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Gender differences in lifespan and mortality rates in two seed beetle species

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Summary

1. In most animals, females live longer than males, and large individuals live longer than small individuals. We examine both gender and body size effects on adult lifespan in two species of seed beetles (*Callosobruchus maculatus* and *Stator limbatus*), and test whether body size differences between males and females can explain gender-differences in mortality rates and lifespan.

2. In both species, the effect of age on mortality rate was best described by a logistic mortality curve. *C. maculatus* females have a higher initial mortality rate than males, while males have a much higher rate of increase of the mortality rate with increasing age. In contrast, *S. limbatus* males had a higher initial mortality rate (opposite to the pattern seen in *C. maculatus*) but males and females did not differ in the rate of increase of mortality with increasing age.

3. Body size was positively correlated with lifespan in both species, but it explained very little of the variance in lifespan ($R^2 < 0{\cdot}09$ for both species) and did not explain the gender difference.

4. Lifespan was heritable for both genders of both populations (h^2 between 0·19 and 0·55), and the shape of the mortality curves varied among families within both species.

Key-words: Ageing, body size, longevity, senescence, sexual dimorphism

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Introduction

In most animals, average lifespan of females is longer than that of males (Hazzard 1986; Smith & Warner 1989), although there are many exceptions (Saha & Raut 1992; Carey *et al*. 1995; Leather *et al*. 1998; Choi *et al*. 2000; Oklejewicz & Daan 2002). Why females live longer than males is generally unknown, in part because few studies have examined differences in mortality patterns between males and females in organisms other than *Drosophila* and humans (but see Tatar & Carey 1994b; Gotthard, Nylin & Wiklund 2000). To address this question, we need first to examine how mortality rates differ between males and females, and then examine what factors explain this difference (Tatar & Carey 1994b; Pletcher, Khazaeli & Curtsinger 2000; Tatar 2001). Differences in lifespan can be due to differences in the onset of age-dependent mortality (Tatar & Carey 1994b), the baseline mortality rate (Fukui, Xiu & Curtsinger 1993; Gotthard *et al*. 2000), the rate of increase in the mortality rate with increasing age (Fukui *et al*. 1993), or the rate of deceleration in mortality rates and/or the time and level at which they reach a plateau. A comparison of separate studies suggests that the gender difference in mortality curves may vary among species (this study), among populations within species (Gotthard *et al*. 2000; Fox *et al*. in press), and may even change as environmental conditions change (White & Bell 1993).

Variation in body size is commonly observed to covary with lifespan and mortality rates. Across species, large animals tend to have longer lifespans than small animals (Gavrilov 1995; Ricklefs & Scheuerlein 2001). However, patterns within species are less clear. Small size of mutant mouse and hamster lines is associated with increased lifespan and reduced risk of mortality (e.g. Oklejewicz & Daan 2002; and references therein), whereas in other mammals large individuals live longer than small individuals (e.g. Berube, Festa-Bianchet & Jorgenson 1999). In most insects, variation in size either does not covary with lifespan (e.g. Nilssen 1997; Strohm & Lechner 2000) or large individuals live longer than small individuals (Møller, Smith & Sibly 1989; Sivinski 1993; Hughes 1995; Oberhauser 1997; Taylor, Anderson & Peckarsky 1998; van Dongen *et al*. 1999). Some studies have shown that the shape and sign of the

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relationship between size and lifespan depends on environmental conditions (Norry & Loeschcke 2002).

Some authors have suggested that gender differences in lifespan may be due to differences in body mass between males and females (e.g. Samaras, Storms & Elrick 2002). In most insect species, females are larger than males and live longer than males. However, within some taxa body size dimorphism varies substantially. For example, in most seed beetles (Chrysomelidae, subfamily Bruchinae) females are larger than males, but males in the genus *Stator* are generally larger than females (e.g. Savalli & Fox 1998). In this study, we examine how lifespan and mortality rates differ between males and females in *Callosobruchus maculatus* (F.), in which females are larger than males, and *Stator limbatus* (Horn), in which males are larger than females.

