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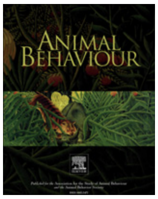

Do male field crickets, *Gryllus pennsylvanicus*, signal their age?

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Older males are often reported to have higher mating success than younger males. To the extent that male quality and survival are positively correlated, this observation raises the possibility that females use male signals to assess age and thus quality. I tested this hypothesis in the fall field cricket, *Gryllus pennsylvanicus*, a species in which females are known to prefer older males, and males call to attract females. Tests were both longitudinal (males recorded early and late in life) and cross-sectional (males recorded once, each at different ages). I measured a variety of temporal and spectral calling song parameters and tested the predictions that: 1) calling song changes with age, and 2) variation in calling song correlates with variation in age. I found significant changes with increased age: calls showed decreased pulse period, decreased pulse duration, decreased pulse peak frequency, more pulses per chirp and increased pulse period variability. Although pulse period and pulse duration were negatively correlated with male age in bivariate correlations, canonical correlation failed to detect any significant relationship between male age and any linear combination of song parameters. I also measured a number of male body size traits and found that the majority of information in male song appears to be related to body size. I discuss the results in relation to the auditory sensitivity of *G. pennsylvanicus*, and suggest a simple mechanism that explains both female preference for older males and female discrimination against heterospecific males.

Older males often have higher mating success than younger males (e.g. Robel 1967; Zuk 1987b, 1988; Conner 1989; Simmons & Zuk 1992; Côté & Hunte 1993; Simmons 1995; Dickinson 2001; Felton et al. 2006; but see Jones et al. 2000; Jones & Elgar 2004; reviewed in Brooks & Kemp 2001). This pattern can be explained by two nonexclusive hypotheses: (1) male survival is not the target of sexual selection per se, but the older-male advantage is simply a by-product of the highest-quality males living long lives, and/or (2) females choose older males precisely because mating with an older male confers some advantage to females such as higher genetic quality, avoidance of inbreeding or increased direct benefits, the so-called age-based indicator mechanism (Trivers 1972; Manning 1985; Kokko 1998; reviewed in Brooks & Kemp 2001). Both hypotheses predict that genetic quality and survival are positively correlated in males, however, only the latter predicts an ontogenetic change in male display to advertise age. As sexually reproducing organisms age, many aspects of their phenotype change (Rose 1991) including male display (e.g. De Luca & Cocroft 2009 and references therein). To the extent that survival and quality are positively correlated in males, age-related phenotypic changes in male display may provide an honest signal of male quality. For example, the adult plumage of male birds often changes with age (e.g. Hill 1996; Delhey & Kempenaers 2006; Doucet et al. 2007; Probst et al. 2007), and females are known to prefer males that have 'older' plumage (Hunt et al. 1998a, b; Sheldon et al. 1999). Other potential examples of age-related quality indicators are the attainment of silver back hair in male gorillas, *Gorilla gorilla* (Levréro et al. 2006) and large body size in male bullfrogs, *Rana catesbeiana* (Howard 1978).

In several species of field crickets (Orthoptera: Gryllidae: Gryllinae), females mate preferentially with older males (Table 1). Male field crickets use forewing stridulation to produce an acoustic signal (calling song) that attracts females (Alexander 1961; Loher & Dambach 1989). In related tettigoniid orthopterans, the forewings wear with age, resulting in changes to song (Hartley & Stephen 1989; Stiedl et al. 1991; Ritchie et al. 1995). Thus, wear-related (age-related) changes in grylline male song could form the basis for the observed mating bias in favour of older males (Zuk 1987b, 1988; Simmons & Zuk 1992; Simmons 1995; Judge 2010), although the substantial individual variation in time spent calling (e.g. Judge et al. 2008) may obscure age-related changes in wear damage. As males age, they may also increase energetic components of calling song in response to their decreasing residual reproductive value (Williams 1966).

In grylline species where females are not known to prefer older males, there is no evidence of age-related changes in calling song

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Table 1
Summary of the studies that have looked for age-related changes in field cricket calling song

Species	Older male bias	Song parameters examined[*]	Experimental design	Relationship with male age	Reference
Acheta domesticus		AMP, PPC, CFQ, ICI	Cross-sectional	None	Gray 1997
Gryllus bimaculatus	Yes[†]	CFQ, Q, CD, ICI, CR, PPC, PD, IPI, PR	Cross-sectional	Older males have more variable PR (not significant after sequential Bonferroni correction)	Simmons & Zuk 1992
G. campestris	Yes[‡]	CFQ, CR, PPC, CD, ICI, E	Longitudinal	Older males have lower CFQ and shorter CD with fewer PPC	Jacot et al. 2007
G. integer (California)		PSB	Longitudinal	None	Hedrick 1986
G. rubens		PR	Longitudinal	None	Walker 2000
G. pennsylvanicus	Yes[§,**]	NCE	Longitudinal	None after 5 days postadult moult	Cade & Wyatt 1984
		PPC	Cross-sectional	Older males have more PPC	M. Zuk, unpublished data, cited in Zuk 1988
		BD	Longitudinal	Older males have shorter BD	Zuk & Simmons 1997
		PR, PPC, ICI, CD	Longitudinal	None	Ciceran et al. 1994
G. texensis		NCE	Longitudinal	None after 5 days postadult moult	Cade & Wyatt 1984
(formerly *G. integer* Texas)		NCE, TCP	Longitudinal	Middle-aged males have greater NCE than young or old males, and males initiate calling earlier in the night as they age	Bertram 2000
		PR, PPT, ITI, PMP	Cross-sectional	None	Souroukis et al. 1992
		PPT	Cross-sectional	None	Gray & Cade 1999
G. veletis	Yes[§]	NCE	Longitudinal	None after 5 days postadult moult	Cade & Wyatt 1984
Teleogryllus africanus		NCE	Longitudinal	None after 5 days postadult moult	Cade & Wyatt 1984
T. oceanicus		Chirp portion: CD, PPC, PR, PD, IPI, CFQ Trill portion: TD, CPT, CR, PD, IPI, ICI, CFQ Entire song: SD, PSC	Cross-sectional	None	Walker & Cade 2003

[*] AMP = amplitude; BD = bout duration; CD = chirp/trill duration; CFQ = carrier frequency; CPT = chirps per trill; CR = chirp rate; E = chirp energy; ICI = interchirp interval; IPI = interpulse interval; ITI = intertrill interval; NCE = nightly calling effort; PD = pulse duration; PMP = proportion of missing pulses; PPC = pulses per chirp; PPT = pulses per trill; PR = pulse rate; PSB = percentage of time spent calling in short bouts = <5 s; PSC = proportion of song that is chirp; Q = Q factor; SD = song duration; TCP = temporal calling pattern (start time, mean time, stop time); TD = trill duration. Song parameters examined also included coefficients of variation for all measured parameters.

