

Acoustic adaptations of periodical cicadas (Hemiptera: *Magicicada*)

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We studied the trade-off between traits that function in mate attraction and those that function in enemy avoidance by contrasting features of acoustic communication in cicadas differentially at risk to predators in the same environment. Two genera of North American cicadas were studied: *Magicicada* and *Tibicen*. *Magicicada* species of periodical cicadas, with 17-year life cycles, seek mates in dense aggregations of calling males that are made possible by the relative ineffectiveness of predators to control their numbers. During the breeding season, *Magicicada* are so abundant that they satiate their predators. From their relative freedom from predation, it is to be expected that traits for attracting mates are emphasized in *Magicicada* compared with the more solitary genus *Tibicen*, which reproduce at much lower densities. Males of solitary species are expected to sing more loudly and at low pitch because both features enhance long-distance transmission. These two features were confirmed by measurement. *Magicicada septendecim* appears to be the most divergent species, evolutionarily, in terms of an unusually sharply tuned sound resonating system, low resonant frequency, and quietness of its song that cannot be entirely explained by body size. These characteristics represent adaptations to the problem of communicating unambiguously to females at close range in a loud and heterogeneous sound environment. Sensitivity to predators, parasitoids, and congeneric species may also have shaped the evolution of their communication systems. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 90, 15–24.

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INTRODUCTION

Advertising or searching for mates is usually accompanied by a risk of attracting predators and parasitoids (Gwynne, 1987; Zuk & Kolluru, 1998; Cooley, 2001); therefore, a trade-off is expected between traits that function in mate attraction and those that function in enemy avoidance. The trade-off is likely to vary among related species that are differentially at risk. North American cicadas are interesting in this regard because adult cicadas in the genus *Magicicada*, emerging at 13- or 17-year intervals, are so abundant in their 4–6-week breeding season (Dybas & Davis, 1962; Dybas & Lloyd, 1974) that they satiate their predators (Lloyd & Dybas, 1966; Karban, 1982; Williams & Simon, 1995). Densities of emerging periodical

cicadas can reach to over 3.5 million per hectare (Dybas & Davis, 1962; Leonard, 1964), and such abundance makes per capita risk of predation extremely low (Karbon, 1982). These densely aggregated species are expected to have traits that are advantageous in mate attraction relatively unmodified by risk of predation, whereas solitary species in the same environment, such as *Tibicen* species, should display adaptations that reduce the risk of being eaten or parasitized. One set of traits in the periodical cicada species (*Magicicada*) has been identified and labelled ‘predator foolhardy’ (Lloyd & Dybas, 1966). All members of the genus fly slowly and are easily approached on the vegetation (White *et al.*, 1983). Lack of wariness and insensitivity to disturbance may be advantageous during the frequent interactions that occur during mate seeking and courtship (Lloyd & Dybas, 1966; Grant, 2005). *Tibicen*, on the other hand, and other nonperiodical cicada species are far more wary and fly faster (Oberdörster & Grant, 2006a).

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In the present study, we ask whether features of acoustic advertising reflect the altered trade-off between attracting mates and avoiding enemies. We do so by contrasting two species of gregarious *Magicicada* species with two species of solitary *Tibicen* species living in the same environment.

Individual *Magicicada* males gain a collective advantage in long-distance transmission by calling simultaneously in dense aggregations. Visual cues also stimulate mating, but songs are more critical (Dybas, 1969). Being physically close to other males, cicadas experience strong competition for mates. This competition has been studied in male *Magicicada septendecim*. Males acoustically interfere with other approaching males while courting females (Marshall & Cooley, 2000; Cooley & Marshall, 2001, 2004).

Three species of the genus *Magicicada*, members of the *-decula*, *-decim*, and *-cassini* groups, are synchronous and coextensive over the majority of their respective geographical ranges in North America (Alexander & Moore, 1962; Williams & Simon, 1995; Marshall & Cooley, 2000; Cooley & Marshall, 2001). They overlap broadly in the use of habitat, although some degree of habitat partitioning occurs by tree species, soil type, and oviposition site (Dybas & Lloyd, 1974; White, 1980). Given loud chorusing at the same time from the same vegetation, there should be a selective advantage for males broadcasting unambiguous signals to females against a loud and heterogeneous background. Ambiguity would be minimized and effectiveness maximized if songs have a species-specific fundamental frequency (Alexander & Moore, 1958; Simmons, Wever & Pylcka, 1971a; Huber *et al.*, 1990; Hennig *et al.*, 1994; Marshall & Cooley, 2000; Cooley *et al.*, 2001) produced from sharply tuned resonators (Bennet-Clark & Young, 1992, 1994). Calling songs of three species of *Magicicada* are known to differ in frequency, length, and temporal patterning (Alexander & Moore, 1958; Simmons *et al.*, 1971a; Cooley & Marshall, 2001). Songs of males of the solitary *Tibicen* species in the same environment are similarly differentiated. In addition, they are expected to sing more loudly and at low pitch because both features enhance long-distance transmission and communication with potential mates (MacNally & Young, 1981).