Materials and methods

STUDY POPULATIONS

Callosobruchus maculatus is a cosmopolitan pest of stored legumes (Fabaceae), particularly beans of the genus *Vigna*. *Stator limbatus* is not a pest, but is widely distributed from northern South America to the south-western United States (Johnson & Kingsolver 1976; Johnson, Kingsolver & Teran 1989). In both species, females cement their eggs to the surface of host seeds and larvae complete development and pupate inside the seed. They emerge from the seed as adults. In the laboratory, *S. limbatus* mating and egg laying begin approximately 24–48 h post-emergence, whereas *C. maculatus* adults will begin mating and ovipositing almost immediately after emerging from their host seed.

The *S. limbatus* population used for these experiments was initiated with ≈200 beetles collected in August 2000 from seeds of *Acacia greggii* along Hwy 77 and adjacent roads in Oracle, Pinal County, Arizona (≈32°38′ N, 110°48′ W). The laboratory population was reared on *A. greggii* for ≈12 generations at 30 °C, 15 : 9 h L:D prior to this experiment. The *C. maculatus* colony we used was collected in 1979 from infested pods of mung bean, *Vigna radiata* (L.) Wilczek, and the closely related black gram, *Vigna mungo* (L.) Hepper, in Tirunelveli, India (Mitchell 1991) and has been maintained in the laboratory at ≈25–26 °C ever since. This population has been referred to as the SI (South India) population in previous studies (e.g. Fox *et al*., in press).

EXPERIMENTAL DESIGN

We used a traditional half-sib design to quantify genetic variation in lifespan and the genetic correlation between male and female lifespan in both species. To create half-sib families, virgin male beetles were each mated sequentially to between two and four different virgin females. *S. limbatus* females are substantially less fecund than *C. maculatus* females, so we created extra *S. limbatus* families to compensate for the smaller family sizes (102 males for *Stator limbatus* and 43 males for *C. maculatus*). We opted for larger families of *C. maculatus* to allow more precise estimation of mortality curves within each family. For *C. maculatus*, each virgin male was mated sequentially in a 35-mm Petri dish with virgin females that were <12 h post-emergence, after which females were transferred to a new dish containing 25 mung seeds (*Vigna radiata*; their native host) and allowed to lay eggs. For *S. limbatus*, females rarely mate quickly, so pairs were confined in a 35-mm Petri dish containing 12–15 *A. greggii* seeds until the female laid at least one egg (dishes were checked twice per day), after which the male was transferred to another dish containing a different virgin female. These procedures were repeated until males successfully fertilized four females, or died. Dishes containing egg-laying females were checked for eggs at 12-h intervals, and seeds bearing eggs were replaced with clean seeds until a female had laid eggs for 48 h. We did not use eggs from older females because of a significant maternal age effect on lifespan known to occur in *C. maculatus* (Fox, Bush & Wallin, in press).

All eggs were reared to the adult stage on seeds of *A. greggii* (for *S. limbatus*) or *V. radiata* (*C. maculatus*) at densities of one larva per seed (excess eggs were scraped off). Emerging beetles were collected twice daily, at 12-h intervals. Body mass at adult emergence was recorded after which adults were confined in 35 mm Petri dishes, without seeds or mates, until death. Beetles were scored twice daily for whether they had died. In total, 2885 *S. limbatus* and 2855 *C. maculatus* offspring were reared to adult and scored for adult body mass and/or lifespan.

Because the two species are reared at different temperatures in their laboratory colonies, we reared them at different temperatures during the experiment (30 °C, L:D 15 : 9 for *S. limbatus* and 26 °C, L:D 15 : 9 for *C. maculatus*). This created a 'natural' rearing environment for each species, and avoided confounding our experiment with temperature-based maternal effects (Atkinson *et al*. 2001). However, this prohibits direct comparison between species in mean lifespan and mortality rates. We thus restrict our analyses to the differences between the genders *within* species and do not make any between-species comparisons for mean traits or parameters of the mortality curves.