[†] Simmons & Zuk (1992).

[‡] Simmons (1995).

[§] Zuk (1987b, 1988).

[**] Judge (2010).

(*Acheta domesticus*: Gray 1997; *Gryllus integer*: Hedrick 1986; *G. rubens*: Walker 2000; *G. texensis*: Cade & Wyatt 1984; Souroukis et al. 1992; Gray & Cade 1999; but see Bertram 2000; *Teleogryllus africanus*: Cade & Wyatt 1984; *T. oceanicus*: Walker & Cade 2003; Table 1). Evidence for age-related changes in calling song is somewhat equivocal for species in which older males are known to have a mating success advantage (*G. bimaculatus*: Simmons & Zuk 1992; *G. campestris*: Simmons 1995; *G. pennsylvanicus*: Zuk 1987b, 1988; Judge 2010; *G. veletis*: Zuk 1987b, 1988). Cade & Wyatt (1984) failed to detect significant changes in male *G. veletis* song with age, but they measured only one parameter of calling song (nightly calling effort). In *Gryllus bimaculatus*, variability in syllable (pulse) rate increases as males age, but this relationship was not statistically significant after controlling for multiple tests (Simmons & Zuk 1992). Ageing male *G. campestris* have significantly decreased carrier frequency, shortened chirp durations and fewer syllables (pulses) per chirp in their calling songs (Jacot et al. 2007).

In the fall field cricket, *G. pennsylvanicus*, age information is conveyed through calling song, since females prefer older males when they are exposed only to calling song (Zuk 1987b). A subsequent analysis of *G. pennsylvanicus* calling song showed no change in male song with age (Ciceran et al. 1994); however, Ciceran et al.'s study did not adequately control for male age, and their sample sizes for song parameters and individuals were small. Additionally, M. Zuk reported that, as male *G. pennsylvanicus* age, they both shorten the duration of song bouts (Zuk & Simmons 1997) and increase the number of pulses per chirp (M. Zuk, unpublished data cited in Zuk 1988). As a result, there is a lack of consensus about the effect of male age on song in *G. pennsylvanicus*.

I tested the hypothesis that male age affects song in *G. pennsylvanicus* by conducting a longitudinal analysis in which I compared the songs of males recorded early and late in life. My experiment improves upon a previous attempt (Ciceran et al. 1994) by increasing the sample size, measuring more song parameters and controlling for male age more precisely. I also conducted a cross-sectional analysis to address the hypothesis that variation in male song is correlated with variation in male age. In this analysis I also looked for correlations between male song and body size, because research on other gryllines has shown body size to have an important influence on male song (e.g. Brown et al. 1996; Simmons & Ritchie 1996). To do this I used a multivariate approach (canonical correlation analysis and redundancy analysis) to relate calling song to male age and body size. This cross-sectional approach is important to ensure that there is sufficient variation in male song to enable females to choose males of different ages. For example, a longitudinal analysis may detect relatively subtle age-related changes in calling song, but these changes may not convey enough information for females to predict male age. Multivariate analyses also have the benefit of conserving statistical power to test the hypothesis of interest. Loss of statistical power has been an issue in previous studies examining correlations between song and other aspects male phenotype (e.g. Simmons & Zuk 1992).

Recent work on the neurobiology and phonotactic behaviour of *G. pennsylvanicus* has demonstrated that females are sensitive to variation in carrier frequency and pulse period (Jeffery et al. 2005), as are other gryllines (Schildberger et al. 1989). Jeffery et al. (2005) found that females are most attracted to calling song models with a carrier frequency of 5 kHz and a pulse period of 40 ms. So, in addition to conducting multivariate tests, I also conducted univariate tests to determine whether these song parameters: (1) change as individual males age (longitudinal study) and (2) are correlated with male age across a sample of males (cross-sectional study).

METHODS

Study Animals

I used first-generation offspring of crickets captured in late August and early September 2002 from the grounds of the University of Toronto Mississauga (43°32′50.51″N, 79°39′37.80″W).

I housed all juvenile crickets in large plastic containers (48 × 35 × 31 cm, length × width × height) at 25 °C, 70% relative humidity and a 12:12 h light:dark cycle. All crickets were fed Purina® cat chow (ground pellets for the first 2–3 weeks of life, and whole pellets afterwards) and provided with water in cotton-plugged plastic vials. Layers of egg cartons provided shelter and a substrate on which to moult. I added new food every 3–4 days and changed water vials as needed. I moved larger nymphs to a separate bin to reduce cannibalism of smaller individuals. I isolated penultimate-instar nymphs in individual containers (polyethylene, 9 cm diameter, 8 cm high) with food (changed weekly), a cotton-plugged microfuge tube filled with water (changed biweekly or more frequently if needed), and a small piece of egg carton.

Recording Calling Song

All recordings were conducted in a sound-attenuating room, under red light and at 26 °C. When a male started to sing, I moved him gently to another table where I replaced the lid of his individual container (i.e. his rearing container) with one containing a screen window (to increase access to his song). I then placed his container under the microphone, which was positioned 2 cm directly above the screen of the container (approximately 10 cm above the floor of the container). When he resumed singing, I started recording his calling song using an Audio-Technica AT815b line cardioid/electret condenser microphone (±1 dB SPL (re. 20 μPa) between 3 and 6 kHz, unpublished data) connected to a Tascam DA-P1 digital audio tape recorder (48 kHz sampling rate). Reverberation did not seem to be a problem (data not shown); this may have been because of the directionality of the microphone, the relatively short distance from cricket to microphone, and the thin (<1 mm) container walls. Recordings were stopped after 3–4 min of continuous singing or at least one bout of continuous singing. If the male failed to resume singing, he was returned to the pool of unrecorded males. At the end of an evening's recording, all of the recorded males were weighed to the nearest 0.1 mg using a Mettler AE 50 balance. All recordings used in this paper have been archived with the Macaulay Library at the Cornell Lab of Ornithology (http://macaulaylibrary.org; search for "*Gryllus pennsylvanicus*"; look for recordings by the author).

