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Size and carrier in the bog katydid, *Metrioptera sphagnum* (Orthoptera: Ensifera, Tettigoniidae)

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Abstract

Among crickets and katydids calling carrier frequency is often inversely related to body size. Within species, this relationship is so far found consistently for species employing nonresonant stridulation, but not always among those using resonant stridulation. *Metrioptera sphagnum*, is an unusual acoustic species in making two different spectra, one by nonresonant, one by resonant, stridulation. The nonresonant carrier of this insect correlates inversely with body size; the carrier of the elastic-resonant song part does not. Complex-wave pulses made over the distal half of the stridulatory file, give a nonresonant spectrum with a broad audio band, peaked near 19 kHz; sinusoidal pulses, made over the proximal half of the file, give an ultrasonic peak near 35 kHz. The sometime absence of a body-size effect in resonant stridulation may arise from the importance in this mechanism of tooth-contact rates: these provide a way of affecting carrier independent of isometry. Another possible factor in expressing body size acoustically is that nonresonant radiators may show less departure from natural vibration modes. Sound intensity in *M. sphagnum*, though affected by temperature, could not be correlated with size.

Introduction

It is a common perception that size and frequency of sound-generating devices are inversely related: the larger the tuning fork the lower its pitch. This is also somewhat true of acoustically signalling animals: carrier frequency is often — but not always — inversely related to body size (Gerhart & Huber 2002, p 41). In this paper I review body size and carrier in acoustic Ensifera (crickets and katydids) in the context of the two basic stridulatory generating mechanisms used by these insects: resonant and nonresonant stridulation (Elsner & Popov 1978).

I then consider a katydid species *Metrioptera sphagnum* (F. Walker, 1869), in which the signalling of body size to conspecifics is likely to be important. This is because males of *M. sphagnum* attract females by calling (Morris 1975) and because the males, of this and many other katydid species, provide a large food gift to the female: singing can signal "...aspects of the phenotype correlated with the ability to supply direct or indirect genetic benefits" (Gwynne, p.175, Table 7.2). So size might be important in *M. sphagnum*'s choice of mates. And it may also be important in this species because males engage in song-mediated spacing and aggression (Romer & Morris in prep.), size being in animals "the most commonly observed determinant of winning or losing a fight" (Bradbury & Vehrenkamp 1998, p.681).

The bog katydid is remarkable in using both resonant and non-resonant stridulation to make two distinct carriers: it alternates between an ultrasonic and an audio-dominated frequency spectrum, each spectrum associated with distinctive tegminal motion patterns (Morris 1970). I sought for body-size correlations to this dual-car-

rier stridulation. Results find body-size information encoded in the audio, but not the ultrasonic portion of the male calling song of this species.

Size and carrier.—Sound frequencies of a singing animal are often negatively related to its body size (Bennet-Clark 1998, Gerhardt & Huber 2002, p.41-43, Cocroft & De Luca 2006). Just as bigger steam whistles on bigger steamships, toot at lower frequencies: larger radiators, on larger katydids or crickets can be expected to emit lower carrier frequencies. Carrier frequency — used here to mean the most intense frequency in a spectrum — will be, for a "reasonably equiaxial" sound-radiating membrane, determined by the membrane's tension, thickness and area; and the radiator's fundamental frequency mode will be "inversely proportional to the square root of the area of the membrane" (Fletcher 1992, p.70). It is this 'area of the membrane' that leads us to expect the ensiferan carriers of ensiferan generators to be inversely affected by body size.

Changes in the carrier of an insect in the course of evolution occur as 1) the effect of indirect selection on body size itself; this is the pleiotropic effect of isometry — the degree to which radiator development is in phase with the growth schedule of nonacoustic body parts. Carrier is also the product of 2) direct selection: e.g., selection acting to favor a pure-tone wavelength that functions in localization (Michelsen & Lohe 1995), or that avoids masking interference (Gerhardt & Huber 2002, p. 42), or through allometry, that encodes adaptive information discriminated by potential conspecific mates or rivals.

"Correlations between carrier frequency and body size can confound the effects of selection on either trait" (Gerhardt & Huber, p. 46) and become a "nuisance" for those trying to understand how carrier has evolved. Carrier will be the result of interplay between indirect body-size effects and direct selection for adaptive frequency upon the generator/radiator. For example, where carrier is determined isometrically, natural selection for smaller body size could counter strong sexual selection imposed by female preferences for lower carriers, or natural selection for larger body size could combine with female-choice sexual selection to enhance male size.

The relation between body size and carrier can be tested either among species or among the individuals of a single species. Bennet-Clark (1998) says not much is known "about how, within an insect taxon, song frequency scales with body size"; but that "over a wide range of tettigoniid species with song frequencies between 4 and 50 kHz, the song frequency is inversely proportional to the square of the length of the mirror frame, the primary resonator in the sound producing structure" (Morris & Pipher 1967; Bailey 1970; Sales & Pye 1974; Gerhardt & Huber, p. 43). Among 48 new and old-world species of Pseudophyllinae, call carrier frequency is

Table 1. Summary of within-species literature testing inverse relation between carrier and size. R, resonant; NR, nonresonant; 'elastic' see text p.

¹ Author(s)	Species	Measure of size	R/NR	Carrier (kHz)	Corr. size?
This paper	<i>Metrioptera sphagnorum</i> ultrasonic mode	Pronotum midline length	R (elastic)	35	No
Morris <i>et al.</i> 1994	<i>Myopophyllum speciosum</i>	Pronotum midline length	R (elastic)	81 (67-95)	No
Gwynne & Bailey 1988	<i>Kawanaphila nartee</i>	Left (functional file) tegmen area	R (?)	51 (47-58)	Yes
This paper	<i>Metrioptera sphagnorum</i> audio mode	Pronotum midline length	NR	18	Yes
Bailey <i>et al.</i> 2007	<i>Anabrus simplex</i> solitary phase	Inverse sq root of mirror area	NR	13.55	Yes
Bailey <i>et al.</i> 2007	<i>Anabrus simplex</i> gregarious phase	Inverse sq root of mirror area etc.	NR	12.24	Yes
Howard & Hill 2006	<i>Gryllotalpa major</i>	Body length	R	2.0	Yes
Brown <i>et al.</i> 1996	<i>Oecanthus nigricornis</i>	PC: teg. width & length, length head, hindwing, foretibia	R	3.75 (field) 3.62 (lab)	Yes
Ponce-Wainer <i>et al.</i> 2008	<i>Oecanthus niveus</i>	PC: tegmen length & width, hind femur length	R	~2.25	Yes
Simmons & Ritchie 1996	<i>Gryllus campestris</i>	Harp area	R	4.5	Yes
Scheuber <i>et al.</i> 2003	<i>Gryllus campestris</i>	Harp area	R	4.7	Yes
Judge 2009	<i>Gryllus pennsylvanicus</i>	Harp area, head width, pronot. width & length, femur length	R	4.6 (field) 5.0 (lab)*	Yes
Bateman <i>et al.</i> 2004	<i>Gryllus bimaculatus</i>	Thorax width	R	3.5-6.7	No
Ferreira & Ferguson 2002	<i>Gryllus bimaculatus</i>	PC: thorax width, length, head width, length etc.	R	4.4-4.7	No
Champagnon & Cueva del Castillo 2008	<i>Gryllodes sigillatus</i>	PC: thorax width, wing width, length, 3 rd femur length	R	6.8	No