ANALYSES

To describe the shape of the mortality curves we estimated the parameter values of a logistic mortality model of the form

$$u(t) = \frac{ae^{bt}}{\left[1 + \left(\frac{as}{b}\right)(e^{bt} - 1)\right]}$$

where a is the intercept of the relationship $u(t) = ae^{bt}$ (often referred to as the initial mortality rate, or the 'extrinsic' mortality rate), b is the rate of exponential increase in mortality at young ages, and s describes the degree of deceleration in mortality with increasing age (Vaupel 1990; Pletcher 1999a,b). This model is similar to a Gompertz mortality model except that it incorporates a term (s) to account for the slowing of the increase in mortality rate with age (Pletcher & Curtsinger 1998); when $s = 0$ the logistic model reduces to the Gompertz model. Parameters were estimated using the maximum likelihood estimation procedure of WinModest (Pletcher 1999b). A Cox proportional hazards model was used to test for gender differences in $u(t)$ (Allison 1995). We used the log-likelihood-ratio test of WinModest (Pletcher 1999b) to test whether individual parameter estimates (a, b and s) differed significantly between males and females, and between large and small size classes (individuals above and below median size).

We used standard analysis of covariance to test for body size effects on lifespan and to test whether body size could explain the difference in lifespan between the sexes (details in the Results section). Genetic variances and covariances for lifespan were calculated using the restricted maximum likelihood variance component estimation procedure of SAS Proc VARCOMP (Littell, Freund & Spector 1991), with V_A (the additive genetic variance) = $4 \times V_S$ (the among sire variance component), and the heritability (h^2) = V_A/V_P (Roff 1997). Additive genetic correlations were calculated both between traits within genders and between genders. Between-trait genetic correlations (r_A) were estimated using standard varcomp procedures in S-Plus (Venables & Ripley 1997). We calculated cross-gender additive genetic correlations for adult lifespan and body mass from the various maximum likelihood variance components (Fry 1992; Lynch & Walsh 1998), as $r_A = \sigma^2_{\text{sire–mixed}}/\sigma_{\text{sire-male}}\,\sigma_{\text{sire-female}}$, where $\sigma^2_{\text{sire–mixed}}$ is the estimated sire main effect variance component from the complete mixed model analyses of variance, with progeny gender treated as factor, and $\sigma_{\text{sire-male}}$ and $\sigma_{\text{sire-female}}$ are the estimated sire main effect variance components from the two reduced models [one for each gender; data were standardized to Normal (0,1) to correct for differences in mean and variance between the genders]. Only the sire (co)variance components were used to avoid bias due to dominance and maternal effects. This cross-gender genetic correlation considers a trait in each sex as if they were separate traits and estimates the degree to which they are under the same genetic control in both genders. Standard errors for V_A, h^2, and r_A were calculated via jackknifing the variance/covariance component estimates across sires (within populations) using S-Plus (Venables & Ripley 1997).

Results

PATTERNS OF MORTALITY

Consistent with previous observations, *C. maculatus* females were 32% larger than males, whereas *S. limbatus* females were 5% smaller than males (Fig. 1). However, in both species, females lived longer (on average) after emerging from their seed than did males (Fig. 1; gender effect in the complete ANOVA including sire, dam and gender effects, $F_{(1,2488)} = 1149$ for *C. maculatus*, $F_{(1,2396)} = 242$ for *S. limbatus*, $P < 0{\cdot}001$ for both species). The mortality (hazard) functions also differed substantially between males and females for each population (Cox proportional hazards, $\chi^2_{(1)} = 1076$ for *C. maculatus*, $\chi^2_{(1)} = 160$ for *S. limbatus*, $P < 0{\cdot}001$ for both species; Breslow ties handling; Fig. 2). For *C. maculatus*, all three parameters of the logistic mortality curve differed between males and females (where a is the intercept, b is the rate of exponential increase in mortality at young ages, and s describes the degree of deceleration in mortality with increasing age; log-likelihood-ratio test, $\chi^2_{(1)} > 16{\cdot}8$, $P < 0{\cdot}001$ for each; WinModest, Pletcher 1999b; Table 1); although females had a higher initial mortality rate than males (a) the rate of exponential increase in mortality with increasing age was substantially greater in males (i.e. there was a higher slope, b, than in females). The higher initial mortality rate (a) produces the shift in the $u(t)$ and $\log[u(t)]$ curves for females relative to males that can be seen in Fig. 2c,e. In contrast, none of the parameters of the logistic mortality model differed significantly between males and females of *S. limbatus*, although there was a trend toward males having a higher initial mortality rate (a) than females ($\chi^2_{(1)}$=

