

# Scale effects and constraints for sound production in katydids (Orthoptera: Tettigoniidae): correlated evolution between morphology and signal parameters

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## Keywords:

acoustic communication;  
bioacoustics;  
comparative analysis;  
evolution of stridulation;  
scale effects;  
Tettigoniidae;  
ultrasounds.

## Abstract

Male katydids (Orthoptera: Tettigoniidae) produce mating calls by rubbing the wings together, using specialized structures in their forewings (stridulatory file, scraper and mirror). A large proportion of species (ca. 66%) reported in the literature produces ultrasonic signals as principal output. Relationships among body size, generator structures and the acoustic parameters carrier frequency ( $f_c$ ) and pulse duration ( $p_d$ ), were studied in 58 tropical species that use pure-tone signals. A comparative analysis, based on the only available katydid phylogeny, shows how changes in sound generator form are related to changes in  $f_c$  and  $p_d$ . Anatomical changes of the sound generator that might have been selected via  $f_c$  and  $p_d$  are mirror size, file length and number of file teeth. Selection for structures of the stridulatory apparatus that enhance wing mechanics via file-teeth and scraper morphology was crucial in the evolution of ultrasonic signals in the family Tettigoniidae.

## Introduction

Acoustic calling is a secondary sexual trait expected to be under selection to enhance signal emission, which is in turn, important in mate attraction (Simmons & Ritchie, 1996). Such selection may result in correlated evolution between call parameters and generator design (Endler, 1992). For example, large-dimension generators are associated with low-pitched sound, whereas smaller generators are associated with high pitched sounds (Fletcher, 1992: 110–114). The effect of body size on call parameters has been studied mostly in vertebrates, but only few studies include modern comparative methods (Bohn *et al.*, 2006). Research on arthropods has emphasized correlative evidence of intraspecific macroevolutionary trade-offs between body size and call frequency, and body size or some other physiological processes (Orci *et al.*, 2005; Greenlee *et al.*, 2007).

Sound in Orthoptera occurs largely by stridulation, where two body parts rub against each other (Dumortier, 1963; Ewing, 1989). In the suborder Ensifera (e.g.

Gryllidae: crickets, and Tettigoniidae: katydids), males stridulate by rubbing together their forewings: typically one forewing possesses a vein modified with a series of cuticular teeth (the stridulatory file), whereas the contralateral wing bears a scraper or plectrum (Ewing, 1989). Muscular contractions that generate movement of the wings (rubbing against each other) are relatively slow. During the closure of the wings, the scraper on one wing hits the file teeth on the other. The result is a wing vibration with a spectrum in which the tooth-strike rate (the number of teeth hit per unit time) corresponds to the lowest component in a harmonic series. Stridulation is therefore a frequency multiplication process, which is necessary because muscles are too slow to cause vibration in the kilohertz range (Michelsen, 1998).

Structures that function as scrapers and files, amplifying surfaces and resonant cavities can all determine certain parameters of the output sound [e.g. carrier frequency ( $f_c$ ), pulse duration ( $p_d$ ), etc.] (Bailey, 1970; Bennet-Clark, 1999; Montealegre-Z & Mason, 2005).  $f_c$  is the most energetic (dominant) spectral frequency; and pulse is a rapid change in the amplitude of a signal from a baseline value to a higher or lower value, followed by a rapid return to the baseline value. Katydids produce two types of calls: pure-tone sounds (tonal or musical sounds with narrow frequency spectra) and broadband

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sounds (noisy signals with broad frequency spectra). Pure tones result from resonant stridulation, whereas broad-band songs arise from a non-resonant mechanism.

The effect of body size on  $f_c$  is evident in many vertebrates that generate calling songs by vocalizations (Wallschager, 1980; Ryan & Brenowitz, 1985). Smaller individuals tend to produce high-frequency calls due to resonant cavities and muscular rate contractions scaling with body size (Wallschager, 1980). This effect also applies to stridulating Orthoptera, for which, most studies incorporate intraspecific comparisons (e.g. Brown *et al.*, 1996; Howard & Hill, 2006; Bailey *et al.*, 2007). Other studies at the interspecific level (e.g. Morris & Pipher, 1967; Bailey, 1970; Sales & Pye, 1974; Heller, 1995; Rust *et al.*, 1999; Heller *et al.*, 2006) lack phylogenetic control.

Jost & Shaw's (2006) molecular phylogeny suggests that katydids evolved from a common ancestor that used pure-tone songs at low frequencies. Most extant species of katydids use frequency signals higher (usually ultrasonic) than their hypothetical ancestor, and also exhibit asymmetric forewings. Morphological differences between the forewings are mainly the thickening of the major radiating areas and the massiveness of the file-bearing wing (left forewing).

Crickets using symmetric forewings, have to synchronize the oscillation of the wings' radiating cells, so that they move in phase (Bennet-Clark, 2003). This is achieved by an escapement mechanism analogous to that of a grandfather's clock (Elliott & Koch, 1985), every tooth impact will generate a complete sound cycle (Koch *et al.*, 1988). Therefore,  $f_c$  is a function of tooth impact rate.

In the pure-tone songs produced by katydids and crickets, a sound pulse is built of sustained oscillations, each of which represents a scraper-tooth interaction (e.g. if the stridulatory file has 100 functional teeth, a complete file sweep will produce a pulse with 100 oscillations). The frequency will depend on the speed of the sweep: if teeth are contacted at a high rate, the time period between waves will be shorter (i.e.  $f_c$  will be higher).  $f_c$  also depends on the resonant frequency of wing cells and veins, and when tooth impact rate equals that resonant frequency, the sound output is achieved. The vibration amplitude is much larger at the resonance frequency than at most other frequencies (Fletcher, 1992; Michelsen, 1998). Tooth strike rate is then critical for determining the output  $f_c$ , and tooth strike rate plays an important role in maintaining the sound intensity over distances (Prestwich & O'Sullivan, 2005). But efficient sound emission requires a reasonably large surface to vibrate at large amplitude (Fletcher, 1992; Bennet-Clark, 1998; Michelsen, 1998).

