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ORIGINAL PAPER

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Hearing dimorphism, trait variation and conflicts over space in the thorax of the bushcricket *Requena verticalis* (Listroscelidinae: Tettigoniidae: Orthoptera)

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Abstract The hearing system of *Requena verticalis* is sexually dimorphic. Previous work has shown size of the auditory spiracle determines absolute threshold and as female spiracles are, on average, larger than males, females are more sensitive to the main energy of the male call. In all measured traits in morphology and physiology, females showed lower coefficient of variation than males. This difference was significant for bulla volume and hearing threshold. In addition, female ear size covaries with thorax dimensions but this is not so in males. Such a finding suggests stabilising selection on ear size in females, perhaps explained by the requirement of females to recognise and locate the male. As the auditory bulla is larger in females than males, so occupying thoracic space, we suggest a possible trade-off in this brachypterous species between hearing sensitivity and sound production. Finally, we examine relative growth of body structures not associated with hearing and those that influence hearing sensitivity. Scaling, where traits are under strong selection, may result in allometry. Female hearing traits show positive allometry with absolute size and while the relationship between bulla volume and spiracle area was positively allometric in females this was not the case for males.

Keywords Bushcricket · Hearing · Sexual dimorphism · Allometry · Tettigoniidae

Introduction

While emphasis has been placed on the role of sexual selection on male advertising signals (Andersson 1994), less attention has been directed towards patterns of selection on the sensory system required to track these signals (McClelland et al. 1987; Wilczynski et al. 1993). In practice, selection should influence the morphology and sensitivity of sensory structures in the same way as both sexual and natural selection affect the more commonly studied processes of signalling (Endler 1992; Ryan and Keddy-Hector 1992). Thus, where sexual roles show strong asymmetry with regards to communication processes there should be concomitant sexual differences in both the shape and function of the associated sensory system (Arak and Enquist 1995).

Differential selection on sensory performance between the sexes can be manifest in three ways. First, sexual dimorphism of sensory structures is demonstrated by differences in absolute size, receptor number and physiological performance (Alatalo et al. 1988; Andersson 1994; Shine 1989). Second, sexual differences may involve the manner in which each trait varies between and within each sex with higher variance indicative of a different selective force than where trait variance is less extreme (Pomiankowski and Møller 1995). Third, differences in sensory performance should be reflected by differences in relative growth, more commonly considered as scaling.

Among tympanate insects, the first of these explanations reflects behavioural asymmetry between the sexes where in most species the male calls with specialised sound producing organs and the often-mute female is attracted to the call. Selection under these conditions should favour greater sensitivity in the listening rather than the calling sex (Heller et al. 1997; Bailey 1998). But while signalling asymmetry may explain hearing dimorphism, sexual differences in observed population *variation* in receptor performance may also reflect different levels of selection between the sexes. Interpretation of population variance, particularly of secondary sex characters, is far from straightforward and even more complex for sensory modalities especially where the organ has functions additional to recognising and responding to sexual signals (Butlin 1993; Møller and Swaddle 1997).

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By comparison, traits that are not under direct sexual selection may be considered to follow a simpler rule of low variance, where selection is directional or, alternatively, where variation is high selection may be considered weak (Andersson 1994). Møller and Swaddle (1997) make the point that intense directional selection on signalling should select against genetic modifiers, so reducing additive genetic variation, but cases where this has been applied to sensory, rather the signalling systems are rare (see Butlin 1993). Finally, selection differences between the sexes may also be expressed as relative growth of hearing organs. Commonly, traits that show positive allometry are those most likely to be under sexual selection (Clutton-Brock et al. 1980; Petrie 1988). For example, large males that develop larger ornaments require relatively less energy to develop and maintain these ornaments compared with smaller males (Clutton-Brock et al. 1980). To this end we may expect sensory structures that are subject to strong selection to be disproportionately larger compared to independent measures of body size.

The ears of bushcrickets are set in the tibia of the forelegs and are backed with trachea, which open into larger frequency sensitive bullae in the thorax (see Bailey 1993 for a review). The auditory trachea of tettigoniids are not linked to the main tracheal system and hence have an almost exclusive function in hearing. The bullae occupy space, which is also shared by stridulatory/flight muscles, but since hearing sensitivity, as measured at threshold, is affected by the size of these auditory pathways (Bailey 1998) there may be a trade-off between the space used by sound producing muscles and structures associated with hearing. Within the sex that is apterous or micropterous no such conflict exists, and thoracic space may be used more completely to increase auditory sensitivity [but see Roff (1986) and Zera and Huang (1999) for arguments relating to fecundity]. While thoracic dimensions and muscle mass may be reduced in apterous females we can provide no a priori explanation why tracheal volume in the female should increase.

