Two new species of the tribe Meconematini (Orthoptera: Tettigoniidae: Meconematinae) from China and male song characters of *Pseudocosmetura yaoluopingensis* sp. nov.

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Abstract

This paper describes two new species of the tribe Meconematini from China, *Acosmetura longielata* **sp. nov.** and *Pseudocosmetura yaoluopingensis* **sp. nov.** Data on the male song characters of *Pseudocosmetura yaoluopingensis* **sp. nov.** are also provided. The type specimens of all new species are preserved in the Museum of Hebei University.

Keywords

Acosmetura, calling song, morphology, taxonomic images, type specimens

Introduction

Up to now, 19 brachypterou genera of Meconematini have been recorded from China, 13 of which are endemic to China (Cigliano et al. 2020). While examining the specimens collected from Anhui and Hunan provinces of China, we discovered two new species and analyzed the male calling songs of *Pseudocosmetura yaoluopingensis* **sp. nov.**

Liu (2000) established *Acosmetura* Liu, 2000 with *Acosmetura brevicerca* Liu, 2000 as the type species. Wang et al. (2018) summarized the taxonomic history of the genus and described one new species *Acosmetura longitubera* Wang, Shi & Wang, 2018. At the same time, they provided a supplementary description and morphological photographs of *Acosmetura emeica* Liu & Zhou, 2007. To date, the genus contains 11 species, all endemic to China (Liu 2000, Liu and Zhou 2007, Liu et al. 2008, Bian et al. 2014, Bian and Shi 2015, Wang et al. 2016, 2018).

The genus *Pseudocosmetura* was proposed by Liu et al. (2010) with type species *Pseudocosmetura fengyangshanensis* Liu, Zhou & Bi, 2010. The authors transferred *Tettigoniopsis anjiensis* Shi & Zheng, 1998 and *Acosmetura multicolora* Shi & Du, 2006 into this genus. Subsequently, Shi and Bian (2012) revised this genus, made a key to the known species, and described two new species: *Pseudocosmetura nanlingensis* Shi & Bian, 2012 and *Pseudocosmetura curva* Shi & Bian, 2012. Then Shi and Zhao (2018) reported a new species of this genus from Sichuan: *Pseudocosmetura wanglangensis* Shi & Zhao, 2018. They also thought *Thaumaspis henanensis* Liu & Wang,

1998 may belong to this genus. At this point, this genus includes six species, all of which are endemic to China (Liu et al. 2010, Shi and Bian 2012, Shi and Zhao 2018).

As for acoustic studies of Meconematini from China, only Wang et al. (2020a, b) have analyzed the male calling of the genus *Sinocyrtaspis* Liu, 2000, which are all relatively similar. The Meconematini species richness of China is very high, but acoustics studies are rare and need to be strengthened.

This paper reports two new species—*Acosmetura longielata* **sp**. **nov.** and *Pseudocosmetura yaoluopingensis* **sp**. **nov**.—and their morphological characters are illustrated. All type specimens examined are preserved in the Museum of Hebei University (MHU).

Methods

Specimens were examined with a Nikon-SMZ-1500 stereomicroscope. Morphological images were acquired using a Leica M205A digital imaging system. The following conventions were adopted for the specimen measurements: body length: distance from apex of fastigium verticis to posterior margin of tenth abdominal tergite; pronotum length: distance from anterior to posterior margins of pronotum; hind femur length: distance from base of hind femur to apex of genicular lobes; ovipositor length: distance from base of subgenital plate to apex of ovipositor.

The calling songs of *Pseudocosmetura yaoluopingensis* **sp. nov.** were recorded in the field using a Pettersson D1000X with a sampling rate at 192 kHz. The materials are as follows: *P. yaoluopingensis* **sp. nov.**, three males, 18–19 September 2019, collected by Tao Wang and Yanqing Li. In total, 90 recordings were recorded and analyzed. Sound measurements and power spectra were obtained using Audacity. Spectral analysis was taken from each syllable using the mean of 512 points in a Fast Fourier Transformation weighted with a Hanning window. Oscillogram of the song was acquired using Matlab R2018a. The recordings of *P. yaoluopingensis* **sp. nov.** were recorded at 21 °C. The insects were placed in a nylon cage with a microphone at distances between 10 to 15 cm.

Song terminology.—Echeme: a first-order assemblage of syllables; echeme duration: time period measured from the first syllable to

the last; echeme interval: time period measured from two neighboring echemes; syllable: sound produced during one cycle of tegmina movements; syllable period: time period measured from the start of one syllable to the next (reciprocal value: syllable repetition rate); impulse: a simple, undivided, transient train of sound waves.

Results

Genus Acosmetura Liu, 2000

Type species.—Acosmetura brevicerca Liu, 2000

Diagnosis.—The genus is characterized by the male tenth abdominal tergite with a shallow concavity on posterior margin; subgenital plate longer than wide; genitalia sclerotized, exposed, not surpassing the posterior margin of subgenital plate. Margins of ovipositor smooth or with small teeth.

Acosmetura longielata sp. nov.

http://zoobank.org/F0BA88EA-71FD-494A-B61B-B3E4B93D2980 Fig. 1

Type specimens.—**Holotype:** CHINA • \mathcal{J} , Guangdong, Ruyuan, Nanling, 15.VI.2019, leg. Tao Wang, MHU. **Paratypes:** CHINA • $2\mathcal{J}2\mathcal{Q}$, Guangdong, Ruyuan, Nanling, 15.VI.2019, leg. Tao Wang, MHU.

Description.—Male. Body small. Fastigium verticis conical, narrower than antennal scape, blunt apically and grooved dorsally. Eyes faintly globular, obviously protruding forward and outward. Apical segment of maxillary palpus longer than subapical one; apex slightly swollen, truncate.

Pronotum long, distinctly prolonged posteriorly, reaching middle part of seventh abdominal tergite; anterior margin straight while posterior margin obtusely rounded (Fig. 1A), metazona rather strikingly elevated (Fig. 1B); lateral lobe longer than deep, metazona conspicuously extended ventrally, posterior margin without humeral sinus (Fig. 1B).

Tegmina short, completely covered by pronotum, overlapping, invisible in lateral view; hind wings absent.

All femora unarmed ventrally, genicular lobes with apices obtuse. Fore coxae with 1 short spine; tibiae with 5 spines respectively on both sides of ventral surface, tibial tympana open on both sides, ovoid. Middle tibiae with 5 inner and 6 outer spines on ventral surface. Hind tibiae with 2–3 spines on both sides of ventral surface as well as 22–26 spines on both sides of dorsal surface, bearing two pairs of ventral apical spurs and one pair of dorsal apical spurs.

Lateral margins of ninth abdominal tergite slightly prolonged posteriorly (Fig. 1C) and posterior margin of tenth abdominal tergite with a U-shaped concavity in the middle (Fig. 1G); epiproct triangular, apical area blunt, fused with tenth abdominal tergite. Cerci cylindrical, basal areas somewhat robust, tapering apically; subapical areas significantly bent dorsad, apical areas with a small spine (Fig. 1G–J). Genitalia sclerotized, not surpassing posterior margin of subgenital plate, apical area flat, tongue-shaped (Fig. 11). Subgenital plate faintly trapezoidal, basal half slightly broad, with a triangular concavity at base, apical area with a V-shaped concavity; styli stout and short, inserted on apical areas of lateral lobes of subgenital plate (Fig. 1H).

Female. Pronotum slightly shorter than male, posterior margin reaching middle part of second abdominal tergite; anterior margin somewhat straight while posterior margin obtusely rounded (Fig. 1D); lateral lobe longer than deep, metazona gradually narrowing

(Fig. 1E). Lateral margins and posterior margin of eighth abdominal tergite feebly expanded posteriorly (Fig. 1L). Tenth abdominal tergite a bit short, with a triangular concavity in the middle on posterior margin (Fig. 1K); epiproct peltate, blunt apically. Cerci conical, apical areas subacute. Subgenital plate nearly trapezoidal, basal area broad, lateral margins and apical area somewhat expanded dorsad while posterior margin straight; approximate lateral margins with a V-shaped carina (Fig. 1F). Ovipositor robust, apical half bent dorsad; dorsal and ventral margins smooth (Fig. 1L).

Coloration.—Body yellowish green, green when alive. Eyes brown. Disc of pronotum with 1 broad longitudinal light brown stripe, of which lateral margins black-brown, outer margins of stripe with 1 longitudinal yellowish white stripe, not reaching posterior margin of pronotum (Fig. 1A, D). Dorsal surface of abdomen with 1 longitudinal black brown stripe in the midline. Posterior margin of male genitalia black-brown (Fig. 11). Ovipositor light brown. Apices of all third segment of tarsi and claws blackish-brown and spines of hind tibiae black.

Measurements (mm).—Body: 310.2-11.6, 911.4-12.9; pronotum: 37.5-8.6, 95.8-6.3; hind femora: 310.1-11.3, 911.8-13.0; ovipositor: 7.7–8.2.

Specimens examined.—CHINA • 1 \bigcirc , Guangdong, Ruyuan, Nanling, 11.VI.2019, leg. Tao Wang, MHU • 1 \bigcirc , Guangdong, Ruyuan, Nanling, 13.VI.2019, leg. Tao Wang, MHU • 1 \bigcirc , Guangdong, Ruyuan, Nanling, 15.VI.2019, leg. Tao Wang, MHU • 1 \bigcirc , Hunan, Yizhang, Mangshan, 31.VII.2019, leg. Yarui Xin, MHU.

Distribution.—China (Guangdong, Hunan).

Discussion.—According to the caudal morphological characters of the male, this new species belongs to the genus *Acosmetura*. The differences between this new species and the known species of the genus *Acosmetura* are as follows: pronotum long, distinctly prolonged posteriorly, metazona rather strikingly elevated; female subgenital plate nearly trapezoidal, lateral margins and posterior margin somewhat expanded dorsad while posterior margin straight, approaching lateral margins with a V-shaped carina.

Etymology.—The name of this new species is derived from the male pronotum that is long and the metazona that is strongly elevated. In Latin, *"long-"* means long and *"elat-"* means elevated.

Genus Pseudocosmetura Liu, Zhou & Bi, 2010

Type species.—Pseudocosmetura fengyangshanensis Liu, Zhou & Bi, 2010

Diagnosis.—The genus is characterized by the male tenth abdominal tergite normal, epiproct distinct or absent; cerci long; genitalia sclerotized, somewhat short. Ovipositor stout, moderately bent dorsad.

Pseudocosmetura yaoluopingensis sp. nov.

http://zoobank.org/91D8B281-F536-4DEA-937C-17135734BB47 Figs 2–4

Type specimens.—**Holotype:** CHINA • \Diamond , Anhui, Yuexi, Yaoluoping, 19.IX.2019, leg. Tao Wang, MHU. **Paratypes:** CHINA • $1\Diamond$, Anhui, Yuexi, Yaoluoping, 19.IX.2019, leg. Tao Wang, MHU • $1\heartsuit$, Anhui, Yuexi, Yaoluoping, 18.IX.2019, leg. Yanqing Li, MHU.



Fig. 1. Acosmetura longielata sp. nov.: A–B, D–E. Pronotum: A, D. Dorsal view; B, E. Lateral view; C, G, I, K–L. Apex of abdomen: C, L. Lateral view; G, K. Dorsal view; I. Latero-dorsal view; F, H. Subgenital plate in ventral view; J. Right cercus in lateral view. A–C, G–J. Male; D–F, K–L. Female. Scale bars: 2 mm (A–B, D–E, L); 1 mm (C, F–H, K); 500 µm (I–J).



Fig. 2. Pseudocosmetura yaoluopingensis sp. nov.: A–B, D–E. Pronotum: A, D. Dorsal view; B, E. Lateral view; C, F, G, K. Apex of abdomen: C, K. Lateral view; F–G. Dorsal view; H, J. Subgenital plate in ventral view; I. Right cercus in latero-dorsal view; A–C, G–I. Male; D–F, J–K. Female. Scale bars: 2 mm (K); 1 mm (A–H, J); 500 µm (I).



Fig. 3. Oscillograms at different scales of the male calling song of *P. yaoluopingensis* sp. nov. A. Two echemes; B. Four syllables; C. Syllable. Scale bars: 1.25 s (A); 25 ms (B); 2.5 ms (C).

Description.—Male. Body small, somewhat robust. Fastigium verticis conical, apex obtusely rounded with a longitudinal sulcus on dorsal surface. Eyes approximatively globular and distinctly protruding forward and outward. Apical segment of maxillary palpus longer than subapical one, slightly swollen apically, truncate.

Pronotum feebly long, reaching middle part of second abdominal tergite; anterior margin straight while posterior margin arcshaped (Fig. 2A), metazona slightly raised (Fig. 2B); lateral lobe longer than deep, posterior margin slightly expanded ventrally, without humeral sinus (Fig. 2B).

Tegmina short, covered by pronotum, visible in lateral view; hind wings absent.

All femora unarmed ventrally, genicular lobes with apices obtuse. Fore coxae with 1 small spine; fore tibiae with 5 spines respectively on inner and outer sides of ventral surface, tympanal organs open on both sides, ovoid. Middle tibiae with 4 inner and 5 outer spines on ventral surface. Hind tibiae with 21–24 spines separately on both sides of dorsal surface, bearing one pair of ventral apical spurs and one pair of dorsal apical spurs.

Lateral margins of ninth abdominal tergite strongly prolonged posteriorly (Fig. 2C), terminals obtusely rounded and bent inward. Tenth abdominal tergite expanded posteriorly, with a U-shaped concavity in the middle, lateral lobes conical, bent inward and backward, terminals somewhat blunt (Fig. 2G, I). Epiproct fused with tenth abdominal tergite, peltate. Cerci markedly bent inward, inner margins of 2/3 apical area concave, grooved (Fig. 2I); apical areas with a small odontoid. Genitalia sclerotized, exposed, surpassing posterior margin of tenth abdominal tergite, basal area robust, apical area slim, split in the middle (Fig. 2G, I). Subgenital plate nearly trapezoidal, broad at base, with a triangular concavity in the middle; midline with longitudinal carinae, posterior margin truncate; styli stout and short, inserted on apico-lateral margins of subgenital plate (Fig. 2H).

Female. Pronotum slightly shorter than male, reaching posterior margin of first abdominal tergite, metazona not raised (Fig. 2D, E); metazona of lateral lobe gradually tapering (Fig. 2E). Lateral margins of eighth and ninth abdominal tergum feebly prolonged posteriorly (Fig. 2K). Tenth abdominal tergite short and broad, center of posterior margin concave, lateral angles somewhat blunt (Fig. 2F). Epiproct slightly small, triangular, blunt apically. Cerci conical, apical areas subacute. Subgenital plate trapezoidal, longer than wide, median carinae distinct, posterior margin slightly concave in the middle (Fig. 2J). Ovipositor stout, robust at base, apical half bent dorsad, apical area subacute; dorsal and ventral margins smooth (Fig. 2K).

Coloration.—Body yellowish green, green when alive. Eyes brown. Disc of pronotum with 1 longitudinal light brown stripe, of which lateral margins black brown, outer margins of stripe with yellowish white longitudinal stripe severally (Fig. 2A, D). Dorsal surface of abdomen with 1 longitudinal black brown stripe in the midline. Apical areas of male cerci light brown. Apices of all third segment of tarsi and claws black brown.

Measurements (mm).—Body: ♂ 9.2–10.8, ♀10.3–12.5; pronotum: ∂4.3–4.7, ♀3.6–4.4; hind femora: ∂8.6–9.5, ♀9.5–10.7; ovipositor: 6.6–7.8.

Specimens examined.—CHINA • 1♂, Anhui, Yuexi, Yaoluoping, 18.IX.2019, leg. Yanqing Li, MHU • 2♀, Anhui, Yuexi, Yaoluoping, 18.IX.2019, leg. Tao Wang, MHU.

Acoustics.—The male calling song of this species is performed only at night and is inaudible to humans. Both echeme duration (3–35 s) and echeme interval (1.6–8.5 s) are irregular (Fig. 3). The echeme consists of more than ten syllables, the amplitude of syllables in the beginning part is small, then gradually increasing. The syllable period is 156 ± 7 ms (n = 600) and the syllable repetition rate is 6.41 Hz. A single syllable consists of more than ten impulses, the amplitude of which gradually increases and then decreases (Fig. 3). The calling song has a large proportion in the ultrasonic range (Fig. 4), and the peak frequency is 33.386 ± 1.71 kHz (n = 600).

Distribution.—China (Anhui).

Discussion.—This new species resembles *Pseudocosmetura anjiensis* (Shi & Zheng, 1998), but differs in the following: male tenth abdominal tergite expanded posteriorly, with a U-shaped concavity in the middle, lateral lobes conical, bent inward and backward,





terminals somewhat blunt; female tenth abdominal tergite short and broad, center of posterior margin concave, lateral angles somewhat blunt; subgenital plate trapezoidal, longer than wide.

Etymology.—The name of the new species is derived from the type locality, Yaoluoping.

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New records of exotic crickets in Europe: *Homoeogryllus* species (Orthoptera: Gryllidea: Phalangopsidae)

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Abstract

This short note lists new records of exotic crickets belonging to the genus *Homoeogryllus* (Orthoptera: Gryllidea: Phalangopsidae) in Europe (Poland and Belgium) and discusses the most probable scenarios of their arrival from tropical regions. Photographs and stridulation spectrograms of these crickets are provided. The report concludes that handling terminals and warehouses with tropical plants are the most common sites in Europe where exotic species of different taxa are recorded. The species *Homoeogryllus longicornis* (Walker, 1869) is also reclassified to the genus *Meloimorpha* Walker, 1870.

Keywords

Belgium, identification, Poland, species introductions, spectrogram, tropical plants

Introduction

International trade, with its multiple means and routes, may not only speed up the movements of animals, but also allow the spread of non-native animals far beyond their home ranges. Among anthropogenic vectors of nonindigenous species, rising sea transport is now considered to account for the bulk of introduced species (Sardain et al. 2019). Shipping containers, hull fouling, and ballast waters help small animals, like insects, to reach distant places. Coupled with global warming, introducing non-native species to new habitats as a result of human activities may be a significant source of biological invasions and can cause severe harm to native species communities (Wheeler and Hoebeke 2017).

However, many adventive or exotic species are introduced to new habitats accidentally and do not establish populations. Crickets within the genus *Homoeogryllus* Guérin-Méneville, 1847 are one example of this phenomenon. Out of 16 species within

the Homoeogryllus genus, 15 can be found in Africa: H. adunctus Gorochov, 1988, H. ambo Gorochov, 2018, H. cavicola Chopard, 1950, H. deviatus Desutter-Grandcolas, 1985, H. gabonensis Desutter-Grandcolas, 1985, H. lyristes Gorochov, 1988, H. maroccanus Desutter-Grandcolas, 1985, H. nigresculus Desutter-Grandcolas, 1985, H. nigripennis Chopard, 1942, H. orientalis Desutter-Grandcolas, 1985, H. parvus Chopard, 1936, H. reticulatus (Fabricius, 1781), H. tessellatus (Serville, 1838), H. venosus Saussure, 1878, and H. xanthographus Guérin-Méneville, 1847. The last species, Homoeogryllus longicornis (Walker, 1869) from the Malay Penninsula (Desutter 1985, Gorochov 2018, Cigliano et al. 2020), actually belongs to the genus Meloimorpha Walker, 1870, according to the number of spurs on its hind tibiae (Desutter-Grandcolas and Jaiswara 2012), and, consequently, we propose here the new combination Meloimorpha longicornis (Walker, 1869), comb. nov. Here, we show data on new records of Homoeogryllus crickets in Europe and provide photos and call spectrograms.

Materials

Specimens were found in various situations as described in the Results. They were collected when possible, recorded, and identified by one of us (LDG), except *H. xanthographus* (Guérin-Méneville, 1847) (see Żurawlew 2009).

Recordings of spontaneously stridulating crickets were made using Canon Power Shot A570 IS (*H. xanthographus*), MINT Olympus Digital Dm-1 (*H. cf. reticulatus*) and a dictaphone (*H. tessellatus*). Analog recordings were digitized at a sampling rate of 44.1 kHz/16 bits and visualized using *seewave* package (Sueur et al. 2008) implemented in R (R Core Team 2013) with the following settings: FFT length: 1024, window type: Hann, temporal overlap: 90%. The audio files were uploaded to the Orthoptera Species File Online (Cigliano et al. 2020) and the MNHN Sound Library.

Results

Homoeogryllus cf. reticulatus (Fabricius, 1781) Figs 1, 2

Observed material.—Belgium, Gent, 8 VIII 2010, 1, D. B. Herman leg., specimen not collected, identified based on its calling song.

Stridulation description.—Only two stridulation series were recorded (Fig. 2a). Each consisted of two fast introductory creaks



Fig. 1. *Homoeogryllus* cf. *reticulatus* (Fabricius, 1781). Male found in a crack of a wall near the port of Gent (Belgium) in which wood of tropical trees is stored.

separated by 30 ms pause and a number of chatter syllables with fundamental frequency ca. 4 kHz and harmonics (Fig. 2c). Duration of the first stridulation with 8 syllables (Fig. 2b) was 4.1 s and that with 5 syllables was 2.2 s. Both stridulations were separated by a 7.6 s pause.

Remark.—The specimen was found in a crack of a wall near a port where the wood of tropical trees is stored. The species has been recorded in Egypt, Chad, Senegal, Guinea, Ivory Coast, Benin, Cameroon, Central African Republic, Equatorial Guinea, Gabon, Republic of the Congo, and Democratic Republic of Congo (= Zaire) (Desutter 1985, Gorochov 2018).

Homoeogryllus tessellatus (Serville, 1838) Figs 3, 4

Observed material.—Poland, Warsaw, Łowicka Street, 17–23 VIII 2016, 1승, M. J. Gorazdowski leg., L. Desutter-Grandcolas det., MNHN.

Remark.—The male was found in a snake terrarium. Presumably, the vector was a bromeliad *Neoregelia carolinae* (Beer) L.B. Smith bought in a garden center. The species is native to Ivory Coast, Guinea, and Sierra Leone (Desutter 1985).

Stridulation description.—The stridulation was mostly continuous with repeated creaks of roughly the same length of 0.3 s (Fig. 4a). The beginning of each series consisted of only 3–5 creaks increasing in length (Fig. 4c). The fundamental frequency of stridulation was around 5 kHz (Fig. 4b). The shortest recorded stridulation was 9.3 s and the longest 35.3 s.



Fig. 2. Stridulation of *Homoeogryllus* cf. *reticulatus* (Fabricius, 1781) male from Gent (Belgium): **a.** spectrogram of two recorded stridulation series; **b.** spectrogram of one stridulation series in higher resolution of time domain; **c.** spectrogram of the beginning of stridulation series with three units (syllables) shown. The oscillograms are shown below and the relative amplitude scales (in dB) on the right of the spectrograms. Abbreviations: dB, decibel; s, second; kHz, kilohertz.



Fig. 3. Homoeogryllus tessellatus (Serville, 1838) male observed in Warsaw (Poland).

