Sex differences in nutrient-dependent reproductive ageing

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Summary

Evolutionary theories of aging predict that fitness-related traits, including reproductive performance, will senesce because the strength of selection declines with age. Sexual selection theory predicts, however, that male reproductive performance (especially sexual advertisement) will increase with age. In both bodies of theory, diet should mediate age-dependent changes in reproductive performance. In this study, we show that the sexes exhibit dramatic, qualitative differences in age-dependent reproductive performance trajectories and patterns of reproductive ageing in the cricket *Teleogryllus commodus.* In females, fecundity peaked early in adulthood and then declined. In contrast, male sexual advertisement increased across the natural lifespan and only declined well beyond the maximum field lifespan. These sex differences were robust to deviations from sex-specific dietary requirements. Our results demonstrate that sexual selection can be at least as important as sex-dependent mortality in shaping the signal of reproductive ageing.
Key words: age; diet; nutrition; reproduction; senescence; sexual selection.

Introduction

Nutrient acquisition and allocation are fundamental to organism fitness because investment in reproduction, including sexual advertisement, depends on condition (Andersson, 1982; Kotiaho *et al.*, 2001) and thus on the pool of acquired resources (Rowe & Houle, 1996). Nutrient-mediated trade-offs are therefore central to the evolutionary study of aging (Partridge & Brand, 2005; Simpson & Raubenheimer, 2007; Carey *et al.*, 2008; Lee *et al.*, 2008; Skorupa *et al.*, 2008) and to sexual selection (Andersson, 1982; Kotiaho *et al.*, 2001; Hunt *et al.*, 2004), but to date there has been little integration between these two bodies of research (Promislow, 2003; but see Carranza *et al.*, 2004; Bonduriansky *et al.*, 2008; Maklakov *et al.*, 2008). Further, most work on diet-mediated aging concerns positive effects of dietary restriction on lifespan and actuarial aging (Weindruch & Walford, 1988; Partridge & Brand, 2005; Lee *et al.*, 2008) – the age-dependent increase in mortality rates, rather than reproductive aging – the age-dependent decrease in reproductive capacity. Most importantly, the causes of sex differences in lifespan and aging rate remain poorly understood (Bonduriansky *et al.*, 2008).

Evolutionary theories of aging predict that senescence in reproductive performance, defined here as net reproductive output, will evolve because of the declining power of natural selection with age (Charlesworth, 1994; Hughes & Reynolds, 2005). Evidence exists for reproductive senescence in various species under laboratory (Finch, 1990; Carey, 2003; Reynolds *et al.*, 2007) and field conditions (Bonduriansky & Brassil, 2005; Charmantier *et al.*, 2006; Keller *et al.*, 2008; Reed *et al.*, 2008). At the same time, life-history theory also predicts that reproductive effort (i.e. reproductive investment per unit of available energy), should increase with age, as optimal investment in reproduction increases as survival prospects decline (Williams, 1966), and there are reasons to expect that selection should generally favour a steeper increase in reproductive effort with age in males than in females. While male courtship and mating can be costly (Cordts & Partridge, 1996; Mappes *et al.*, 1996), a male's maximum potential reproductive success is less constrained by the time-investment requirements of offspring production, and is thus usually much higher than a female's. Males can therefore potentially gain more fitness through risky, damaging strategies that sacrifice survival prospects for reproductive opportunities (Bonduriansky *et al.*, 2008). Likewise, game-theoretic models predict that sexually selected male advertisement should increase with age under a wide range of circumstances (Kokko, 1997). Age-dependent increases in sexual signalling could favour the maintenance of somatic condition into advanced age, while also compensating for the effects of senescent deterioration in reproductive traits (Kokko, 1997; Graves *et al.*, 2006; Graves, 2007; Bonduriansky *et al.*, 2008).