ACOUSTIC FEATURES OF CICADAS

The mechanics of a male cicada's loud song have been extensively investigated (Pringle, 1954; Young & Josephson, 1983; Young, 1990; Bennet-Clark & Young, 1992, 1994; Fonseca & Popov, 1994; Hennig *et al.*, 1994; Young & Bennet-Clark, 1995; Fonseca & Hennig, 1996; Bennet-Clark, 1997). Sound is produced by a pair of ribbed tymbals on the abdomen. The tymbal

has been described as an energy storage mechanism that releases energy as the ribs buckle inwards sequentially upon tymbal muscle contraction (Bennet-Clark, 1997). Buckling causes pressure changes in the abdominal cavity, and sound leaves the cavity through a pair of tympani. Tensor muscles modulate the amplitude (Hennig *et al.*, 1994), as does the opening and closing of the opercula overlying the tympani through changes in the posture of the abdomen (Young, 1990; Bennet-Clark & Young, 1992).

The abdominal cavity and tymbals act as a coupled Helmholtz resonator, radiating sound through the acoustically transparent tympani (Bennet-Clark & Young, 1992). Two measurable properties are of value when comparing species. The first is the resonant frequency (f_0). This is related to the volume (V) of the cavity and the area (A) and length (L) of the aperture (tympani) by the general equation:

$$f_0 = (c/2\pi) \cdot \sqrt{(A/LV)} \quad (1)$$

The symbol c is the speed of sound in the fluid, taken as 340 m/s. For two tympani, as in cicadas, A is the combined area of the two tympani and L is 1.7 times the radius of one of them (Bennet-Clark & Young, 1992). The second property is a so-called quality factor, Q . This measures the effective increase in the amplitude of the vibration at resonance and the rapidity with which it changes. It is given by the formula:

$$Q = 2\pi \sqrt{(L^3V/A^3)} \quad (2)$$

Q is a measure of the sharpness of its tuning, and is equal to the resonant frequency divided by the bandwidth at 3 dB below maximum (Bennet-Clark & Young, 1994). A sharply tuned resonator has a high Q . It does not scale with body size and is a constant of the resonator design. A similar sharpness of tuning is potentially available to all species (Bennet-Clark & Young, 1994); therefore, differences among species in Q -values can be interpreted as different evolutionary solutions to problems of communication.

Resonant frequency (f_0) increases with area of the tympani and decreases with volume cavity and hence with abdomen size. Since area (L^2) increases more slowly with body size than does volume (L^3), the net effect of an increase in body size is a decrease in frequency. Bennet-Clark & Young (1994) confirmed the expected relationship with data from 17 species. The correlation between dominant frequency and body length as an index of body size was 0.857. The interspecific comparison assumes that sound-producing structures are similar in all species, and this appears to be true (Bennet-Clark & Young, 1994; Fonseca & Popov, 1997). It also assumes a constant relationship between tympani and abdominal cavities, so that tympanum size can be ignored when relating song frequency to body size. However, data provided by

Bennet-Clark & Young (1992; tables 1, 3) show that this is not correct. The present study was designed to investigate the relationship between tympani and body size, and f_0 and Q -values. We compared the two *Magicicada* species included in the study by Bennet-Clark & Young (1992) with two sympatric nonperiodical (annual) species, *Tibicen linnei* and *Tibicen chloromera*, which were not included. Our predictions were: (1) the two *Magicicada* species would have higher Q -values than the *Tibicen* species and (2) they would have higher resonant frequencies due to their smaller body size.