The pool of males to be recorded on an evening was a haphazard selection of the population of individually housed males alive at that time. If a male's age at first recording was within 3–12 days postadult moult, then I attempted to record his calling song 14 days later. A 14-day span was chosen for the longitudinal analysis because this enabled me to record males twice within approximately the natural age range for this species (Zuk 1987a; Murray & Cade 1995). Males that were successfully recorded twice were included in the longitudinal analysis; other males were included in the cross-sectional analysis. Thus, males included in this study may represent a biased subset of relatively high-effort callers, since males had to call on at least one occasion, and some males did not call when selected for recording. Most of the studies listed in Table 1 suffer from this problem. However, there is little that can be done to force a male to call (but see Wenzel et al. 1998). Furthermore, non-calling males may be displaying an alternative mating tactic (Cade 1979, 1981).

Measuring Song Parameters

All recorded songs were transferred to a PC using Cool Edit 2000 (now Adobe Audition), through a custom-built port connected to the digital input of a Creative SoundBlaster Audigy soundcard. Songs were saved as 48 kHz, 16-bit, mono wave files. For each file, I selected a region of calling song that showed the greatest density and regularity of chirps and then saved a 16-chirp section from one bout of song from that region as an ASCII text file for transfer to a Macintosh computer for analysis. The filenames of these text files were encoded by a third party to allow me to remain blind to the song identity (and thus male age) while I measured song parameters. On the Macintosh, all manipulation and analysis of songs was done using Canary 1.2.4. (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). All text files were converted to Canary files and high-pass filtered at 1 kHz to remove background noise.

I measured a range of temporal and spectral parameters for each song, including chirp duration, chirp period, pulses per chirp, pulse duration, pulse period, chirp peak frequency, pulse peak frequency and pulse bandwidth −3 dB from peak amplitude. I measured chirp peak frequency because carrier frequency varied slightly among pulses within a chirp and this represents a measure of carrier frequency integrated over the entire chirp. However, I also measured pulse peak frequency because I wanted to measure the properties of one individual wing stroke and thus be able to correlate measurements made on the same pulse (i.e. carrier frequency, pulse bandwidth, pulse duration, pulse period). Also, it is unclear which frequency measure may be more relevant to female evaluation of calls, 'instantaneous' (pulse by pulse) or 'average' (chirp) frequency. I also included in analyses the standard deviation of both chirp period and pulse period as estimates of the rhythmicity or cadence of male song. Pulse measurements were made on the second pulse of the chirp (Fig. 1). To ensure a high degree of consistency in the measurement of temporal parameters, I standardized the waveform window within Canary to an on-screen resolution of 0.10 s/inch and 0.50 Pa/inch (temporal and amplitude dimensions respectively) for chirp duration and interchirp interval, and 0.03 s/inch and 0.20 Pa/inch for pulse duration and interpulse interval. To generate frequency spectra, I used a 42.67 ms analysis frame, with an FFT of 2048 points and a Hamming window function. I set the on-screen amplitude resolution to 0.1 dB/inch and

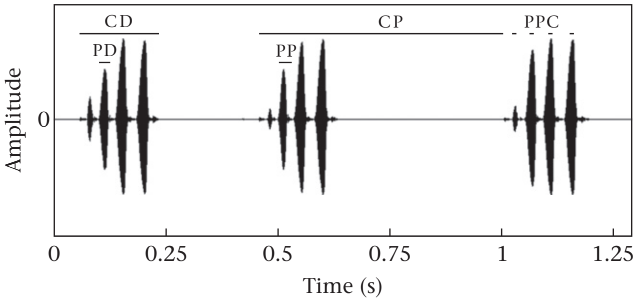

Figure 1. Amplitude by time plot of *G. pennsylvanicus* calling song illustrating the temporal parameters that were measured: chirp duration (CD), pulse duration (PD), chirp period (CP), pulse period (PP) and pulses per chirp (PPC).

frequency resolution to 100 Hz/inch to standardize measurements of peak frequency and bandwidth. Temporal parameters were measured on each of the first 15 chirps, but spectral parameters were measured on only the first five chirps since these measurements were much less variable than temporal parameters. Therefore, all measurements used in the analyses are means (median in the case of pulses per chirp) of either 15 or five measurements.

Morphological Measurements

I used NIH Image (version 1.62 for Macintosh, National Institutes of Health, Washington, D.C., http://rsbweb.nih.gov/nih-image/) to measure: head width, pronotum width, pronotum length, left and right femur length, and left and right harp area on all individuals. The harp is a modified area of the male forewing that serves to radiate song (Bennett-Clark 1989). I did not use the method of Simmons & Ritchie (1996) to estimate harp area, but instead measured it more directly using six easily recognized landmarks around the perimeter of the harp (available from the author upon request). To increase the accuracy of harp area measurements, I measured each harp three times and used the mean area for all analyses. I calculated mean femur length, femur length asymmetry (left−right), mean harp area and harp area asymmetry (left−right). Harp area asymmetry is related to cricket calling song (Simmons & Ritchie 1996), and femur length asymmetry may reflect an individual's ability to buffer developmental instability (Van Valen 1962). Therefore, each male had measurements for eight morphological variables, including mass, in the cross-sectional analysis.

Statistical Analysis

For the longitudinal analysis, I conducted pairwise analyses to test for age-related changes in the 10 song parameters. Then, because many of the song parameters were highly intercorrelated, I also conducted a principal components analysis to reduce the 10 song parameters to a set of orthogonal song principal components. I followed this with a multivariate repeated measures GLM with age class (older versus younger) as the within-subjects factor and the song principal components as dependent variables.

