

Female Mate Choice as a Condition-Dependent Life-History Trait

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ABSTRACT: The acquisition of resources is an important determinant of patterns of variation in and covariation among traits that are costly to produce and are dependent on condition for their expression. However, the extent to which variation in female mate choice behavior is condition dependent, and how this is related to other life-history traits, remains largely unknown. We manipulated the acquisition of dietary protein in the black field cricket, *Teleogryllus commodus*, and measured the effects of this on several important life-history traits and on female mate choice behavior. Females reared on a high-protein diet developed faster, were heavier at eclosion, and lived longer than females reared on a low-protein diet. Two lines of evidence suggest that female mate choice behavior in *T. commodus* is condition dependent. First, females reared on the high-protein diet were more sexually responsive and expressed stronger linear and quadratic preference functions for call rate and dominant frequency, respectively. Second, within treatments, females that developed faster were lighter, generally less sexually responsive, and, in the high-protein-diet treatment, expressed weaker preferences than slower-developing females. Collectively, our findings suggest an important role for resource acquisition in generating variation in mate choice behavior.

Keywords: life history, condition dependence, mate choice, sexual responsiveness, preference function, *Teleogryllus commodus*.

Variation in behavior that influences mate choice occurs not only among populations (Verrell 1999) but also within populations (Jennions and Petrie 1997; Widemo and Sæther 1999) and across an individual's lifetime (Moore and Moore 2001). Mate choice is a powerful agent of sexual selection (Andersson 1994), and variation in mate choice has several important evolutionary consequences (Jennions and Petrie 1997; Badyaev and Qvarnström 2002; Rodriguez and Greenfield 2003). Despite this, the causes of individual variation in mate choice behavior and how it is related to life-history trade-offs by females remain poorly understood.

Until recently, evolutionary biologists have tended to study the evolution of both female mate choice and male sexual traits in relative isolation from the rest of the organism (Partridge and Endler 1987; Kokko 1998; Badyaev and Qvarnström 2002). Several recent empirical (Gustafsson et al. 1995; Kokko et al. 1999) and theoretical (Kokko 1997a, 1998; Kokko et al. 2002) studies have, however, shown that the costs that are integral to sexual traits functioning as signals of quality (Zahavi 1975; Grafen 1990) are best understood through their effects on residual reproductive value. This has generated renewed calls for life-history theory to be integrated into the study of sexual signaling (Höglund and Sheldon 1998; Badyaev and Qvarnström 2002).

Like male sexual traits, female choice is expected to be costly, and these costs are central parameters in models of the evolution of mating preferences (Pomiankowski 1987; Houle and Kondrashov 2002; Kokko et al. 2002). Although the costs of mate choice are notoriously difficult to measure directly (Kotiaho 2001), several innovative studies have measured (Backwell and Passmore 1996) or experimentally manipulated (Milinski and Bakker 1992; Hedrick and Dill 1993; Markow and Clarke 1997; Gray 1999; Moore and Moore 2001; Wong and Jennions 2003) the costliness of choice to demonstrate that females are less discriminating when the costs of mate choice increase. Our understanding of mate choice decisions should therefore also benefit when viewed as an investment into one of many life-history traits (Badyaev and Qvarnström 2002).

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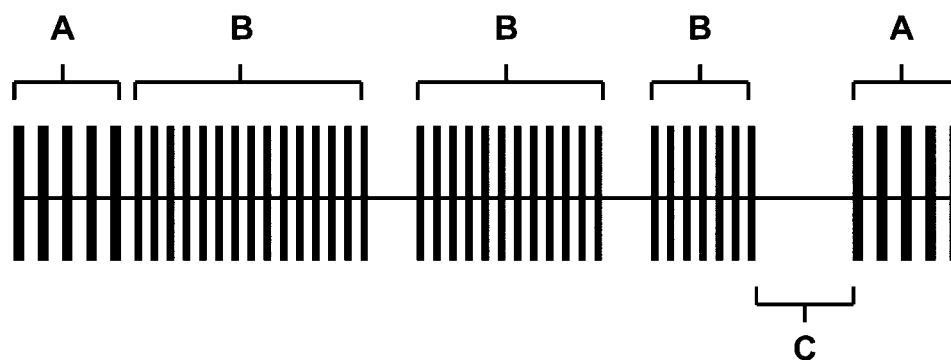


Figure 1: Schematic representation of the advertisement call of *Teleogryllus commodus*. Each call comprises a chirp (A) followed by one or more trills (B). We manipulated the call rate by varying the intercall interval duration (C) or the dominant frequency of the call (not shown on figure). All other call parameters were kept constant.

Condition dependence is a major source of within-population variation in the expression of costly sexual traits (Andersson 1986; Grafen 1990; Rowe and Houle 1996), with important implications for investment of resources into other life-history traits. Following Rowe and Houle (1996), we define condition as the pool of resources an individual has available to allocate to life-history traits. There is now strong evidence from several species that condition dependence lies at the heart of the trade-off between costly sexual traits and other major fitness components such as survival and growth (Kotiaho 2001; Kotiaho et al. 2001; Hunt et al. 2004a, 2004b; Tomkins et al. 2004). There are fewer tests, however, of how condition influences female mate choice decisions (Jennions and Petrie 1997; Widemo and Sæther 1999).

The outcome of female mate choice (i.e., which male or males a female mates with) is a product of both female willingness to invest in choice (choosiness sensu Jennions and Petrie 1997) and the shape of the female preference function. It is possible that condition dependence may generate variation in both aspects of mate choice (Jennions and Petrie 1997; Wagner 1998; Widemo and Sæther 1999; Brooks and Endler 2001). Indeed, empirical studies demonstrate that condition influences both the investment a female is willing to make in assessing and responding to males in general (Poulin 1994; Simmons 1994; Markow and Clarke 1997; Ortigosa and Rowe 2002; Cratsley and Lewis 2003; Syriatowicz and Brooks 2004) and the strength of preferences that females express toward certain male phenotypes (e.g., Brown 1997; Bakker et al. 1999; López 1999; Hingle et al. 2001a, 2001b; Mazzi 2004).