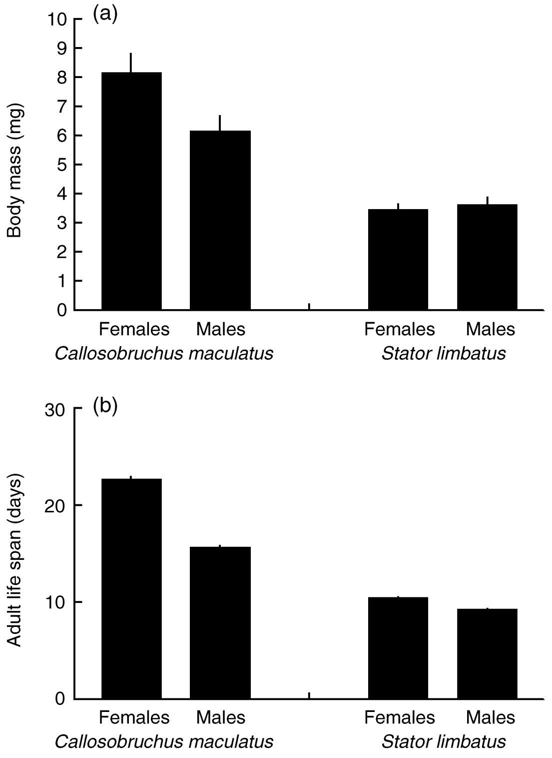

Fig. 1. Mean body mass (a) and adult lifespan (b) for both *Callosobruchus maculatus* and *Stator limbatus*. Note the reverse patterns of sexual size dimorphism (although the difference is small for *S. limbatus*). Both traits differ significantly between males and females, for both species (analysis of variance, with sire and dam (sire) included as fixed effects; $P < 0{\cdot}001$ for each comparison).