To test the hypothesis that male age is conveyed in calling song (cross-sectional analysis), I first conducted a series of pairwise correlations on male age, the morphological variables and the 10 male song variables to identify univariate correlations between song and age, age and male morphology, and song and male morphology. I then conducted a canonical correlation analysis and redundancy analysis with age and the eight morphological variables as dependent variables, and the 10 song parameters as independent variables. Canonical correlation analysis is the full multivariate extension of univariate correlation analysis (Tabachnick & Fidell 2001). In canonical correlation analysis, one set of variables (often referred to as dependents) is related to another set of variables (independents) through the computation of canonical variates, which are linear combinations of the dependent and independent variables that maximize variance shared between canonical variate pairs (i.e. one independent canonical variate and one dependent canonical variate). Canonical correlation analysis computes as many pairs of canonical variates as there are variables in the smaller set, either dependent or independent. Each subsequent canonical variate pair maximizes the proportion of variance explained from that left over from the previous canonical variate pair. Redundancy analysis allows for the evaluation of the proportion of variance in one set of variables that is explained by the canonical variate of the other set (Tabachnick & Fidell 2001). The canonical correlation analysis augments the univariate analyses by revealing additional axes of song variation other than the original measured song parameters.

To examine the amount of information about male age relative to male morphology that is conveyed in song, I conducted three sequential canonical correlation and redundancy analyses. The first analysis had only male age as the dependent variable (equivalent to multiple regression; Tabachnick & Fidell 2001), the second had only the eight male morphological measurements as the dependent variables, and the third had both male age and the eight morphological measurements. The variance in the dependents explained by the song variables in each canonical correlation analysis shows the degree to which song will predict age (see Rotenberry et al. 1996 for a similar use of canonical correlation analysis and redundancy analysis).

I used SPSS 10 for Windows (SPSS, Chicago, IL, U.S.A.) for all statistical analyses. I tested the assumption of normality for all variables using Kolmogorov−Smirnov tests with Lilliefors significance correction. All tests were two tailed and had an a priori type I error rate of 5%.

RESULTS

Longitudinal Analysis

I recorded 28 males at both a young (mean ± SE $= 7.1 \pm 0.6$ days postadult moult) and old (mean ± SE $= 21.4 \pm 0.6$ days postadult moult) age, which is well within the age range found in wild populations of *G. pennsylvanicus* (Zuk 1987a; Murray & Cade 1995). Normality tests revealed that several of the song parameters (chirp period, chirp period standard deviation, pulses per chirp, pulse period standard deviation and pulse bandwidth) deviated significantly from normality (K−S Lilliefors tests: all $P\text{s} < 0.005$). Transformations failed to restore normality for all of these variables, so I performed nonparametric tests for all variables. Results were consistent regardless of whether the data were analysed with parametric or nonparametric statistics (data not shown).

Males lost weight as they aged (mean ± SE mass: young: 431 ± 17 mg; old: 397 ± 16 mg; paired *t* test: $t_{25} = 5.492$, $P < 0.001$). To test whether the age-related change in mass confounded age-related changes in any of the song parameters, I correlated change in mass with change in each song parameter. After correcting for multiple testing using the sequential Bonferroni method (Holm 1979), change in mass was not significantly correlated with change in any song parameters (all $|\text{Spearman's } r_S| < 0.447$, all $P\text{s} > 0.225$).

Given that I could not transform all of the song variables to conform to the assumption of normality, I could not conduct a multivariate repeated measures GLM to test the omnibus hypothesis that song changed with age. Consequently, I tested each song parameter individually using Wilcoxon signed-ranks tests. Song changed significantly with age. In particular, old males had shorter pulse periods, shorter pulse durations, lower pulse peak frequencies, more pulses per chirp and more variable pulse periods compared to when they were young (Table 2, Fig. 2). Age-related changes in pulse period and pulse duration remained statistically significant after correction for multiple testing. I found no effect of age on chirp duration, pulse bandwidth, chirp period standard deviation, chirp peak frequency or chirp period (Table 2).

To further test the prediction that song changes with age in *G. pennsylvanicus*, I conducted principal components analysis (PCA) on the 10 song parameters. Although normality tests revealed that many of the original song parameters were not normally distributed (see above), PCA does not make assumptions about the distribution of variables as long as principal components are not

Table 2
Median and interquartile range (IQR) for each song parameter examined for male *G. pennsylvanicus* at younger and older ages

Parameter	Younger		Older		WSR *Z*[*]	*P*
	Median	IQR	Median	IQR		
Chirp duration (ms)	178.6	168.7–186.0	179.6	172.1–190.6	1.252	0.210
Chirp period (ms)	631.2	562.2–693.8	600.0	498.9–696.8	0.660	0.509
Chirp period variability (SD, ms)	86.4	54.9–119.8	90.4	49.1–168.3	1.002	0.316
Pulses per chirp (pulses)	4	3–5[†]	4	4–6[†]	2.333	0.020
Pulse duration (ms)	21.6	19.4–24.1	18.2	16.3–21.2	2.892	0.004[‡]
Pulse period (ms)	40.2	36.7–42.4	38.0	34.5–40.8	3.393	0.001[‡]
Pulse period variability (SD, ms)	1.4	1.1–2.2	2.0	1.5–2.7	2.049	0.040
Chirp peak frequency (kHz)	4884	4646–5096	4861	4717–4990	0.934	0.350
Pulse peak frequency (kHz)	4838	4604–5041	4774	4577–4875	2.517	0.012
Pulse bandwidth (Hz)	121	88–158	114	88–134	1.207	0.227

[*] Wilcoxon signed-ranks test, normal approximation.
[†] Minimum to maximum instead of IQR.
[‡] Remained statistically significant after correction for multiple testing (Holm 1979).

tested for statistical significance (Tabachnick & Fidell 2001). I included songs for males when they were both young and old since I wanted to compare changes in song within males. PCA extracted five song principal components (SPCs) with eigenvalues greater than one that together explained 88.5% of the variation in the original 10 song parameters. SPC loadings for each song parameter and the variance explained by each SPC are given in Table 3. Normality tests revealed that SPC1 and SPC5 significantly deviated from normal distributions (SPC1: test statistic $= 0.118$, $P = 0.051$; SPC5: test statistic $= 0.125$, $P = 0.030$) and so I proceeded with nonparametric tests.

Change in mass was not significantly correlated with any of the SPCs (all $|\text{Spearman's } r_S| < 0.298$, all $Ps > 0.140$). I tested for age-related changes in the five SPCs by conducting five Wilcoxon signed-ranks tests and then correcting for multiple testing. Song changed significantly with age in only SPC1 (Wilcoxon signed-ranks test: $Z = -3.234$, $P = 0.006$): males had higher values of SPC1 when they were older than when they were younger (mean difference $\pm$ SE $= 0.691 \pm 0.169$), meaning that they tended to increase pulses per chirp, decrease pulse duration, decrease pulse period, increase chirp duration and increase pulse period variability as they aged (see Table 3). I found no differences in any of the other SPCs (all $|Z| < 1.936$, all $Ps > 0.211$).