¹ *pers. comm. K. Judge

found to vary inversely with body size (Heller 1995).

Heller's data are not corrected for phylogeny using independent contrasts (Felsenstein 1985), but where this has been done, the outcome is the same. Cueva del Castillo & Gwynne (2007) found an inverse relation of size to carrier among 58 species of katydids, and attribute it entirely to phylogeny. By contrast, Montealegre (2009), examining the evolutionary relation between mirror (radiator) size and carrier among katydid species that generate sinuoidal calls (as Cueva del Castillo & Gwynne 58 species, but not all the same 58), concludes that "forewings, mirror and file dimensions, are well predicted by body size" and that this correlation increases with the removal of phylogenetic effects.

The widespread nature of this 'inverse pitch' relationship among Ensifera makes it surprising that no significant correlation of "characteristic frequency" was found with either tegmental length or body length among 20 acridid grasshoppers (Meyer & Elsner 1996). In speculating about this exception, Gerhardt & Huber (2002) note that grasshoppers lack specialized wing radiators comparable to those of Ensifera, and that for the broadband signals typical of grasshoppers (nonresonant spectra – see below) it may be problematic to determine a carrier.¹

¹ Obtaining consistencies among spectra produced by nonresonant stridulation is really not problematic. For example *Conocephalus* spp. show extreme stereotypy of spectral subpeak location (Morris & Pipher 1967). Use of moving averages to smooth spectra may have enhanced consistent spectral results in the present paper.

Within mole, field and tree-cricket species (Table 1), workers have often found inverse relationships between calling-song carrier and body size, the latter expressed as the length of generator area, or of some other body part, or some principal-component (PC) combination of body parts. In *Gryllotalpa major*, the prairie mole cricket, carrier is inversely correlated with body length (Howard & Hill 2006). In the field cricket *Gryllus campestris*, carrier decreases with increasing harp area (Simmons 1995, Simmons & Ritchie 1996, Scheuber *et al.* 2003). In the tree cricket *Oecanthus nigricornis*, size (as a PC incorporating head width, hindwing length, foretibia length, forewing length and width) and song frequency are negatively correlated (Brown *et al.* 1996). And yet again, for another tree cricket, *Oecanthus niveus*, carrier is inversely related to body size expressed as a PC of forewing and hind femur dimensions (Ponce-Wainer & Cueva del Castillo 2008). In an extensive study of *Gryllus pennsylvanicus*, every measure of body size employed (head width, pronotum width, pronotum midline length, mean harp area, mean femur length) shows inverse correlation with carrier. The highest correlation coefficient is for harp area, the body part among these others most intimately associated with carrier generation (Judge 2009).

But there are also a number of examples involving crickets where body size is not found to affect carrier. No correlation was seen in *Gryllus bimaculatus* between thorax width and carrier for a huge sample (n=269) of males (Bateman, Ferguson & Ferreira 2004). And an earlier study of the same species reached the same conclusion (Ferreira & Ferguson 2002). For *Gryllodes sigillatus*, using

Table 2. Diagnostic features of resonant and nonresonant stridulation.

Ensiferan stridulation modes:	Resonant stridulation	Nonresonant stridulation
Spectrum	Single dominant frequency, often with harmonics; narrow-peaks; high Q	Multiple adjacent frequencies comprise a band spectrum; low Q
Waveform of pulse	Sinusoidal, reaching amplitude plateau, relatively slow decay	Complex, transient pulses often in trains; relatively rapid decay
Tooth rate	Matched to radiator oscillations, same as carrier frequency	Unmatched, significantly lower than carrier frequency

multiple size measures as a principal component, “body size was not significantly associated with peak frequency” (Champagnon & Cueva del Castillo 2008).

The katydid *Anabrus simplex* (the Mormon ‘cricket’ of western North America) occurs in both solitary and gregarious forms. The solitary males are cryptically green or brown, smaller, and sing at higher carrier frequencies (mean 13.6 kHz); the gregarious males are black, larger and sing with a significantly lower carrier (mean 12.2 kHz) (Bailey *et al.* 2007). In both forms their carriers change negatively with increasing head-capsule width or with increasing mirror (radiator) area.

Myopophyllum speciosum is a pseudophylline katydid, endemic to a valley of the eastern slopes of the Ecuadorean Andes (Morris *et al.* 1994). *Kawanaphila nartee* is a zaprochiline, a pollen and nectar-feeding katydid of western Australia (Gwynne & Bailey 1988). In both these species, individuals generate high ultrasonic carriers of very high Q (extremely narrowly peaked); in both the carrier frequency varies among individuals. In *M. speciosum* average carrier is 81 kHz (range 67 to 95 kHz). In *K. nartee* average carrier within the “higher mode” of carriers (ranging between 47 and 58 kHz) is 51 kHz. For *M. speciosum*, male body size, as pronotum midline length, is not predicted by its carrier (Morris *et al.* 1994); but the opposite is true in *K. nartee* where there is a significant negative correlation between carrier and body size (midline pronotum length) and between carrier and forewing radiator (Gwynne & Bailey 1988).

Overall then, though an inverse correlation between carrier and body size is commonly found among and within katydid and cricket species, there are also clear exceptions, such as *Gryllus bimaculatus* or *Myopophyllum speciosum*. The present paper adds another exception, the ultrasonic mode (see below) of *M. sphagnum*.

