Sexual Dimorphism in Life History: Age, Survival, and Reproduction in Male and Female Field Crickets *Teleogryllus commodus* under Seminatural Conditions

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ABSTRACT: Males and females differ in their reproductive strategies. Accordingly, sexually dimorphic optima in the allocation of resources to reproduction should select for sex-specific life histories, including sex-specific resolution of the key trade-off between reproduction and longevity. While males are expected to increase reproductive effort with increasing age under sexual selection theory, female reproductive effort should rather decrease after maturity, due to waning selection pressure at older ages. Sex differences in reproductive trade-offs and in the external mortality hazards experienced during the population's evolutionary history are both likely to shape sex differences in reproductive and actuarial (age-specific mortality) aging. Despite the importance of small-bodied, short-lived animals as laboratory models for life-history and aging studies, very little is known about sex differences in life-history patterns under natural conditions. Here, we tested for sex-specific patterns of reproductive and actuarial aging in field crickets under near-natural conditions. Both males and females showed actuarial senescence, with females exhibiting more rapid aging than males but with a later onset. Female and male reproductive effort showed a senescent decrease, with the peaks at different ages. Our findings provide the first demonstration of sexual dimorphism in age-dependent patterns of both survival and reproduction in an insect under near-natural conditions.

Keywords: reproductive aging, field enclosures, insects, mortality rates, senescence, sex differences.

Introduction

Detrimental effects of aging, also known as senescence, can be observed in most organisms (Charlesworth 2000) and are generally characterized by a decline in fecundity (reproductive aging) and by an increase in age-dependent mortality rates (actuarial aging) with advancing age (Partridge and Barton 1996). This definition can be broadened by including adverse direct and indirect effects of declines in fitness components (Williams and Day 2003), for example, mating behavior (Moore and Moore 2001) and performance traits (Grotewiel et al. 2005). Methods to detect signatures of aging have shifted away from analyzing maximum life span of organisms to embrace more powerful biodemographic approaches to estimating age-specific mortality rates (Pletcher 1999). While this has meant a substantial improvement in the way the effects of aging on longevity are described, life span is neither the only nor the most important trait that is subject to senescence (Stearns 1992; Partridge and Barton 1996; Williams 1999; Williams et al. 2006).

Lifetime reproductive output of an individual depends on age-dependent reproductive effort, which is subject to a trade-off with residual reproductive value (Stearns 1992). Longevity and reproductive effort are therefore linked (through trade-offs) in life-history theory (Roff 1992), and many of the mechanistic bases of these links are becoming well resolved (Partridge and Gems 2002). As trade-offs are notoriously plastic (e.g., Glazier 1999; Messina and Fry 2003), mortality rates on their own are not sufficient to characterize whether and how animals age (Partridge and Barton 1996). Information about age-dependent reproductive effort forms a useful complement to our understanding of aging and senescence.

Most tests of evolutionary theories of aging are carried out under laboratory settings (Rose and Charlesworth 1980; Tatar and Carey 1993; Tucic et al. 1996; Zwaan 1999; Stearns et al. 2000; Phelan et al. 2003; Hunt et al. 2006; Zajitschek et al. 2007). This approach allows specific questions about aging to be answered while controlling many confounding environmental effects. However, these studies have in common the fact that they remove most forms of external death hazard that are present in nature (e.g., pathogens, predators, variable weather conditions), including those that shaped the genetic makeup of the population

before it was brought into the laboratory environment (e.g., Chippindale et al. 1994; Promislow et al. 1996; Carey et al. 1998).

Theory tells us that the magnitude and nature of external mortality risks determine the evolution of aging patterns. A higher extrinsic death hazard (that is not dependent on age or condition of the organism that experiences it) is predicted to result in an earlier onset and higher rate of aging (Williams 1957; Hamilton 1966; Abrams 1993; Reznick et al. 2004; Bronikowski and Promislow 2005; Williams et al. 2006; but see Baudisch 2005). One exception to this prediction is when there are density-dependent effects on population growth (Abrams 1993). Under such circumstances the competitive release under high extrinsic mortality (e.g., high predation in guppies; Reznick et al. 2004) can sometimes result in less rapid senescence. In addition, external mortality rate may largely determine life expectancy and, hence, the mean fitness costs of aging. Furthermore, because laboratory environments eliminate most sources of physiological stress (e.g., pathogens and parasites, hunger, thirst, adverse weather, etc.), the expression of aging under laboratory conditions may differ markedly from that of natural populations (Kawasaki et al. 2008).

Most available data on patterns of senescence of wild animal populations come from vertebrates (mammals [Promislow 1991; Loison et al. 1999; Nussey et al. 2006], fish [Bryant and Reznick 2004; Reznick et al. 2004], and birds [Møller et al. 2005; Charmantier et al. 2006]). The vast majority of studies on senescence in invertebrates— albeit with a large bias toward only a few species such as the vinegar fly *Drosophila melanogaster* (e.g., Curtsinger et al. 1995; Hughes 1995; Charlesworth 2001) and the nematode *Caenorhabditis elegans* (e.g., McCulloch and Gems 2003; Kaeberlein et al. 2006; Sedensky and Morgan 2006)— have been carried out under laboratory conditions.