Homoeogryllus xanthographus (Guérin-Méneville, 1847) Figs 5, 6

Observed material.—Poland, Gołuchów, Pleszew District, 20 I–10 III 2009, 1♂, A. Biernat leg., S. W. Heads det. (see Żurawlew 2009).

Remark.—The male was found in a wicker basket with potted plants inside a residential building. It had probably been transported, as an egg or a nymph, with the coconut bedding into which the plants were potted.

Stridulation description.—Recorded stridulations (n = 9) consisted of 4 to 9 elements (Fig. 6a). Two types of elements could be distinguished: shorter creaks repeated 3 to 8 times and a longer, terminating creak (Fig. 6c). One series had two terminating elements (Fig. 2b). The fundamental frequency of stridulation was around 4 kHz.

Discussion

In this short note, we report new records of two species of *Homoeogryllus* genus, *H.* cf. *reticulatus* and *H. tessellatus*, in Belgium and Poland, respectively. In addition, we newly describe the stridulations of *H. xanthographus*, another *Homoeogryllus* species which, as an egg or nymph transported in soil substratum, was previously introduced in Poland (Fig. 5; Żurawlew 2009). So far, of the species of *Homeogryllus*, only the stridulations of *H. tessellatus*, *H. tessellatus*, H. cf. *reticulatus*, *H. nigresculus*, and *H. xanthographus* have been described (Desutter 1985, Żurawlew 2009).

These tropical crickets were probably introduced into Europe by being shipped from Africa, which is a source of tropical plants for Europe. Shipping-mediated introductions of



Fig. 4. Stridulation of *Homoeogryllus tessellatus* (Serville, 1838) male from Warsaw (Poland): **a**. spectrogram of recorded stridulation; **b**. spectrogram of one stridulation series in higher resolution of time domain; **c**. spectrogram of the beginning of stridulation series with three units (syllables) shown. The oscillograms are shown below and the relative amplitude scales (in dB) on the right of the spectrograms. Abbreviations: dB, decibel; s, second; kHz, kilohertz.



Fig. 5. *Homoeogryllus xanthographus* (Guérin-Méneville, 1847) male observed in Gołuchów, Pleszew District (Poland).

Eugaster spinulosa (Johansson, 1763) (Bazyluk and Liana 2000) from Africa, *Amphiacusta nauta* (Desutter-Grandcolas, 1997) from the Caribbean, and that of *H. xanthographus* support this scenario. In fact, studies show that ports and garden centers in Europe are places where many species of tropical insects and spiders have been recorded (Rozwałka et al. 2016). Apart from the accidental introduction of species associated with woody plants, another pathway that largely contributes to the spread of non-native species is trade and breeding as pets (owing to their pleasant songs) or as food for vertebrate and invertebrate pets. Indeed, some *Homoeogryllus* species are reported to be kept in terrariums, but their true origin and identification have not been confirmed.

As a consequence of accidental introductions, some species may start new populations, which is a threat to local biodiversity (Hulme 2009). They could also invade hot, human-made places, such as bakeries, houses, or underground electric railroad, as is the case of *Acheta domesticus* (Linnaeus, 1758), known as the "grillon du métro" in Paris. Examples of tropical Orthoptera species that were introduced to Europe or North America that can now be found in palm houses, greenhouses, and houses include *Tachycines asynamorus* Adelung, 1902, and *Diestrammena japanica* Blatchley, 1920, (Głowaciński et al. 2012, Epps et al. 2014). These species have also been found in Cuba where they are believed to have established new populations (https://www.saltatoria.info/arten%C3%BCbersicht-a-z-species-az/homoeogryllus-sp-kuba/), even though they are not listed among the Orthoptera of Cuba (Yong and Perez-Gelabert 2014).

Continuous monitoring of all the exotic species found in Europe can contribute greatly to correct identifications in the future, the collection of new information on their biology, and the identification of new potentially invasive species. For instance, in the Czech Republic, as many as 595 non-native species have been recorded (Šefrová and



Fig. 6. Stridulation of *Homoeogryllus xanthographus* (Guérin–Méneville, 1847), male observed in Gołuchów, Pleszew District (Poland): **a.** spectrogram of recorded stridulation series; **b.** spectrogram of one stridulation series in higher resolution of time domain; **c.** spectrogram of two type units (syllables). The oscillograms are shown below and the relative amplitude scales (in dB) on the right of the spectrograms. Abbreviations: dB, decibel; s, second; kHz, kilohertz.

Laštůvka 2005). In Poland, 305 species are non-native with insects being most common, followed by molluscs, shellfishes, flatworms, nematodes, arachnids, cnidarians, and annelids (Głowaciński et al. 2012). The difficulty is in evaluating the potential of these tropical species to actually invade and settle, especially in terms of resistance to cold weather and changes in the available resources.

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Initial impact of a soil disturbance technique (disc harrowing) on Orthoptera in a grass heath in Breckland, UK

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Abstract

On a Breckland grass heath in eastern England, soil disturbance methods such as disc harrowing employed to benefit endangered plants such as tower mustard, *Arabis glabra*, could also create exposed ground for localized insects, specifically the mottled grasshopper, *Myrmeleotettix maculatus*. Orthoptera of disc-harrowed strips on a grass heath at Santon Warren in Norfolk, UK, were monitored in 2018 and 2019. Data analysis focused on two target species, field grasshopper, *Chorthippus brunneus*, and *M. maculatus*, which are likely to respond positively to the creation of early successional habitat. Of the two species, *M. maculatus* was found in significantly high abundance on the disc-harrowed strips, whereas *C. brunneus* was not. The species richness of Orthoptera did not appear affected by harrowing, although three species at this location (lesser marsh grasshopper, *Chorthippus albomarginatus*, longwinged conehead, *Conocephalus fuscus*, and Roesel's bush-cricket, *Roseliana roeselii*) need taller vegetation than was present on the disc-harrowed strips.

Keywords

Acrididae, bare earth, bush-crickets, conservation, grasshoppers, heath-land, Tettigoniidae

Introduction

Breckland is a biodiversity hotspot in the UK; 25,500 species were recorded in a recent audit led by the University of East Anglia (Dolman et al. 2012). Over 2,000 of these species were of national conservation concern. The flora includes over 120 nationally rare and threatened plant species with many dependent on the remaining dry grassland and heathland that survived afforestation in the 20th century (Robertson and Hawkes 2017). The grasshopper fauna (Orthoptera: Acrididae) of Breckland is relatively impoverished in comparison, with only six native species (55% of the national total of 11 species) (Richmond 2001, Gardiner 2018a). Despite the dearth of species, grasshoppers are an important component of grassland ecosystems, consuming up to 8% of net primary production (Köhler et al. 1987). Grasshoppers are a crucial link in food chains as prey for spiders and avian predators in particular (Latchininsky et al. 2011). Densities of grasshoppers often exceed 3 adults/m² in dry acid grassland and heathland, indicating that they can be an abundant food source (Gardiner et al. 2002). Be-

cause of this, grasshoppers have been listed as a key invertebrate group in the Breckland Natural Area profile.

Different grasshopper species have contrasting microclimatic preferences (humidity and temperature) that drive the diversity of assemblages (Gardiner et al. 2002, Gardiner and Dover 2008). Short grassland and heathland swards may be unfavorable for some grasshoppers due to high microclimatic temperatures (>44°C) at 10 cm above the soil surface (Gardiner and Hassall 2009), which can lead to shade-seeking behavior and vigorous escape responses in several grasshopper species. The optimum air temperature for the development of grasshoppers in the UK is thought to be 35–40°C (Willott 1997), although at high elevations in the Alps (>2000 m above sea level), temperatures never reach these levels, limiting the reproductive potential of the common green grasshopper, *Omocestus viridulus* (Berner et al. 2004).

Responses to microclimatic temperatures differ between species. For example, the mottled grasshopper, *Myrmeleotettix maculatus*, is a short sward specialist, and its small size may be an adaptation for the high temperatures it experiences (Willott 1997). Contrastingly, *O. viridulus*, a tall grass species in the UK (Marshall and Haes 1988), is a large insect that can overheat in short, hot grasslands/heathlands and, therefore, avoids those habitats (Gardiner 2010). Tall grassland may also have higher humidity that is more favorable for this grasshopper (Berner et al. 2004).

Warren and Büttner (2009) highlighted that disturbance caused by military activities can help conserve populations of the bluewinged grasshopper, Oedipoda caerulescens, which needs plentiful (30-50%) bare earth in its habitat. Many insects can be classified as either disturbance-dependent or disturbance-averse, depending on the level of disturbance of the vegetation cover they need to persist. Bare earth provides sites where grasshoppers can bask to warm up (exposed soil is often much hotter than surrounding vegetation; Key 2000) and where adult females of species such as the field grasshopper, Chorthippus brunneus, which lay their egg pods in exposed soil (Choudhuri 1958), can deposit their egg load after mating. Bare earth is the earliest stage of succession and is often lacking in grasslands due to a dearth of soil disturbance caused by an absence of grazing livestock. Grasslands without management can become tall and rank and have little exposed soil (Grayson and Hassall 1985, Ausden and Treweek 1995, Gardiner 2018b).

Myrmeleotettix maculatus was the scarcest species recorded in a recent survey of Breckland (Gardiner 2013, 2018a), being observed at only two sites (East Wretham Heath and Thetford Warren Lodge). In the Breckland survey, there seemed to be an absence of the open ground for this disturbance-dependent grasshopper. At Thetford Warren Lodge, it was abundant on lichen heath, a seemingly scarce habitat at the other survey sites.

It is the aim of this short communication to determine the initial impact of the soil disturbance technique of disc harrowing on Orthoptera of a grass heath in Breckland, UK, focusing on two disturbance-dependent species: *C. brunneus* and *M. maculatus*.

Methods

Site.—The study site on Santon Warren (52°27'43.2468"N, 0°40'23.8224"E) in Breckland, Suffolk, UK, was a grass heath composed of fine-leaved grasses (*Agrostis* and *Festuca* spp.) with rare annual plants (tower mustard, *Arabis glabra*) dependent on soil disturbance for their persistence. The grass and lichen heath developed on a sandy soil (with flint) and underlying chalk bedrock. Formerly, rabbit (*Oryctolagus cuniculus*) grazing checked grass growth and scrub development, but since the myxomatosis outbreak in the 1960s, this influence has declined. Therefore, other methods of creating bare ground were required to encourage the proliferation of rare plants.

Soil disturbance technique.—Two strips of grass heath (300 m length) with little exposed bare ground (<10%) were randomly selected for soil disturbance with agricultural discs attached to the back of a tractor. The primary aim of disc harrowing in this area was to promote the abundance of the plant *A. glabra* (Neal Armour-Chelu personal communication). The vertical discs harrowed the surface and upper layers of the soil (Robertson and Hawkes 2017) to a width of 2.5 m and a depth between 8–18 cm. Disc harrowing has been regularly employed in Breckland in recent years to conserve rare plant populations and promote invertebrate abundance (Robertson and Hawkes 2017). The two strips were disc-harrowed in February 2018 with adjacent grass heath left untouched (Fig. 1). Vegetation was allowed to naturally regenerate on the strips.

Orthoptera sampling methods.—In each disc-harrowed strip and in an adjacent control strip, a 1-m wide x 300-m long transect (the same length for the disc-harrowed strip and the control) was established, closely following the methodology of Gardiner et al. (2005) and Gardiner and Hill (2006). The disc-harrowed and control strips were parallel to each other but at least 10 m apart to reduce the risk of double counting. Two target species, C. brunneus and the more localized M. maculatus, were the focus of adult monitoring, although individuals of all species were also recorded to determine assemblage composition and species richness. The former grasshopper is an abundant species in Breckland, while M. maculatus is localized and probably declining in response to the lack of soil disturbance on grass heath (Gardiner 2018a). The two target species should be model insects for studying the responses to disc harrowing as both require bare earth during their life cycle for basking and oviposition (Marshall and Haes 1988). It is acknowledged that the narrow nature of the disc-harrowed strips meant that frequent movements of grasshoppers between bare earth and surrounding unmanaged heath were unavoidable. Therefore, the surveys were a snapshot of strip usage, indicating their favorability for basking or oviposition, rather than as a selfcontained breeding habitat.



Fig. 1. Disc-harrowed strips in May 2018, three months after disc harrowing, showing partial revegetation and variation in exposed substrate.

Each transect was walked at a slow, strolling pace (2 km/hr) from May–July of 2018 and 2019 (5 surveys in each year, 10 in total). Nymphs flushed from a 1-m wide band in front of the observer were recorded along the center of the 2.5 m harrowed strip and in the control. As it is difficult to distinguish between species in the early instars, nymphs of both species were lumped together for recording purposes. The surveys were undertaken in vegetation sufficiently short (<50 cm) to minimize the possibility of overlooking nymphs in tall grass (Gardiner et al. 2005). With practice, it was relatively easy to ascertain the species of adults without capture (Gardiner and Hill 2006). In addition to nymphs and adults of the two grasshopper species, other orthopteran species were counted on transects to provide an estimate of assemblage abundance and species richness. The weather conditions on survey days were favorable for insect activity, being largely sunny and warm (>17°C).

Statistical analysis.—The counts for each transect were standardized to 0.1 ha to give a clearer indication of usage of strips and control. To correct for non-normality, the data for both grasshopper species and the species richness were square-root transformed (Heath 1995). The mean density/0.1 ha of nymphs, adults of *C. brunneus* and *M. maculatus*, and overall species richness were compared between the disc-harrowed strips and control in both years using a 2-way ANOVA.

Results

A total of 811 nymphs (70% of total recorded) were observed on the disc-harrowed strips in both years combined, compared to 353 on the control transects. Adults of both species were numerous (both years combined, *C. brunneus*: 729 individuals, *M. macu*- *latus*: 559). The disturbance-dependent species *M. maculatus* was almost exclusively recorded on the disc-harrowed transects (552 adults observed, 99% of total) compared to the control (just 7 adults). Adults of *C. brunneus* were more evenly distributed (434, or 60%, on disc-harrowed transects and 295 on control).

Densities of nymphs (Fig. 2) were not significantly different between disc-harrowed strips and controls (F = 6.77, P = 0.06) or year (F = 2.18, P = 0.21) with no interaction between factors (F = 0.01, P = 0.93). Densities of *C. brunneus* adults were not significantly different between disc-harrowed strips and controls (F = 0.98, P = 0.38) or year (F = 1.14, P = 0.35) with no interaction between treatment and year (F = 0.21, P = 0.67). In contrast to *C. brunneus*, densities of *M. maculatus* adults were significantly different between disc-harrowed strips and controls (F = 299.58, P = 0.0001) but not between years (F = 3.35, P = 0.14) and with no interaction between factors (F = 0, P = 1).

Overall, five species of Orthoptera were recorded on the sparsely vegetated disc-harrowed strips and eight on the controls (Table 1). All species apart from *C. brunneus* and *M. maculatus* were in low abundance (≤ 20 adults). Common green grasshop-



Fig. 2. Nymph (both species combined) and adult density for two grasshopper species.

 Table 1. Species of Orthoptera recorded on disc-harrowed strips and unmanaged controls.

Species	Disc-harrowed	Control	Total
Chorthippus brunneus	434	295	729
Myrmeleotettix maculatus	552	7	559
Stenobothrus lineatus	15	16	31
Omocestus viridulus	4	16	20
Roeseliana roeselii	0	11	11
Pseudochorthippus parallelus	2	5	7
Chorthippus albomarginatus	0	3	3
Conocephalus fuscus	0	2	2
Total	1007	355	1362

per, *Omocestus viridulus*, lesser marsh grasshopper, *Chorthippus albomarginatus*, meadow grasshopper, *Pseudochorthippus parallelus*, and stripe-winged grasshopper, *Stenobothrus lineatus*, were all more numerous on the controls than the disc-harrowed strips (Table 1). No bush-crickets were recorded on the harrowed strips, with longwinged conehead, *Conocephalus fuscus*, and Roesel's bush-cricket, *Roeseliana roeselii*, being confined to the taller vegetation (>30 cm) of the control heath. Despite the differing species lists, disc harrowing had no impact on species richness (F = 3.46, P = 0.14) nor did it differ with years (F = 0.54, P = 0.50), with no interaction between treatment or year (F = 0.76, P = 0.43).

Discussion

In many grasslands, grazing can create patches of bare earth (through trampling of the soil by hooves) that provides an environment for grasshopper oviposition and basking (Bazelet and Gardiner 2018, Gardiner 2018b). In the absence of grazing animals, such as sheep and cattle, artificial methods of soil disturbance can be used to establish exposed soil (Robertson and Hawkes 2017, Hawkes et al. 2019a,b). In this study, disc harrowing was utilized to encourage the germination of rare plant species such as *A. glabra* in Breckland. In turn, it appears that disc harrowing also benefited the localized grasshopper *M. maculatus*, which is a species found in early successional ground with bare earth and lichen cover (Marshall and Haes 1988).

In this study, *M. maculatus* was almost exclusively found on the soil disturbed strips when compared to unmanaged dry heath, a similar situation to other Breckland soil disturbance studies. In research plots at nearby Stanford Training Area (STANTA), 60 *M. maculatus* were recorded in pitfall traps on cultivated grass heath, whereas none were captured in undisturbed controls (Robert Hawkes personal communication). The grasshopper is at an advantage on exposed soil, particularly where there is a high stone content, due to its mottled coloration that provides excellent camouflage (Gardiner 2014).

In the pioneering Breckland study by Dolman and Sutherland (1994), shallow rotavation produced bare soil interspersed with fragments of vegetation including the remains of grass tussocks, moss, and lichen. It appears that disc harrowing produces a similar diverse habitat. The microhabitats of the harrowed strips varied from unvegetated mobile sand, stony ground, to soil sparsely covered with lichens and mosses. *Myrmeleotettix maculatus* was recorded in all of these situations (Fig. 3), and it is likely that the continued presence of this localized grasshopper may be dependent on the provision of an appropriate matrix of exposed soil and early successional vegetation in Breckland.

The most abundant grasshopper, *C. brunneus*, had no preference for the disc-harrowed strips. In a study of its response to sward height in Essex, *C. brunneus* preferred grasslands with swards

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Fig. 3. Typical *Myrmeleotettix maculatus* habitat: stony, exposed soil with little vegetation. Photo credit: T. Gardiner.

10–20 cm in height (Gardiner et al. 2002), suggesting that the harrowed strips lacked the required patches of tall grass for shelter and feeding (Bernays and Chapman 1970a,b), despite an abundance of oviposition habitat. Consequently, without taller refuges from the often excessive microclimatic temperatures of bare soil, larger species (*C. brunneus* at 15–25 mm as compared to *M. maculatus* at 12–19 mm; Marshall and Haes 1988) may disperse to unmanaged vegetation to seek shade (Gardiner and Hassall 2009).

The 2.5 m-wide strips were probably too narrow to fulfil all the needs of either grasshopper species, probably with frequent movements between the exposed soil and adjacent grass heath. Adults of *M. maculatus* were abundant on the strips: perhaps they utilized the exposed ground for basking and oviposition.

In reality, soil disturbance is undertaken to conserve rarer species than the orthopterans recorded in this study. The primary driver at Santon Warren is the conservation of the endangered plant *A. glabra*. The favorable habitat for *M. maculatus* demonstrates a knock-on benefit for a non-target insect. It is possible that disc harrowing may also benefit other invertebrates that require soil disturbance, such as the declining small heath butterfly, *Coenonympha pamphilus*, that was regularly sighted on the strips. Green tiger beetles, *Cicindela campestris*, were also seen on the disc-harrowed strips along with many species of Hymenoptera.

Hawkes et al. (2019a) report that ground-disturbance increased the numbers of woodlark, *Lullula arborea*, while multi-taxa invertebrate responses were mixed in response to various ground treatments (Hawkes et al. 2019b), with only 'priority' carabid beetles influenced by cultivation treatment. Hawkes et al. (2019b) further outlined that landscapes with soil disturbance treatments had a higher species richness of ants, beetles, and true bugs than those without.

This small-scale study presents evidence that soil disturbance on a grass heath using a disc harrow may produce enhanced habitat for localized disturbance-dependent species such as *M. maculatus*. Although orthopteran species richness was unaffected by disc harrowing, the strips may be too hot or bare of vegetation for species not recorded on the strips, such as the bush-crickets *C. fuscus* and *R. roeselii* (Table 1). Therefore, soil disturbance should be embedded within the management of a grass heath mosaic that includes long grassland benefitting the full range of Orthoptera present (Table 1).

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Presence of the four-spined pygmy devil, *Arulenus validispinus* (Orthoptera: Tetrigidae), confirmed in Bukidnon region on the island of Mindanao, Philippines

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Abstract

The four-spined pygmy devil (*Arulenus validispinus* Stål, 1877) is an endemic species to the Philippines. It was described more than 140 years ago from a single female specimen. Since its description, only a single new record was known, reported by Skejo from the Lanao region in 2017 and based on a specimen from eBay. Here, we record the species from the Bukidnon Mountains. We present measurements of a male and a female we collected, with the description of the species morphology and habitat. This species differs from its congeneric Mia's pygmy devil (*A. miae* Skejo & Caballero, 2016) by the sharp dorsal and lateral spines.

Keywords

Arulenus miae, habitat, morphology, Mt. Pantaron, taxonomy

Introduction

The Philippines is biogeographically one of the most diverse countries due to its high number of islands (Mittermeier et al. 1998). Mindanao, a major island of the Philippines, is located on the southern part of the archipelago. Recently, discoveries of a new species and records of pygmy grasshoppers were made in Mindanao (Skejo and Caballero 2016, Tan et al. 2019, Mohagan et al. 2020). The Bukidnon is located in the central part of Mindanao and contains one of the most extensive mountain massifs of the island—the Mt. Pantaron Range—which is a major part of the central cordillera (Gronemeyer et al. 2014). The mountain region has a high biodiversity value (Coritico et al. 2018). A faunistic inventory was recently conducted in the area, during which an interesting species of pygmy grasshopper was collected, *Arulenus validispinus*, which had not been recorded for more than a century.

The four-spined pygmy devil (*A. validispinus* Stål, 1877) is an obscure species that was, until today, known only from the holo-type female collected by Semper in the Philippines without specified locality (Stål 1877, Skejo and Caballero 2016, Skejo 2017)

and a female specimen on eBay from the Lanao region of the island of Mindanao. The other species of the genus, Mia's pygmy devil (*A. miae* Skejo & Caballero, 2016), inhabits the area west of *A. validispinus'* distribution (Skejo 2017).

Our study presents, for the first time, measurements and habitat of a male *A. validispinus*.

Materials and methods

Entry protocol and permits.—Compulsory permits, such as an approved Gratuitous Permit (GP) from the Department of Environment and Natural Resources in compliance with RA 9147 for the collection of the specimens and Institutional Animal Care and Use Committee (IACUC), were obtained.

Field sampling, collection of specimens, photography, and measurements.—The study was conducted in the lower and upper montane forest of Mt. Pantaron, Sitio Miaray, Barangay Mandahican, Cabanglasan (8°27'73.0"N, 125°36'54.6"E; 1004 m.a.s.l.; 03–14 February 2020) (Fig. 1). The combination of standard belt-transect and opportunistic and random sampling was implemented in the study. The collection of specimens was conducted along an established 2-km transect covering 10 m x 5 m on both sides.