Ensiferan stridulation modes.—Stridulation in Ensifera involves rubbing tegmina (forewings) together as a “pick-and-file energy source” (Fletcher 1992, p.240): a pick (plectrum or scraper) at the anal margin of one wing is caught successively on teeth of a ventrally toothed vein (file) of the other wing; each sudden release of the pick makes the insect’s sound radiators oscillate. Two common mechanisms of pick-and-file excitation among ensiferan Orthoptera may be termed resonant and nonresonant (Elsner & Popov 1978, Montealegre & Morris 1999, Montealegre & Mason 2005). They are distinguished by differences in the waveform (time domain) and spectrum (frequency domain), as well as by how the contacts of the pick are timed in relation to the oscillations of the sound radiators (Table 2).

Resonant stridulation mechanisms give rise to a high-Q spectrum dominated by a single narrow frequency peak and often with narrowly peaked harmonics. Nonresonant (‘damped resonant’, Bennet-Clark 1998) stridulation results in a low-Q wide-band spectrum of many adjacent frequencies: an energy ‘aggregate’ typically tens of kHz in width.

Sinusoidal pulses, *i.e.*, simple sine waves, characterize the pulses of resonant mechanisms. The pulses of nonresonant mechanisms are

damped and transient (Bennet-Clark 1998, Fig. 7), decaying rapidly and comprised of complex waves, whereas in resonant mechanisms pulse amplitudes build and decay more gradually and pulses last longer. Resonant pulses are typically sustained over multiple waves, slowly building, then keeping, an amplitude plateau over tens of waves, before finally dying away again relatively slowly.

Tooth contact rates in resonant stridulation keep a critically timed relation to sound-radiator oscillations — one tooth is passed by the scraper for each generated wave — so as to reinforce the oscillation of the radiator at its single dominant frequency (*e.g.*, Walker 1962, Bennet-Clark & Bailey 2002). The radiators are operating at song resonance and act as “regulators” of the song frequency (Bennet-Clark 2003, p. 1480). For nonresonant stridulation, tooth-scraper interaction rates are lower, usually much lower, than the generated carrier. Thus successive pulses usually have time to die away completely, producing a pulse series or pulse train, *i.e.*, a group of distinct or only slightly time-overlapped, rapidly decaying, impulses.

Metrioptera sphagnum calling song.—*Metrioptera sphagnum* (F. Walker, 1869) of the subfamily Tettigoniinae (at one time Decticinae) is classified in the Orthoptera Species File (see refs) as *Sphagniana sphagnum*. ‘Bog katydid’ is a convenient common name. In summer, males call day and night, from tamarack (*Larix*) and black spruce (*Tsuga*) in sphagnum bogs (Morris 1970).

Structure of the two-mode song is illustrated in Fig. 1. The insect sings steadily for minutes at a time, switching without pause between two stroking methods. Acoustic output changes (every quarter second or so) from an audio mode [AM] to an ultrasonic mode [UM] then back again *etc.* Fig. 1A shows three complete ultrasonic modes separated by two complete audio modes.

Using a photo-cell to relate flash photographs of dorsally viewed wing overlap with records of the distinctive time-domain patterning of sound pulses, Morris & Pipher (1972) found that separate file regions are used to generate the two modes. The audio is produced upon the distal half of the file, the ultrasonic upon the proximal. Though the teeth of these two file regions are distinctive, being much broader proximally than distally, these differences grade into one another along the file.

Sound occurs on both opening (fro) and closing (to) of the forewings. The fro sound emission (labelled as such Fig. 1B,C) contributes regularly to the spectra of both modes: it is a brief complex wavetrain, occurring as the scraper moves distad along the file and away from the wing base. The more intense pulse groups in between fros are *pulse trains*. Each mode has its own kind of higher-intensity train, both kinds made on tegminal closure. For the audio mode, this train is comprised of rapidly decaying pulses (~18 such in each of the two complete trains shown in Fig. 1B). For the ultrasonic mode this train is of short, spaced, tonal pulses [SSTP] (four such in each of the two complete trains shown in Fig 1C). These simple sine waves typically plateau in amplitude, creating a distinctive ‘flat’ envelope over the first 15 waves or so of a pulse (inset Fig. 1E; the gap in this pulse between waves 7 and 8 is atypical).

