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Sex differences in the effects of juvenile and adult diet on age-dependent reproductive effort

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Abstract

Sexual selection should cause sex differences in patterns of resource allocation. When current and future reproductive effort trade off, variation in resource acquisition might further cause sex differences in age-dependent investment, or in sensitivity to changes in resource availability over time. However, the nature and prevalence of sex differences in age-dependent investment remain unclear. We manipulated resource acquisition at juvenile and adult stages in decorated crickets, *Gryllodes sigillatus*, and assessed effects on sex-specific allocation to age-dependent reproductive effort (calling in males, fecundity in females) and longevity. We predicted that the resource and time demands of egg production would result in relatively consistent female strategies across treatments, whereas male investment should depend sharply on diet. Contrary to expectations, female age-dependent reproductive effort diverged substantially across treatments, with resource-limited females showing much lower and later investment in reproduction; the highest fecundity was associated with intermediate lifespans. In contrast, long-lived males always signalled more than short-lived males, and male age-dependent reproductive effort did not depend on diet. We found consistently positive covariance between male reproductive effort and lifespan, whereas diet altered this covariance in females, revealing sex differences in the benefits of allocation to longevity. Our results support sex-specific selection on allocation patterns, but also suggest a simpler alternative: males may use social feedback to make allocation decisions and preferentially store resources as energetic reserves in its absence. Increased calling effort with age therefore could be caused by gradual resource accumulation, heightened mortality risk over time, and a lack of feedback from available mates.

Introduction

An individual's lifetime fitness is a function of its early reproductive rate, the pattern of change in reproductive rate with age and lifespan (Bonduriansky *et al.*, 2008). Fitness is thought to be optimized through age-specific selection on the allocation of acquired resources to current and future reproduction; males and females are predicted to be subject to different sexual selection pressures, however, causing divergence between the sexes in the optimal pattern of resource allocation (Promislow, 2003; Graves, 2007; Bonduriansky *et al.*, 2008).

The limiting factors for achieving reproductive success are also expected to be sex-specific, with females typically constrained by the resources and time requirements of constructing eggs, whereas male mating success is mediated more by competition with other males for access to females (Bateman, 1948; Trivers, 1972; Andersson, 1994). Females should generally adopt fairly low-risk strategies of resource investment and engage in less risky behaviour than males (Wedell *et al.*, 2006). In many species, fathers invest less in each offspring than do mothers, in part so that resources may be redirected towards acquiring additional mates (Trivers, 1972). Reproductive effort is predicted to increase

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with age (because reproduction is increasingly the best option for resource investment when the risk of mortality from intrinsic sources grows; Kirkwood, 1977), and males may also sacrifice longevity in favour of increased allocation to current reproductive effort (Vinogradov, 1998). Theoretical models have demonstrated circumstances in which males with greater access to resources invest disproportionately in costly sexual traits to the extent that they suffer lower survival rates than males with fewer resources (Kokko, 1997, 1998; Höglund & Sheldon, 1998; Kokko *et al.*, 2002; Hunt *et al.*, 2004b). Despite this theory, a trade-off between reproductive effort and lifespan in males is not often discernible in empirical data: most studies report that preferred males also survive the longest (Jennions *et al.*, 2001; but see also Hunt *et al.*, 2004a; Robinson *et al.*, 2006). One possible explanation is that differences in resource acquisition ability ('condition', *sensu* Rowe & Houle, 1996) mask this trade-off within populations, because males with high levels of resource acquisition invest heavily in both reproduction and survival (Van Noordwijk & De Jong, 1986; Reznick *et al.*, 2000; Roff & Fairbairn, 2007).

Current acquisition ability is also likely to be heavily influenced by prior allocation (e.g. during the juvenile stage) to traits involved in gathering or processing food. Environmental conditions encountered during juvenile development could, therefore, have long-term repercussions (Grafen, 1988; Metcalfe & Monaghan, 2001; Monaghan, 2008). Discerning the effects of diet manipulations at specific life stages can be difficult (e.g. Scheuber *et al.*, 2003). The only way to study the relationship between juvenile and adult acquisition is by manipulating diet across these life stages, which clarifies the separate effects of stage-dependent investment on fitness-related traits (Whattam & Bertram, 2011). As males and females should optimize fitness in different ways, changes in nutritional requirements with development are also likely to be sex-specific (Maklakov *et al.*, 2008). Applying juvenile and adult diet manipulations to both sexes can therefore help assess whether differences in sexual selection have led to divergence across the sexes in allocation strategies.

Crickets are ideal organisms for studying sex-specific patterns of survival and reproductive investment, primarily because we can easily measure age-dependent reproductive effort in both sexes. Male crickets produce an energetically costly long-range calling song through stridulation of their wings (Kavanagh, 1987; Hunt *et al.*, 2004a), and a male's calling effort is a strong predictor of mating success (Hunt *et al.*, 2004a; Bentsen *et al.*, 2006; Rodríguez-Muñoz *et al.*, 2010). Female reproductive effort can be quantified by counting the number of eggs produced (Zajitschek *et al.*, 2007). The costs of reproductive effort are likely to differ between the sexes, and recent studies using several cricket species have shown that males and females exhibit dramatically different patterns of reproductive ageing (Maklakov *et al.*, 2009; Zajitschek *et al.*, 2009c, 2012; Archer *et al.*, 2012).

The relationship between resource acquisition, reproductive effort and ageing in crickets appears complex and depends on sex and context. Among males, a pattern of increasing calling effort until later ages is widespread across several species (Judge *et al.*, 2008; Maklakov *et al.*, 2009; Zajitschek *et al.*, 2009c; Archer *et al.*, 2012), and reproductive effort and lifespan are genetically correlated in *Teleogryllus commodus* and *Gryllodes sigillatus* (Zajitschek *et al.*, 2007; Archer *et al.*, 2012). However, male crickets can follow distinct diet-dependent allocation strategies (Hunt *et al.*, 2004a), and artificial selection experiments have demonstrated antagonistic pleiotropy between calling effort and longevity in male *T. commodus* under some environmental conditions (Hunt *et al.*, 2006). The nutrient requirements for optimizing fitness in crickets are sex-specific, with increased protein intake augmenting egg production in females, whereas increased carbohydrate or overall caloric intake leads to higher calling effort in males (*T. commodus*: Maklakov *et al.*, 2008; *Gryllus veletis*: Harrison *et al.*, 2014). Unlike males, patterns of age-dependent reproductive effort in female crickets appear to be less dependent on diet: female fecundity typically peaks early in adulthood and then declines (Zajitschek *et al.*, 2009a; Archer *et al.*, 2012), and this pattern appears to hold irrespective of nutritional manipulations (Maklakov *et al.*, 2009; Zajitschek *et al.*, 2009c). Further work is needed to investigate whether investment patterns depend on individual condition.