Despite a growing recognition that sexual selection may influence aging and vice versa (Promislow, 2003; Maklakov *et al.*, 2005, 2007; Graves, 2007; Bonduriansky *et al.*, 2008), the evolution of sex differences in reproductive aging has not been tested experimentally. Here, we address this deficit directly by measuring lifetime age-dependent sexual advertisement in males and fecundity in females under experimental diets known to affect reproduction and lifespan in field crickets, *Teleogryllus commodus*, an omnivorous insect that inhabits pastures and grasslands of southern Australia. We have studied a population of crickets from Smith's Lake, N.S.W. since 2002, and the body of field and laboratory research we have published on these crickets makes them an ideal model for studies of sex-dependent reproductive costs and aging. Experiments in field enclosures have suggested that males and females differ in both the rate and onset of actuarial aging (females age more rapidly but later than males) and in reproductive senescence (females senesce but males do not) under near-natural conditions (Zajitschek *et al.*, 2009a). It is reasonable to predict that differences in senescence may be associated with differences in the nature and nutritional basis of reproductive effort. Males call by transverse stridulation of their wings, and females preferentially mate with males with high calling effort (Hunt *et al.*, 2004; Bentsen *et al.*, 2006). High calling effort is phenotypically costly (Hunt *et al.*, 2004) and depends primarily on carbohydrate energy content of the food (Maklakov *et al.*, 2008). There is a genetic trade-off between calling and male lifespan (Hunt *et al.*, 2006). In addition, calling may raise exposure to potential predators and parasites, as has been shown for congener *T. oceanicus* (Bailey & Haythornthwaite, 1998). By contrast, female reproductive effort is in the form of the number of eggs laid, and is maximized on an intake of approximately equal amounts of protein and carbohydrate by weight (Maklakov *et al.*, 2008).

We employ the Geometric Framework (GF) of nutrition (Simpson & Raubenheimer, 2007) to study the role of macronutrients in mediating age-dependent reproductive performance. Food availability is crucial for the expression of condition-dependent reproductive traits but the relationship between relative availability of key nutrients in the diet and fitness components can be complex (Carey *et al.*, 2008; Lee *et al.*, 2008; Maklakov *et al.*, 2008). The GF is a state-space multivariate approach to understanding the nutritional requirements of animals and the performance consequences of particular diets (Raubenheimer & Simpson, 1997; Simpson *et al.*, 2004; Simpson & Raubenheimer, 2007). The nutritional relationship of an animal to its environment is modelled in *n*-dimensional nutrient space, where each dimension is one nutrient, and the animal's nutritional state at any time is a point in that space (Simpson & Raubenheimer, 2007). With its emphasis on both experimental manipulation of multiple nutrients and on the measurement of performance consequences, the GF is a promising approach to understanding the nutritional basis of aging (Simpson & Raubenheimer, 2007). It has already resulted in insights into the complex consequences of nutrition for both aging and fitness in *Drosophila melanogaster* (Lee *et al.*, 2008) and was successfully used to identify nonlinear effects of nutrient intake on fitness components in *T. commodus* crickets (Maklakov *et al.*, 2008).
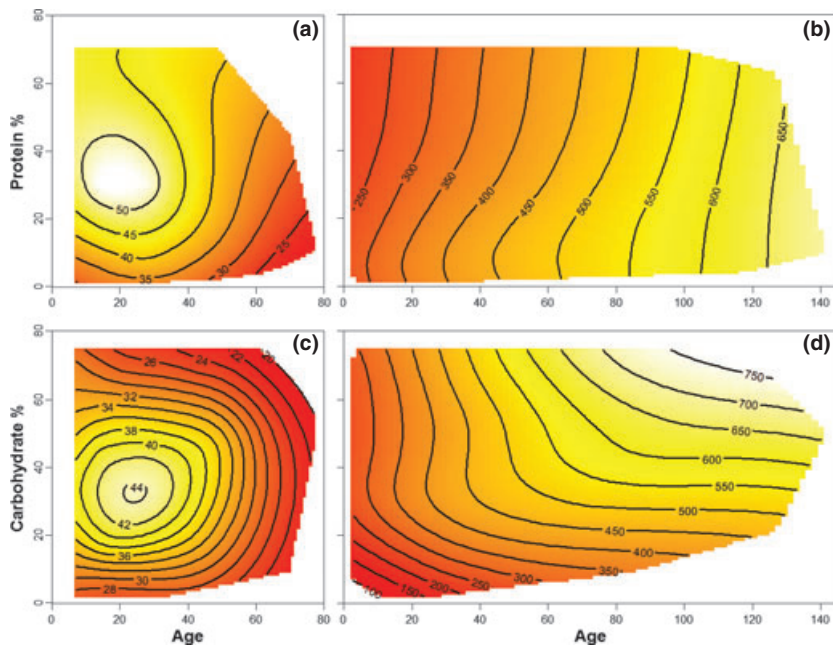
We used artificial diets to deliver controlled concentrations and ratios of proteins and carbohydrates. Previously (Maklakov *et al.*, 2008), we showed that lifespan in both sexes, and male calling effort, were maximized on high carbohydrate, low protein diet, whereas female egg laying was maximized on a 1:1 protein:carbohydrate ratio.

