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The dissimilar costs of love and war: age-specific mortality as a function of the operational sex ratio

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Abstract

Lifespan and ageing are strongly affected by many environmental factors, but the effects of social environment on these life-history traits are not well understood. We examined effects of social interaction on age-specific mortality rate in the sexually dimorphic neriid fly *Telostylinus angusticollis*. We found that although interaction with other individuals reduced longevity of both sexes, the costs associated with variation in operational sex ratio were sex specific: males' early-life mortality rate increased, and lifespan decreased, with increasing male bias in the sex ratio, whereas surprisingly, the presence of males had no effect on early-life mortality or lifespan of females. Intriguingly, early-life (immediate) mortality costs did not covary with late-life (latent) costs. Rather, both sexes aged most rapidly in a social environment dominated by the opposite sex. Our findings suggest that distinct reproductive activities, such as mating and fighting, impose different age-specific patterns of mortality, and that such costs are strongly sex specific.

Introduction

Life-history theory postulates that organisms will evolve to schedule use of energy reserves and resources over the lifetime to optimally balance reproduction with longevity (Stearns, 1989; Roff, 1992). The most efficient scheduling of resources therefore will be dependent on the environment, and organisms may evolve facultative strategies (adaptive plasticity) that enable them to maximize their fitness in a range of environments. However, the environment may also impose constraints on organisms' ability to optimize their reproductive strategies (e.g. by limiting access to resources, or imposing irreparable somatic damage). Lifespan and ageing – two life-history traits closely related to fitness – are known to be highly environment dependent (Kawasaki *et al.*, 2008). In particular, many studies have shown that mating and reproduction impose life-history costs in the form of reduced survival prospects (e.g. Ernsting & Isaaks, 1991; Chapman *et al.*, 1993, 1995). Such costs are central to theory on the evolution of reproductive strategies and the evolution of ageing (Williams, 1957; Hamilton, 1966). However, little is known about how these costs are affected by variation in a key environmental parameter – the nature and frequency of social interactions.

The social environment can impose a variety of costs, and the nature and severity of these costs may differ between sexes. Social interaction in any form is likely to carry heavy costs, resulting from competition for food and space (Boyd, 1982; Krause & Ruxton, 2002), and exposure to parasites from other individuals and their waste products that necessitates increased immune function (Alexander, 1974; Krause & Ruxton, 2002). But when variation occurs in the operational sex ratio, organisms will face altered frequencies and intensities of interaction with same- and opposite-sex individuals, and differential exposure to various components of reproductive activity, such as agonistic interactions (combat), courtship and mating. Indeed, sex ratios are likely to be highly variable across space and time (reviewed in Kvarnemo & Ahnesjo, 1996). Variation in the sex ratio may therefore affect life-history costs and, because the sexes pursue very different reproductive strategies, these costs may be highly sex specific.

Life-history costs of encountering the opposite sex (intersexual interaction) are well established in the literature as costs of mating (Daly, 1978) and costs of

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reproduction (Stearns, 1989; Roff, 1992). For males, mating costs result from the energetic demands of courtship and mating, struggling with resistant females, mate guarding, and producing sperm and accessory gland proteins (Walker, 1980; Dewsbury, 1982; Andersson, 1994; Arnqvist & Rowe, 2005). For females, intersexual interaction carries survival costs resulting from heavy investment in offspring, as well as male harassment and persistent courtship, injury by the male, exposure to parasites and sexually transmitted diseases, or manipulative or damaging seminal substances (Stockley, 1997; Jennions & Petrie, 2000).

Costs of intrasexual interactions, on the other hand, are not well understood. These costs are not likely to be trivial, as males often fight for access to females (Darwin, 1871; Trivers, 1972), and females of some species fight for access to resources (Trivers, 1972; Wrangham, 1980). Few studies have examined the costs of intrasexual interactions, particularly in females, or compared the costs of inter- and intrasexual interactions. One recent study (Maklakov & Bonduriansky, 2009) found that in both seed beetles *Callosobruchus maculatus* and carrion flies *Prochyliza xanthostoma*, male–male interactions carried about equal costs (measured as reductions in lifespan) to males as interactions with females, whereas for females, interacting with males was significantly more costly than interacting with other females. Similarly, in the dung fly *Sepsis cynipsea*, females housed in mixed-sex pairs were found to suffer much higher survival costs than when housed in same-sex pairs, but the opposite trend was found in males, with same-sex interactions reducing longevity to a far greater degree than mixed-sex interactions (Mühlhäuser & Blanckenhorn, 2002). In contrast, female dung beetles *Onthopagus binodis* were shown to suffer no change in longevity when housed in mixed-sex population cages vs. same-sex cages, whereas male longevity was lower in mixed-sex cages than same-sex cages (Kotiaho & Simmons, 2003). The above findings therefore suggest that the mortality costs of intrasexual interactions can be very high, as well as sex specific. In contrast, Clutton-Brock & Langley (1997) measured lifespan in tsetse flies *Glossina morsitans morsitans* housed in different sex ratios and found that for both sexes, longevity declines when housed in an opposite-sex-biased sex ratio. Thus, in tsetse flies, intersexual interactions appear to carry greater lifespan costs than intrasexual interactions, as might be expected generally in species with high costs of mating.