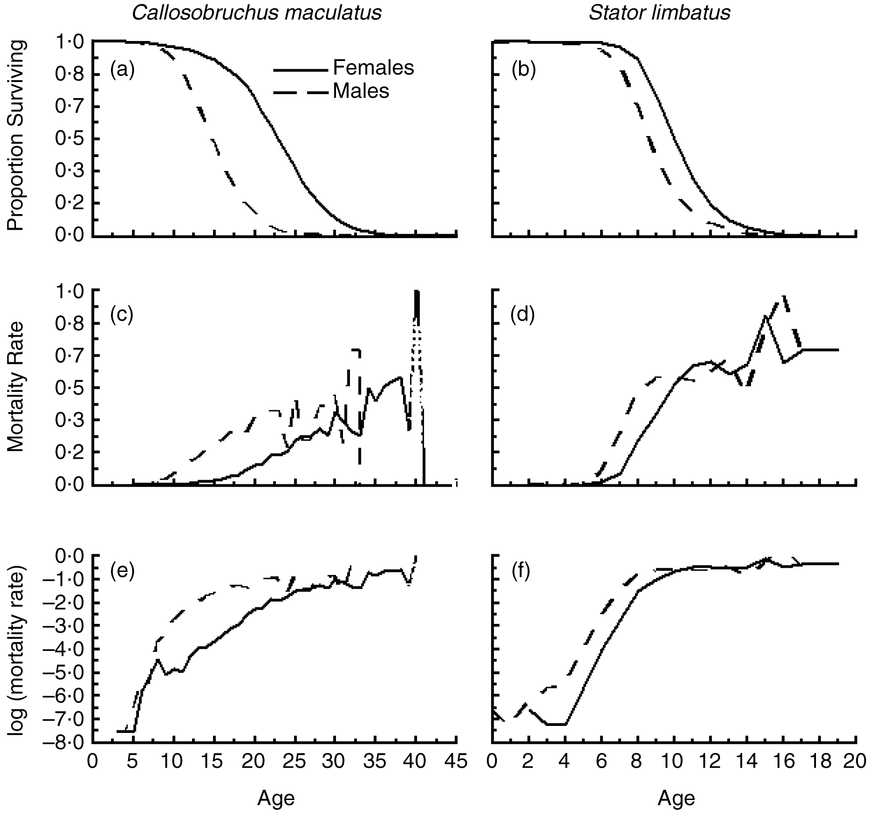

Fig. 2. Survivorship (a,b) mortality curve [$u(t)$] (c,d), and log-transformed mortality curve, $\log[u(t)]$ (e,f), for male and female *Callosobruchus maculatus* and *Stator limbatus*. The mortality curves were best explained by the logistic mortality model, $u(t) = ae^{bt}/[1 + (as/b)(e^{bt}-1)]$, where a is the initial mortality rate, b is the rate of exponential increase in mortality at young ages, and s describes the degree of deceleration in mortality with increasing age (see parameters values in Table 1).

2·29, $P = 0{\cdot}13$; $\chi^2_{(1)} < 0{\cdot}49$, $P > 0{\cdot}52$ for b and s) producing the shift in the $u(t)$ and $\log[u(t)]$ curves for females relative to males in Fig. 2d,f.

EFFECTS OF BODY SIZE ON LIFESPAN AND MORTALITY RATES

Body size was positively correlated with both male and female adult lifespan for both species of beetles (R^2 from linear regression of lifespan vs. mass = 0·09 for both males and females of *S. limbatus*, $R^2 = 0{\cdot}07$ and 0·05 for males and females of *C. maculatus*, respectively; $F > 40$, $P < 0{\cdot}001$ for all analyses, ANCOVA with sire and dam effects included as fixed effects). This was consistent with the likelihood analysis (Cox proportional hazards) that demonstrated a large body mass effect on the shape of the male and female mortality functions ($\chi^2_{(1)} > 26$, $P < 0{\cdot}001$ for both genders of both species). However, the within-gender relationships between body mass and adult lifespan were not adequate to explain the difference in mean lifespan between the genders; in both species, the difference between the adult lifespan of males and females remained highly statistically significant even when the effects of body mass were removed (ANCOVA, $F > 117$, $P < 0{\cdot}001$ for both species). There was no evidence that the relationship between body mass and lifespan differed between the genders ($F < 1{\cdot}41$, $P > 0{\cdot}23$) or among sire families ($F < 1{\cdot}25$, $P > 0{\cdot}13$) for either species. Interestingly, the relationship between body mass and lifespan was slightly concave for female *C. maculatus* (significant mass^2 term in linear regression, $t = -2{\cdot}57$, $P = 0{\cdot}01$). However, there was no evidence that

Table 1. Parameter values for the logistic mortality model, $u(t) = ae^{bt}/[1 + (as/b)(e^{bt} - 1)]$

	Parameter Estimates (95% Confidence Intervals)		
	a (×10^{-5})	b	s
Stator limbatus			
Female offspring	0·202	1·32	2·16
	(0·065–0·631)	(1·19–1·47)	(1·81–2·57)
Male offspring	0·612	1·39	2·23
	(0·236–2·00)	(1·26–1·52)	(1·92–2·59)
Callosobruchus maculatus			
Female offspring	3·8	0·277	0·72
	(2·6–5·4)	(0·257–0·297)	(0·58–0·88)
Male offspring	1·0	0·598	2·06
	(0·5–1·8)	(0·543–0·658)	(1·74–2·43)

a = initial mortality rate, b = rate of exponential increase in mortality at young ages, and s describes the degree of deceleration in mortality with increasing age.