MATERIAL AND METHODS

Periodical cicadas of Brood X (Williams & Simon, 1995) and annual cicadas were collected by hand from the campus of Princeton University, New Jersey, USA, in May to August 2004. All measurements were made on males. Lengths of body from head to tip of abdomen and lengths of abdomen separately were measured to the nearest mm with a ruler. The length of the opercula covering the sound-transmitting tympani was measured from the base in the abdominal midline to the furthest point distally of one of them, and the width of the two opercula combined was measured at the base between lateral ridges on the abdomen that run antero-posteriorly. The two opercula measurements were made to the nearest 0.1 mm with calipers. The volume of the abdomen was measured by placing it vertically in a cradle of modelling clay and injecting water from a 1-mm³ syringe up to the level of the tympani.

The tympanum of most species is a taut thin membrane. Area of the tympanum was determined by dissection, mounting on a slide, photographing it using RS Image 1.9.1 for Windows, and then measuring with IPLab 3.7 for Macintosh. The more elastic tympanum of *M. septendecim* was dissected with some loss or distortion and, as a result, our area estimates are minima. We report the mean of the area estimates but use the somewhat larger published mean of 8.44 mm² (Bennet-Clark & Young, 1992) in calculations. For comparison of all our data with the available published data, we calculated correction factors from the differences between our measurements of *M. cassini* and previously published ones of this species, and then applied the correction factors to our measurements.

Bennet-Clark & Young (1994) compared resonant frequencies of 17 species with their body lengths. We increased the sample of species with *T. linnei* and *T. chloromera* from the present study, *Tibicen lyricen* ($N = 4$) from a study of morphology in the same study area (Oberdörster & Grant, 2006a), and *Magicicada septendecula*. In the absence of direct measurements of body length of *M. septendecula*, we added 5% to the

body length of *M. cassini* on the basis of their relative proboscis lengths given by Dybas & Lloyd (1974). Calling songs ($N = 1$) of all four species, as well as *M. septendecula* and *T. lyricen*, were obtained from the University of Michigan's cicada website (Cooley, Marshall, & O'Brien, 2005). Resonant frequencies and power spectra were determined from spectrograms with the program RAVEN, version 1.2.1 (Cornell Bioacoustics Laboratory, Ithaca, New York, USA) suitable for a Macintosh computer. Resonant frequencies for *M. septendecim* (1.3 kHz) and *M. cassini* (5.8 kHz) were close to published values of 1.3 kHz and 6.0 kHz, respectively (Young & Josephson, 1983), and are therefore considered to be reliably estimated for the other species. Q -values could not be reliably estimated due to vagaries of amplitude curves. Measured values at 3 dB below maximum (Bennet-Clark & Young, 1994) of ~18 for both *Magicicada* species deviate from published values for *M. septendecim* ($Q = 25$) and *M. cassini* ($Q = 5$) (Young & Josephson, 1983), and values for the other species were even higher, perhaps as a result of amplitudes of the recordings (50–60 dB) being only approximately one half the field-recorded maxima (Sanborn & Phillips, 1995).

Sound pressure levels were recorded with an analogue display Radio Shack Sound Level Meter placed at 1.5 m above ground beneath dense aggregations of *Magicicada* species calling at ~10–20 m in tree canopies (Oberdörster & Grant, 2006b). Recordings of maximum levels were made at three sites at 4-day intervals during the months of May and June, and species composition of each chorus was noted. Statistical analyses were performed with t -tests, analysis of variance or multivariate analysis of variance (MANOVA) for testing differences between population means, and with reduced major axis regression and confidence ranges for testing allometric scaling relationships (Rayner, 1985).

RESULTS

MORPHOLOGY

The four species differ in morphological features associated with sound transmission (Table 1). Abdomen volumes are significantly heterogeneous ($F_{3,19} = 60.108$, $P < 0.0001$), and all species differ from each other by Bonferroni/Dunn post-hoc tests ($P = 0.0001$ – 0.0004) except for the pair *M. septendecim* and *T. linnei* ($P = 0.6540$). Tympanum area also varies among the three species investigated ($F_{2,11} = 89.480$, $P < 0.0001$); *T. chloromera* has a larger area than *T. linnei* and *M. cassini* ($P < 0.0001$), but the area of *T. linnei* exceeds that of *M. cassini* at only $P = 0.0150$. Tympanum shape deviates from a pure circle, as indicated by radial standard deviations greater

Table 1. Mean measurements of male cicadas in mm (area measured in mm², volume in mm³)