Costs of mating may be particularly high for females when male harassment or physical coercion is prevalent (Arnqvist & Rowe, 2005), and theory predicts that females should evolve behavioural responses to an increasingly male-biased sex ratio, to minimize these costs (Arnqvist, 1992). Furthermore, empirical evidence has shown that females may even evolve frequency-dependent morphological responses to elevated male harassment of a particular phenotype (Gosden & Svensson, 2007). Heavily male-biased sex ratios may be costly for males as well when males fight for access to females, as exemplified by the reduced longevity for male dung flies housed in same-sex cages (Mühlhäuser & Blanckenhorn, 2002), whereas the presence of females could potentially influence the degree of male-male fighting and thus the degree of costs. The magnitude and nature of the costs of inter- and intrasexual interactions may therefore vary considerably among species, and further research on animals with different mating systems is required to gain a general understanding of such variation.

Reproductive activity may impose mortality costs that are immediate (i.e. a short-term increase in mortality risk) or latent (i.e. an accumulation of somatic wear-and-tear that causes increased mortality rate late in life). Immediate costs are generally reflected in an increase in early-life mortality, whereas latent costs result in increased late-life mortality or increased ageing rate (Tatar *et al.*, 1993; Kotiaho, 2001). Ageing (senescence) is a decline in reproductive value with advancing age (Partridge & Barton, 1996) that can reflect increasing mortality rate (actuarial ageing) and/or decreasing reproductive rate (reproductive ageing). We focus on actuarial ageing in this study. Factors that impose immediate and latent mortality costs may operate differently on different individuals in a population, such that what kills some individuals may simply weaken others, or may operate as selective pressures on the population, weeding out the most susceptible (Service *et al.*, 1998; Reznick *et al.*, 2004). However, it remains unclear whether different types of reproductive activity (e.g. fighting and mating) tend to impose different types of mortality costs. Although theory clearly predicts a positive relationship between early-life mortality rate and ageing rate on an evolutionary scale (Williams, 1957; Hamilton, 1966), it is less clear how within-generation effects of environmental parameters (such as sex ratio) on early-life mortality rate (or mean lifespan, which will largely reflect variation in early-life mortality if most individuals die young) might covary with effects on ageing rate. Few studies have examined variation in both early-life mortality rate or mean lifespan and late-life mortality or ageing rate, particularly in an experimental context (reviewed in Bonduriansky *et al.*, 2008).

The mortality costs associated with different social environments have implications for the evolution of reproductive strategies and life histories (Bonduriansky *et al.*, 2008). Mortality costs are an important component of selection on various reproductive activities such as agonistic interactions and mating, and can drive the evolution of facultative behavioural strategies that mitigate such costs. For example, high costs of male–male interactions may favour males that suppress aggression towards rivals when the operational sex ratio becomes strongly male-biased and immediate mating opportunities are scarce, whereas high costs of mating may favour

choosiness (Parker, 1983). The reproductive strategy may, in turn, affect life expectancy and influence the evolution of somatic maintenance and ageing (Williams, 1957; Hamilton, 1966; Kirkwood, 1977).

The sexually dimorphic fly *Telostylinus angusticollis* (Diptera: Neriidae) exhibits distinctive patterns of sexual interaction (Bonduriansky, 2006, 2007) and has become a model for research on environmental effects on the expression of morphological and life-history traits (Bonduriansky, 2006, 2007; Bonduriansky & Head, 2007; Kawasaki *et al.*, 2008). Males are on average significantly larger than females (Bonduriansky, 2007) and often stand guard over the female during and sometimes after mating. Males pursue resistant females at length in an effort to mate, during which the male continually attempts to mount the female and initiate copulation, and the female may reject these attempts by moving away from the male and pressing her ovipositor to the ground. Males engage in spectacular combat for dominance at oviposition sites (small patches of rotting tree bark) where females aggregate. Females also interact agonistically with males and other females at oviposition sites. In addition, operational sex ratio appears to be highly variable across space in the wild. Females tend to aggregate at oviposition sites that are guarded by one or a few males, and other males are often found aggregating without females at surrounding sites, perhaps awaiting the chance to dominate an oviposition site, recuperating from combat or else pursuing an alternate reproductive strategy. This species is found in closed canopy forest in coastal areas of south-eastern Australia. The adults feed, mate and oviposit on the trunks of trees, and larvae develop in the rotting bark (M.I. Adler & R. Bonduriansky, unpublished observations).