Specimens of *Arulenus validispinus* were collected by handpicking when encountered during the diurnal (07:00 h–15:00 h) and nocturnal (17:00 h–22:00 h) period. They were then put in vials filled with 95% ethyl-alcohol for preservation. Specimens were air-dried and mounted. Images of *A. validispinus* were taken using a DSLR Canon EOS 700D camera combined with an AmScope stereomicroscope. Final images of the species were edited using licensed Adobe Photoshop CS software. An ocular micrometer was used to measure the specimens. The standard methodology of Skejo and Bertner (2017), Tumbrinck and Skejo (2017), and Muhammad et al. (2018) were used for gathering measurements.

The following measurements were taken: Body length (from fastigium to the end of pronotum), pronotum length (PL) (from

the anterior margin to the caudal apex of the pronotum), **pronotum** lobe width (PW) (between the lateral lobes), pronotum height (PH) (lateral view from the bottom of the paranota to the tip of the highest spine), fore femur length (FFL) (in lateral view, its greatest length from the tip of the dorso-basal lobe to the tip of the knee), fore femur width (FFW) (in lateral view, its greatest width), mid femur length (MFL) (in lateral view, its greatest length from the tip of the dorso-basal lobe to the tip of the knee), mid femur width (MFW) (in lateral view, its greatest width), hind femur length (HFL) (in lateral view, its greatest length from the tip of the dorsobasal lobe to the tip of the knee), hind femur width (HFW) (in lateral view, its greatest width), vertex width (VW) (between the supraocular lobes in dorsal views or between the eyes in frontal view), compound eve width (CEW) (dorsal or frontal view), and antennal length (AL) (from scapus to the tip of the last segment). The specimens collected and examined in this study were deposited in Central Mindanao University, University Museum, Zoological Section, Tetrigidae collection. All measurements are shown in millimeters.



Fig. 1. Map of A. the Philippines and B. Mindanao showing the known distribution of *A. validispinus* in C. Mt. Pantaron, Sitio Miaray, Barangay Mandahican, Cabanglasan where the specimens were collected (red circles) and in Lanao region based on a specimen from eBay (blue triangle).

Results and discussion

Diagnosis of the genus.—The genus can be easily distinguished from similar genera by the following characters: a single paranotal lobe present, tegmina and alae absent, lateral paranotal lobes turned outwards, pronotum surface smooth, slightly wrinkled, and high spines present on pronotal discus. The genus can be separated from *Discotettix* by the shape of paranota, absence of wings, pronotum that is not wrinkled and not tuberculated, and smooth femora surface (Skejo 2017).

Diagnosis of the species.—We collected two specimens, a male and a female, from Bukidnon. Our specimens are very similar to Stål's type specimen, which is from an unknown locality, as well as to the specimens reported by Skejo (2017) in his diploma thesis, which came from Lanao, 105.41 km from Bukidnon. The specimens of fourspined pygmy devils are dark in coloration, and as in *A. miae*, have reddish markings. Dorsum of pronotum bears four long spines: a pair between the shoulders on the bulky elevation of the discus and a pair in the metazona. Our specimens have slightly larger spines and longer ventrolateral projections (Fig. 2) than the holotype (see holotype of *A. validispinus* in Orthoptera Species File, Cigliano et al. 2020). The holotype has a third pair of wart-like spines located at the anterior apex that are not observed in our specimens.

Comparison with congeners.—The genus *Arulenus* is endemic to the Philippines with only two known species, *A. miae* and *A. validispinus*. *A. validispinus* is similar to *A. miae* Skejo & Caballero, 2016, and can be distinguished by the set of the following characters: (i) prozona of pronotum granulated, very wrinkly (slightly granulate, more or less smooth in *A. miae*), (ii) metazona of pronotum from 2.8/10 to 4.5/10 of pronotum length, bearing the first pair of spines higher than the second (more than 2×), from 5.1/10 to 6.5/10 of the length bearing the second pair of spines high, hind femora more robust (length/maximal width ratio 2.4 in male and 2.5 in female), and with dorsal margin undulate and tuberculate, and (iii) notable spiky ventrolateral projections of the lateral lobes (paranota).

Material examined.—PHILIPPINES • (2/2) 1319. Bukidnon, Cabanglasan, Barangay Mandahican, Sitio Miaray, Mt Pantaron, 8°27'73.0"N, 125°36'54.6"E, 1,004 masl, 03–14 Feb. 2020, AM-011, A.B. Mohagan, R.R. Patano Jr., M.S. Acola, D.O. Amper, F.P. Coritico, and V.B. Amoroso, Central Mindanao University, University Museum, Zoological Section.

Type locality.—The Philippines, no specified locality of the holotype label. Type series: a single female holotype, labeled Ins. Philipp., originates from Semper's collection and is deposited in the entomological collections of the Naturhistoriska Riksmuseet in Stockholm, Sweden.

Distribution.—Inhabiting tropical mountainous rainforests on Mindanao (the Philippines) at 800–1,100 m above sea level: known from Lanao and Bukidnon Region (present study).

Measurements.—Male (N=1). BL 11.1; PL 10.4; PW 6.2; PH 5.0; FFL 4.0; FFW 0.8; MFL 4.5; MFW 0.6; HFL 6.1; HFW 2.5; VW 1.2; CEW 1.0; AL 7.2.

Female (N=1). BL 12.0; PL 10.8; PW (between the tips of the spines) 6.5; PH 5.2; FFL 4.15; FFW 0.14; MFL 4.6; MFW 0.65; HFL 6.52; HFW 2.65; VW 1.24; CEW 1.1; AL 7.6.

Habitat and ecology.—The species is found on tree bark in the montane forest (Fig. 3), similar to the habitat of *A. miae* and *Spartolus pugionatus* Stål, 1877 (Mohagan et al. 2020). The associated vegetation consists of the following species of trees: *Shorea* spp., *Lithocarpus* spp., *Ficus* spp., *Pinanga* spp.; and ferns: *Sphaeropteris elemeri*, *S. polypoda*, *Alsophila fuliginosa*, *Taenitis blechnoides*, *Schizaea dichotoma* and *Selaginella* spp. Besides the Lanao region (Skejo 2017), here we report the species from the Bukidnon region, more specifically Mt. Pantaron, Sitio Miaray, Barangay Mandahican, Cabanglasan. These records finally confirm that *A. validispinus* inhabits Mindanao island in the Philippines—an answer to a 140-year old question of this species' distribution.



Fig. 2. Habitus of the four-spined pygmy devil, *Arulenus validispinus* Stål, 1877, a male from Bukidnon (Mt. Pantaron) in A. dorsal and B. lateral view.



Fig. 3. Habitat of the four-spined pygmy devil, *Arulenus validispinus* Stål, 1877, in A. lower and B. upper lowland dipterocarp rainforest of Mt. Pantaron (about 1,004 masl).

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Supplementary material 1

Authors: Alma B. Mohagan, Romeo R. Patano Jr., Mescel A. Acola, Daniel O. Amper, Fulgent P. Coritico and Victor B. Amoroso Data type: Morphometric data

- Explanation note: We provide supplementary data on Arulenus validispinus morphometric data and comparing to its sibling Arulenus miae.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/ odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
- Link: https://doi.org/10.3897/jor.29.53718.suppl1

Calling songs of Neotropical katydids (Orthoptera: Tettigoniidae) from Panama

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Abstract

Understanding the ecology and evolution of animal communication systems requires detailed data on signal structure and variation across species. Here, we describe the male acoustic signals of 50 species of Neotropical katydids (Orthoptera: Tettigoniidae) from Panama, with the goal of providing data and recordings for future research on katydid communication, evolution, ecology, and conservation. Male katydids were recorded individually using an ultrasound-sensitive microphone and high-sampling rate data acquisition board to capture both audible and ultrasonic components of calls. Calls varied enormously in duration, temporal patterning, peak frequency, and bandwidth both across and within subfamilies. We confirm previous studies showing that katydid species within the subfamily Pseudophyllinae produced short calls (<250 ms) at long intervals and we confirm that this is true for species in the subfamily Phaneropterinae as well. Species in the Conocephalinae, on the other hand, typically produced highly repetitive calls over longer periods of time. However, there were exceptions to this pattern, with a few species in the Conocephalinae producing very short calls at long intervals, and some species in the Phaneropterinae producing relatively long calls (1-6 s) or calling frequently. Our results also confirm previous studies showing a relationship between katydid size and the peak frequency of the call, with smaller katydids producing higher frequency calls, but the slope of this relationship differed with subfamily. We discuss the value of documenting the diversity in katydid calls for both basic studies on the ecology, evolution, and behavior of these species as well as the potential conservation benefits for bioacoustics monitoring programs.

Keywords

acoustic signals, bioacoustics monitoring, bushcrickets, insect communication, ultrasound

Introduction

Understanding the ecology and evolution of animal communication systems requires detailed data on signals and how they

vary across species (Cocroft and Ryan 1995, Endler et al. 2005, Arnegard et al. 2010, Liénard et al. 2014, Tobias et al. 2014). In many animal taxa, males produce conspicuous acoustic signals to attract females for mating (Myrberg et al. 1986, Catchpole 1987, Gerhardt and Huber 2002, Smotherman et al. 2016), providing opportunities for both basic studies on communication and applied studies through bioacoustic monitoring (Sueur 2002, Chek et al. 2003, de Solla et al. 2005, Gasc et al. 2013, Krause and Farina 2016, Grant and Samways 2016). Acoustic signal production by males is particularly conspicuous and ubiquitous in the Orthoptera (Römer 1998, Gerhardt and Huber 2002), making species in this taxon ideal for the types of studies mentioned above (e.g., Diwakar and Balakrishnan 2007a, Schmidt et al. 2012, Jain et al. 2014, Frederick and Schul 2016, Roca and Proulx 2016, Bailey et al. 2019). Here we describe male acoustic signals of 50 species of Neotropical katydids (Orthoptera: Tettigoniidae) from Panama, with the goal of providing data and recordings for future research on katydid communication, evolution, ecology, and conservation.

Katydids, also known as bushcrickets, are a highly diverse group of insects (Mugleston et al. 2018) in which males produce acoustic signals, or calls, to attract females. In most subfamilies, males call and females walk to males by tracking the source of the sound, a behavior called phonotaxis (Bailey et al. 1990, Schul and Schulze 2001, Guerra and Morris 2002, Kowalski and Lakes-Harlan 2011, Dutta et al. 2017). In the subfamily Phaneropterinae, however, males and females usually produce an acoustic duet, with the female producing a call in a short, and species-specific, latency after the male call (reviewed in Bailey 2003, Heller et al. 2015). Phaneropterine males walk to the replying female or, in some phaneropterine species, both sexes move toward each other (Heller et al. 2015). Male katydids call by rubbing a plectrum on one forewing across a file on the underside of the other forewing (Bailey 1970, Montealegre-Z and Mason 2005), a form of sound generation termed stridulation. Depending on the species, sound can be produced during wing clos-



Fig. 1. Representative call of *Orophus conspersus* with labelled acoustic parameters: **A.** Spectrogram; **B.** Oscillogram; and **C.** Power spectrum. Temporal parameters – PD: pulse duration, PP: pulse period, WO: wing-opening sound. Spectral parameters – BW: bandwidth, HF: high frequency, LF: low frequency, PF: peak frequency.

ing, wing opening, or both wing opening and closing movements (Suga 1966, Morris and Pipher 1972, Walker and Dew 1972, Hartley et al. 1974, Walker 1975a, Morris and Walker 1976, Heller 1988, Montealegre-Z 2012, Stumpner et al. 2013, Chivers et al. 2014). In addition to acoustic signals, many katydid species in the subfamilies Conocephalinae and Pseuodophyllinae produce vibrational signals that travel through plants (Morris 1980, Belwood and Morris 1987, Belwood 1988a, Saul-Gershenz 1993, Morris et al. 1994, Römer et al. 2010, Stumpner et al. 2013, Sarria-S et al. 2016), and in at least one pseudophylline species, males and females perform an acoustic-vibratory duet (Rajaraman et al. 2015).

Calling songs have been described for many katydid species across the world, and the acoustic properties of these calls are extraordinarily diverse (Ragge and Reynolds 1998, Naskrecki 2000, Rentz 2001, Diwakar and Balakrishnan 2007a, Cole 2010, Cheng et al. 2016, Hemp and Heller 2017, Chamorro-Rengifo et al. 2018, Sevgili et al. 2018). Similar to crickets (Otte 1992), the temporal structure of the call usually differs between sympatric species and appears to be an important parameter for identifying a potential mate of the same species (Bailey and Robinson 1971, Tauber and Pener 2000, Deily and Schul 2004, Bush and Schul 2006, Cole 2010, Hartbauer and Römer 2014). Unlike crickets, most of which produce sounds in a relatively narrow band of frequencies between 2-8 kHz (Otte 1992, Diwakar and Balakrishnan 2007a, but see Robillard and Desutter-Grandcolas 2004, Robillard et al. 2015), katydids show enormous variation in the dominant frequency of their calls, ranging from as low as 0.6 kHz (Tympanophyllum arcufolium from Malaysia, Pseudophyllinae: Heller 1995) all the way up to the extreme ultrasound of 150 kHz (Supersonus aequoreus from Colombia and Ecuador, Meconematinae: Sarria-S et al. 2014). In the past, the high frequencies produced by many katydid species for communication required specialized and costly microphones and recording equipment, which has sometimes limited the recording and documentation of calls of these species. In recent years, more affordable equipment has become available that can record these higher frequencies (e.g., Audiomoth: https:// www.openacousticdevices.info).

Katydid calls and calling behavior are shaped by many selective forces including female preferences (Bailey et al. 1990, Ritchie 1996, Dutta et al. 2017), male-male competition (Greenfield 1983, Dadour 1989), interactions between female preferences and male-male competition (Morris et al. 1978, Deily and Schul 2009, Greenfield et al. 2016), parasites and predators that eavesdrop on prey signals (Belwood and Morris 1987, Hunt and Allen 1998, Lehmann and Heller 1998, Falk et al. 2015, Lakes-Harlan and Lehmann 2015), and features of the environment that influence transmission of the signal (Greenfield 1988, Stephen and Hartley 1991, Römer 1993, Schmidt and Balakrishnan 2015). The role of predators in shaping katydid calls has been a focus of research in the Neotropics due to an endemic family of bats (Phyllostomidae) that contains several species known to eavesdrop on katydid calls to locate them as prey (Belwood 1988b, Kalko et al. 1996, Falk et al. 2015, Denzinger et al. 2018), often preving on them in very large numbers (Belwood 1988a, Römer et al. 2010, ter Hofstede et al. 2017). It has been suggested that the very low calling rate of most forest-dwelling Neotropical katydids could be a result of this intense predation pressure (Rentz 1975, Belwood and Morris 1987, Belwood 1988a, Morris et al. 1994). By documenting the calls of many sympatric Neotropical species, we hope to gain a better understanding of how these numerous selective forces interact to shape patterns of acoustic signals within a community. Future work will incorporate phylogenetic data, which is not currently available for most of these species, to assess the evolution of signal types.

In addition to being interesting animals for basic studies on the ecology and evolution of acoustic communication, the conspicuous and species-specific calls produced by katydids make them ideal animals for bioacoustic monitoring projects. Compared to birds and mammals, most insects, including Neotropical katydids, have relatively small home ranges, meaning that their population dynamics will reflect local environmental conditions and will more accurately track heterogeneous conditions across a landscape (French 1999, Lang and Römer 2008, Fornoff et al. 2012, Campos-Cerqueira et al. 2019). In addition, Neotropical katydids occur at the nexus of food webs, eating many species of plants and small prey (Coley and Kursar 2014, Symes et al. 2019) and being eaten by a diversity of predators (Belwood 1990), many of which are heavily dependent on particular sizes or species of



Fig. 2. Representative power spectra (dBFS/Hz) of katydid calls shown with 90% confidence intervals (CI). The number (*n*) of clips, containing calls of the focal species, used in determining the aggregated values are indicated in the respective plots. Species are arranged from lowest to highest peak frequency (top to bottom, then left to right).

Species	Individuals (calls)	Call Duration (ms)	Number of Pulses in Call	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
Conocephalinae							
Acantheremus major	3 (7)	$1,779.2 \pm 1,405.7$	135.0 ± 110.0	22.1 ± 0.3	20.0 ± 0.8	24.9 ± 0.6	5.0 ± 1.0
Agraecia festae	3 (15)	$1,950.9 \pm 373.9$	26.5 ± 5.2	40.3 ± 1.4	32.1 ± 0.5	52.0 ± 2.0	19.9 ± 1.7
Copiphora brevirostris	8 (115)	30.0 ± 5.2	2.5 ± 0.4	32.9 ± 1.2	27.8 ± 0.9	34.7 ± 1.1	6.9 ± 1.5
Eppia truncatipennis	3 (11)	21,292.1 ± 8,320.1	69.6 ± 27.5	50.2 ± 2.2	37.2 ± 1.5	63.4 ± 9.0	26.1 ± 8.9
Erioloides longinoi	3 (41)	1,384.6 ± 336.1	157.9 ± 42.8	30.1 ± 1.7	25.7 ± 2.9	37.4 ± 2.4	11.7 ± 5.1
Neoconocephalus affinis	5 (25)	16,827.2 ± 7,471.4	468.1 ± 207.8	14.9 ± 2.0	9.5 ± 0.3	30.9 ± 3.0	21.4 ± 2.9
Subria sylvestris	3 (37)	125.0 ± 0.4	2.0 ± 0.0	38.9 ± 2.0	23.7 ± 6.2	49.3 ± 0.8	25.6 ± 6.8
Vestria punctata	3 (23)	31.4 ± 1.5	1.9 ± 0.1	29.7 ± 1.3	24.1 ± 2.0	36.9 ± 1.8	12.8 ± 2.9
Phaneropterinae							
Aegimia elongata - call type 1	3 (37)	204.6 ± 24.0	3.5 ± 0.5	10.2 ± 0.1	6.9 ± 0.7	20.4 ± 0.6	13.5 ± 1.1
Aegimia elongata - call type 2	2(7)	740.2 ± 242.1	7.1 ± 1.5	10.2 ± 0.1	7.5 ± 0.3	19.9 ± 0.2	12.4 ± 0.5
Aegimia maculifolia	5 (52)	$1,397.9 \pm 214.7$	16.2 ± 2.2	17.0 ± 1.4	10.2 ± 0.4	22.8 ± 0.4	12.5 ± 0.7
Anapolisia colossea	9 (116)	$1,964.5 \pm 430.0$	5.6 ± 0.8	20.1 ± 0.6	12.2 ± 2.4	25.4 ± 1.0	13.2 ± 2.8
Anaulacomera furcata	3 (53)	21.2 ± 1.5	2.0 ± 0.0	29.4 ± 1.0	24.3 ± 0.8	35.9 ± 0.4	11.7 ± 0.9
Anaulacomera "goat"	3 (15)	1.7 ± 0.5	1.0 ± 0.0	27.0 ± 0.6	23.2 ± 0.6	33.0 ± 3.4	9.9 ± 3.8
Anaulacomera "ricotta"	3 (16)	59.0 ± 2.0	2.0 ± 0.0	33.8 ± 1.8	29.3 ± 2.4	39.1 ± 1.6	9.8 ± 1.5
Anaulacomera spatulata	3 (59)	43.0 ± 2.5	2.0 ± 0.0	24.5 ± 3.5	21.8 ± 3.5	29.3 ± 3.1	7.5 ± 1.3
Anaulacomera "wallace"	4 (19)	34.3 ± 2.5	3.1 ± 0.3	25.0 ± 0.6	20.4 ± 1.4	31.1 ± 3.9	10.7 ± 4.7
Arota festae	10 (83)	21.4 ± 3.2	8.0 ± 0.7	12.7 ± 1.5	7.8 ± 0.2	18.5 ± 1.1	10.7 ± 1.2
Arota panamae	10 (156)	15.3 ± 2.2	4.9 ± 0.6	24.4 ± 2.6	15.1 ± 2.3	33.2 ± 2.1	18.1 ± 3.9
Ceraia mytra	9 (71)	75.5 ± 9.4	9.7 ± 0.7	10.7 ± 0.9	6.7 ± 0.5	20.3 ± 1.2	13.6 ± 1.5
Chloroscirtus discocercus	12 (157)	139.1 ± 14.2	6.4 ± 0.5	19.2 ± 2.2	11.3 ± 0.9	25.7 ± 3.3	14.4 ± 3.8
Dolichorcercus latipennis	3 (19)	329.8 ± 26.7	15.6 ± 0.7	26.2 ± 1.0	20.9 ± 0.3	31.6 ± 1.3	10.7 ± 1.0
Ectemna dumicola	5 (83)	465.9 ± 59.0	9.9 ± 1.3	15.1 ± 2.5	10.0 ± 0.7	26.2 ± 1.8	16.1 ± 1.7
Euceraia atryx	3 (14)	$1,093.2 \pm 474.6$	13.8 ± 2.6	13.2 ± 1.4	11.1 ± 1.1	15.9 ± 1.2	4.8 ± 0.2
Euceraia insignis	3 (21)	1,618.6 ± 266.8	16.3 ± 1.8	12.7 ± 0.7	10.3 ± 0.4	14.7 ± 0.5	4.4 ± 0.9
Hetaira sp.	3 (13)	36.2 ± 2.9	3.0 ± 0.0	24.9 ± 1.0	21.8 ± 1.2	29.5 ± 1.6	7.8 ± 0.4
Hyperphrona irregularis	3 (15)	8.8 ± 1.9	1.0 ± 0.0	16.1 ± 1.0	15.3 ± 1.1	19.2 ± 1.1	3.9 ± 0.2
Lamprophyllum bugabae	14 (207)	614.8 ± 48.3	6.9 ± 0.7	9.7 ± 0.4	7.1 ± 0.2	19.3 ± 0.8	12.2 ± 0.7
Lamprophyllum micans	11 (55)	803.4 ± 49.2	8.0 ± 0.2	17.4 ± 1.3	12.9 ± 0.6	23.8 ± 0.8	10.9 ± 0.6
Microcentrum championi	4 (20)	471.8 ± 54.1	3.1 ± 0.1	10.3 ± 0.4	6.8 ± 0.2	16.7 ± 1.5	9.9 ± 1.6
Microcentrum "polka"	8 (73)	6,322.1 ± 1,932.6	7.6 ± 1.9	9.7 ± 0.4	7.3 ± 0.3	13.6 ± 0.6	6.3 ± 0.5
Montezumina bradlevi	3 (18)	31.9 ± 6.7	1.0 ± 0.0	29.8 ± 4.7	18.7 ± 1.0	46.5 ± 3.3	27.8 ± 3.1
Orophus conspersus	4 (40)	70.4 ± 13.1	3.0 ± 0.7	11.1 ± 0.5	7.4 ± 0.5	19.0 ± 1.0	11.6 ± 1.1
Philophyllia ingens	9 (114)	6.4 ± 2.2	1.0 ± 0.0	10.8 ± 0.8	9.3 ± 1.4	13.0 ± 0.6	3.7 ± 1.4
Phylloptera dimidiata	12 (213)	20.7 ± 2.6	7.7 ± 1.1	15.8 ± 1.8	10.5 ± 1.0	25.0 ± 1.5	14.5 ± 2.0
Phylloptera quinquemaculata	3 (15)	53.1 ± 4.0	9.3 ± 1.5	11.8 ± 0.4	8.9 ± 0.3	19.8 ± 3.3	10.9 ± 3.5
Pycnopalpa bicordata	3 (14)	33.4 ± 10.1	5.0 ± 1.0	26.1 ± 0.9	22.5 ± 0.8	31.7 ± 2.4	9.2 ± 1.7
Steirodon stalii	10(93)	208.5 + 14.9	3.0 ± 0.0	18.6 ± 1.2	13.4 + 1.0	24.4 + 1.1	11.0 + 1.4
Viadana brunneri	11(195)	8.6 + 0.6	2.0 ± 0.0	16.1 ± 0.5	14.7 ± 0.5	18.9 ± 0.8	4.2 ± 0.7
"Waxy" sp.	3 (13)	69.3 + 2.3	6.5 ± 0.8	11.7 ± 0.5	9.9 ± 0.8	17.6 ± 1.1	7.7 ± 1.8
Pseudophyllinae	. ()						
Acanthodis curvidens	3 (48)	64.0 ± 7.1	5.3 ± 0.4	15.6 ± 1.0	9.6 ± 0.4	21.7 ± 1.7	12.1 ± 1.3
Balboana tibialis	4 (20)	125.3 ± 16.5	6.6 ± 1.1	14.4 ± 1.5	9.1 ± 0.9	17.5 ± 1.0	8.4 ± 1.5
Cocconotus wheeleri	6 (108)	247.3 ± 80.1	11.4 ± 3.3	24.8 ± 1.0	20.7 ± 1.0	27.4 ± 1.4	6.7 ± 1.1
Docidocercus gigliotosi	7 (140)	117.5 ± 97.0	1.6 ± 0.6	24.4 ± 0.6	23.5 ± 0.6	26.1 ± 0.8	2.6 ± 0.8
Eubliastes pollonerae	5 (100)	37.4 ± 3.1	2.0 ± 0.0	24.2 ± 1.5	21.1 ± 1.5	25.5 ± 1.7	4.3 ± 1.7
Idiarthron maior	3 (26)	45.4 ± 2.1	2.0 ± 0.0	24.4 ± 0.7	19.6 ± 0.8	29.4 ± 1.9	9.8 ± 1.4
Ischnomela gracilis	4 (12)	10.8 ± 1.3	1.0 ± 0.0	73.9 ± 2.1	66.5 ± 2.9	90.6 ± 6.0	24.1 ± 7.7
Ischnomela tulchrittennis	3 (15)	68.8 + 1.8	2.0 ± 0.0	13.6 ± 0.2	12.2 ± 0.2	15.4 ± 0.2	3.2 ± 0.1
Pristonotus tuberosus	3 (9)	17.5 ± 0.8	1.0 ± 0.0	10.9 ± 1.7	83+01	173 + 28	9.0 ± 2.7
Scopiorinus fraoilis	3 (15)	60.4 + 7.3	1.0 ± 0.0 1.0 ± 0.0	25.6 ± 0.7	21.7 ± 0.1	31.7 ± 1.0	10.0 ± 2.7
Thamnohates subfalcata	3 (15)	30.6 + 2.8	2.0 ± 0.0	18.8 ± 0.3	17.7 ± 0.4	21.1 ± 0.7	3.4 + 0.4