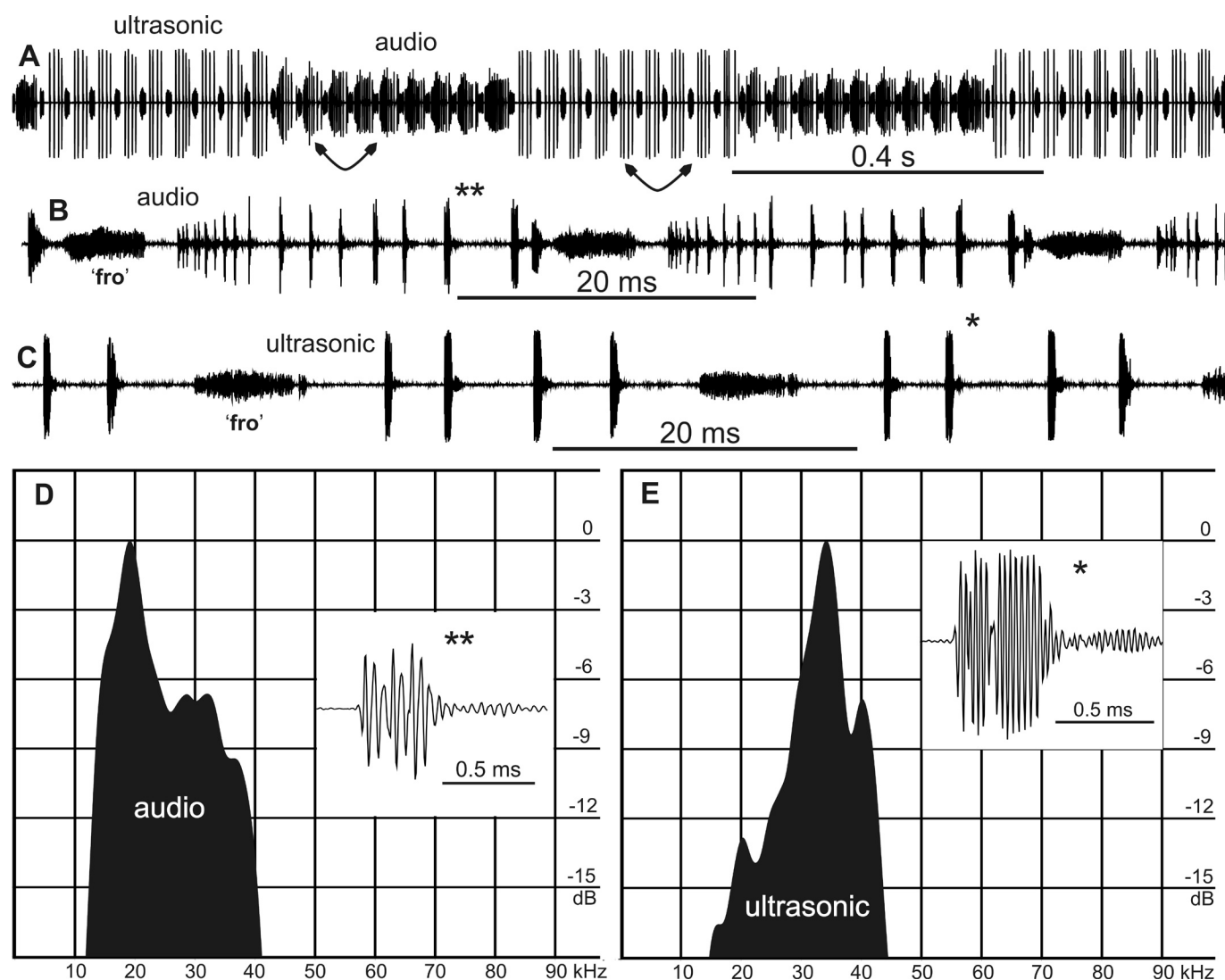


Fig. 1. Records of one of the study specimens, illustrating time-domain structure and Welch-smoothed spectra. A. Three complete ultrasonic and two complete audio modes (each mode of about 9 phonotomes). B. Higher resolution audio-mode time sample (16384 points) taken from A (see region arrowed); this time sample is the basis of the Welch-smoothed audio spectrum in D. C. Higher resolution ultrasonic-mode time sample (16384 points) extracted from A (see region arrowed); this time sample is the basis of the Welch-smoothed ultrasonic-dominated spectrum in E. D and E. Power spectra of audio and ultrasonic modes. High and low kHz values 3 dB down from the peak, determined midpeak values. Inset within Fig. 1D is a single audio transient pulse (see ** in B) showing its complex waveform. Inset within Fig. 1E is a single ultrasonic pulse (see * in C) showing its sinusoidal form. (Note that minor pulse trains coinciding with tegminal opening contribute to both modes; this singer exhibits an audio mode with fewer than normal rapid-decay pulses in each of his major pulse trains; the brief amplitude envelope drop within the ultrasonic pulse is not a consistent feature of these pulses.) A phonatome is all of the sound produced by a cycle of tegminal movement (Walker & Dew 1972)

Spectra of the modes are distinct. That of the audio (Fig. 1D) is a frequency band, peaking near 18 to 19 kHz; at 15 dB down from peak this band is about 25 kHz wide. Having more intense frequencies below 20 kHz, this mode sounds more loudly to a human listener (hence 'audio mode'). The spectrum of the ultrasonic mode (Fig. 1E), which is actually the more intense of the two, has a single dominant carrier peak near 34 to 35 kHz; this peak is created by the SSTP pulses (inset Fig. 1E); the apparent breadth of the spectrum owes much to the fros that accompany the SSTP pulses.

The specimen whose song comprises Fig. 1 has an unusually low rate of transient pulses in its audio-mode trains. Seen at a low resolution toward the end of the trains, some pulses seem to approach the same appearance as the SSTP pulses. That this is not the case is illustrated by the two insets of Fig. 1D and Fig. 1E: the double

asterisked audio pulse is a complex wave of variable amplitude envelope, the single-asterisked ultrasonic pulse is sinusoidal and of a relatively uniform high amplitude (sometimes with momentary amplitude departures as here).

There is a variant of resonant stridulation I will refer to as 'elastic' resonant. Elastic resonant stridulation is powered by the energy of cuticle distortion. Elasticity of cuticle bent during file-scraper engagement is released over a very short time interval (hence with greater power). The nature of elastic resonant stridulation has now been observed with high-speed video in three tettigoniid species: the first two (Montealegre *et al.* 2006) being an undescribed species related to the pseudophylline *Myopophyllum speciosum* and a species, also undescribed, of listroseline katydid in the genus *Arachnoscelis*. The third species is *M. sphagnorum*, which is also the species in which

elastic resonant stridulation was first hypothesized to explain the ultrasonic mode (Morris & Pipher 1972).

High speed video, obtained recently by Fernando Montealegre, shows that during ultrasonic-mode tegminal closures the forewings are nearly paused during most of each interpulse interval. Only the high-amplitude part of the pulse, *i.e.*, actual sound emission, coincides with tegminal displacement. This is interpreted as follows: the scraper lodges at intervals along the file, engaging the two wings. While thus engaged, and with the tegmina paused, the contracting closer muscles force the scraper region of the right tegmen to bend and store elastic energy. This state continues until the scraper's changing angle of engagement (its distortion) permits it to slip free. Slipping free, scraper (and tegmina) advance a short distance across a series of file teeth at high velocity, before lodging again. Alternating trap, storage and release, form the basis of generating the four relatively well-spaced sinusoidal pulses per tegminal closure seen in Fig. 1C.

Elastic resonant stridulation utilizes energy stored in scraper distortion to achieve extreme rates of tooth-scraper contact, but is only possible for small groups of teeth at a time (~ 15 in *M. sphagnorum*). Time-domain patterns of *Ensifera* are thus suspect as involving elastic resonance/distortion storage if they consist of a series of well-spaced sinusoidal ultrasonic pulses, *i.e.*, if they involve, per phonatome, short spaced tonal pulses (SSTP) separated by relatively substantial silent pauses. This resonant stridulation mechanism usually produces *ultrasonic* pure-tone frequencies. That is, though the acoustic end result of this resonant mechanism is, as with that of crickets — a simple sine wave — these sine waves are at ultrasonic frequencies. While each wave in a pulse is still based upon one scraper-tooth passage, pick contacts are made at a much higher velocity.

