ORIGINAL ARTICLE

Ontogenetic timing as a condition-dependent life history trait: High-condition males develop quickly, peak early, and age fast

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Within-population variation in ageing remains poorly understood. In males, condition-dependent investment in secondary sexual traits may incur costs that limit ability to invest in somatic maintenance. Moreover, males often express morphological and behavioral secondary sexual traits simultaneously, but the relative effects on ageing of investment in these traits remain unclear. We investigated the condition dependence of male life history in the neriid fly *Telostylinus angusticollis*. Using a fully factorial design, we manipulated male early-life condition by varying nutrient content of the larval diet and, subsequently, manipulated opportunity for adult males to interact with rival males. We found that high-condition males developed more quickly and reached their reproductive peak earlier in life, but also experienced faster reproductive ageing and died sooner than low-condition males. By contrast, interactions with rival males reduced male lifespan but did not affect male reproductive ageing. High-condition in early life is therefore associated with rapid ageing in *T. angusticollis* males, even in the absence of damaging male–male interactions. Our results show that abundant resources during the juvenile phase are used to expedite growth and development and enhance early-life reproductive performance at the expense of late-life performance and survival, demonstrating a clear link between male condition and ageing.

KEY WORDS: Condition dependence, costs of secondary sexual traits, life history, reproductive ageing, senescence, sexual selection.

Ageing, the decline in performance with age, is a highly variable trait that can have important consequences for lifetime fitness (Bouwhuis et al. 2012; Jones et al. 2014). Classic theory on the evolution of ageing and life history offers explanations for differences in these traits between species and populations (Medawar 1952; Williams 1957; Kirkwood 1977), and similar principles can be applied to between-sex differences as well (Promislow 2003; Bonduriansky et al. 2008; Maklakov and Lummaa 2013; Adler and Bonduriansky 2014). Yet, the factors that generate and maintain variation in these traits within sex and population remain poorly understood. If stable sex-specific optima exist and variation in ageing and life-history patterns is largely genetically determined, then alleles that optimize these sex-specific phenotypes should be fixed, leaving de novo mutation and gene flow as the only sources of genetic variation within populations. Genetic variation within populations could also be maintained by balancing or conflicting selection, such as sex-specific selection and intralocus sexual conflict (Berg and Maklakov 2012). However, another potentially important source of variation in ageing and life history within sex and population is developmental

plasticity, which could generate phenotypic differences in response to environmental heterogeneity.

Previous research suggests that variation in individual condition (i.e., the amount of metabolic resources available for allocation to different fitness-related traits; Andersson 1982; Nur and Hasson 1984; Rowe and Houle 1996)—a key predictor of fitness that encompasses genetic, epigenetic, and environmental sources of variation (Hill 2011)—could be an important source of variation in ageing rates within species. For example, female red deer with high early life reproductive performance experienced faster rates of reproductive ageing than lower quality females (Nussey et al. 2006). A similar pattern was also found in a wild population of antler flies—large males had higher mating rates in early life, but aged faster than small males (Bonduriansky and Brassil 2005). However, the relationship between condition and ageing rate also varies between species. For example, contrary to the pattern found in red deer, bighorn sheep exhibit a positive relationship between body mass, early life fecundity, and late life fecundity (Bérubé et al. 1999). Intriguingly, one study in crickets similarly found that male condition, reproductive effort, and longevity were positively correlated (Judge et al. 2008), yet in another study of a closely related species high-condition males had shorter life spans (Hunt et al. 2004).

The relationship between condition and ageing rate may depend on both the relative and absolute costs of investment in reproductive traits. Individuals with access to abundant resources (i.e., high condition) may be able to increase investment across multiple fitness-related traits, including reproduction and somatic maintenance. If relative costs of reproductive investment are lower for high-condition individuals, then high-condition individuals may be able to maintain high reproductive performance while avoiding accelerated ageing, potentially resulting in a positive relationship between early- and late-life reproduction and life span (e.g., bighorn sheep; Bérubé et al. 1999). Conversely, trade-offs between reproduction and somatic maintenance may lead to rapid ageing in high-condition individuals (Bonduriansky and Brassil 2005). Such trade-offs may be especially pronounced in males, as increased condition is often associated with increased investment in secondary sexual traits, such as sexual displays (Mappes et al. 1996; Hunt et al. 2004; Judge et al. 2008) and weapons (Emlen 1997). Investment in these types of traits is expected to impose significant costs on the bearer (Kotiaho 2001). Thus, if high condition is associated with a shift toward a life history strategy geared toward maximizing reproductive performance, the absolute costs of reproduction could increase disproportionately with condition even if relative costs decline. In other words, high-condition males may achieve higher reproductive performance but also pay higher latent costs than low-condition males and, as a result, high-condition males may suffer accelerated ageing.

There is a great variety of morphological features that are associated with high condition in males and have the potential to incur many types of costs, and which in turn may influence life-history trade-offs. In particular, high condition is often associated with exaggerated expression of weapons or sexual ornaments, and increased body size (Nur and Hasson 1984; Andersson 1994), and costs of these morphological secondary sexual traits are well documented. For example, development costs of exaggerated weapons can limit investment in postcopulatory traits, both across and within species (Simmons and Emlen 2006; Liu et al. 2015). In addition to production costs, secondary sexual traits can also require constant energetic input, imposing significant maintenance costs on males that bear these traits, for instance, through constant pigment production (Hooper et al. 1999) or grooming (Walther and Clayton 2005). One potential consequence of this demand on resources is a trade-off between secondary sexual trait expression and immunocompetence (Faivre et al. 2003; also see Folstad and Karter 1992). Maintenance of a large body size may also impose energetic costs on high-condition males (Blankenhorn 2000). For example in wolf spiders, metabolic rate per gram body weight increases with total body size (Kotiaho et al. 1998). These examples suggest that, although high-condition individuals are able to afford the initial investment in sexual ornaments, weapons, or increased body size as predicted by the handicap hypothesis (Zahavi 1975, 1977; Nur and Hasson 1984), maintenance costs of these traits throughout adulthood have the potential to divert resources away from other fitness-related traits, including those related to ageing.

Males also typically exhibit condition-dependent behaviors. Energetic costs of sexual displays or signaling, as well as male-male combat behaviors, have been shown across many species including fish (Castro et al. 2006; Ros et al. 2006), birds (Höglund et al. 1992; Eberhardt 1994), frogs (Prestwich et al. 1989), and arthropods (Mac Nally and Young 1981; Watson and Lighton 1994). Importantly, these costs have been shown to influence male performance across multiple life-history traits, reducing survival (Mappes et al. 1996), lifespan (Cordts and Partridge 1996), and growth rates (Gosling et al. 2000). Additionally, agonistic interactions expose males to increased somatic damage, which has the potential to reduce male performance (e.g., Sinclair et al. 2011). High rates of aggression have also been associated with increased hormonal stress levels in some species (Creel et al. 1996; Cavigelli 1999). High-condition males may be especially likely to engage in damaging behavioral interactions, and these interactions may cause irreparable wear and tear (e.g., damage to the exoskeleton in insects: Bonduriansky and Brassil 2005; Adler et al. in press), imposing latent costs manifested as accelerated ageing.