In this study, we investigate the effect of juvenile and adult diet on patterns of allocation to life history traits in both sexes of the decorated cricket *G. sigillatus*. We manipulate nutrient content to vary resource acquisition among males and females at both the juvenile and adult stages and examine the consequences for allocation to development, reproductive effort and survival. For both sexes, we predicted that nutrient-rich diets at the juvenile stage would result in individuals developing to adulthood at larger size and at a faster rate. However, we expected to see divergence between male and female patterns of investment in reproductive effort at adulthood: sex differences in the strength of sexual selection, in tandem with age-specific selection, might result in dramatic differences in age-dependent reproductive effort (Bonduriansky *et al.*, 2008). We predicted that the resource and time demands of egg production among females – giving relatively lower returns on resource investment per unit of time – would result in moderate ('live slow, die old') strategies, with those given access to nutrient-rich diets peaking earlier or sustaining higher levels of reproductive effort. In contrast, we predicted that male investment should depend sharply on diet: whereas nutrient-deprived males should increase calling effort with age, nutrient-rich

adult males should sacrifice longevity for greater early reproductive effort.

Materials and methods

Cricket maintenance

Gryllodes sigillatus used in this study were descended from 500 adult crickets collected in Las Cruces, New Mexico, in 2001, and used to initiate a laboratory culture maintained at a population size of approximately 5000 crickets and allowed to breed panmictically (Ivy & Sakaluk, 2005). New genetic material was introduced periodically from cultures at other institutions. Crickets were housed in a 15-L plastic container in an environmental chamber maintained at 32 ± 1 °C on a 14-:10-h light/dark cycle. Crickets were provided with a standard diet of ground cat food (Friskies Go-Cat Senior®; Purina, London, UK) and water in 60-mL plastic test tubes plugged with cotton wool *ad libitum*, in addition to egg cartons for shelter. As soon as adults were detected, moistened cotton wool was provided in a petri dish (10 cm diameter) as an oviposition substrate. Each generation was maintained at a density of approximately 300 crickets per container.

Experimental design

We used two different diet treatments to manipulate resource acquisition in experimental subjects. These diets were defined by high and low levels of a range of nutrients – particularly protein – and were selected on the basis of their similarity to diets used in previous studies of life history allocation in crickets (Hunt *et al.*, 2004a; Judge *et al.*, 2008; Zajitschek *et al.*, 2009c). Diet treatments used in nutritional geometry studies to target specific nutrient combinations precisely (e.g. Maklakov *et al.*, 2008, 2009; Harrison *et al.*, 2014) were not suitable for our experiment as juvenile crickets cannot be reared on them (J. Hunt, pers. comm.). The high-nutrient, protein-rich diet (H) consisted of 100% ground dry cat food (Purina, 32% protein), the standard diet on which our laboratory stocks are maintained. The low-nutrient, protein-poor diet (L) was a mixture comprising 50% ground dry cat food and 50% ground oatmeal (Aberfeldy Oatmeal, 11% protein).

We collected 360 cricket nymphs within 24 h of hatching from eggs harvested from laboratory stock cultures. Nymphs were assigned randomly to either diet treatment ($N = 180$ for each juvenile diet treatment) and reared individually in clear plastic containers (5 × 5 × 5 cm) containing a piece of egg carton as shelter, a water bottle plugged with cotton wool and the food treatment *ad libitum*. We cleaned the cricket containers weekly, providing each individual with fresh food and water.

From the fifth larval instar onwards, we checked individuals daily for eclosion to adulthood. On the day of eclosion, we measured body mass using a high-precision electronic balance (Denver Instrument, model PI-225DA) and photographed individuals through a microscope (Motic, model SMZ-168 equipped with Moticam 2000) to obtain measurements of pronotum length using NIH ImageJ software (Schneider *et al.*, 2012). We calculated body condition at eclosion for each cricket using the scaled mass index (Peig & Green, 2009, 2010), with mean and scaling exponent calculated separately for each sex.

We assigned each newly eclosed individual at random to an adult diet, resulting in 4 lifetime diet treatment groups: HH, HL, LH and LL (with the first letter designating the juvenile diet and the second the adult diet). Individuals in treatment groups HH and LL were maintained on the same diet at both juvenile and adult life stages; those in treatment groups HL and LH were switched to the alternate diet following eclosion to adulthood. We maintained adults in the same manner as nymphs and checked each individual daily for survival.

Measuring male age-dependent reproductive effort

We quantified male reproductive effort as his 'calling effort', the duration of time (in seconds) that each individual spent broadcasting his long-distance sexual advertisement call. We measured each male cricket overnight for 12 h every 7 days, beginning at 7 days post-eclosion, until death. On the day of measurement, we replaced the lid of each male's container with a lid in which a microphone (C1163, Dick Smith Electronics) was mounted; we then placed each container into a hollowed-out cube of sound-proofing foam to minimize outside disturbance and ensure there was no crosstalk between containers. An electronic acoustic recording system (Bertram & Johnson, 1998) sampled from the microphone of each individual cricket container 10 times per second to determine whether or not a male was calling.

Measuring female age-dependent reproductive effort

We quantified female reproductive effort as the number of eggs produced in a 4-week period after mating. We gave each female the opportunity to mate 7 days after eclosion, by housing her with a single random stock male overnight. Mated females were provided with moist cheesecloth as a substrate for oviposition immediately after being separated from the male. We collected eggs and provided new cheesecloth every 7 days, beginning at 7 days after mating, for a total of 4 weeks.