We therefore test hypotheses concerning sexual asymmetry in the calling and listening roles of the bushcricket, *Requena verticalis*. We examine structural differences in hearing function and relate these findings with previously published studies on variation in hearing sensitivity (Bailey 1998). We attempt to explain our observed differences in both variation and relative growth of hearing structures in terms of different calling and searching strategies of each sex.

Material and methods

Morphology

Adult *R. verticalis*, collected from the campus gardens of the University of Western Australia, were immediately frozen and stored. Pronotum length and hind tibial length were measured using an eyepiece linear graticule. Spiracle area was measured using a grid graticule estimating the irregular area covered by the grid. Measures of spiracle area using this direct technique were later confirmed using the area program of "Optimus". There was no significant difference between the two techniques ($t = 0.27$, $P = 0.79$).

Bulla volume was obtained by measuring the length, width and breadth of casts. Injecting epoxy resin into the bushcricket's auditory spiracle until it flowed out of the cut fore-femur allowed us to make casts of the tracheal system. Bushcrickets were left at room temperature for 24 h to ensure hardening of the epoxy resin. After this treatment specimens were placed in 4% sodium hydroxide solution for 2–3 days to dissolve tissue so that casts could be easily extracted.

Relative muscle mass was estimated by weighing the thorax after separating it from the head, abdomen and legs and removing the gut. After which the soft tissue was then dissolved in the way describe above, and the remaining cuticle weighed, which allowed an estimation of muscle mass.

Data were analysed using parametric tests and to ensure normality data were log transformed. Allometry of log values was examined comparing regression slopes to isometric slope of 1. Differences in variance were analysed using coefficients of variation (CV), where differences between measures were examined using a two-tailed variance ratio test (*F*). Such a test is considered valid where CVs are less than 30% (Lewontin 1966). Lande (1977) points out that although values of CV have no units, comparisons of traits should have the same dimensionality and be of similar complexity. We apply measures of CV (variance ratio test) to linear, squared and cubed metrics, and although the ideal relationship between the magnitudes of CV for line, area and volume is the ratio 1:2:3, where measures are of complex structures a simple transformation of area and volume will lead to significant underestimates of CV. For this reason, while stating the calculated CV (Table 1) as an un-transformed value we have only used these estimates to compare like dimensions with like.

To test for allometry data were raised to the power of square root (area measures) or cube root (volume measures) and then log transformed. Both model I, least-squares regression and model II, reduced major axis regression (Sokal and Rolf 1981; Harvey and Pagel 1991) were performed on transformed data, comparing slopes between sexes and for deviation from isometry where there would be a slope of one. As both measures are expected to vary in the same manner and have similar degrees of error model II estimates are considered more likely to reflect true deviation from isometry (Harvey and Pagel 1991; Petrie 1988).

All parameters were tested for repeatability. Repeated-measures ANOVA comparing three measures for each trait ($n = 10$) were log transformed. Spiracle areas using the grid technique ($F = 1.19$, $P = 0.31$) and image analysis ($F = 0.91$, $P = 0.41$) were not significantly different nor were measures of bulla volume ($F = 0.82$, $P = 0.46$).

Acoustic behaviour

The call of *R. verticalis* consists of a series of short syllables (wing movements) of about 15 ms separated by an inter-syllable interval of 10–12 ms (Fig. 1b, c). The syllables are grouped into chirps. Chirp length tends to be highly variable and may consist of almost

Table 1 Coefficient of variation (CV) of male and female traits expressed as a percentage

	CV (%)	
	Males	Females
Pronotum length (mm)	7.3	4.6
Hind tibial length (mm)	8.1	6.8
Spiracle area (mm^2)	15.8	11.1
Bulla volume (mm^3)	18.8	16.6