We investigated the mortality costs of social interaction in male and female *T. angusticollis* by comparing age-specific mortality rate and lifespan in individually housed flies with flies housed in groups, as well as flies housed under a range of sex ratios (all-female, female-biased, even, male-biased, all-male). This enabled us to compare the mortality costs of inter- and intrasexual interactions for males and females. In addition, we investigated the effects of these different social environments on both immediate and latent mortality costs by examining variation in early-life mortality rate, mean lifespan, late-life mortality rate and ageing rate (Gompertz *b*). We were thus able to ask whether immediate and latent mortality costs covary among social environments.

Materials and methods

Source and rearing of flies

The laboratory stock used in this experiment was derived from > 100 individuals of both sexes collected from aggregations on the trunks of *Acacia longifolia* trees in Fred Hollows Reserve in Sydney, Australia, and maintained in the laboratory as a large, outbred population for about 25 generations, supplemented annually with new wild-collected individuals. Larval medium consisted of 30 mL of blackstrap sugarcane molasses (Conga Foods, Preston, Vic. Australia), 30 mL of liquid barley malt (Colonial Farms; Select Foods, Smithfield, NSW, Australia) and 32 g of soy protein powder (Nature's Way, Pharm-A-Care, Warriewood, NSW, Australia) per litre of dry cocopeat hydrated with 800 mL of water. The food mixture was homogenized thoroughly using a handheld blender and frozen at −20 °C until the day of use.

Experimental procedures

To obtain flies for the experiment, eggs were collected from stock cages and transferred into containers of fresh medium provided *ad libitum*. Adult flies, which attain sexual maturity a few days after emergence from the puparium, were transferred randomly to experimental treatment cages on the day of adult emergence, such that all flies began the experiment at age 0 (where 'age' is defined as time since adult emergence). Flies assigned to group treatments (n = 390) were transferred in groups of 10 flies into 1-L cages, and flies assigned to the individual treatment (n = 41 males and 43 females) were transferred individually into 250-mL cages. Group treatments consisted of virgin males in groups of 10 (n = 7 cages), virgin females in groups of 10 (n = 9 cages), equal sex ratio groups of five males and five females (n = 7 cages), male-biased cages with eight males and two females (n = 7 cages), and female-biased cages with eight females and two males (n = 7 cages).

Experimental cages were covered in mesh stockings to allow for ventilation. Cocopeat was spread onto the bottom of each cage and moistened to prevent desiccation and provide a source of water. The larval medium described earlier was provided to adult flies as a source of food as well as an oviposition medium, and changed every 10 days. Group cages were provided with 70 mL of larval medium, whereas individual cages received a 12-mL petri dish full of medium. As an additional source of food for adults, all cages also contained separate dishes filled with brown sugar and instant dried yeast. Sugar and yeast dishes were changed if they became mouldy. All cages were watered and checked every other day for dead flies until all the flies in the experiment had died (97 days). Dead flies were removed from group cages and sexed. Flies were kept on a 12 h–12 h light–dark cycle using a combination of broad-spectrum fluorescent and incandescent lighting, at an approximately constant temperature of 26 °C at 50% humidity.

Statistical analysis

Analyses of variation in mortality rate and lifespan were based on cage means as observational units. Early-life

mortality rate was estimated as the probability of dying before age 20 days, calculated as the number of individuals alive at age 20 days divided by the number of individuals alive at age 0 days. Late-life mortality rate was estimated as the probability of dying between age 30 and 50 days, calculated as the number of individuals alive at age 50 days divided by the number of individuals alive at age 30 days. Because mortality data for individually housed flies were non-normally distributed (there were many zeros), mortality rates for individually housed and group-housed flies were compared using nonparametric tests. However, among group treatments, cage means were normally distributed for each measure of mortality rate, as well as mean lifespan, and were therefore compared using parametric tests. Sex ratios in mixed-sex experimental cages changed over the course of the experiment as individual flies died, although the average difference in sex ratio between male-biased, even and female-biased treatments was maintained throughout most of the experiment. We report results in relation to the sex ratios established at the start of the experiment.