	<i>Magicicada septendecim</i>	<i>Magicicada cassini</i>	<i>Tibicen linnei</i>	<i>Tibicen chloromera</i>
Body length				
<i>N</i>	10	10	9	22
Mean ± SD	27.5 ± 1.247	23.75 ± 0.635	31.56 ± 1.184	33.61 ± 0.872
Abdomen length				
<i>N</i>	10	10	9	10
Mean ± SD	16.05 ± 0.94	14.25 ± 0.69	18.1 ± 0.979	20.07 ± 0.8
Abdomen width				
<i>N</i>	10	10	8	4
Mean ± SD	10.04 ± 0.381	8.59 ± 0.351	12.28 ± 0.469	14.45 ± 0.436
Abdomen volume				
<i>N</i>	5	5	5	5
Mean ± SD	0.68 ± 0.061	0.23 ± 0.076	0.22 ± 0.038	0.4 ± 0.067
Tympanum area				
<i>N</i>	5	5	4	5
Mean ± SD	6.43 ± 0.296	9.91 ± 0.425	12.7 ± 1.157	21.67 ± 2.13
Radial SD				
<i>N</i>	–	5	4	5
Mean ± SD	–	14.66 ± 1.092	13.88 ± 3.078	15.51 ± 2.483
Opercula length				
<i>N</i>	10	10	8	19
Mean ± SD	4.94 ± 1.008	4.75 ± 0.308	7.94 ± 0.588	10.75 ± 0.488
Opercula width				
<i>N</i>	10	10	8	19
Mean ± SD	8.42 ± 0.573	7.42 ± 0.386	8.86 ± 0.342	9.96 ± 0.568

Radial standard deviation (SD) is a measure of the ellipticity of the tympanum.

than zero (Table 1). The three species do not differ in tympanum shape ($F_{2,11} = 0.329$, $P = 0.7264$).

Body size is not a good predictor of either abdominal volume or tympanal area. *M. septendecim* has the largest volume, even though it is shorter in body length than the two *Tibicen* species (Table 1). However, according to data in Bennet-Clark & Young (1992), its mean tympanal area (8.44 mm²) is smaller than that of its smaller congener *M. cassini* (8.81 mm²), and therefore much smaller than the two *Tibicen* species. Body length is not a good predictor because the genera differ in the shape of the abdomen. In *Magicicada*, the abdomen is fusiform but, in *Tibicen*, it is dorsoventrally flattened and broad. For example, the abdomen is 1.60-fold longer than wide in *M. septendecim* and 1.66-fold longer in *M. cassini*, but only 1.47-fold longer in *T. linnei* and 1.39-fold longer in *T. chloromera* (Table 1).

As expected from differences in the dimensions of abdomens, opercula dimensions are highly heterogeneous among species (MANOVA; Wilk's lambda = 0.024, $F_{6,86} = 77.560$, $P < 0.0001$). All species differ from each other in opercula length and width at $P < 0.0001$, with two exceptions; *M. cassini* and *M. septendecim* have the same lengths ($P = 0.0416$), and *M. septendecim* and *T. linnei* have the same

widths ($P = 0.0585$; $P_{\text{crit}} = 0.0083$). The largest differences are in opercula length between the *Magicicada* and *Tibicen* species, both absolutely and in relation to abdomen length (Table 1). The opercula cover approximately 30% of the abdomen length of *M. septendecim* and 31% of the *M. cassini* abdomen length, whereas they cover 43% and 56% of the abdomen lengths of *T. linnei* and *T. chloromera*, respectively.

QUALITY OF SONG

The quality factor Q is predicted to be higher in the two *Magicicada* species than in the two *Tibicen* species on the basis of their anatomy. The measured Q -value is especially high in *M. septendecim* but not in *M. cassini* (Table 2). As expected, there is no correlation between predicted Q -values and body size for all six species ($r = 0.239$, $P = 0.325$), or for the five without *M. septendecim* ($r = 0.311$, $P = 0.329$).

RESONANT FREQUENCY

Measured resonant frequencies generally correspond with the calculated values, except for the notably low measured frequency for *M. septendecim*. Moreover, *T. linnei* has the highest predicted resonant fre-

Table 2. Predicted and measured quality (Q) and resonant frequencies (f_0) of six species of cicadas

Species	N	Q predicted	Q measured	f_0 predicted	f_0 measured
<i>Magicicada septendecim</i>	5	14.04§	25.0*	4.00‡§	1.3*
<i>Magicicada cassini</i>	5	7.84§	5.0*	7.00‡§	6.0*
<i>Tibicen linnei</i>	4	6.33§	–	7.66§	5.3§
<i>Tibicen chloromera</i>	5	5.73§	–	6.47§	4.9§
<i>Cyclochila australasiae</i>	5	5.43‡§	6.3‡	4.56‡	4.3†
<i>Macrotristria angularis</i>	5	6.97‡§	9.2‡	4.41‡	4.0*

Cyclochila australasiae and *Macrotristria angularis* are Australian species.