Condition-dependent variation in mate choice may have important evolutionary implications both within and among populations (Jennions and Petrie 1997; Rolff 1998; Wagner 1998; Pfennig and Tinsley 2002). Variability

among individuals in the shape, direction, or strength of their preference functions can potentially influence the form, direction, and intensity of sexual selection in the population as a whole (Jennions and Petrie 1997; Widemo and Sæther 1999). When there is individual variation in preference functions, the net population preference function may differ markedly from that of individual females. For example, differences among individuals in directional linear preference functions may lead to a population-level preference function that generates stabilizing, frequency-dependent (Partridge and Hill 1984; Potts et al. 1991; Lesna and Sabelis 1999), or disruptive (Turner and Burrows 1995) selection.

In the black field cricket, *Teleogryllus commodus*, males broadcast an advertisement call from a simple burrow structure to attract a mate (Loher and Rence 1978; Evans 1988). The advertisement call begins with a single chirp sequence followed by a variable number of trill sequences that are repeated at a faster rate (fig. 1; Bentley and Hoy 1972; Hill et al. 1972). Female preference for call structure has been extensively studied in *T. commodus*, and both temporal (Loftus-Hills et al. 1972; Pollack and Hoy 1979, 1981) and spectral call properties (Hill 1974; Hennig and Weber 1997) are important in eliciting positive female phonotaxis.

Here we investigated how condition influences both female mate choice decisions and key life-history traits in *T. commodus*. We reared offspring from hatching on diets that differed in protein content and measured several life-history traits that are related to the acquisition and allocation of condition. We then conducted phonotaxis trials to measure female sexual responsiveness and preferences for calls that differed in either dominant frequency or call rate. This allowed us to test for the effects of female condition on female responsiveness and both a directional

(call rate) and a stabilizing (dominant frequency) preference function (Brooks et al. 2005).

Methods

Experimental Animals

Crickets used in this experiment were the third-generation descendents of approximately 200 adult female *Teleogryllus commodus* collected at Smith's Lake (32°22'S, 152°30'E), New South Wales, Australia, in March 2002. Field-collected females were isolated in individual plastic containers (5 cm × 5 cm × 5 cm) and were provided with commercially produced cat food (Friskies Go-Cat Senior), water, and a petri dish containing moist cotton wool for egg laying. Cultures were maintained by rearing the offspring of 100 randomly created adult pairs per generation in six stock culture containers (80 L) in a constant-temperature room at 28° ± 1°C with a 14L : 10D light regime. At the start of the experiment, we collected 600 nymphs within 24 hours of hatching and randomly assigned each to a low-, medium-, or high-protein diet (= 200 nymphs/diet).

Experimental Manipulation of Female Condition

We experimentally manipulated female condition by varying the protein content of their diet through their life span (from hatching until death). We varied protein content of the diet by producing food pellets with different mixtures of high-protein fish-rearing pellets (Pisces Enterprises, 45% protein) and oatmeal (Farmland, 12% protein). The high-, medium-, and low-protein-diet treatments consisted of a dry weight mixture of 100%, 75%, or 50% fish-rearing pellets to oatmeal. We created food pellets by grinding fish pellets and oatmeal and then adding water and placing the mixture into a custom-built Plexiglas mold in a drying oven at 60°C for 12 hours. This produced dry pellets with an average weight of 121 ± 2 mg.

Each nymph was reared in an individual plastic container (5 cm × 5 cm × 5 cm) and was provided with water, three diet pellets, and a piece of egg carton for shelter. Food and water were replenished weekly and the container cleaned and nymph survival recorded. On reaching the fifth instar, nymphs were checked daily for eclosion. On eclosion, all females were weighed using an electronic balance, and pronotum widths were measured using an eyepiece graticule in a binocular microscope. A total of 64, 80, and 66 females eclosed from the low-, medium-, and high-protein-diet treatments, respectively. Adult females were kept in their original containers until their use in phonotaxis trials 10 days after their eclosion. During

this period, females were provided with water and their treatment diet and were weighed every second day.

Condition Dependence of Female Mate Choice

To examine the condition dependence of female mate choice, we randomly assigned 10-day-old females to two experiments. Each experiment consisted of a series of phonotaxis trials in which females were given a choice between a standard and a focal call. The calls were identical in structure, with the exception of the trait being examined, which was either dominant frequency or call rate. To create the standard call, we used the mean call properties from a sample of males recorded at 20° ± 2°C. In the dominant frequency experiment, the focal call had a dominant frequency that differed from the standard call by -3, -2, -1, 1, 2, or 3 SD. In the call rate experiment, we altered the duration of the intercall interval to be either -1 (highest call rate), 1, 2, 3, 4, or 5 (lowest call rate) SD from that of the standard call. The actual dominant frequency and call rate values of focal calls are presented in figures 5 and 7.

We synthesized calls using CoolEdit Pro (version 1.2). The standard and focal calls were created on separate channels of a stereo computer file and played back to females as a continuous loop. The sound files were saved in an AIFF format. In the dominant frequency experiment, calls were presented alternately. In the call rate experiment, the relative start times of the two calls changed throughout the loop, and the starting point in the loop was assigned haphazardly to remove any consistent "leader-follower" effects (e.g., Dyson and Passmore 1988; Dyson et al. 1994; Greenfield 1994).

We broadcast calls using SoundEdit 16 software (version 2.0) on a G3 Macintosh computer connected to two Koss HD50 speakers. The two speakers were positioned centrally on opposite sides of a 106 × 106-cm arena with their surface flush against the arena walls. The arena was fitted with sound insulation acoustic foam to reduce reverberation. A BOSS BA-250 audio amplifier was used to ensure that calls had an amplitude of 75 dB (RMS) at the center of the arena. A Radio Shack sound pressure-level meter (catalog no. 33-2055) was used before every trial to calibrate the peak amplitude of both calls. The sound pressure-level meter was set to fast response time and a C weighting.