This study explores the evolution of sound generator anatomy arising from selection acting upon acoustic variables in the Tettigoniidae. The following questions are addressed: as katydids evolved, how were changes in

sound generator morphology related to changes in  $f_c$ ? Because the structure of the sound generator probably scales with body size,  $f_c$  should be affected by body size. So one expects  $f_c$  to be higher in smaller species. Thus (i) smaller individuals will have sound generators with relatively smaller areas available for sound radiation; (ii) smaller sound radiating areas will coexist with shorter stridulatory files, a shortening which might take the form of smaller more compact teeth, shorter inter-tooth distances and/or higher tooth density; and (iii) this last expectation (shorter files) opens another possibility: because in pure-tone singing, one sound oscillation represents a single tooth impact, and because small individuals would tend to have short files with high tooth density, small individuals might be expected to make shorter pulses with shorter wavelengths. In other words, species that use high frequencies would evolve to make shorter sound pulses.

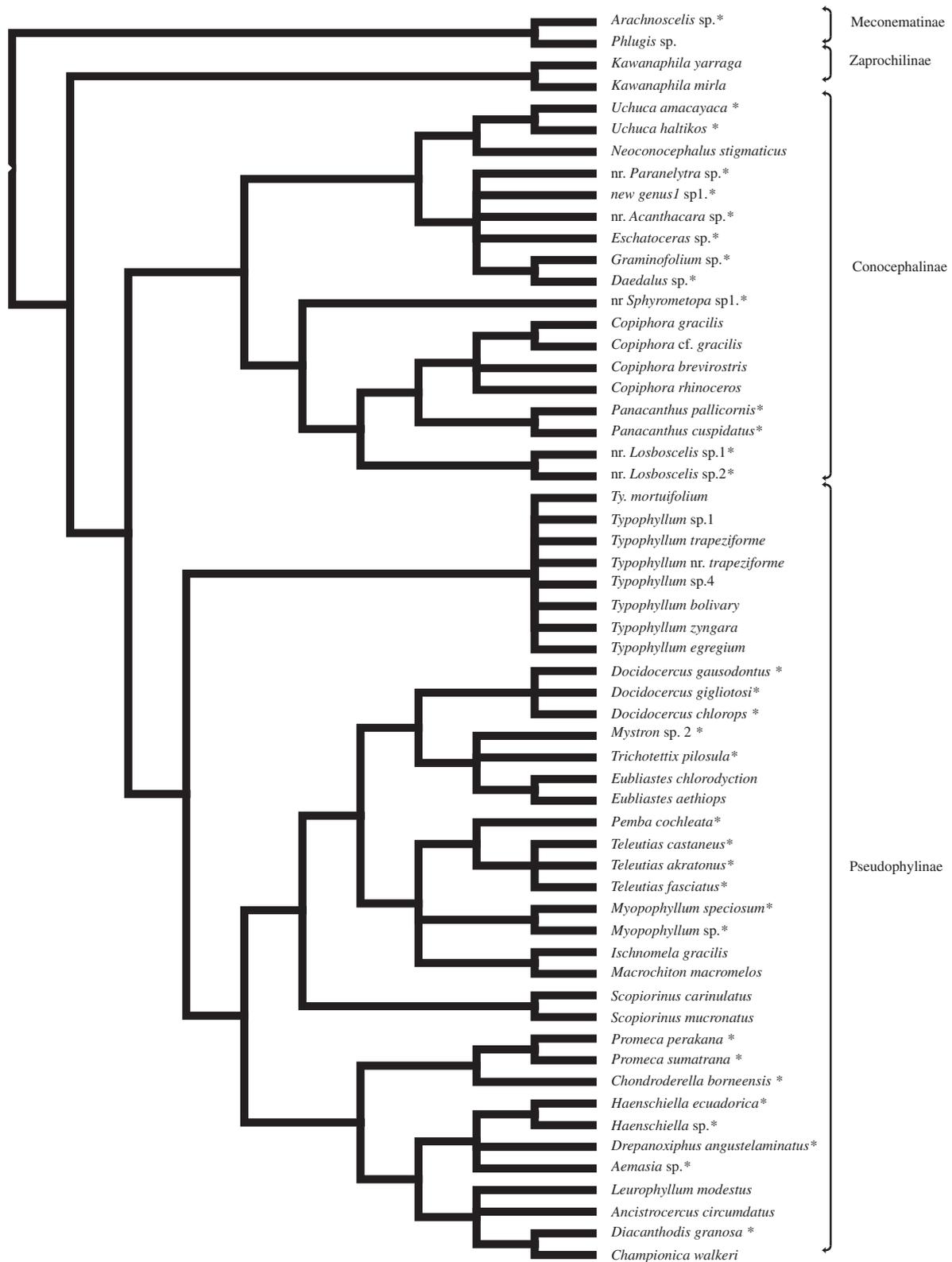
Scaling of sound variables has not previously been undertaken for this family in a phylogenetically controlled analysis. This is also one of the first tests, related to acoustic communication in the order Orthoptera, of a hypothesis of association between sound generator anatomy and the physical characteristics of the calling song.

## Materials and methods

### Species sampling

I performed measurements of katydid song properties, male body size and the dimension of sound generators in 58 species (Fig. 1, Table S1). Acoustic measurements of 39 species were taken from the literature. Measurements for the remaining 19 species were obtained directly from sound recordings made under laboratory conditions (for details see Montealegre-Z, 2005). Of all studied species, only the palaeotropical katydids *Promeca* spp. and *Chondroderella* sp. were not available for morphological measurements. Their measurements were taken from Heller (1995) and by contacting the author (K. G. Heller, personal communication). All morphological measurements are shown in millimetres (mm). Pronotal length was used as an estimate of body size. Other morphological measurements include: mirror length, stridulatory file length and number of teeth on the stridulatory file. These measurements were used to estimate tooth density (teeth  $\text{mm}^{-1}$ ). Acoustic variables measured were  $f_c$  and  $p_d$ .  $p_d$  was measured from the first detectable low amplitude oscillations of the building part to the last few oscillations of the free decay.