Statistical analysis

We performed all statistical analyses using R 3.0.2 (R Core Team, 2013). For generalized linear models

(GLMs) and generalized linear mixed models (GLMMs), categorical input variables such as sex, juvenile diet and adult diet were coded using binary dummy variables to aid interpretation of standardized coefficients (Gelman & Hill, 2007). Numeric input variables such as age or lifespan were standardized by centring (subtracting the mean) and scaling (dividing by 2 standard deviations), putting them on a common scale with each other and with the binary predictors, and aiding the interpretation of main effects (Gelman & Hill, 2007; Gelman, 2008; Schielzeth, 2010). Independence between linear and quadratic forms of numeric predictors (e.g. age and age^2, lifespan and lifespan^2) was achieved by standardizing the input variable before squaring (Gelman & Hill, 2007).

Unless otherwise stated, model simplification was performed by dropping nonsignificant terms from the full model sequentially and using an *F*-test (lifespan) or chi-squared test (survival, lifetime reproductive effort) to compare the new model with the previous one. We retained more complex models whenever simplification resulted in a significant increase in model deviance. Further details of individual analyses are provided in Appendix S1.

Adult survival and lifetime reproductive effort

We also used Cox regression survival analysis to build separate survival curves for different combinations of sex and treatment group.

For males, lifetime reproductive effort was the sum of all measurements of their nightly calling effort; for females, it was the total number of eggs laid within the 4-week period after mating. We estimated the effects of diet treatment and lifespan on lifetime reproductive effort separately for each sex using generalized linear models with negative binomial error distributions.

Age-dependent reproductive effort

We used the R package MCMCglmm (Hadfield, 2010) to separately determine for each sex the effects of juvenile diet, adult diet, age at measurement, lifespan, and interactions between these predictors on age-dependent reproductive effort.

Female weekly egg count measurements were analysed using the 'Poisson' family in MCMCglmm, which handled the overdispersion of the data automatically. Weekly male calling effort was overdispersed and zero-inflated, and no data transformation adequately addressed both problems. For this analysis, we fitted a zero-altered Poisson (ZAP) model, a two-part model that includes a logistic regression for the zeroes in the data and a Poisson regression for the zero-truncated counts. The use of a ZAP model enabled us to ask two separate questions (Atkins *et al.*, 2013): which factors affect whether there is calling or no calling (i.e. zero or nonzero), and which affect the amount of calling when it occurs?

Visualization of age-dependent reproductive effort

Graphic representations of the relationship between weekly reproductive effort measurements, diet treatment and lifespan were created by fitting nonparametric thin-plate spline contour plots separately for each sex, using the Tps function in the R package fields (Furrer *et al.*, 2009).

Results

Of the 320 nymphs reared individually from hatching, 205 eclosed to adulthood successfully: this represents 99 from the high-nutrient (H) diet, and 106 from the low-nutrient (L) diet, altogether comprising 100 males and 105 females. We found no significant effect of diet treatment on survival to eclosion ($\chi^2_1 = 0.489$, $P = 0.485$; proportion surviving $\pm$ binomial S.E.: L = 0.663 $\pm$ 0.037, H = 0.619 $\pm$ 0.038). The proportion of individuals surviving to eclosion was not dissimilar to that found in similar studies, although more typically there is a (frequently nonsignificant) trend towards greater survival among those on higher quality diets (Hunt *et al.*, 2004a; Judge *et al.*, 2008; Zajitschek *et al.*, 2009c). Of the 99 crickets surviving to eclosion on the H diet, 57 were female and 42 were male; of the 106 on the L diet, 48 were female and 58 were male. We found no significant skew in the sex ratio of those surviving to eclosion overall or in each diet (overall: $\chi^2_1 = 0.122$, $P = 0.727$; H diet: $\chi^2_1 = 2.273$, $P = 0.132$; L diet: $\chi^2_1 = 0.943$, $P = 0.331$).

Male lifetime diet treatments had the following sample sizes: LL = 27, LH = 31, HL = 24, and HH = 18. The asymmetry in treatment group size was due to individuals being assigned a new diet randomly upon reaching eclosion. A single male (diet HH) died prior to the first call effort recording, and another 3 (1 each of LL, LH and HH) did not call at all during measurement periods; these 4 males were therefore excluded from the analysis of reproductive effort, leaving a total of 96. Three females died prior to mating (one each of diets LH, HL and HH); the remaining 102 make up the following sample sizes: LL = 22, LH = 25, HL = 33, and HH = 22. A further 15 females failed to lay any eggs throughout the 4-week period and were excluded from the analysis of reproductive effort, leaving a total of 87 remaining: LL = 16, LH = 23, HL = 29, and HH = 19. Models retaining females with zero fecundity were qualitatively similar and are not presented here.

Juvenile development rate and adult morphology

Sex explained most of the variation in developmental rate and adult morphology (pronotum length and scaled mass index, SMI) at eclosion ($F_{3,201} = 323.950$, $P < 0.001$), and there was also a significant effect of diet treatment ($F_{3,201} = 3.610$, $P = 0.014$). Juvenile crickets reared on the high-nutrient juvenile diet

treatment group (H) had greater pronotum lengths and weighed more than those in the low-nutrient (L) group, although univariate ANOVAs showed that within-sex diet effects were only significant in males (male pronotum length: low nutrient = 2.362 ± 0.025 mm, high nutrient = 2.438 ± 0.028 mm, $F_{1,98} = 4.131$, $P = 0.045$; female pronotum length: low nutrient = 2.768 ± 0.029 mm, high nutrient = 2.806 ± 0.033 mm, $F_{1,103} = 0.726$, $P = 0.396$; male SMI: low nutrient = 0.194 ± 0.010, high nutrient = 0.234 ± 0.013, $F_{1,98} = 6.023$, $P = 0.016$; female SMI: low nutrient = 0.246 ± 0.013, high nutrient = 0.274 ± 0.016, $F_{1,103} = 1.856$, $P = 0.176$). High-nutrient diet males tended to have a higher rate of development to eclosion than did low-nutrient males (1/days from hatching to eclosion), but this was not significant (male development rate: low nutrient = 0.0200 ± 0.0005, high nutrient = 0.0212 ± 0.0005, $F_{1,98} = 3.060$, $P = 0.083$; female development rate: low nutrient = 0.0206 ± 0.0004, high nutrient = 0.0211 ± 0.0005, $F_{1,103} = 0.678$, $P = 0.412$).