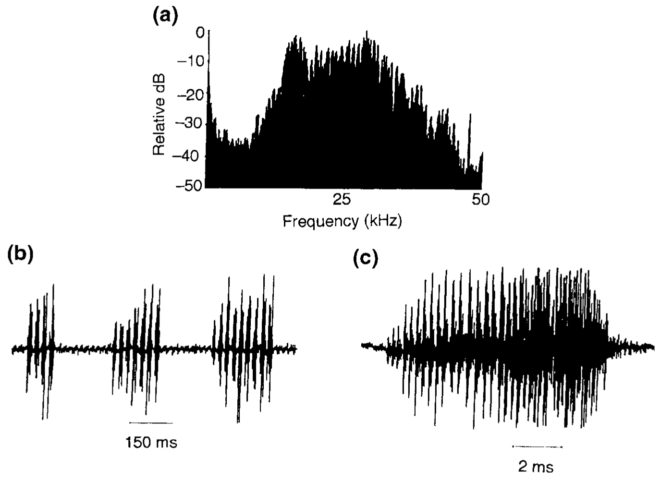

Fig. 1 The call of *Requena verticalis* showing the frequency spectrum with peaks of energy close to 16 and 28 kHz (a) and the temporal structure of a series of syllables (b and c)

continuously produced chirps, lasting several seconds, or repeated chirps in groups of five or seven syllables with an inter chirp interval of 150–200 ms (Schatral and Bailey 1991). Like many bushcrickets the call's energy is a broad frequency band, but with pronounced peaks at 16 kHz and 28 kHz (Fig. 1a), and, as in most tettigoniids, males use their call to both compete with other males and also to attract receptive females. Call intensity has been shown to co-vary with body size in a number of tettigoniid species including *Mygalopsis marki* (Römer and Bailey 1986) and importantly in *R. verticalis* (Bailey et al. 1990).

Ear morphology

The structure of the ear of *R. verticalis* is typical of most tettigoniid species (Bailey 1990, 1993, and Fig. 2). The tibial crista acustica, beneath the knee of the foreleg is attached medially to a paired tympanic membrane opening forward and backwards on the tibia. The axons of the tonotopically arranged mechanoreceptors lead through the leg nerve along the femur to the auditory neuropile in the prothoracic ganglion (reviewed in Lakes and Schikorski 1990). A common trachea backs the tympana, and this trachea acts as a sound guide through the permanently open thoracic spiracle and expanded tracheal bulla in the thorax to the tympanic membranes. Sound effectively interacts both with the external surface of the tympana and in a more major way through the internal pathway of expanded trachea and open spiracle (Michelsen et al. 1994).

The size of the spiracular opening determines the amount of sound entering the trachea (Nocke 1975; Bailey 1998), and the bulla is presumed to act as a resonator or high pass filter (Michelsen et al. 1994; for a review see Bailey 1993). Critical to this discussion is the relative size of the spiracle and the associated bulla.

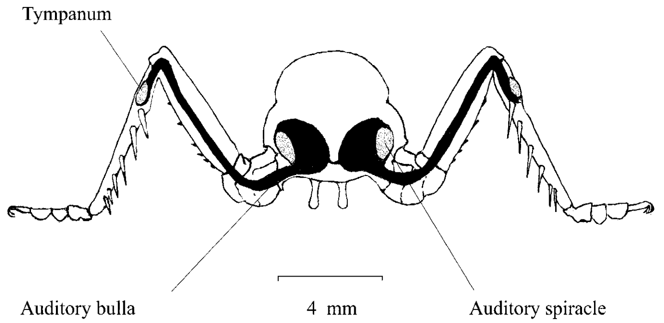

Fig. 2 A schematic view of the auditory tracheal anatomy of *R. verticalis* looking anterior from the bisected insect

Results

Sexual dimorphism and allometry

Males have smaller spiracle openings than females ($t=-12.47$; $P<0.0001$): larger individuals, as measured by prothorax length, have relatively larger spiracle openings. We found that both sexes showed a strong positive relationship between spiracle area and pronotum length. A model I least-squares regression of log spiracle area against log of the square of pronotum length provides a significant positive relationship for both sexes (LSR: males: $y = 0.88x - 0.99$; df 33; $F=59.61$; $P<0.0001$: females: $y = 0.67x - 0.69$; df 38; $F=16.23$; $P=0.0003$). Model II (reduced major axis) regression of the same measures for both sexes also provided a significant positive relationship, but the slopes, in both cases were not different from unity (males: $\beta=1.10$; NS compared to 1; $P=0.41$: females: $\beta=1.22$; $P=0.12$). The relationship between spiracle area and thoracic length is isometric.