Ageing rate was estimated from the Gompertz model,

$$\mu_x = ae^{bx} \quad (1)$$

where μ_x is the probability of death per unit time (hazard rate) at age x (in days), a is a scaling parameter and b reflects the rate of increase in hazard with age, generally interpreted as the actuarial ageing rate (Carey, 2001). The Gompertz model provided a good fit to the data for each treatment (see Results). Gompertz b was estimated for each treatment as the ordinary least squares slope of the regression of log-hazard rate (mean over 5-day age-intervals) against age (interval mid-point) (see Carey, 2001). Because relatively large sample sizes are needed to obtain meaningful estimates of ageing rate, it was not possible to obtain separate estimates of Gompertz b for each cage. Mean mortality rate in late life (i.e. between age 30 and 50 days), which could be estimated for each cage, was calculated as an alternative estimate of latent costs.

Six of the 474 flies used in the experiment (~1%) withdrew from the experiment because of factors unrelated to treatment effects, such as escape or accidental death from handling. These individuals were excluded from the analysis.

Results

Early-life mortality

Probability of death within the first 20 days following adult emergence was slightly greater among individually housed males than group-housed males (Mann–Whitney U-test: N = 30 group cages and 41 individual cages; Z = −2.21, P = 0.0270), whereas females showed the opposite pattern (N = 32 group cages and 43 individual cages; Z = −3.91, P < 0.0001). There was no overall difference between sexes in this measure of early-life mortality (N = 75 cages containing females and 71 cages containing males; Z = 0.50, P = 0.55). Among male flies housed in groups, probability of death within the first 20 days increased with increasing proportion of males per cage (linear regression: $F_{1,28}$ = 9.73, P = 0.0042), whereas for females in groups, the proportion of males per cage had no effect ($F_{1,30}$ = 0.09, P = 0.76) (Fig. 1a).

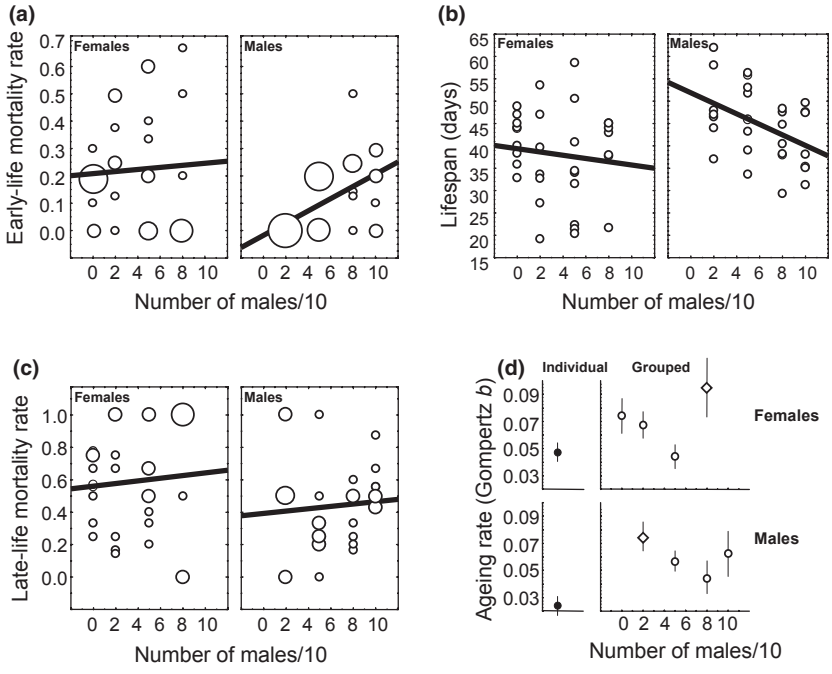

Fig. 1 The effect of sex ratio (number of males in a group of 10 flies) on (a) early-life mortality rate (probability of dying at ages 0–19 days), (b) lifespan, (c) late-life mortality rate (probability of dying at ages 30–50 days) and (d) ageing rate (Gompertz b). In (a–c), points represent cage means (point size reflects the number of cages represented), and lines represent ordinary least squares regressions. In (d), points represent estimates of Gompertz b for each treatment and sex, and bars represent the standard error of the estimate (inferred from the standard error of the linear slope of log hazard on age). Open diamonds denote the opposite-sex-biased treatment for each sex (i.e. females in male-biased sex ratio and males in female-biased sex ratio).