Table 2. Nested ANOVA and estimated variance components for adult lifespan of *Stator limbatus* and *Callosobruchus maculatus*

	Analysis of variance			Variance components	
Source	d.f.	MS	*F*	Observational	Genetic
Stator limbatus					
Females	100	11·81	2·35***	V_{Sire} = 0·54	V_{a} = 2·17
Sire	106	5·03	1·63***	V_{Dam} = 0·37	h^2 = 0·55 ± 0·021
Dam (sire)	1194	3·08		V_{Error} = 3·06	R^2 = 0·34
Error				V_{P} = 3·97	
Males					
Sire	100	11·26	1·82**	V_{Sire} = 0·42	V_{a} = 1·68
Dam (sire)	108	6·27	2·02***	V_{Dam} = 0·52	h^2 = 0·42 ± 0·024
Error	1202	3·10		V_{Error} = 3·09	R^2 = 0·35
				V_{P} = 4·03	
Callosobruchus maculatus					
Females	42	96·90	1·55*	V_{Sire} = 1·57	V_{a} = 6·28
Sire	118	68·98	2·56***	V_{Dam} = 5·27	h^2 = 0·19 ± 0·009
Dam (sire)	1216	26·92		V_{Error} = 26·94	R^2 = 0·30
Error				V_{P} = 33·78	
Males					
Sire	42	80·97	2·64***	V_{Sire} = 1·82	V_{a} = 7·30
Dam (sire)	116	33·72	2·61***	V_{Dam} = 2·44	h^2 = 0·43 ± 0·018
Error	1287	12·90		V_{Error} = 12·92	R^2 = 0·34
				V_{P} = 17·19	

Type III sums of squares were calculated using SAS general linear models procedure (Littell, Freund & Spector 1991; PROC GLM). *F* ratios were calculated using the 'random/test' option of SAS Proc GLM. Variance components were estimated using the restricted maximum likelihood method of SAS VARCOMP. $V_{\mathrm{a}} = 4V_{\mathrm{S}} \times V_{\mathrm{Sire}}$, among sire variance component; V_{Dam}, among dam variance component; V_{Error}, error variance in ANOVA; V_{P}, total phenotypic variance; V_{a}, additive genetic variance.
$^*P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; $^{***}P < 0{\cdot}001$.

the relationship was nonlinear for male *C. maculatus* or for either gender of *S. limbatus* ($|t| < 0{\cdot}31$, $P > 0{\cdot}75$).

To test which parameters of the mortality function (a, b, or s) differed between large and small individuals, we divided individuals of each gender within each species into two classes (above or below the median size), and then tested whether the three parameters of the mortality function differed between large and small individuals. None of the parameters differed significantly between size classes for female *S. limbatus*, but all three parameters differed significantly between size classes for male *S. limbatus*; small males had baseline mortality rates (a) almost 200 times higher than did large males ($\chi^2_{(1)} = 20{\cdot}1$, $P < 0{\cdot}0001$), but the mortality rate increased more slowly for small males (b = 1·95 vs. 1·24; $\chi^2_{(1)} = 14{\cdot}0$, $P = 0{\cdot}001$). For female *C. maculatus*, the baseline mortality rate (a) was higher for small individuals than for large individuals (0·00193 vs. 0·00069; $\chi^2_{(1)} = 6{\cdot}5$, $P = 0{\cdot}01$), but there was no significant difference in the rate of increase in mortality (b; $\chi^2_{(1)} = 3{\cdot}5$, $P = 0{\cdot}07$). There were no significant differences in any of the parameters between large and small male *C. maculatus* ($\chi^2_{(1)} < 1{\cdot}82$, $P = 0{\cdot}18$).

GENETIC VARIATION IN LIFESPAN AND MORTALITY RATES

The shapes of mortality curves varied significantly among sire families, and among dam families (nested within sires) within both beetle species, indicating genetic variation in the shapes of mortality curves (SAS Proc Lifereg: $\chi^2 > 270$, $P < 0{\cdot}001$ for each). This variation among families translated into genetic variation in adult lifespan. The heritability (h^2) of lifespan (e.g. the proportion of the total phenotypic variation due to additive genetic effects) ranged between 0·19 and 0·55 (significantly greater than zero for both genders of both species; Table 2).