"With the same tegminal apparatus *M. sphagnorum* produces two distinctive spectra" (Morris 1970). No other tettigoniid species is known to alternate its calling between resonant and nonresonant spectra.

Methods

Specimens.—In the boreal forest of Canada (150 km northwest of Thunder Bay, Ontario and ~ 20 km west of Upsala) the Trans-Canada highway runs close by the Canadian Pacific rail line. In this area there are frequent and extensive bogs carpeted with sphagnum moss; these poorly drained areas intersperse with slightly higher sand and rock covered by black-spruce forest. One such bog is in Trewartha Township [lat 49°08.04' N, long 90°46.21'W], and another near Niblock, a rail location, lat 49° 5.4' N, long 90° 41.55' W; elevation of these study sites is ~ 467 m. The spruce and tamarack trees in the bog areas are sparsely distributed, and stunted to varying degrees, giving the appearance of a tree-dotted open meadow. Males of *M. sphagnorum* sing from these trees or low shrubs both day and night during late July and early August. A combined sample of 50 adult male specimens was obtained here: 21 in 1994, 29 in 2006. Each singer was stalked acoustically during the daytime and localized with the help of a heterodyning device (U25 Ultrasound Advice), its microphone mounted for mobility on the end of a fishing rod. Via earphones the device operator hears the ultrasonic output of a singer shifted into the low-audio range; sound gradients then enable localization.

When first viewed, most singers are perched head to the sky on the trunk or terminal shoot of a (<1 -m high) spruce (Fig. 3B). They can then often be 'guided' by hand proximity to jump into

an open insect net held below. Sometimes the insect's response to human disturbance is not to cease his song, but to leave out the ultrasonic component while continuing to sing in the audio mode. Some individuals actually approach the observer in a 'bold-male behavior', while lengthening or prolonging their audio modes (Morris, unpub.). Commonly a disturbed male leaps downward to the sphagnum surface, where 'freezing' on landing (Fig. 3), together with their cryptic coloration, makes them virtually invisible.

In 2006 the field-collected specimens were transported ~ 1400 km to Mississauga ON and maintained there over the next few weeks singly in screen cylinder cages (10-cm high, 4-cm diameter) pinned to a foam base; from these cages they sang as a sample of their calling song was digitized to a computer. In 1994 most were recorded in a similar manner, but in a residence near their collection site: only 5 were transported south for recording.

Recording.—For the 21 specimens recorded in 1994 a $\frac{1}{4}$ " Bruel & Kjaer microphone (4135) was clamped to a stand and directed normal to the insect's dorsum; it was alligned overtop the sound generator at a 10-cm distance. The output of this microphone went via a preamplifier (B&K 2633) and cable (0027) to a measuring amplifier (B&K 2606). The analog output signal obtained was then double low-pass filtered from 100 kHz (Krohn Hite 3202) and digitized with a PC computer board (DAS50 Keithley) running at 200,000 samples/s. This recording system is flat in its response to ultrasonic frequencies up to 70 kHz.

For recording of singing males in 2006 the output of a Bruel & Kjaer $\frac{1}{4}$ " microphone (4939) went to a B&K sound level meter (2204) set to linear response on its 100 range; output was band-pass filtered (Krohn-Hite 3202, 2-70 kHz) and conveyed to a PC card (Ines 616f), which digitized the signal into a PC computer at a sampling rate of 201,544 samples/s. This digitizing process utilized a user-friendly 'macro' within MATLAB (created by Peter Wall). Temperatures for all these recordings (1994 and 2006) ranged between 18.3 and 28.9 °C, median 24.4 °C.

Measurements and analysis.—For each of the recorded males, we measured midline pronotal length in mm to the nearest 0.1 mm, using a stereomicroscope with an ocular micrometer.

A time-domain sample of 16384 y-values (~ 80 ms duration, ~ 2 audio phonatomes or $\sim 2+$ ultrasonic phonatomes) was obtained from the middle region of each stridulatory mode (Fig. 1 B,C). Upon this time base we calculated power density spectra (psd) using Welch smoothing (Welch method of psd estimation, DADiSP 6.0, DSP Development Corp.). During smoothing each time-sample is divided into 256 serial segments of 128 values each; each segment overlaps the previous by 64 values; a FFT (Fast Fourier Transform) is calculated on each time segment and these are averaged to give the final psd estimate. The peak value of the psd estimate spectrum is taken as 0 and the y values expressed as dB relative to this peak. A single peak (middle) frequency was determined from high and low bracketing frequency values 3 dB down (Fig. 1 D,E).²

Testing for a relation between body size and peak values of

² Sound spectra involve presentation problems. Using a log or a linear scale on the y axis creates very different impressions of peak prominence: linear displays of relative energy make peaks look dramatic. It is also often misleading to present too broad a range of values on the y axis, since only the most intense components will survive background noise in a real environment, many lower peaks should be considered biologically afunfunctional. Setting the most intense frequency in the spectrum as zero and expressing other values in dB relative to this reference is useful, but there is not much value in ranging beyond 18 dB below this peak on the y axis.

Table 3. Measures associated with *M. sphagnum* male cohort (n = 50): body size (pronotum midline length), mode carriers, recording temperatures.

	Pronotum length (mm)	Audio Carrier (Hz)	Ultrasonic Carrier (Hz)	Temperature °Celsius
Range	1.64	7022.1	6.889.4	10.6
Min	4.12	16282.3	32019.0	18.3
Max	5.76	23304.4	38908.4	28.9
Median	5.10	18267.1	34256.2	24.4
Mean, \bar{x}	5.07	18637.4	34549.5	23.7
SEmean, $s_{\bar{x}}$	0.06	240.0	219.9	0.34
Coeff. of Variation %	7.6	9.1	4.5	10.2

each of the two carriers, I calculated a multiple linear regression in which pronotum length was treated as the dependent variable. The effect of the unavoidable variations in recording temperature were assessed by making temperature one of the three independent variables, so partitioning it. The other two independent variables were audio-mode carrier peak and ultrasonic-mode carrier peak. The rationale for these being 'independent' is that a female, making an approach to a singing male as a potential mate, or a male competitor making an agonistic approach to an opponent, can be viewed as predicting male size from information contained in the singer's two carrier-frequency spectra.

