developers (figure 2). Accordingly, the majority of fast-developing males never experienced senescence-related mortality costs, and most that did were at higher risk of death for only a small a portion of their lives. These results highlight the distinction between lifespan and senescence *per se*. All else being equal, faster senescing individuals will have a shorter lifespan on average, but longevity is also influenced by the baseline mortality rate and timing of onset of senescence. Therefore, variation in lifespan among groups may not simply reflect variation in senescence rate, and can differ in direction, as in our study. Researchers wanting to make inferences about senescence must be sure to measure changes in performance through time, rather than relying on lifespan (and *vice versa*).

Slow-developing male antler flies had a higher average mating rate than fast developers (figure 3). This result is surprising, especially because slow developers were smaller on average and large male antler flies are more successful in territorial combat [45] and are preferred by females [64]. Furthermore, a previous study of male mating success in antler flies found that larger males had a high daily mating rate [43]. Notably, because slow developers also lived shorter lives on average, there was no net effect of development time on LMS. The high average mating rate of these slower developing males may represent an alternative mating strategy which either compensates for, or contributes to, their short lifespan. In yellow dung flies, for example, small males which cannot compete on dung successfully mate on patches of apple pomace where male–male combat is low [65]. Small male antler flies may similarly localize to areas of the antler where males do not defend territories, such as the underside (whichever side of the antler happens to face the ground) [45]. They may also be more willing to accept matings from less fecund females that high-quality males would reject [64].

Despite their high average mating rate, slow-developing males may not have achieved as equal fitness as their peers. We only recorded mating success, which does not take into account variation in female fecundity or postcopulatory effects including sperm viability, sperm competition and female choice [66]. These males might be more susceptible to copulatory take-overs by rivals [62], be willing to accept less fecund females [64], lose paternity owing to sperm expulsion by females [62] or produce semen with a reduced stimulatory effect on egg production (see [67]). If these mechanisms of postcopulatory selection act against slow-developing males, their siring success could be lower than other males, despite similar LMS.

Our detection of actuarial senescence in male antler flies in the wild is consistent with multiple previous studies and further reinforces the existence of senescence in a short-lived insect in nature [39,43,46]. Previous studies have also reported reproductive senescence in this species [39,43,46], but we did not find a significant decline in male mating rate with age, although the trend was negative. Reproductive declines may simply be difficult to detect at smaller sample sizes, as Mautz *et al*. [39] detected clear reproductive senescence in male antler flies in one year ($n = 432$ males), but found only low support in the other ($n = 219$) in which sample size was similar to the current study.

Wing length had a small effect on male actuarial senescence (Weibull scale) and no effect on average mating rate in our results. In our study, large males tended to live longer. Similarly, Bonduriansky & Brassil [43] found that larger male size was associated with greater longevity and mating success, but faster reproductive senescence in antler flies. Interestingly, Mautz *et al*. [39] reported differing effects of body size between years: large males experienced substantially higher mortality in one year, but slightly lower mortality in the other and slightly higher mating rate in both years. However, none of these past studies measured development time, so they could not partition the effects of development time and body size, which are correlated in antler flies (figure 1*b*; [68]). Thus, the significant effects of body size on lifespan, mating success and senescence reported by Bonduriansky & Brassil [43] may in fact be consistent with the effects of development time reported here.

This is the first study, to our knowledge, to experimentally test for silver spoon effects in an insect in nature [42] and one of the first to investigate early–late life trade-offs in wild insects (but see [18]). Overall, our findings suggest that development time is an important contributor to adult life-history traits and senescence, and that this depends on early life environmental quality. However, the phenotypic consequences of variation in development time were mixed and were consistent with a silver spoon effect on some adult traits, but not others. More research is required to elucidate the mechanism behind the paradoxical high average mating rate of otherwise apparently low-quality males and to determine whether their postcopulatory performance is similarly high. Owing to the antler flies' complex phenotypic response, larval diet will probably affect fitness differently as environmental and social conditions vary through time and space. For example, living longer could be critical if female encounter rates are reduced in a particular year or location (e.g. because of bad weather). Much work remains to be done to characterize factors that influence the life-history traits and fitness of insects in nature.

Ethics. This research was carried out under the authorization of the Ontario Ministry of the Environment, Conservation and Parks.

Data accessibility. Data used in this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2rbnzs7jj [69].

Authors' contributions. M.J.O. and H.D.R. conceived the study design with input from R.B. M.J.O. and B.S.M. performed the experiment and collected data. C.S.A. and N.O.R. performed data analysis. C.S.A. and M.J.O. drafted the manuscript. All authors contributed to interpretation and manuscript revisions.

Competing interests. We declare we have no competing interests.

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