Costs arising from investment in secondary sexual traits, therefore, have the potential to cause accelerated ageing in

high-condition individuals and, because condition typically has a large environmental component (Andersson 1982; Rowe and Houle 1996; Hill 2011; Bonduriansky et al. 2015), variation in condition arising from environmental heterogeneity could contribute to the maintenance of variation in male ageing and life history within populations. However, few explicit tests of the effects of these costs on ageing patterns have been carried out. In particular, when condition is associated with the expression of both morphological and behavioral secondary sexual traits, the relative costs of these traits and their influence on ageing remain unknown. Understanding the nature of such costs may provide insight on variation in ageing rates within populations, and the contrasting patterns of condition-dependent ageing observed across species.

We used the neriid fly, *Telostylinus angusticollis*, to investigate how the costs of condition-dependent secondary sexual traits influence male reproductive ageing patterns. In this species, adults form large aggregations on the trunks of native Australian *Acacia longifolia* trees, as well as the introduced Brazilian coral tree hybrid, *Erythrina x sykesii*, where females oviposit in patches of rotting bark. Areas near oviposition sites are often defended by large, dominant males, which are frequently observed engaging in combat for control of territories (pers. obs.). Body size is highly condition dependent, with flies (particularly males) that have access to more nutrient resources during development emerging as larger adults (Bonduriansky 2007). High-condition males also express exaggerated morphological secondary sexual traits (elongated antennae, head capsule, and forelimbs; Bonduriansky 2007; Sentinella et al. 2013). These traits are employed as weapons, and their expression enhances performance in male-male combat (Fricke et al. 2015). Moreover, high-condition males are more likely to engage in combat (Bath et al. 2012). Investment in condition-dependent morphological and behavioral traits is therefore likely to impose costs on high-condition males, potentially affecting their rate of ageing.

To investigate effects of early-life condition on ageing, we manipulated nutrient concentration in the larval diet, generating "low-condition" males with small body size and reduced secondary sexual traits and "high-condition" males with large body size and exaggerated secondary sexual traits. To test for effects of investing in male–male contest (combat and scramble) behaviors on ageing patterns, each focal male was then housed together with another male and either permitted or prevented from engaging in male–male contests, in a fully factorial design. We predicted that high-condition males would achieve higher mating success than low-condition males in early life, and asked how early-life condition and opportunity to engage in male–male contests would influence rates of ageing in reproductive traits (reproductive ageing), as well as longevity. To quantify reproductive ageing, we measured multiple aspects of male reproductive

performance as a function of male age, including male performance in no-choice pairings with females and under competitive conditions.

Materials and Methods
REARING FLIES AND EXPERIMENTAL SETUP

Laboratory stock used in experiments was derived from individuals collected from a naturally occurring population in Fred Hollows Reserve in Sydney, Australia (33°54′44.04″S 151°14′52.14″E). Experimental flies in this study were grand-offspring of wild caught flies. Larval medium used to rear stock flies consisted of 32.8 g of protein (Nature's Way soy protein isolate; Pharm-a-Care, Warriewood, Australia) and 89 g of carbohydrate (brown sugar; Coles brand, Bundaberg, Australia) per 600 mL of reverse osmosis water and 170 g of cocopeat. Because flies in stock cages were allowed to oviposit on the same batch of larval medium (provided to larvae ad libitum) over several days, larvae experienced a range of nutritional conditions, preventing adaptation to a particular nutrient concentration. Hence, any experimental effects of condition are unlikely to have been influenced by adaptation to particular diet treatment.

We manipulated the amount of resources available to flies during development by rearing flies on either a nutrient-rich or a nutrient-poor larval diet. Diets were chosen from Sentinella et al., with the aim of maximizing size differences between treatments, while keeping the protein to carbohydrate ratio the same across diets (1:3). The body sizes of high-condition (larger) and low-condition (smaller) males produced in this experiment were well within the range of natural variation observed in the wild (Bonduriansky 2006). The "rich" larval diet provided to high-condition treatment males consisted of 32.8 g of protein (soy protein isolate) and 89 g of carbohydrate (brown sugar) per 600 mL of reverse osmosis water and 170 g of cocopeat. The "poor" larval diet provided in the low-condition treatment consisted of 5.5 g protein and 14.8 g carbohydrate for the same amount of water and cocopeat. Larval medium was thoroughly homogenized using a hand-held beater, then frozen at –18°C until day of use.

To obtain experimental animals, 2960 eggs from the lab stock were transferred to fresh larval medium (40 eggs per 200 g of medium). Larvae were incubated at 25°C and watered to keep the larval medium moist until first adult eclosion. Focal adult males were then transferred to 400 mL cages fitted with mesh stockings to allow for ventilation, and moist cocopeat lined the bottom to provide water. Focal males were provided with a dish of oviposition medium (rich larval medium) and housed together with a companion male reared on an intermediate ("standard") larval diet (10.9 g protein and 29.7 g carbohydrate per 600 mL
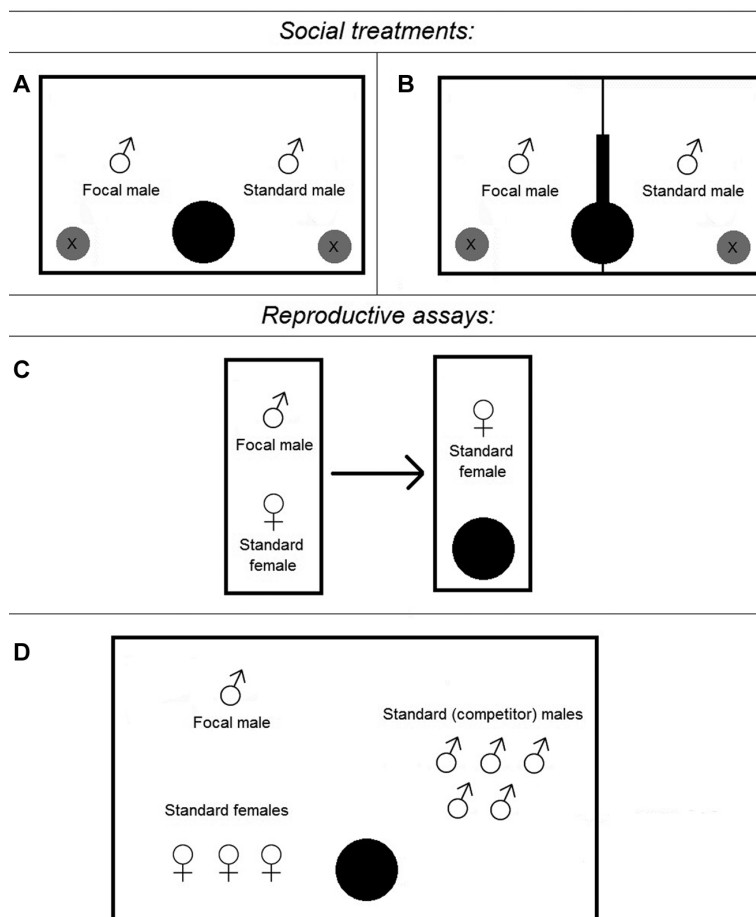
Figure 1. Social treatments (A and B) and reproductive assays (C and D): (A and B) Housing setup of flies in the fighting (A) and nonfighting (B) social treatment groups: focal males were housed with one companion male, and the two flies were either able to freely interact (fighting; A), or physical contact was restricted (nonfighting; B) by partitioning the container; (C) no-choice reproductive assay: each focal male was paired with a standard female for one hour; (D) competitive assay: each focal male was placed in an arena with five competitor males and three standard females.

water and 170 g cocopeat), which produced flies of an intermediate size (Sentinella et al. 2013; A. K. Hooper, pers. obs.). If the companion male died prior to the focal male, the companion male was replaced with a new male of similar age. Focal males had ad libitum access to food (brown sugar and dried yeast) throughout their life. Focal males were marked on the thorax with enamel paint (Model Master; Testor, Rockford, IL; Kawasaki et al. 2008) to distinguish them from competitor males.