Furthermore, most studies of reproductive aging and the relationship between reproductive aging and longevity have focused on only one sex. In the aging literature this is most often females, due to the ease of counting eggs (Tatar et al. 1996; Rauser et al. 2000; Norry et al. 2006), whereas in the sexual selection literature this is more often males because of their exaggerated sexually selected traits (Kotiaho 2000; Hunt et al. 2004*a*). Sexually selected differences in male and female reproductive effort (Trivers 1972; Clutton-Brock et al. 2006) might result in dramatically different sex-specific patterns of senescence (Promislow 2003; Graves 2007; Bonduriansky et al. 2008). While the variation between taxa and mating systems shows no clear pattern of sex differences in senescence, or the relation between senescence and longevity, males are expected under many circumstances to benefit from trading off life span against increasing mating possibilities and to

increase their reproductive effort throughout life (Kokko 1997; Bonduriansky et al. 2008). In addition, males (especially those bearing conspicuous secondary sexual traits) will often be subject to higher internal and external mortality hazards, leading to elevated aging rates (Bonduriansky et al. 2008). Females, however, generally have to invest more resources and time into offspring production than males and are thus constrained by relatively low returns per unit of time compared to males, leading to a "live slow, die old" strategy (Bonduriansky et al. 2008). Further, males and females seldom have identical evolutionary interests regarding a given reproductive event (Parker 2006), and this sexual conflict has the potential to drive sex differences in aging patterns through antagonistic coevolution between the sexes (Promislow 2003; Bonduriansky et al. 2008).

In the past, it was commonly assumed that short-lived organisms such as insects die too young in the wild to see any signature of senescence (Comfort 1978; Kirkwood and Austad 2000). This dogma has been rejected recently in antler flies *Protopiophila litigata*, in which age-dependent mating and survival rate of males in a natural population were observed to decline later in life (Bonduriansky and Brassil 2002, 2005). Very recently, actuarial aging has also been reported in wild populations of the neriid fly *Telostylinus angusticollis* (Kawasaki et al. 2008) and the black field cricket *Teleogryllus commodus* (Zajitschek et al. 2009). However, none of these studies have been able to quantify both actuarial and reproductive aging in both sexes under natural conditions. The reasons are mostly practical, as most insects are shorter lived and smaller than vertebrates, such that it is difficult to mark and monitor a suitably large sample and extremely difficult to measure reproductive effort in the wild. However, the use of large outdoor enclosures makes it possible to overcome many of these difficulties, permitting the collection of longitudinal data to estimate age dependence of reproductive rate under seminatural conditions that preserve most of the sources of external mortality and stress experienced by wild populations.

Here we tested for signatures of senescence in males and females of the field cricket *Teleogryllus commodus* under near-natural conditions. We were especially interested in testing for sex-specific differences in senescent patterns and in the relationship between the amount and timing of reproductive effort and longevity and whether short-lived and long-lived crickets pursued distinct life-history strategies.

Methods

We collected 391 last-instar nymphs of the black field cricket *Teleogryllus commodus* from February 9 to March

2, 2006, from a cow pasture near Smith's Lake, New South Wales, Australia (32°22′S, 152°30′E). Nymphs were transferred to the University of New South Wales Smith's Lake field station, 6 km away from the collection site and introduced to field enclosures on the following day.

Enclosure Design

We built eight field enclosures on level ground under partial cover of broad-leaved paperbark (*Melaleuca quinquenervia*) trees at the field station. Enclosures were 180 cm × 180 cm with 50-cm-high walls built of black Corflute (Corex Plastics). The walls were buried to a depth of 10 cm and sealed with papier-mâché. We covered the top of each enclosure with plastic mesh, sized 1 cm × 1 cm. The floor of each enclosure was approximately half bare earth and half short grass (under 15 cm in height). We provided egg cartons covered with Corflute as shelter in the middle of each enclosure. To provide partial cover against rain and sunlight, we balanced a piece of Corflute (40 cm × 40 cm) on the mesh on top of each enclosure. Enclosures were never totally in full sunlight. We provided animals with water-soaked cotton wool in a petri dish that was kept wet and renewed every second day. The food in the enclosure was supplemented with cat food (Friskies Go-Cat Senior, 32% protein; 57 mg individual^{-1} day^{-1} = approximately half the amount that is normally fed to an individual cricket in laboratory experiments: three pieces 7 days^{-1}). Enclosures permitted exposure to pathogens and parasites, small predators such as spiders, and the full range of ambient weather conditions (temperature, humidity, precipitation, natural sunlight, and light-dark cycle) experienced by the natural population of crickets. They differed from nature mainly in preventing the entry of bird predators (which would otherwise have quickly decimated the enclosed crickets) and in simulating the hiding places (clumps of tall grass) and food resources (vegetation and cow dung) using artificial shelters (egg cartons) and food (cat food). Thus, although not fully natural, these enclosures approximated natural conditions far better than laboratory environments.