Wing-stroke rate is affected by temperature (Walker, 1975; Prestwich & Walker, 1981) and thus  $p_d$  and, to a less extent,  $f_c$ . This is because muscle contraction and stroke rate, increase with temperature (Josephson, 1984); thus at higher temperatures, pulses tend to be shorter, and  $f_c$  higher. To correct for this effect,  $p_d$  and  $f_c$



**Fig. 1** Phylogenetic relationship between 58 species of katydids used in the calculation of the independent contrasts. Asterisks show species of some genera not included in Naskrecki's (2000) phylogeny.

were adjusted (using linear equations) for those specimens from which recordings at different temperatures were available to an extrapolated temperature of 25 °C or nearly so (as most of the recordings obtained from published literature were at this temperature or at a close value).

This analysis is based only on species whose calls are the product of resonant stridulation (pure tones). This mechanism of generation produces wing-closing pulses that are highly sinusoidal because they reflect one dominant frequency (or few harmonically related frequencies) rather than a band. Species using broad-band songs were avoided because only in pure-tone signals can the 1 : 1 relationship between tooth impacts and oscillation of the sound generator be inferred (Elliott & Koch, 1985; Bennet-Clark, 1999; Montealegre-Z & Mason, 2005). This facilitates association between pulse duration, number of cycles and the segments of the file used during sound production.

For exploring morphological data, variables were log<sub>e</sub>-transformed. The effect of body size on different characters was controlled by obtaining the residuals of these interactions, which were then used in subsequent statistical analysis. The number of file teeth did not correlate with body size. Teeth do not result from a multiplicative developing process, and their number remains constant throughout an insect's adult life (Stärk, 1958). Therefore, the removal of body size effect on number of teeth was avoided.

Ordinary least square (OLS) was used to explore the interaction of variables. For example,  $f_c$  and  $p_d$  were log<sub>e</sub> transformed for linearization and as they are function of body size, their residuals were obtained to control for this effect as explained above (Garland *et al.*, 1992). Tables S2 and S3 show the results of OLS analysis of all variables without phylogenetic correction. As predicted,  $p_d$  showed a significant negative relationship with  $f_c$ , and  $f_c$  with body size. These data were used in a subsequent comparative analysis.

### Comparative analysis

For comparative analysis, I used the method of phylogenetically independent contrasts (PIC) (Felsenstein, 1985; Harvey & Pagel, 1991) and the most recent phylogenetic hypothesis available for Tettigoniidae, as proposed by Naskrecki (2000). This phylogeny was built on 300 morphological characters and mostly resolved at tribe and subfamily level, incorporating 198 genera. Thirty-three species were not originally included in Naskrecki's phylogeny, but are incorporated in this study (Fig. 1). Therefore, their position in the topology was established using their phylogenetic or taxonomic relationships on Naskrecki's phylogeny (i.e. they were inserted into the clades of their respective subfamilies or tribes, or genera). For those subfamilies or tribes for which just one or two species were available, species

allocation was straightforward, whereas three or more species of the same group (genus or tribe) ended sometimes in polytomies (Fig. 1).

Phylogenetically independent contrast analysis of morphological and acoustic variables employed the *PDAP* package (Midford *et al.*, 2008) of *MESQUITE* Software, version 1.12 (Garland *et al.*, 1992; Maddison & Maddison, 2006); positivizing contrasts in  $x$ -axes (Garland *et al.*, 1992). PICs were obtained from the log-transformed character data. Equal branch lengths (length = 1.0) was assumed, except in polytomies where the branch length was 0, as resolved by the program. A total of 16 polytomies were resolved and a bifurcating tree, from which 57 contrasts were extracted, was obtained. Fifty-six degrees of freedom was used to conduct the PIC analysis, but to produce a more conservative analysis, polytomies were taken into account and a second test performed, reducing the degrees of freedom by the number of polytomies, to 40.

Phylogenetically independent contrast analysis followed the same protocol used for phylogenetically uncorrected data. Briefly, contrasts obtained with the *MESQUITE PDAP* package were standardized for subsequent analysis. OLS through the origin was performed between contrasts of log body size with contrasts of other variables that correlated with body size, obtaining the residuals (free from body size effect) of these regressions for subsequent analysis. Residuals of the variables of interest were regressed through the origin (Garland *et al.*, 1992).

Just & Shaw (2006) found conflicts between morphological and molecular data, concluding that this may indicate a high degree of morphological homoplasy in Ensifera, particularly in regard to acoustic characters (such as forewing structures). The phylogeny of Tettigoniidae used in this study might be questionable because it was based on morphology, and my assumption that this phylogeny is accurate might compromise the analysis. From Naskrecki's (2000) phylogeny, information about taxonomy and possible phylogenetic relationships is available. Therefore, to reinforce the analysis I assumed that the phylogeny provided by Naskrecki was only partially known. Briefly, to further evaluate phylogenetic tree topology and branch length uncertainty (Housworth & Martins, 2001), I used a random branching process on the same tree used in the analysis, and also generated 1000 trees from a Bayesian analysis. For these analyses, I report slope estimates, correlation coefficients, standard errors, confidence intervals and variances of standardized independent contrasts using *MESQUITE*. The same analysis performed with 1000 simulated trees yielded similar results (Table S4).