Univariate ANOVA showed no significant difference between the sexes in the rate at which they developed to adulthood, regardless of diet (development rate between-sex differences: low nutrient = 0.00059, $F_{1,104} = 0.956$, $P = 0.331$; high nutrient = 0.00006, $F_{1,97} = 0.007$, $P = 0.935$). Females were larger and had greater SMI than males at eclosion in both diet treatment groups (pronotum length between-sex differences: low nutrient = 0.406 mm, $F_{1,104} = 114.0$, $P < 0.001$; high nutrient = 0.369 mm, $F_{1,97} = 66.180$, $P < 0.001$; SMI between-sex differences: low nutrient = 0.052, $F_{1,104} = 10.640$, $P = 0.002$; high nutrient = 0.041, $F_{1,97} = 3.520$, $P = 0.064$).

Adult survival and lifetime reproductive effort

Cox regression survival analysis showed no significant effects of juvenile diet quality, adult diet quality, sex or any interactions on survival, either before or after model simplification (Table S1).

Total lifetime male calling effort was best described by a simplified model with a single significant term, a positive linear effect of lifespan (1.051 ± 0.214, $z_{1,95} = 4.922$, $P < 0.001$). The lack of significant interactions between lifespan and diet treatment indicates that longer-lived males called more during their lifetime, but that the relationship between lifespan and total lifetime calling effort did not depend on diet. As males that live longer had more opportunities to call, we ran a model with mean calling effort (an individual's total calling effort divided by the number of measurements taken) as the response variable (and the same set of predictors) to investigate whether longer-lived males also called more per night on average. After removal of a single outlier (see Appendix S1 for details), the final model showed a positive linear relationship whereby longer-lived males called more on average per night (0.598 ± 0.210, $z_{1,94} = 2.853$, $P = 0.004$; Figure S1).

The final model for total female egg production also required removal of a single outlier; the effect of lifespan in this model was curvilinear, such that total fecundity increased with lifespan to intermediate values, but decreased at higher values (lifespan = 1.642 ± 0.325, $z_{1,85} = 5.055$, $P < 0.001$; lifespan^2 = −2.425 ± 0.396, $z_{1,85} = -6.123$, $P < 0.001$; Fig. 1). The linear effect of lifespan depended on adult diet (−1.749 ± 0.461, $z_{1,85} = -3.794$, $P < 0.001$): total fecundity increased with lifespan at a lower rate for

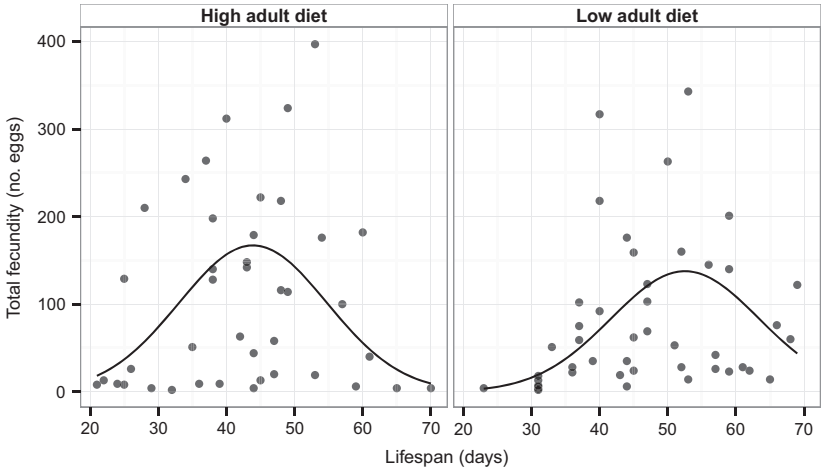

Fig. 1 Total female fecundity plotted against lifespan, separately for high- and low-quality adult diets (pooled across juvenile diet treatments). Lines are predicted slopes from a negative binomial regression with a second-order polynomial (see text for further details), showing the change in total fecundity as a function of lifespan: overall, females of intermediate lifespan have higher fecundity independent of adult diet. Females assigned to the high-nutrient adult diet have peak total fecundity at lesser lifespans, whereas a fecundity benefit of long lifespan is only evident in females on low-nutrient adult diet.

females on high-nutrient adult diet. The main effect of high-nutrient adult diet on fecundity was significantly positive (0.471 ± 0.216, $z_{1,85} = 2.175$, $P = 0.030$). These effects are manifest in females fed a high-nutrient adult diet having peak total fecundity at earlier ages and a fecundity benefit to long lifespan only in low-nutrient adult diet females.

Age-dependent reproductive effort

Male

The final model for age-dependent calling consisted of two parts, one of which (the zero-altered component) described aspects affecting the likelihood of calling (as opposed to remaining silent), whereas the other (a Poisson model) described the intensity of calling among males that called. The whole model included juvenile and adult diet treatments and both linear and quadratic forms of the standardized age term, as well as all interactions between these; it also included the standardized lifespan term and an interaction between age and lifespan (Table 1). By retaining lifespan in the model, a portion of change in performance can be described as within-individual ageing (Van de Pol & Verhulst, 2006). Although there were several significant interactions (described further below) affecting both the probability of calling and the intensity of effort per night, the patterns of age-dependent calling effort were similar across diet treatments: calling increased with age, and longer-lived males called more at all ages (Fig. 3).

In the zero-altered part of the model, a positive significant term indicates that a variable predicts reduced likelihood of zeroes, whereas a negative significant term indicates an excess of zeroes (zero inflation) (Hadfield,

Table 1 Results from mixed model analysis of male weekly calling effort (using the 'zero-altered Poisson' distribution specified with MCMCglmm). Fixed effects are shown separately for the zero-altered and Poisson parts of the final model; random effects are presented as variance components. The baseline category for diet treatment group is LL (*e.g.* 'juvenile diet (H)' indicates treatment group HL).