Table 1. Call parameters for 50 species of katydids recorded on Barro Colorado Island, Panama. Values are mean ± standard deviation.

katydids (Gradwohl and Greenberg 1982, Peres 1992). Changes in vegetation or predator communities are likely to be reflected in the katydid community and changes in the katydid community will have direct impacts on vegetation and predator resources (Kalka et al. 2008). Consequently, acoustic monitoring of orthopterans is now being used as an indicator of habitat quality and change as well as for the direct conservation and management of insect populations (Fischer et al. 1997, Braun 2011a, Hugel 2012, Penone et al. 2013, Lehmann et al. 2014, Jeliazkov et al. 2016, Newson et al. 2017).

The purpose of this study was to describe the calls of many katydid species within the same community to facilitate future studies on the behavioral ecology, community ecology, conservation biology, and evolutionary biology of these insects. To this end, we provide detailed descriptions of the calls of 50 katydid species from three subfamilies (Conocephalinae, Phaneropterinae, and Pseudophyllinae) from Panama.

Methods

Katydids were collected at night from vegetation in the forest and from lights around buildings on Barro Colorado Island (BCI), Panama (9°09'53"N, 79°50'12"W), during the dry season (January to April) in 2007, 2011, 2014, and 2016–2018. We identified katydids to species, when possible, using a combination of published resources (Nickle 1992, Naskrecki 2000, Cigliano et al. 2020). Some of the species are not yet described (Robillard et al. in prep.), and to provide continuity within the literature, we use provisional manuscript 'names'; these names are disclaimed as unavailable per Article 8.3 of the ICZN. We follow the subfamilies as listed in the Orthoptera Species File (Cigliano et al. 2020), recognizing that the classifications of these higher-level taxa are unstable and currently being revised (Mugleston et al. 2013, 2018, Braun 2015a).

Katydids were housed in mesh cages with ad libitum water and food (cat food and apple) until recording. Male mass was determined to the nearest mg using an AWS Gemini-20 scale within 24 hours of capture. Recordings of male calls were made in a screened building close to the forest to maintain katydids at natural ambient temperature, humidity, and acoustic background, factors that appear to be important for male singing behavior. Although temperature can affect calling in katydids (Walker 1975b), the temperature and humidity of tropical rainforests is very stable compared to temperate environments. We took temperature and humidity measurements (n = 64) in the screened recording building at approximately 1800 and 0000 hours most nights. The mean temperature was 25.4 ± 1.2 °C with a range of 23.0–28.7 °C. The humidity was $81.3 \pm 6.3\%$ with a range of 64-92%. During call recording, individual males were placed in cylindrical metal mesh cages (72 × 150 mm, D × H) that were surrounded by acoustic foam to reduce sound reflections. A condenser microphone (CM16, Avisoft Bioacoustics, Berlin Germany) placed 30 cm from the cage, an A/D converter (UltraSoundGate 416H, Avisoft), and a laptop running Avisoft Recorder software with a sampling rate of 250 kHz were used to record calls produced by the focal male.

We quantified acoustic parameters for 2,859 calls from 265 individuals from 50 species from three subfamilies (Conocephalinae; Phaneropterinae; Pseudophyllinae). We used Avisoft SASLAB PRO acoustic analysis software (Specht 2019) to measure acoustic parameters for male calls (3–14 individuals/species, 1–20 calls/ individual). Before measuring spectral parameters, we applied a frequency response filter that was the inverse of the microphone

frequency response to correct for the frequency response of the microphone and generate audio files with accurate power spectra. Filtered recordings are deposited in the sound library of the Muséum national d'Histoire naturelle (MNHN: https://sonotheque. mnhn.fr/); sound inventory numbers are given as MNHN-SO*** with each species' song descriptions. Whenever possible, recorded individuals were deposited as voucher specimens in the MNHN collection for further studies. Sound recordings are also available through Dryad and GBIF. We follow the terminology and definitions for "call" and "pulse" from Morris et al. (1988). Specifically, a call is "the most inclusive repetitive time-amplitude pattern in the insect's sound emission" and a pulse is "a wave train, isolated in time by an amplitude modulation that declines to background noise level" (Morris et al. 1988). We do not have data on the wing movements during calling, preventing us from using more precise terminology (Ragge and Reynolds 1998). Most calls were also very simple and could be described without the terminology needed to describe complex calls seen in some other katydid species (Morris and Walker 1976). Very quiet sounds that consistently precede louder pulses are assumed to be wing opening sounds and are only described in cases where they are consistently long and of relatively high amplitude across individuals compared to other wing opening sound (Acanthodis curvidens, Eubliastes pollonerae, and Vestria punctata). Figures of example calls (oscillograms and spectrograms) were made using the R package Seewave (Version 2.0.5, Sueur et al. 2008).

Calls generally consisted of multiple short sound pulses (Fig. 1). For each call, we counted the number of pulses and measured three temporal parameters and four spectral parameters. From the oscillogram, we measured the following temporal parameters: 1) pulse durations (time from the start to the end of each pulse, in ms), 2) pulse period (time from the start of one pulse to the start of the next pulse, in ms), and 3) call duration (the time from the start of the first pulse to the end of the last pulse in the call, in ms). For spectral analyses, we used the automatic parameter measurement feature in Avisoft SASLAB PRO (FFT length 512, Hamming window, 98.43% overlap) with a spectral resolution of 488 Hz and a temporal resolution of 0.032 ms. For each individual pulse and for the entire call, we measured the following spectral parameters: 1) peak frequency (frequency with the most energy, in kHz), 2) lowest frequency (-20 dB below the peak, in kHz), 3) highest frequency (-20 dB below the peak, in kHz), and 4) bandwidth (highest frequency minus lowest frequency, in kHz). When setting the threshold for the lowest and highest frequencies, the "total" option was not selected in the automatic parameter measurement software options, which meant that additional peaks outside the main peak were not considered for lowest and highest frequencies. For most calls, this reduced the variance in the lowest and highest frequency values due to noise. A few species, however, had calls with a strong harmonic structure and multiple frequency peaks that were not included in our measurements, and for those species we describe additional frequency peaks in the text. In some cases, the automatic parameters feature included background noise as the lowest frequency, in which case, we measured the low frequency directly from the power spectrum. For each katydid species, the mean value for each call parameter was calculated by first averaging the value across calls for each individual, and then averaging across the means for each individual to calculate the mean value for the species. Standard deviations reported in the text and tables are standard deviations of the means for each individual. This was used instead of pooled means and standard deviations to reflect variation across individuals.

In addition to the measurements described above, we estimated spectral profile curves using both analyzed and additional recordings to visualize the variation in frequencies produced by species in this community (Fig. 2). All recordings (except those of Ischnomela gracilis) were band-pass filtered between 3.2-59.6 kHz and downsampled to 120 kHz. These parameters ensure modest amounts of data reduction and noise suppression without affecting the signals of interest. For Ischnomela gracilis, since the dominant frequency was between 70-80 kHz, the upper extent of the band-pass filter was set to 93.75 kHz and the recordings were downsampled to 187.5 kHz. Following resampling, the recordings were split into 1 s clips with an overlap of 12.5%. The clips were screened to retain only those that contained calls of the focal species. The waveforms in the resulting clips for each species were scaled to fit the amplitudes in the range [-1.0, 1.0], and then power spectral density (PSD) spectrograms were computed using short-time discrete Fourier transforms (using 4.25 ms Hann windows with 50.5% overlap). The ensuing time and frequency resolutions were 2.1 ms and 234.4 Hz, respectively. The lower extent of the dynamic range of the spectrograms was restricted to -60 dBFS/ Hz. Representative spectral profiles of the call(s) contained in each clip were extracted by taking the maxima from each frequency bin. Since each clip is dominated by the call(s) of focal species, the representation is indicative of the true spectral profile. The representative spectral profiles were normalized to suppress effects of amplitude and background level differences between clips, and they are presented as aggregations of the per-species representative spectral profiles.

Results

Conocephalinae

Acantheremus major Naskrecki, 1997 Fig. 3 [MNHN-SO-2019-206, -207, -208]

Acantheremus major is a mid-sized (0.57 g, n = 1), light green katydid with a broad and flat face, a prominent pointed cone on its head (an elongated fastigium), and black mouthparts (Fig. 3A, B). This species is only known from Panama (Cigliano et al. 2020).

The call consists of a rapid series of pulses (Fig. 3C, D), with a total call duration that is highly variable, ranging from 0.2-4.8 s with a mean of ~1.8 s (Table 1). The peak frequency of the entire call is 22 kHz with a -20 dB frequency range spanning 20–25 kHz, giving a bandwidth of 5 kHz (Table 1). The amplitude of the pulses varies across the call. In one individual, the amplitude always increased across the call, whereas in a second individual, amplitude increased and then decreased across the call (Fig. 3C).

The pulses in the call are all very similar in their temporal and spectral properties. Pulse durations are 7.1 \pm 1.5 ms (mean \pm SD; 3 individuals, 7 calls, 68 pulses) and pulse periods are 15.9 \pm 5.3 ms. The peak frequency of the pulse is 22.2 \pm 0.3 kHz with a -20 dB frequency range spanning 20.6 \pm 0.7–24.8 \pm 0.9 kHz, giving a bandwidth of 4.2 \pm 1.1 kHz, similar to values taken for the call as a whole (Table 1). Each pulse is very slightly frequency modulated, sweeping from ~24 to ~21 kHz (Fig. 3D). All three recorded individuals were similar in call spectral properties, but two individuals produced longer duration pulses (mean 7.7 and 8.2 ms) with shorter periods (12.3 and 13.4 ms) than the third individual (mean duration 5.5 ms, period 22.0 ms).

This appears to be the first description of the call of this species.



Fig. 3. Photographs and calling song spectrograms of *Acantheremus major*. A. Male; B. Face; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and 14 pulses from the same call (D). Photo credit: H. ter Hofstede.

Agraecia festae Griffini, 1896 Fig. 4 [MNHN-SO-2019-220, -221, -222]

Agraecia festae is a very small $(0.20 \pm 0.04 \text{ g}, n = 18)$, light green katydid with nearly translucent areas on the body and mouthparts that are red and yellow (Fig. 4A). This species was originally described by Griffini (1896), but the type specimens are currently unavailable for examination. Chamorro-Rengifo et al. (2015) treat it as *incertae sedis* and suggest that it could be transferred to another genus. This species is only known from Panama (Cigliano et al. 2020).

The call consists of a rapid series of pulses (Fig. 4B, C) with a total call duration that is highly variable, ranging from $\sim 1-3.5$ s

with a mean of ~2 s (Table 1). The peak frequency of the entire call is 40 kHz with a -20 dB frequency range spanning 32–52 kHz, giving a bandwidth of 20 kHz (Table 1). The amplitude of the pulses is similar across the call, although the first few pairs of pulses are usually of a lower amplitude than the rest of the pulses in the call (Fig. 4B). Individuals will call frequently at night and are commonly recorded in the forest on BCI.

Pulses are arranged in pairs, and individual tooth strikes are visible on the oscillogram (Fig. 4B, C). The duration of the first pulse in a pair is shorter than the second pulse (Table 2). The spectral properties of each pulse type are the same (Table 2).

This appears to be the first description of the call of this species.



Table 2. Call pulse parameters of Agraecia festae (3 individuals, 15 calls; mean ± SD); n = number of pulses measured.

Pulse Type (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (199)	14.7 ± 1.1	129.7 ± 7.7	40.0 ± 0.7	33.0 ± 0.8	50.4 ± 1.9	17.3 ± 1.9
2 (199)	22.3 ± 3.1	26.0 ± 2.8	39.8 ± 0.8	32.0 ± 0.5	51.1 ± 1.9	19.1 ± 1.8

Copiphora brevirostris Stål, 1873 Fig. 5 [MNHN-SO-2019-329, -330, -331, -332, -333, -334, -335, -336]

Copiphora brevirostris is a large $(1.63 \pm 0.31 \text{ g}, \text{n} = 51)$, green katydid with a broad, flat, and yellow face and a powerful bite (Fig. 5A, B). Unlike many other species of *Copiphora*, the fastigium is not elongated (i.e., no cone-like structure on the top of the head). In females, the ovipositor is longer than the body (Fig. 5B). This species is known from Panama (Nickle 1992) and Colombia (Cigliano et al. 2020).

The call consists of 1–4 pulses (Fig. 5C, D) with a mean call duration of 30 ms (Table 1). Pulses usually increase in amplitude across the call, and relatively high-amplitude wing-opening sounds can be seen before some pulses (Fig. 5D). The call has strong harmonics with the fundamental (~16 kHz) and first harmonic (~33 kHz) produced at similar amplitudes (Fig. 2). The first harmonic usually has more energy than the fundamental, but in some calls the fundamental can be the same or slightly higher in amplitude than the first harmonic. The peak frequency of the harmonic is 33 kHz with a -20 dB range spanning ~28–35 kHz, giving

a bandwidth of 7 kHz (Table 1). Males call very rarely and tend to call more frequently after midnight.

Pulse durations are typically 6–9 ms (Table 3), although pulse durations are highly variable and can range from 2–12 ms. The second pulse is often slightly longer than the first pulse. Pulse periods are ~15 ms (Table 3). The spectral properties of the individual pulses are very similar to each other and the entire call (Table 3). The peak frequency of the fundamental is ~16 kHz, and the first harmonic is ~32 kHz, with a -20 dB range spanning 29–34.5 kHz, giving a bandwidth of 5.5 kHz (Table 3). The bandwidth reported here is just for the first harmonic. The fundamental was usually of a lower amplitude than the first harmonic, but the difference in amplitude was highly variable across calls and pulses. Each pulse is frequency modulated, either sweeping from higher to lower frequencies (~34 to 30 kHz) or shaped like an upside-down U (ranging from ~33 up to 35 and down to 30 kHz; Fig. 5D).

Calls of this species were previously described by Belwood and Morris (1987), Belwood (1988a), Morris et al. (1994), Falk et al. (2015), and Symes et al. (2016). In addition to acoustic signals, both males and females produce vibrational signals (described in Belwood 1988a).



Fig. 5. Photographs and calling song spectrograms of *Copiphora brevirostris*. A. Male (photo credit: H. ter Hofstede); B. Female (photo credit: C. Wilson); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 3. Call pulse parameters of *Copiphora brevirostris* (8 individuals, 115 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (115)	6.7 ± 1.7		32.9 ± 1.2	29.8 ± 1.7	34.7 ± 1.2	5.0 ± 2.3
2 (113)	8.4 ± 1.5	13.6 ± 1.9	32.7 ± 1.0	29.1 ± 1.5	34.2 ± 1.2	5.1 ± 1.8
3 (55)	7.0 ± 1.4	16.0 ± 1.4	31.2 ± 1.2	26.6 ± 1.8	34.0 ± 2.4	7.4 ± 3.6

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Eppia truncatipennis Stål, 1875 Fig. 6 [MNHN-SO-2019-611, -642, -646]

Eppia truncatipennis is a large $(1.18 \pm 0.15 \text{ g}, \text{n} = 2)$, mottled, brown katydid with abruptly truncated wings, a black face, and red mouthparts (Fig. 6A). This species was redescribed by Naskrecki (2000). It is known from southern Mexico, Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a sequence of "chirps" (term used in Naskrecki 2000) composed of 10–12 pulses produced with almost no silence between them (Fig. 6B, C). Chirps are produced at very regular intervals, with a chirp period of ~280 ms (Table 1). Sequences of chirps are produced for long periods of time (11.3–44.7 s with a mean of 21.3 s; Table 1). The peak frequency of an entire sequence of chirps is ~50 kHz with a -20 dB frequency range spanning ~37–63 kHz, giving a bandwidth of ~26 kHz (Table 1).

The chirps are all very similar in their temporal and spectral properties. Chirp durations are 114.4 ± 9.1 ms (3 individuals,

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11 calls, 110 chirps). There is always an even number of pulses within a chirp, usually 10 or 12 (mean 11.4 ± 1.1). Pulse durations within a chirp range from ~7–14 ms. It is possible that sound is produced both during the wing opening and wing closing movements, resulting in pulses that vary in amplitude but have almost no silence between them (Fig. 6C). High-speed video of males singing would be helpful in confirming that this is the mechanism responsible for these chirps that lack silence between pulses.

The peak frequency of the chirps is 49.7 ± 2.5 kHz with a -20 dB frequency range spanning $37.5 \pm 1.2-63.0 \pm 8.3$ kHz, giving a bandwidth of 25.5 ± 8.1 kHz (3 individuals, 11 calls, 110 chirps). There is also significant energy at 10-12 kHz, and, in some calls, this frequency range is the same or greater in amplitude than the typical peak frequency of ~50 kHz.

Calls of this species were previously described by Naskrecki (2000), but they were recorded at a lower sampling rate that did not capture the higher frequencies described here.



Fig. 6. Photograph and calling song spectrograms of *Eppia truncatipennis*. A. Male (photo credit: L. Symes); B. and C. Spectrogram (top panel) and oscillogram (bottom panel) of the start of one call (B) and one chirp from the same call (C).



Erioloides longinoi Naskrecki & Cohn, 2000 Fig. 7 [MNHN-SO-2019-649, -650, -651]

Erioloides longinoi is a small $(0.36 \pm 0.07 \text{ g}, \text{ n} = 8)$, cylindrical, green katydid with blue mouthparts, red and yellow markings on the ventral surface of the abdomen, and an agile bite (Fig. 7A, B). This species is known from Mexico, Costa Rica, and Panama (Cigliano et al. 2020).

The call consists of a rapid series of pulses (Fig. 7C, D) with a total call duration ranging from 1.0-1.9 s and a mean of 1.4 s (Table 1). The peak frequency of the entire call is 30 kHz with a -20 dB frequency

range spanning 25–37 kHz, giving a bandwidth of 12 kHz (Table 1). The amplitude of the pulses gradually increases for the first 10–15 pulses and then remains constant for the rest of the call (Fig. 7C).

The pulses in the call are all very similar in their temporal and spectral properties. Pulse durations are 4.4 ± 0.7 ms (3 individuals, 41 calls, 410 pulses) and pulse periods are 8.9 ± 0.5 ms. The peak frequency of the pulse is 30.2 ± 1.9 kHz with a -20 dB frequency range spanning $26.6 \pm 2.9-38.2 \pm 4.3$ kHz, giving a bandwidth of 11.6 ± 7.2 kHz. Each pulse is frequency modulated, sweeping from ~32 to 28 kHz (Fig. 7D).

This appears to be the first description of the call of this species.



Fig. 7. Photographs and calling song spectrograms of *Erioloides longinoi*. A. Male; B. Female hanging upside down from a plexiglass plate, showing coloration of abdomen and mandibles; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and 10 pulses from the same call (D). Photo credit: H. ter Hofstede.

Neoconocephalus affinis (Palisot de Beauvois, 1805) Fig. 8 [MNHN-SO-2019-1458, -1465, -1466, -1467, -1468]

Neoconocephalus affinis is a mid-sized $(0.76 \pm 0.10 \text{ g}, \text{n} = 4)$, cylindrical, green katydid with an elongated fastigium (Fig. 8A). This species is polymorphic, with both green and brown individuals observed at BCI. The species was redescribed by Naskrecki (2000). This species is known from the United States (Florida), southern Mexico, the Caribbean, Costa Rica, Panama, and northern South America (Nickle 1992, Cigliano et al. 2020).

The call consists of a rapid series of pulses (Fig. 8B, C) that can last just a few seconds or continue for many minutes continuously. Total call duration for the calls analyzed here ranged from 0.5-106 s, with a mean of ~17 s (Table 1). The peak fre-

quency of the entire call is ~15 kHz with a -20 dB range spanning ~10–30 kHz, giving a bandwidth of ~20 kHz (Table 1). The call also has significant energy at higher frequencies in the range of 50-60 kHz (Fig. 8B, C).