*Young & Josephson (1983); †Young (1990); ‡Bennet-Clark & Young (1992); §present study; † or ‡§ refer to our recalculations (§) of original data († or ‡).

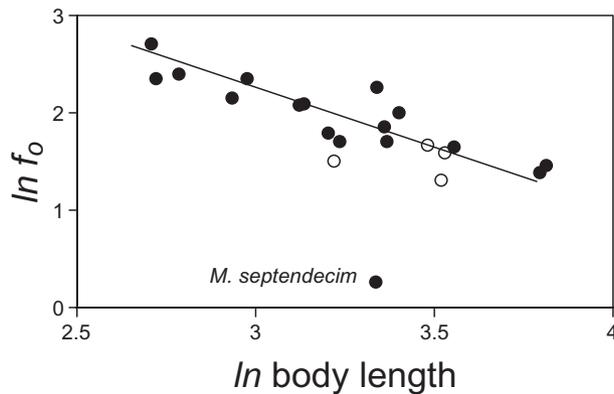


Figure 1. Reduced major axis model of resonant frequency scaled with body size as indexed by body length. *Magicicada septendecula* and three *Tibicen* species (indicated by open circles) were added to the data of 17 species (closed circles) taken from Bennet-Clark & Young (1994).

quency but not the highest measured frequency. Resonant frequency scales with body size as indexed by body length. *Magicicada septendecim* is a notable outlier, having a much lower frequency than is predicted from its size (Fig. 1). When this is excluded, the slope for the 16 species studied by Bennet-Clark & Young (1994) is -1.080 (95% confidence interval = 1.057 – 1.103). This is close to but significantly different from the value of -1.0 , which is theoretically expected if frequency scales isometrically with linear body dimensions (eqn. 1). The effect of adding *M. septendecula* and three *Tibicen* species to the sample of 16 species is to increase the slope to -1.23 , which departs even more strongly from expectation (99% confidence interval = 1.167 – 1.293). The change in slope is caused by the addition of species with resonant frequencies that are low in relation to their body size: *M. septendecula* (4.47 kHz), *T. lyricen* (3.58 kHz), *T. chloromera* (4.87 kHz) and *T. linnei* (5.30 kHz).

LOUDNESS

Sound pressure levels (SPL) were in the range 54–89 dB on 8 days of recording. Aggregations of *M. septendecim* lacking *M. cassini*, and *M. septendecula* produced consistently quieter songs (mean \pm SE = 65.2 ± 2.23) than those of *M. cassini* (and a few *M. septendecula*) (79.1 ± 1.19) (paired $t_7 = 15.165$, $P < 0.0001$). Because there was no obvious difference in numbers between the two sets of choruses, the large difference implies that *M. septendecim* songs are individually quieter than *M. cassini* songs. Mean recording levels for the mixed species group were consistently intermediate between the recording levels of the pure species.

DISCUSSION

In the absence of a phylogeny for cicadas, we have contrasted *Magicicada* with *Tibicen* and all other species that have been studied to date to investigate variation in sound production in relation to features of the acoustic apparatus. On the basis of these comparisons, *M. septendecim* appears to be the most divergent species, evolutionarily, in terms of the quietness of its song, a low resonant frequency, and a high Q -value at that frequency.

QUIETNESS

As expected from their dense calling aggregations, *Magicicada* species produce quieter song calls than the solitary *Tibicen* species. Past studies have shown that individual *M. septendecim* produce a quieter song (~ 70 dB SPL) than *M. cassini* (~ 80 – 85 dB SPL) (Young & Josephson, 1983; Weber, Moore Huber & Klein, 1987), and the songs of both are markedly quieter than the songs of *T. chloromera* (97.1–103.4 dB SPL) and *T. linnei* (101.9–107.1 dB SPL) (Sanborn & Phillips, 1995). Only three of the 30 species studied by Sanborn & Phillips (1995) had song calls as quiet as *M. cassini*, and none had songs or alarm calls as quiet

as *M. septendecim*. Our uncontrolled field recordings are consistent with the published difference in loudness between *M. septendecim* and *M. cassini*.