Cross-sectional Analysis

I recorded 104 male *G. pennsylvanicus* for the cross-sectional analysis, however, upon measurement of morphology, two males were excluded from analysis because their left forewing was either missing or grossly deformed. The remaining 102 males ranged in age from 4 to 27 days postadult moult (mean $\pm$ SE $= 14.1 \pm 0.6$ days). Male *G. pennsylvanicus* were directionally asymmetric for femur length (one sample Kolmogorov–Smirnov test: $Z = 1.426$, $P = 0.034$), but not harp area ($Z = 0.948$, $P = 0.311$), although femur length asymmetry and harp area asymmetry were positively correlated (Spearman rank correlation: $r_S = 0.245$, $P = 0.013$). Males' right femurs were longer than their left femurs ($\text{median}_{L-R} = -0.03$ mm, interquartile range -0.07 to 0.04 mm). Given that field cricket stridulation is inherently directionally asymmetric, with males usually stridulating with the right forewing on top of the left (Masaki et al. 1987; personal observation), I retained the directionality of harp area asymmetry measurements in all subsequent analyses even though I did not detect directional asymmetry in harp area.

Normality tests revealed that many of the song variables (chirp duration, chirp period, chirp period standard deviation, pulses per chirp, pulse period standard deviation and pulse bandwidth) and several of the morphological variables (harp area asymmetry, femur length asymmetry and body mass) deviated significantly from normality (K–S Lilliefors tests: all $Ps < 0.016$). Transformations failed to normalize many of the variables (data not shown), so I tested for pairwise correlations using nonparametric Spearman rank correlations. Male age was significantly correlated with only pulse period ($r_S = -0.255$) and pulse duration ($r_S = -0.222$) (Table 4). Pulse duration was positively correlated with all of the measures of body size, and pulse period was negatively correlated with harp area asymmetry (Table 4). Both chirp peak frequency and pulse peak frequency were negatively correlated with all of the measures of body size, but most strongly with mean harp area (Table 4).

Canonical correlation analysis, like multiple regression, is sensitive to multicollinearity (Tabachnick & Fidell 2001). Therefore, I reduced five of the measures of body size (body mass, head width, pronotum width, pronotum length and mean femur length) to a summary measure of body size using principal components analysis (PCA). Although harp area was strongly positively correlated with these five measurements (all Pearson's $r_S > 0.690$, all $Ps < 0.001$), I did not include harp area in the PCA because this structure is directly related to production of calling song (Bennett-Clark 1989). PCA resulted in one principal component with an eigenvalue greater than 1 (PC1 eigenvalue $= 4.626$) and that explained 92.5% of the variation in the original five variables. Variable loadings on PC1 (henceforth called body size) were as follows: body mass (0.961), head width (0.977), pronotum width (0.955), pronotum length (0.961) and mean femur length (0.955).

When age, body size, harp area, harp area asymmetry and femur length asymmetry (collectively male phenotype) were entered into a canonical correlation analysis as dependents, calling song correlated significantly with male phenotype on two canonical variate pairs (CVPs) (CVP1: $F_{50,400.15} = 2.363$, $P < 0.001$; CVP2: $F_{36,331.51} = 1.477$, $P = 0.043$). The first canonical correlation was 0.681 (46.3% shared variance) and the second was 0.500 (25.0% shared variance). Redundancy analysis showed that within the first two canonical variate pairs, calling song accounted for 18.1% of the variance in the dependent variables (Table 5). Following Tabachnick & Fidell (2001), I considered only variable loadings of 0.3 or greater when interpreting the canonical variate pairs. Within the first canonical variate pair, lower pulse peak frequency (-0.861), lower chirp peak frequency (-0.839) and longer pulse duration (0.360) were positively correlated with harp area (0.980) and body size (0.650) (Table 5). And within the second canonical variate pair, shorter pulse duration (-0.547), shorter pulse period (0.530), greater pulse period variability (0.491) and more pulses per chirp (0.342) were negatively correlated with harp area asymmetry