Lifespan

Both males and females housed in groups had shorter mean lifespans than those housed individually (ANOVA: $F_{1,142} = 15.57$, $P = 0.0001$), but there was no overall difference in mean lifespan between sexes ($F_{1,142} = 0.79$, $P = 0.38$), nor an interaction between sex and type of housing (individual vs. grouped) ($F_{1,142} = 0.81$, $P = 0.37$) (Fig. 2). Among grouped flies, male mean lifespan declined with increasing proportion of males per cage (linear regression: $F_{1,28} = 6.53$, $P = 0.0164$), whereas for females, the proportion of males per cage did not affect mean lifespan ($F_{1,30} = 0.37$, $P = 0.55$) (Fig. 1b).

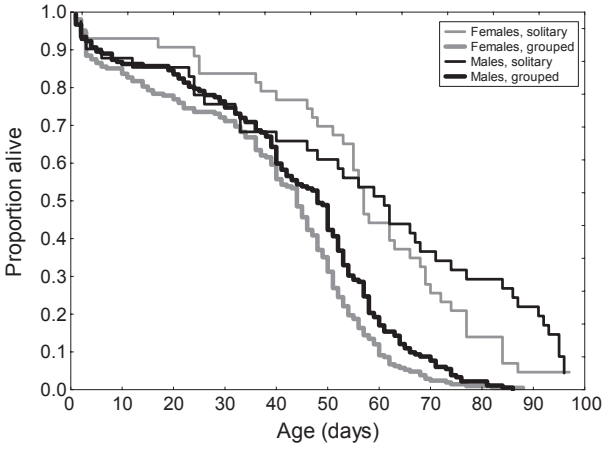

Fig. 2 Survivorship (lx) curves for males and females housed individually and in groups (all grouped treatments pooled within-sex).

Late-life mortality

Late-life mortality rate (i.e. probability of death between 30 and 50 days following adult emergence) was higher for flies housed in groups than those housed individually for both males (Mann–Whitney U-test: $N = 30$ group cages and 41 individual cages; $Z = 4.24$, $P < 0.0001$) and females (Mann–Whitney U-test: $N = 32$ group cages and 43 individual cages; $Z = 5.46$, $P < 0.0001$). Among grouped flies, late-life mortality rate was not affected significantly by sex-ratio treatment for either sex (linear regressions: $F_{1,28–30} < 0.18$, $P > 0.67$) (Fig. 1c).

Ageing rate

The Gompertz b parameter provided a useful estimate of variation among treatments in ageing rate, as indicated by the strong linear relationship of age-specific log-hazard rate with age for each treatment (Fig. 3). Gompertz b was generally lower in individually housed flies than in group-housed flies. However, as can be seen from an inspection of Fig. 1d, Gompertz b did not exhibit any tendency to increase with the proportion of males within groups. Interestingly, the highest ageing rate was observed for males under a female-biased sex ratio, and for females under a male-biased sex ratio (i.e. in the