Trials were conducted under red light to minimize observer disturbance and at the same temperature at which male calls were originally recorded (20° ± 2°C). The female was first placed in the center of the arena under a piece of egg carton (which acted as a refuge) and a plastic container (5 cm × 5 cm × 5 cm) with mesh sides. The calls were then played for 1 min before we lifted the plastic

Table 1: Descriptive statistics (mean \pm SE) examining the effect of diet on female life-history traits

	Treatment means			Univariate tests	
	High protein	Medium protein	Low protein	<i>F</i>	<i>P</i>
Pronotum width (mm)	6.82 (.03)	6.91 (.04)	6.85 (.03)	1.63	.199
Mass at adult eclosion (g)	.733 (.011)	.714 (.011)	.682 (.12)	6.66	.002
Mass at 10 days posteclosion (g)	.918 (.018)	.822 (.16)	.772 (.16)	20.60	.000
Development time (days)	96.9 (1.4)	100.0 (1.3)	114.8 (2.0)	28.06	.000
Adult survival (days)	53.2 (1.9)	46.8 (1.5)	33.8 (1.5)	28.43	.000
<i>N</i>	64	80	62		

Note: Standard errors are provided in parentheses. For univariate tests, $df = 2, 203$. MANOVA: Pillai's trace = 0.569, $F = 15.90$, $df = 10, 400$, $P = .000$.

container. An observer then watched the female until she entered the 6.5-cm radius semicircular choice zone in front of a speaker or 20 min had elapsed. On the rare occasion (23 out of 1,248 trials) when a female did not respond to the call stimuli within 20 min, she was tested later on the same day to the same call stimuli. In each instance, when a female was retested, she responded and expressed a preference for one call. When a female responded (entered the choice zone), we noted her preferred call and her response time (the time taken to enter the choice zone).

Each female was used in six phonotaxis trials run over consecutive days. Both trial order per female and the side of the arena from which the standard call was broadcast in the first trial were randomized. We then alternated which speaker broadcast the standard call for the remaining five trials. Moreover, the order in which females were tested on a given day was randomized with regard to diet. Because each female was tested with all six focal calls, we could calculate both individual females' preference functions and treatment mean preference functions. We obtained measures from 101 females (32 high-, 39 medium-, and 30 low-protein diet) in the dominant frequency trials and 105 females (32 high-, 41 medium-, and 32 low-protein diet) in the call rate trials.

Statistical Analysis

We scored a female's preference as -1 (standard call preferred) or 1 (focal call preferred). We also calculated a weighted preference score, which incorporated a female's responsiveness. The weighted preference score was calculated by multiplying a female's absolute preference score by the following weighting factor:

$$\text{weighting} = \frac{1}{\sqrt{t}} - \frac{1}{\sqrt{1,200}},$$

where t is the individual female's response time. This time-weighted preference score is normally distributed. A rapid

response to the standard call gives the lowest possible score (-1), a very slow response to either call gives a score close to 0, and a rapid response to the focal call gives the highest possible score (1).

We calculated the mean preference functions (both absolute and time weighted) for each treatment by taking the mean preference score for each stimulus and fitting a first-order (call rate experiment) or a second-order polynomial (dominant frequency experiment) regression to the relationship between female preference and the call values. Our justification for treating preference functions as coefficients from first- and second-order polynomials was the finding of strong directional and stabilizing selection on call rate and dominant frequency in an earlier study on this population (Brooks et al. 2005). We estimated individual preference functions by fitting separate regressions for each female using her time-weighted scores as the response variable. The linear preference coefficient is the linear coefficient from a simple linear regression. The quadratic coefficient was estimated from a regression model including both linear and quadratic terms. This method is similar to that described by Brooks and Endler (2001).

We used MANOVA with Type III sums of squares to test an effect of diet treatment on life-history measures. We then used MANOVA to test for effects of diet treatment and life-history covariates on female mean response time and individual linear and quadratic preference functions in each of the two phonotaxis experiments. We used hierarchical (Type I) sums of squares in these MANOVA models because we wished to first test for treatment effects and then for the effect of fitting covariates and treatment by covariate interactions. To satisfy assumptions of homogeneity of variances, we transformed preference coefficients by adding a constant to make all values positive and then log transformed them.

To test whether there were significant differences between diet treatments in their effect on preference functions (both linear and quadratic), we employed random-

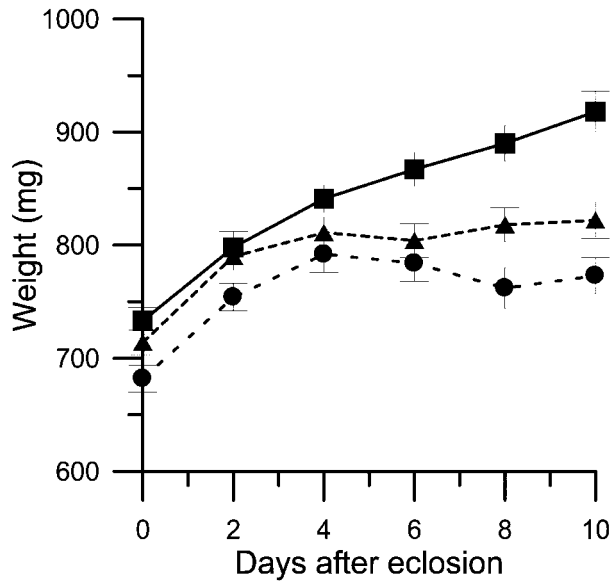


Figure 2: Acquisition of body weight in the first 10 days posteclosion for females reared on the high- (squares, solid line), medium- (triangles, large-dashed line), and low- (circles, small-dashed line) protein diets. The phonotaxis trials on individual females started on day 10 posteclosion.

ization tests. In each test, we randomly drew (with replacement) response scores from the original distribution of values from the behavior experiment 9,999 times. We then calculated the stimulus mean values and the linear and quadratic preference coefficients for each treatment. To provide a two-tailed probability for each contrast, we calculated the number of times we would expect to see pairwise differences in coefficients equal to or larger than the observed differences.

