Studying the allometric relationships between morphological traits and body size is important to understand the evolutionary patterns of within-species variations in morphology (Shingleton et al. 2007, 2008). Many morphological characters are phenotypically plastic and correlate with body size, often owing to the influence of environmental conditions (Shingleton et al. 2009). Some of the morphological characters under the influence of selection can become disproportionately larger or smaller with increasing body size (i.e., hyperallometry) (Shingleton et al. 2007, 2008, Rodríguez and Eberhard 2019). For example, sexual selection tends to favor the hyperallometry of secondary sexual traits (Bonduriansky and Day 2003; Bonduriansky 2007). Studying the allometric relationships between these traits and body size can offer insights into patterns of sexual selection.

For animals that communicate using sound to find and attract mates, the acoustic signals produced by males can sometimes reveal information about the male condition and/or quality to the female (Bennet-Clark 1998, Bentsen et al. 2006, Brown et al. 2006). The sound generator characters responsible for producing the acoustic signals can thus be subjected to female preference, male–male competition, and sexual selection, and consequently exhibit hyperallometry (Anichini et al. 2017, Rebrina et al. 2020). In some instances, larger sound generator characters are an indication of better body condition, because developing and maintaining these structures can be energetically costly (Del Castillo and Gwynne 2007). Hence, females can exhibit a preference for acoustic signals produced by larger sound generator characters. Furthermore, larger sound generator characters can also be more resistant to wear and tear, conferring males with larger sound generator characters to be more competitive in producing sound to locate and attract mates than males with smaller ones (Ritchie et al. 1995, Anichini et al. 2017).

In many species of katydids (Tettigonioidae Krauss, 1902), males also produce sound to attract females, and the sound generator characters are found on their asymmetrical tegmina (Montealegre-Z. 2009, Montealegre-Z. et al. 2017). These include the stridulatory file, a specialized serrated vein on the left tegmen that produces sound when the teeth hit against the scraper on the right tegmen, as well as the mirror, a specialized cell membrane on the right tegmen that helps amplify the sound and dictate resonance and frequency (e.g., Morris and Pipher 1967, Bailey 1970, Montealegre-Z. and Postles 2010). The biophysical mechanics of sound production, allometry of sound generator characters in katydids, and how they play a role in attracting mates and avoiding predators have been well studied (e.g., Bailey 1967, 1970, Sales and Pye 1974, Heller 1995, Ritchie et al. 1995, Bennet-Clark 1998, Morris

Acoustic communication, including allometry of secondary sexual traits and body size, can differ among katydid species from different parts of the world. However, Neotropical species tend to be better studied than their Southeast Asian relatives. This is true for the tribe Copiphorini (Orthoptera, Tettigoniidae). To allow for future comparative studies of Neotropical and Palaeotropical Copiphorini, the allometric relationships between sound generator characters and body size of Euconocephalus pallidus from Singapore were examined. Five sound generator characters—tégmen length, stridulatory file length, tooth width, teeth density, and mirror area—were correlated with pronotum length as the proxy for body size. Stridulatory file length, tooth width, and teeth density were also correlated with the mirror area. The relationships were subsequently tested for difference between scaling slope and isometry based on 29 male adults from a single population. All sound generator characters except teeth density exhibited significant positive correlations with pronotum length, whereas teeth density exhibited significant negative correlation with pronotum length. Among them, only tooth width and teeth density scaled hyperallometrically, while the other characters scaled isometrically. As males produce a continuous buzzing call over long durations, larger teeth (i.e., larger tooth width and lower teeth density to accommodate larger teeth) are probably more resistant to age-related abrasion. This may imply that males with larger teeth can produce calls recognized and/or favored by the females over a longer part of the males’ adult lifespan.
materials and methods

study subject.—Euconocephalus pallidus inhabits open grassland and is among the largest orthopterans and best fliers from this habitat (Tan 2011, 2020, Tiwari and Diwakar 2019). At night, males produce a distinct loud buzz for a substantially long duration. The dominant frequency of the calls is around 12 kHz (Tan 2020). Multiple males have been observed to call concurrently (Tan 2011).

sampling.—Between 6 February and 2 April 2019, 29 adult males were collected from an open grassland in Singapore (1.34279N, 103.87751E) known formerly as Bidadari Cemetery. The site has since been cleared for residential development. The katydids were identified using a key in Tan (2011). The katydids were euthanized by freezing, dried and pinned, and subsequently deposited in the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, Singapore. Collections were carried out from this single site within a short period of time, which minimizes potential confounding effects of population, generational, and temporal differences.

measurement of body size and sound generator characters.—All measurements were done using ImageJ 1.51j8 (Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA) following the approach in Tan et al. (2020).