### Allometry of the sound generator

To study the anatomical scaling of sound generator variables, I conducted analyses on species data and on

PIC among morphological variables with the method of standardized major axis (SMA). SMA is recommended for allometric comparisons and can be used with PIC (Warton *et al.*, 2006). Morphological variables were tested against the null hypothesis of isometry, with slopes of one for the log of sound generator morphology (file length, number of file teeth, tooth density and mirror length) vs. log body size. The log of number of teeth, and log of tooth density, vs. log of file length were also tested. Allometry analysis involved the log of species data, and the PIC data. For SMA on PIC, the line was forced to pass through the origin (Garland *et al.*, 1992; Warton *et al.*, 2006). The effect of body size was uncorrected in both cases. All statistical analyses were carried out with the program *SMATR* (Falster *et al.*, 2006).

## Results

### The effect of body size on other morphological variables

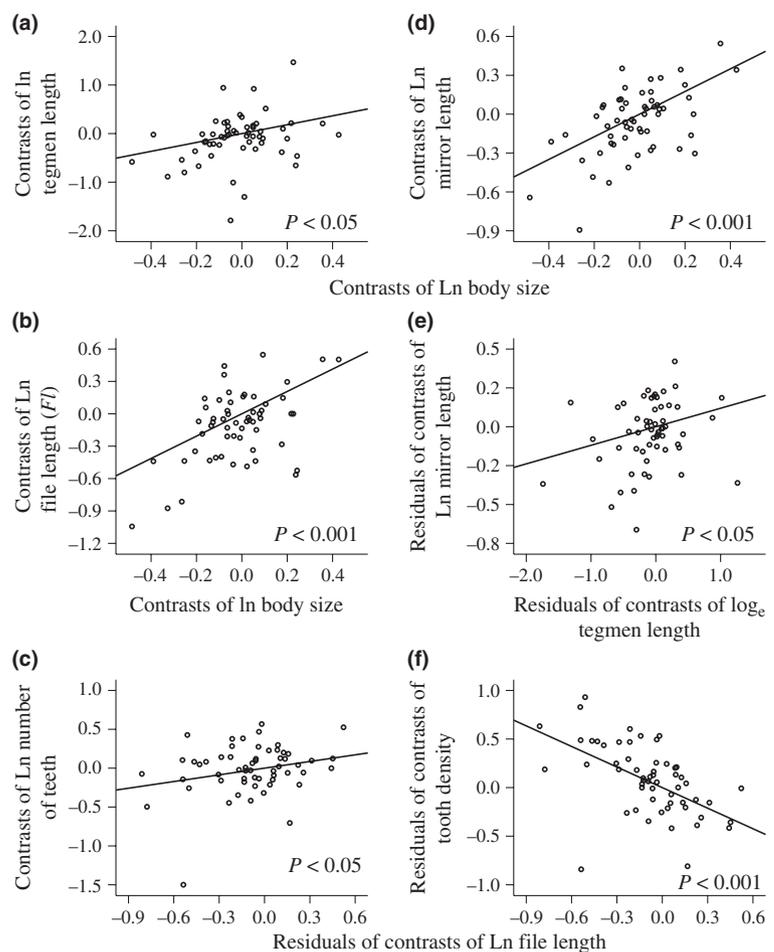
Forewings, mirror and file dimensions are well predicted by body size. Body size significantly explains only a low

percentage of variation in forewing length, but it does predict mirror and file dimensions (Fig. 2a,b,d, Table 1). In both cases, the correlation increases after the phylogenetic effect is removed. Forewing length explains the changes in mirror dimension only by a low amount (Fig. 2e); the correlation decreased ca. 65% after controlling for phylogeny. Conversely, forewing size does not predict file length (Table 1).

After controlling for phylogeny, the number of file teeth was still positively correlated with file length (Fig. 2c), but a strong decrease in the correlation was observed (Table 1). Increasing file length negatively affects tooth density and this interaction was highly significant for the analysis with species data and that with PIC, with similar slopes in each case (Fig. 2f, Tables 1 and S2). Thus, in katydids, larger files tend to have a larger number of teeth, and also to have teeth more openly spaced.

### Allometry of the sound generator

The slope of all sound generator characters (except number of teeth) against body size was significant;



**Fig. 2** (a,b) Regressions between the independent contrasts of body size (re-pronotal length) file and tegmen length. (c) Relationship between residual of contrast of file length with residuals of contrasts of number of teeth. (d,e) The effect of body size and tegmen length on mirror dimensions. (f) Correlation between file length and tooth density. Phylogenetic independent contrasts applied to the log-transformed data of all variables; residuals obtained by regressing contrasts of allometric variables on contrasts of body size. For details of statistical analyses and interactions of other variables see Table 2.

**Table 1** Regression (through the origin) of morphological variables with phylogenetic correction on species means.

	$F_{1,56}$	$r^2$	$P$ -value	Slope	95% CI	SE
Ln body size related scaling						
File length*	19.70	0.26	0.000	1.03	0.57, 1.50	0.23
Number of file teeth*	2.31	0.04	0.134	0.38	-0.12, 0.88	0.25
Mirror length*	25.81	0.32	0.000	0.87	0.53, 1.22	0.17
Tegmen length*	6.28	0.10	0.015	0.93	0.19, 1.67	0.37
Ln tegmen length related scaling†						
File length†	2.43	0.04	0.13	0.12	-0.04, 0.28	0.08
Mirror length†	4.33	0.10	0.042	0.12	0.00, 0.23	0.06
Ln file length related scaling‡						
Tooth density‡	26.44	0.32	0.000	-0.71	-0.98, -0.43	0.14
Number of teeth	4.17	0.07	0.046	0.5	0.01, 0.57	0.14

All equations of the form:  $\text{Ln } Y = \text{slope} \times \text{Ln } X$ .

\*Phylogenetic independent contrasts (PIC) analysis applied to the log of all morphological data.

†The effect of body size (re pronotum length) was removed from all variables that scale with body dimension by obtaining the residuals from the regression of contrasts of  $\text{Ln } Y = \text{slope} \times \text{Ln body size}$ .

however, none of these variables scales isometrically with body size. These results apply to both uncorrected data and PIC (Table 2). Conversely, tooth density and number of file teeth scale isometrically with file length, in both situations, with species data and with PIC (Table 2).