Results and discussion

We observed a striking difference between sexes in the age-dependent trajectories of reproductive output (Figs 1 and 2). These differences are most probably due to fundamental differences in life histories, as well as in the nutrient and energetic requirements for reproduction. Female fecundity generally declined with age except near the balanced protein:carbohydrate ratio that we have previously shown is optimal for lifetime egg production (Maklakov *et al.*, 2008), at which female egg laying increased to peak at 3–4 weeks old and then declined (Table 1, Fig. 1a,c). Longer-lived females generally laid more eggs at a given age, and it was only in these females that fecundity increased to a peak and then declined (Fig. 2a,c, interaction between age and lifespan in Table 1a). Although reproductive output was nutrient-dependent, age-related reproductive senescence was not: there was no interaction between age and either macronutrient. The general age-dependent decline in female fecundity and the interaction between age and lifespan were both significant after the effects of nutrients had been included in the model (Table 1).

In contrast, male calling effort generally increased with male age. Male calling effort was independent of protein content in the diet (Fig. 1d), but it did increase more rapidly and plateau at a higher level with increased carbohydrate availability (Table 1, Fig. 1b). The significant interaction between age and lifespan (Table 1) reflects the fact that calling does not decline with age in short-lived males but peaks and then declines in the longest-lived males (Fig. 2b,d). The interaction between carbohydrate and age indicates that age-specific reproductive effort depends on availability of this nutrient in males.

To relate our results to selection in nature, we compare our data with median and maximum lifespan estimates for the wild source population (Zajitschek *et al.*, 2009b). In our laboratory experiment, female egg-laying rate peaked between 7 and 28 days (Fig. 1a), whereas, in the wild, adult females have a median lifespan of 22.7 days and an estimated maximum of 73.3 days (Zajitschek *et al.*, 2009b). Thus, the senescent decline in the laboratory commenced just before the age corresponding to the median adult life expectancy in the field population. Moreover, females that lived for less than 30 days in our experiment started to senesce from the first week after eclosion (Fig. 2c). These results suggest that reproductive
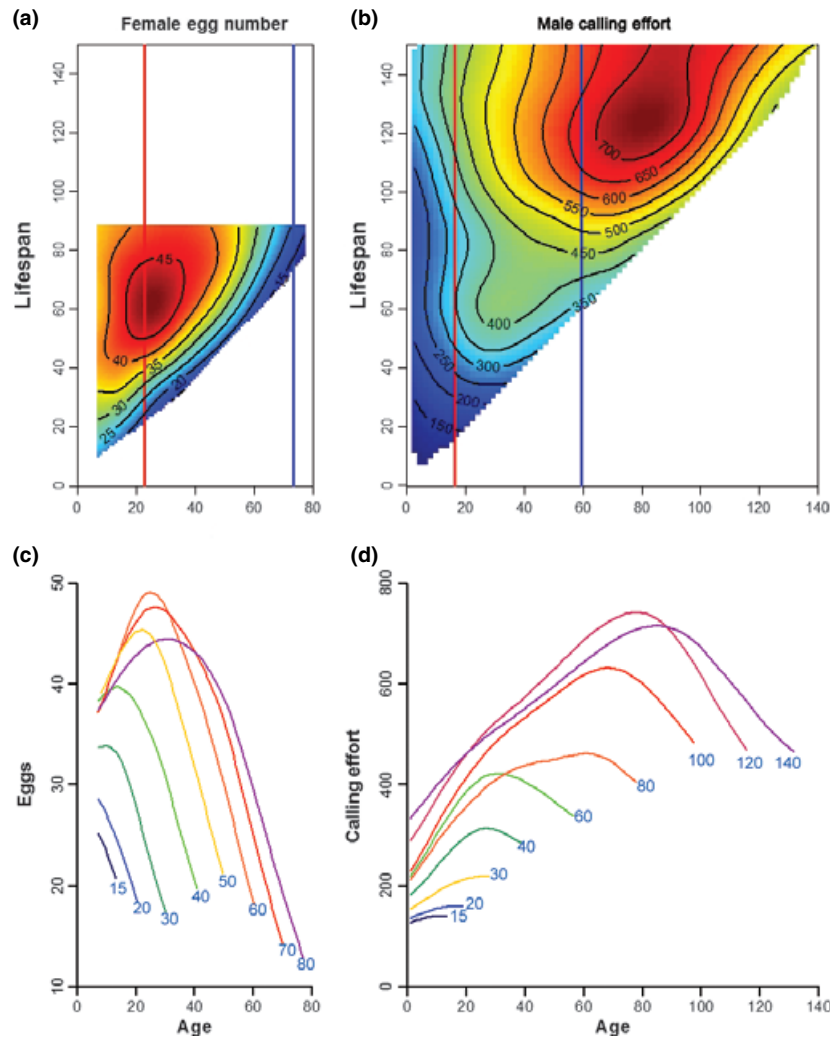
Fig. 1 Age-dependent reproductive performance in relation to dietary protein and carbohydrates. Female weekly egg laying in relation to age and dietary protein (a) and carbohydrate (c). Male calling (seconds spent calling per hour of measurement) in relation to age and dietary protein (b) and carbohydrate (d).