Results

Condition Dependence of Life-History Traits

With the exception of adult pronotum width, diet treatment significantly influenced all measured life-history traits (table 1). Nymphs were more likely to survive to eclosion when reared on higher-protein diets (Hunt et al. 2004a). Females reared on a high-protein diet matured faster, lived longer as adults (Cox regression, $\text{Wald}_2 = 63.44$, $P < .001$; all pairwise contrasts $P < .01$), and were consistently heavier at eclosion than those from lower-protein diets (table 1). Females reared on the high-protein diet were 7% heavier at eclosion than those reared on the low-protein diet, and they were heavier relative to their body size (ANCOVA, diet: $F = 21.50$, $df = 2, 206$, $P < .0001$). They also increased in weight faster after eclosion and for a longer period

than those reared on the medium- and low-protein diets. After 10 days, high-protein-diet females were 19% heavier than those reared on the low-protein diet (fig. 2; repeated-measures ANOVA, diet \times day: $F = 4.62$, Greenhouse-Geisser $df = 5.92, 609.4$, $P < .001$).

Across diet treatments, faster development was associated with greater body mass (table 1), but within each diet treatment, females that matured faster were lighter at eclosion (univariate ANCOVA, diet: $F = 5.69$, $df = 2, 204$, $P = .004$; development time: $F = 11.90$, $df = 1, 204$, $P = .001$; fig. 3). The slope of the relationship between development time and longevity did not differ among diet treatments (ANCOVA, diet treatment \times development time: $F = 0.8$, $df = 2, 208$, $P = .419$). Both across and within diet treatments, females that developed faster lived longer as adults (fig. 4; ANCOVA, diet: $F = 20.3$, $df = 2, 210$, $P = .0001$; development time: $F = 4.2$, $df = 1, 210$, $P = .041$). Neither weight at eclosion nor weight at 10 days after eclosion explained a significant amount of variation in longevity.

Female Preference for Dominant Frequency

On average, females showed a preference for calls with an intermediate to high dominant frequency. In all three diet

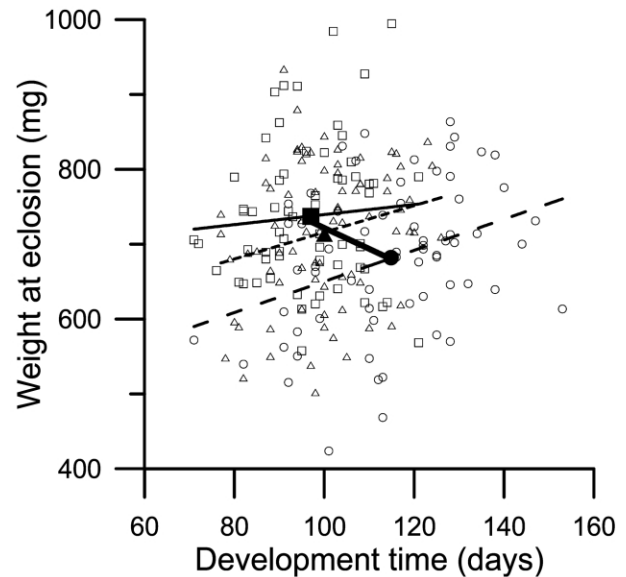


Figure 3: Relationship between female development time and body weight at eclosion. Although there is a negative relationship between development time and body weight across diet treatments (filled symbols, thick line), this relationship is positive within each of the three diet treatments. Squares, solid line = high-protein diet; triangles, large-dashed line = medium-protein diet; circles, small-dashed line = low-protein diet.

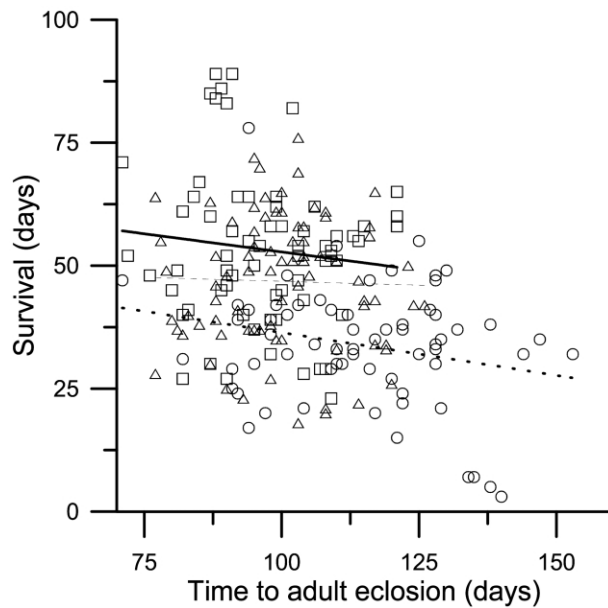


Figure 4: Influence of diet and development time on the adult longevity of females. Squares, solid line = high-protein diet; triangles, dashed line = medium-protein diet; circles, dotted line = low-protein diet.

treatments, the most preferred call had a frequency of 3.96 KHz, which is 1 SD higher than the population mean dominant frequency (i.e., the standard call; population-level preference functions are in fig. 5). The three diet treatments did not differ in the most preferred dominant frequency (randomization tests, all pairwise comparisons $P > .5$). Time-weighted linear preference gradients were stronger in the high- and medium-protein treatments than in the low-protein treatment (fig. 5*b*; high- vs. low-protein diet, $P = .0001$; medium- vs. low-protein diet, $P = .006$; high- vs. medium-protein diet, $P > .05$), but there was no difference among diet treatments in the absolute linear preference gradients (fig. 5*a*; all $P > .05$). Moreover, the quadratic preference gradient that describes the curvature about the preferred dominant frequency was stronger in the higher-protein treatments than the low-protein treatment (absolute preference: high- vs. low-protein diet, $P = .006$; other contrasts, $P > .05$; time-weighted preference: high- vs. low-protein diet, $P = .002$; medium- vs. low-protein diet, $P = .004$; high- vs. medium-protein diet, $P > .05$).

Our diet treatments had significant effects on all individual measures of female mate choice (table 2; fig. 6). Females reared on the high-protein diet responded more rapidly, had stronger linear preferences for calls of higher frequency, and also expressed stronger stabilizing (concave-down) preference functions, as illustrated by their more negative quadratic preference scores.

Development time was the only life-history trait that was significantly associated with mate choice, but its effect on response time differed between the diet treatments. Faster-developing females in the high- and medium-protein-diet treatments responded more slowly, but this was not the case for females in the low-protein-diet treatment (fig. 6). There was also a marginally nonsignificant difference among diet treatments in the effect of development time on females' linear preference functions ($P = .07$). Slower-developing females fed a low-protein diet tended to express weaker linear preferences, whereas there was a weak relationship in the opposite direction for females on high- and medium-protein diets (fig. 6).