Fig. 1. Measurements of body size and sound generator characters. A. Male habitus in dorsal view; B. Stridulatory file on the left tegmen in ventral view, scale bar = 0.5 mm; C. Mirror area on the right tegmen in dorsal view, scale bar = 1.0 mm. PronL = pronotum length, TL = tegmen length, FileL = file length, ThD = teeth density, ThW = tooth width, d = length of 10 teeth in the middle region of the file.

1999). These enabled more recent works that examined allometry of sound generator characters in a broad range of species while accounting for phylogenetic relatedness (e.g., Montealegre-Z 2009) and that focused on targeted species to build on studies of sexual selection in katydids (e.g., Anichini et al. 2017, Rebrina et al. 2020). The comparative study by Montealegre-Z (2009) also demonstrated that many sound generator characters exhibited hyperallometry with body size, but Anichini et al. (2017) and Rebrina et al. (2020) showed that this is not necessarily the case in Poecilimon Fischer, 1853 (subfamily Phaneropterinae).

While Anichini et al. (2017) and Rebrina et al. (2020) based their investigation on temperate model species, Montealegre-Z (2009) provided a comparative study of 58 tropical species—most of which are from the Neotropics. Heller (1995) previously demonstrated that the acoustic signaling in Neotropical and Palaeotropical Pseudophyllinae is highly variable owing to different predation pressures in different parts of the world. Likewise, it is also plausible that allometric relationships between sound generator characters and body size can differ among taxonomically related but geographically distant species. Therefore, expanding the investigation of allometry in sound generator characters to less known species may reveal new insights and, consequently, provide a more comprehensive understanding of the evolutionary patterns related to these sound generator characters.

Here, the allometric relationships between sound generator characters and body size of a Palaeotropical katydid species from the tribe Copiphorini Karny, 1912 is examined, specifically from the genus Euconocephalus Karny, 1907. Very little is known, apart from a few anecdotal observations, about the katydids from this region (e.g., Tan 2011, 2020, Tiwari and Diwakar 2019). In comparison, Neotropical Copiphorini have been used extensively as study subjects in various studies on acoustic communication (e.g., Montealegre-Z and Mason 2005, Montealegre-Z and Postles 2010, Sarria-S et al. 2016, Celiker et al. 2020). These also include Neoconocephalus Karny, 1907, a genus very similar morphologically to Euconocephalus (e.g., Counter Jr 1977, Schul and Patterson 2003, Deily and Schul 2004). Building up information about acoustic communication in Euconocephalus, including examining their allometry, may eventually allow for comparative inference between species from the Neotropics and Palaeotropics.

For this study, Euconocephalus pallidus (Redtenbacher, 1891) was collected, as the species is a relatively large katydid with well-developed sound generator characters suitable for studying allometry with body size. Being the most abundant and widely distributed Euconocephalus from Singapore and highly adaptable to both urban and peri-urban habitats (Tan 2011, 2020). E. pallidus has the potential to be an important model species to examine acoustic communication of katydids in the context of urbanization. The following questions were investigated: (1) What is the relationship between body size and sound generator characters (both stridulatory structures and mirror)? (2) What is the relationship between the different sound generator characters on different tegmina (e.g., stridulatory file length on the left tegmen vs. mirror area on the right tegmen)? And if, as predicted, these relationships are significant, (3) can their isometric or hyperallometric relationships allow for inference about the selection pressures acting on these sound generator organs? By using a similar methodology and addressing similar questions as previous species-targeted studies (see Anichini et al. 2017, Rebrina et al. 2020), the aim was to also examine how generalizable the patterns observed in Poecilimon are in the taxonomically more distant E. pallidus.
Pronotum length (PronL), measured between the middle of the anterior margin and that of the posterior margin (Fig. 1A), was used as a proxy for body size (Montealegre-Z 2009). To measure the PronL and tegmen length (TL), the dried-pinned specimens were photographed using a Canon EOS 700D digital SLR camera with a Canon EF 100 mm f/2.8 Macro USM lens (Fig. 1A).