To manipulate male opportunity to engage in male–male contest behaviors, focal males were randomly allocated to one of two social treatments: fighting or nonfighting (Fig. 1A, B). In the fighting treatment, focal males and the companion male were allowed to freely interact and engage in contests for control over the oviposition dish in the center of the container. In the nonfighting treatment, a barrier of fly mesh was placed down the center of the container and across the oviposition dish, splitting the area into two so each male could independently defend its own oviposition site, and preventing the flies from engaging in any tactile interactions. In addition, a smaller solid black barrier was placed down the middle of the oviposition dish in the center of the flyscreen to prevent males from receiving visual cues from the other male while on the oviposition dish. This design therefore provided males in each social treatment with the same amount of space, food, and oviposition medium (which is used as a food source by adults) per male. As males in the nonfighting treatment could also sense each other through the fly mesh both visually and chemically, social cues across treatments were similar; the only difference between the two treatment groups was opportunity to engage in interactions involving physical contact, and therefore to incur mechanical damage and allocate energy to combat. This resulted in a fully factorial design (fighting, high condition, $N = 53$; fighting, low condition, $N = 53$; nonfighting, high condition, $N = 53$; nonfighting, low condition, $N = 53$).

Every two days, focal enclosures were checked and any deaths were recorded. After death, focal males were photographed with wings removed. We used thorax length as a measure of adult body size (Bondurianskiy 2006), and wing area missing at the time of death as a measure of lifetime accumulated somatic damage (Downer and Laufer 1983). All photos were taken using a Leica DFC digital camera mounted on a Leica MS5 stereomicroscope, and body dimensions were quantified from images using ImageJ software (National Institutes of Health, Bethesda, Maryland, USA).

Reproductive performance of males was tested in two ways: no-choice assays (Fig. 1C) and competitive assays (Fig. 1D). All focal males were tested repeatedly in both no-choice and competitive assays. All assays were conducted under standard lighting conditions. A double fluorescent light fixture with electronic ballast housing fitted with Repti Glo 2.0 UVB full spectrum terrarium lamp (Exo Terra, Rolf C. Hagen Inc., Montreal, Canada) and Repti Glo 5.0 UVB tropical terrarium lamp (Exo Terra, Rolf C. Hagen Inc., Montreal, Canada) was used to create a high UVB light environment, simulating natural light. All standard females used in reproductive trials were reared on a standard diet, and housed in female-only groups provided with ad libitum food. Standard females were 15 (±1) days old at the time of reproductive assays, and therefore gravid with mature eggs.

NO-CHOICE ASSAYS

To test male ability to produce viable offspring independently of competition, males were paired with a standard female in a glass scintillation vial for 1 h (Fig. 1C). During this hour, we recorded the latency to first mating, number of matings that occurred in the hour, as well as duration of matings. Males were first tested in this assay when they were 15 days old, and then retested every 10 days (with a new standard 15 days old female) until the male's death.

After 1 h, if mating occurred, females were transferred to a 250-mL container with food and an oviposition dish, and left for 96 h to lay eggs. After 48 h, the oviposition dish was swapped for a fresh dish. We recorded the number of eggs the female laid on each dish. At either 48 or 96 h (depending on availability of eggs), 20 eggs were collected and transferred to 100 g of standard larval medium and incubated at 25°C. Where less than 20 eggs were present on the dish, all eggs were collected. Date of first offspring emergence was recorded, and after 10 days all emerged flies were euthanized by freezing. Offspring were then counted, sexed, and thorax length of up to five males and five females measured for each brood. Any containers that failed to produce any adult flies 10 days after adult emergence from the last container from the same egg transfer date were scored as having zero emergence.

Figure 2. Two *Telostylinus angusticollis* males locked together in characteristic vertical contact posture of fully escalated combat (photo: R. Bondurianskiy), while in this vertical posture, males repeatedly strike each other with their head and "chest", raise and strike each other with their forelegs, and sometimes wrap a foreleg around their competitor's neck in a "head-lock." (see Supporting Information video).

COMPETITIVE ASSAYS

As males frequently compete with other males for access to females, we also tested male ability to achieve matings under competition. Male performance in competitive arenas was tested when males were 15 and 35 days old to gain a measure of performance at young and old ages for each individual.

Males were placed in an arena with five competitor males and an oviposition dish (Fig. 1D). Competitor males were derived from a stock founded by *T. angusticollis* individuals collected in Brisbane, Queensland (Cassidy et al. 2014), and were reared on a standard larval diet and housed communally in large population cages before and between assays. The Brisbane stock was used to facilitate paternity assignment (which was not undertaken as part of this study). To allow males to establish dominance hierarchies, focal males were left in the competitive arena for at least 8 h before any behavioral observations.

At the beginning of the competitive assay, three standard females were introduced to the arena, resulting in a high-competition environment for the focal male (Fig. 1D). Competitive arenas were then observed for 1 h. We recorded the total number of matings that occurred, noting how many were performed by the focal and by the competitor males. All contest interactions involving the focal male were also noted. We defined a contest interaction as a physical encounter between two males that ended with a clear retreat by one male. These were further classified as either a full combat (which occurs when males lock together in a

characteristic vertical contact posture and strike each other with their bodies, heads, and forelegs; Fig. 2), or a noncombat contest interaction (i.e., not involving vertical contact posture). We also recorded any chasing behavior, as when there was a clear approach and retreat between two males without touching. Where possible, we recorded whether the focal or competitor male initiated the encounter, and which male retreated (i.e., "lost" the contest). As a measure of resource defense strategy, we also recorded whether the interaction occurred on or next to the oviposition dish. After the hour was complete, focal and competitor males were returned to their respective enclosures.

MALE–MALE CONTEST INTERACTIONS IN ENCLOSURES

Before each "no-choice" assay at each age up until 45 days old, we observed male behaviors in the fighting social treatment for 30 min and recorded all contest interactions. We did this to determine the relative rates of contest behaviors experienced by high- and low-condition males in their enclosures.

STATISTICAL ANALYSES

All analyses were performed in R version 3.2.0 (R development Core Team 2008). Means are presented plus-minus standard error.