Pulses are arranged in pairs and individual tooth strikes are visible on the oscillogram (Fig. 8C). The duration of pulse type 1 is shorter and usually lower amplitude than pulse type 2, and the period between pulse type 1 and 2 is shorter than the pulse period between pulse type 2 and 1 (Table 4). The spectral properties of each pulse type are the same (Table 4).

Calls of this species were previously described by Greenfield (1983), Walker and Greenfield (1983), Belwood and Morris (1987), Naskrecki (2000), Bush et al. (2009), and ter Hofstede et al. (2010).



Table 4. Call pulse parameters of *Neoconocephalus affinis* (5 individuals, 25 calls; mean ± SD); n = number of pulses measured.

Pulse Type (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (125)	20.7 ± 2.0	29.7 ± 2.5	14.6 ± 2.0	9.6 ± 0.4	29.3 ± 4.8	19.8 ± 4.5
2 (125)	29.0 ± 2.8	42.2 ± 3.4	14.6 ± 2.1	9.6 ± 0.4	27.0 ± 3.5	17.3 ± 3.3

Subria sylvestris Naskrecki & Morris, 2000 Fig. 9 [MNHN-SO-2019-1814, -1815, -1816]

Subria sylvestris is a small to mid-sized $(0.55 \pm 0.09 \text{ g}, \text{n} = 11)$ katydid with both green and brown morphs, slightly translucent exoskeleton, and black markings on the posterior edge of the pronotum (Fig. 9A, B). This species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of two pulses with a very consistent mean call duration of 125 ms (Table 1; Fig. 9C, D). Calls can be produced singly or repeated at an interval of 1-3 s for long periods of time.

The peak frequency of the entire call is ~40 kHz with a -20 dB range spanning ~24–50 kHz, giving a bandwidth of ~26 kHz (Table 1). There is also significant energy at lower frequencies in the range of 20–25 kHz (Fig. 9D).

The pulses are often equal in amplitude and individual tooth strikes are visible on the oscillogram (Fig. 9D). The first pulse is usually longer than the second pulse (Table 5). The spectral properties of each pulse type are the same (Table 5).

Calls of this species were previously described by Naskrecki (2000), but they were recorded at a lower sampling rate that did not capture the higher frequencies described here.



Fig. 9. Photographs and calling song spectrograms of *Subria sylvestris*. A. Male, green morph (photo credit: H. ter Hofstede); B. Female, brown morph (photo credit: T. Robillard); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 5. Call pulse parameters of Subria sylvestris (3 individuals, 37 calls; mean ± SD); n = number of pulses measured.
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Pulse number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (37)	32.2 ± 1.7		38.9 ± 1.7	24.2 ± 5.4	49.1 ± 0.9	24.9 ± 6.1
2 (37)	26.6 ± 1.5	98.4 ± 1.3	38.6 ± 1.9	24.2 ± 6.8	49.2 ± 1.0	25.0 ± 7.7

Vestria punctata (Redtenbacher, 1891) Fig. 10 [MNHN-SO-2019-1820, -1821, -1822]

Vestria punctata is a mid-sized (0.66 g, n = 1), green katydid with very distinctive markings (Fig. 10A, B). The facial markings are particularly striking, with brownish-yellow mouthparts, a band of dark green across the middle of the face, and white circular patches across the top. There are two white spots on the posterior edge of the pronotum and the abdomen is green on the dorsal surface, pale yellowish-green on the ventral surface, and has black spots on the sides. This species was redescribed by Naskrecki (2000), who mentioned several undescribed species of *Vestria* from Central America and the need for a critical taxonomic revision of the genus. This species is known from Costa Rica, Panama, Colombia, and Peru (Cigliano et al. 2020).

The call consists of two main pulses with what appear to be relatively high amplitude wing-opening sounds before each pulse

(Fig. 10C, D). The first wing-opening sound is long and can be greater in amplitude than the first pulse, whereas the second wingopening sound is very short. The total call duration is ~30 ms not including the first wing-opening sound (Table 1) and ~47 ms with the wing-opening sound. The peak frequency of the entire call is 30 kHz with a -20 dB range spanning 24–37 kHz, giving a bandwidth of 13 kHz (Table 1).

The first pulse is much shorter and lower in amplitude than the second pulse (Table 6; Fig. 10D). The spectral properties of each pulse are the same (Table 6). Individual tooth strikes are visible on the oscillogram for pulse 1 and 2, but not for the presumed wing-opening sounds (Fig. 10D).

Calls of this species were previously described by Naskrecki (2000), but they were recorded at a lower sampling rate that did not capture the higher frequencies described here.



Fig. 10. Photographs and calling song spectrograms of *Vestria punctata*. A. Male; B. Female; inset: close-up of face; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: H. ter Hofstede.

Table 6. Call pulse parameters of *Vestria punctata* (3 individuals, 23 calls; mean \pm SD); WO = long wing-opening sound at start of each call; n = number of pulses measured.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
WO (23)	11.0 ± 0.5		26.8 ± 2.6	21.4 ± 2.5	36.6 ± 3.6	15.1 ± 1.7
1 (23)	7.3 ± 0.4	15.6 ± 3.5	30.3 ± 1.5	23.7 ± 1.7	37.2 ± 1.6	13.5 ± 2.0
2 (22)	14.0 ± 2.2	18.6 ± 1.3	29.6 ± 1.3	24.7 ± 2.2	36.9 ± 1.9	12.2 ± 3.3

Phaneropterinae

Aegimia elongata Rehn, 1903 Fig. 11 [MNHN-SO-2019-212, -213, -214]

Aegimia elongata is a mid-sized (no weight data available), leafmimicking, green katydid with rounded tegmina, an elongated horn-like projection on the top of the head, and hind legs that are laterally flattened (Fig. 11A). This species is distinguished from *Aegemia maculifolia* by having a mainly green horn and legs (i.e., no completely brown leg segments). This species was redescribed by Dias et al. (2012). This species is known from Costa Rica, Panama, and Colombia (Nickle 1992, Cigliano et al. 2020).

Two call types can be produced by the same individual (two of the three recorded individuals produced both call types). There was no clear pattern for when the two call types would be produced; it appeared somewhat random whether the individual would produce call type 1 or 2. The spectral properties of the two call types are the same, with a peak frequency of ~10 kHz and a -20 dB range spanning ~7–20 kHz, giving a bandwidth of ~13 kHz (Table 1; Fig. 11B–E). The temporal properties of the two call types differ. Call type one starts with a long, low amplitude pulse followed by ~20 ms of silence, then a second higher amplitude, medium duration pulse followed by ~100 ms of silence, and ends with 1–3 very short pulses (Table 7; Fig. 11B, C). Individual tooth strikes are visible on the oscillogram for pulse one. Total pulses per call range from 3–5 with a mean call duration of ~200 ms (Table 1).

Call type two starts with a long, low amplitude pulse, followed after ~400 ms of silence by a series of 5–9 very short pulses that increase in amplitude (Table 8; Fig. 11D, E). The short pulses are repeated at regular intervals (Table 8). Total pulses per call range from 6–10, with a mean call duration of ~740 ms (Table 1). There are also very low amplitude pulses produced between the short pulses that are not characterized in detail here. These low amplitude pulses are irregular in duration and amplitude with tooth strikes visible on the oscillogram but have similar spectral properties to the other described pulses (Fig. 11D, E).

This appears to be the first description of the call of this species.



Fig. 11. Photograph and calling song spectrograms of *Aegimia elongata*. A. Male with identification number written in ink; B. and C. Spectrogram (top panel) and oscillogram (bottom panel) of call type 1 at different time scales; D. and E. Spectrogram (top panel) and oscillogram (bottom panel) of call type 2 at different time scales. Photo credit: H. ter Hofstede.
Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (36)	35.4 ± 5.4		11.9 ± 0.9	7.7 ± 0.3	20.4 ± 0.7	12.7 ± 0.8
2 (36)	8.0 ± 0.4	57.6 ± 6.0	9.8 ± 0.2	7.7 ± 0.2	19.8 ± 0.3	12.2 ± 0.5
3 (36)	3.8 ± 1.3	116.9 ± 3.0	10.6 ± 0.7	7.8 ± 0.4	16.0 ± 1.9	8.2 ± 1.5
4 (13)	4.9 ± 1.2	50.0 ± 5.7	10.4 ± 0.6	7.7 ± 0.6	16.8 ± 0.8	9.0 ± 0.2

Table 7. Call pulse parameters of Aegimia elongata call type 1 (3 individuals, 36 calls; mean ± SD); n = number of pulses measured.

Table 8. Call pulse parameters of *Aegimia elongata* call type 2 (2 individuals, 7 calls; mean \pm SD); n = number of pulses measured. Only one individual produced calls with more than 6 pulses; thus, there is no SD for pulses 7–9.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (7)	55.4 ± 6.9		10.2 ± 0.1	7.6 ± 0.5	20.1 ± 0.5	12.5 ± 1.0
2 (7)	3.1 ± 0.0	458.4 ± 139.6	10.0 ± 0.2	7.7 ± 0.5	19.0 ± 1.4	11.3 ± 1.9
3 (7)	3.1 ± 1.2	51.5 ± 3.3	10.0 ± 0.2	7.7 ± 0.5	19.2 ± 0.4	11.5 ± 0.9
4 (7)	4.2 ± 0.1	50.7 ± 1.3	10.0 ± 0.4	7.7 ± 0.5	19.3 ± 0.4	11.6 ± 0.2
5 (7)	5.2 ± 0.5	51.9 ± 1.9	10.1 ± 0.1	7.9 ± 0.2	16.8 ± 3.1	8.9 ± 2.9
6 (7)	5.2 ± 0.3	54.4 ± 1.9	10.2 ± 0.1	8.1 ± 0.2	18.9 ± 0.1	10.8 ± 0.1
7 (6)	5.5	57.2	10.0	8.0	19.0	11.0
8 (6)	6.0	61.2	10.0	7.8	19.2	11.4
9 (1)	1.9	95.9	9.7	7.8	19.0	11.2

Aegimia maculifolia Dias, Rafael, & Naskrecki, 2012 Fig. 12 [MNHN-SO-2019-215, -216, -217, -218, -219]

Aegimia maculifolia is a mid-size (0.63 ± 0.1 g, n = 16), leafmimicking, green katydid with rounded tegmina, an elongated horn-like projection on the top of the head, and hind legs that are laterally flattened (Fig. 12A, B). This species is distinguished from *Aegemia elongata* by having a completely brown mid-tibia and a brown tip to the horn. This species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 10–23 pulses (mean: 16) produced in groups (Fig. 12C, D), with a total call duration that is highly variable, ranging from 630-2,440 ms and a mean of ~1,400 ms (Table 1). The peak frequency of the call is ~17 kHz, with a -20 dB range spanning ~10–23 kHz, giving a bandwidth of ~13 kHz (Table 1). Pulses increase in amplitude across the call.

The pulses are similar in spectral properties (Table 9), with individual tooth strikes visible on the oscillogram and the peak frequency of the tooth strikes decreasing from ~19 to 13 kHz over

each pulse (Fig. 12D). The call usually starts with pulses being produced in groups of four (pulse group type 1), then one or two groups of three pulses (pulse group type 2), and ending with pulses grouped in pairs (pulse group type 3; Table 9). The first pulse of each pulse group is longer than the other pulses (Table 9) and has 2-3 distinct gaps in the tooth strike pattern (Fig. 12D, first pulse), whereas the other pulses in a group are shorter and tooth strikes are evenly spaced (Fig. 12D, second pulse). The most common call has 15 pulses arranged as two groups of four pulses, followed by one group of three pulses, followed by two pairs of pulses (Table 9), however many variations are produced by the same individual, including calls that lacked the three pulse group, have two three-pulse groups, or have 1-3 pairs of pulses at the end. The call in Fig. 11 provides an example of a particularly long call with three groups of four, two groups of three, and two groups of two pulses. Pulse durations range from 14-75 ms and pulse periods range from 50-230 ms, with means that vary depending on pulse group and pulse number within the group (Table 9).

This appears to be the first description of the call of this species.



Fig. 12. Photographs and calling song spectrograms of *Aegimia maculifolia*. A. Male (photo credit: T. Robillard); B. Male on female (photo credit: C. Kernan); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and two pulses from the same call (D). PGT# refers to pulse group type (see Table 9).

Table 9. Call pulse parameters of *Aegimia maculifolia* (5 individuals, 52 calls; mean \pm SD); n = number of pulses measured. Values are given for the most common call type (pulses grouped as 4, 4, 3, 2, 2).

Pulse Group	Pulse Number	Pulse Duration	Pulse Period	Peak Frequency	Low Frequency	High Frequency	Bandwidth
Туре	(n)	(ms)	(ms)	(kHz)	(kHz)	(kHz)	(kHz)
1	1 (52)	42.7 ± 3.0		16.1 ± 1.0	12.0 ± 0.4	21.6 ± 0.2	9.7 ± 0.4
1	2 (52)	35.8 ± 4.0	67.8 ± 3.5	16.4 ± 0.9	11.1 ± 0.5	21.9 ± 0.5	10.8 ± 0.9
1	3 (52)	32.9 ± 2.0	61.0 ± 6.9	14.9 ± 0.7	9.5 ± 0.4	20.9 ± 0.8	11.4 ± 1.0
1	4 (48)	26.7 ± 4.0	60.7 ± 2.2	13.8 ± 0.9	9.0 ± 0.6	20.1 ± 1.3	11.0 ± 1.1
1	5 (44)	58.0 ± 4.5	74.3 ± 9.7	16.4 ± 1.2	12.3 ± 0.6	22.1 ± 0.4	9.9 ± 0.7
1	6 (44)	35.9 ± 2.8	83.5 ± 6.6	16.8 ± 0.7	11.3 ± 1.2	22.0 ± 0.5	10.7 ± 1.7
1	7 (44)	33.3 ± 2.2	59.9 ± 5.6	15.6 ± 1.1	9.7 ± 0.5	21.0 ± 0.7	11.3 ± 0.9
1	8 (44)	25.1 ± 1.6	62.3 ± 2.1	13.9 ± 0.4	9.3 ± 0.3	20.1 ± 1.4	10.8 ± 1.4
2	9 (49)	63.0 ± 5.1	75.8 ± 3.1	17.4 ± 1.7	12.1 ± 1.2	22.2 ± 0.3	10.1 ± 1.4
2	10 (49)	35.2 ± 2.5	89.2 ± 8.4	18.2 ± 0.7	12.3 ± 0.9	22.1 ± 0.4	9.8 ± 1.1
2	11 (49)	32.4 ± 3.3	61.3 ± 2.7	15.7 ± 1.3	9.9 ± 0.5	21.4 ± 0.4	11.5 ± 0.6
3	12 (52)	65.4 ± 5.1	131.9 ± 8.6	17.4 ± 1.7	11.9 ± 1.3	22.2 ± 0.4	10.4 ± 1.6
3	13 (52)	37.2 ± 2.4	92.9 ± 7.5	18.2 ± 0.7	12.5 ± 1.0	22.1 ± 0.5	9.6 ± 1.3
3	14 (50)	65.5 ± 6.3	189.2 ± 11.2	17.5 ± 1.0	12.0 ± 1.0	22.1 ± 0.4	10.1 ± 1.3
3	15 (50)	34.3 ± 3.7	95.2 ± 8.6	17.5 ± 1.0	12.4 ± 1.0	22.0 ± 0.4	9.6 ± 1.2

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Anapolisia colossea (Brunner von Wattenwyl, 1878) Fig. 13 [MNHN-SO-2019-223, -224, -225, -226, -227, -228, -229, -230, -231]

Anapolisia colossea is a mid-size $(0.91 \pm 0.08 \text{ g}, \text{n} = 112)$, green katydid with yellowish mouthparts and vertical bands on the broad wings that alternate between dark green and translucent with green specks (Fig. 13A, B). This species is known from Panama and Colombia (Nickle 1992, Cigliano et al. 2020).

The call consists of a series of 3-10 (mean: 5.6) short, broadband pulses (Fig. 13C, D) with a total call duration that is highly variable, ranging from ~0.8–4.0 s and having a mean of 2 s

(Table 1). The peak frequency of the entire call is ~ 20 kHz, with a -20 dB range spanning $\sim 12-25$ kHz, giving a bandwidth of ~ 13 kHz (Table 1). The amplitude of the pulses can vary across the call, but not in a consistent manner. Sometimes the pulses within a call are all equal in amplitude, and sometimes they increase or decrease in amplitude across the call.

The pulses in the call are all very similar in their temporal and spectral properties (Table 10), but with the first pulse being slightly longer in duration than the others. The pulse period, however, gradually increases across the call (Table 10).

The calls of this species were previously described by Falk et al. (2015) and Symes et al. (2016).



Fig. 13. Photographs and calling song spectrograms of *Anapolisia colossea*. A. Male (photo credit: C. Kernan); B. Female (photo credit: H. ter Hofstede); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and one pulse from the same call (D).

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (116)	13.4 ± 1.4		19.7 ± 0.7	9.6 ± 0.7	26.3 ± 1.0	16.7 ± 0.8
2 (116)	11.6 ± 1.4	376.0 ± 11.7	19.8 ± 0.6	9.8 ± 0.9	26.4 ± 1.0	16.6 ± 1.2
3 (116)	11.3 ± 1.5	394.0 ± 18.7	19.8 ± 0.7	9.7 ± 0.8	26.4 ± 1.1	16.7 ± 1.1
4 (112)	11.6 ± 1.5	423.5 ± 19.5	19.8 ± 0.6	9.6 ± 0.7	26.5 ± 1.0	16.9 ± 1.1
5 (84)	11.3 ± 1.9	435.7 ± 25.1	19.9 ± 0.5	9.8 ± 0.9	26.3 ± 1.0	16.6 ± 1.3
6 (59)	11.0 ± 2.1	460.9 ± 23.3	19.8 ± 0.5	9.6 ± 1.0	26.3 ± 1.1	16.6 ± 1.8
7 (35)	11.7 ± 2.1	516.1 ± 69.6	19.8 ± 1.2	9.8 ± 1.5	26.6 ± 1.3	16.7 ± 2.5
8 (10)	12.1 ± 1.1	465.9 ± 96.6	19.4 ± 0.7	9.8 ± 1.7	26.8 ± 1.4	17.0 ± 3.0
9 (3)	13.5 ± 1.1	519.2 ± 15.4	20.1 ± 0.5	9.2 ± 0.0	27.4 ± 0.5	18.2 ± 0.5

Anaulacomera furcata Brunner von Wattenwyl, 1878 Fig. 14 [MNHN-SO-2019-232, -233, -234]

Anaulacomera furcata is a very small $(0.14 \pm 0.04 \text{ g}, \text{n} = 43)$, green katydid with narrow wings, a solid green face, three black spots on the posterior edge of the pronotum, light yellow stripes along the dorsal margins of the pronotum, and male cerci that are forked, having two branches at the end (Fig. 14A, B). This

species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of two short pulses of equal amplitude produced ~20 ms apart (Table 11; Fig. 14C, D). The peak frequency of the entire call is ~29 kHz, with a -20 dB range spanning ~24–36 kHz, giving a bandwidth of ~12 kHz (Table 1). The two pulses have similar temporal and spectral properties (Table 11).



Fig. 14. Photographs and calling song spectrograms of *Anaulacomera furcata*. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: C. Kernan.

Fable 11. Call pulse parameters of Anaulacomera f	rcata (3 individuals, 53 calls; mean ± SD); n = number of pulses measured
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Pulse number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (53)	0.8 ± 0.1		29.2 ± 1.1	24.8 ± 1.1	35.0 ± 0.7	10.2 ± 1.3
2 (53)	0.9 ± 0.1	20.2 ± 1.5	29.8 ± 0.7	25.0 ± 0.7	35.8 ± 0.3	10.8 ± 0.7

Anaulacomera "goat"

Fig. 15

Anaulacomera "goat" is a very small $(0.16 \pm 0.02 \text{ g}, \text{ n} = 12)$, green katydid with narrow wings, a dark line through the eye, and

temporary species name "goat" due to the unique eye patterning. The calls recorded from these individuals are all the same and can be readily distinguished from the other species of Anaulacomera we collected in Panama.

The call consists of a single pulse with a duration ~2 ms (Taa dark brown stridulatory area in males (Fig. 15A, B). We were ble 1; Fig. 15C, D). The peak frequency of the call is ~27 kHz, with not able to identify these individuals to species and provide the a -20 dB range spanning 23–33 kHz, giving a bandwidth of 10 kHz.



Fig. 15. Photographs and calling song spectrograms of Anaulacomera "goat". A. Male (photo credit: C. Wilson); B. Female (photo credit: C. Kernan). Inset shows dark line through eye; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Anaulacomera "ricotta"

Fig. 16

Anaulacomera "ricotta" is a very small $(0.12 \pm 0.02 \text{ g}, \text{ n} = 7)$, green katydid with narrow wings, a white and green mottled body, and male cerci that are forked, having two branches at the end, one of which ends in a spiral coil (Fig. 16A, B). We were not able to

identify these individuals to species and provide the temporary species name "ricotta" due to the unique white mottling on the body.

The call consists of two short pulses of equal amplitude produced ~60 ms apart (Table 12; Fig. 16C, D). The peak frequency of the entire call is ~34 kHz, with a -20 dB range spanning ~29–39 kHz, giving a bandwidth of ~10 kHz (Table 1). The two pulses have similar temporal and spectral properties (Table 12).



Fig. 16. Photographs and calling song spectrograms of *Anaulacomera* "ricotta". A. Male (photo credit: H. ter Hofstede); B. Female (photo credit: C. Kernan); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 12. Call pulse parar	meters of Anaulacomera	"ricotta"	(3 individuals,	16 calls; mean ± SI)); n = number of	pulses measured
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Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(KHZ)	(KHZ)	(KHZ)	
1 (16)	1.0 ± 0.2		33.2 ± 2.5	29.5 ± 2.1	38.0 ± 0.2	8.4 ± 1.9
2 (16)	1.0 ± 0.2	58.0 ± 1.9	33.9 ± 1.5	30.1 ± 1.6	38.0 ± 0.1	7.9 ± 1.6

Anaulacomera spatulata Hebard, 1927 Fig. 17 [MNHN-SO-2019-238, -239, -240]

Anaulacomera spatulata is a small $(0.30 \pm 0.08 \text{ g}, \text{n} = 129)$, green katydid with very narrow wings. Males have a dark brown stridulatory area and spatulate cerci (Fig. 17A, B). This species is known from Panama, Colombia, and Suriname (Cigliano et al. 2020).

The call consists of two short pulses of equal amplitude produced ~40 ms apart (Table 13; Fig. 17C, D). The peak frequency of the entire call is ~25 kHz, with a -20 dB range spanning ~22– 29 kHz, giving a bandwidth of ~7 kHz (Table 1). The two pulses have similar temporal and spectral properties (Table 13).



Fig. 17. Photographs and calling song spectrograms of *Anaulacomera spatulata*. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: C. Wilson.