Five sound generator characters were examined: TL; stridulatory file length (FileL), tooth width (ThW), and teeth density (ThD) on the left tegmen; and mirror area (MA) on the right tegmen. Measurements of these traits follow those of Rebrina et al. (2020). To measure the sound generator characters, the tegmina were dissected and the stridulatory areas on both left and right tegmen were photographed using the dSLR camera with a Canon MP-E 65 mm f/2.8 USM (1–5×) lens. The FileL was measured as the total length of the stridulatory file on the ventral side of the left tegmen (Fig. 1B). This was done by connecting the posterior ends of the cusp of each tooth of all the visible teeth using the ‘segmented line’ function in ImageJ. The ThW was determined by obtaining the average tooth width of the teeth in the middle region of the file. The middle region of the file was defined as the central tooth on the file plus five teeth to the basal end and four to the anal end (Fig. 1B). Tooth width was measured between the posterior ends of the cusp of the tooth. The ThD was calculated as the ratio of the 10 teeth previously chosen to the length of the middle region of the file (measured along the edge of the tooth) (Fig. 1B). The MA on the right tegmen was measured using the ‘polygon selection’ function in ImageJ to connect the inner margin of the vein surrounding the membrane making up the mirror (Fig. 1C).

Analysis

All statistical analyses were done using R software version 4.1.0 (R Core Team 2019). Prior to modeling, all traits were log_{10}-transformed to normalize the distribution and reduce heteroscedasticity (Packard et al. 2011). To examine the allometric scaling of sound generator characters with body size, the approach used by Anichini et al. (2017) and Rebrina et al. (2020) was adopted: a standardized major axis (SMA) regression was fitted for each sound generator character using the ‘smatr’ R package (Warton et al. 2012), with the PronL as a fixed effect. SMA regression is preferred over ordinary least square (OLS) regressions owing to the lower expected error of the former (Warton et al. 2006, Smith 2009). Moreover, SMA is preferred because both the sound generator characters and body size have similar levels of error as a result of the measurements being collected using the same method and having similar magnitudes (Warton et al. 2006, Smith 2009).

The coefficient of determination, \( R^2 \), was reported as a measure of the strength of regressions (Kasuya 2019). Effect sizes were interpreted as high (\( R^2 > 0.25 \)), medium (\( R^2 > 0.09 \)), or low (\( R^2 > 0.01 \)) (Cohen 1992). To test for significant difference between the scaling slope and isometry for each sound generator character, the ‘slope.test’ function of the ‘smatr’ package was used. ‘Slope = 1’ was used when a one-dimensional character (e.g., TL, FileL, ThW, and ThD) was scaled with body size (PronL, also one-dimensional). For MA, ‘slope = 2’ was used since the (two-dimensional) surface area of the mirror increases as a square of body length. This is to account for the assumption that a body grows equally in all three dimensions, i.e., that structure surface area should grow as a square of body length (Hirst et al. 2017, Rebrina et al. 2020).

Results

The average and range (minimum to maximum) of each sound generator character of the 29 males were as follows: PronL = 7.8 mm (7.0–8.7 mm); TL = 40.3 mm (35.4–44.5 mm); FileL = 1.8 mm (1.6–2.0 mm); ThW = 0.12 mm (0.07–0.14 mm); ThD = 39.4 mm{\(^{-1}\)} (29.7–49.0 mm{\(^{-1}\)}); MA = 4.4 mm{\(^2\)} (3.7–5.0 mm{\(^2\)}).

All sound generator characters exhibited significant correlations with PronL (Fig. 2), with strong effect sizes (i.e., \( R^2 \)) of the SMA models ranging from 0.3 to 0.5, except for ThD (Table 1). With the exception of ThD, the remaining sound generator characters were log_{10}-transformed. The thicker lines indicate hyperallometric relationships, and the thinner lines indicate isometric relationships.