Fixed effects	Estimate	95% CI (lower, upper)	*P*
Zero-altered			
(Intercept)	0.194	(−0.255, 0.745)	0.316
Juvenile diet (H)	−0.230	(−1.305, 0.646)	0.568
Adult diet (H)	0.026	(−0.946, 0.877)	0.961
Juvenile diet (H) × adult diet (H)	−0.438	(−1.772, 1.153)	0.663
Age	−0.940	(−1.985, −0.007)	0.045*
Age^2	0.438	(−1.689, 1.971)	0.802
Juvenile diet (H) × age	1.257	(0.008, 2.792)	0.041*
Juvenile diet (H) × age^2	−1.975	(−4.237, 0.589)	0.110
Adult diet (H) × age	−0.372	(−1.890, 0.497)	0.253
Adult diet (H) × age^2	−0.668	(−2.917, 1.686)	0.644
Juvenile diet (H) × adult diet (H) × age	−1.459	(−3.598, 0.314)	0.124
Juvenile diet (H) × adult diet (H) × age^2	3.529	(0.273, 6.812)	0.041*
Lifespan	−0.066	(−0.846, 0.631)	0.810
Lifespan × age	0.747	(−0.561, 2.026)	0.317
Poisson			
(Intercept)	6.417	(5.981, 6.824)	<0.001***
Juvenile diet (H)	0.198	(−0.605, 0.661)	0.905
Adult diet (H)	0.304	(−0.314, 0.837)	0.310
Juvenile diet (H) × adult diet (H)	−0.036	(−0.818, 0.961)	0.944
Age	0.244	(−0.361, 0.908)	0.399
Age^2	−1.361	(−2.601, −0.065)	0.059
Juvenile diet (H) × age	−0.503	(−1.352, 0.461)	0.323
Juvenile diet (H) × age^2	2.512	(0.243, 3.503)	0.019*
Adult diet (H) × age	0.354	(−0.591, 1.006)	0.457
Adult diet (H) × age^2	0.248	(−1.238, 1.858)	0.693
Juvenile diet (H) × adult diet (H) × age	0.670	(−0.611, 2.018)	0.300
Juvenile diet (H) × adult diet (H) × age^2	−2.847	(−4.904, −0.591)	0.015*
Lifespan	0.406	(−0.083, 0.808)	0.087
Lifespan × age	0.947	(−0.127, 1.556)	0.092

Variance components	Estimate	95% CI (lower, upper)
Zero-altered		
ID	0.587	(0.194, 1.059)
Poisson		
ID	0.251	(0.097, 0.576)
Residual	1.718	(1.514, 2.080)

*$P < 0.05$, *$P < 0.01$, ***$P < 0.001$.

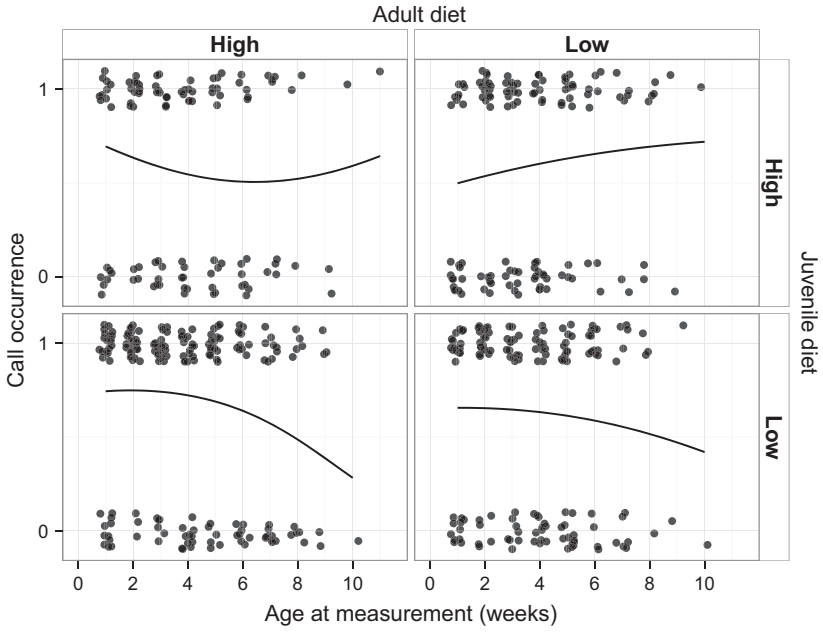

Fig. 2 Age-dependent binary call occurrence data (0 = no call, 1 = call) with fitted binomial GLM quadratic regression slope, separately for each diet treatment (HH, top left; HL, top right; LH, bottom left; LL, bottom right).

2010); positive main effects can therefore be read as increasing the likelihood of recording a call, whereas negative main effects indicate decreased likelihood of calling. The zero-altered part of the model showed that the age-related response of male call likelihood depends on both juvenile diet and adult diet (Table 1, Fig. 2). The significant interaction between the quadratic age term and diet treatment at both stages is manifest in the curvature of the response among HH males, where the likelihood of calling levels off after an initial decreases. The main linear effect of age was to decrease the likelihood of calling with age, but this was dependent on juvenile diet: the likelihood of calling increased with age among males in diet group HL (Fig. 2).

The Poisson part of the model predicts the calling effort when males did call. The effect of age on calling effort depended on both juvenile and adult diet treatments: males that had access to the high-quality diet at juvenile and adult stages (HH) decreased calling effort at later ages, although this was only evident among longer-lived males (Table 1, Fig. 3). Males fed the high-quality diet at only the juvenile stage (HL) increased calling effort sharply at later ages. The main effect of the quadratic age term was marginally nonsignificant