Although the female has a smaller prothorax compared with the male, measures of spiracle area and bulla volume showed that females have significantly larger ears than males (spiracle area: $t=-12.47$, $df=59$, $P<0.01$; bulla volume: $t=-9.77$, $df=53$, $P<0.01$; Fig. 3a, b). Ear size, determined as spiracle area, was related to prothorax size. In both sexes there was a significant and positive relationship between spiracle area and thorax length (males: log square-root area to log prothorax length; $r^2=0.65$; $df=33$; $F=59.61$; $P<0.0001$: females: $r^2=0.31$; $df=38$; $F=16.23$; $P=0.0003$). Similarly, bulla size is dimorphic. Females have significantly larger auditory bulla than males ($t=2.0$; $df=57$; $P<0.0001$; Fig. 3b). The relationship between thorax size and bullae volume in females is isometric; bulla volume increases with spiracle area in females ($F=14.32$; $P=0.00068$) but not in males ($F=0.29$; $P=0.60$; Fig. 3c).

We measured hind tibia length as an independent estimate of size. The relationship between log prothorax length and log hind tibia length is not, as expected, isometric. The slopes are significantly less than unity with larger individuals with proportionately larger prothorax dimensions (male: $\beta=0.76$, $t=9.53$, $df=22$, $P<0.05$: $\beta=0.86$, $t=6.91$, $df=40$, $P<0.05$). Females have longer hind tibia than males ($t=-5.8$, $df=38$, $P<0.01$).

Thorax size is arguably influenced by the presence of the auditory bullae in females, but in males the volume occupied by the bulla may compete with muscles used for stridulation. Males are brachypterous and use their short wings for sound production while females are wingless; thus, one explanation for the observed size

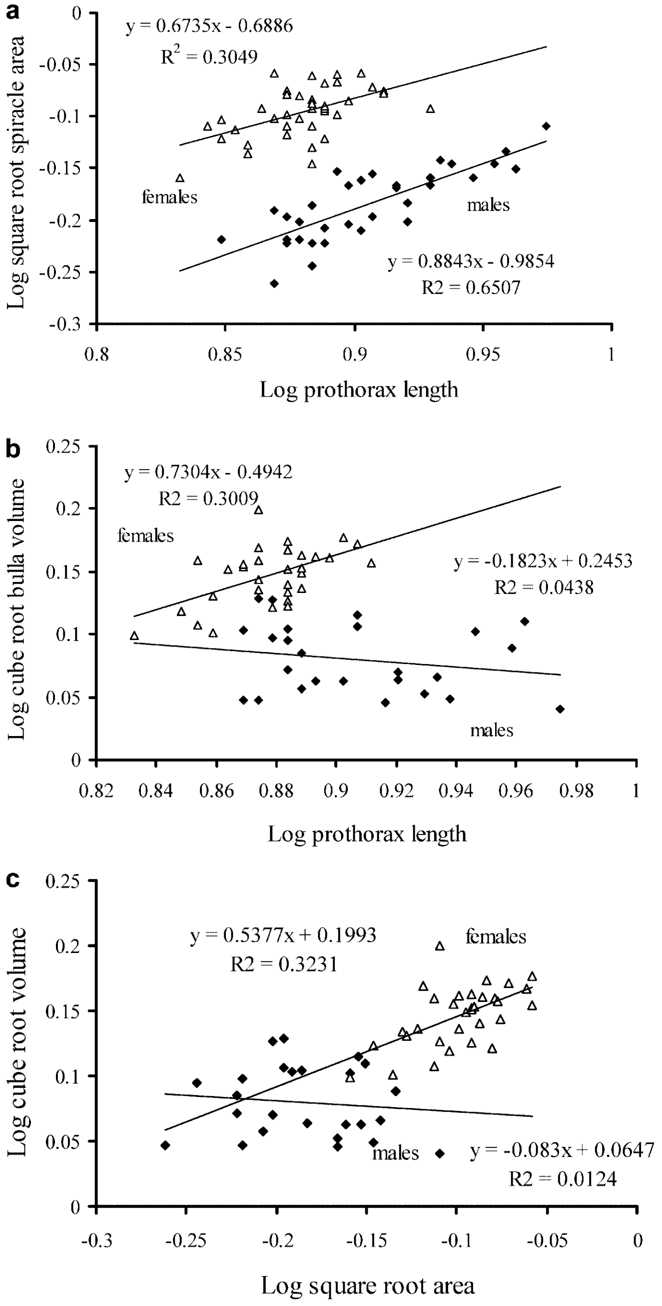

Fig. 3 a The relationship between spiracle area (mm^2) as the log square root, and the log of prothorax length (mm) of male and female *R. verticalis*. (**b**) The relationship between log cube root auditory bulla volume (mm^3) and log prothoracic length (mm) of male and female. (**c**) The relationship between log cube root auditory bulla volume (mm^3) and log square root spiracle area (mm^2) of male and female

differences may be the relative mass of thoracic musculature. For males this mass was significantly larger than in females (males; mean = 0.57 ± SE 0.03 g: females; 0.41 ± SE 0.05 g; $t = 2.57$; $df = 18$; $P = 0.019$), and the positive isometric correlation between total body mass and absolute thoracic muscle mass in males ($r^2 = 0.67$; $df = 9$; $F = 16.02$; $P = 0.0039$) indicates that larger males have proportionately more muscle. No such relationship exists for females.