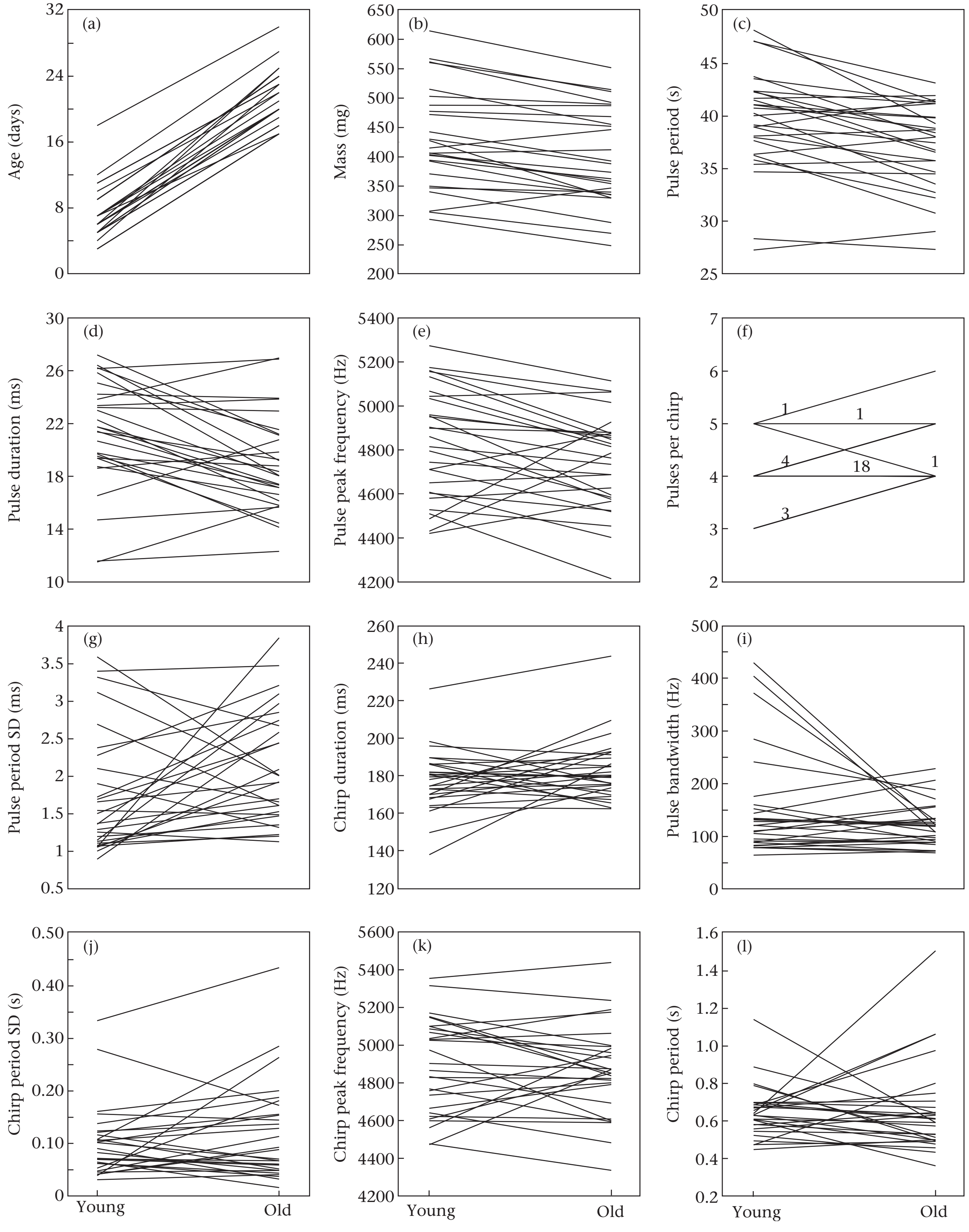

Figure 2. Plot of changes in *G. pennsylvanicus*: (a) age, (b) mass and (c–l) calling song parameters from the longitudinal analysis. The nine song parameters are listed in order of decreasing statistical significance based on Wilcoxon signed-ranks tests (see Table 2 for statistical values): (c) pulse period, (d) pulse duration, (e) pulse peak frequency, (f) pulses per chirp, (g) pulse period standard deviation, (h) chirp duration, (i) pulse bandwidth, (j) chirp period standard deviation, (k) chirp peak frequency, (l) chirp period. Each line represents the change in calling song for an individual male.

Table 3
Principal components analysis of male song in the longitudinal analysis

Parameter	Song principal component				
	1	2	3	4	5
Chirp duration	**0.594**	0.332	0.365	0.428	0.380
Chirp period	0.324	**0.669**	**0.511**	−0.152	−0.146
Chirp period variability	0.298	**0.502**	0.411	**−0.520**	−0.340
Pulses per chirp	**0.852**	0.061	0.133	0.383	0.143
Pulse duration	**−0.735**	0.382	0.088	0.217	0.323
Pulse period	**−0.734**	0.428	0.346	−0.060	0.196
Pulse period variability	**0.558**	−0.191	−0.416	−0.343	0.173
Chirp peak frequency	0.078	**−0.782**	**0.576**	−0.144	0.126
Pulse peak frequency	−0.149	**−0.760**	**0.585**	−0.123	0.146
Pulse bandwidth	−0.141	−0.242	0.180	**0.544**	**−0.698**
Eigenvalue	2.711	2.427	1.588	1.124	0.998
% Variance	27.106	24.269	15.882	11.237	9.981

Principal component loadings greater than 0.5 are in bold.

(−0.721; i.e. right harp increasing in area relative to the left) and body size (−0.521) (Table 5). Male age did not load strongly (i.e. above 0.3, Tabachnick & Fidell 2001) on either of the two canonical variate pairs (Table 5).

Canonical correlation analysis between one dependent and several independent variables is equivalent to multiple regression (Tabachnick & Fidell 2001); therefore, I conducted a multiple regression of age on the 10 song parameters. This multiple regression was not statistically significant ($F_{10,91} = 1.592$, $P = 0.121$). Removal of age from the full canonical correlation analysis did not greatly change canonical correlation between song and male phenotype (canonical $\text{correlation}_{\text{morphology}} = 0.680$, canonical $\text{correlation}_{\text{age+morphology}} = 0.681$). Redundancy analysis showed that calling song accounted for 16.9% of variation in the first canonical variate when just male morphology was included, whereas it accounted for 13.5% of variation in the first canonical variate when both age and morphology were included.

DISCUSSION

Older male *G. pennsylvanicus* field crickets are more attractive to females than are younger males (Zuk 1987b, 1988; Judge 2010), even when females have only calling song on which to base their mate choice (Zuk 1987b). This finding demonstrates that the calling song of older males differs from that of younger males. This may result from (1) ontogenetic changes in male song, (2) differential survival by a subset of males with calling songs that differ from those of other males in the population, or (3) both. In this study, I tested the hypothesis that male song changes with age in *G. pennsylvanicus*. Males recorded at 7 days postadult moult (young males) and 21 days postadult moult (old males) showed significant changes in song. When they were older, males had shorter pulse period, shorter pulse duration, lower pulse peak frequency, more pulses per chirp and more variable pulse period than when they were younger (Fig. 2). Males also weighed less when they were older; however, mass loss probably did not confound age-related changes in song because there were no statistically significant correlations between mass loss and changes in any song parameter. In a separate cross-sectional analysis, pulse period and pulse duration were negatively correlated with male age, although these results should be interpreted with caution because of the loss of statistical significance with correction for multiple testing (Table 4). When correlations with male morphology were taken into account with canonical correlation analysis, linear combinations of song parameters did not explain a significant portion of the variance in male age (Table 5).