senescence may be expressed in wild females. In contrast to females, there is little evidence of senescence in calling rate in short-lived males (less than 40 days lifespan; Fig. 2b,d). There is modest senescence at the end of life in males that lived 40–80 days, and the most dramatic late-life decline in male reproductive performance begins at around 70–90 days for the longest-lived (lifespan > 80 days) males, well beyond the maximum estimated male lifespan in the wild (~60 days, Zajitschek *et al.*, 2009b). These results suggest that reproductive senescence may be undetectable in males in the wild population.

Calling effort represents a major reproductive investment in male crickets (Hunt *et al.*, 2004) and is under strong sexual selection in the wild because females preferentially mate with males with the highest calling effort (Hunt *et al.*, 2004). Kokko (1997) showed, theoretically, that investment in sexually selected traits is predicted to increase with age under a wide range of conditions, including those applicable to male calling in crickets. Age-dependent increase in trait expression is particularly likely when males can acquire and store resources over their adult lifetime. We have shown previously that male crickets on high carbohydrate diets tend to accumulate fat more readily than females (Maklakov *et al.*, 2008), ostensibly as storage to meet the energetic demands of future calling. Furthermore, high-quality males in Kokko's (1997) model often start advertising earlier and advertise more than low-quality males early in life, but never the other way round. This prediction is also consistent with our findings, as long-lived males on high-quality diets [low protein, high carbohydrate (Maklakov *et al.*, 2008)] called more early in life and throughout their life than short-lived males on low-quality diets (Fig. 2d).

Classic aging theory suggests that the sex that experiences a higher rate of extrinsic mortality (e.g. from sex-specific pre-