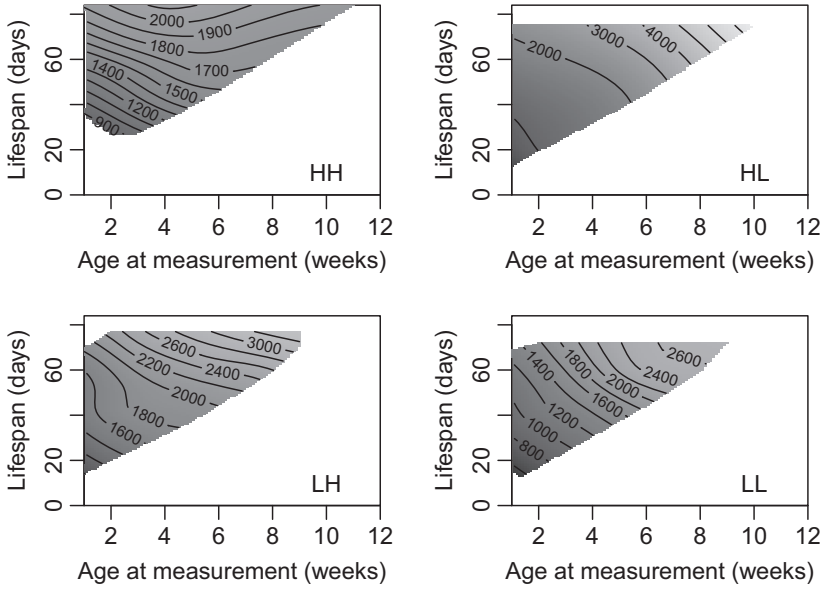

Fig. 3 Age-dependent male calling effort in relation to lifespan, excluding zero calls and plotted separately for each lifetime diet treatment combination (HH, top left; HL, top right; LH, bottom left; LL, bottom right). Lighter shades represent higher values.

and showed that the rate of increase in male calling effort tended to slow at later ages. Lifespan and the interaction between lifespan and measurement age also had marginally nonsignificant positive effects, suggesting that longer-lived males tended to call more and that the effect of age was especially acute in longer-lived males.

Female

The final model for weekly female egg production indicated that the effect of lifespan depended on both juvenile diet and adult diet (Table 2). Because there were no 3-way interactions between juvenile diet, adult diet and age, we pooled the adult diet treatments in Fig. 4a (to illustrate the effects of juvenile diet) and the juvenile treatments in Fig. 4b (to illustrate the effects of adult diet). Juveniles provided with a high-protein diet tended to show marked senescence, with their highest egg outputs early during life (Fig. 4a). Furthermore, in this treatment, females who lived longest had the highest fecundity. In the low-protein juvenile diet treatment, by contrast, fecundity during weeks 2–5 increased as a function of age and was negatively related to longevity. The effects of adult diet on age-specific fecundity were notably different (Fig. 4b). Females on high-protein diets tended to senesce (were most fecund early in life), but longevity in this treatment covaried negatively with fecundity during weeks 2–5. In the low-protein diet treatment, fecundity did not seem to depend strongly on age, but was positively correlated with total lifespan.

Discussion

Consuming a nutrient-rich juvenile diet resulted in larger and heavier adults of both sexes, as well as increasing the rate of development to adulthood, but without imposing differential mortality during this period. Both male and female crickets exhibited distinct effects of diet quality on how they allocated resources to reproductive effort across their lifespan. Male crickets displayed a positive relationship between lifespan and calling effort, with longer-lived males calling more overall and on average regardless of diet. We also found a positive relationship between weekly calling effort measurements and lifespan across all diets, as well as between calling, lifespan and age, indicating that longer-lived males called more each night and increased their calling with age at a higher rate than other males. Unlike males, in females, we found differences across diets in both the presence and pattern of reproductive senescence, as well as in the covariance between longevity and fecundity. Whereas most other studies have shown diet-dependent plasticity in males, here we report intriguing changes in the age-dependent patterns of investment by females due to variation in resource acquisition.

Male life history strategies

Resource acquisition at both juvenile and adult stages affected the precise trajectories of age-dependent calling effort in males, yet the overall patterns among calling males were strikingly similar: calling effort increased with age, and longer-lived males called more. These

Fixed effects	Estimate	95% CI (lower, upper)	*P*
Poisson			
(Intercept)	0.382	(−1.145, 1.956)	0.635
Juvenile diet (H)	−1.044	(−3.036, 0.954)	0.289
Adult diet (H)	0.150	(−1.985, 2.188)	0.909
Juvenile diet (H): adult diet (H)	1.314	(−1.380, 4.409)	0.364
Age	3.593	(1.479, 5.859)	0.001***
Age^2	−1.859	(−6.666,3.164)	0.470
Lifespan	0.566	(−1.467, 2.864)	0.618
Juvenile diet (H): age	−3.288	(−5.802, −0.504)	0.016*
Juvenile diet (H): age^2	3.577	(−2.525, 10.033)	0.268
Juvenile diet (H): lifespan	0.240	(−2.529, 3.138)	0.855
Adult diet (H): age	−2.952	(−5.758, −0.287)	0.030*
Adult diet (H): age^2	1.392	(−4.969, 7.998)	0.673
Adult diet (H): lifespan	−1.163	(−4.506, 1.823)	0.468
Juvenile diet (H): adult diet (H): age	2.093	(−1.403, 6.071)	0.267
Juvenile diet (H): adult diet (H): age^2	−5.507	(−14.870, 2.794)	0.208
Juvenile diet (H): adult diet (H): lifespan	−0.386	(−4.620, 3.306)	0.847
Variance components	Estimate	95% CI (lower, upper)	
ID	0.142	(0, 0.537)	
Residual	12.500	(9.316, 15.940)	

Table 2 Results from mixed model analysis of female weekly fecundity (using the 'Poisson' distribution specified with MCMCglmm). Fixed effects are shown for the final model; random effects are presented as variance components. The baseline category for diet treatment group is LL (*e.g.* 'juvenile diet (H)' indicates treatment group HL).