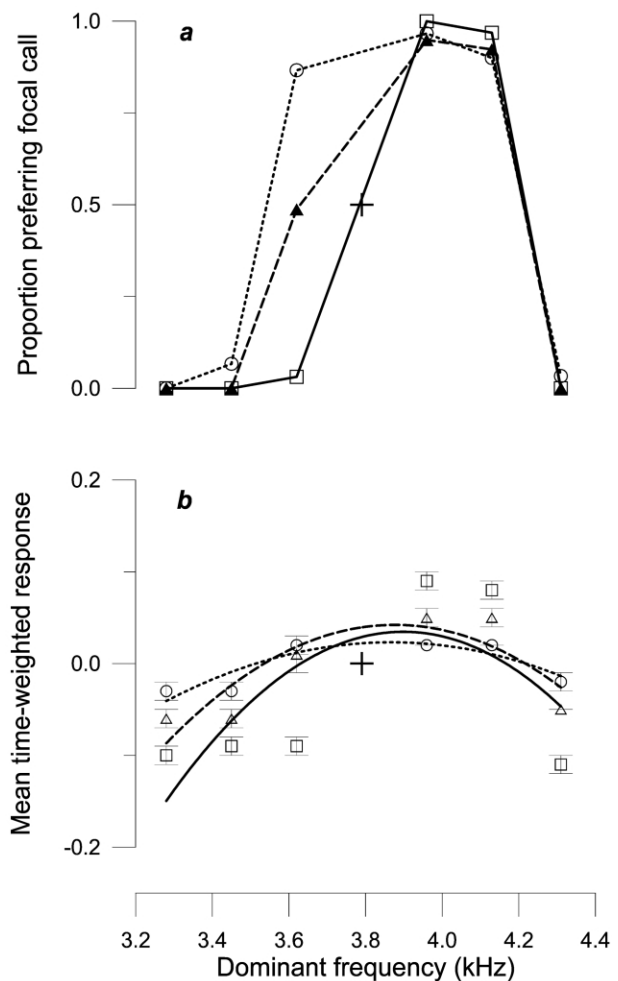


Figure 5: Mean preference functions for dominant frequency by females in each of the three diet treatments. *a*, Proportion of females that chose the focal call over the standard call. *b*, Mean time-weighted preference for the focal call over the standard call with second-order polynomial fitted. Squares, solid line = high-protein diet; triangles, large-dashed line = medium-protein diet; circles, small-dashed line = low-protein diet.

Table 2: MANCOVA examining the effects of diet and life-history covariates on the three components of female mate choice in the dominant frequency preference trials

	Multivariate tests		
	Diet treatment	Development time	Treatment × development time
Pillai's trace	.810	.011	.198
<i>F</i>	21.31	.33	3.45
df	6, 188	3, 93	6, 188
<i>P</i>	.000	.804	.003
	Univariate tests		
	df	<i>F</i>	<i>P</i>
Source and dependent variable:			
Diet treatment:			
Mean response time	2, 95	143.53	.000
Linear preference function β	2, 95	15.69	.000
Quadratic preference function γ	2, 95	9.32	.000
Development time:			
Mean response time	1, 95	.650	.422
Linear preference function β	1, 95	.072	.789
Quadratic preference function γ	1, 95	.040	.842
Treatment × development time:			
Mean response time	2, 95	8.89	.000
Linear preference function β	2, 95	2.79	.066
Quadratic preference function γ	2, 95	.82	.444

Female Preference for Call Rate

On average, females on all three diets preferred a higher call rate (fig. 7). The linear preference gradient for higher call rate was strongest for females on the high-protein diet and weakest for those on the low-protein diet (randomization tests: absolute preference: high- vs. low-protein diet, $P = .0001$; medium- vs. low-protein diet, $P = .001$; high- vs. medium-protein diet, $P = .836$; time-weighted preference: high- vs. low-protein diet, $P = .0001$; medium- vs. low-protein diet, $P = .0001$; high- vs. medium-protein diet, $P = .011$; fig. 7). There were similar differences in the quadratic preference gradients across diet treatments, with a positive curved preference function for the population reared on a high-protein diet and negative curved preference functions for the population reared on a low-protein diet (absolute preference: all contrasts, $P < .001$; time-weighted preferences: high- vs. medium-protein diet, $P = .006$; high- vs. low-protein diet, $P < .001$; medium- vs. low-protein diet, $P < .1$).

Consistent with the trend at the diet treatment level of analysis, individual females on the high-protein diet responded most rapidly and had the strongest linear preference gradients for high call rates (fig. 8; table 3). There were also significant differences in individual females' quadratic preference gradients among treatments. Females on the high-protein diet had more concave preference func-

tions (positive coefficients), whereas females on the medium- and low-protein diets tended to have convex functions (negative coefficients).

Again, development time was the only life-history variable that was significantly associated with individual females' mate choice behavior (table 3; fig. 8). Within each diet treatment, faster-developing females responded more slowly and showed a marginally nonsignificant trend ($P = .08$) to express more positive quadratic preference functions (fig. 8). The effect of development time on linear preference functions differed among diet treatments (fig. 8; table 3). There was no relationship for low-protein-diet females, but for high-protein-diet females, those that developed more slowly had stronger linear preference functions.