dation) will evolve a life history characterized by a higher rate of senescence (Williams, 1957). However, this hypothesis can be challenged on several grounds (Bonduriansky *et al.*, 2008). High predation or intra-sexual competition (particularly in males) may select for maintenance of good physiological condition, delaying the onset and/or decelerating the rate of senescence (Abrams, 1993). Moreover, higher extrinsic mortality and lower mean lifespan do not necessarily lead to accelerated physiological senescence if reproductive success increases with age (Reznick *et al.*, 2004; Graves, 2007). Sexual selection can result in older males gaining disproportionate access to females compared with younger males, thereby imposing strong selection on late life performance (Graves, 2007). Selection can also favour increasing reproductive effort as a response to declining survival probability. Males are expected to elevate their reproductive effort more steeply with age than females because males stand to gain more by sacrificing survival for immediate reproductive opportunity (Bonduriansky *et al.*, 2008). Male *T. commodus* have a higher extrinsic (background) mortality rate and shorter life expectancy than females in the field (Zajitschek *et al.*, 2009b), possibly because of increased exposure to predators and parasitoids while calling. However, males do not exhibit faster actuarial aging than females in the wild (Zajitschek *et al.*, 2009b), and do not exhibit detectable reproductive aging during biologically significant part of their lives in the laboratory (Fig. 2a–d). Moreover, under laboratory conditions that eliminate most extrinsic mortality sources, males substantially outlived females. (This was not due to the fact that females were mated whereas males were virgin in our study: a subsequent experiment shows that while mating significantly reduces female lifespan it does not affect male lifespan; see on-line Data S1, Tables S1 and S2, Fig. S1, Supporting

(a) Female egg number

(b) Male calling effort

(c)

(d)

Fig. 2 The relationship between lifespan and age-dependent female egg-laying (a, in eggs per week) or male calling (b, in seconds calling per night). Red lines indicate median adult lifespan and blue lines indicate maximum predicted adult lifespan for each sex, from a capture–recapture study of adults in the wild at the site where collections were made for the stock used in this study (Zajitschek *et al.*, 2009b). (c, d) Age-specific trajectories of egg-laying (females, c) and calling effort (males, d) for cohorts of individuals of different lifespans (indicated in blue numbers next to the trajectory curves).

Table 1 Results of linear and nonlinear response surface analysis of the effects of dietary protein and carbohydrate percentage, age and lifespan on reproductive effort for females (a) and males (b)

	Linear effect	Nonlinear effect			
		Protein	Carbohydrate	Age	Lifespan
a. Female fecundity					
Protein	0.401*	−0.021*			
Carbohydrate	−0.105	−0.022*	−0.018*		
Age	−2.686*	−0.039	0.002	−2.116*	
Lifespan	0.559*	0.004	−0.006	0.409*	−0.011
b. Male calling effort					
Protein	−0.985	0.026			
Carbohydrate	2.100*	−0.047	−0.098		
Age	2.752*	0.047	0.058*	−0.121*	
Lifespan	1.844*	−0.041	0.025	0.102*	−0.033

Gradients were estimated by GLMM with individual identity fitted as a random effect. Asterisks indicate significance at $\alpha = 0.05$.

Information.) Our results are consistent with the hypothesis that sexual selection drives the evolution of late-life performance in males, conferring the physiological capacity to out-

live females when males are released from the high extrinsic mortality they experience in the field. Our findings thus demonstrate that sexual selection's role in shaping the life history is key to interpreting sex differences in age-dependent trajectories of reproductive performance.

Conclusions

To conclude, we found that the pattern of age-specific reproductive performance differs dramatically between the sexes. We argue that this disparity is a result of very different forms of selection on age-specific female fecundity and male sexual advertisement. Female fecundity rapidly declined with age as predicted by the evolutionary theory of aging, whereas males showed increasing calling effort with age, and evidence of reproductive senescence was limited to very old age, as predicted by models of age-dependent sexual advertisement. Our results are consistent with two nonexclusive mechanisms: either sexual selection has resulted in delayed aging by promoting late-life performance in males, or sexual selection has favoured an age-dependent increase in male reproductive

effort that counteracts (and obscures) concomitant deterioration in reproductive capacity (i.e. aging). Our findings thus suggest that, as a consequence of sexual selection, the signal of reproductive aging may often be weaker in males than in females. This may explain why, despite the prevalence of male-biased mortality rates in many taxa, empirical studies have provided little evidence of male-biased aging rates (Bonduriansky et al., 2008). Given the theoretical and practical importance of the relationships between reproduction, diet and aging, empirical data on how natural selection and sexual selection shape age-specific reproduction and senescence across different taxa are urgently needed.

Experimental procedures

Experimental animals

The crickets used in this experiment were derived from a laboratory stock collected in February 2006 at Smith's Lakes, N.S.W and kept at UNSW. This population is maintained on cat food (Friskies Go-Cat® Senior; Nestle, Vervey, Switzerland) and water ad libitum and propagated by rearing the offspring of > 100 randomly paired adults per generation in six different containers (80 L). Both the stock population and experimental animals were kept at 28 ± 1 °C and a 10D:14L light regime.