Table 4
Matrix of Spearman rank correlations among male phenotypic variables and song parameters

	Phenotypic variables									Song parameters								
	Age	Mass	HW	PW	PL	MHA	ASHA	MFL	ASFL	CD	CP	CPSD	PPC	PD	PP	PPSD	CPKF	PPKF
Phenotypic variables																		
Mass	−0.025																	
HW	−0.037	**0.922**																
PW	0.056	**0.896**	**0.922**															
PL	−0.024	**0.872**	**0.913**	**0.882**														
MHA	−0.047	**0.698**	**0.729**	**0.681**	**0.648**													
ASHA	−0.044	−0.089	−0.077	−0.062	−0.088	−0.134												
MFL	−0.079	**0.883**	**0.891**	**0.834**	**0.899**	**0.707**	−0.107											
ASFL	−0.127	−0.069	−0.025	−0.007	0.008	0.116	0.245	0.022										
Song parameters																		
CD	0.010	0.148	0.163	0.156	0.144	0.172	0.063	0.193	0.047									
CP	0.083	0.069	0.013	0.000	−0.016	0.038	−0.195	−0.010	0.077	0.135								
CPSD	0.009	−0.015	−0.067	−0.036	−0.112	−0.062	−0.076	−0.063	0.025	0.025	**0.684**							
PPC	0.163	−0.129	−0.080	−0.051	−0.092	−0.048	0.179	−0.069	0.029	**0.640**	0.062	0.053						
PD	−0.222	0.298	0.309	0.197	0.277	0.259	−0.147	0.324	−0.046	−0.014	−0.252	−0.160	−0.276					
PP	−0.255	0.183	0.119	0.098	0.119	0.037	−0.207	0.146	−0.028	−0.005	0.044	0.113	**−0.532**	**0.504**				
PPSD	−0.136	−0.152	−0.170	−0.134	−0.149	−0.015	0.129	−0.212	0.000	0.031	−0.030	0.137	0.120	−0.239	−0.221			
CPKF	−0.092	**−0.343**	−0.295	−0.307	−0.310	**−0.516**	0.122	**−0.373**	−0.124	−0.056	−0.120	−0.089	0.070	−0.115	−0.032	0.024		
PPKF	−0.096	−0.313	−0.261	−0.287	−0.282	**−0.518**	0.046	−0.322	−0.173	−0.078	−0.130	−0.103	0.000	−0.054	0.035	−0.050	**0.943**	
PBW	−0.024	0.028	0.067	0.126	0.050	−0.081	0.116	−0.002	−0.074	−0.087	−0.056	0.039	0.052	−0.253	−0.074	0.092	0.029	0.014

Age = age at recording; Mass = mass at recording; HW = head width; PW = pronotum width; PL = pronotum length; MHA = mean harp area; ASHA = asymmetry in harp area; MFL = mean femur length; ASFL = asymmetry in femur length; CD = chirp duration; CP = chirp period; CPSD = chirp period standard deviation; PPC = pulses per chirp; PD = pulse duration; PP = pulse period; PPSD = pulse period standard deviation; CPKF = chirp peak frequency; PPKF = pulse peak frequency; PBW = pulse bandwidth. Values in bold were statistically significant at $P < 0.05$ following correction for multiple testing ($N = 102$ for all cells).

Table 5
Results of the canonical correlation analysis

Canonical variate	Canonical variate pair	
	1	2
Dependent variable		
Age	−0.038	0.210
Body size	0.650	−0.521
Mean harp area	0.980	−0.134
Harp area asymmetry	0.031	−0.721
Femur length asymmetry	−0.257	−0.243
Redundancy (%)	13.5	4.6
Independent variable		
Chirp duration	0.164	0.028
Chirp period	−0.049	−0.154
Chirp period variability	−0.040	−0.009
Pulses per chirp	−0.076	0.342
Pulse duration	0.360	−0.547
Pulse period	0.059	−0.530
Pulse period variability	0.029	0.491
Chirp peak frequency	−0.839	−0.021
Pulse peak frequency	−0.861	−0.189
Pulse bandwidth	−0.270	−0.238
Redundancy (%)	16.9	10.6
Canonical correlation	0.681	0.500

Includes canonical loadings of dependent and independent variables on their respective canonical variates, the percentage variance of each canonical variate explained by variables from the other set (Redundancy), and the canonical correlation for each pair of canonical variates.

Do Male G. pennsylvanicus *Signal Their Age?*

Recently, Jacot et al. (2007) found that male *G. campestris* produce calling song with lower carrier frequency and more pulses per chirp as they age. Thus, the older-male mating advantage in this species (Simmons 1995) may be at least partially explained by this age-related decrease in carrier frequency (Jacot et al. 2007) since females prefer lower carrier frequencies (Scheuber et al. 2004). Previous work on *G. pennsylvanicus* calling song (Ciceran et al. 1994) failed to detect statistically significant age-related changes in song. However, Ciceran et al. (1994) reported increases in pulses per chirp, interchirp interval, chirp duration and pulse rate (inverse of pulse period) as males aged. All of these effects, except increased interchirp interval (not analysed), were statistically significant in the current study (Table 3).

The results of the current longitudinal study are consistent with the hypothesis that female preference for older males is based on ontogenetic changes in calling song. However, for this preference to work, females must be able to discriminate male age on the basis of calling song. Although age was related to both pulse period and pulse duration in bivariate correlations (Table 4), calling song did not significantly predict male age when correlations with body size were taken into account. Furthermore, removal of age from the canonical correlation analysis did not decrease the amount of variance in male phenotype explained by calling song. Thus, there seems to be relatively little information about age in male calling song on which female *G. pennsylvanicus* could base a mating preference for older males. However, if females pay attention to specific song parameters (as is the case in many other gryllids), such as pulse period or pulse duration, then it may be possible for females to choose older males.

Interestingly, Jeffery et al. (2005) found that the attractiveness of *G. pennsylvanicus* calling song varied with pulse period, attaining peak attractiveness at 40 ms. In the current study, individual males decreased the pulse period of their calling song from 40 ms when they were younger to 38 ms when they were older. This might suggest that age-related changes in calling song may make older males less attractive. However, as Jeffery et al. (2005) tested females with calling song models with pulse periods of 35 and 40 ms, the true peak in attractiveness may lie between 35 and 40 ms, close to the older male pulse period of 38 ms found in the current study. Furthermore, other age-related changes, such as an increase in pulses per chirp (e.g. Fig. 2), which increases the duty cycle (proportion of time filled with male signal) of male song, may interact with decreases in pulse period and pulse duration to cause male *G. pennsylvanicus* to increase in attractiveness with age. Future work on the phonotactic preferences of female *G. pennsylvanicus* should present females with song models that represent the full range of song parameter combinations to more fully describe the selection that females exert on all song parameters (e.g. Brooks et al. 2005).

What Information is Conveyed in Male Song?