Discussion

Dietary protein significantly influenced important life-history traits and several key aspects of female mate choice behavior in the black field cricket, *Teleogryllus commodus*. Our results are the first to demonstrate simultaneous effects of female condition on both choosiness (measured as how long a female listened to calls before responding) and preference functions (which calls they chose; Jennions and Petrie 1997). Moreover, we demonstrated condition

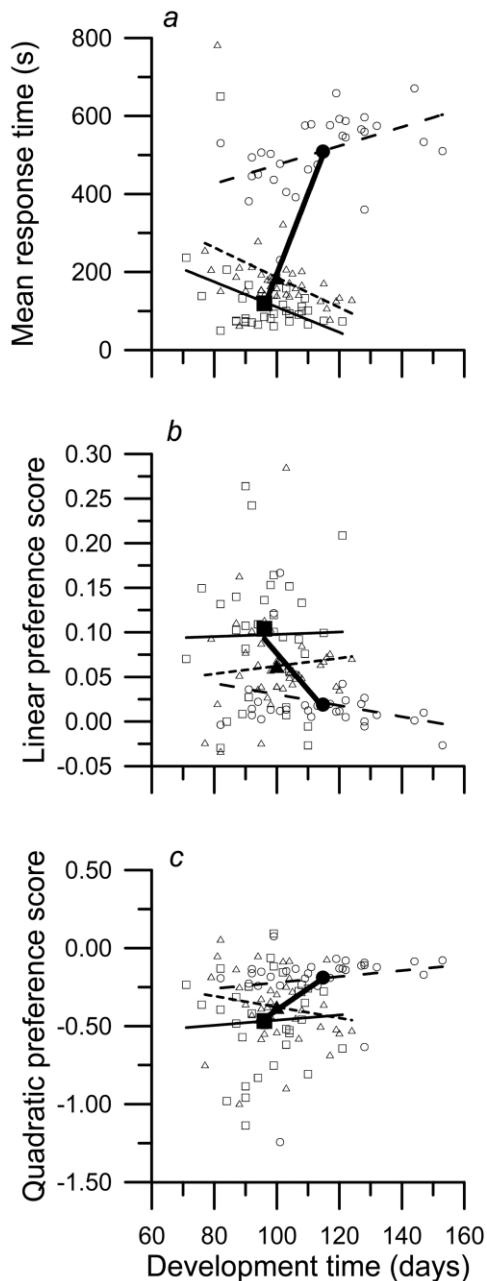


Figure 6: Influence of diet and development time on (a) mean response time, (b) linear preference coefficients, and (c) quadratic preference coefficients of individual females in the dominant frequency experiment. Multivariate and univariate significance tests of diet treatment, development time, and their interactions are presented in table 2. *Squares, solid line* = high-protein diet; *triangles, large-dashed line* = medium-protein diet; *circles, small-dashed line* = low-protein diet. The filled symbols and thick solid line represent the relationship between measures of mate choice and development time across diet treatments.

dependent of both a preference that exerts directional selection (for call rate) and one that exerts stabilizing selection (for dominant frequency) on male call structure.

The Acquisition and Allocation of Resources to Life-History Traits

Early discussions of the importance of condition to sexual selection used the term to summarize the general health and vigor of an individual (Andersson 1982, 1986; Nur and Hasson 1984; Charlesworth 1987; Zeh and Zeh 1988). More recently, however, Rowe and Houle (1996) placed condition within the context of life-history theory by narrowing the definition to the total pool of resources that is available to allocate to fitness-related traits. While many subsequent authors have highlighted the value of a life-history perspective to studying condition dependence (Badyaev and Qvarnström 2002; Hunt et al. 2004b; Tomkins et al. 2004), only a few empirical studies of mate choice have accomplished this goal (Cotton et al. 2004). Ours is the first study to simultaneously examine the relationship among female condition, mate choice behavior, and other important life-history fitness components, such as development rate, adult life span, and adult weight gain, that are related to the acquisition of resources.

The sign and strength of the relationships between key life-history traits depend on the amount of resources that individuals acquire and how these are then allocated among various traits (van Noordwijk and de Jong 1986; Houle 1991; de Jong and van Noordwijk 1992; Reznick et al. 2000). Positive covariation among life-history traits is theoretically predicted when variation in resource acquisition is sufficient to obscure allocation trade-offs (van Noordwijk and de Jong 1986; de Jong and van Noordwijk 1992). In our experiment, we manipulated the protein content of the diet fed to *T. commodus* to mimic lifelong differences in females' ability to acquire and assimilate valuable resources. We therefore interpret treatment differences in female sexual responsiveness and mating preference, survival to eclosion, adult life span, development time, and weight gain as revealing condition-dependent traits. In *T. commodus*, the acquisition of dietary protein appears to be an important component of female condition, a finding supported in several other insect species (reviewed by Nylin and Gotthard [1998]).

Within diet treatments, we expect that differences among females will be due to individual variation in both resource acquisition and allocation. The increased importance of variation in allocation at this level should reveal more often negative covariation among traits due to trade-offs in resource allocation (van Noordwijk and de Jong 1986; Houle 1991; de Jong and van Noordwijk 1992). Indeed, within diet treatments, we found several negative

relationships between life-history traits that are consistent with trade-offs in resource allocation. In particular, within each diet treatment, females that developed faster eclosed at a lighter body weight. This phenotypic trade-off is often seen in insects (Gebhardt and Stearns 1988; Møller et al. 1989; Simons and Roff 1994; Nunney 1996; Blanckenhorn 1998) if not ectothermic animals in general (reviewed by Kozłowski 1992; Atkinson and Sibly 1997; Roff 2000). Without knowing the relationships between each fitness component and total fitness, however, it is impossible to determine the adaptive significance of these life-history trade-offs (Hunt et al. 2004b).

Our finding that, within diet treatments, females that developed faster lived longer as adults contrasts with the more commonly reported negative correlation between juvenile development and adult survival (Partridge and Fowler 1992; Promislow and Bugbee 2000). Chippindale et al. (1997) have argued that rapid nymph development may signal reduced ability to acquire and/or assimilate resources. This is consistent with our finding that fast-maturing females eclosed at lighter weights both on an absolute scale and relative to their body size.

Condition Dependence of Female Mate Choice

Two lines of evidence suggest that female sexual responsiveness and the expression of preferences for higher call rates and intermediate frequency calls are condition dependent. First, differences among diet treatments in these important aspects of female choice suggest a direct link to resource acquisition. Second, the relationships within diet treatments between development time and mate choice suggest that choice may be influenced by, or even subject to, fundamental life-history trade-offs in *T. commodus*. This, in turn, suggests that mate choice is costly and that the ratio of benefit to costs of choice is probably lower for females in poorer condition. Although the costs of mate choice are important for models of the evolution of mating preferences (Pomiankowski 1987; Houle and Kondrashov 2002; Kokko et al. 2002), they have been extremely difficult to measure directly (Kotiaho 2001). Studying the condition dependence of mate choice in a life-history context may provide a worthwhile approach to better understanding the costs of choice.