Artificial diets

Twenty-four different dry foods that varied in protein and carbohydrate content were prepared according to established protocol (Simpson & Abisgold, 1985). The details are provided in Maklakov et al. (2008). Briefly, the diets consisted of proteins (3:1:1 mixture of casein, albumen and peptone), carbohydrates (1:1 sucrose:dextrin), Wesson's salts, ascorbic acid, cholesterol and vitamin mix. The combinations of diets used in this experiment are shown in Table 2.

Data collection

We collected females and males as final instar nymphs from the stock and assigned 8–10 of each sex at random to each of the 24 diets (see Maklakov et al., 2008).

We measured age-specific calling effort in males overnight on the third and seventh night posteclosion and then every week thereafter using an a custom-built electronic monitoring device (see Hunt et al., 2004) that monitored males from 6:00 PM to 9:00 AM. Briefly, the device consists of 64 microphones attached to the lids of male containers that are connected to the sensor; the sensor is connected to DaqBook 120, IO Tech data logger and personal computer, which is programmed to check for signal from each microphone 10 times per second. The signal is recorded as 1 when 10 dB higher than the level of background noise, otherwise as 0. Males were kept in individual containers (14 × 8.5 × 7.5 cm),

Table 2 The composition and relative ratio of protein and carbohydrate content of diets used in the experiment

Per cent composition

Protein	Carbohydrate	P + C	P:C ratio
10	2	12	5:1
30	6	36	5:1
50	10	60	5:1
70	14	84	5:1
9	3	12	3:1
27	9	36	3:1
45	15	60	3:1
63	21	84	3:1
6	6	12	1:1
18	18	36	1:1
30	30	60	1:1
42	42	84	1:1
3	9	12	1:3
9	27	36	1:3
15	45	60	1:3
21	63	84	1:3
2	10	12	1:5
6	30	36	1:5
10	50	60	1:5
14	70	84	1:5
1.33	10.66	12	1:8
4	32	36	1:8
6.66	53.33	60	1:8
9.33	74.66	84	1:8

which were then placed in styrofoam containers (23 × 17 × 12.5 cm) to keep males in acoustic isolation.

Female reproductive performance was measured by estimating their weekly fecundity rate. We mated females to random stock males on a weekly basis. After mating, each female was provided a fresh, moist sand pad into which she laid her eggs for the next week. The removed pads were stored in 95% ethanol and all eggs in a sample were counted.

Statistical analysis

We used General Linear Mixed Models (GLMM) to fit multivariate response surfaces (Lande & Arnold, 1983; Phillips & Arnold, 1989; Blows & Brooks, 2003; Chenoweth & Blows, 2005). The statistical approach that we used also relies on including lifespan as a factor in the mixed model with male identity included as a random factor when analysing age-specific performance. This statistical approach takes into account both within-individual and between-individual variation in age-specific performance within the same general model (e.g. van de Pol & Verhulst, 2006; McCleery et al., 2008). For each sex, we conducted two separate GLMM. (i) Only the linear effects of protein (P), carbohydrate (C), age (A) and lifespan (L) and (ii) adding the nonlinear effects of P, C, A and L to model 1. The estimated gradients for P, C and A were similar with lifespan included in or excluded from these models. The data were analysed in SPSS13 and

visualized using nonparametric thin-plate splines in R (version 2.5.1) [33]. Both the GLMM analyses and the thin-plate spline visualizations fit curves based on the effects of the continuous variables on all observations across the entire data set.

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Author contributions

AAM, SJS, DR, RB and RCB conceived and designed the project; AAM, MDH, JD, FC, FZ, SPL performed the experiments; AAM, MDH, FZ and RCB analysed the data; AAM, SJS, DR, FZ, SPL, RB and RCB wrote the paper.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Data S1 The effect of mating on survival of male and female crickets under different diets.

Fig. S1 Cumulative survival curves of mated (blue line) vs. virgin (green line) animals.

Table S1 The effect of diet and mating on female survival.

Table S2 The effect of diet and mating on male survival.

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