### PIC on acoustic and morphological variables

$p_d$  was negatively correlated with  $f_c$ , supporting my predictions (Fig. 3a, Table 3); a reduction of only 12% in the coefficient of determination was observed after controlling for phylogeny.  $p_d$  was also positively correlated with file length and with number of file teeth (Fig. 3b,c, Table 3). Body size on the other hand, explains ca. 19% of any change in  $f_c$  (Fig. 3d, Table 3).

**Table 2** Standardize major axis (SMA, Warton *et al.*, 2006) fitting on morphological data with and without phylogenetic correction on species means.

	SMA fitting on phylogenetically uncorrected data						SMA fitting on PIC									
	$r^2$	$P_{\text{SMA}}$	Slope	95% CI	int.	$Sl_{\text{Hyp}}$	$F_{1,56}$	$P_{\text{Hyp}}$	$r^2$	$P_{\text{SMA}}$	Slope	95% CI	$Sl_{\text{Hyp}}$	$F_{1,55}$	$P_{\text{Hyp}}$	
Ln body size related scaling																
File length	0.20	0.000	1.77	1.40, 2.25	-2.51	1.0	25.70	0.000	0.24	0.000	1.96	1.56, 2.46	1.0	38.64	0.000	
No. file teeth	0.24	0.002	1.77	1.40, 2.23	1.87	1.0	26.63	0.000	0.06	0.063	2.04	1.58, 2.64	1.0	35.45	0.000	
Tooth density	0.00	0.789	1.49	1.14, 1.94	1.79	1.0	9.29	0.004	0.06	0.065	-2.07	-2.67, -1.61	1.0	37.50	0.000	
Mirror length	0.19	0.001	1.40	1.11, 1.78	-1.69	1.0	8.21	0.006	0.27	0.000	1.51	1.20, 1.89	1.0	13.65	0.000	
Tegmen length	0.20	0.000	2.47	1.95, 3.14	-1.31	1.0	74.96	0.000	0.10	0.013	2.89	2.25, 3.70	1.0	100.76	0.000	
Ln tegmen length related scaling																
File length	0.36	0.000	0.72	0.58, 0.89	-1.57	1.0	10.12	0.002	0.14	0.003	0.68	0.53, 0.87	1.0	10.34	0.002	
Mirror length	0.39	0.000	0.57	0.46, 0.70	-0.95	1.0	32.87	0.000	0.18	0.001	0.52	0.41, 0.66	1.0	32.92	0.000	
Ln file length related scaling																
Tooth density	0.19	0.001	-0.84	-1.06, -0.66	4.86	1.0	2.18	0.146	0.24	0.000	-1.06	-1.33, -0.84	1.0	0.24	0.630	
No. teeth	0.42	0.000	1.00	0.82, 1.22	4.38	1.0	0.00	0.987	0.22	0.000	1.04	0.826, 1.32	1.0	0.13	0.719	

Effect of body size included for purposes of scaling. Equations of the form:  $\text{Ln } Y = \text{intercept} + \text{slope} \times \text{Ln } X$ .  $P_{\text{Hyp}}$  = null hypothesis.

$f_c$  is also predicted by file length (Fig. 3e), but curiously neither number of file teeth nor tooth density correlate with  $f_c$  (Fig. 3f, Table 3). Therefore, elongate files with a large number of teeth evolved in the context of producing pulses (sound produced during a single closing stroke) of long duration, but not necessarily of high frequency.

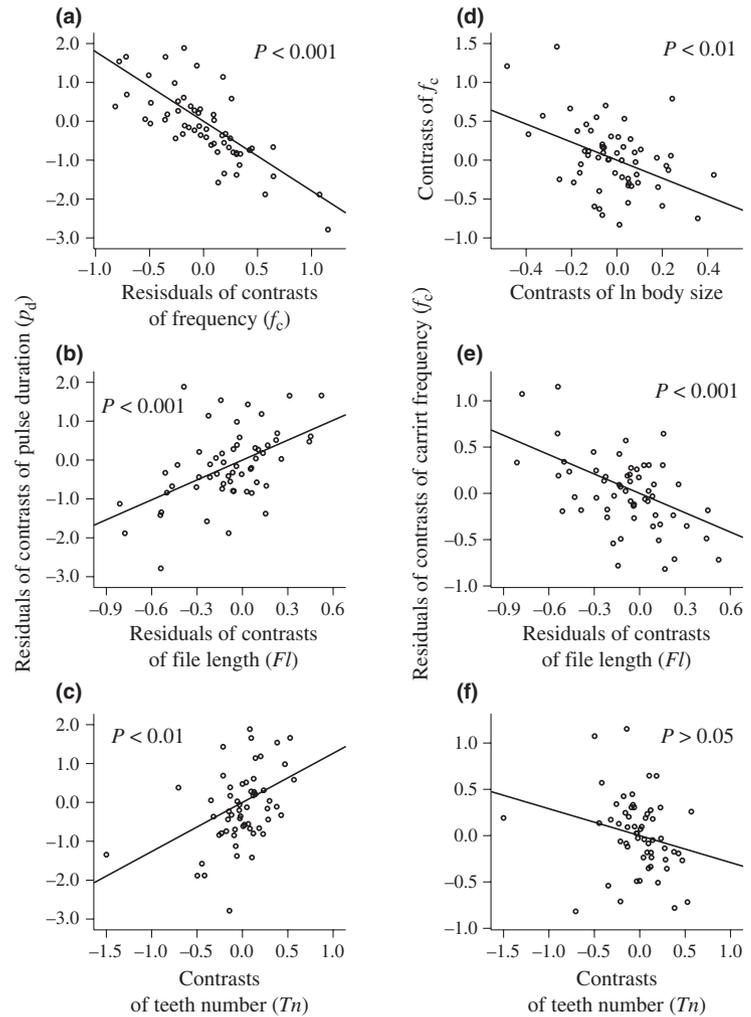
Similar results were obtained by assuming random branch lengths on the topology shown in Fig. 1, and also assuming inaccurate phylogeny (Table S4).