Two enclosures were used exclusively for nymphs, and nymph density in each enclosure was adjusted in order to have equal numbers in each enclosure. There were never more than 130 nymphs in one enclosure. We checked nymphs daily and captured newly eclosed adults. We then measured their pronotum width to the nearest 0.01 mm with an electronic caliper and tagged them by attaching a laser-printed numbered paper label with clear nail polish (Maybelline) to the top of their pronotum. This tagging method does not affect life span or behavior of *T. commodus* in the laboratory (F. Zajitschek and R. Bonduriansky, unpublished data). We then transferred the newly

eclosed adults to one of four enclosures that contained only adults. A total of 79 males and 134 females eclosed into adulthood from February 12 to March 13, 2006. We kept no more than 50 adults in an enclosure at any time. Males and females were kept together to allow them to mate. The sex ratio, defined as the number of eclosed males divided by the total number of eclosed adults, was 0.47 after the first 5 days of the experiment, 0.38 after 15 days, and 0.37 after all animals had eclosed. In order to keep the sex ratio in each enclosure very close to these values of the whole enclosure population, we added random males or females that were captured in the field. Animals were monitored individually by recording the presence of all marked individuals on each day and noting deaths. Marked crickets were caught in the afternoon of days 5, 12, and 19 after eclosion and every 4 days from then on and kept overnight in individual plastic containers for measurement of reproductive effort, after which they were released back into their enclosure.

After most of the experimental animals had died, the remaining animals (three males, or 3.8%, and 39 females, or 29.1%) were taken to Sydney on April 22, 2006, and housed for the remainder of their lives in a plastic container (40 cm × 55 cm × 30 cm) that was covered with mesh and kept in a covered area outdoors. The bottom of the container was covered with a 5-cm-deep layer of earth that was taken from the ground where the enclosures had been installed in the field. To imitate natural moisture conditions, we sprinkled the earth in the container with water when it rained. The sex ratio was maintained as in the enclosures, by adding randomly chosen animals of the needed sex from our laboratory stock culture. Maintaining animals under these conditions, which were similar to the conditions experienced in the enclosures, made it possible to use data from animals that died in Sydney in the final analysis.

Longevity and Mortality Rates

For the mortality analysis, deaths of all animals (those that died in the enclosures at the field site and in Sydney) were included. The significance of the difference in male and female average longevity was tested using Cox proportional hazards regression analysis. We used the program WinModest (Pletcher 1999) to fit four models (Gompertz, Gompertz-Makeham, Logistic, Logistic-Makeham) to the age-specific mortality rates, to find the model that fitted best using log-likelihood ratio tests, to estimate the parameters of the best-fit model, and to test for significant differences in parameter values between best-fit models, separately in males and in females. In each case, either the Gompertz model

$$\mu_x = \alpha\, e^{\beta x} \qquad (1)$$

or the Gompertz-Makeham model

$$\mu_x = c + \alpha\, e^{\beta x} \qquad (2)$$

turned out to provide the best fit. In both models, the age-dependent mortality hazard (μ_x) at age x is described by the baseline mortality (α) and the exponential increase in mortality with age (β). The Gompertz-Makeham model has one additional parameter, the age-independent mortality rate (c), and the model reduces to the Gompertz model when c takes on the value zero. We used WinModest to compare parameters among groups by constraining one parameter to be the same for both groups and comparing the log-likelihood value of this constrained model to the unconstrained model of both groups. To compare the model parameters between two groups that had different best-fit models, we used the more complex of the two models for both groups (Pletcher et al. 2000).

Measuring Reproductive Effort

In order to test for reproductive aging, we quantified reproductive effort in marked individuals at regular intervals until death. Female *T. commodus* are sexually receptive during their whole adult life. In mated females, egg laying is not dependent on the number of matings, but matings stimulate an increase in egg deposition in the 2–24 h after a mating occurs (Loher and Edson 1973; Loher et al. 1981). Females were put separately into a plastic container for 1 night at age 5, 12, and 19 days after eclosion and every 4 days from then on and were provided with a cotton wool-plugged water tube and a petri dish filled with damp sand in which they could oviposit. On the following day, we counted the number of eggs laid. Fecundity of females that were taken to Sydney was recorded until they died. We observed males at Smith's Lake at the same age as females' fecundity was measured, for 2 h, from 11 p.m. until 1 a.m., and noted every 5 min whether a male was calling. No measurements of calling effort in Sydney were taken from the three males that died in Sydney (age at last measurement for these three males: 39, 51, 51 days). Producing long-distance advertisement calls, or calling effort, is not the only component of male reproductive effort, but it has been shown to be very costly (Hunt et al. 2004*a*), and it is under strong sexual selection in the field (Bentsen et al. 2006). The number of measurements recorded in total was 1,199 for females and 397 for males. Minimum ambient air temperature was recorded every night.