Pearson product-moment correlation coefficients were calculated for the three variables whose samples were determined to be drawn from normally distributed populations: the two modal carrier peaks and pronotum length. Because temperature values were non-normal (Shapiro-Wilk 0.951, $p = 0.04$) a nonparametric Spearman's rank correlation was also carried out, involving the same three variables

and temperature.

For a subset of the 50-male sample: impulse sound-level readings (re 20 μ Pa) were obtained using the measuring amplifier, for 20 of the 21 males taken in 1994. Measures were made at a dorsal aspect to the singing insect, the long axis of the microphone directed by eye normal to the plane of the insect's back; a metric rule, held beside the singer and a few cm to the side of the clamped microphone, helped to position the microphone tip 10 cm from the singer's generator. Distance error is within 0.5 cm.

The insect's two modes present themselves to the human ear at different intensities: the audio is heard much more loudly. Set on 90-range, the needle of the measuring amplifier shifts and stabilizes (fluctuating) regularly between a lower and higher deflection. Viewing the AM pattern of the signal on an oscilloscope, it is apparent that the higher deflection values coincide with and so measure the sound levels of the ultrasonic modes. We took these higher readings of the 20 males as our data, but they were found to be from a non-normal population (Shapiro-Wilk 0.892, $p = 0.03$). So a (nonparametric) Spearman's rank correlation was calculated, examining the joint properties of sound levels, body size and temperature.

Systat (version 12) software was used to perform the regressions and parametric correlations. Spearman rank correlations were performed using SPSS (ver. 10.0.7, SPSS Inc.).

Results

Dimension and peak carriers.—General statistics for body size, carriers and recording temperatures are summarized in Table 3. Pronotum lengths for the 50 specimens ranged from 4.12 to 5.76 mm (mean 5.07 mm, coefficient of variation 0.076). The average audio-mode carrier peak was 18637 Hz (range 16282-23304 Hz, CV = 0.09); the average ultrasonic-mode carrier peak was 34550 Hz (range 32019-38908, CV = 0.05). The insects were recorded at temperatures between 18.3 and 28.9 °C (10.6 °): the median recording temperature was 24.4 °C.

Significance of the multiple linear regression is indicated by an ANOVA ($F = 3.55$, $p = 0.02$) (Table 4) and these data are shown to have come from a normally distributed population (Shapiro-Wilk

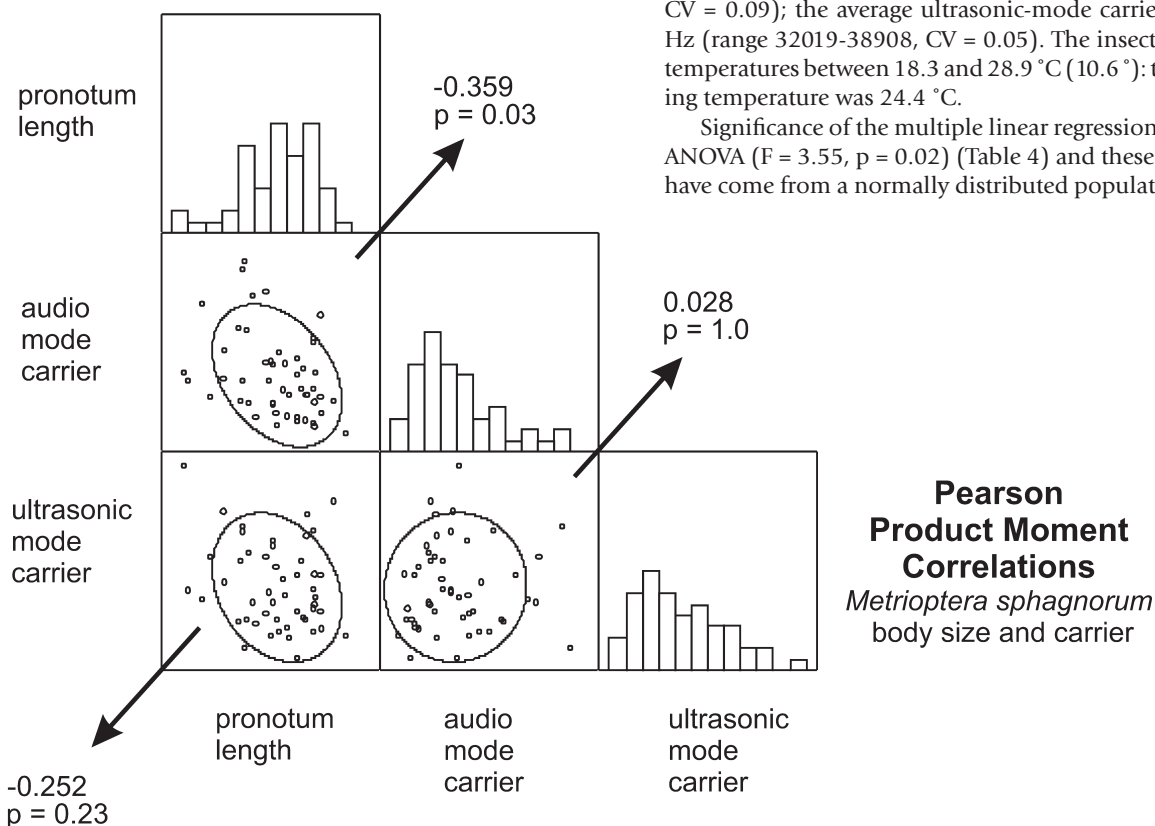


Fig. 2. Pearson correlation scatterplot matrix with Bonferroni-corrected probabilities, expressing relationships between pronotum length and the two different carriers of *M. sphagnum*.

Table 4. ANOVA of multilinear regression of carriers, size and temperature.

Source	SS	df	MS	F	p
Regression	1.373	3	0.458	3.55	0.02
Residual	5.928	46	0.129		

Table 5. Results of multiple linear regression: song modes and temperature related to body size in *M. sphagnorum*.