## Discussion

Evolutionary correlations are shown here between some structures of the male stridulatory apparatus, and the acoustic parameters  $p_d$  and  $f_c$ . These correlations suggest a simple micromutational process that could lead to anatomical modification of the katydid stridulatory organ through selection acting on acoustic signals (Toms, 1993): that is, adaptation and natural selection acting on song characters could have led to changes in the number of file teeth, tooth distribution and mirror (area) reduction. Below I present a broad discussion on this topic.

### The effect of body size on morphological and acoustic variables

Allometric scaling of acoustic organs with body size suggests evolutionary influences on  $f_c$  other than body size. The low correlation (although highly significant) between  $f_c$  and body size found in this study, together with the results of Del Castillo & Gwynne (2007), showing that  $f_c$  is not explained by body size, indicates a certain phylogenetic association between both traits. In contrast to vertebrates, katydid body size alone cannot explain the changes in  $f_c$  in all situations.



**Fig. 3** (a–c) Pulse duration ( $p_a$ ) and its relationship to acoustic and morphological variables. Note the strong interaction between  $p_a$  and  $f_c$  (a), file length (b), and the number of teeth in the file (c). (d–f) The effect of body size (re-pronotal length) and some other structures of the pars stridens on  $f_c$ . See Table 3 for details of statistical analyses.

An explanation for this might be that some species of relatively large size have evolved disproportionately small sound generators, whereas still others have developed biomechanical strategies to produce different  $f_c$  during calling. *Myopophyllum* spp., *Metrioptera sphagnorum* and *Ischnomela gracilis* are the examples of these situations.

Males of *Myopophyllum* spp. generate pure-tone calls with individual carriers falling between 68 and 90 kHz; they are of relatively large size compared with other ultrasonic katydids (e.g. *Arachnoscelis* sp., *Haenschiella* sp.) and exhibit a notable reduction in mirror area (Montealegre-Z, 2005; Montealegre-Z *et al.*, 2006). *Metrioptera sphagnorum*, exhibit two stridulatory modes related to two intensity levels, in which each one involves a particular audio (ca. 17 kHz) and ultrasonic (ca. 33 kHz)  $f_c$  (Morris, 1970). For each mode, the scraper sweeps different file regions, with morphologically different teeth (Morris & Pipher, 1972). *Ischnomela gracilis* has two similar intensity levels at 15 kHz and ca. 80 kHz, but

stridulatory movements suggest that tooth strikes occur to excite the 15 kHz component whereas the 80 kHz result from a higher mode of vibration (Montealegre-Z, 2005). Thus, mirror dimension and/or the biomechanical properties for exploitation of different  $f_c$  on the same generator could have been selected for building-in ultrasounds independent of body size, at least in some groups.

Additionally, body size and  $f_c$  can be strongly associated in some species that use ultrasounds. Because ultrasonics lose energy more rapidly with distance, especially in humid air (Römer, 1993), it seems questionable they would aid in enticing distant females. Using such frequencies a caller limits the reach of his broadcast and (possibly) increases his cost, because equivalent intensity levels must be maintained. Therefore, ultrasonic singing should be energetically more demanding (Bailey *et al.*, 1993). Male size seems to be related to the metabolic cost of gonad production (Blanckenhorn *et al.*, 2007), and the energetics of singing affects

**Table 3** Regression (through the origin) of acoustic variables.

	$F_{1,56}$	$r^2$	P-value	Slope	95% CI	SE
Regression on body size						
Carrier frequency	13.35	0.19	0.001	-1.16	-1.80, -0.52	0.32
Pulse duration	9.83	0.15	0.003	2.35	0.85, 3.86	0.75
Regression on file length						
Carrier frequency	19.86	0.26	0.000	-0.70	-1.01, -0.38	0.16
Pulse duration	21.84	0.28	0.000	1.70	0.98, 2.44	0.37
Regression on mirror length						
Carrier frequency	54.97	0.50	0.000	-1.30	-1.65, -0.95	0.18
Pulse duration	38.07	0.405	0.000	2.78	1.88, 3.68	0.45
Regression on tegmen length						
Carrier frequency	1.82	0.03	0.183	-0.15	-0.36, 0.07	0.11
Pulse duration	3.76	0.06	0.058	0.49	-0.02, 0.99	0.25
Regression on number of file teeth*						
Carrier frequency	3.19	0.05	0.080	-0.29	-0.62, 0.04	0.16
Pulse duration	12.49	0.18	0.001	1.26	0.55, 1.98	0.36
Regression on tooth density						
Carrier frequency	2.48	0.03	0.121	0.21	-0.06, 0.49	0.14
Pulse duration	0.21	0.00	0.650	-0.15	-0.81, 0.51	0.33
Regression on carrier frequency						
Pulse duration	75.22	0.57	0.000	-1.79	-2.20, -1.38	0.21

PIC, phylogenetic independent contrasts.

\*The effect of body size was removed from most variables, except from number of file teeth (see Materials and methods), by obtaining the residuals from the regression  $\ln Y = \text{slope} \times \ln \text{body size}$  (Garland *et al.*, 1992).

spermatophore production in katydids (Bailey *et al.*, 1993; Simmons & Gwynne, 1993; Gwynne, 2001; Robinson & Hall, 2002; Del Castillo & Gwynne, 2007). Therefore, the trade-off between spermatophore size and  $f_c$  could constrain an increase in males' body size in some katydids (Del Castillo & Gwynne, 2007), especially in those species using rapid (energetically demanding) wing-stroke rates (Bailey *et al.*, 1993; Montealegre-Z *et al.*, 2006). Nevertheless, a few species have incorporated elastic energy into the generating process so that the scraper moves much faster whereas wings and muscles move at lower speeds [an adaptive mechanism of energy conservation (Montealegre-Z *et al.*, 2006)]. Therefore, the fact that  $f_c$  can be altered by behavioural and/or biomechanical strategies of the sound generator, and that body size depends on vital physiological processes, might add noise to the interaction between  $f_c$  and body size, and produce the low correlation observed here and also by other authors. Thus, the highly significant interaction observed in the phylogenetically uncorrected data between body size and  $f_c$  (Table S3) is explained in part by the evolutionary relationships of the katydid species.