Table 13. Call pulse parameters of Anaulacomera spatulata (3 individuals, 59 calls; mean ± SD); n = number of pulses measured.

Pulse number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (59)	1.3 ± 0.2		24.6 ± 3.2	22.2 ± 3.3	29.3 ± 2.5	7.1 ± 1.3
2 (59)	1.4 ± 0.3	41.4 ± 2.3	24.3 ± 3.7	22.0 ± 3.3	29.3 ± 2.0	7.3 ± 1.4

Anaulacomera "wallace" Fig. 18

Anaulacomera "wallace" is a very small $(0.22 \pm 0.05 \text{ g}, \text{ n} = 28)$, green katydid with narrow wings, a green and white mottled face, eyes that are half green and half white, and highly reduced cerci in males (Fig. 18A, B). We were not able to identify these individuals to species, and we provide the temporary species name "wallace."

The calls recorded from these individuals are all the same and can be readily distinguished from the other species of *Anaulacomera* that we collected in Panama.

The call consists of three short pulses of equal amplitude produced ~16 ms apart (Table 14; Fig. 18C, D). The peak frequency of the entire call is ~25 kHz, with a -20 dB range spanning ~20– 31 kHz, giving a bandwidth of ~11 kHz (Table 1). The three pulses have similar temporal and spectral properties (Table 13).



Fig. 18. Photographs and calling song spectrograms of *Anaulacomera* "wallace". A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: C. Kernan.

Pulse number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (19)	1.2 ± 0.2		25.3 ± 1.7	21.4 ± 0.7	29.1 ± 2.6	7.7 ± 3.1
2 (19)	1.0 ± 0.2	16.5 ± 0.7	25.0 ± 0.6	21.5 ± 1.3	29.7 ± 3.4	8.2 ± 4.3
3 (18)	0.9 ± 0.2	16.2 ± 1.1	25.1 ± 0.9	21.7 ± 1.2	29.9 ± 3.4	8.2 ± 4.2

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Arota festae (Griffini, 1896)

Fig. 19 [MNHN-SO-2019-241, -246, -247, -248, -249, -250, -251, -252, -253, -254]

Arota festae is a mid-sized $(0.98 \pm 0.15 \text{ g}, \text{ n} = 34)$, light green katydid with broad, rounded tegmina that cover nearly all of the hindwings (<3 mm visible beyond the apex of the tegmina) (Fig. 19A, B). This species is known from Panama, Colombia, and Suriname (Cigliano et al. 2020).

The call consists of a series of 7-10 (mean: 8) short pulses (Fig. 19C, D) with a total call duration ranging from ~15-28 ms and having a mean of 21 ms (Table 1). The peak frequency of the entire call is ~13 kHz with a -20 dB frequency range spanning

~8-19 kHz, giving a bandwidth of ~11 kHz (Table 1). The amplitude of the pulses varies across the call. In most cases, the pulses increase in amplitude (Fig. 19D), but sometimes they increase and then decrease in amplitude.

Pulse durations are short and increase slightly in duration over the call, whereas pulse period stays constant across the call (Table 15). The peak frequency of each pulse increases across the call (Table 15). The low and high frequencies of each pulse also increase across the call, with bandwidths ranging from 5-9 kHz, depending on the pulse (Table 15).

The calls of this species were previously described by Symes et al. (2016).



Fig. 19. Photographs and calling song spectrograms of Arota festae. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: C. Wilson.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (83)	0.8 ± 0.2		8.7 ± 0.3	6.7 ± 0.6	15.8 ± 2.2	9.1 ± 2.3
2 (83)	1.0 ± 0.2	3.0 ± 0.5	8.8 ± 0.2	7.3 ± 0.4	14.3 ± 2.2	7.0 ± 2.4
3 (83)	1.0 ± 0.2	2.7 ± 0.4	9.2 ± 0.3	7.7 ± 0.2	13.2 ± 2.2	5.5 ± 2.3
4 (83)	1.0 ± 0.2	2.7 ± 0.4	9.7 ± 0.4	8.0 ± 0.3	13.7 ± 2.1	5.7 ± 2.0
5 (83)	1.0 ± 0.1	2.7 ± 0.5	10.6 ± 0.5	8.4 ± 0.3	15.0 ± 2.2	6.6 ± 2.1
6 (83)	0.9 ± 0.1	2.8 ± 0.4	11.9 ± 1.0	9.1 ± 0.6	17.1 ± 2.4	8.0 ± 2.4
7 (83)	1.2 ± 0.3	2.9 ± 0.3	13.5 ± 0.8	10.4 ± 1.3	17.9 ± 1.5	7.5 ± 2.0
8 (62)	1.3 ± 0.2	2.9 ± 0.3	14.4 ± 0.9	10.9 ± 1.0	19.3 ± 2.7	8.4 ± 2.5
9 (26)	1.4 ± 0.2	2.8 ± 0.5	14.3 ± 0.8	11.4 ± 0.4	18.1 ± 1.2	6.7 ± 1.0

Arota panamae (Hebard, 1927)

Fig. 20 [MNHN-SO-2019-255, -256, -288, -289, -290, -291, -292, -293, -294, -295]

Arota panamae is a mid-sized (0.57 ± 0.11 g, n = 68), light green katydid with broad wings and hindwings that extend >3 mm beyond the apex of the tegmina (Fig. 20A, B). This species is known from Panama and Colombia (Cigliano et al. 2020).

The call consists of a series of 3-6 (mean: 5) short pulses (Fig. 20C, D) with a total call duration ranging from $\sim 8-25$ ms and having a mean of ~ 15 ms (Table 1). The peak frequency of the entire call is ~ 24 kHz with a -20 dB frequency range span-

ning \sim 15–33 kHz, giving a bandwidth of \sim 18 kHz (Table 1). The amplitude of the pulses varies across the call. The pulses either increase in amplitude or they increase and then decrease in amplitude across the call (Fig. 20D).

Pulse durations are short and increase over the call, whereas pulse period stays constant (Table 16). The peak frequency of each pulse increases across the call (Table 16). The low and high frequencies of each pulse also increase across the call, with bandwidths ranging from 10–20 kHz depending on the pulse (Table 16).

The calls of this species were previously described by Falk et al. (2015) and Symes et al. (2016).



Fig. 20. Photographs and calling song spectrograms of *Arota panamae*. A. Male (photo credit: C. Wilson); B. Female (photo credit: M. Ayres); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 16. Call pulse parameters of Arota panamae (10 individuals, 156 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (156)	0.4 ± 0.1		12.1 ± 1.4	7.5 ± 0.9	25.2 ± 4.1	17.8 ± 4.0
2 (156)	0.5 ± 0.1	3.3 ± 0.8	14.3 ± 2.5	9.7 ± 1.7	26.9 ± 3.3	17.1 ± 3.1
3 (156)	0.5 ± 0.1	3.6 ± 0.5	18.2 ± 3.0	13.2 ± 2.7	28.9 ± 3.5	15.7 ± 3.4
4 (151)	0.7 ± 0.2	3.6 ± 0.4	23.2 ± 3.2	16.3 ± 3.0	31.6 ± 2.5	15.3 ± 3.2
5 (118)	1.0 ± 0.3	3.6 ± 0.5	26.8 ± 1.7	20.2 ± 3.4	34.7 ± 3.5	14.4 ± 5.1
6 (48)	1.1 ± 0.2	3.3 ± 0.3	27.9 ± 1.0	23.0 ± 1.5	34.7 ± 3.6	11.7 ± 4.7

Ceraia mytra Grant, 1964

Fig. 21 [MNHN-SO-2019-302, -303, -304, -305, -306, -307, -308, -309, -310]

Ceraia mytra is a large $(1.30 \pm 0.28 \text{ g}, \text{n} = 31)$, green katydid with narrow wings, reddish cerci, and reddish-purple hindlegs (Fig. 21A, B). This species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 6-13 (mean: 10) short pulses (Fig. 21C, D) with a total call duration ranging from ~40–96 ms and having a mean of ~76 ms (Table 1). The peak frequency of the entire call is ~11 kHz with a -20 dB frequency range spanning ~7–20 kHz,

giving a bandwidth of ~13 kHz (Table 1). The amplitude of the pulses varies across the call. The pulses either increase in amplitude (Fig. 21D) or they increase and then decrease in amplitude across the call.

The pulses in the call are all very similar in their temporal and spectral properties (Table 17). Pulses sometimes have silent gaps within them, making it look like there are two shorter pulses separated by a very short silent period (e.g., pulse six in Fig. 21D). The peak frequency of each pulse decreases slightly across the call (Table 17). The low and high frequencies of each pulse also decrease slightly across the call (Table 17).

The calls of this species were previously described by Falk et al. (2015).



Fig. 21. Photographs and calling song spectrograms of *Ceraia mytra*. A. Male (photo credit: H. ter Hofstede); B. Female (photo credit: L. Symes); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (71)	1.4 ± 0.5		12.0 ± 1.1	7.9 ± 0.9	17.4 ± 1.7	9.5 ± 2.2
2 (71)	1.6 ± 0.6	7.9 ± 1.2	11.9 ± 1.0	8.0 ± 1.1	17.7 ± 1.9	9.7 ± 2.5
3 (71)	1.7 ± 0.3	7.6 ± 0.6	11.6 ± 0.9	7.8 ± 1.0	17.4 ± 1.4	9.6 ± 1.7
4 (71)	1.5 ± 0.3	8.0 ± 0.7	11.3 ± 0.7	7.7 ± 0.7	16.9 ± 1.3	9.2 ± 1.7
5 (71)	1.3 ± 0.3	8.0 ± 0.5	11.1 ± 0.9	8.0 ± 0.7	16.1 ± 1.4	8.1 ± 1.7
6 (71)	1.4 ± 0.4	8.0 ± 0.5	11.1 ± 0.8	7.6 ± 0.6	16.5 ± 1.7	8.9 ± 1.6
7 (68)	1.6 ± 0.6	8.1 ± 0.5	10.9 ± 0.7	7.8 ± 0.8	17.1 ± 2.3	9.3 ± 2.8
8 (63)	1.6 ± 0.4	8.4 ± 0.6	10.3 ± 1.0	7.5 ± 0.7	16.8 ± 1.5	9.3 ± 2.0
9 (48)	1.8 ± 0.6	8.5 ± 0.8	9.8 ± 0.8	7.1 ± 0.6	15.3 ± 2.3	8.2 ± 2.8
10 (16)	1.1 ± 0.4	8.3 ± 0.3	9.2 ± 0.8	6.7 ± 0.4	14.6 ± 1.2	7.9 ± 1.6

Chloroscirtus discocercus Rehn, 1918 Fig. 22 [MNHN-SO-2019-311, -312, -313, -314, -315, -316, -317, -318, -319, -320, -321, -322]

Chloroscirtus discocercus is a mid-sized $(0.59 \pm 0.22 \text{ g}, \text{ n} = 79)$, green katydid with narrow wings, sometimes with light yellow stripes along the dorsal margins of the pronotum (Fig. 22A, B). This species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 4–8 (mean: 6) short pulses (Fig. 22C, D) with a total call duration ranging from \sim 85–173 ms and having a mean of \sim 140 ms (Table 1). The peak frequency of the entire call is \sim 20 kHz with a -20 dB frequency range spanning \sim 11–26 kHz, giving a bandwidth of \sim 15 kHz (Table 1). Pulses are

fairly constant in amplitude, but the first or last pulse is often of a lower amplitude than the rest of the pulses.

The first pulse in the call is longer in duration than the other pulses, which are similar in duration (Table 18). The first pulse period is also longer in duration than the other periods, which are similar in duration (Table 18). The pulses in the call are all similar in their spectral properties (Table 18). Pulses are usually frequency-modulated, with the first half consisting of a constant frequency component at ~13 kHz, with visible tooth strikes in the oscillogram, followed by a frequency-modulated sweep up to ~20 kHz, often followed by a steep vertical tail at the end (Fig. 22D).

The calls of this species were previously described by Symes et al. (2016).



Fig. 22. Photographs and calling song spectrograms of *Chloroscirtus discocercus*. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: H. ter Hofstede.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (157)	13.7 ± 2.5		17.0 ± 2.7	10.0 ± 1.2	26.9 ± 2.5	16.9 ± 2.8
2 (157)	8.7 ± 2.2	30.0 ± 3.1	18.8 ± 2.5	12.2 ± 2.0	26.1 ± 3.5	13.9 ± 4.4
3 (157)	7.4 ± 2.1	24.2 ± 1.3	18.5 ± 2.8	13.0 ± 2.4	25.5 ± 3.1	12.4 ± 4.5
4 (157)	7.1 ± 1.8	22.7 ± 1.0	19.1 ± 2.3	13.1 ± 2.2	24.8 ± 3.1	11.7 ± 4.3
5 (156)	7.3 ± 1.7	22.1 ± 1.1	19.0 ± 2.2	13.1 ± 2.1	24.5 ± 2.5	11.4 ± 3.8
6 (148)	7.9 ± 1.3	22.3 ± 1.6	19.2 ± 2.4	12.7 ± 1.5	25.5 ± 2.6	12.8 ± 3.6
7 (60)	7.6 ± 1.4	23.3 ± 1.3	18.5 ± 2.2	12.2 ± 1.5	25.4 ± 2.1	13.1 ± 3.3

Dolichocercus latipennis (Brunner von Wattenwyl, 1891) Fig. 23 [MNHN-SO-2019-344, -345, -346]

Dolichocercus latipennis is a very small $(0.21 \pm 0.03 \text{ g}, \text{n} = 40)$ and mostly brown katydid with hind wings that extend significantly beyond the tips of the sharply-angled and narrow tegmina, reminiscent of a wind-dispersed seed (Fig. 23A, B). The dorsal surface of the abdomen is bright green. This species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 14-17 (mean: 16) short pulses (Fig. 23C, D) with a total call duration ranging from $\sim 282-370$

ms and having a mean of ~330 ms (Table 1). The peak frequency of the entire call is ~26 kHz with a -20 dB frequency range spanning ~21–32 kHz, giving a bandwidth of ~11 kHz (Table 1). Pulses usually increase in amplitude over the call with the last two pulses then decreasing in amplitude (Fig. 23C).

The pulses increase in duration across the call (Table 19). The pulse periods are similar in duration (Table 19). The pulses in the call are all similar in their spectral properties (Table 19). Each pulse is a short, downward frequency modulated sweep from ~28–21 kHz (Fig. 23D). In some calls, some pulses have silent gaps within them.

This appears to be the first description of the call of this species.



Fig. 23. Photographs and calling song spectrograms of *Dolichocercus latipennis*. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and nine pulses from the same call (D). Photo credit: H. ter Hofstede.

Table 19. Call pulse parameters of Dolichocercus latipennis (3 individuals, 19 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (19)	1.0 ± 0.5		27.1 ± 2.2	23.2 ± 0.9	32.0 ± 2.1	8.8 ± 1.4
2 (19)	1.0 ± 0.4	22.5 ± 0.9	26.5 ± 1.8	23.1 ± 1.3	32.0 ± 1.4	8.9 ± 1.7
3 (19)	1.1 ± 0.3	22.9 ± 1.2	26.1 ± 1.1	22.9 ± 0.7	31.3 ± 1.2	8.4 ± 1.0
4 (19)	1.1 ± 0.3	23.2 ± 1.2	26.0 ± 0.9	23.0 ± 0.9	31.1 ± 0.9	8.1 ± 0.8
5 (19)	1.1 ± 0.3	23.2 ± 0.9	26.1 ± 0.8	22.8 ± 0.8	31.1 ± 1.1	8.3 ± 0.6
6 (19)	1.3 ± 0.3	23.0 ± 1.1	26.0 ± 0.6	22.6 ± 0.6	31.1 ± 0.9	8.5 ± 0.6
7 (19)	1.4 ± 0.2	23.1 ± 1.0	25.9 ± 0.4	22.9 ± 0.7	30.9 ± 0.7	8.0 ± 0.5
8 (19)	1.5 ± 0.3	22.9 ± 0.8	26.1 ± 0.6	22.9 ± 0.5	30.8 ± 1.1	7.9 ± 1.2
9 (19)	1.6 ± 0.2	22.8 ± 1.0	26.0 ± 0.6	22.6 ± 0.4	30.4 ± 1.1	7.8 ± 1.3
10 (19)	1.8 ± 0.5	22.8 ± 0.7	26.0 ± 0.6	22.4 ± 0.4	30.6 ± 1.3	8.2 ± 1.5
11 (19)	1.9 ± 0.5	22.8 ± 0.7	25.9 ± 0.6	22.3 ± 0.4	30.7 ± 1.5	8.4 ± 1.5
12 (19)	2.2 ± 0.8	22.5 ± 1.0	26.1 ± 1.0	22.1 ± 0.2	30.8 ± 1.9	8.7 ± 1.9
13 (19)	2.3 ± 0.8	21.8 ± 1.5	25.9 ± 0.9	21.6 ± 0.1	30.8 ± 1.8	9.1 ± 1.8
14 (19)	2.4 ± 0.8	21.3 ± 1.7	25.5 ± 0.8	21.4 ± 0.0	30.9 ± 2.3	9.5 ± 2.3
15 (16)	2.6 ± 1.0	19.9 ± 2.0	25.0 ± 0.4	21.0 ± 0.2	31.5 ± 2.2	10.5 ± 2.4
16 (13)	3.1 ± 0.3	17.9 ± 0.6	23.8 ± 1.0	19.1 ± 0.3	33.2 ± 2.9	14.0 ± 2.9

Ectemna dumicola Saussure & Pictet, 1897 Fig. 24 [MNHN-SO-2019-347, -348, -608, -609, -610]

Ectemna dumicola is a mid-sized $(0.66 \pm 0.11 \text{ g}, \text{n} = 10)$, green katydid with narrow wings and a thin white and purple stripe running from the eyes, across the lateral surface of the pronotum, and continuing on the leading edge of the tegmen (Fig. 24A, B). This species is known from Panama and Colombia (Cigliano et al. 2020).

The call consists of a series of 3-14 (mean: 10) short pulses (Fig. 24C–F) with a total call duration ranging from $\sim 123-678$ ms

and having a mean of ~466 ms (Table 1). The peak frequency of the entire call is ~15 kHz with a -20 dB frequency range spanning ~10–26 kHz, giving a bandwidth of ~16 kHz (Table 1). Pulses usually increase in amplitude over the call with the last two pulses often decreasing in amplitude (Fig. 24C–F).

The pulses increase slightly in duration from across the call (Table 20), whereas pulse periods decrease over the call (Table 20). The pulses in the call are all similar in their spectral properties (Table 20).



Fig. 24. Photographs and calling song spectrograms of *Ectemna dumicola*. A. Male (photo credit: L. Symes); B. Female (photo credit: H. ter Hofstede); C. and D. Spectrogram (top) and oscillogram (bottom) of one call with 11 pulses at different time scales; E. and F. Spectrogram (top) and oscillogram (bottom) of one call with three pulses at different time scales.

Table 2	20.	Cal	l pu	lse j	parameters	of Ect	emna	dumicol	a (!	5 in	divic	iuals	6, 83	call	s; 1	mean ±	SD); 1	n = num	ber of	pu	lses	meas	surec
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Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (83)	5.5 ± 0.6		14.0 ± 1.4	10.0 ± 0.8	24.9 ± 2.2	14.9 ± 2.3
2 (83)	6.2 ± 0.7	60.0 ± 3.7	14.7 ± 1.8	10.3 ± 1.1	24.8 ± 3.5	14.4 ± 3.7
3 (83)	6.2 ± 0.8	56.1 ± 2.3	14.8 ± 1.9	10.4 ± 1.0	24.9 ± 3.4	14.5 ± 3.6
4 (81)	5.9 ± 0.8	57.4 ± 1.6	14.9 ± 2.0	10.4 ± 1.0	24.8 ± 3.3	14.4 ± 3.5
5 (81)	6.0 ± 0.9	56.5 ± 3.1	15.0 ± 2.4	10.4 ± 0.9	24.7 ± 3.2	14.3 ± 3.4
6 (81)	6.4 ± 1.2	54.6 ± 3.7	15.3 ± 2.5	10.5 ± 0.8	25.6 ± 1.7	15.2 ± 1.6
7 (80)	6.8 ± 1.5	52.9 ± 4.6	15.2 ± 2.3	10.4 ± 0.8	26.0 ± 1.6	15.6 ± 1.4
8 (70)	6.9 ± 1.3	48.5 ± 4.4	15.3 ± 2.5	10.3 ± 0.7	26.0 ± 1.4	15.7 ± 1.4
9 (58)	7.4 ± 0.9	41.8 ± 4.3	15.9 ± 2.6	10.3 ± 0.8	26.0 ± 1.2	15.7 ± 1.3
10 (53)	7.0 ± 1.0	39.2 ± 3.6	15.9 ± 2.9	10.2 ± 0.9	25.7 ± 1.1	15.4 ± 1.5
11 (27)	7.0 ± 0.9	38.4 ± 2.2	15.7 ± 2.9	10.3 ± 1.0	24.6 ± 1.5	14.3 ± 2.1
12 (12)	6.9 ± 1.3	38.4 ± 1.7	14.1 ± 0.2	10.7 ± 0.6	23.5 ± 4.3	12.9 ± 4.9

Euceraia atryx Grant, 1964 Fig. 25 [MNHN-SO-2019-662, -663, -666]

Euceraia atryx is a mid-sized $(0.67 \pm 0.15 \text{ g}, \text{n} = 56)$, green katydid with narrow wings, orange tarsi, and a pronotum that is yellow on the sides and brown on the dorsal surface (Fig. 25A, B). This species is known from Costa Rica, Panama, Colombia, and Suriname (Cigliano et al. 2020).

The call consists of a series of 11-17 (mean: 14) short pulses (Fig. 25C, D) with a total call duration ranging from ~0.7-1.7 s

and having a mean of ~ 1.1 s (Table 1). The peak frequency of the entire call is ~13 kHz with a -20 dB frequency range spanning ~11-16 kHz, giving a bandwidth of ~5 kHz (Table 1). Pulses usually increase and then decrease in amplitude over the call (Fig. 25C, D).

Pulse durations are short, and both pulse durations and pulse periods are consistent across the duration of the call (Table 21). The pulses in the call are all similar in their spectral properties (Table 21).



Fig. 25. Photographs and calling song spectrograms of Euceraia atryx. A. Male (photo credit: H. ter Hofstede); B. Female (photo credit: C. Kernan); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and three pulses from the same call (D).