In line with the prediction that bulla volume competes with space in the restricted prothorax with muscle mass in males, we found that bulla volume of females increases with thorax size ($r^2 = 0.16$; $df = 31$; $F = 5.79$; $P = 0.0225$). However, no such relationship exists for males ($r^2 = 0.44$; $df = 24$; $F = 1.05$; $P = 0.32$; Fig. 3b). Not surprisingly, given this “relaxed” use of thoracic space in females, we found that spiracle area covaried positively with bulla volume in females (log cube-root bulla volume on log square-root spiracle area $r^{2=}0.32$; $df = 31$; $F = 13.33$; $P = 0.0007$; Fig. 3c). By comparison, in males there was a trend towards a negative relationship between volume and auditory spiracle area ($r^2 = 0.01$; $df = 24$; $F = 0.29$; $P = 0.597$).

Coefficients of variation

We made the assumption that where differences in variation of each trait occurred between the sexes this may indicate different levels of selection. To this end we calculated the CV for each of our measures. Absolute ear size showed a higher total variance than hind tibia length (a measure of absolute size), and so we tested if CV of absolute trait values differed between the sexes for both ear parameters. In all measured traits females showed a lower CV than males (Table 1) and this difference was significant for bulla volume ($F = 2.36$; $df = 31$, 25; $P < 0.05$). By comparison spiracle area showed no significant difference ($F = 1.40$; $df = 39$, 34; NS). Further, there was a significantly higher variation in pronotum length ($F = 5.76$; $df = 37$, 32; $p < 0.05$) but not hind tibial length for females compared with males ($F = 1.25$; $df = 40$, 25; $p < 0.05$). As indicated above, comparisons between CV of measures with different dimensionalities (pronotum and femur lengths, area of spiracle and volume of bulla) were not straightforward and so were not used in this study.

Hearing sensitivity

The distribution of energy within the call shows two dominant peaks, the lower at 16 kHz and the higher peak at 28 kHz (Bailey and Yeoh 1988; Fig. 1). As determined in a previous study (Bailey 1998), males and females differ in hearing sensitivity. Males show their greatest sensitivity to call frequencies in the lower frequency band, while females are sensitive across a broader spectrum, with greater sensitivity towards higher frequencies compared to males (Bailey 1998). Mean (± SD) threshold at 16 kHz for males was 45.9 ± 9.1 dB SPL, while that at 28 kHz was 60.4 ± 8.4 dB SPL. In females, threshold to the lower frequency was 43.2 ± 2.6 dB SPL and for the higher frequencies was 45.26 ± 3.46 dB SPL. Hearing sensitivity between the two sexes differed, and as expected from the higher variance in ear measures, variation (CV) of male sensitivity was significantly higher for all frequencies (variance ratio test F 0.05 (2) 23, $30 = 4.82$: $F = 9.92$: $P < 0.001$), as well as at both 16 kHz ($F = 9.7$: $P < 0.001$) and 28 kHz ($F = 3.17$: $P < 0.05$; Fig. 4).

Discussion

Trait variation – conflict for space

This paper confirms and extends an earlier finding that hearing processes are dimorphic in *R. verticalis* (Bailey 1998). The simplest explanation of sexual differences in hearing performance amongst the ensiferan Orthoptera is that acoustic signalling is asymmetric; in most cases the male calls and females search for the male's signal. However, our primary question related to sexual differences in trait variation and the possible influence of sexual selection on the scaling of these traits. We make two assumptions: first, where there is selection by one sex on the sensory structures of the other, trait variation should be relatively lower. Second, if there is a trait size-advantage to an individual, and such a trait is heritable resulting in more or better mates, then resulting selection should lead to positive allometry (Petrie 1988).