Effect	Coefficients	t	Probabilities
Audio Mode Carrier	-7.9(10 ⁻⁵)	-2.531621	0.015
Ultrasonic Mode Carrier	-5.8(10 ⁻⁵)	-1.667345	0.102
Temperature °C	-3.87(10 ⁻³)	-0.168135	0.867
Constant	8.64	6.862758	0.000

Y (Body size) = -7.9(10⁻⁵)(AMcarrier)-5.8(10⁻⁵)(UMcarrier)-3.87(10⁻³) (Temperature) + 8.64

0.985, $p = 0.75$). Peak audio carrier gives a significant amount of information about a singer's body size ($t = -2.532$, $p = 0.015$); peak ultrasonic carrier does not ($t = -1.667$, $p = 0.102$) (Table 5). The negative value of the audio-mode partial regression coefficient (-7.9×10^{-5}) is consistent with sound frequency having larger values for larger body sizes. Temperature effects, as one would expect, do not contain useful information about body size and are not significant here ($t = 0.168$, $p = 0.87$); but the procedure (multiple linear regression) has partitioned temperature effects so that they do not confound the testing of the size and carrier relationships.

Pearson correlation coefficients (parametric) are presented in Fig. 2; probabilities are Bonferroni corrected. The null of no linear relation between the two peak carrier variables, audio mode and ultrasonic mode, must be accepted ($r = 0.028$, $p = 1.0$). Likewise for the ultrasonic mode carrier peak compared with pronotum length: there is no evidence of a linear correlation relationship ($r = 0.252$, $p = 0.23$). But the null is rejected in favor of a significant correlation between audio mode and pronotum length: here there is a significant linear relationship between the variables ($r = -0.359$, $p = 0.03$). Size is thus reflected in the audio-mode spectral peak, but not in the ultrasonic. This difference between the two modes is consistent with their having no significant correlation with each other.

For temperature, Spearman's rank correlations indicate a significant effect on carrier ($r = 0.277$, $p = 0.05$, ultrasonic mode; $r = 0.291$, $p = 0.04$, audio mode). There is also a significant correlation of audio mode with pronotum length ($r = -0.367$, $p = 0.009$) but nonsignificant correlation between ultrasonic mode and pronotum length ($r = -0.176$, $p = 0.22$) and between the two carrier modes ($r = 0.05$, $p = 0.73$). The results of the rank correlations are consistent with those of the multiple linear regression.

Dimension and intensity.—For the twenty singers whose sound levels were measured, ultrasonic-mode intensities ranged over almost 10 dB (9.5 dB); mean sound level at a 10-cm distance was 97.53 dB. The minimum measured ultrasonic-mode sound level was 91.5 dB, maximum 101.0 dB. Spearman's rank correlation coefficients and their associated probabilities are given in Table 6. For recording temperatures we reject the null hypothesis: ranks of sound levels do covary with ranks of temperature. Males recorded at higher temperatures tend to be more intense. But the null is accepted for body size and level: size did not significantly affect the intensity of the singer's ultrasonic mode.

Table 6. Spearman's rank correlation tests, coefficients (ρ) and associated probabilities (prob.) for covariance of ranks of ultrasonic-mode sound levels with size and recording temperatures. *significant.

	Level	Size
Size	$\rho = -0.22$ prob. = 0.35	
Recording Temperature	$\rho = 0.44$ prob. = 0.05*	$\rho = -0.14$ prob. = 0.55

Discussion

One generator and two spectra: a harmonic hypothesis.—The tegmina of many Tettigoniidae are asymmetric (Montealegre *et al.* 2009b), with the right scraper-bearing wing often appearing more specialized for sound radiation than the left. Specialization can take the form of modified wing cells called specula³ (sing. speculum): glassy areas in the anal regions of forewings. *M. sphagnorum* has such specula (see Fig. 1 of Morris & Pipher 1972) in its right tegmen. And among these, the largest is an ovoid wing cell, sometimes referred to as the mirror. Mirrors are no doubt the principal radiators of sound in this, and many, katydid species.

If the mirror functions as the main or only sound radiator of the bog katydid, then it must alternate between producing a broad-band, strongly audio, carrier with a peak at 18 kHz (during the insect's audio mode) and a predominantly ultrasonic carrier, with a narrow 35-kHz peak (during its ultrasonic mode). How could a single wing-cell radiate two different carriers?

Harmonics (exact integer multiples of the fundamental frequency, Fletcher 1992, p.274) offer an hypothesis. Pierce p.280, citing Lord Rayleigh 1894, describes the *modes*⁴ of vibration for a clamped circular elastic disc: "The gravest [fundamental mode] [= first harmonic, Fletcher 1992, p.274] which has the lowest frequency, has nodal positions only along the circle of clamping. The next higher frequency [second harmonic] has this nodal circle, and another between it and the center". So the mirror of *M. sphagnorum* in radiating the audio mode, might move with a single nodal circle at its vein-supported periphery: the mirror would move mostly in the 'gravest' way. Then, with the insect switching to the ultrasonic mode, the same wing cell could oscillate with two nodal circles, creating ultrasonic tooth-rate frequencies through its elastic resonance; these frequencies would become effective and dominate in the spectrum by virtue of the mirror moving with nodal positions of the second harmonic.

Such hypothetical behavior by the mirror is consistent with the observation that the peak of the audio carrier (mean 18.6 kHz) is close to being the fundamental (first harmonic) of the peak of the ultrasonic carrier (mean = 34.6 kHz). Two times 18.6 is 37.2 kHz. *M. sphagnorum* may have evolved the second harmonic of its calling song into a second song component. Arguing against this hypothesis however is the fact that only one harmonic shows a correlation with body size. If the mirror functions as a single radiator of harmonically related carriers, one supposes both harmonics should show an effect of body size. It is also the case that radiation of the putative fundamental of 18.6 kHz must be different to the degree that the sound produced comprises a low-Q band rather than a narrow high-Q peak.

³ Defined in Torre-Bueno 1962: "glassy areas at base of tegmina in male Orthoptera that serve as sounding boards".

⁴ The term mode is used here in its standard acoustic meaning, rather than as previously in this paper to describe the two parts of *M. sphagnorum*'s song.

A more complex generator?—So how is it that the ultrasonic mode shows no correlation with body size? Perhaps the generator is not best viewed as a unitary organ, radiating both modes from a single mirror. Perhaps the other specula do not function in phase with the mirror. There are reasons to regard the generator as more complex: the making of each mode occurs upon different nonoverlapping file regions — the audio from a range of teeth farther from the teeth base, the ultrasonic from a tooth series closer to the wing base (Morris & Pipher 1972). The angle of tegminal engagement should be steeper for the audio mode than the ultrasonic, so there is likely a difference between these modes in the vectors of developed forces. Distinctive tooth shape seems to reflect such differences, being broad for the ultrasonic, narrow for the audio. These structural features combine to suggest that specula of the scraper-bearing wing might be differently activated for ultrasonic than audio-mode emission. This being so, perhaps the resonance of the ultrasonic mode radiators is more allometrically distanced from body size than the audio — so that no carrier and size correlation is seen.