Table 21.	Call	pulse	parameters	of Eucera	a atryx	(3	individuals,	14 calls	; mean	± SD); n =	= number	of	pulses	measu	red
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Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (14)	2.2 ± 0.5		12.8 ± 1.4	11.1 ± 0.9	15.6 ± 1.9	4.5 ± 1.0
2 (14)	2.7 ± 0.2	91.0 ± 19.1	13.1 ± 1.2	11.1 ± 1.0	15.3 ± 1.4	4.2 ± 1.0
3 (14)	3.1 ± 0.3	88.1 ± 17.8	13.1 ± 1.2	11.1 ± 1.1	15.2 ± 1.3	4.1 ± 0.8
4 (14)	3.2 ± 0.1	88.3 ± 17.7	13.1 ± 1.3	11.1 ± 1.3	15.2 ± 0.7	4.1 ± 0.6
5 (14)	3.1 ± 0.2	87.0 ± 18.0	13.0 ± 1.1	11.3 ± 1.1	15.1 ± 0.7	3.8 ± 0.5
6 (14)	2.9 ± 0.3	85.3 ± 17.1	13.1 ± 1.2	11.4 ± 1.0	15.3 ± 0.8	3.9 ± 0.5
7 (14)	2.6 ± 0.3	84.3 ± 17.4	13.2 ± 1.3	11.3 ± 1.1	15.1 ± 1.2	3.8 ± 0.1
8 (14)	2.3 ± 0.6	87.5 ± 16.2	13.3 ± 1.1	11.3 ± 0.9	15.5 ± 1.4	4.2 ± 0.8
9 (14)	2.5 ± 0.5	83.1 ± 16.9	13.4 ± 1.2	11.6 ± 1.5	15.2 ± 0.9	3.6 ± 0.6
10 (14)	2.4 ± 0.6	81.8 ± 17.6	13.3 ± 1.3	11.7 ± 1.4	15.4 ± 0.9	3.7 ± 0.7
11 (14)	2.4 ± 0.8	82.5 ± 17.3	13.3 ± 1.4	11.6 ± 1.5	15.4 ± 1.0	3.8 ± 0.9
12 (11)	2.2 ± 0.7	83.0 ± 17.0	13.4 ± 1.2	11.7 ± 1.5	15.1 ± 0.9	3.4 ± 0.8
13 (8)	2.4 ± 0.8	90.4 ± 15.9	13.0 ± 1.6	11.4 ± 1.4	14.8 ± 1.5	3.4 ± 0.0
14 (6)	2.7 ± 0.5	95.8 ± 10.0	12.8 ± 1.2	10.9 ± 1.0	14.5 ± 0.8	3.6 ± 0.3

Euceraia insignis Hebard, 1927 Fig. 26 [MNHN-SO-2019-1090, -1091, -1092]

Euceraia insignis is a mid-sized (0.58 ± 0.08 g, n = 37) katydid with narrow wings, a neon green pronotum, orange tarsi, and hind femurs that are green at the proximal end and black at the distal end (Fig. 26A, B). This species is widely distributed throughout Central America (Nicaragua, Costa Rica, and Panama) and northeastern South America (Cigliano et al. 2020).

The call consists of a series of 12-18 (mean: 16) short pulses (Fig. 26C, D) with a total call duration ranging from ~1.0-1.9 s

and having a mean of ~1.6 s (Table 1). The peak frequency of the entire call is ~13 kHz with a -20 dB frequency range spanning ~10–15 kHz, giving a bandwidth of ~5 kHz (Table 1). Pulses usually increase and then decrease in amplitude over the call (Fig. 26C, D).

The first two pulses are shorter than the rest of the pulses in the call, and the pulse period decreases slightly over the call (Table 22). The pulses in the call are all similar in their spectral properties (Table 22).

This appears to be the first description of the call of this species.

Fig. 26. Photographs and calling song spectrograms of *Euceraia insignis*. A. Male (photo credit: C. Kernan); B. Female (photo credit: C. Wilson); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and two pulses from the same call (D).



Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (21)	1.5 ± 0.2		12.1 ± 0.5	10.3 ± 0.9	14.5 ± 0.3	4.3 ± 0.7
2 (21)	1.7 ± 0.1	110.8 ± 3.2	12.5 ± 0.1	11.2 ± 0.1	14.3 ± 0.2	3.1 ± 0.2
3 (21)	2.0 ± 0.3	108.0 ± 4.3	12.8 ± 0.3	11.4 ± 0.5	14.6 ± 0.5	3.1 ± 0.3
4 (21)	2.7 ± 0.4	108.4 ± 3.7	12.8 ± 0.3	10.9 ± 0.3	14.6 ± 0.5	3.7 ± 0.7
5 (21)	3.2 ± 0.6	106.7 ± 4.0	12.7 ± 0.5	10.7 ± 0.5	14.5 ± 0.7	3.8 ± 1.2
6 (21)	3.3 ± 0.4	105.6 ± 5.2	12.7 ± 0.6	10.6 ± 0.2	14.4 ± 0.7	3.9 ± 0.8
7 (21)	3.1 ± 0.3	104.9 ± 5.6	12.8 ± 0.5	10.6 ± 0.6	14.4 ± 0.7	3.8 ± 1.2
8 (21)	3.0 ± 0.1	104.3 ± 6.3	12.8 ± 0.5	10.3 ± 0.4	14.6 ± 0.9	4.3 ± 1.2
9 (21)	3.1 ± 0.4	103.6 ± 6.2	12.6 ± 0.5	10.3 ± 0.3	14.5 ± 0.8	4.2 ± 1.1
10 (21)	3.0 ± 0.2	104.0 ± 7.3	12.8 ± 0.5	10.5 ± 0.2	14.5 ± 0.8	4.0 ± 0.9
11 (21)	3.1 ± 0.2	102.8 ± 6.3	12.5 ± 0.9	10.5 ± 0.3	14.5 ± 0.7	4.0 ± 1.0
12 (21)	3.1 ± 0.4	103.5 ± 7.3	12.7 ± 0.7	10.5 ± 0.2	14.5 ± 0.8	4.0 ± 1.0
13 (20)	3.3 ± 0.5	103.5 ± 7.0	12.7 ± 0.7	10.4 ± 0.3	14.4 ± 0.7	4.0 ± 1.0
14 (19)	2.9 ± 0.1	102.4 ± 6.1	12.5 ± 0.8	10.4 ± 0.3	14.6 ± 0.8	4.2 ± 1.1
15 (17)	3.0 ± 0.1	103.5 ± 7.3	12.7 ± 0.6	10.6 ± 0.1	14.5 ± 0.8	3.9 ± 0.9
16 (11)	2.8 ± 0.2	102.6 ± 6.8	12.7 ± 0.6	10.7 ± 0.0	14.5 ± 0.8	3.8 ± 0.7



Hetaira sp. Fig. 27

Hetaira is a very small $(0.15 \pm 0.02 \text{ g}, \text{n} = 6)$ katydid with green and brown coloration, white tarsi, and a solid green dorsal surface of the pronotum (Fig. 27A). We were not able to identify this katydid to species. The calls recorded from these individuals are all the same and can be readily distinguished from other katydid species collected in Panama.

The call consists of a series of three pulses (Fig. 27B, C) with a total call duration ranging from 33–40 ms and having a mean

of \sim 36 ms (Table 1). The peak frequency of the entire call is \sim 25 kHz with a -20 dB frequency range spanning \sim 22–30 kHz, giving a bandwidth of \sim 8 kHz (Table 1). Pulse amplitudes are constant or can increase across the call (Fig. 27C).

Pulse durations increase slightly across the call, whereas pulse periods are similar to each other (Table 23). The pulses in the call are all similar in their spectral properties (Table 23). Pulses sometimes have short silent gaps within them, such that they appear like two very short pulses produced in rapid succession.



Table 23. Call pulse parameters of *Hetaira* sp. (3 individuals, 13 calls; mean \pm SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (13)	1.1 ± 0.3		24.8 ± 0.8	22.0 ± 1.4	28.6 ± 1.3	6.6 ± 2.4
2 (13)	1.2 ± 0.4	17.2 ± 1.5	25.0 ± 1.2	22.4 ± 1.3	28.0 ± 2.1	5.6 ± 0.8
3 (13)	1.4 ± 0.2	17.5 ± 1.5	25.0 ± 1.2	22.3 ± 1.7	29.0 ± 1.7	6.6 ± 0.3

Hyperphrona irregularis Brunner von Wattenwyl, 1891 Fig. 28 [MNHN-SO-2019-1093, -1094, -1095]

Hyperphrona irregularis is a mid-sized (0.98 ± 0.29 g, n = 25), green katydid with highly conspicuous blue and black banding on the dorsal surface of the abdomen and three small, dark spots on the broad tegmina (Fig. 28A, B). This species is known from Nicaragua, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a single pulse with a duration ~9 ms (Table 1; Fig. 28C, D). The peak frequency of the call is ~16 kHz, with a -20 dB range spanning 15–19 kHz, giving a bandwidth of ~4 kHz. The frequency increases slightly over the call from ~15 to 18 kHz in a sine-shaped wave (Fig. 28D).



Fig. 28. Photographs and calling song spectrograms of *Hyperphrona irregularis*. **A.** Male, inset showing blue stripes on dorsal surface of abdomen (photo credit: H. ter Hofstede); **B.** Female (photo credit: C. Wilson); **C.** and **D.** Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Lamprophyllum bugabae Hebard, 1927

Fig. 29 [MNHN-SO-2019-1283, -1284, -1285, -1286, -1287, -1288, -1289, -1290, -1291, -1292, -1293, -1294, -1295, -1296]

Lamprophyllum bugabae is a large $(1.61 \pm 0.28 \text{ g}, \text{n} = 101)$, green katydid with broad wings and a black and yellow line on the leading edge of the tegmen (Fig. 29A). This species is only known from Panama (Cigliano et al. 2020).

The call consists of a series of 3-8 (mean: 7) long pulses (Fig. 29C, D) with a total call duration ranging from ~260–750 ms and having a mean of ~615 ms (Table 1). The peak frequency of the entire call is ~10 kHz with a -20 dB frequency range spanning ~7–

19 kHz, giving a bandwidth of ~12 kHz (Table 1). Pulses usually increase and then decrease in amplitude over the call (Fig. 29C, D).

Pulse durations usually increase and then decrease across the call, whereas pulse periods are similar in duration (Table 24). The pulses in the call are all similar in their spectral properties (Table 24). Individual tooth strikes in each pulse are clearly visible on the oscillogram and are much more closely spaced than in *Lamprophyllum micans* (compare Fig. 29C and Fig. 30D). The peak frequency of each tooth strike decreases across each pulse from ~15 to 9 kHz.

The calls of this species were previously described by Falk et al. (2015).



Table 24. Call pulse parameters of Lamprophyllum bugabae (14 individuals, 207 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (207)	60.5 ± 9.4		10.0 ± 0.5	6.5 ± 0.2	17.9 ± 1.8	11.4 ± 1.9
2 (207)	72.7 ± 7.6	82.6 ± 9.3	9.8 ± 0.6	6.8 ± 0.2	18.4 ± 1.5	11.6 ± 1.6
3 (207)	74.8 ± 7.2	94.3 ± 8.1	9.9 ± 0.6	7.1 ± 0.2	19.0 ± 1.1	11.9 ± 1.1
4 (206)	73.4 ± 7.1	96.3 ± 7.5	9.9 ± 0.6	7.2 ± 0.2	19.4 ± 0.9	12.2 ± 0.9
5 (202)	71.3 ± 8.0	95.9 ± 6.7	9.7 ± 0.4	7.2 ± 0.2	19.5 ± 0.8	12.3 ± 0.7
6 (199)	70.1 ± 7.5	93.9 ± 6.6	9.8 ± 0.6	7.2 ± 0.2	19.5 ± 0.8	12.3 ± 0.8
7 (157)	64.4 ± 7.5	94.8 ± 10.3	9.9 ± 0.9	7.1 ± 0.4	19.5 ± 0.7	12.4 ± 0.8
8 (62)	59.8 ± 5.5	87.6 ± 2.7	10.3 ± 0.8	6.9 ± 0.3	19.3 ± 1.2	12.4 ± 1.1

Lamprophyllum micans Hebard, 1924

Fig. 30 [MNHN-SO-2019-1297, -1298, -1299, -1300, -1301, -1302, -1303, -1304, -1305, -1306, -1307]

Lamprophyllum micans is a medium-to-large $(0.99 \pm 0.17 \text{ g}, \text{n} = 153)$, green katydid with broad wings, a thin black and yellow line on the leading edge of the tegmen, and a black eye stripe that extends below the eye (Fig. 30A, B). Males have a black saddle across the stridulatory area. This species is known from Nicaragua, Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 7-9 (mean: 8) long pulses (Fig. 30C, D) with a total call duration ranging from $\sim 675-900$ ms and having a mean of ~ 800 ms (Table 1). The peak frequency

of the entire call is ~17 kHz with a -20 dB frequency range spanning ~13–24 kHz, giving a bandwidth of ~11 kHz (Table 1). Pulses usually increase and then decrease in amplitude over the call (Fig. 30C, D).

Pulse durations usually increase across the call, whereas pulse periods are more similar in duration (Table 25). The pulses in the call are all similar in their spectral properties (Table 25). Individual tooth strikes in each pulse are clearly visible on the oscillogram and are fewer and much more sparsely spaced than in *Lamprophyllum bugabae* (compare Fig. 30D and Fig. 29C). Unlike for *L. bugabae*, the peak frequency of each tooth strike is the same.

The calls of this species were previously described by Symes et al. (2016).



Fig. 30. Photographs and calling song spectrograms of *Lamprophyllum micans*. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and one pulse from the same call (D). Photo credit: C. Wilson.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (55)	43.8 ± 5.4		17.0 ± 1.2	13.3 ± 0.7	23.3 ± 0.8	10.0 ± 0.8
2 (55)	44.2 ± 2.4	105.6 ± 5.6	17.1 ± 1.1	13.4 ± 0.7	23.2 ± 0.5	9.8 ± 0.6
3 (55)	45.0 ± 2.7	107.3 ± 5.0	17.1 ± 1.2	13.1 ± 0.6	23.4 ± 0.6	10.3 ± 0.7
4 (55)	46.9 ± 3.1	102.8 ± 7.3	17.1 ± 1.2	13.0 ± 0.6	23.5 ± 0.7	10.6 ± 0.7
5 (55)	49.6 ± 4.6	102.1 ± 5.2	17.3 ± 1.3	13.0 ± 0.6	23.7 ± 0.8	10.7 ± 0.6
6 (55)	57.3 ± 7.6	101.7 ± 6.8	17.5 ± 1.4	13.1 ± 0.8	23.6 ± 0.8	10.5 ± 0.8
7 (55)	63.3 ± 8.6	106.7 ± 4.3	17.7 ± 1.4	13.1 ± 0.9	23.7 ± 1.0	10.6 ± 0.9
8 (52)	67.9 ± 5.6	112.1 ± 8.6	17.7 ± 1.3	12.9 ± 0.8	23.7 ± 0.9	10.7 ± 0.8

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Microcentrum championi Saussure & Pictet, 1898 Fig. 31 [MNHN-SO-2019-1308, -1309, -1310, -1311]

Microcentrum championi is a mid-sized $(0.93 \pm 0.08 \text{ g}, \text{ n} = 62)$, robust, green katydid with broad wings and yellow mouth-parts (Fig. 31A, B). This species is known from Panama and Colombia (Cigliano et al. 2020).

The call consists of a series of three pulses (Fig. 31C, D) with a total call duration ranging from ~370-668 ms and having a

mean of ~472 ms (Table 1). The peak frequency of the entire call is ~10 kHz with a -20 dB frequency range spanning ~7-17 kHz, giving a bandwidth of ~10 kHz (Table 1). Pulses increase in amplitude over the call (Fig. 31C, D).

The first pulse is shorter in duration than the other two pulses (Table 26). The pulses in the call are all similar in their spectral properties (Table 26). Individual tooth strikes in each pulse are clearly visible on the oscillogram (Fig. 31D).



Fig. 31. Photographs and calling song spectrograms of Microcentrum championi. A. Male (photo credit: H. ter Hofstede); B. Female (photo credit: C. Wilson); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and one pulse from the same call (D).

Table 26. Call pulse parameters of *Microcentrum championi* (4 individuals, 20 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (20)	38.8 ± 7.1		10.1 ± 0.4	6.8 ± 0.2	15.3 ± 1.3	8.5 ± 1.3
2 (20)	48.3 ± 4.9	195.1 ± 23.4	10.2 ± 0.5	7.0 ± 0.2	15.5 ± 1.3	8.5 ± 1.3
3 (20)	49.1 ± 4.8	215.4 ± 24.0	10.2 ± 0.4	7.1 ± 0.2	16.4 ± 1.1	9.3 ± 1.0

Microcentrum "polka" Fig. 32

Microcentrum "polka" is a large $(1.20 \pm 0.12 \text{ g}, \text{n} = 117)$, green katydid with yellow dots along the leading edge of the tegmen (Fig. 32A, B). We were not able to identify these individuals to species and provide the temporary species name "polka" because of the yellow dots on the wings. The calls recorded from these individuals are all the same and can be readily distinguished from other katydid species collected in Panama.

The call consists of a series of 3–15 short pulses (mean: 8; Fig. 32C, D) with a total call duration ranging from 2.2–13.6 s and having a mean of ~6.3 s (Table 1). The peak frequency of the entire call is ~10 kHz with a -20 dB frequency range spanning ~7–14 kHz, giving a bandwidth of ~7 kHz (Table 1). The pulse amplitude is highly variable within and between individuals and can increase, decrease, or stay constant in amplitude.

Both pulse durations and pulse periods are consistent across the duration of the call (Table 27). The pulses in the call are all similar in their spectral properties (Table 27).



Fig. 32. Photographs and calling song spectrograms of *Microcentrum* "polka". A. Male (photo credit: C. Kernan); B. Female (photo credit: L. Symes); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call (C) and one pulse from the same call (D).

Table	e 27.	Call	puls	se parameters of	Microcentrum	"polk	a″ ([8 in	dividu	als, '	73 cal	ls; m	nean ±	SD); n	= num	ber of	pu	lses measure	d.
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Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (73)	1.7 ± 0.3		9.7 ± 0.4	7.2 ± 0.3	13.4 ± 0.5	6.2 ± 0.6
2 (73)	1.7 ± 0.3	971.0 ± 46.5	9.7 ± 0.4	7.2 ± 0.3	13.5 ± 0.5	6.3 ± 0.5
3 (73)	1.9 ± 0.3	964.9 ± 44.2	9.7 ± 0.5	7.3 ± 0.3	13.6 ± 0.6	6.3 ± 0.5
4 (72)	2.0 ± 0.3	947.6 ± 47.0	9.7 ± 0.5	7.3 ± 0.3	13.5 ± 0.6	6.2 ± 0.5
5 (67)	2.0 ± 0.4	935.9 ± 51.4	9.8 ± 0.5	7.3 ± 0.3	13.6 ± 0.7	6.3 ± 0.5
6 (56)	2.1 ± 0.3	936.9 ± 55.2	9.7 ± 0.4	7.3 ± 0.4	13.6 ± 0.6	6.3 ± 0.5
7 (42)	2.1 ± 0.4	938.8 ± 57.8	9.8 ± 0.5	7.4 ± 0.4	13.7 ± 0.6	6.3 ± 0.4
8 (31)	2.0 ± 0.5	940.6 ± 65.6	9.6 ± 0.5	7.4 ± 0.4	13.7 ± 0.8	6.3 ± 0.5
9 (20)	2.2 ± 0.5	949.3 ± 75.4	9.5 ± 0.6	7.4 ± 0.4	13.9 ± 0.8	6.5 ± 0.6
10 (13)	2.7 ± 0.5	961.7 ± 79.9	9.7 ± 1.0	7.4 ± 0.5	13.5 ± 0.8	6.1 ± 0.5

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Montezumina bradleyi Hebard, 1927 Fig. 33 [MNHN-SO-2019-1312, -1313, -1314]

Montezumina bradleyi is a very small $(0.16 \pm 0.03 \text{ g}, \text{n} = 15)$, green katydid with narrow tegmina, hind wings that stick out significantly past the tips of the tegmina, elongated eyes, and an "E"-shaped marking on the inner surface of the forefemur (Fig. 33A). This species is known from Costa Rica and Panama (Cigliano et al. 2020).

The call consists of a single pulse with a duration of ~32 ms (Table 1; Fig. 33B, C). The peak frequency of the call is ~30 kHz,

with a -20 dB range spanning 19-47 kHz, giving a very broad bandwidth of ~28 kHz. The peak frequency decreases over the call from ~40 kHz at the start of the call to ~20 kHz at the end of the call (Fig. 33C). Individual tooth strikes are visible on the oscillogram (Fig. 33C).

This appears to be the first description of the call of this species. The stridulatory file is described by Nickle and Carlysle (1975), and the song of the congeneric species M. modesta is described by Nickle (1984).



Orophus conspersus (Brunner von Wattenwyl, 1878) Fig. 34 [MNHN-SO-2019-1574, -1575, -1576, -1577]

Orophus conspersus is a large $(1.1 \pm 0.13 \text{ g}, n = 13)$ species with broad wings and is highly variable in color. Morphs range from bright green through tan, brown, and a deep reddish brown, a color most often seen in females (Fig. 34A, B). The tympana of this species are often white (Fig. 34B). This species is known from Guatemala, Nicaragua, Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 1-4 pulses (mean: 3; Fig. 34C, D) with a total call duration ranging from 9-96 ms and having a

mean of ~70 ms (Table 1). The peak frequency of the entire call is ~11 kHz with a -20 dB frequency range spanning ~7–19 kHz, giving a bandwidth of ~12 kHz (Table 1). Pulse amplitudes either consistently increase or they increase and then decrease across the call (Fig. 34D).

Pulse durations and pulse periods vary slightly over the call (Table 28). The pulses in the call are all similar in their spectral properties (Table 28).

The calls of this species were previously described by Taliaferro et al. (1999).



Fig. 34. Photographs and calling song spectrograms of *Orophus conspersus*. A. Male (photo credit: C. Wilson); B. Female with a spermatophore (photo credit: H. ter Hofstede); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 28. Call pulse parameters of Orophus conspersus. (4 individuals, 40 calls; mean \pm SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(KHZ)	(KHZ)	(KHZ)	
1 (40)	12.9 ± 5.3		11.2 ± 0.1	7.7 ± 0.6	18.4 ± 1.1	10.7 ± 1.4
2 (37)	13.5 ± 4.7	30.8 ± 8.3	11.1 ± 0.3	7.5 ± 0.4	18.9 ± 1.0	11.4 ± 1.2
3 (28)	11.1 ± 3.4	27.4 ± 1.2	11.3 ± 1.0	7.5 ± 0.5	18.4 ± 0.1	10.8 ± 0.5
4 (18)	8.4 ± 0.1	27.1 ± 3.8	11.7 ± 0.6	7.4 ± 0.4	18.2 ± 0.3	10.8 ± 0.3

Philophyllia ingens Hebard, 1933 Fig. 35 [MNHN-SO-2019-1578, -1579, -1580, -1581, -1582, -1583, -1584, -1585, -1586]

Philophyllia ingens is a very large $(3.43 \pm 0.65 \text{ g}, \text{ n} = 38)$, green katydid with broad wings, yellow spots on the tegminal margin, and white stripes on the face that extend from the eye to the base of the mandible (Fig. 35A, B). This species is known from Nicaragua, Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a single pulse with a duration ~6 ms (Table 1; Fig. 35C, D). The peak frequency of the call is ~11 kHz with a -20 dB range spanning 9–13 kHz, giving a narrow bandwidth of ~4 kHz. The call usually has a very strong harmonic structure. The fundamental frequency of the call is 5 kHz, with the first harmonic (10–11 kHz) being of a higher amplitude than the fundamental and the other harmonics (Fig. 35D).