In the study by Sanborn & Phillips (1995), sound pressure level variation among 30 species recorded at a distance of 50 cm from the calling male was found to scale positively with body size (mass in mg) on a semi-log plot. Large males produce a loud and low-pitched song, and this carries further than the song of smaller cicadas (MacNally & Young, 1981) and thus has the potential to reach a greater number of conspecific individuals without the singer changing calling perches (Sanborn & Phillips, 1995). *Magicicada septendecim* departs conspicuously from the interspecific pattern in having an unusually quiet song, absolutely and in relation to its large size. It is also unusual in having maximum sensitivity, in both males and females, to the resonant frequency of male calling song (Huber *et al.*, 1980; Huber *et al.*, 1990). In *M. cassini* and other species, males sing louder at frequencies higher than the peak in acoustic sensitivity.

Sound output is loudest between tympani and opercula (Young, 1990). Opening the opercula increases the amplitude by 10 dB (Young, 1990), as well as increasing the resonant frequency by ~10% (Bennet-Clark & Young, 1992). The present study has shown that *Magicicada* species have a much smaller pair of opercula than *Tibicen* species. It is possible that the significance of small opercula is a greater ability to increase amplitude in the context of courting females and deterring other males (Cooley & Marshall, 2001; 2004). The disadvantage could be an easier entrance for small (and unknown) parasitoids and fungal spores (Soper, Delyzer & Smith, 1976a). Periodical cicadas suffer from a host-specific fungal parasite, *Massospora cicadina*, which only affects the abdomen of the cicada (White & Lloyd, 1985). If our suggestion is correct, the trade-off between traits that maximize mate acquisition and those that maximize enemy avoidance has shifted in *Magicicada* towards mate acquisition traits.

QUALITY OF SOUND AT RESONANCE

The high *Q*-values predicted for *Magicicada* species conform to an expectation based on the reasoning that cicadas in dense mixed species aggregations of courting males should have sharply tuned sound producing resonators. Our results confirm those obtained in a previous study of the same two species (Young & Josephson, 1983; Bennet-Clark & Young, 1992), although there are minor differences. Using data provided by Bennet-Clark & Young (1992), we calculate expected values of *Q* for *M. septendecim* and *M. cassini* of 12.02 and 8.53, which are close to expected values from our own data of 14.04 and 7.84, respectively. Values for both species of *Magicicada* are

higher than values calculated for the other four species studied to date; two *Tibicen* species in the present study and two Australian species previously studied (Bennet-Clark & Young, 1992).

Q-values for the two *Magicicada* species obtained directly by measurement were 25 for *M. septendecim* and 5 for *M. cassini* (Young & Josephson, 1983). The first is higher than the predicted value of 14.04 and the second is lower than the predicted value of 7.84. The correspondence between predicted and measured *Q*-values is only slightly better for the two Australian species. Measurement of *Q*-values in realistic field situations presents a great technical challenge (for extensive discussions, see Young & Josephson, 1983; Young, 1990; Bennet-Clark & Young, 1992; Young & Bennet-Clark, 1995).

The high *Q*-value of *M. septendecim* is especially notable. The calling song of *M. septendecim* is unusually sharply tuned, with $Q_{3\text{ dB}} = 25$, meaning that the peak frequency of 1.3 kHz is 25 times the band width at -3dB (below 0 = maximum intensity). The sharp tuning can be explained physiologically as a result of an increase in the inertance or effective mass of the orifice of the resonating chamber, as well as by a reduction in the effective area of the tympanum (Young & Josephson, 1983).

The first explanation is supported by the fact that the tympanum of *M. septendecim* is unusually thick and pliable in comparison with *M. cassini* and other species, as reported by Bennet-Clark & Young (1992) and observed by us in the present study. With regard to the second explanation, cicadas are able to reduce tympanal areas by folding the tympanal membranes when singing (Pringle, 1954; Young, 1990; Hennig *et al.*, 1994), and it is possible that *M. septendecim* does so more extensively or effectively than other species. Membrane folding in *T. linnei* increases auditory thresholds across the whole frequency range by up to 20 dB (Hennig *et al.*, 1994) and avoids stimulus overload or damage to the auditory nerves, at the same time as preserving the ability to hear other chorusing males nearby, as well as predators and parasitoids (Pringle, 1954; Simmons *et al.*, 1971b; Hennig *et al.*, 1994). Membrane folding could affect the *Q*-value at resonance.