Reproductive Aging

To analyze patterns of age-dependent changes in reproductive effort, we used generalized linear mixed models with a negative binomially distributed error term and a log link function (PROC GLIMMIX, SAS Institute). To avoid problems with multicollinearity, variables were standardized before the analyses (Jaccard and Turrisi 2003). We modeled age at measurement (age), its quadratic term (age^2), and life span as fixed effects. Interactions between age and life span and age^2 and life span were added to test for heterogeneity in life-history strategies between shorter- and longer-lived individuals. Individual identity was included as a random effect in all models to account for correlated longitudinal data within individuals. Additionally, minimum air temperature was included as a random effect in all models. Reproductive effort in females, not in males, was measured both at Smith's Lake and in Sydney. Therefore, we included a binary variable that defined the location, and, accordingly, the two different housing conditions, together with its two-way interaction terms with age, age^2, and life span in the full model for female reproductive effort. For model selection, nonsignificant variables were dropped from the full model, and the model was refitted to the data until all of the remaining variables were significant at a level of $P < .05$.

For a graphic presentation of the relationship of reproductive effort with age and life span, we fitted nonparametric thin-plate splines using the TPS function in the fields package in R 2.7.2 (R Development Core Team 2007). Due to the difference in how reproductive effort was measured in the two sexes, we analyzed male and female reproductive effort using distinct models and separate tests. Note that sample size, and therefore power to detect significant patterns, is smaller in males than in females.

To evaluate the relationship between age-independent reproductive effort and life span, we estimated total (lifetime) reproductive investment of each male and female as the sum of all measurements of calling effort in males, and egg numbers in females, taken during an animal's life span. While we could not strictly measure lifetime reproductive investment (i.e., total quantity of resources spent on reproduction), our indexes of reproductive investment should provide a good approximation for this variable. Mean reproductive effort of an individual was calculated as total reproductive effort divided by the number of days on which reproductive effort was quantified for that individual.

We then fitted linear and quadratic regression models, with life span as the dependent variable and total and mean reproductive effort as the independent variable, separately

Table 1: Mean/median life span and parameter values from Gompertz-Makeham mortality models of males and females

Sex	Mean adult life span ± SE (days)	Mortality parameters		
		α	β	c
Male	29.07 ± 1.67 (28)	.011 (.007, .017)	.049 (.039, .061)	6.63E−16 (0, 4.90E−15)
Female	41.71 ± 2.43 (47)	8.28E−12 (0, 9.78E−7)	.280 (.172, .454)	.020 (.016, .024)

Note: α = baseline mortality; β = increase in mortality; c = age-independent mortality. Median adult life span and lower and upper 95% confidence intervals for the parameter estimates are given in parentheses.

to all animals within each sex. We used software packages SAS 9.1, SPSS 16.0, and Microsoft Excel for analyses.

Results

Longevity and Mortality Rates

Females lived on average 13 days longer than males (difference in mean adult life span, table 1; Cox regression: $\chi^2 = 30.09$, df = 1, $P < .0001$). The Gompertz model showed the best fit for mortality rates in males (H_0: Gompertz-Makeham vs. Gompertz model, $P > .9999$), and the Gompertz-Makeham model described the data best in females ($P < .0001$). When we compared male and female mortality rates using the Gompertz-Makeham model, we found that all three parameters were significantly different between the sexes (df = 1 for all comparisons; for parameter α, $\chi^2 = 25.31$, $P < .001$; for parameter β, $\chi^2 = 20.32$, $P < .0001$; for parameter c, $\chi^2 = 6.07$, $P = .0137$; table 1; fig. 1). Baseline mortality α was higher in males, whereas increase in mortality rate β and age-independent mortality rate c were higher in females.

Reproductive Aging

Models of male and female reproductive effort showed significant linear and quadratic relationships between reproductive effort and age at measurement (table 2). Males with life spans shorter than 45 days increased their calling effort at early ages and then plateaued (fig. 2A). In males that lived 45 days and longer, calling effort peaked in the range between 25 and 30 days and decreased thereafter (fig. 2A). In females, life span and its interaction terms with age and age² were significant (table 2). This means that the curvature of the function describing the number of eggs laid per age depended on a female's life span. For females that died before 40 days of adult life, fecundity increased or plateaued after an initial increase before they died. Fecundity of females with life spans between 40 and 80 days increased until around 20 days of age and then decreased again. Interestingly, in females that reached life spans above 80 days, there seems to be an extended or even a later peak until around 60 days. Housing condition was not a significant predictor of female fecundity, which suggests that the senescent decrease in fecundity is not

attributable to the change in how female crickets were kept at very late ages.