To test which specific parameters of the mortality curves varied among sires, we calculated the mortality parameters (a, b and s) separately for each dam family (using WinModest) and then tested whether the parameters varied among sires. As observed in our prior analysis (see 'Patterns of mortality' above), the parameters b and s differed significantly between males and females for *C. maculatus* ($F_{(1,279)} > 18{\cdot}7$, $P < 0{\cdot}001$). Interestingly, this analysis also detected significant gender effects on both a and b in *S. limbatus* ($F_{(1,312)} > 4{\cdot}42$, $P < 0{\cdot}036$ for both), in contrast to the analysis that pooled offspring into a common data set (see 'Patterns of mortality' above; the previous analysis suggested that a differed between the genders, but standard errors were large; Table 1). Of the three parameters in the two species, we detected genetic variation only for the slope of the female *S. limbatus* mortality curve (b) ($F_{(100,312)} = 1{\cdot}74$, $P < 0{\cdot}001$).

Although phenotypic correlations between body size and adult lifespan were significantly positive for both genders of both species ($r_P > 0{\cdot}19$ for *C. maculatus* and $r_P > 0{\cdot}24$ for *S. limbatus*, SEM < 0·05 for each estimate), estimates of the additive genetic correlations did not differ from zero for either gender of either species (*C. maculatus*; $r_A = 0{\cdot}02 \pm 0{\cdot}30$ for females and $r_A = -0{\cdot}22 \pm 0{\cdot}35$ for males; *Stator limbatus*, $r_A = 0{\cdot}17 \pm 0{\cdot}30$ for females, $r_A = 0{\cdot}21 \pm 0{\cdot}34$ for males). The lifespan of male beetles was genetically correlated to that of their sisters; the additive genetic correlations between male and female lifespan (between-gender genetic correlations) were significantly greater than 0 for both species (*C. maculatus*, $r_A = 0{\cdot}97 \pm 0{\cdot}02$; *S. limbatus*, $r_A = 0{\cdot}86 \pm 0{\cdot}05$).

Discussion

As in the majority of animals, female *S. limbatus* and *C. maculatus* live longer than males despite a difference between species in the direction of body size dimorphism. However, the parameters of the mortality model that explained the gender-difference in lifespan differed between the species; in *C. maculatus* females have a higher initial mortality rate (*a*) than males, but males have a much higher rate of increase of the mortality rate (*b*) with increasing age, whereas in *S. limbatus* males had a higher initial mortality rate but males and females did not differ in the rate of increase of mortality. Our results for *C. maculatus* are consistent with results from a previous study of this population (South India) and one other population (Burkina Faso) of *C. maculatus* (Fox *et al*. in press); although males had lower initial rates of mortality (*a*) they had higher rates of increase in mortality (*b*) in both populations (but see Tatar & Carey 1994b who tested beetles under different environmental conditions). This difference in results between species indicates that the mechanistic explanation for gender differences in lifespan must necessarily differ among species, and possibly even among populations within species.

In both *S. limbatus* and *C. maculatus*, body size was positively correlated with adult lifespan, and small individuals had a higher baseline mortality rate than did large individuals. In humans (Kushner 1993; but see Samaras *et al*. 2002) and some laboratory mice (Gartner 1992) the relationship between size and lifespan tends to be convex – intermediate sized individuals live the longest, probably because excessively small or large individuals tend to be unhealthy. Convex relationships between body size and lifespan are typically not observed in natural populations. Instead, body size generally correlates positively with lifespan (e.g. Berube *et al*. 1999) consistent with the patterns observed in comparative studies (Gavrilov 1995; Ricklefs & Scheuerlein 2001). We found some evidence that the relationship between size and lifespan was convex for female *C. maculatus*, but the relationship was linear for male *C. maculatus* and for both genders of *S. limbatus*.

Although body size was positively correlated with adult lifespan in both *C. maculatus* and *S. limbatus*, this phenotypic correlation did not reflect an underlying positive genetic correlation, indicating that lifespan is unlikely to co-evolve with body size (consistent with results of Tatar & Carey 1994a; but contrary to the results of Møller *et al*. 1989 and Messina & Fry 2003; each of whom examined *C. maculatus* in different test environments). Instead, it appears that environmental conditions that influence body size also influence adult longevity, creating an environmentally based positive correlation between these traits that has no underlying genetic basis. For example, our *S. limbatus* are raised on seeds collected from nature, which may vary in their suitability for larval development. Beetles that develop on higher-quality seeds may mature larger and with more resources available for adult functions, and thus live longer. The source of this environmental covariation requires further investigation.