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

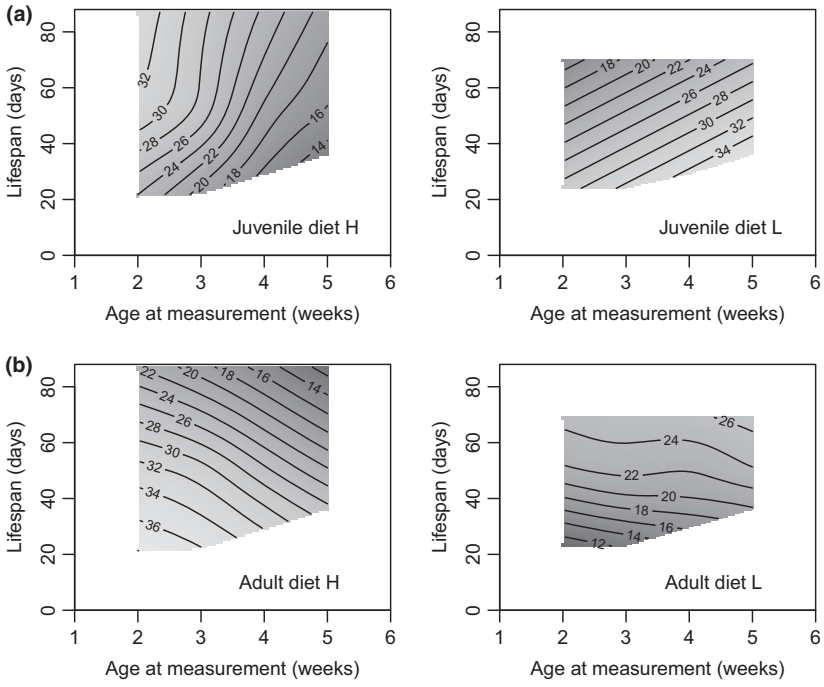

Fig. 4 The effect of (a) juvenile and (b) adult diet on age-dependent female reproductive effort (weekly egg counts) in relation to lifespan. (a) High-nutrient juvenile diet, left; low-nutrient juvenile diet, right. Data are pooled across adult diet treatment groups (*i.e.* high juvenile diet = HH + HL; low juvenile diet = LH + LL). (b) High-nutrient adult diet, left; low-nutrient adult diet, right. Data are pooled across juvenile diet treatment groups (*i.e.* high adult diet = HH + LH; low adult diet = HL + LL). Lighter shades represent higher values.

results conform to the hypothesis that the marginal benefits of investment in reproductive effort (rather than survival) increase with age (Kirkwood, 1977), and other studies that indicate covariance between secondary sexual trait expression and longevity (Jennions *et al.*, 2001). Using a zero-altered model, we were able to assess – within a single statistical framework – the effects of these variables on not only the amount of calling effort when a male called, but also the likelihood of a male to call. Whereas overall patterns indicate age-related increases in calling effort, and a positive correlation between lifespan and total calling effort, these patterns mask more subtle differences between individuals in how resources are invested in reproductive effort.

Calling effort levels among males on the low-nutrient diet as juveniles increased with age, yet the likelihood of actually recording a call decreased. Such patterns suggest these males may have been saving resources for less frequent but more intense bouts of calling (perhaps due to low reserves from the juvenile stage that might otherwise underpin adult energy requirements). By contrast, males assigned to the HL treatment increased both their likelihood and amount of calling with age; decreased acquisition in adulthood might lead individuals to invest more in current reproductive effort to compensate for their lowered future reproductive value in comparison with high-condition individual. Whattam & Bertram (2011) found that male *Gryllus assimilis* assigned to a low-quality adult diet produced more calling bouts per night on average than those on high-quality diets, a possible indicator of efficacy-based selection: frequent and vigorous display is required when females are unpredictable in space and time (Ryan & Cummings, 2005).

Our statistical separation of the likelihood of calling and the amount of calling also mirrors the integral difference between the sexes in how they accumulate fitness through reproductive effort. For females, the equation is generally straightforward: fecundity is amassed by the gathering of resources and the time required for converting these resources to useful forms. For males, resource acquisition is also a strong requirement for investment in energetically costly signalling, but allocation decisions are subject to greater uncertainty. Male reproductive success first requires the presence of available and willing females; optimal signalling then depends both on an individual's condition and the competition that he faces at any time (Houston & McNamara, 1987; Kokko, 1997; Lindström *et al.*, 2009). Males therefore need to sample the social environment far more than do females, which may select for strong phenotypic plasticity in male signalling decisions (Bretman *et al.*, 2011). Our results show that males exhibit acquisition-related plasticity in both when and how much to call, and previous studies have shown that manipulation of the competitive social environment induces plasticity of cricket calling behaviour: perceived future competition (Kasumovic *et al.*, 2012) and the presence of rivals (Callander *et al.*, 2013) both affect how males invest in calling effort. In other species that are able to alter signalling behaviour dynamically, males invest more when females are present (Mappes *et al.*, 1996)

or are of higher quality (Wong & Svensson, 2009), yet such factors have thus far been ignored in studies of investment in reproductive effort by male crickets.

Honesty in signalling

Despite being assigned to the nutrient-poor diet as adults, HL males recorded the highest overall single measurements of weekly calling effort. However, this was restricted to a few long-lived individuals at late measurement ages. Theory predicts that low-quality males can signal 'dishonestly' if some proportion of condition can be transferred from one age to the next: suppression of signalling at earlier ages by low-quality males enables the storage of unused resources for later use, such that these males could have higher trait expression value at some late age than that of high-quality males (Kokko, 1997). In line with predictions from Kokko's model (Kokko, 1997), Hunt *et al.* (2004a) showed that male *T. commodus* on a low-protein diet delayed the onset of calling compared to males fed a medium- or high-protein diet, gaining more weight during this period and then calling more at late ages than other males. The proportion of these 'dishonest' males in the population should be small due to age-related increases in mortality rates; females selecting a male with a high trait value will therefore most likely obtain a high-quality male, regardless of the apparent mismatch between calling effort and quality late in the season.

Female life histories

While female crickets fed the high-nutrient juvenile diet were larger and heavier than those fed the low-nutrient diet, these differences were smaller than between-diet effects in males and were not statistically significant. We also found no effect of juvenile diet on lifespan or total reproductive effort. Female field (*G. veletis*) and black field crickets (*T. commodus*) are more dependent on protein (one of the main differences between our diet treatments) than are males for maximizing reproductive effort (Maklakov *et al.*, 2008; Harrison *et al.*, 2014); here, low-quality diet females may have increased their feeding rate at the juvenile stage to compensate for the lower protein content of their diet. Adult diet did affect the coefficients describing the relationship between lifespan and total fecundity among females, but did not change its overall shape: in line with predictions, the highest levels of fecundity were achieved by individuals of intermediate age. These patterns suggest that the best female allocation strategies are moderate, with equal investment between reproduction and survival being optimal due to the limiting factors of the nutrients and time required to construct eggs.