In summary, we found declines of reproductive effort at late ages for both males and females, indicating reproductive senescence. Senescent declines occurred only in males and in females that lived longer than 45 and 40 days, respectively. In those individuals, reproductive effort peaked later in males than in females.

Associations between Total Reproductive Effort and Longevity

Males that lived longer called more in total during their lifetime than shorter-lived males ($F_{1,78} = 60.151$, $P < .001$; fig. 3a), and this relationship persisted when males that did not call at all were excluded ($F_{1,55} = 26.185$, $P < .001$). Mean nightly calling effort increased with age ($F_{1,78} = 8.100$, $P = .006$; fig. 3b), but this seems to be driven by the large group of shorter-lived males that did not call at all, because the linear effects were no longer significant when we excluded data of these males that did not call ($F_{1,55} = 0.062$, $P = .804$).
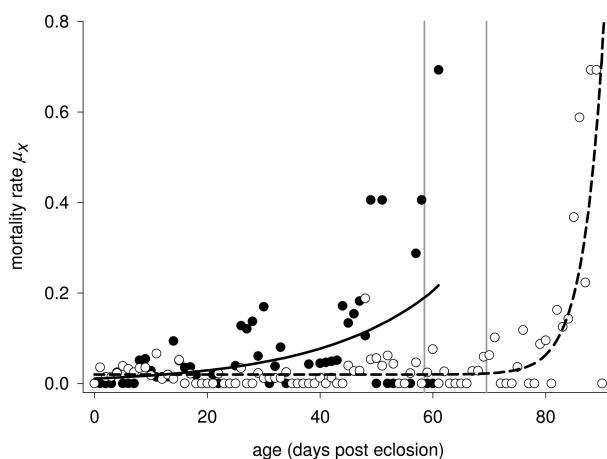
Figure 1: Age-dependent mortality rate μ_x of males (*filled circles, solid black line*) and females (*open circles, dashed black line*). Black lines represent fitted Gompertz-Makeham functions (for parameterization, see table 1). Gray vertical lines depict ages below which animals that died in seminatural outdoor enclosures (see "Methods") were used to calculate daily mortality rates (*left line*, males; *right line*, females).

Table 2: Models for age-dependent reproductive effort in males and females

Term	df	F	Estimate ± SE	P
Male:				
Age	1, 297	9.75	.0605 ± .0194	.0020
Age^2	1, 297	8.22	−.0013 ± .0005	.0044
Female:				
Age	1, 1,011	13.35	.3132 ± .0857	.0003
Age^2	1, 1,011	13.57	−.0089 ± .0024	.0002
Life span	1, 1,011	7.33	.0847 ± .0313	.0069
Age × life span	1, 1,011	7.99	−.0101 ± .0036	.0048
Age^2 × life span	1, 1,011	9.11	.0003 ± .0001	.0026

Note: Male N_{ind} = 79, N_{obs} = 397, and female N_{ind} = 134, N_{obs} = 1,199, where ind = individuals and obs = observations.

Females that lived longer showed higher lifetime fecundity than short-lived females ($F_{1,133}$ = 102.331, $P < .001$; fig. 4a), and this was qualitatively the same when we excluded data from 39 females that did not lay any eggs during their lifetime ($F_{1,94}$ = 27.615, $P < .001$). Mean nightly fecundity showed an increase with increasing longevity but then plateaued ($F_{2,133}$ = 19.231, $P < .001$; fig. 4b). However, as in males, this relationship was not existent when data of females that laid no eggs during their entire lives were excluded ($F_{1,94}$ = .003, $P = .957$; fig. 4b).

Discussion

Under the near-natural conditions of our enclosures, *Teleogryllus commodus* showed a clear signature of sex-dependent senescence. Both males and females show exponential increase in mortality rates at later ages. In females, actuarial senescence started much later and was more rapid than in males. Female fecundity also showed signs of senescence, increasing up to approximately the age of female mean longevity and decreasing thereafter. By contrast, reproductive senescence in males was not as pronounced and started at older ages compared to females. We found no evidence of a negative relationship between reproductive effort and longevity. Together, these findings support the emerging view that reproductive and actuarial senescence do occur in relatively short-lived insect species in the wild (Bonduriansky and Brassil 2002, 2005; Kawasaki et al. 2008; Zajitschek et al. 2009) and that patterns of senescence differ substantially between sexes due to differences in the timing and nature of reproductive investment.