Of the phenotypic variables considered in the cross-sectional analysis (male age, body size, harp area, harp area asymmetry, femur length asymmetry), *G. pennsylvanicus* calling song appears to convey information mostly about male harp area and body size. Males with both lower carrier frequency (both pulse and chirp peak frequency) and longer pulse duration were larger in both harp area and body size (Tables 4, 5), although song was most strongly associated with harp area within the first canonical variate pair. This is perhaps not surprising since the harp is directly involved in radiating calling song (Bennett-Clark 1989), and larger harps resonate at a lower frequency (Nocke 1971). In addition, pulse duration is controlled by the duration of contact between forewings during the closing stroke of stridulation (Bennett-Clark 1989). Larger male *G. pennsylvanicus* have larger forewings and thus longer files (part of the stridulatory apparatus on the forewing), and so may have pulses of longer duration because their forewings are in contact for longer during stridulation. This assumes that males do not vary the proportion of their forewings used or the speed of forewing closure during stridulation.

Why do male *G. pennsylvanicus* reliably signal harp area and body size in calling song? In most Gryllidae, calling song attracts females and can ward off rival males (Alexander 1961; Loher & Dambach 1989), so reliable information about body size in calling song may be important in both competition with rivals and signalling male quality. Jeffery et al. (2005) found that a carrier frequency of 5 kHz was most attractive to female *G. pennsylvanicus*. Given that the males in the cross-sectional analysis had a mean pulse peak frequency of 4920 ± 30 Hz, carrier frequency and thus harp area may be under stabilizing selection by female choice, contrary to the usual pattern of females favouring larger males (see below). In contrast, male–male competition probably exerts directional selection on harp area since larger male *G. pennsylvanicus* win more fights than smaller males (Souroukis & Cade 1993). Field crickets stridulate during aggressive interactions (Alexander 1961), and reliable information about body size conveyed through aggressive song may help males reduce the costs of fighting when body size differences are great. Therefore, male–male competition may maintain the correlation between body size and carrier frequency (i.e. positive correlational selection), so selection for larger body size would result in selection for larger harps and lower carrier frequency.

Evidence that larger male body size is favoured by sexual selection in *G. pennsylvanicus* is mixed. In a field enclosure experiment where sex ratio was manipulated, Souroukis & Cade (1993) detected significant total selection and directional selection on male weight, although the result depended on sex ratio. In the wild, there is some evidence for directional sexual selection: males found paired with females were significantly larger in only one of two body size dimensions than males found alone (Zuk 1988). However, in studies where males were prevented from competing physically, there was no significant selection for larger males (Zuk 1987b; Judge 2010). These results suggest that male–male competition may be more important than female choice in selecting for larger male body size.

Body size is also an important determinant of male mating success in other grylline crickets. In *Acheta domesticus*, larger males win more fights (Hack 1997; Savage et al. 2005), are preferred by females (Gray 1997; Savage et al. 2005) and sing calling songs with more pulses per chirp than smaller males (Gray 1997). Larger male *G. campestris* are more attractive to females (Simmons 1992, 1995), and information about body size is conveyed through carrier frequency: larger males have larger harps and lower carrier frequencies (Simmons 1995; Simmons & Ritchie 1996). Larger male *G. bimaculatus* win more fights (Simmons 1986a; Hofmann & Schildberger 2001) and are preferred by females (Simmons 1986b). Simmons & Zuk (1992) found that larger males had longer pulse durations than smaller males. Another gryllid (Oecanthinae) in which larger male body size is sexually selected is the black-horned tree cricket, *Oecanthus nigricornis*. Larger males win more aggressive contests (Brown 1994) and are preferred by females (Bussière et al. 2005), which receive higher-quality proteinaceous food gifts from larger males (Bussière et al. 2005). Larger male *O. nigricornis* have songs with lower carrier frequency and shorter pulse duration, although only the former is important in attracting females (Brown et al. 1996). In each of these studies, sexual selection seems to consistently favour larger males through both male–male competition and female choice. Clearly, further work is needed on the extent to which fitness of male *G. pennsylvanicus* is determined by male–male interactions versus female choice.

An Alternative Hypothesis to Explain Increased Attractiveness of Older Male G. Pennsylvanicus*?*

Female *G. pennsylvanicus* that appear to be choosing older males may actually be discriminating against heterospecific matings with *G. firmus*. These two closely related gryllines hybridize across a wide area in the northeastern United States (Harrison & Arnold 1982). *Gryllus pennsylvanicus* matures earlier than *G. firmus*, and the extent of overlap in breeding phenology between the two species varies across the hybrid zone (Harrison 1985). *Gryllus pennsylvanicus* has both shorter pulse periods and shorter pulse durations than *G. firmus* (Alexander 1957; Doherty & Storz 1992). Thus, in areas of sympatry, female *G. pennsylvanicus* that prefer shorter pulse periods and/or shorter pulse durations and thus older (earlier-maturing) male *G. pennsylvanicus*, are less likely to hybridize with *G. firmus* than females that do not express the preference. However, in areas of allopatry such as my study area, why is the preference for shorter pulse period and thus older males maintained? Such a preference, if exercised strictly, is likely to be costly since the oldest males represent a small fraction of males in the wild (Zuk 1987a; Murray & Cade 1995) and calling males are relatively widely dispersed (French et al. 1986). Gene flow between areas of sympatry and allopatry (Walker 1974) may maintain the preference, although this is unlikely due to potential costs of the preference and limited dispersal since most *G. pennsylvanicus* lack flight wings (Harrison 1979). Alternatively, females may gain direct benefits by choosing older males if these males defend territories rich in food resources (Rost & Honegger 1987). High-condition male *G. pennsylvanicus* (as manipulated through diet) lived longer and called more per day (i.e. higher duty cycle) than low-quality males (Judge et al. 2008), and females are attracted to calling songs of higher duty cycle (unpublished data). Thus, if the ability to acquire larval resources (condition) is heritable (Rowe & Houle 1996), then females may gain indirect benefits by mating with older males. These benefits may play a role in keeping *G. pennsylvanicus* and *G. firmus* from introgressing into a single species, since matings between female *G. pennsylvanicus* and male *G. firmus* produce viable and fertile hybrid offspring (Harrison 1983). Further experiments using female *G. pennsylvanicus* from the hybrid zone that examine phonotaxis to calling songs of varying pulse periods, coupled with studies of age-related changes in male calling song from these populations would clarify the role that phonotactic preferences play in preventing hybridization between *G. pennsylvanicus* and *G. firmus*.

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