RESONANT FREQUENCY

A third acoustical feature that distinguishes *M. septendecim* is its resonant frequency. The observed frequency of 1.3 kHz is exceptionally low and, although the relatively small areas of the tympani contribute to the low frequency, it is well below the frequency of 4.0 kHz predicted from the Helmholtz equation using measurements of the tympani and resonance chamber. The observed frequency of the

related *Magicicada neotredecim* is similar, at 1.4–1.7 kHz (Marshall & Cooley, 2000). By contrast, five other species, including *M. cassini*, have resonant frequencies close to those predicted from properties of their sound producing anatomies. Resonant frequencies are predicted by the Helmholtz equations better than are the Q -values.

Allometric analysis also shows that the resonant frequency of *M. septendecim* is unusually low. Using ordinary least squares regression analysis, Bennet-Clark & Young (1994) found that resonant frequency of 16 species scales negatively with body size as indexed by body length. We repeated the analysis, adding three *Tibicen* species and *M. septendecula*, and using a reduced major axis model that is more appropriate for allometric analysis of functional relationships (Rayner, 1985). *Magicicada septendecim* is an outlier; the recorded frequency for *M. septendecim* (1.3 kHz) is well below the frequency of approximately 6.2 kHz expected from its body length (Table 2, Fig. 1). For this reason, *M. septendecim* was excluded from the calculation of the slope of the interspecific relationship between body size and resonant frequency. The isometric expectation for the slope is -1.0 because, according to eqn. 1, f_0 is proportional to $A/L \cdot V$, or $L^2/L \cdot L^3$, which simplifies to $1/L$ (Bennet-Clark & Young, 1994). A proportional increase in L is accompanied by the same proportional decrease in f_0 . However, even without *M. septendecim*, the slope is statistically different from the theoretically expected 1.0 , even beyond the 99% confidence range (1.167–1.293). This suggests heterogeneity in the data, perhaps caused by variation in tympanal area to some extent independent of body size.

Our study additionally identified abdomen shape as a source of variation in the relationship between frequency and body size. The abdomen is fusiform in *Magicicada* but dorsoventrally flattened and broad in *Tibicen* and, as a result, body length is not a good predictor of abdominal volume, tympanal area or resonant frequency. *Magicicada septendecim* has the largest volume, even though it is shorter in body length than the two *Tibicen* species. Yet, according to data in Bennet-Clark & Young (1992), and as confirmed by us, its tympanal area is smaller than that of *M. cassini*, and therefore much smaller than the two *Tibicen* species. Future studies might find body weight (mass) to be a better predictor of resonant frequency than body length.

LOW RESONANT FREQUENCY OF *M. SEPTENDECIM*

The anomalous frequency of *M. septendecim* has been attributed to an unusually thick tympanum, an attribution supported by experimental evidence (Bennet-Clark & Young, 1992). This species displays other,

apparently unique, features of the acoustic apparatus that may be relevant, including properties of tymbal and tensor muscles (Young & Josephson, 1983; Hennig *et al.*, 1994), resilin pads, and the mass and elasticity of the tymbal ribs (Young & Bennet-Clark, 1995; Bennet-Clark, 1997).

Biomechanical analyses answer the ‘how’ but not the ‘why’ question of sound production. Hitherto, no attempt has been made to interpret the significance of the anomalously low *M. septendecim* frequency in terms of ecological context. We did not derive an expectation based on the dense calling aggregations. Two possible evolutionary explanations can be suggested, one involving acoustic avoidance of other cicada species, and the other involving an association with predator detection. These two explanations may be complementary.

With regard to the first explanation, premating isolation of related species occurs when their respective courtship signals are minimally ambiguous (Coyne & Orr, 2004). Isolation may be enhanced by sympatric divergence of signals and responses to them. Indeed, reproductive character displacement in pitch has been demonstrated in 13-year periodical cicadas of the *-decim* group. A shift in male songs of *M. neotredecim* from 1.4 kHz in the absence of *Magicicada tredecim* to 1.7 kHz in their presence is matched by a shift in female preference (Marshall & Cooley, 2000; Simon *et al.*, 2000; Cooley *et al.*, 2001). Therefore, resonant frequency of the *-decim* group of species may have shifted downwards early in their evolutionary history as a result of interactions with other species, resulting in elimination of overlap in calling and reception characteristics. However, the frequencies of the calling songs of the *-decim* species are so far below the resonant frequencies of 4.5 kHz (*M. septendecula*) and 6.0 kHz (*M. cassini*) that an avoidance of these two congeneric species appears to be an unlikely explanation for the low frequency of songs in the *-decim* group. On the other hand, response functions are consistent with a hypothesis of acoustic avoidance.