Fig. 2. Relationships between the five sound generator characters with pronotum length (PronL) as body size based on SMA. A. Tegmen length; B. Stridulatory file length; C. Tooth width; D. Teeth density; E. Mirror area. All traits were log_{10}-transformed. The thicker lines indicate hyperallometric relationships, and the thinner lines indicate isometric relationships.
characters correlated positively with PronL. Furthermore, there was strong evidence of ThW and ThD scaling hyperallometrically with PronL: ThW increased hyperallometrically about 2.7 times faster than PronL, whereas ThD decreased hyperallometrically about 2.4 times faster than PronL (Table 1). There was very little evidence of TL and FileL scaling more than slope = 1 with PronL, indicating that these characters scale isometrically (Table 1). Likewise, there was also very little evidence of MA scaling more than slope = 2 with PronL, indicating that MA also scales isometrically (Table 1).

FileL exhibited significant correlation with MA (Fig. 3), with moderate effect size (i.e., $R^2$ of the SMA models = 0.15) (Table 1). However, there was very little evidence of FileL scaling more than slope = ½ with MA. ThW and ThD did not correlate significantly with MA (Fig. 3, Table 1).

Discussion

In the investigated paleotropical katydid, there was significant hyperallometric scaling of tooth width and teeth density with pronotum length. Mainly, larger males of *E. pallidus* bear disproportionately broader teeth and have disproportionately less densely arranged teeth. The rest of the sound-producing characters scaled isometrically with body size. Specifically, larger *E. pallidus* males were found to bear significantly longer tegmina and stridulatory file and larger mirror than smaller males. These results corroborate previous studies showing the influence of male body size on sound generator characters in other katydids, including a comparative study of 38 species by Montealegre-Z (2009) and species-based studies of *Poecilimon* (Anichini et al. 2017, Rebrina et al. 2020).

ThW and ThD exhibited hyperallometric scaling with body size, which has also been reported in *Poecilimon* (Anichini et al. 2017, Rebrina et al. 2020). One possible explanation is that these traits are subjected to positive sexual selection (Bonduriansky 2007) and may be crucial for aggressive male–male competition or as an exhibition of male quality (Eberhard et al. 2018, Rodríguez and Eberhard 2019). The striking of teeth against the scrape can cause wear and tear to the teeth (damage or loss) (Hartley and Stephen 1989). A possible hypothesis is that, since larger teeth are probably more resistant to age-related abrasion, males with larger teeth (i.e., larger ThW and lower ThD to accommodate larger teeth) are more likely to produce calls with signal properties that are recognized and/or preferred by the females over a longer period of their adult life span (Ritchie et al. 1995, Anichini et al. 2017). This could be true for *Euconocephalus* because males produce a continuous buzzing call over long durations. The continuous striking of teeth in such call types can lead to the teeth being more susceptible to wear and tear than katydids that produce shorter schemes.

The sound generator characters FileL and MA exhibited isometric scaling. This is perhaps indicative of stabilizing selection driven by their functions (Bennet-Clark 1998, Anichini et al. 2017). Specifically, FileL and MA are important morphological determinants of the carrier frequency that females tend to rely on for recognizing conspecific males, in which longer FileL and larger MA tend to scale negatively with carrier frequency in katydids (Morris et al. 1994, Montealegre-Z 2009, Montealegre-Z et al. 2017, Rodríguez and Eberhard 2019). This also implies that the variations in FileL and MA within a species should correlate with the normal distribution of wing resonance and carrier frequency to ensure conspecific recognition. Therefore, FileL and MA are probably less likely to be subjected to positive sexual selection.

However, in *Poecilimon*, MA scaled hyperallometrically with body size and was postulated to be under positive sexual selection facilitated by female preference for louder signals (Rebrina et al. 2020), the mirror structure also being important for the amplification of sound (Morris and Pipher 1967, Bailey 1970, Chivers et al. 2017). The same cannot be said for *E. pallidus*, because whether the mirror structure is under sexual selection would be out of the scope of this paper when data on the acoustics and female prefer-
ence of *E. pallidus* were not available. Nonetheless, this illustrates how the scaling of sound generator characters with body size is not always generalizable.

Lastly, TL scaled isometrically with body size in the macropterous *E. pallidus* because the wings of this species are likely to be more important for flight. This species was observed in Singapore to call on tree canopies along streets, suggesting that they can fly and disperse over long distances along green corridors (Tan 2011). A plausible explanation for the positive coupling of TL and body size may be associated with the correlated growth of TL and body size during development, and consequently, the TL becoming fixed in the adult after the final molt (Rebrina et al. 2020). A larger male, therefore, probably has longer wings to facilitate effective flight.