Longevity of focal males was analyzed using a Cox proportional hazards regression model using the *coxme* package. Condition treatment, social treatment, and their interaction were entered as predictor variables, with age at death as the response, and focal larval container included as a random effect. The interaction between condition and social treatment was tested using a likelihood ratio test. Additionally, we investigated actuarial ageing rates (i.e., age-specific changes in mortality rates) using the Bayesian Survival Trajectory Analysis (BaSTA) package (Colchero et al. 2012); (See Supporting Information materials for details).

Males with no wing damage at time of death were used to estimate the linear relationship between body size and wing area (Supporting Information Material and Table S3). This was then used to predict full wing size of all males from thorax length. The actual wing area remaining at time of death was then subtracted from predicted full wing size for each wing to give a measure of wing damage for all males. This value was then analyzed using a linear mixed effects model using the package *lme4*, with condition, social treatment, and their interaction as fixed predictors of wing damage. Life span was included as a covariate because wing damage accumulates with age (reviewed in Burkhard et al. 2002). Individual ID and larval container were included as random effects.

The total number of contest interactions observed in experimental enclosures prior to no-choice assays was analyzed using a generalized linear mixed effects model with Poisson error structure. Fixed effects are listed in Table S5. Male ID and larval container were entered as random effects, as well as an observation-level random effect to correct for overdispersion (Harrison 2014).

To investigate male–male contest behaviors during competitive assays, we first carried out principle component analysis of all contest behaviors recorded (total number of contest interactions, proportion of interactions that escalated to full combat, proportion that occurred near oviposition dish, proportion initiated by the focal male, proportion won by the focal male; Fig. S3; Table S6). From this, we determined that the behavior that was the best predictor of overall performance in male–male contest interactions (i.e., the behavior with the highest loading on PC1) was the proportion of fights where the focal male "won" the interaction (Supporting Information Material and Table S6). We then analyzed this behavior as the response variable in a generalized linear mixed effects model to determine which factors affected contest performance. Data were analyzed as a matrix of successes and failures, with binomial error structure. Fixed effects are listed in Table 1. Individual ID and focal larval container were included as random effects. Proportion of total matings obtained by the focal male (relative to all matings achieved by the focal and competitor males) was analyzed similarly with a generalized linear mixed effects model using the same fixed and random effects (Table 1).

Table 1. Generalized linear mixed effects models of the proportion of contest interactions won and proportion of matings attained by the focal male in competitive assays.

Fixed effects	Proportion contests "won"		Proportion matings attained	
	Estimate	SE	Estimate	SE
(Intercept)	0.344	0.292	**–1.613**	**0.132**[***]
Condition treatment	**–1.750**	**0.480**[***]	0.257	0.181
Social treatment	–0.100	0.397	0.235	0.166
Age	**1.091**	**0.419**[**]	**0.534**	**0.216**[*]
Condition × social treatment	–0.138	0.665	–0.401	0.236
Condition × age	**–1.414**	**0.679**[*]	**0.694**	**0.283**[*]
Social treatment × age	–0.069	0.529	–0.033	0.271
Condition × social treatment × age	0.785	0.884	0.031	0.365

Bold values denote *P*-value < 0.05, *P-value < 0.05, **P-value < 0.01, ***P-value < 0.001.

Table 2. Generalized linear mixed effects models of reproductive performance measures from males mated to standard virgin females in no-choice assays.

Fixed effects	Latency to first mating		Duration of matings		Probability of mating		No. of matings during assay		No. of eggs laid by female		Egg to adult viability	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
(Intercept)	**2.499**	**0.104*****	**1.882**	**0.063*****	**3.214**	**0.673*****	**0.586**	**0.064*****	**3.690**	**0.188*****	–0.634	0.586
Condition treatment	**0.380**	**0.145****	0.000	0.077	**–3.840**	**1.015*****	**0.364**	**0.082*****	–0.027	0.256	**2.421**	**0.639*****
Social treatment	0.067	0.141	0.031	0.085	–0.099	0.847	–0.149	0.088	–0.316	0.244	0.593	0.617
Age	**0.009**	**0.003****	–0.002	0.002	**–0.045**	**0.019***	–0.060	0.063	**–0.581**	**0.193****	**–0.107**	**0.009****
Hours after assay eggs collected	–	–	–	–	–	–	–	–	–	–	**–0.006**	**0.002****
Mating order	–	–	**–0.013**	**0.006***	–	–	–	–	–	–	–	–
Condition × social treatment	–0.333	0.197	–0.043	0.105	**3.650**	**1.311****	0.077	0.113	0.302	0.330	–0.789	0.836
Social treatment × age	0.002	0.004	0.000	0.002	–0.002	0.024	–0.010	0.086	–0.264	0.257	–0.005	0.013
Condition × Age	**–0.018**	**0.004*****	0.001	0.002	**0.169**	**0.039*****	**0.250**	**0.078****	**0.561**	**0.254***	–0.006	0.012
Condition × social treatment × age	**0.011**	**0.006***	0.001	0.003	**–0.136**	**0.045****	–0.151	0.106	–0.014	0.336	0.019	0.016

Bold values denote *P*-value < 0.05, *P-value < 0.05, **P-value < 0.01, ***P-value < 0.001.

As most males had died by the age of 65 days, only data from no-choice assays performed up to age of 55 days were included in analyses. Random effects of individual ID and focal larval container were included in all the following mixed effects models, and fixed effects are listed in Table 2. Latency to first mating and duration of matings during the no-choice assay were analyzed using linear mixed effects models. Data in these analyses were log-transformed to improve normality of errors. Number of matings attained by males in the no-choice assay and number of eggs laid by the female were similarly analyzed using generalized linear mixed effects models with Poisson error structure. An observation-level random effect was included to correct for overdispersion in the model of female egg output. The probability of males performing any successful matings during the no-choice assay was similarly analyzed with a binomial error structure. Egg to adult viability was analyzed as a binomial matrix of successes and failures, modeled with a binomial error structure. In this analysis, the number of hours after mating when eggs were collected (either 48 or 96) was included as a covariate to account for any effect of female latency to lay eggs on egg-to-adult viability.

Body size of offspring was analyzed using linear mixed effects models with fixed effects listed in Table 3. As the sample sizes for each treatment became very unbalanced after the first assay (age 15 days), only offspring produced in the no-choice reproductive assay at day 15 were used in this analysis (age was therefore not included as a fixed effect). Random effects included in the model were individual ID and larval container of the focal sire.

Results
BODY SIZE AND DEVELOPMENT TIME
High-condition males (thorax length 3.03 ± 0.009 mm) were larger than low-condition males (thorax length 2.57 ± 0.019 mm; Welch two-sample *t*-test: $t_{147.46} = 22.3$, $P < 0.001$). Development time was shorter in high-condition males (25.9 ± 0.09 days) than low-condition (28.7 ± 0.13 days) males (Welch two-sample *t*-test: $t_{187.87} = -17.9$, $P < 0.001$).

LIFE SPAN AND MORTALITY RATE
Low-condition males had a longer life span than high-condition males (mean lifespan low-condition males = 60.8 days, mean lifespan high-condition males = 49.3 days, hazard ratio = 0.685, $P = 0.007$), and males in the nonfighting social treatment also had a longer life span compared to males in the fighting treatment (hazard ratio = 0.580, $P < 0.001$). There was no significant interaction between these factors ($\chi^2(1) = 0.155$, $P = 0.694$; Fig. 3A).