### Stridulatory file and acoustic parameters

The evolutionary history of acoustic communication by katydids appears to have taken a direction of ultrasound exploitation. Katydids are the only group of Ensifera

using ultrasonic or extreme ultrasonic  $f_c$ . Of all species whose acoustic features are adequately reported in the literature (ca. 400 species), about 66% have spectra dominated by ultrasonic frequencies (i.e. > 20 kHz, Suga, 1966; Heller, 1988; Morris *et al.*, 1994; Heller, 1995; Montealegre-Z & Morris, 1999; Braun, 2002; Montealegre-Z, 2005).

The sound generator of katydids has been dramatically modified to achieve such high-frequency signals. But there must be a trade-off between the area utilized for sound radiation and the wavelength of the sound produced (Fletcher, 1992). For a 'roughly circular' radiating source, such as the katydid mirror, the minimum dimension for good source-to-medium loading should be a radius of ca. 1/6 the carrier wavelength (Bennet-Clark, 1998). In this way, high frequency production in katydids could have constrained the selection for specific file morphology to optimize tooth strikes and to adapt sound wavelengths to the size of the radiator.

One would then expect files with high tooth density to be correlated with short wavelengths (high frequencies), because file teeth work as frequency multipliers (Michelsen, 1998). Therefore, assuming all file teeth are struck in sequence, the higher the tooth density on a short file segment, the more teeth struck during a scraper sweep and the shorter the wavelengths of the produced pulse (i.e. the higher  $f_c$ ). However, in this study neither tooth density nor tooth number correlates with  $f_c$  (Fig. 3f, Table 3). High frequencies tend to be generated by individuals with a small number of teeth in their files, which shows that high tooth numbers are not necessary to achieve high frequencies.  $f_c$  is a function of file length, and file length in turn, scales isometrically with tooth number and tooth density (Table 2); but there should be an upper limit on the number of teeth a file can accommodate. Thus, one can observe that body-size selection might constrain the evolution of small files with high tooth densities (Fig. 2b,f), but that such files are not necessarily selected to produce high frequencies (Table 3). It might seem that the observed insignificant correlation between  $f_c$  and tooth density and tooth number is related to a mechanism that enables the control of  $f_c$  independent of tooth distribution (similar to the escapement used by crickets), where the control of  $f_c$  is achieved by the radiator. But, katydids do not use an escapement mechanism because forewings are asymmetrical (Montealegre-Z, 2005; Montealegre-Z & Mason, 2005).

In Gryllidae and Gryllotalpidae, gradual changes in the stridulatory file through selection, especially  $f_c$ , should be more difficult to determine as the  $f_c$  range exploited by most species is usually limited to a small range (2–8 kHz). Actually, some authors have searched for correlations between morphology of the stridulatory apparatus including the file and the acoustic parameters across different species of crickets and mole crickets (Rakshpal,

1960; Walker & Carlyle, 1975; Toms, 1993; Desutter-Grandcolas, 1995, 1998; Hoffart *et al.*, 2002), but with the exception of harp dimension vs.  $f_c$ , so far no obvious interaction has been found. This can be related to the use of an escapement mechanism: if escapement is universal in Gryllidae, absent in Tettigoniidae, there should be less variation in cricket file morphology than in that of katydids. The wide range of  $f_c$  used by katydids without the restriction of an escapement mechanism may have allowed several possibilities of stridulatory technique and morphological adaptation to be explored. This has presumably influenced the evolution of ultrasound production in this family.

The highly significant relationship between  $p_d$  and  $f_c$  (Fig. 3a) is explained by the anatomical design of the sound generator. Small katydids tend to have short files (Fig. 2b, Table 1) and the isometric relationship between file length, tooth density and tooth number (Table 2) shows that teeth are packed more closely together in short files than in large files: in large files tooth density is lower (perhaps tooth thickness, not measured in this study, is the key scaling factor explaining these file features) (Fig. 2f). If the number of teeth represents the number of driven oscillations in a pulse, then a short file holding many teeth could be scraped quickly, generating a short pulse, dense in oscillations (i.e. a high-frequency pulse). However, such a theoretical 'fast multi-impact scraping' model apparently was not the mechanism selected over the evolution of Tettigoniidae [at least for species with  $f_c$  above 40 kHz (Montealegre-Z *et al.*, 2006)]. The trade-off between radiator size and wavelength, and the fact that high frequency sounds attenuate more rapidly due to spreading and atmospheric absorption than low frequency ones (Wiley & Richards, 1978) are limiting factors in the production of ultrasounds with optimal intensity levels. But maintaining equivalent intensity levels is relevant for species survival in acoustic animals. Therefore, I suggest that tooth strike optimization (derived from scraper and file adaptations) was the mechanism, selected during ultrasonic communication in the family Tettigoniidae. Intensity optimization in small radiators adapted for high-frequency production can be obtained by increasing momentum and transfer of kinetic energy from scraper-file interactions to the radiating forewing regions.