The summed activity of the auditory nerve of male and female *M. septendecim* has a lowest threshold at 1.4 kHz, close to the main peak in the calling song spectrum and, above this value, the mean auditory threshold rises sharply with increasing song frequency to 80–90 dB at 4 kHz (Huber *et al.*, 1990). As a consequence, most of the sound energy in the calling songs of the two congeneric species (which is above 4 kHz) is unlikely to be perceived by *M. septendecim*. Filtering out these songs can be interpreted as an adaptation to loud mixed species choruses that enable *M. septendecim* individuals to focus on conspecifics and avoid interactions with the other species. Deafness to congeneric song could be the result of character displacement.

The second possible evolutionary explanation is that the *-decim* group of species evolved low frequency communication under the influence of predator pressure. Most receptor cells of cicada auditory organs are maximally sensitive to frequencies of 1–4 kHz (Huber *et al.*, 1990; Popov, 1990). Because these frequencies are below the maximum energy band of male song in most cicada species, some studies have suggested a main function of hearing might be the detection of predators (Popov, 1990; Hennig *et al.*, 1994), in addition to the recognition and localization of cicada songs that necessarily must be loud (except for *M. septendecim*). Most species of cicadas have a single peak of sensitivity but *Okanagana rimosa* is unusual in having two peaks, one at approximately 0.7 kHz in the conjectured predator-sensitive zone and the other at 7–10 kHz in the conspecific-sensitive zone that is typical for cicadas of its size. Bimodality suggests two separate functions. The peaks in frequency occur in both airborne sounds and in airborne-induced substrate vibrations (Stölting, Moore & Lakes-Harlan, 2002).

The argument for predator-sensitivity is supported by studies of directionality of sound reception. Directionality is achieved in *Cicada barbara* by the functioning of the tympani as pressure difference receivers (Fonseca & Popov, 1997). Females of this species show highly directional mechanical responses to experimental stimulation in the entire frequency range of < 1–20 kHz, whereas male directional sensitivity shows two strong peaks, one at 6–7 kHz corresponding to the frequency of its song and another well below this at 1.8 kHz (Fonseca & Popov, 1997). The two peaks are close to the fundamental frequencies of *M. cassini* and *M. septendecim* calling songs, respectively. Thus, a possible reason for the large difference in resonant frequencies of the two *Magicicada* species is that one species (*M. cassini*) has retained a frequency to be expected from its body size whereas the other (*M. septendecim*) underwent an evolutionary shift into a predator-sensitive channel through modification of tympanal anatomy. This would have enabled the singers, when they were singing, to be directionally sensitive to acoustic signals from predators, other singers, and possibly parasitoids that are sensitive to their songs (Soper, Shewell & Tyrrell, 1976b; Robert, Miles & Hoy, 1999; Lakes-Harlan, Stölting & Moore, 2000). If so, not all traits of *M. septendecim* are ‘predator-foolhardy’ as previously believed.

CONCLUSIONS

The present study has provided evidence of acoustic adaptation in periodical cicadas to the dense aggregations of calling males that are made possible by the relative ineffectiveness of predators to control their

numbers owing to their uniquely long and periodic 13- or 17-year life cycles. Through the influence of the intervening variable of high density, the trade-off between traits that function in mate attraction and those that function in enemy avoidance has shifted in these species towards greater emphasis of mate attracting traits, including features of their acoustic communication. In future investigations, it would be worth examining the possibility of an additional trade-off in *Magicicada* between mate attraction (males) and fecundity (females). Sexual selection on mate attracting traits of females could affect the fecundity of females if there is an intersexual genetic correlation between abdomen volumes of males and females and if fecundity scales with abdomen volume. Other species of periodical cicadas, especially *M. septendecula*, should also be studied, with particular attention given to measuring *Q*-values and determining auditory thresholds of females. Finally, a phylogeny would be a great help in enabling an interpretation to be made of the evolutionary history of this unusual group of insects. Even in its absence, the many traits in which *M. septendecim* differs from *M. cassini* is suggestive of a large amount of elapsed time since they shared a common ancestor (Simon *et al.*, 2000; Grant, 2005).

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