Actuarial Aging

Male and female longevities differed significantly. Sex differences in longevity have been shown in many taxa, although which sex lives longer seems to vary to a great extent between species (Rose 1994; Murray and Cade 1995; Zajitschek et al. 2007). Our results demonstrate that in *T. commodus* under field enclosure conditions, sex-dependent longevity is driven by sex differences in age-dependent mortality: the female cohort senesced later but much more rapidly than males. Hamilton (1966) used the product of survival and reproduction in the general Euler-Lotka equation to model fitness as the Malthusian parameter, r,
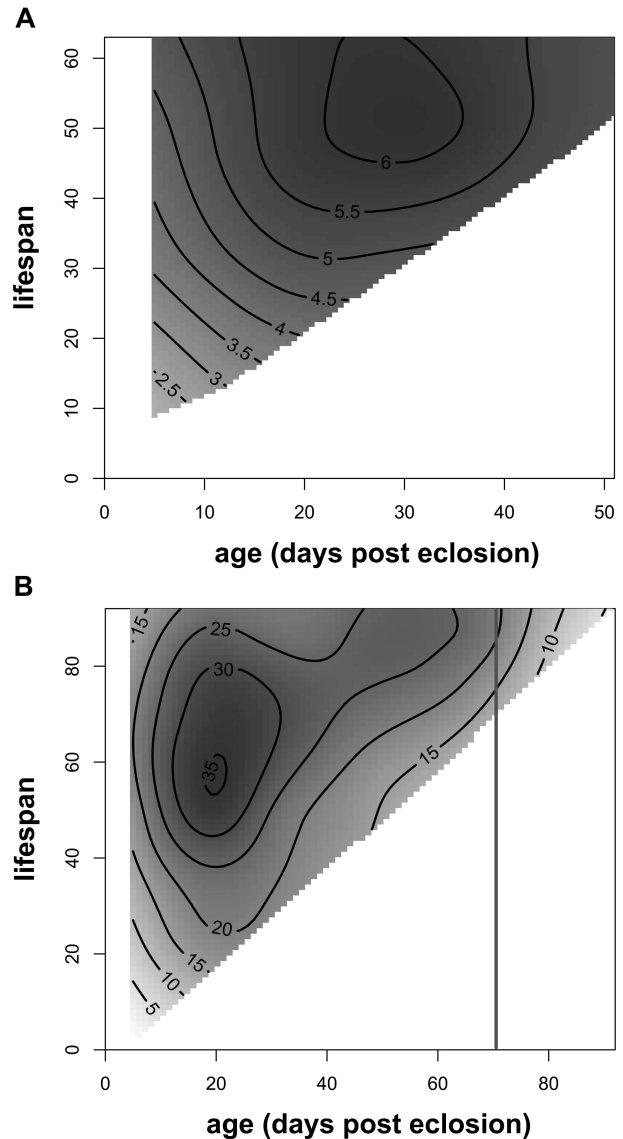
Figure 2: Age-dependent reproductive effort in relation to life span. The surface for males (*A*) represents nightly calling effort (see "Methods" for measurement scale). In females (*B*), number of eggs laid per night is shown. Darker shades of gray indicate higher values of reproductive effort. For females (*B*), the vertical line depicts the maximum age of animals that died in seminatural outdoor enclosures.
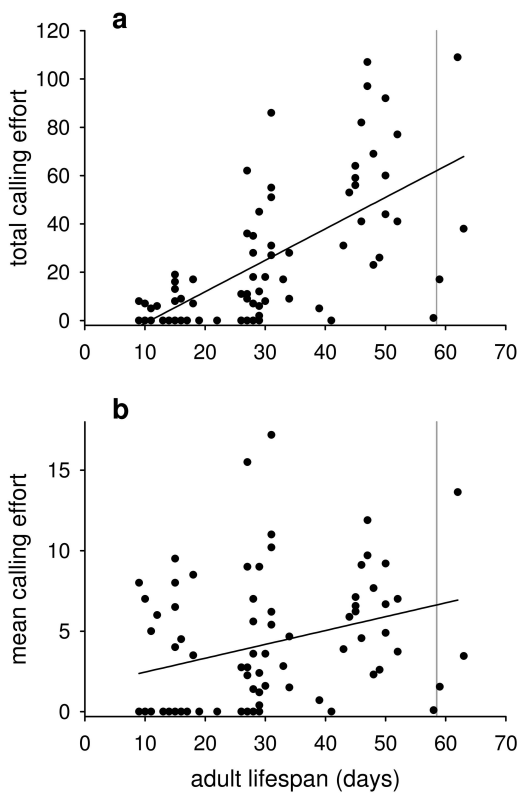
Figure 3: Relationship between male calling effort and life span. Total calling effort (*a*) is the sum of all calling effort measurements during the lifetime of a male; mean calling effort (*b*) is the mean nightly calling effort. In both panels, the black solid line shows the overall model for all males. The life span above which only animals that died in Sydney were used in the plot is depicted by the vertical line.

and thus to generate predictions about the factors that shape senescence. He predicted that high rates of senescence and reduced life spans are both likely to result from higher extrinsic mortality under some but not all circumstances. In so doing, however, he generally equated high mortality rate with rapid senescence. In our study, males have higher overall mortality rates and therefore shorter life spans than females. If, however, we use the Gompertz parameter β as our measure of senescence, females senesce more rapidly, even though they are longer lived. This situation of a late onset yet a steep incline of senescence in females was best described by the Gompertz-Makeham model. This underlines the important fact that the mortality patterns we estimated in males and females cannot be well characterized with just one descriptive parameter such as β because females have a much higher aging rate than males but only later in life, expressed by the very low estimated value of α in females. Initial mortality rates, represented by the sum of parameters α and c (Ricklefs

1998), are quite similar in males and in females, but males have higher overall mortality rates.