The following analysis is offered: collisions between two objects are governed by laws of momentum and energy transfer (Serway & Jewett, 2004). Increments in velocity of two objects in opposite direction (e.g. scraper and file teeth) will result in large momenta and consequently in increments of the amounts of energy dissipated after the impact has occurred (Tipler & Mosca, 2004). Therefore, the amount of kinetic energy directed into the forewing oscillator will be proportional to the momentum (Prestwich & O'Sullivan, 2005). In crickets and mole crickets, the relationship between peak amplitude of each sound oscillation and inter-tooth distance is

linear (Bennet-Clark, 1970, 1987; Prestwich & O'Sullivan, 2005), and this is also common in other singing Ensifera, including katydids (Montealegre-Z, 2005). According to this, a working hypothesis would be that widely spaced teeth might allow escalating scraper velocity and, in turn, momentum, which might result in stronger impacts and dissipation of large amounts of energy into the forewing oscillator. The propagation of high frequencies demands higher metabolic energy to maintain an equivalent intensity over several metres (Bailey *et al.*, 1993). Increased kinetic-energy transfer will require a minimum tooth space for effectiveness, which is difficult to achieve in a small file over-packed with teeth. For effectiveness, such a model would also require a mechanism that propels the scraper at elevated speeds between teeth, which involves elastic energy (Montealegre-Z *et al.*, 2006). For efficiency, optimal tooth impacts produced by this mechanism should match the resonant properties of the radiator.

Katydid are constrained by a metabolic factor from producing sustained tonal calls above ca. 40 kHz (referred to as 'critical carrier'). Below this frequency closing wing speed matches the speed of tooth impacts and correlates positively with  $f_c$ . Tooth distribution differs in species singing above and below the critical carrier. Below the critical carrier, pure-tone singers tend to exhibit stridulatory files designed for continuous scraper sweeps in which inter-tooth space gradually increases in the same direction of scraper movement (Montealegre-Z, 2005; Montealegre-Z & Mason, 2005). In contrast, files of species singing above the critical carrier are designed for interrupted scraper movements with more erratic and unpredictable file distribution, therefore, systematic tooth distribution is not important in these species (Montealegre-Z *et al.*, 2006). Indeed, in extreme ultrasonic singers where file length scales with body size (Fig. 2b), files densely packed with teeth may cause problems for the correct performance of the elastic energy mechanism explained above. Observations of reduced tooth number and a more erratic tooth distribution in extreme frequency species support this idea (Montealegre-Z, 2005).

## Conclusions

This article explains the evolutionary relationships between the sound generator structures and the acoustic features of the produced sound in katydids, and suggests that anatomical designs that enhance tooth strike rates should be considered as critical factors during the evolution of stridulation in this group of insects. The insignificant correlation between  $f_c$  and tooth density, and  $f_c$  and number of stridulatory file teeth suggests that a mechanism, other than files with high density of teeth, designed to provide frequency multiplication and to maintain the equivalent sound intensity gain, was selected during the evolution of ultrasonic exploitation

in katydids. Such a mechanism should facilitate appropriate scraper-tooth drive, momentum, and kinetic energy transfers. This can only be attained with elongated flexible scrapers (Montealegre-Z *et al.*, 2006) and minimum optimal average inter-tooth spacing, which provides the displacement, and the scraper recoiling velocity, necessary to reinforce momentum. Adaptations of the stridulatory file structure and scraper anatomy should facilitate this mechanism (Montealegre-Z *et al.*, 2006). This analysis also suggests that during the evolution of acoustic communication in the Tettigoniidae, mirror, file length and tooth number were the anatomical structures influenced through selection of  $p_d$  and  $f_c$ . Selection could act on the song, by female choice preference for calls with certain characteristics, and this would lead to directional selection in the morphology of the stridulatory organs. For example, mirror reduction in the case of high frequencies (Table 3), elongated files to accommodate more teeth (Fig. 2c), and special anatomical designs of file teeth and scraper to enhance tooth strikes. The phenotypic and genetic variation in the stridulatory file, the intraspecific correlation observed between variation in call parameters ( $p_d$  and  $f_c$ ) and variation in the stridulatory organs (i.e. mirror, file length, file-tooth number), and the problems of attenuation of high frequency signals suggest that female selection on call parameters affects the morphology and the mechanics of the male stridulatory organ.

Finally, I want to emphasize the tentative nature of this study in referring to shared features of all katydids that are particular to those using pure tones (i.e. resonant stridulation). A large number of species of katydids employ noisy signals [non-resonant stridulation, e.g. *Conocephalus* spp., and many others, see Heller's (1988) revision]. It is possible that the  $f_c$  in this species is controlled by some of the factors studied here, especially mirror dimension (Sales & Pye, 1974). But the complex features of non-resonant stridulation make it difficult to study these species from some of the perspectives used in this work, especially the correlation between file morphology and pulse duration. However, because katydids seem to have descended from an ancestor that employed resonant stridulation (Jost & Shaw, 2006), the approach adopted in this study (including only resonant stridulation) proves to be an important step for understanding the evolution of stridulation in the family Tettigoniidae.

## Acknowledgments

This study was supported by Natural Sciences and Engineering Research Council of Canada, operating grant (4946) to Glenn K. Morris (University of Toronto). I gratefully acknowledge discussion and support from Glenn K. Morris during the execution of this project. David I. Warton provided feedback and guidance during the SMA analysis. Raúl Cueva del Castillo gave feedback

in the comparative analysis. Measurements of palaeotropical katydids were supplied by Klaus G. Heller. The Colombian environment Ministry approved permits to conduct fieldwork in Colombian national parks (decree 309 of the 25 February 2000), special thanks to Margarita Gnecco-O, Nancy Murillo-B, and Luz Aida Angel-P for processing permits. Erika Morley and Thorin Jonsson helped reviewing the document. Special thanks to my wife Liliana Castano-R for all her support, our daughter Camille Marie was born on the day this article was submitted.

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## Supporting information

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

**Table S1** Morphological and acoustic data used in the comparative analysis.

**Table S2** LSO analysis of morphological data without phylogenetic correction on species means.

**Table S3** Conventional regression of acoustic variables on sound generator morphology without phylogenetic correction on species means.

**Table S4** Randomization tests using the method of independent contrasts.

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Received 25 June 2008; revised 16 September 2008; accepted 11 October 2008