Our study demonstrates that body size differences between males and females do not explain the differences in mortality patterns and average lifespan between the genders – even after removing effects of body size on lifespan, females still outlive males. lifespan differences are thus not simply the by-product of sexual and natural selection on body size. We propose that either metabolic differences or differences in patterns of resource allocation between males and females probably account for the gender difference in lifespan. Some authors have suggested that decreasing metabolic rate extends longevity (review in Rollo 2002; but see Oklejewicz & Daan 2002) consistent with the pattern that larger species, which generally have lower metabolic rates, generally have longer lifespans. Alternatively, males may allocate a greater proportion of their biomass to reproduction, or allocate those resources sooner, such that they become resource-stressed at a younger age. Both *C. maculatus* and *S. limbatus* are facultatively aphagous (e.g. *C. maculatus* is well adapted to a storage environment, in which food and water are not available). Adults must thus use larval-acquired resources for somatic maintenance and even small differences in metabolic rate or rate of allocation of resources to reproduction cannot be offset by increased ingestion of food or water in a storage environment. For *S. limbatus*, we know that virgin males lose mass faster than virgin females (Savalli & Fox 1998) suggesting that males either maintain a higher metabolic rate than females or are less efficient at avoiding water loss. We thus propose that a gender-difference in energy expenditure explains at least some of the gender-difference in lifespan. This hypothesis needs to be evaluated further by simultaneously manipulating adult reproduction and diet.

Differences in mortality rates between the genders may result from different patterns of extrinsic mortality experienced by young adults. In general, lower rates of extrinsic mortality experienced by young adults favour alleles that delay senescence, and thus extend lifespan (Williams 1957; Ricklefs 1998; but see Abrams

1993). Although we have no field data on activity rates of males and females, beetle behaviour in the laboratory suggests that males are more active than females and may thus be under greater risk of extrinsic mortality allowing the accumulation of alleles that reduce lifespan. Other factors that affect the amount of selection for long lifespan in males (relative to selection on female lifespan), such as the phenology of reproductive behaviours (Gotthard *et al*. 2000), have yet to be identified for these two beetle species.

Adult lifespan was heritable in both seed beetle species, with the heritability ranging between 0·19 and 0·55 depending on the gender and species. These values are comparable to estimates found in other studies of *C. maculatus* (Møller *et al*. 1989; Fox *et al*., in press), other seed beetles (Nomura & Yonezawa 1990; Tucić *et al*. 1991; Tanaka 1993) and other insects (Roff 1992). However, for senescence to evolve in response to natural selection there must be genetic variation in the shape of the mortality curve, and not just in the mean lifespan. Because of the need for very large sample sizes, studies of genetic variation in mortality curves are most easily performed on organisms where large numbers of genetically identical or very similar animals can be raised per line, such as *Drosophila*. Genetic variation in all three parameters of the logistic mortality model has been detected in *Drosophila* (Curtsinger *et al.* 1992; Hughes & Charlesworth 1994; Hughes 1995; Promislow *et al*. 1996). Tatar & Carey (1994a) have also previously demonstrated genetic variation in the slope of the mortality curve in *C. maculatus*. We found significant genetic variation within populations in the shape of mortality curves (variation among families in overall shape), but when examining individual parameters we detected significant genetic variance only in the slope of the mortality curve for *S. limbatus*, probably because our family sizes were not large enough to accurately estimate the other parameters of the mortality model separately for each family (a constraint imposed by the fecundity of females; Tatar & Carey 1994b; Promislow *et al*. 1996).

Conclusions

This study thus demonstrates that mortality curves differ in shape between males and females, but that the way that the mortality curves differ between the genders depends on the species. It is thus likely that no single mechanism will explain why males generally have shorter lifespans than females. Although body size is phenotypically correlated with lifespan, body size differences between the genders cannot account for the differences in mortality. For these two beetle species we propose that at least some of the difference in lifespan and mortality rates between genders is due to faster energy/water loss in males than in females, although differences in extrinsic risks of mortality (such as that due to predation) may also contribute. These hypotheses are the subject of ongoing investigation.

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