Several previous studies have manipulated the quality and/or quantity of food provided to females to reveal a positive relationship between condition and the expression of mating preferences (Brown 1997; Lesna and Sabelis 1999; Hingle et al. 2001a; but see Syriatowicz and Brooks 2004). Other studies have provided correlational evidence for an association between female preferences and condition indexes (e.g., body size, Jennions et al. 1995; residual body mass, Rintamäki et al. 1998; body mass : length ratio,

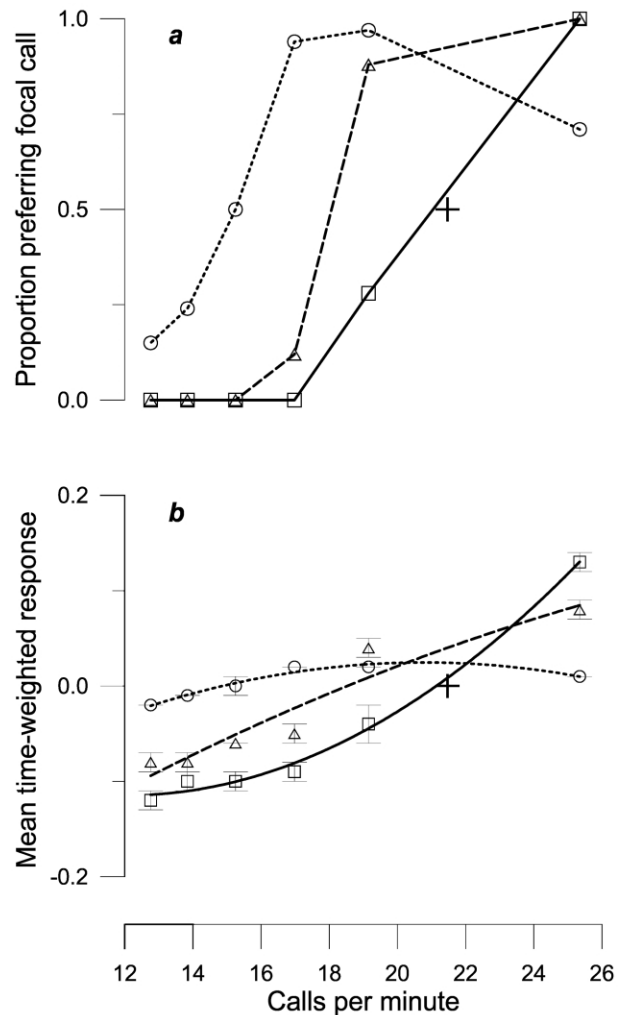


Figure 7: Treatment mean preference functions for call rates by females in each of the three diet treatments. *a*, Proportion of females that chose the focal call over the standard call. *b*, Mean time-weighted preference for the focal call over the standard with second-order polynomial fitted. Squares, solid line = high-protein diet; triangles, large-dashed line = medium-protein diet; circles, small-dashed line = low-protein diet.

Bakker et al. 1999; Hingle et al. 2001b; Beeler et al. 2002; hip : waist ratio, Penton-Voak et al. 2003). There is also growing evidence from correlational (Poulin 1994; Pfennig and Tinsley 2002) and manipulative (López 1999; Mazzi 2004) studies that parasite infection weakens mating preferences. Collectively, these studies, along with ours, generally show that females in better condition exert stronger preferences.

The relationship between female choosiness or responsiveness and condition, however, seems more variable and may depend on the species' mating biology. In species where females receive a nutritious food gift from a male,

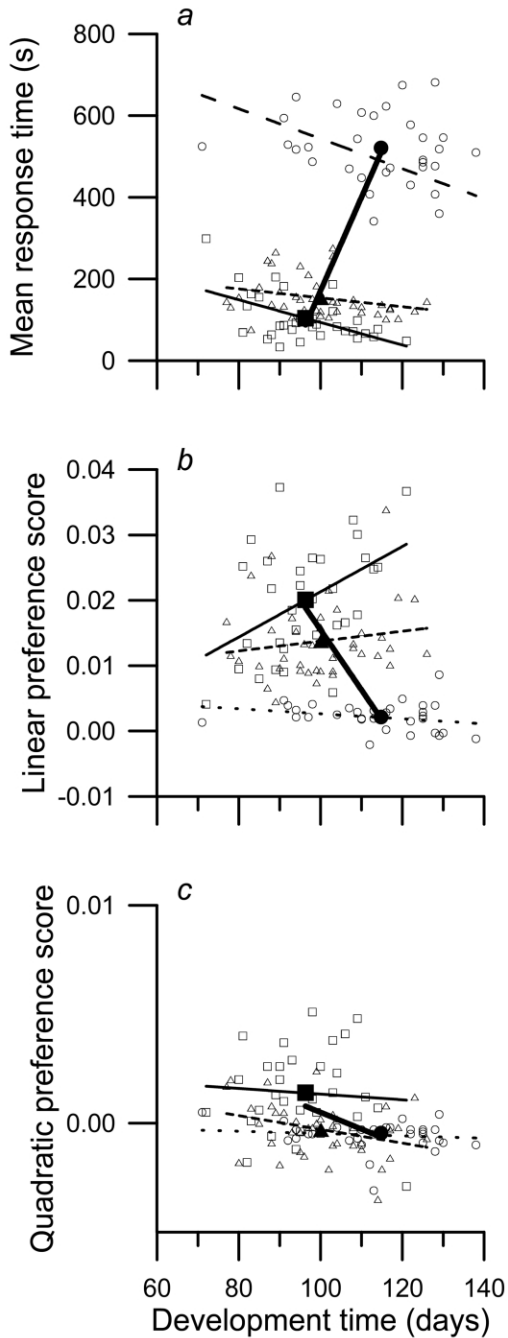


Figure 8: Influence of diet and development time on (a) mean response time, (b) linear preference coefficients, and (c) quadratic preference coefficients of individual females in the call rate experiment. Multivariate and univariate significance tests of diet treatment, development time, and their interactions are presented in table 3. Squares, solid line = high-protein diet; triangles, large-dashed line = medium-protein diet; circles, small-dashed line = low-protein diet. The filled symbols and thick solid line represent the relationship between measures of mate choice and development time across diet treatments.