Mortality rates were best estimated using a Weibull model with simple shape (Supporting Information Material and Table S1). Mortality rate was highest in the high-condition males in the fighting treatment, and lowest in the low condition males in the nonfighting treatment (Fig. 3B; Supporting Information
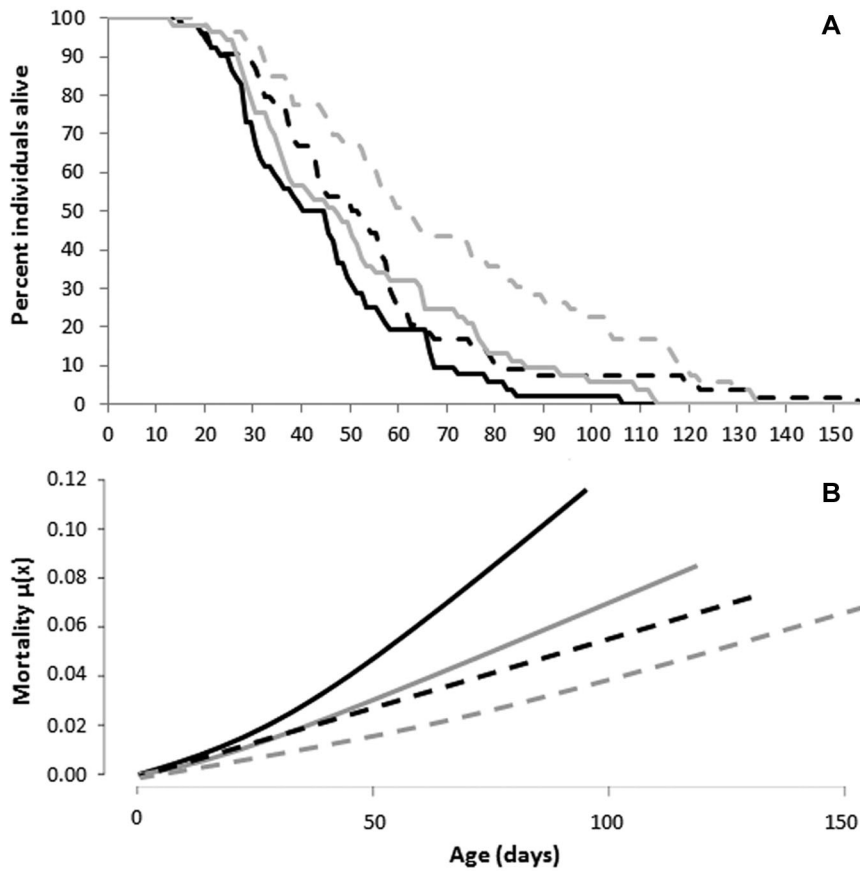
Figure 3. (A) Survivorship curves for high- and low-condition males housed in fighting and nonfighting social treatments. (B) Mortality curves estimated by BaSTA analysis (See Supporting Information Materials for details). Black lines represent high-condition males, gray lines represent low-condition males, solid lines represent males in the fighting social treatment, and dashed lines represent males in the nonfighting treatment.

Table 3. Linear mixed effects model of body size of offspring produced in a no-choice pairing.

Fixed effects	Est.	SE
(Intercept)	**2.194**	**0.223**[***]
Condition treatment	0.001	0.030
Social treatment	–0.027	0.029
Offspring sex	**0.436**	**0.008**[***]
Hours after mating eggs collected	0.000	0.000
Standardized development time (focal parent)	–0.007	0.009
Standardized thorax length (focal parent)	–0.007	0.009
Virgin female development time	0.014	0.009
Condition (low) × social treatment (nonfighting)	0.012	0.036

Bold values denote *P*-value < 0.05, ***P*-value < 0.001.

Materials and Fig. S1). This difference in mortality trajectory between treatment groups appears to be driven by differences in the scale (b_1) parameter, rather than the shape (b_0) parameter.

COMPETITIVE ASSAYS

There was a significant interaction between condition and age on the proportion of male–male combat interactions won by the focal male (Table 1; Fig 4A). There was no change with age in the proportion of combat interactions won by low-condition males, whereas high-condition males won more interactions when older. There was also an overall effect of condition with high-condition males winning more interactions against competitors than low-condition males at both ages.

There was a significant interaction between condition treatment and age on male mating success under competition (Table 1; Fig. 4B). At age 15 days, there was no difference in mating success between high-condition and low-condition males. However at age 35 days, low-condition males had higher mating success than high-condition males relative to the competitor males.
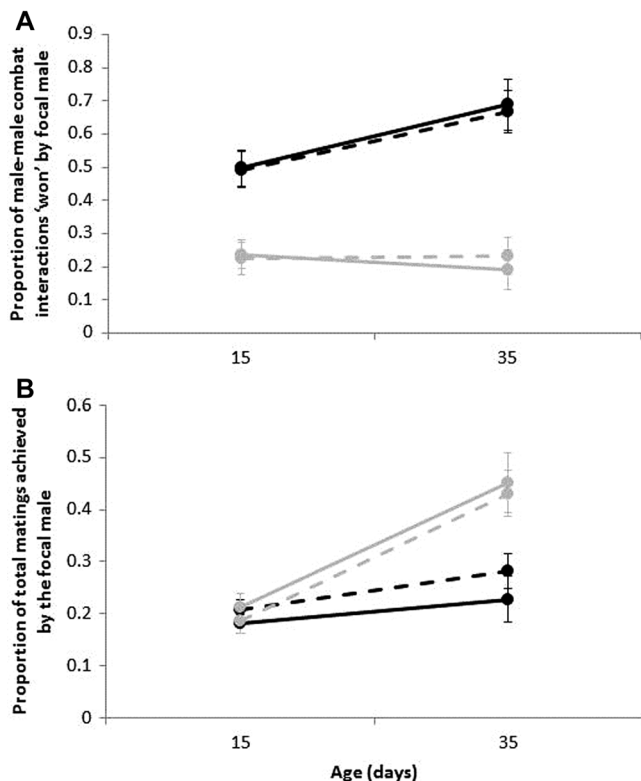
Figure 4. Focal male performance in competitive assays at 15 and 35 days of age: (A) The proportion of male–male contests won by the focal male; (B) proportion of matings obtained by the focal male. Black lines represent high-condition males, gray lines represent low condition males, solid lines represent males in the fighting treatment group, and dashed lines represent males in the nonfighting treatment group.

NO-CHOICE ASSAYS

Average latency to first mating was 795 ± 13 sec. There was an interaction between condition and age on the average latency to first mating (Table 2; Fig. 5A). At the age of 15 days, high-condition males achieved mating more quickly than low-condition males. At all other ages, low-condition males had a shorter latency to mating than high-condition males. This occurred because latency to first mating increased with age in high-condition males, but did not change with age in low-condition males.

Average duration of matings that occurred during the no-choice assay was 74.6 ± 0.7 sec. The only significant effect on mating duration was mating order, whereby matings became successively shorter over the course of the assay (Table 2).