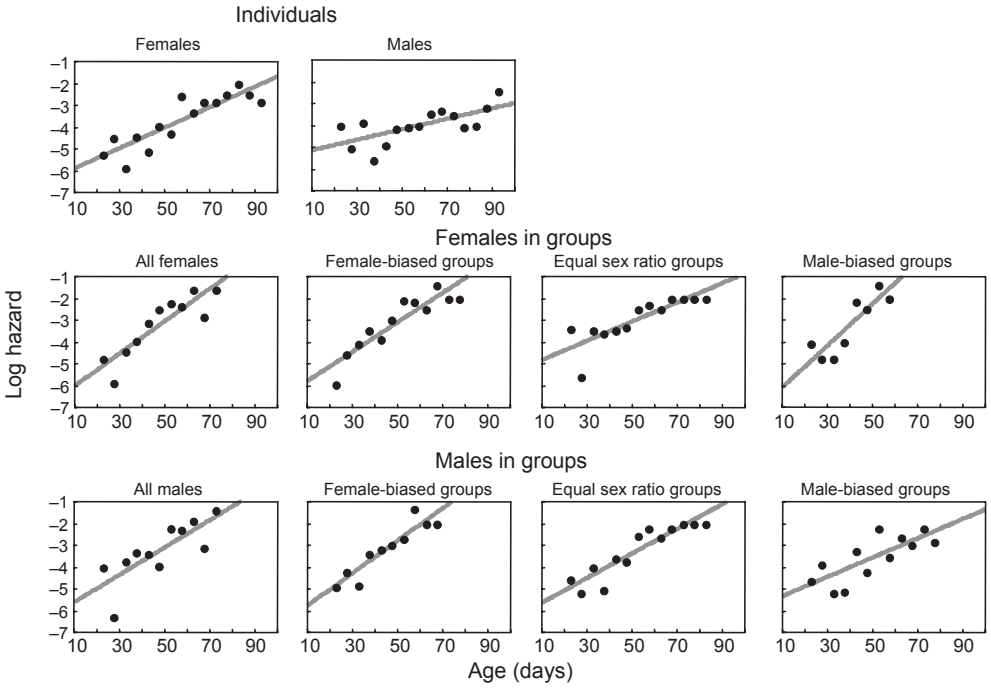

Fig. 3 Log-hazard rate as a function of age for each sex within each treatment. The slope of this relationship represents ageing rate (Gompertz b).

opposite-sex-biased treatment). This pattern has tentative statistical support: The mean Gompertz *b* for both sexes was greater in the opposite-sex-biased treatment than the mean Gompertz *b* for other grouped treatments combined (Mann–Whitney *U*-test: $N_{\text{opposite-sex-biased}} = 2$, $N_{\text{other}} = 6$, $Z = -2.00$, $P = 0.0455$).

Covariation among measures of mortality

Among grouped-treatment cages, early-life mortality rate was correlated negatively with lifespan, but this relationship was significant only for males (Pearson correlation: females: $r_{32} = -0.22$, $P = 0.24$; males: $r_{30} = -0.57$, $P = 0.0011$). Likewise, late-life mortality rate was correlated negatively with lifespan, but significantly so only for males (females: $r_{32} = -0.23$, $P = 0.21$; males: $r_{30} = -0.55$, $P = 0.0016$). Early-life mortality rate was correlated negatively with late-life mortality rate, but the relationship was significant only for females (Pearson correlation: females: $r_{32} = -0.49$, $P = 0.0041$; males: $r_{30} = -0.11$, $P = 0.56$). Among treatment means, there was no evidence of covariation between ageing rate and early-life mortality rate or lifespan for either sex ($P > 0.26$ for all correlations). However, we detected a near-significant positive correlation among treatments between Gompertz *b* and late-life mortality rate for males ($r_5 = 0.87$, $P = 0.0554$). We also detected a substantial (but nonsignificant) positive correlation between Gompertz *b* and late-life mortality rate for females ($r_5 = 0.58$, $P = 0.31$).

Discussion

Our results show that both males and females lived longest, had a lower rate of late-life mortality and tended to age (i.e. experience an increase in mortality rate with age) less rapidly, when housed individually. We also found that males showed an increase in early-life mortality and a decrease in mean lifespan as the proportion of males in the group increased, whereas for females, there was no effect of sex ratio on early-life mortality or mean lifespan. Variation in late-life mortality and ageing rate was not significantly related to variation in sex ratio for either sex. However, for both sexes, the highest ageing rate was recorded in the opposite-sex-biased treatment.

Our results suggest a generalized cost to social interaction, for both sexes, in nearly all measures of mortality. Living in a crowded environment likely results in increased exposure to parasites and bacteria in waste products (Alexander, 1974; Krause & Ruxton, 2002), and competition for resources (Boyd, 1982; Krause & Ruxton, 2002). Social interaction may also cause mechanical damage, even from nonaggressive physical interaction with other individuals (Krause & Ruxton, 2002) – a cost that may be especially important for insects because they cannot repair damage to the exoskeleton (Bonduriansky & Brassil, 2005).

In contrast to previous findings (Clutton-Brock & Langley, 1997; Reguera *et al.*, 2004; Maklakov & Bonduriansky, 2009), the proportion of males in a cage appeared to have no consistent effect on early-life mortality rate or lifespan of females. This was surprising, as males are expected to impose costs on females through mating and associated behaviours, such as physical persistence and mate guarding, which may result in reduced opportunity for feeding or increased somatic damage (reviewed in Arnqvist & Kirkpatrick, 2005; Arnqvist & Rowe, 2005). However, the magnitude of such costs probably varies a great deal among species, depending on the extent to which males harass females and thereby interfere with female foraging or impose physical damage, and depending on the toxicity of male ejaculate fluids. Some of these costs may also be masked in the relatively benign environment of the laboratory, where predators and many parasites are excluded and food is readily available (Sgrò & Partridge, 2000; Linnen *et al.*, 2001; Kawasaki *et al.*, 2008). Chapman *et al.* (1998) reviewed the literature on mating costs to females in Diptera and report that interacting with males (mating) has been shown to decrease longevity in 10 species, whereas it has no effect on longevity in nine other species. As Kotiaho & Simmons (2003) point out, where females do not suffer a longevity cost associated with male interaction, as in our study and theirs, this may not be surprising given that males may transfer important seminal nutrients to females that could be used for somatic maintenance and egg production.