Unfortunately, the examination of the relationships between the sound generator characters, body size, and acoustic signal properties (see Montealegre-Z 2009, Montealegre-Z et al. 2017) was not possible in this study, as acoustic data were unavailable. As a result, inferences about female preference in *E. pallidus* are only speculative and require further testing. Nonetheless, this study provides the basis for further studies into acoustic communication in *E. pallidus* and Southeast Asia Copiphorini. Future studies examining the allometric relationships between sound generator characters and body size among different populations of *E. pallidus*—from urban and peri-urban habitats—can provide insights into the microevolution of these characters. It may also be worth looking into comparative studies by including sympatric congeners (e.g., *E. mucro* [Haan, 1843]) and/or relatives (e.g., *Xestophrys horvathi* Bolívar, 1905) (see Tan 2011).

**Acknowledgments**

The author thanks Fran Rebrina and Fernando Montealegre-Z for their comments and suggestions to improve the manuscript and Huiqing Yeo, a native English speaker from Singapore, for improving the writing. The study was funded by the Wildlife Reserves Singapore Conservation Fund (WRSCF). The author thanks the Orthopterists' Society and the Journal of Orthoptera Research for their comments and suggestions to improve the manuscript. The writing. The study was funded by the Wildlife Reserves Singapore Conservation Fund (WRSCF). The author thanks the Orthopterists' Society and the Journal of Orthoptera Research for their comments and suggestions to improve the manuscript. The study was funded by the Wildlife Reserves Singapore Conservation Fund (WRSCF).

**References**

Anichini M, Kuchenreuther S, Lehmann GCG (2017) Allometry of male sound-producing structures indicates sexual selection on wing size and stridulatory teeth density in a bushcricket. Journal of Zoology 301: 271–279. https://doi.org/10.1111/jzo.12419

Bailey WJ (1967) Further investigations into function of mirror in Tettigonioida (Orthoptera). Nature 215: 762–763. https://doi.org/10.1038/215762a0

Bailey WJ (1970) The mechanics of stridulation in bush crickets (Tettigonioida, Orthoptera) I. Tegmental Generator. Journal of Experimental Biology 52: 495–505. https://doi.org/10.1242/jeb.52.3.495

Bennet-Clark HC (1998) Size and scale effects as constraints in insect sound communication. Philosophical Transactions: Biological Sciences 353: 407–419. https://doi.org/10.1098/rstb.1998.0219

Bentsen CI, Hunt J, Jennions MD, Brooks R (2006) Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus*. The American Naturalist 167:102–116. https://doi.org/10.1086/503176

Bonduriansky R (2007) Sexual selection and allometry: a critical reappraisal of the evidence and ideas. Evolution 61: 838–849. https://doi.org/10.1111/j.1558-5646.2007.00081.x

Bonduriansky R, Day T (2003) The evolution of static allometry in sexually selected traits. Evolution 57: 2450–2458. https://doi.org/10.1111/j.0014-3820.2003.tb01490.x

Brown WD, Smith AT, Moskalik B, Gabriel J (2006) Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. Animal Behaviour 72: 225–233. https://doi.org/10.1016/j.anbehav.2006.01.012

Celiker E, Jonsson T, Montealegre-Z F (2020) On the tympanic membrane impedance of the katydid *Copiphora gorgonensis* (Insecta: Orthoptera: Tettigoniidae). The Journal of the Acoustical Society of America 148: 1952–1960. https://doi.org/10.1121/10.0002119

Chivers BD, Béthoux O, Sarria-S FA, Jonsson T, Mason AC, Montealegre-Z F (2017) Functional morphology of tegmina-based stridulation in the relict species *Cyphoderus monstrosus* (Orthoptera: Ensifera: Prophalangopsidae). Journal of Experimental Biology 220: 1112–1124. https://doi.org/10.1242/jeb.153106

Cohen J (1992) A power primer. Psychological Bulletin 112: 155–159. https://doi.org/10.1037/0033-2909.112.1.155

Counter Ir SA (1977) Bioacoustics and neurobiology of communication in the tettigoniid *Neosconocephalus robustus*. Journal of Insect Physiology 23: 993–1008. https://doi.org/10.1016/0022-1910(77)90127-5

Delly JA, Schul J (2004) Recognition of calls with exceptionally fast pulse rates: female phonotaxis in the genus *Neosconocephalus* (Orthoptera: Tettigoniidae). Journal of Experimental Biology 207: 3532–3539. https://doi.org/10.1242/jeb.015779