From what we know about crickets in natural populations, extrinsic mortality hazards are likely to be higher in males than in females because their calling behavior might be exploited by phonotactic predators and parasitoids (Walker and Masaki 1989; Bailey and Haythornthwaite 1998; Zuk and Kolluru 1998; Kolluru et al. 2004). Our capture-mark-recapture study (Zajitschek et al. 2009), conducted at the same time as our study at the field site where nymphs for our experiment were caught, showed that males were both less likely to be recaptured at all and that they had a higher age-independent mortality rate than females in the wild. Estimated median life spans of males and females in the wild were about half of the median life spans in our seminatural enclosures. Aging rate (β, as estimated in Gompertz models for both sexes) did not vary between the sexes and was lower than our estimates for both males and females in enclosures (Zajitschek et al.
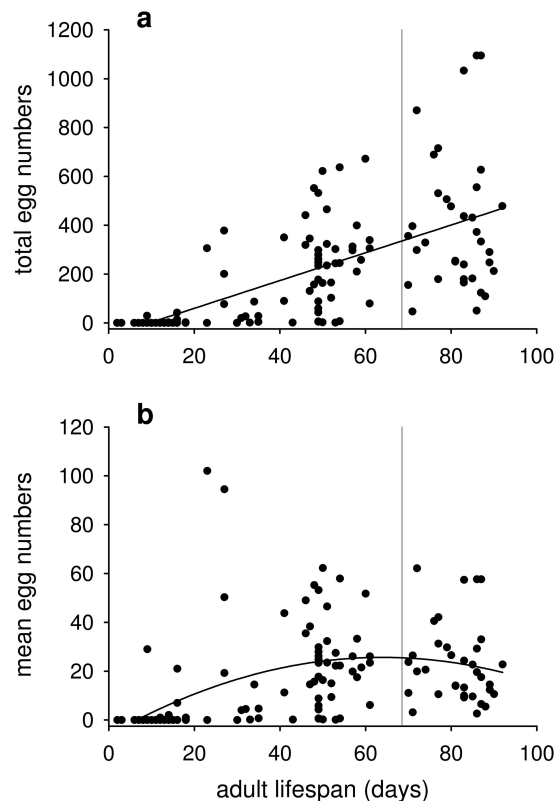

Figure 4: Relationship between number of eggs a female laid and life span. Total egg numbers (*a*) are the sum of eggs a female laid during her lifetime; mean egg numbers (*b*) are the mean nightly numbers of eggs a female laid. In both panels, the black solid line shows the overall model for all females. The life span above which only animals that died in Sydney were used in the plot is depicted by the vertical line.

2009). Disregarding the potential effects of methodological differences between these two studies, this suggests that animals in enclosures indeed experienced less overall mortality hazards than in the wild. We found no higher background mortality in males compared to females, as was the case in wild animals (Zajitschek et al. 2009). Additionally, in enclosures, without access of large predators, there seems to be no trade-off between total calling effort and life span. The fact that the effect of large predators such as birds and bats on male mortality rates is excluded in enclosures might be responsible for this positive relationship. Alternatively, it could reflect a condition-dependent effect—males in good condition call more but are also able to better escape from large predators and therefore live longer. Of course, these two explanations are not mutually exclusive, and it should be interesting to see estimates of mortality rates and reproductive effort, together with a quantitative estimate of predation in this species in the future.

The rapid aging rate in females was driven by deaths from animals that died while kept in a small outdoor container in Sydney rather than in the original field enclosures. But even if the changed conditions affected the female mortality pattern at late ages, the onset of aging would still be much later in females than in males, and the conclusion that the difference between male and female mortality patterns is mainly due to a higher male baseline mortality rate still seems robust. In addition, while the rapid aging rate could reflect the change in how the animals were kept, we argue that this is not likely to be the case. If differing conditions changed mortality rates, we would expect a change in the opposite direction, that is, animals that are kept in a container should live longer than animals that live in outdoor enclosures, because of the reduced exposure to environmental conditions, resulting in a flatter mortality curve, rather than the rapidly accelerating pattern of mortality with age observed in very-long-lived females.

Reproductive Aging

Male reproductive effort appeared to increase and plateau in males with low and medium life spans. Calling effort of males that reached higher life spans, however, increased until it peaked and declined again at later ages. This can be interpreted as evidence that only long-lived males exhibit reproductive aging (i.e., declining calling effort with age).