they tend to become more sexually responsive when either diet quality is reduced (Brown 1997; Cratsley and Lewis 2003) or the prevalence of parasitism is increased (Simmons 1994). For example, in the tree cricket, *Oecanthus nigricornis*, females fed a low-quality diet are less likely to reject male mating attempts (Brown 1997). This is presumably because females wish to obtain nutrients from male glandular secretions and are therefore less choosy. Where there are no material benefits of mate choice, however, females seem to become less sexually responsive when in poor dietary condition (Proctor 1991; Markow and Clarke 1997; Ortigosa and Rowe 2002; Syriatowicz and Brooks 2004) or when suffering from high parasite loads (Poulin 1994; López 1999). For example, in the cockroach, *Nauphoeta cinerea*, females maturing in a high-quality environment were more sexually responsive to male courtship attempts than those reared in a lower-quality environment (Clark et al. 1997). These findings suggest that variation in female responsiveness is influenced not only by resource availability but also by whether the value of a mating depends on female condition. Our finding of a positive association between condition and sexual responsiveness in *T. commodus* is typical for a species in which nutritional benefits of mate choice appear to be absent.

Mate choice is most likely to be condition dependent if the costs are greater for females in poor condition (Badyaev and Qvarnström 2002). Therefore, to understand why females in poorer condition took longer to respond to call stimuli and expressed weaker preference functions, it is crucial to understand the costs experienced when choosing a mate. While female crickets often experience an increased probability of falling victim to predators or parasitoids when responding to a male's call in the field (Sakaluk and Belwood 1984; Gray and Cade 1999), it is difficult to conceive how this risk would vary with female condition. An alternate, and more likely, explanation is that decreased responsiveness and weaker preferences occur if mate choice is more costly for females in low condition as a result of depleted energy stores (Wagner and Harper 2003). A number of empirical studies suggest that there are substantial energetic costs associated with sampling potential mates (Milinski and Bakker 1992; Wong and Jennions 2003). While these costs are reduced in laboratory studies, females in low condition may still allocate more of their limited resources to foraging and rebuilding condition rather than assessing and responding to males. This would particularly be the case if females in poor condition were attempting to forgo the costs of mating until they have sufficient resources to allocate to offspring (Syriatowicz and Brooks 2004). Which of these potential costs are most pertinent to mate choice decisions in *T. commodus* remains to be empirically tested.

Table 3: MANCOVA examining the effects of diet and life-history covariates on the three components of female mate choice in the dominant frequency preference trials

	Multivariate tests		
	Diet treatment	Development time	Treatment \times development time
Pillai's trace	1.146	.119	.116
<i>F</i>	43.83	4.38	2.01
df	6, 196	3, 97	6, 196
<i>P</i>	.000	.006	.66
	Univariate tests		
	df	<i>F</i>	<i>P</i>
Source and dependent variable:			
Diet treatment:			
Mean response time	2, 99	437.80	.000
Linear preference function β	2, 99	80.15	.000
Quadratic preference function γ	2, 99	20.16	.000
Development time:			
Mean response time	1, 99	9.58	.003
Linear preference function β	1, 99	4.97	.028
Quadratic preference function γ	1, 99	3.16	.079
Treatment \times development time:			
Mean response time	2, 99	1.19	.310
Linear preference function β	2, 99	5.65	.005
Quadratic preference function γ	2, 99	.47	.622

Implications for Sexual Selection

Our finding that condition significantly influenced female mate choice decisions has several implications for the way that sexual selection operates on male calling in *T. commodus*. Condition-dependent female sexual responsiveness may influence the strength of sexual selection in either of two opposing ways (Jennions and Petrie 1997; Syriatowicz and Brooks 2004). Because females in poorer condition expressed weaker preferences for call rate and for dominant frequency, they are more likely to mate with a wider range of males. This will reduce the variance in male mating success and weaken selection on male calling. Alternatively, if low female responsiveness increases the threshold level of attractiveness that is required for a male to obtain a mating, then only extremely attractive males will mate, thereby increasing sexual selection on male calls.

Condition-dependent variation among individual females in the shape of their preference functions can also potentially influence both the net strength and direction of sexual selection in the population (Jennions and Petrie 1997; Widemo and Sæther 1999). Because the strength of both the linear and quadratic terms describing preferences for dominant frequency and call rate were dependent on female condition, resource availability within cricket populations may strongly influence the strength of sexual selection on these male traits.

While our individual measures of female responsiveness and preference functions give us some insight into their relationships with other life-history traits, it is the diet-treatment-level preference functions that ultimately reveal how sexual selection will act on male calling within populations with a given level of food availability. We demonstrated that female condition influenced the diet-treatment-level preference function in much the same way that it influenced individual females' preference functions. This is an important finding because population-level preference functions emerge from the decisions of individual females and may differ in shape or form from the functions expressed by individuals (Wagner 1998).

Our results raise the testable prediction that differences in the strength of sexual selection across populations can be related to resource availability. Indeed, in guppies, many of the differences between populations in life-history (Grether 2000; Grether et al. 2001) and male color patterns (Grether et al. 1999), once attributed largely to differences in predation regime (e.g., Endler 1995), also appear to be influenced by differences in resource availability. Condition-dependent mate choice in guppies could potentially reinforce sexually selected differences across guppy populations (Syriatowicz and Brooks 2004).

Fluctuations in resource availability may lead to variation in the strength and/or direction of sexual selection.

Both theoretical (Kokko 1997b) and empirical studies (Neff 2000; Randerson et al. 2000) suggest that variation in female mate choice decisions may offer a partial resolution to the lek paradox. In particular, if the genes governing female mate choice are dependent on environmental conditions for their expression, as has been demonstrated in wax moths (*Achroia grisella*) reared at different temperatures (Rodriguez and Greenfield 2003), genotype by environment interactions may be an important factor maintaining genetic variation in female condition and thus potentially driving heterogeneity in sexual selection on male sexual traits. Exploring the genetic basis of condition and condition-dependent mate choice in *T. commodus* is the next important step in understanding the broader evolutionary implications of variation in female mate choice decisions.

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