We detected a three-way interaction between condition, social treatment, and age on the probability of males achieving any matings in the no-choice assay (Table 2; Fig. 5B). At young age (15 days), low-condition males in the fighting social treatment had a lower probability of achieving any matings. The probability of mating decreased with age in high-condition males, but did not change with age in low-condition males, with the exception of age 55 days, where probability of mating was slightly decreased for low-condition males in the nonfighting treatment compared to low-condition males in the fighting treatment.

There was an interaction between condition and age on the number of matings performed in the no-choice assay (Table 2; Fig. 5C). At young age (15 days), there was no difference between high-condition and low-condition males in the number of matings achieved during the assay. With increasing age, low-condition males increased the number of matings performed, but there was no effect of age on the number of matings performed by high-condition males.

There was an interaction between condition and age on the number of eggs produced by females mated to males in the no-choice assay (Table 2; Fig 5D). At young age (15 days), high-condition males induced females to lay more eggs, whereas at all other ages females mated to low-condition males had higher egg output.

Egg-to-adult viability of offspring was affected by male condition, with females paired with low-condition males producing more viable eggs at all ages (Table 2; Fig. 5E). There was also an overall effect of age, with egg-to-adult viability decreasing with increasing male age in both condition treatments. When eggs were collected at 96 h after mating (rather than 48 h), there was a slight decrease in egg-to-adult viability.

There was no effect of male condition treatment, social treatment, or age on size of offspring produced by males in the no-choice assay (Table 3). There was, however, an effect of offspring sex on body size.

WING DAMAGE

Residual wing damage was not affected by either individual condition or social treatment, nor the interaction between these factors. However, life span had a significant effect, with longer lived flies having more wing damage at time of death (Supporting Information Material and Table S4).

COMBAT BEHAVIORS IN ENCLOSURES

Neither condition nor social treatment or age affected the number of male–male contest interactions recorded in experimental enclosures (Supporting Information Material and Table S5). This indicates that males in both high- and low-condition treatments interacted at similar rates with the companion males throughout their lives.

Discussion

Many studies have linked abundant resources and high condition to increased investment in sexual signals and weapons that enhance mating success and demonstrated a trade-off between
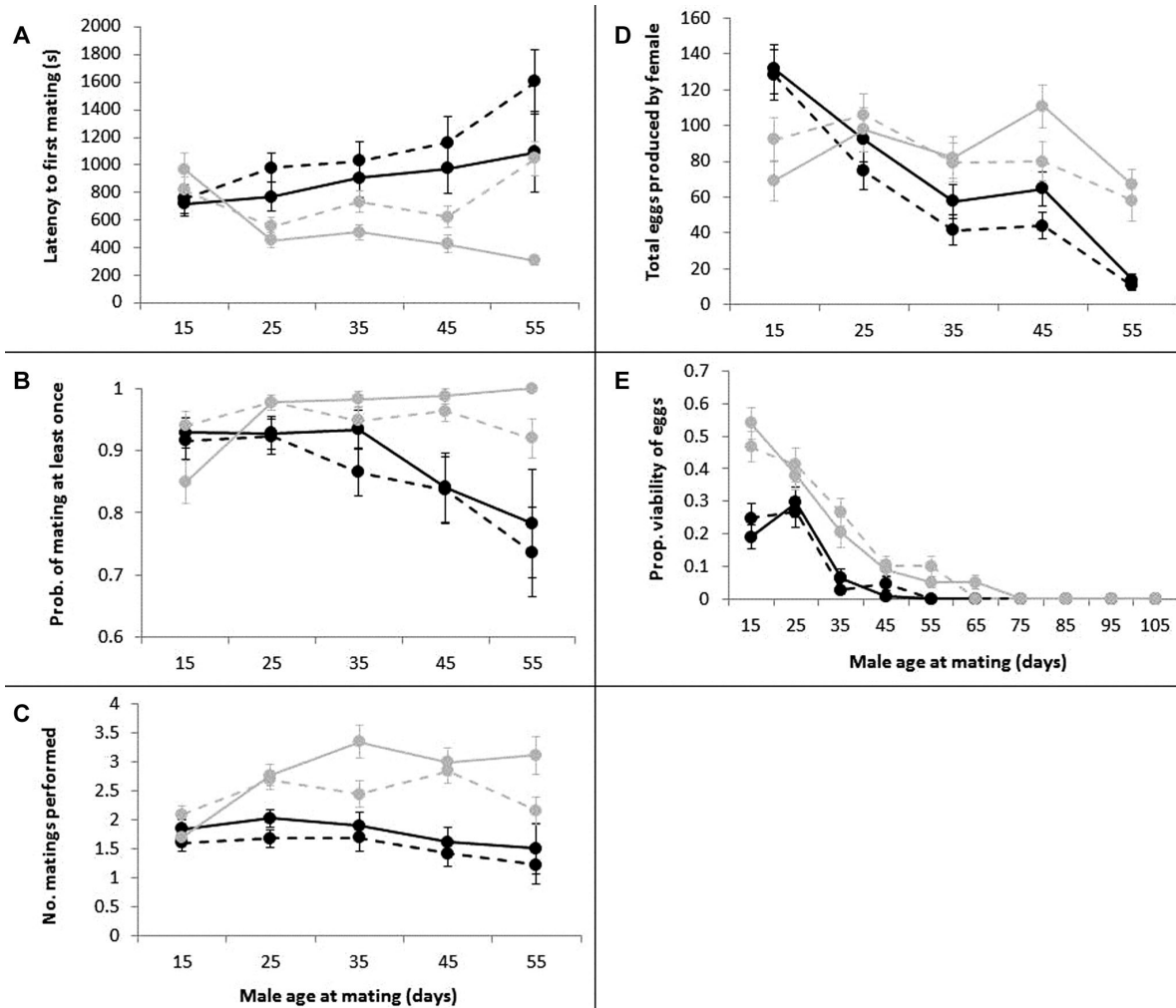
Figure 5. Male performance in a no-choice assay (A: latency to first mating; B: probability of mating at least once; C: number of matings performed), and reproductive output by standard females mated to males in a no-choice assay (D: total number of eggs laid in 96 h; E: egg-to-adult viability of those eggs). Black lines represent high-condition males, and low-condition males are represented by gray lines, solid lines represent males in the fighting social treatment, and dashed lines represent males in the nonfighting treatment.

reproduction and survival. Our study provides new insight by showing that ontogenetic timing is a central element of condition-dependent life-history strategies (Fig. 6). We found clear evidence that high-condition *T. angusticollis* males peaked earlier than low-condition males in most reproductive performance measures. Moreover, we found no evidence that reproductive performance peaked at higher levels in high-condition males. These findings suggest that *T. angusticollis* males use abundant nutrients during the juvenile phase to achieve earlier reproduction, perhaps without attaining a higher reproductive peak. However, the accelerated ontogeny of high-condition males imposed severe latent costs manifested in rapid ageing across all measures of reproductive performance and resulted in shortened lifespan. Although males that interacted with other males throughout life died sooner and had a higher mortality rate, male–male interactions had little effect on reproductive performance, indicating that accelerated

ageing in high-condition *T. angusticollis* males results primarily from costs associated with the development and maintenance of the high-condition body rather than from damaging male–male interactions. Our results suggest that the principal advantage enjoyed by high-condition *T. angusticollis* males is an accelerated ontogeny reflected in rapid growth and development and an early reproductive peak, and show that condition-dependent investment in reproductive traits that are fixed during development is a key source of variation in ageing rate in males of this species.