However, we found some evidence that interacting with males imposed latent costs on females. Although the proportion of males in cages did not affect females' late-life mortality rate, we found that females in male-biased cages had the highest ageing rate (i.e. Gompertz *b*) of any female treatment. This suggests that when females are exposed to a high mating rate and an increased probability of male harassment, they incur cumulative somatic wear-and-tear that increases the probability of death at late ages. A number of studies in insects have shown that increased mating rate is costly for females, even when copulating more does not result in an increase in egg production (Fowler & Partridge, 1989; Chapman *et al.*, 1993). Such costs could reflect mechanical internal damage from the male intromittent organ, external damage from male harassment during courtship, reduction in immune function, toxicity of accessory gland proteins (all reviewed in Arnqvist & Rowe, 2005), or depletion of nonreplenishable energy reserves such as the pupal fat body (Stoffolano *et al.*, 1997). Such factors may impose latent rather than immediate costs if each interaction causes only a slight increase in somatic wear-and-tear that does not result in a short-term increase in mortality risk, but accumulated damage over several weeks ultimately results in a decline in somatic condition manifested in a rapid increase in mortality rate at late ages.

For males, as the proportion of males in a cage increased, early-life mortality rate increased and lifespan decreased. This contrasts with results for tsetse flies, where males experience the greatest lifespan reductions in female-biased cages (Clutton-Brock & Langley, 1997) and likely reflects the high frequency and intensity of male-male combat in *Telostylinus angusticollis*, which may result in severe somatic damage and an immediate increase in probability of death. Males likely have an even more adverse effect on each other in the wild, where somatic damage may often result in reduced escape ability from predators. Somatic damage is not simply an artefact of artificial conditions and extended longevity in laboratory-housed insects (Cartar, 1992). In *T. angusticollis*, we have observed severe wing damage, the loss of one or more legs and/or a reduced ability to escape from simulated attack in a substantial proportion of individuals in the wild (M.I. Adler & R. Bonduriansky, in preparation).

Interestingly, for males, latent costs did not increase with exposure to other males: there was no evidence of covariation of late-life mortality rate or ageing rate with the sex ratio. Rather, males aged most rapidly when subjected to a female-biased sex ratio. This suggests that, as for females, males may incur latent costs from mating. Mating is likely to be energy-intensive for males as well as females. Although males invest less than females in each offspring, an increased mating rate likely means an increase in sperm production and accessory gland proteins, which may be very costly to produce (Dewsbury, 1982; Cordero, 1995). Unlike combat, however, such energetic costs may not elevate short-term mortality rate but, rather, impose latent costs by increasing the rate of somatic deterioration at later ages. These findings differ to those from a study in *Drosophila melanogaster*, in which male mortality rate immediately increased with the introduction of females, but dropped to the rate of virgin males once females were removed (Partridge & Andrews, 1985). Partridge & Andrews interpreted these results as suggesting that mating costs for male fruit flies are immediate but not latent. However, their lifespan measurements were not carried out until all individuals were dead (in the two longest lived treatments, lifespans were not reported for approximately 75% of males in the no-female treatment, and approximately 10% of males in the females-removed treatment), and thus they may have failed to detect latent costs expressed as elevated ageing rate late in life. Also, reproduction may have acted as a selective force in that experiment, and males in poor condition may have been more vulnerable to extrinsic sources of mortality and died, but males in good condition may have survived and would also have been fairly robust to deterioration late in life (see Reznick *et al.*, 2004; Bronikowski & Promislow, 2005). The possibility of reproduction acting as a selective force is relevant to our results as well, but the finding that males in female-biased cages had the highest ageing rate suggests that if such selection did take place, it was not enough to overcome the latent costs of reproduction.