Although overall investment in survival and reproduction was similar across diets, age-dependent fecundity in females differed markedly depending on both juvenile and adult diet. These differences were not predicted, but there are some plausible explanations for them. Females fed a high-quality diet at the juvenile stage displayed increased fecundity early in life and senesced rapidly; accumulated protein may have enabled these individuals to build more eggs early in adulthood, with metabolism then declining as a function of reproductive activity. By contrast, low-nutrient juvenile diet females probably eclosed to adulthood with less protein for building eggs and therefore required more time as adults to accumulate resources. Differences in the covariance between fecundity and lifespan across treatments are likely due to changes in the marginal value of investment across traits that trade off: for example, the negative covariance among females fed a low-quality diet may be due to diverting resources to extending survival for more time to accumulate and convert resources to eggs.

Females that were fed high-nutrient adult diets showed high initial fecundity, presumably because of access to greater amounts of protein at early adulthood. As with those fed a high-nutrient diet as juveniles, this group showed rapid reproductive senescence, which may be due to negative effects of reproductive activity. Such effects would also explain why those with high early fecundity also exhibited reduced survival. Fecundity in females fed a low-nutrient adult diet was reduced compared to other diets and showed little change with age, suggesting that low diet females cannot accumulate enough protein to mature more eggs. Equal investment in both survival and reproductive effort would enable individuals to live longer to gather enough resources to build more eggs.

Sex differences may arise from sex-specific selection pressures

While the overall pattern among males was to increase calling with age, females exhibited reproductive senescence on some diet treatments. Male calling patterns were consistent with several previous studies of age-dependent reproductive effort in crickets (Judge *et al.*, 2008; Maklakov *et al.*, 2009; Zajitschek *et al.*, 2009c, 2012; Archer *et al.*, 2012). In females, we found that the effects of high-quality diet at juvenile and adult stages were similar, increasing early fecundity but with senescent effects on reproductive effort shortly thereafter (a pattern also consistent with previous studies of age-dependent reproductive effort in crickets; Maklakov *et al.*, 2009; Zajitschek *et al.*, 2009c; Archer *et al.*, 2012). The relationship between lifespan and both total and age-dependent reproductive effort indicate differences between the sexes in the potential benefits of allocation to longevity. In males – regardless of

diet – lifespan and total calling were positively correlated, and the longest-lived males called the most at any given age. Peak calling effort also tended to occur beyond the average lifespan (median male adult lifespan: 46.5 ± 2.39 days). In contrast, total female fecundity was highest in those that lived to intermediate ages, and there was no consistent relationship between age-dependent reproductive effort and lifespan among females. Furthermore, fecundity among females fed a high-quality diet at either juvenile or adult stage peaked early, well before the average lifespan (median female adult lifespan: 44.0 ± 1.80 days). Similar results were shown in the study by Maklakov *et al.* (2009), who used median and maximum predicted adult lifespan from a separate study of wild crickets (Zajitschek *et al.*, 2009b) to show that *T. commodus* female median lifespan occurred around peak fecundity, whereas male calling effort peaked beyond the maximum predicted lifespan in the wild. The marked differences between male and female patterns of age-dependent reproductive effort suggest that optimal resource allocation is driven by sex-specific selection pressures.

Conclusions

Calling effort is an important determinant of mating success in male crickets (Hunt *et al.*, 2004a; Bentsen *et al.*, 2006; Rodríguez-Muñoz *et al.*, 2010), and we found that males – regardless of dietary treatment at either the juvenile or adult stage – tended to increase their effort with age, with this trend continuing beyond the average lifespan. Our results, along with those of Maklakov *et al.* (2009), lend support to the hypothesis that sexual selection drives the evolution of increased male performance in later life (Graves, 2007). However, given that longer-lived males called most in all treatment groups, another possible explanation for such a trend is that female choice for increased calling effort exerts directional selection on male condition. Selection might then favour genes with positive pleiotropic effects on lifespan and whole-organism performance (Lailvaux & Irschick, 2006). Positive genetic correlations between lifespan and measures of calling effort at several ages have been found previously in male *G. sigillatus* (Archer *et al.*, 2012); manipulating resource acquisition in genetically related individuals would help simultaneously assess genetic and environment-dependent male plasticity in allocation. Furthermore, the importance of female cues on how male crickets allocate resources to signalling effort has thus far been largely neglected in the literature and could yield greater insights into whether age-related increases in calling are due to strategic decisions or are governed more by residual reproductive value.

The positive correlations between reproductive effort and lifespan in males should not, perhaps, be surprising: within-treatment variation in male quality can cause some individuals to have more resources to spend on all fitness-enhancing traits (Van Noordwijk & De Jong, 1986; Reznick *et al.*, 2000). This begs the question of why positive correlations between reproductive effort and lifespan are not seen in females. One potential explanation stems from studies of field crickets (*T. commodus* and *G. veletis*), which showed that both reproductive effort and longevity could be maximized using similar nutritional profiles in males; by contrast, females maximized reproductive effort via protein intake and longevity via carbohydrates (Maklakov *et al.*, 2008; Harrison *et al.*, 2014). Variation in male quality in our study might therefore be related to sheer metabolic efficiency, where the ability to acquire and convert resources to an all-purpose store enables positive correlations between life history traits. Females, meanwhile, are constrained by particular nutrient mixtures in how they maximize fitness, resulting in a necessary compromise between reproduction and longevity, which is ameliorated or deepened depending on the particular sequence and composition of diets through development.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Further details of statistical analyses.

Figure S1 Total lifetime calling effort plotted against lifespan (pooled across all diet treatments). Shown is the predicted slope with 95% confidence intervals from a negative binomial regression (see text for further details): longer-lived males call more overall, regardless of diet.

Table S1 Cox regression survival analyses. Complete full factorial model (i) and effects of juvenile and adult diets in males and females (ii, iii). χ^2 for full model, Wald for separate variables.

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