Del Castillo RC, Gwynne DT (2007) Increase in song frequency decreases spermaphore size: correlative evidence of a macroevolutionary trade-off in katydids (Orthoptera: Tettigoniidae). Journal of Evolutionary Biology 20: 1028–1036. https://doi.org/10.1111/j.1420-9101.2006.01298.x

Eberhard WG, Rodríguez RL, Huber BA, Speck B, Miller H, Buzzato BA, Machado G (2018) Sexual selection and static allometry: the importance of function. Quarterly Review of Biology 93: 207–250. http://doi.org/10.1086/699410

Fischer LH (1853) Orthoptera Europea. G. Engelmann Lipsiae, Leipzig, 454 pp.

Hartley JC, Stephen RO (1989) Temporal changes in the quality of the song of a bush cricket. Journal of Experimental Biology 147: 189–202. https://doi.org/10.1242/jeb.147.1.189

Heller KG (1995) Acoustic signaling in palaeotropical bushcrickets (Orthoptera: Tettigonioida: Pseudophyllidae): does predation pressure by cavedropping enemies differ in the Palaeo and Neotropics? Journal of Zoology 237: 469–485. https://doi.org/10.1111/j.1469-7998.1995.tb07775.x

Hierst AG, Lilley MKS, Glazier DS, Atkinson D (2017) Ontogenetic body-mass scaling of nitrogen excretion relates to body surface area in diverse pelagic invertebrates. Limnology and Oceanography 62: 311–319. https://doi.org/10.1002/lno.10396

Karny HH (1907) Revisio Conopoidea. Abhandlungen der K.K. Zoologisch-botanischen Gesellschaft Wien 4(3): 1–114.

Karny HH (1912) Orthoptera. Fam. Locustidae. Subfam. Copiphorinae. Genera Insectorum 139: 1–50, 6 pls.

Kasuya E (2019) On the use of r and r squared in correlation and regression. Ecological Research 34: 235–236. https://doi.org/10.1111/1440-1703.10181

Krauss HA (1902) Die Namen der ältesten Dermaptera- (Orthopteren-)Gattungen und ihre Verwendung für Familien- und Unterfamilien-Benennungen auf Grund der jetzigen Nomenklaturregeln. Zoologischer Anzeiger 25(676): 530–543.

Montealegre-Z F (2009) Scale effects and constraints for sound production in katydids (Orthoptera: Tettigoniidae): correlated evolution between morphology and signal parameters. Journal of Evolutionary Biology 22: 355–366. https://doi.org/10.1111/j.1420-9101.2008.01652.x

Montealegre-Z F, Mason AC (2005) The mechanics of sound production in *Panacanthus pallicornis* (Orthoptera: Tettigoniidae: Conocephalinae): The stridulatory motor patterns. Journal of Experimental Biology 208: 1219–1237. https://doi.org/10.1242/jeb.01526

Montealegre-Z F, Ogden J, Jonsson T, Soulsbury CD (2017) Morphological determinants of signal carrier frequency in katydids (Orthoptera): a comparative analysis using biophysical evidence of wing vibration. Journal of Evolutionary Biology 30: 2068–2078. https://doi.org/10.1111/jeb.13179
Montealegre-ZF, Postles M (2010) Resonant sound production in Copiphora gorgonensis (Tettigoniidae: Copiphorini), an endemic species from Parque Nacional Natural Gorgona, Colombia. Journal of Orthoptera Research 19: 347–355. https://doi.org/10.1665/034.019.0223

Morris GK (1999) Song in arthropods. In: Davey KG (Ed.) Encyclopedia of Reproduction, vol. 4. Academic Press, San Diego. 508–517.