When interpreting results from laboratory studies, particularly those relating to life-history traits, it is important to consider the relevance of the experimental conditions to conditions the organism might experience in a more natural environment, as well as the conditions that would have shaped the species' evolutionary trajectory. A previous study on this species (Kawasaki *et al.*, 2008) found that life expectancy in the wild was much lower than in the laboratory. This might negate the importance to fitness of late-life effects seen in the laboratory. However, end-of-life decline that manifests late in the benign conditions of the laboratory may be analogous to the decline seen much earlier in the harsh conditions of the wild. Indeed, Kawasaki *et al.* (2008) found that ageing rate was higher for males in the wild than in the laboratory, suggesting that latent costs may be especially important in the wild. On the other hand, factors that contribute to variation in longevity and ageing may be somewhat different in the laboratory and the wild. For example, these environments are likely to differ in the nature and abundance of parasites, absence vs. presence of predators and stability of ambient conditions such as temperature and humidity. In addition, the constant availability of *ad libitum* food in the laboratory could result in increased reproduction, which may translate to different costs, but also provide additional resources for somatic maintenance.

As might be expected, both early-life and late-life mortality rates covaried negatively with average lifespan, although this relationship was much stronger in males than in females. However, early-life and late-life mortality rates covaried negatively in both sexes, although this relationship was significant only in females. Negative covariation between early- and late-life mortality rates could result from selection removing low-quality individuals in early life, such that the remaining individuals may survive better at late ages. Because only a single estimate of ageing rate (Gompertz *b*) could be obtained for each treatment, statistical analysis of variation in ageing rate among treatments is complicated by the small number of observations ($N = 5$ estimates of Gompertz *b* for each sex: Fig. 1d). There was no evidence of covariation between early-life mortality rate or lifespan and ageing rate for either sex, but late-life mortality rate was near-significantly, positively correlated with ageing rate for males. As can be seen from an inspection of Fig. 1d, there is also no evidence that increasing number of males in groups was associated with more rapid ageing for males, in contrast with findings for early-life mortality rate and lifespan.

While ageing rates may reveal accumulated damage that causes the organism to decline rapidly late in life, measures of early-life mortality rate and average lifespan may largely reflect factors that result in immediate elevation of mortality risk because most affected

individuals will die before exhibiting signs of senescence. Our findings suggest that different aspects of reproductive activity, such as mating and fighting, impose immediate and latent costs to different degrees. Our results also caution against using lifespan as a proxy for ageing rate and suggest that experiments should be continued until all individuals are dead, to gain a more accurate measure of late-life decline. However, measures of actuarial ageing are still likely to give an incomplete picture of life-history optimization strategies, and other measures, such as reproductive ageing, are also likely to be important in revealing patterns of age related declines in fitness (Partridge & Barton, 1996).

Our findings have potential implications for the evolution of reproductive strategies and life histories. We found evidence that male-male interactions impose greater immediate mortality costs for males than do male-female interactions (Fig. 1). One interesting implication of this finding is that if males employ alternative reproductive strategies based on combat and territoriality vs. sneaking and scrambling (whether as discrete alternatives, or as a continuum), then the combat/territoriality strategy may be associated with relatively weaker selection on longevity than the sneaking/scrambling strategy. Males that fight to gain access to females will experience high immediate mortality costs (offset, for winners, by abundant mating opportunities) and suffer a reduced life expectancy that may, in turn, select for reduced investment in somatic maintenance, whereas males that employ noncombat strategies may be selected to prolong life (Kirkwood, 1977; Kirkwood & Rose, 1991). Our findings therefore support a potential mechanism mediating the apparent trade-off between a high-condition phenotype and the ability to maintain somatic condition with advancing age (Bonduriansky & Brassil, 2005; M.I. Adler & R. Bonduriansky, in preparation). Our findings do not predict such intraspecific variation in selection on longevity among females, however, because there is no evidence that increased reproductive activity (e.g. increased female–female competition for resources that can be used to produce eggs, or elevated mating rate) is associated with increased immediate mortality risk and reduced life expectancy for females. Our results thus offer an example of how sex-specific reproductive strategies may select for sexually dimorphic life histories (see Promislow, 2003; Bonduriansky *et al*., 2008).

In conclusion, our findings reveal that social environment is an important factor in determining lifespan and ageing rate, but the costs of inter- and intrasexual interaction are distinct and sex specific. For males, it appears that fighting with other males results in immediate mortality costs, increasing early-life mortality rate and reducing lifespan. Mating at a high frequency is costly for males as well, but these costs seem to manifest later in life, increasing ageing rate for males when housed in female-biased cages. For females, interacting with males does not appear to carry higher immediate mortality costs than interacting with other females. But as for males, a high frequency of mating and its associated behaviours may result in latent costs for females, increasing ageing rate for females when housed in male-biased cages. Moreover, we found some evidence that the social environment can have contrasting effects on immediate and latent costs. The lack of covariation in these measures reveals potentially important differences in the effects of social interactions on the dynamics of reproductive and life-history scheduling.

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