Although it is predicted by theory (Andersson 1994; Williams 1966) and it has been shown empirically (Cordts and Partridge 1996; Kotiaho and Simmons 2003; Hunt et al. 2004a) that male reproductive effort can be extremely costly, studies of reproductive aging in wild populations have largely focused on female age-dependent fecundity (Gustafsson and Pärt 1990; Mysterud et al. 2002; Møller et al. 2005; Nussey et al. 2006). Most of these studies presenting data for both sexes are on vertebrates (e.g., Promislow et al. 1992; Loison et al. 1999), and, only recently, Reed et al. (2008) showed sex differences in reproductive aging in a vertebrate for the first time: in the common guillemot (*Uria aalge*), a long-lived sea bird, breeding success of both males and females declined at later ages, but the decline was slightly faster in females than in males. To our knowledge, reproductive senescence (in males only) so far has been reported for only one insect species, the fly *Protopiophila litigata*, in the wild (Bonduriansky and Brassil 2002, 2005). Here, we show that calling effort in male *T. commodus* with high longevity also declined with increasing age.

Female fecundity declined after reaching an earlier peak, which is a pattern of reproductive aging also seen in female red deer (*Cervus elaphus*; Nussey et al. 2006) and choughs (*Pyrrhocorax pyrrhocorax*; Reid et al. 2003) when tested under natural conditions. This pattern of age-dependent fecundity is interesting because theory predicts that fecundity should generally peak shortly after the age of the onset of reproduction (Hamilton 1966; Emlen 1970). Yet in our study, and in the studies on red deer and choughs cited above, the senescent decline is much later after the predicted onset at maturity (age of maturity of female *T. commodus* is 5–10 days of adult life; red deer, 3 years; choughs, 2–3 years; age of onset of senescent decline in fecundity in *T. commodus* is 20 days; red deer, 8 years; choughs, 7–8 years; Reid et al. 2003; Nussey et al. 2006). One variation to the prediction is that when there is indeterminate growth and fecundity is associated positively with size, then fecundity should increase and senescence should be delayed and weakened (but never totally offset; Hamilton 1966). This is a pattern typical of fish in which increasing fecundity is very likely due to indeterminate growth and the positive relationship between body size and fecundity (Reznick et al. 2002). The pattern that we document is surprising because there is no increase in body size in crickets once they eclose to adulthood and because under laboratory conditions mean fecundity is not correlated with pronotum width or weight of a female (Zajitschek et al. 2007). The observed increase in reproductive effort up to a certain age does not appear to reflect a tendency for individuals to elevate their reproductive effort as their survival prospects decline since age-specific mortality rate remained virtually constant in females until very late ages. However, there was evidence for such a terminal increase of reproductive effort in females that reached very high life spans.

Associations between Total Reproductive Effort and Longevity

The association between longevity and fitness may be positive or negative, depending on how the trade-offs between reproductive effort and life span are resolved (Hansen and Price 1995; Kokko 1998; Kokko et al. 2002; Bondurianksy and Brassil 2005; Bondurianksy et al. 2008). In many cases the resolution of these trade-offs depends on both the resources that an individual has acquired (condition; sensu Rowe and Houle 1996) and the way in which these resources are subsequently allocated to fitness components including reproductive effort and somatic maintenance (Houle 1991; Rowe and Houle 1996; Hunt et al. 2004*b*). When male and female reproductive efforts differ as fundamentally as they do in field crickets, it is possible for the way in which an acquired condition is allocated to reproductive effort to differ so dramatically that the relationships among fitness, age-dependent reproductive effort, and life span are radically different between the sexes (Beck et al. 2003; Hunt et al. 2004*a*). We found that both male and female longevity were associated with greater lifetime reproductive effort. This suggests that, under field enclosure conditions, the trade-offs between reproduction and longevity were not so extreme as to generate a negative correlation between reproduction and longevity. This is consistent with quantitative genetic evidence from our laboratory that under benign conditions, reproductive effort and life span were positively genetically correlated (Zajitschek et al. 2007). Laboratory studies have also shown that trade-offs between life span and reproduction in *T. commodus* are mediated by diet (Hunt et al. 2004*a*; Maklakov et al. 2008), and, thus, our ability to identify such trade-offs could be limited by the fact that we used only one type of diet in this experiment.

In conclusion, this study provides evidence of senescence in both males and females of a short-lived species under near-natural conditions. The observed senescence is stronger in females than in males, with females showing a later but more rapid age-dependent increase in mortality than males. Females and males exhibited a clear signature of reproductive aging that was dependent on longevity. Generally, onset of the senescent decline in reproductive effort was much earlier in females than in males. The evolutionary basis of sex-dependent senescence presents fertile ground for experimental and comparative study.

Acknowledgments

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