Morris GK, Mason AC, Wall P, Belwood JJ (1994) High ultrasonic and tremulation signals in neotropical katydids (Orthoptera: Tettigoniidae). Journal of Zoology 233: 129–163. https://doi.org/10.1111/j.1469-7998.1994.tb05266.x

Morris GK, Pipher RE (1967) Tegmental amplifiers and spectrum consistencies in Neoconocephalus nigropleurum (Bruner), Tettigoniidae. Journal of Insect Physiology 13: 1075–1085. https://doi.org/10.1016/0022-1910(67)90109-6

Packard GC, Birchard GF, Boardman TJ (2011) Fitting statistical models in bivariate allometry. Biological Reviews 86: 549–563. https://doi.org/10.1111/j.1469-185X.2010.00160.x

R Core Team (2019) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rebrina F, Anichini M, Reinhold K, Lehmann GU (2020) Allometric scaling in two bushcricket species (Orthoptera: Tettigoniidae) suggests sexual selection on song-generating structures. Biological Journal of the Linnean Society 131: 521–535. https://doi.org/10.1093/biolinnean/blaa122

Redtenbacher J (1891) Monographie der Conocephaliden. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 41: 315–562.

Ritchie MG, Couzin ID, Snedden WA (1995) What’s in a song? Female bushcrickets discriminate against the song of older males. Proceedings of the Royal Society B: Biological Sciences 262: 21–27. https://doi.org/10.1098/rspb.1995.0171

Rodriguez RI, Eberhard WG (2019) Why the static allometry of sexually-selected traits is so variable: the importance of function. Integrative and Comparative Biology 59: 1290–1302. https://doi.org/10.1093/icb/icz039

Sales GD, Pye JD (1974) Ultrasonic Communication in Animals. Chapman and Hall, London. 281 pp. https://doi.org/10.1007/978-94-011-6901-1

Sarria-S FA, Buxton K, Jonsson T, Montealegre-Z F (2016) Wing mechanics, vibrational and acoustic communication in a new bush-cricket species of the genus Copiphora (Orthoptera: Tettigoniidae) from Colombia. Zoologischer Anzeiger-A Journal of Comparative Zoology 263: 55–65. https://doi.org/10.1016/j.jcz.2016.04.008

Schul J, Patterson AC (2003) What determines the tuning of hearing organs and the frequency of calls? A comparative study in the katydid genus Neoconocephalus (Orthoptera, Tettigoniidae). Journal of Experimental Biology 206: 141–152. https://doi.org/10.1242/jeb.00070

Shingleton AW, Estep CM, Driscoll MV, Dworkin I (2009) Many ways to be small: different environmental regulators of size generate distinct scaling relationships in Drosophila melanogaster. Proceedings of the Royal Society B: Biological Sciences 276: 2625–2633. https://doi.org/10.1098/rspb.2008.1796

Shingleton AW, Frankino WA, Flatt T, Niijhout HF, Emlen DJ (2007) Size and shape: the developmental regulation of static allometry in insects. BioEssays 29: 536–548. https://doi.org/10.1002/bies.20584

Shingleton AW, Mirth CK, Bates PW (2008) Developmental model of static allometry in holometabolous insects. Proceedings of the Royal Society B: Biological Sciences 275: 1875–1885. https://doi.org/10.1098/rspb.2008.0227

Smith RJ (2009) Use and misuse of the reduced major axis for line-fitting. American Journal of Physical Anthropology 140: 476–486. https://doi.org/10.1002/ajpa.21090

Tan MK (2011) The Copiphorini (Orthoptera: Tettigoniidae: Conocephalinae) in Singapore. Nature in Singapore 4: 31–42.

Tan MK (2020) Soundscape of urban-tolerant crickets (Orthoptera: Gryllidae, Trigonidiidae) in a tropical city, Singapore. Bioacoustics 30: 469–486. https://doi.org/10.1080/09524622.2020.1813627

Tan MK, Ingrisch S, Wahab RHA, Japir R, Chung AV (2020) Ultrasonic bioacoustics and stridulum morphology reveal cryptic species among Lipotactes big-eyed katydids (Orthoptera: Tettigoniidae: Lipotactinae) from Borneo. Systematics and Biodiversity 18: 510–524. https://doi.org/10.1080/14772000.2019.1676923

Tiwari C, Diwakar S (2019) Singers in the grass: call description of conehead katydids (family: Tettigoniidae) and observations on avoidance of acoustic overlap. Bioacoustics 28: 522–538. https://doi.org/10.1080/09524622.2018.1499553

Warton DI, Duursma RA, Falster DS, Taskinen S (2012) smatr 3 – an R package for estimation and inference about allometric lines. Methods in Ecology and Evolution 3: 257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biological Reviews of the Cambridge Philosophical Society 81: 259–291. https://doi.org/10.1017/S1464793106007007