Nonresonant stridulation and body size.—Table 1 lists all literature in which taxa have been examined for body-size correlation with carrier. These are grouped by stridulation type – elastic resonant, nonresonant and resonant.

For nonresonant stridulators, correlation of carrier with body size has so far been sought in only two taxa: *M. sphagnorum* and *A. simplex* (Table 1). A significant correlation was found in both the gregarious and solitary phases of the Mormon cricket, as also for the bog katydid in its audio mode. Grasshopper spectra to the contrary (Meyer & Elsner 1996), at present the peak of all *ensiferan* nonresonant carriers examined correlates with body size. Though of course this sample is tiny.

One may puzzle at the apparent lack of interest in testing for body-size correlation among nonresonant stridulators. This arises perhaps from a concern that band spectra are too inherently variable to characterize (Gerhart & Huber 2002). But there is evidence this is not the case, e.g., the band spectra of *Conocephalus* katydid spp. show highly consistent spectral subpeaks (See Footnote 1 present paper; Morris & Pipher 1967).

Nonresonant stridulation is characterized by a band of frequencies, and so is more complex than spectra produced by resonant mechanisms. This suggests, in great contrast to the radiators of resonant systems, an absence of selection for any single carrier frequency. Any body part, though unspecialized for sound generation, once set into vibration in air must make sound; the 'default' spectrum of such a structure would no doubt be a broad and noisy band – certainly not a musical tone. Because the radiator/mirror of nonresonant stridulators is by definition less narrowly tuned: it is presumably less constrained by selection for radiation of particular harmonically related frequencies or a single high-Q frequency. Perhaps therefore, such radiators are freer to be governed by body isometry and so able to more closely reflect the effects of body size.

Resonant stridulation and body size.—Of 10 resonant-stridulating taxa (Table 1), there are seven cricket and three katydid species. All the crickets produce dominant pure-tone carriers in the low audio range, between 2 and 6.8 kHz. Carrier is inversely related to body size in five of these crickets, unrelated in two: so an inverse correlation of body size and carrier appears not to be a consistent feature of cricket resonant stridulation. The escapement mechanism of crickets is credited with making it possible to generate carriers lower than those of other orthopterans of comparable size (Gerhardt & Huber,

p. 42); to the extent this is so, cricket carriers could be expected to exhibit less body-size effect than other taxa.

The three resonant-stridulating katydids of Table 1 produce ultrasonic carriers. Two of these species are known to be using elastic resonance, which means that their scraper advance is governed by elastic recoil. This is a very different mechanism from that of the crickets, in which it is the oscillation of their radiators that regulates scraper advance (Bennet-Clark 2003, Montealegre *et al.* 2009b). This difference means that the katydids should be able to drive their radiator at a tooth-contact frequency that has little to do with the radiator's isometrically determined size. (This may also explain the very large variance in individual carriers observed among individuals of *M. speciosum* (Morris *et al.* 1994.)). For both the ultrasonic mode carrier of *M. sphagnorum* and the carrier of *Myopophyllum speciosum*, no inverse correlation with body size was found. Except for *Kawanaphila nartee*, one might suppose an absence of correlation between carrier and body size is characteristic of elastic resonance.

Song structure is known for 3 spp. of the Australian Zaprochiline genus *Kawanaphila* (Gwynne & Bailey 1988, Mason & Bailey 1998). Typically they produce a series of short-duration pure-tone impulses in the range of 40 to 70 kHz. The sinusoidal amplitude-plateaued form of these pulses indicates resonance stridulation. But it is difficult to reconcile *Kawanaphila* file morphology with these high frequency pulses on a 'one-wave and one file-tooth' basis. In *K. nartee* there are only ~15 rather peg-like teeth (Fig. 3 of Gwynne & Bailey 1988). In *M. sphagnorum*, in the file region making the ultrasonic mode, tooth density is much higher and teeth are broadly transverse. (see Figs 4-7 of Morris & Pipher 1972). It is difficult to envisage an elastic-resonant mechanism in *Kawanaphila*. Perhaps the generation mechanism is like that suggested as 'impulsive excitation' (Fletcher 1999, p. 232): the teeth of *Kawanaphila*'s file might provide input energy, by temporarily lodging a part of the radiator wing and allowing distortion energy to build up. "At some suitable displacement the vibrator slips out...and thereafter vibrates and radiates freely." There are probably many different tegmino-tegminal mechanisms yet to be understood among Ensifera.

Size and song intensity: shouting by insects?—In insect muscle, force and twitch rate, and therefore power, increase with increasing temperature over the viable range (Josephson 1981). At higher temperatures ectothermic insects sing with increasing rates of tegminal movement (Gerhardt & Huber 2002). More sound output per unit time means higher power and should give higher sound-level readings, as indeed was the case here. But size showed no influence on the measured song intensity levels. Surely the bigger of two equally warm singers should have shown higher intensities.

This result might be rationalized as insects varying their sound levels as individuals, depending on context. The lack of observed correlation between size and intensity could result from the fact that under the relatively uniform recording conditions, singers tended to settle on a sound level below the loudest of which they were capable at any given temperature. In other words to detect correlation with size we need to assess their relative sound levels as singers when "shouting" (Zahavi 1978, 1997). Intensity may well vary with size when the singer is at his output capacity.

I have often marked a gradual increase in readings of peak dB levels for a katydid beginning singing activity. They rise slowly in level measures to stabilize around a value after having sung for several minutes. They are in other words, able to increase their singing intensity beyond that dictated by temperature effects. It is difficult to make accurate measurements of sound level in the

A



B

Fig. 3. *M. sphagnum* male. (A) walking within spruce branches and (B, Inset) shown silhouetted against the sky in a typical head-up, bent-abdomen, stridulation posture. Photos by Dita Klimas. See Plate V.

context of interactive behaviors, so there is little in the literature about 'voluntary' sound level changes. But there is probably much about intensity that is adaptive.

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Fig. 4. A black spruce and sphagnum bog near Upsala in northern Ontario is the habitat of *M. sphagnorum*. See Plate V.