Our first task was to separate the effects of sound production from those of hearing, particularly as in males the thorax houses both inflated tracheal bullae and also the stridulatory and ambulatory muscles. Hence, within this space it is conceivable that selection for stridulatory muscles (sound production) competes for space with ear size (sound reception); both sexes walk and so ambulatory muscle differences are neutral. One prediction is that where there is no space-conflict bulla dimensions should covary with thorax size, and where there is a conflict with increase thorax size, muscle mass should increase with thorax size at the expense of bulla volume. It appears that female *R. verticalis* conform to the "space-conflict" model; hearing sensitivity covaries with the dimensions of the ear while this is not the case for males. In the male, thorax size appears linked with the dimensions of hearing structures and the requirement of the male to stridulate. There was no significant relationship between thorax size and bulla size but there was a strong relationship between thorax and muscle mass. Hence, larger males with larger wings had proportionately more muscle. For females, without the demands for stridulation, bulla volume increases proportionately with thorax size; the ears of larger females were correspondingly more sensitive than those for smaller females.

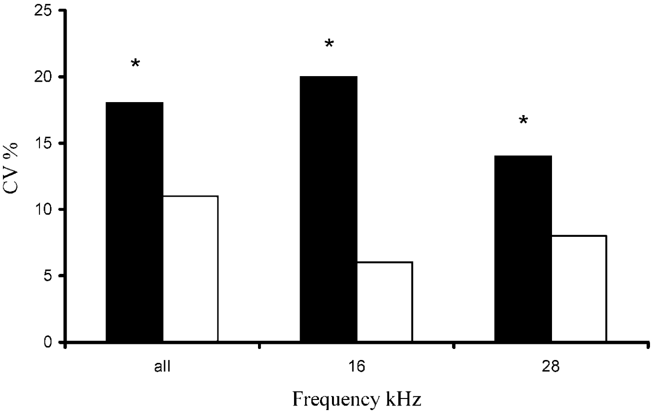

Fig. 4 A comparison between the Coefficients of Variation (CV %) between absolute auditory thresholds of male and female *R. verticalis* for all frequencies and at the two main peaks of energy in the call 16 kHz and 28 kHz. (* $p < 0.05$). (Summary data extracted from Bailey 1998)

Within-sex variation and ear size

Ear morphology showed no sexual difference in the respective coefficients of variation in regard to ear size, but there was a significant difference in the variance of bulla volume. With this significant relationship between bulla volume and thorax size we would expect that female bulla size would show a high variance. This was not so, rather females had lower variance in this character compared with males. One explanation for difference in variance may be that females, rather than males optimise bullae size for mate location; in some species ear size influences a female's ability to locate its mate (Gwynne and Bailey 2000). As to whether stabilising selection existed for all sexually dimorphic tettigoniid hearing systems depends on which sex is doing the searching and so traits associated with searching should then be under stabilising selection.

The prothorax can be considered a confounding and perhaps unreliable indicator of size where, in females there was high variance in prothorax length compared with males, yet low variance in relation to a second size trait such as tibia length. A negative relationship between measures of thorax and leg suggests there is positive selection on optimum thorax size in both sexes, perhaps in males, to optimise hearing and sound production and in females, greater sensitivity for mate location. In *R. verticalis* there is an association between high structural variance and measured variance in hearing thresholds; males show high threshold variance at the critical frequencies of the call compared with females (Bailey 1998). In the context of sexual signalling it may be argued that whereas males are only required to be aware of the proximity and general locality of a calling rival, females must locate males and in some cases distinguish between male calling traits.

Selection on hearing traits

Finally, we made the prediction that where structures are under strong directional or stabilising selection, having relatively larger bullae provides an advantage for larger animals. In this way large males should be more sensitive to the sounds of their conspecifics and large females to more distant males. In this case female hearing traits should show positive allometry with absolute size and in line with this prediction bulla volume and spiracle area did show positive allometry (LSR).

Concordant with the "space-conflict" model we found no allometric relationship in males between bulla volume and size in males. We suggest that in species where the auditory spiracle represents the primary auditory input and, where females search for the calling male, there is a possible trade-off between increased hearing sensitivity with its high-pass filter characteristics (Michelsen et al. 1994), and the space occupied by muscles used in stridulation. However, the space-conflict model cannot be universal among tettigoniid families as among many duetting phaneropterines males have far larger auditory bullae than females (Bailey 1993) and, in these genera, males either search for females or at least the searching roles are shared. Further, pseudophylline tettigoniids have almost non-existent spiracular openings, and even less developed bullae. In such groups the spiracular input may be far less important, and sound entry may be through the tympanal slits beneath the knees (Mason et al. 1991).

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