EFFECTS OF CONDITION ON AGEING
High-condition males had an advantage in some aspects of reproductive performance at young ages (15–25 days), and were better fighters at both young and old ages. High-condition males exhibited shorter latency to first mating and higher probability of achieving at least one mating in the 15 days no-choice
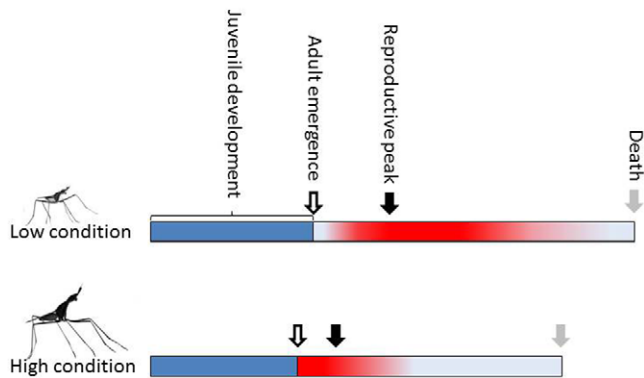
Figure 6. Ontogenetic timing of high- and low-condition males. High-condition males experience accelerated ontogeny but age faster and die sooner compared to low-condition males. The lengths of developmental and adult ontogenetic phases are based on observed means for low- and high-condition males. Although the precise positions of reproductive performance peaks cannot be determined from our data, the approximate relative positions of these peaks in high- and low-condition males are shown.

assay, suggesting that high-condition males were more attractive to females when young. Females paired with high-condition males also laid more eggs in the 15 days no-choice assay, suggesting that high-condition males outperform low-condition males in fecundity stimulation (which may involve the transfer of seminal proteins such as sex peptide; Chapman 2001) at early ages. However, we observed accelerated ageing in high-condition males, manifested in poor performance at old age relative to low-condition males. These results suggest that high-condition males invest more in early life at the expense of late life performance. One possible cause of this trade-off is maintenance costs of larger body size or exaggerated weapons in high-condition males. In *T. angusticollis*, nutrient abundance during the larval feeding phase has a large influence on the development of adult body size and secondary sexual traits and, because *T. angusticollis* is a holometabolous species, males are unable to alter their exoskeleton after metamorphosis is complete. These traits could potentially impose energetic costs on high-condition individuals by increasing overall metabolic demands (Kotiaho et al. 1998) or increasing energetic requirements of locomotion and feeding (Møller 1989; Basolo and Alcaraz 2003), thus reducing their ability to invest in somatic maintenance. In addition, high-condition *T. angusticollis* males have more fragile bodies (Adler et al. in press), and this greater fragility may be a cost of building a body geared to enhanced reproductive performance in early life.

High-condition males may also divert resources away from somatic maintenance and into accelerated development. Although high-condition males exhibited their maximum performance at the earliest age examined (15 days), low-condition males improved with age in some aspects of reproductive performance,

including number of matings in the no-choice assay, and mating success under competition, suggesting that they reached their reproductive peak later in life. As low-condition males also experience slower juvenile development, this suggests that abundant nutrients in the larval diet affect the male life-history strategy by allowing high-condition males to accelerate both the juvenile and adult phases of their ontogeny. In the wild, mortality rate is high and lifespans of *T. angusticollis* males are much shorter than those experienced under benign lab conditions (Kawasaki et al. 2008). Under lab conditions, high extrinsic mortality has been shown to select for faster development time and shorter lifespan in *Drosophila* (Stearns et al. 2000). Thus, if development rate is resource limited in *T. angusticollis*, high-condition males may benefit by using increased resources to accelerate growth and development and increase early-life fitness at the cost of late-life performance. Costs of accelerated growth and development rate are well established (Metcalfe and Monaghan 2003), and it is possible that low-condition individuals are unable to bear these costs.

Our results are concordant with the findings of Hunt et al. (2004), who showed that abundant dietary protein throughout life accelerated growth and development, increased early-life calling effort, but shortened life span in male crickets. Similarly, in wild antler flies (*Protopiophila litigata*), large males achieved higher mating success in early life but suffered more rapid reproductive ageing than small males (Bonduriansky and Brassil 2005). These patterns fit with a number of other studies, which show that accelerated growth or larger body size is associated with accelerated ageing rates within species. For example, larger dog breeds tend to suffer more rapid ageing than smaller breeds (Kraus et al. 2013). It has also been shown that lifespan is increased in multiple mutant strains of mice that have decreased production of or sensitivity to growth hormone, suggesting that growth and body size are important determinants of lifespan in this species (Bartke et al. 2001). Thus, accelerated growth is often associated with high mortality or rapid ageing, and the costs of accelerated growth may also result in rapid ageing in high-condition individuals.

As well as investing in early-life performance, our results suggest that high-condition males are also investing more in precopulatory performance, because high-condition males outperformed low-condition males in all measures of contest performance in male–male interactions. Surprisingly, however, high-condition males achieved equal mating success to low-condition males in competitive assays at the age of 15 days, and performed worse than low-condition males in competitive assays at the age of 35 days. Selection is often context dependent, and performance under laboratory conditions may therefore differ from performance in natural environments (Miller and Svensson 2014). In our experiment, low-condition males may have benefited from the limited space available in competitive assay arenas, because

increased density increases interference rates from competitor males, potentially decreasing the relative mating success of large, aggressive males (Conner 1989; Knell 2009). Additionally, environment complexity can also affect the relative fitness of different behavioral phenotypes (Lukasik et al. 2006), and this may have affected our behavioral results. Nonetheless, as for most other measures of performance, the competitive mating success of high-condition males peaked at an early age (15 days), and declined thereafter relative to that of low-condition males.

Selection for increased precopulatory performance in high-condition males could further select for low-condition males to maintain postcopulatory performance into older ages. As low-condition males perform poorly in male–male contests, it is likely that they rely on sneak matings in the wild. It has been shown in other species that behaviorally subordinate males can compensate for fewer mating opportunities by producing more competitive sperm (Gage et al. 1995; Simmons et al. 1999; Vladić and Järvi 2001; Smith and Ryan 2010). Additionally, if low-condition males rely on sneak matings, they are more likely to encounter females who have previously mated, and thus face greater levels of sperm competition, further increasing selection for investment in sperm performance in low-condition males (Parker 1990a,b). Indeed, it was previously shown that low-condition *T. angusticollis* males engage in longer copulations and confer higher egg-hatching success than high-condition males (Fricke et al. 2015), indicating that increased investment in postcopulatory performance by low-condition males is a consistent response in this species. These selection pressures could further select for low-condition males to increase investment in postcopulatory traits and delay the onset of reproductive ageing relative to high-condition males at the cost of precopulatory (combat) performance.

EFFECTS OF MALE–MALE CONTESTS ON AGEING

In comparison to the large effects of nutrients in the larval diet, which determine early-life condition, on the life history of *T. angusticollis* males, opportunity to engage in male-male contests had little or no effect on reproductive performance or reproductive ageing. Nonetheless, males that had the opportunity to engage in male–male contests throughout life experienced increased mortality and reduced lifespan, suggesting that such contests are in fact costly. Although intrasexual competition has been shown to affect actuarial ageing rates in other species (Mysterud et al. 2005; Maklakov and Bonduriansky 2009), to our knowledge, only one other study has tested the effects of intrasexual combat interactions on reproductive ageing patterns (see Bretman et al. 2013). Sharp and Clutton-Brock (2011) found that increased aggression between female meerkats negatively affected reproductive output, and accelerated rates of reproductive senescence in those females. Our results suggest that the costs imposed by male–male contests are more latent than immediate. We found no effect of

social treatment on the amount of wing damage at time of death. However, a previous study on this species showed that male–male interactions can result in substantial wing damage when males are maintained at higher densities (Adler et al. in press), and such damage has been reported in other species as well (Alcock 1996). Latent costs of male–male combat behaviors in *T. angusticollis* might also arise from a decrease in feeding behaviors, reduced immunocompetence, or from stress or fatigue (Creel et al. 1996; Cornwallis and Birkhead 2008), which have the potential to negatively affect lifespan (Monaghan et al. 2008). However, it is not clear why male–male contests do not appear to affect reproductive ageing in this species.

Surprisingly, we also found little evidence of interactions between social treatment and condition on reproductive ageing patterns. Only one such was detected for probability of mating at least once in no-choice assays. However, high-condition males that interacted throughout life with other males had increased, not decreased probability of mating. This suggests that high-condition males might obtain some social cue in a highly competitive environment to increase mating effort. However, as none of our other results indicate that this is the case, it is unclear why social treatment had this effect. As we did not find evidence of a higher cost of exposure to fighting behaviors in high-condition males, this suggests that high-condition males are not actually investing more in combat behaviors per se, as we initially expected. Alternatively, high-condition males may be able to compensate for increased energetic expenditure, for example, through compensatory feeding (Marler and Moore 1991).

ONTOGENETIC TIMING AS A CONDITION-DEPENDENT LIFE-HISTORY STRATEGY

Classic condition-dependence theory suggests that abundant resources are allocated to morphological and behavioral secondary sexual traits that enable high-condition males to achieve high mating success (Andersson 1982; Nur and Hasson 1984; Rowe and Houle 1996). Although it is widely acknowledged that physiological traits (such as immunocompetence and development rate) can also be condition dependent (Hill 2011), the role of such traits in male reproductive strategies has received far less attention than the role of signals and weapons. Moreover, although it is widely recognized that investment in reproductive traits (including secondary sexual traits) often trades off with somatic maintenance and survival (Williams 1957; Kirkwood 1977; Kirkwood and Rose 1991; Maklakov and Immler 2016), and some empirical studies have suggested a positive relationship between condition and ageing rate (Hunt et al. 2004; Bonduriansky and Brassil 2005; but see Maklakov et al. 2009; Zajitschek et al. 2009), the link between condition and ageing is complex and remains poorly understood.

By investigating the effects of nutrient abundance during the juvenile phase on male performance in a broad range of

fitness-related traits across the life span, we were able to identify ontogenetic timing as a central component of condition-dependent life-history strategy. Our results suggest that, rather than simply using abundant nutrient resources to increase mating success relative to low-condition males, *T. angusticollis* males use these resources to increase the rate of juvenile growth and development and achieve an earlier peak in reproductive performance. We found little evidence that peak performance of high-condition males exceeded that of low-condition males. Given that high-condition males had a clear advantage in combat performance, it is possible that high-condition males effectively exclude low-condition males from prime oviposition sites and monopolize matings under natural conditions, and thus perhaps achieve higher peak mating success than low-condition males in the wild. Nonetheless, the results of our competitive and noncompetitive assays suggest that high-condition males benefit largely by shifting their peak reproductive capability to an earlier age. Coupled with their more rapid juvenile development, this shift may allow high-condition males to reproduce several days earlier, on average, than low-condition males (Fig.6). Accelerated juvenile development may be advantageous given high larval mortality from predation (AH, pers. obs.) Additionally, given the very high extrinsic mortality risk experienced by *T. angusticollis* individuals in natural populations (Kawasaki et al. 2008), earlier reproduction is likely to result in a substantial fitness advantage for high-condition males. High-condition males appear to achieve this earlier reproductive peak by investing more in weapons and male–male contest behaviors. Our results suggest that this enhanced early-life reproductive effort allows high-condition males to achieve high mating success soon after adult emergence. However, investment in such traits imposes latent costs manifested in rapid ageing, and may also elevate immediate mortality risk from injury and predation. Ontogenetic timing, therefore, appears to be a key component of the condition-dependent reproductive strategy in *T. angusticollis* males. Ontogenetic timing also appears to mediate the relation between condition and the rate and pattern of ageing in this species.

Conclusions

Although previous studies (e.g., Hunt et al. 2004) have shown that high condition can trade off against longevity, our study yields several novel insights. First, we show that, in *T. angusticollis* males, high-condition males are prone to rapid ageing irrespective of opportunity to engage in costly, condition-dependent behaviors. Second, we provide clear evidence that high early-life condition is associated with accelerated reproductive ageing across a broad range of reproductive traits. Third, our results suggest that high condition results in an earlier but not higher peak in male reproductive performance, such that high-condition *T. angusticollis* males benefit primarily from earlier reproduction rather than from

an increased reproductive rate throughout life. Our findings provide strong evidence that ontogenetic timing—the rate of juvenile growth and development, and the rate of attainment of the adult reproductive peak—is a key, condition-dependent element of the life-history strategy of *T. angusticollis* males. Our results also show that access to nutrient resources during development can be an important source of variation among individuals in the rate and pattern of ageing.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supplementary video. Fully escalated male–male combat behaviour in *Teleostylinus angusticollis*.

Figure S1. Mortality (c) and survivorship (d) curves with 95% confidence intervals for each treatment as fitted by Weibull mortality model, where b_0 is the shape parameter (a) and b_1 is the scale parameter (b).

Figure S2. Kullback–Leibler divergence calibration (KLDC) values comparing parameter posterior distributions between our treatment groups.

Figure S3. Principle component analysis of male–male combat behaviors recorded in a competitive arena by large and small males.

Table S1. Model selection for the 10 models run in the BaSTA analysis (based on deviance information criterion, DIC).

Table S2. Parameter estimates for each treatment group for the best fitting model (Weibull with simple shape).

Table S3. Linear regression of full wing area on thorax length (fighting, high condition, $N = 50$; fighting, low condition, $N = 51$; nonfighting, high condition, $N = 56$; nonfighting, low condition, $N = 49$).

Table S4. Generalized linear mixed effects model of the effects on social environment and condition on residual wing damage at time of death.

Table S5. Generalized linear mixed effects model of the effects on competitive behaviors in the fighting treatment.

Table S6. Loadings of PC1 of male–male combat behaviors observed in competitive assay.