The calls of this species were previously described by Falk et al. (2015).



Fig. 35. Photographs and calling song spectrograms of *Philophyllia ingens*. **A.** Male (photo credit: C. Wilson); **B.** Female (photo credit: H. ter Hofstede); **C.** and **D.** Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Phylloptera dimidiata Brunner von Wattenwyl, 1878 Fig. 36 [MNHN-SO-2019-1587, -1588, -1589, -1590, -1591, -1592, -1593, -1594, -1595, -1788, -1789, -1790]

Phylloptera dimidiata is a mid-sized (0.54 ± 0.08 g, n = 115), green katydid with broad wings, pink legs, and a black saddle on the posterior third of the pronotum (Fig. 36A, B). This species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 5-13 very short pulses (mean: 8; Fig. 36C, D) with a total call duration ranging from 11-29 ms and

having a mean of ~21 ms (Table 1). The peak frequency of the entire call is ~16 kHz with a -20 dB frequency range spanning ~10–25 kHz, giving a bandwidth of ~15 kHz (Table 1). Pulse amplitudes typically increase and then decrease across the call (Fig. 36D).

Pulse durations increase across the call, whereas pulse periods decrease slightly across the call (Table 29). The peak frequency of each pulse decreases across the call (Table 29). The low and high frequencies of each pulse also decrease slightly across the call (Table 29).

The calls of this species were previously described by Symes et al. (2016).



Fig. 36. Photographs and calling song spectrograms of *Phylloptera dimidiata*. **A.** Male (photo credit: C. Wilson); **B.** Female (photo credit: H. ter Hofstede); **C.** and **D.** Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 29. Call pulse parameters of Phylloptera dimidiata	(12 individuals, 204 calls; mean ± SI	D); n = number of pulses measured
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Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (204)	0.4 ± 0.1		20.5 ± 1.3	15.4 ± 2.0	26.4 ± 0.9	9.9 ± 2.2
2 (204)	0.5 ± 0.1	3.3 ± 0.6	20.2 ± 1.4	15.8 ± 1.7	25.8 ± 0.8	9.9 ± 1.6
3 (204)	0.6 ± 0.1	3.3 ± 0.6	18.9 ± 1.4	15.2 ± 1.3	24.9 ± 1.0	9.7 ± 1.0
4 (204)	0.8 ± 0.1	3.1 ± 0.6	17.2 ± 1.4	13.7 ± 1.5	24.2 ± 1.2	10.4 ± 1.7
5 (204)	0.9 ± 0.2	2.9 ± 0.5	15.5 ± 1.4	12.3 ± 1.5	23.1 ± 1.2	10.8 ± 1.7
6 (200)	0.9 ± 0.2	2.8 ± 0.5	14.1 ± 1.6	11.2 ± 1.4	23.0 ± 2.2	11.8 ± 2.4
7 (163)	0.9 ± 0.2	2.6 ± 0.5	13.1 ± 1.6	10.3 ± 1.4	23.2 ± 2.4	12.9 ± 2.9
8 (83)	0.8 ± 0.1	2.3 ± 0.4	12.4 ± 1.5	9.5 ± 1.0	23.3 ± 2.1	13.9 ± 2.3
9 (26)	0.9 ± 0.5	2.0 ± 0.4	12.9 ± 1.6	9.2 ± 0.9	23.6 ± 1.5	14.4 ± 1.5
10 (13)	0.8 ± 0.2	2.1 ± 0.5	13.8 ± 1.1	9.2 ± 1.9	22.7 ± 1.2	13.5 ± 0.9
11 (8)	0.8 ± 0.0	1.6 ± 0.2	13.2 ± 0.8	9.2 ± 1.7	22.8 ± 2.7	13.6 ± 0.9
12 (6)	0.9 ± 0.3	2.0 ± 0.2	12.6 ± 0.2	8.6 ± 2.8	23.5 ± 0.2	15.0 ± 2.5

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Phylloptera quinquemaculata Bruner, 1915 Fig. 37 [MNHN-SO-2019-1791, -1792, -1793]

Phylloptera quinquemaculata is a mid-sized $(0.79 \pm 0.25 \text{ g}, \text{n} = 8)$, green katydid with pink legs that are strongly banded with black and five spots (or clusters of spots) on the tegmina (Fig. 37A, B). This species has not been previously recorded from Panama. It is known from Colombia and central Brazil (Cigliano et al. 2020).

The call consists of a series of 6-11 pulses (mean: 9; Fig. 37C, D) produced in two groups, with a total call duration ranging from 46-60 ms and having a mean of \sim 53 ms (Table 1). The peak fre-

quency of the entire call is ~12 kHz with a -20 dB frequency range spanning ~9–20 kHz, giving a bandwidth of ~11 kHz (Table 1). Pulse amplitudes typically increase and then decrease across each pulse group (Fig. 37D).

The call looks very similar to two short *Phylloptera dimidiata* calls produced ~24 ms apart (Table 30). Pulse durations and pulse periods are consistent across the call (Table 30). The peak frequency of each pulse decreases across each pulse group (Table 30). The low and high frequencies of each pulse also decrease slightly across the call (Table 30).

This appears to be the first description of the call of this species.



Fig. 37. Photographs and calling song spectrograms of *Phylloptera quinquemaculata*. A. Male (photo credit: C. Wilson); B. Female (photo credit: H. ter Hofstede); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 30. Call pulse parameters of Phylloptera quinquemaculata (3 ind	lividuals, 15 calls; mean \pm SD); n = number of pulses measured
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Pulse Group	Pulse Number	Pulse Duration	Pulse Period	Peak Frequency	Low Frequency	High Frequency	Bandwidth
	(n)	(ms)	(ms)	(kHz)	(kHz)	(kHz)	(kHz)
1	1 (15)	0.9 ± 0.2		15.5 ± 1.0	12.3 ± 0.4	19.0 ± 0.7	6.7 ± 0.3
1	2 (15)	1.1 ± 0.1	4.3 ± 0.6	14.4 ± 1.1	10.8 ± 0.6	19.4 ± 3.1	8.6 ± 3.5
1	3 (13)	1.4 ± 0.2	4.1 ± 0.4	12.2 ± 0.6	10.2 ± 0.4	16.2 ± 1.5	5.9 ± 1.2
1	4 (12)	1.2 ± 0.4	3.8 ± 0.4	11.3 ± 0.4	9.5 ± 0.3	14.1 ± 0.7	4.6 ± 0.6
1	5 (5)	1.3 ± 0.3	3.8 ± 1.0	11.5 ± 0.4	8.5 ± 0.2	15.0 ± 0.5	6.5 ± 0.3
2	1 (15)	0.7 ± 0.1	23.5 ± 2.4	15.8 ± 1.0	12.4 ± 1.5	19.3 ± 1.0	6.8 ± 1.0
2	2 (15)	1.1 ± 0.1	3.7 ± 0.3	15.3 ± 1.2	11.3 ± 1.3	19.4 ± 1.7	8.1 ± 2.5
2	3 (15)	1.4 ± 0.2	4.1 ± 0.5	12.9 ± 0.7	10.3 ± 0.9	18.5 ± 2.8	8.2 ± 3.6
2	4 (15)	1.4 ± 0.3	3.7 ± 0.4	11.7 ± 0.5	9.6 ± 0.5	14.7 ± 1.2	5.0 ± 0.8
2	5 (13)	1.4 ± 0.3	3.3 ± 0.2	11.1 ± 0.1	8.4 ± 0.3	14.8 ± 2.0	6.4 ± 2.1
2	6 (6)	1.2 ± 0.4	3.8 ± 1.3	10.4 ± 0.3	8.4 ± 0.8	15.1 ± 0.7	6.8 ± 0.1

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Pycnopalpa bicordata (Saint-Fargeau & Serville, 1825) Fig. 38 [MNHN-SO-2019-1797, -1798, -1799]

Pycnopalpa bicordata is a very small $(0.12 \pm 0.02 \text{ g}, \text{n} = 16)$ katydid with green and brown coloration, white tarsi, transparent windows in the wings that look like dead patches in a leaf, and two heart-shaped green markings on the pronotum (Fig. 38A, B). This species is known from southern Mexico, Honduras, Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 4-6 pulses (mean: 5; Fig. 38C, D) with a total call duration ranging from 25-47 ms and having a mean

of ~33 ms (Table 1). The peak frequency of the entire call is ~26 kHz with a -20 dB frequency range spanning ~23–32 kHz, giving a bandwidth of ~9 kHz (Table 1). Pulse amplitudes either consistently increase or they increase and then decrease across the call (Fig. 38D).

Pulse durations and pulse periods are quite consistent across the call (Table 31). The pulses in the call are all similar in their spectral properties (Table 31). Pulses often have short silent gaps within them, such that they appear like two very short pulses produced in rapid succession (Fig. 38D).

The calls of this species were previously described by Falk et al. (2015).



Fig. 38. Photographs and calling song spectrograms of *Pycnopalpa bicordata*. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: H. ter Hofstede.

Table 31. Call pulse parameters of *Pycnopalpa bicordata* (3 individuals, 14 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (14)	1.3 ± 0.2		28.2 ± 3.6	23.1 ± 1.9	34.7 ± 5.3	11.6 ± 3.5
2 (14)	0.9 ± 0.4	7.5 ± 0.3	26.5 ± 1.6	23.1 ± 1.1	31.9 ± 3.4	8.8 ± 2.7
3 (14)	1.1 ± 0.4	7.5 ± 0.6	26.1 ± 1.2	23.8 ± 1.0	30.5 ± 2.8	6.7 ± 2.2
4 (14)	1.5 ± 0.7	7.9 ± 0.6	26.2 ± 0.8	23.3 ± 1.3	30.3 ± 1.8	7.0 ± 0.6
5 (10)	1.8 ± 0.1	7.8 ± 1.8	26.3 ± 0.6	23.4 ± 0.7	30.5 ± 1.0	7.0 ± 1.7

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Steirodon stalii (Brunner von Wattenwyl, 1878) Fig. 39 [MNHN-SO-2019-1803, -1804, -1805, -1806, -1807, -1808, -1809, -1810, -1811, -1812, -1813]

Steirodon stalii is a very large $(4.16 \pm 0.49 \text{ g}, \text{ n} = 22)$, green katydid with yellow-tipped ridges along the edge of the pronotum (Fig. 39A). This species is known from Nicaragua, Costa Rica, Panama, Colombia, and Brazil (Nickle 1992, Cigliano et al. 2020).

The call consists of a series of three pulses (Fig. 39B, C) with a total call duration ranging from 187-247 ms and having a mean

of ~209 ms (Table 1). The peak frequency of the entire call is ~19 kHz with a -20 dB frequency range spanning ~13-24 kHz, giving a bandwidth of ~11 kHz (Table 1). Pulse amplitudes usually increase across the call (Fig. 39C).

Pulse durations and pulse periods are quite consistent across the call (Table 32). The pulses in the call are all similar in their spectral properties (Table 32).



Table 32. Call pulse parameters of *Steirodon stalii* (10 individuals, 92 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (92)	4.8 ± 2.3		19.0 ± 1.5	13.6 ± 1.2	24.2 ± 1.0	10.6 ± 1.5
2 (92)	4.8 ± 2.0	94.5 ± 7.6	18.9 ± 1.1	13.5 ± 1.0	24.3 ± 1.1	10.8 ± 1.6
3 (92)	5.6 ± 2.3	107.6 ± 7.8	18.7 ± 1.7	13.2 ± 1.0	24.4 ± 1.3	11.2 ± 1.7

Viadana brunneri Cadena-Castañeda, 2015 Fig. 40 [MNHN-SO-2019-1823, -1824, -1825, -1826, -1827, -1828, -1829, -1830, -1831, -1832, -1833]

Viadana brunneri is a small $(0.38 \pm 0.07 \text{ g}, n = 70)$ and delicate green katydid with broad wings that give a strong impression of a single new leaf (Fig. 40A). This species was described by Gorochov and Cadena-Castañeda (2015), and they note that the species identified as *V. zetterstedti* in Panama by Hebard (1927, 1933) and Nickle (1992) corresponds with this species. This species is known from Panama and Colombia (Cigliano et al. 2020).

The call consists of a series of 2 pulses (Fig. 40B, C) with a total call duration ranging from 4–10 ms and having a mean of 8.6 ms (Table 1). The peak frequency of the entire call is ~16 kHz with a -20 dB frequency range spanning ~15–19 kHz, giving a bandwidth of ~4 kHz (Table 1). The second pulse is usually greater in amplitude than the first pulse (Fig. 40C).

The two pulses in the call are similar in their temporal and spectral properties (Table 33).

The calls of this species were previously described by Falk et al. (2015) and Symes et al. (2016) (identified as *V. zetterstedti* in these papers).



Table 33. Call pulse parameters of *Viadana brunneri* (11 individuals, 195 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (195)	1.3 ± 0.2		16.2 ± 0.5	14.6 ± 0.5	18.3 ± 0.8	3.7 ± 0.5
2 (195)	1.6 ± 0.2	6.9 ± 0.5	16.2 ± 0.5	14.9 ± 0.5	18.3 ± 0.7	3.4 ± 0.6

Phaneropterinae gen. "Waxy sp." Fig. 41

Phaneropterinae gen. "Waxy sp." is a mid-sized $(0.73 \pm 0.18 \text{ g},$ n = 73) katydid with very rounded and tough tegmina that have a waxy surface (Fig. 41A, B). We believe that this might be an undescribed species and provide the temporary name "Waxy sp." due to the unusually waxy feel of the wings. The calls recorded from these pulse periods within pulse groups are similar (Table 34). The individuals are all the same and can be readily distinguished from the other katydids we recorded in Panama.

The call consists of a series of 6-8 pulses (mean: 6.5; Fig. 41C, D) produced in two groups with a total call duration

ranging from 65–73 ms and having a mean of ~70 ms (Table 1). The peak frequency of the entire call is ~12 kHz with a -20 dB frequency range spanning \sim 10–18 kHz, giving a bandwidth of \sim 8 kHz (Table 1). Pulse amplitudes typically increase across each pulse group (Fig. 41D), but they can also be constant or decrease in amplitude.

Pulse durations increase within each pulse group, whereas peak frequency of each pulse decreases within each pulse group (Table 34). The low and high frequencies of each pulse also decrease slightly within each pulse group, with a bandwidth of ~5-7 kHz (Table 34).



Fig. 41. Photographs and calling song spectrograms of "Waxy" sp. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: C. Wilson.

Table 34. Call pulse parameters of "Waxy sp." (3 individuals, 13 calls; mean ± SD); n = number of pulses measur	ed.
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Pulse Group	Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1	1 (13)	0.7 ± 0.2		15.5 ± 0.3	12.5 ± 0.8	18.0 ± 0.5	5.5 ± 0.6
1	2 (13)	0.9 ± 0.2	4.5 ± 0.4	13.3 ± 0.2	10.6 ± 1.0	17.0 ± 0.4	6.4 ± 1.2
1	3 (13)	1.6 ± 0.1	4.0 ± 0.4	11.5 ± 0.3	10.2 ± 0.6	15.3 ± 0.7	5.1 ± 1.2
2	1 (13)	0.7 ± 0.2	47.4 ± 3.2	15.1 ± 0.3	11.6 ± 0.8	18.0 ± 0.4	6.4 ± 1.0
2	2 (13)	1.1 ± 0.5	5.1 ± 0.1	12.9 ± 0.5	10.6 ± 0.9	16.7 ± 0.9	6.1 ± 1.7
2	3 (13)	1.6 ± 0.1	4.6 ± 0.2	11.5 ± 0.5	10.3 ± 0.4	15.3 ± 0.6	5.0 ± 0.9

Pseudophyllinae

Acanthodis curvidens (Stål, 1875) Fig. 42 [MNHN-SO-2019-209, -210, -211]

Acanthodis curvidens is a very large $(2.98 \pm 0.2 \text{ g}, \text{n} = 6)$, brown and green mottled katydid with a blue and white face, purple markings on the ventral surface, and prominent hooked spines on the hind limbs (Fig. 42A, B). It is very well-camouflaged when resting on lichen-covered bark. This species is known from Panama and Colombia (Cigliano et al. 2020).

The call begins with a long, low amplitude sound, likely a wing opening sound, followed by 3–4 short pulses and ends with a longer, higher amplitude pulse (Table 35; Fig. 42C, D). Wing-opening sounds are often also seen before each short pulse (Fig. 42D). The

total call duration, not including the first wing-opening sound, ranges from 65–73 ms and has a mean of 64 ms (Table 1). The peak frequency of the call is ~16 kHz with a -20 dB range spanning ~10–22 kHz, giving a bandwidth of ~12 kHz (Table 1).

The peak frequency and the amplitude of the pulses increase across the call (Table 35). The initial wing-opening sound is long, and the short pulses that follow the wing-opening sound tend to increase in both duration and peak frequency (Table 35). The final pulse is longer, greater in amplitude, and has a higher peak frequency than the preceding pulses. The pulse periods of the call are fairly consistent (Table 35).

The calls of this species were previously described by Belwood (1988a) and Falk et al. (2015). In addition to acoustic signals, both males and females produce vibrational signals (described in Belwood 1988a).



Fig. 42. Photographs and calling song spectrograms of *Acanthodis curvidens*. A. Male (photo credit: T. Robillard); B. Face (photo credit: H. ter Hofstede); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 35. Call pulse parameters of *Acanthodis curvidens* (3 individuals, 38 calls; mean \pm SD); WO: wing-opening sound at start of each call; LP: last pulse, which is either pulse 4 or 5; n = number of pulses measured.

Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
WO (38)	19.3 ± 0.7		11.7 ± 0.8	8.8 ± 1.1	20.2 ± 1.0	11.4 ± 0.5
1 (38)	4.0 ± 1.5	34.4 ± 4.5	12.6 ± 0.1	8.8 ± 0.5	19.7 ± 1.3	10.9 ± 0.9
2 (38)	4.8 ± 1.8	15.0 ± 1.5	12.7 ± 0.2	9.2 ± 0.2	20.0 ± 0.8	10.7 ± 0.6
3 (38)	5.2 ± 2.0	15.6 ± 0.8	13.6 ± 0.9	9.3 ± 0.1	20.2 ± 0.9	10.9 ± 0.7
4 (15)	5.9 ± 0.2	16.0 ± 1.8	14.7 ± 0.6	9.6 ± 0.1	19.6 ± 2.3	10.0 ± 2.4
LP (38)	12.9 ± 4.3	13.9 ± 0.7	16.1 ± 0.9	11.2 ± 1.4	20.2 ± 2.0	8.9 ± 2.8

Balboana tibialis (Brunner von Wattenwyl, 1895) Fig. 43 [MNHN-SO-2019-298, -299, -300, -301]

Balboana tibialis is a very large $(4.76 \pm 0.75 \text{ g}, \text{n} = 6)$ and robust dark brown katydid with black patches at the base of the forewings and bright green male cerci (Fig. 43A, B). This species is known from Nicaragua, Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of a series of 5–8 pulses (mean: 7; Fig. 43C, D) with a total call duration ranging from 105–156 ms and having a mean of ~125 ms (Table 1). The peak frequency of the entire call is ~14 kHz with a -20 dB frequency range spanning ~9–18 kHz, giving a bandwidth of ~9 kHz (Table 1). Pulse amplitudes either

consistently increase or they increase and then decrease across the call (Fig. 43D).

Pulse durations, periods, and peak frequencies all increase across the call (Table 36). The low and high frequencies also increase across the call and the bandwidth of each pulse can vary from 5–9 kHz. Some calls have a conspicuous initial wing-opening sound with a duration of 11.6 ± 0.9 (n = 11 calls).

The calls of this species were previously described by Belwood and Morris (1987), Belwood (1988a), ter Hofstede et al. (2010), Jones et al. (2014), Falk et al. (2015), and Symes et al. (2016). In addition to acoustic signals, both males and females produce vibrational signals (described in Belwood 1988a).



Fig. 43. Photographs and calling song spectrograms of *Balboana tibialis*. A. Male (photo credit: H. ter Hofstede); B. Female (photo credit: C. Kernan); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 36. Call pulse parameters of Balboana tibialis (4 individuals, 20 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (20)	3.8 ± 0.8		12.4 ± 1.8	8.4 ± 1.0	16.8 ± 1.6	8.5 ± 2.2
2 (20)	6.1 ± 1.1	19.5 ± 2.3	13.0 ± 1.5	8.8 ± 0.5	16.2 ± 1.7	7.4 ± 2.1
3 (20)	7.6 ± 1.6	20.4 ± 1.6	13.2 ± 1.0	9.5 ± 1.2	16.7 ± 1.3	7.1 ± 2.3
4 (20)	8.6 ± 1.5	21.0 ± 2.0	14.1 ± 1.6	10.7 ± 1.8	16.1 ± 1.9	5.4 ± 3.3
5 (20)	10.2 ± 0.9	21.4 ± 2.2	14.1 ± 1.3	11.1 ± 1.5	16.2 ± 1.8	5.0 ± 3.0
6 (16)	9.8 ± 1.8	21.8 ± 1.6	14.4 ± 1.4	11.1 ± 2.1	17.1 ± 0.9	5.9 ± 2.8
7 (11)	9.2 ± 0.4	23.8 ± 1.0	14.9 ± 2.2	9.5 ± 1.9	17.5 ± 1.2	8.0 ± 2.3

Cocconotus wheeleri Hebard, 1927 Fig. 44 [MNHN-SO-2019-323, -324, -325, -326, -327, -328]

Cocconotus wheeleri is a large $(1.32 \pm 0.21 \text{ g}, \text{n} = 18)$, cylindrical, tan katydid with green markings on the wings, significantly darker dorsal surface of pronotum (black to dark brown) compared to tan colored sides of pronotum, and five black vertical lines on the face (Fig. 44A, B). This species is only known from Panama (Cigliano et al. 2020).

The call consists of a series of 4-16 (mean: 11) pulses (Fig. 44C, D) with a total call duration ranging from $\sim 79-355$ ms and having a mean of ~ 250 ms (Table 1). The peak frequency of the entire call is ~ 25 kHz with a -20 dB frequency range spanning

 \sim 20–27 kHz, giving a bandwidth of \sim 7 kHz (Table 1). The first 2–3 pulses are much lower in amplitude than the rest of the pulses, which are usually quite constant in amplitude (Fig. 44C, D), although in some individuals the pulse amplitudes increase and then decrease over the call.

The first two pulses are shorter in duration than the rest of the pulses (Table 37). Excluding the first two pulses, both pulse duration and pulse period increase slightly across the call (Table 37). The pulses in the call are all similar in their spectral properties (Table 37).

The calls of this species were previously described by Belwood and Morris (1987), Belwood (1988a), and Symes et al. (2016). In addition to acoustic signals, both males and females produce vibrational signals (described in Belwood 1988a).



Fig. 44. Photographs and calling song spectrograms of *Cocconotus wheeleri*. A. Male, inset showing striped face (one of the five black lines is obscured by white glare; photo credit: H. ter Hofstede); B. Female (photo credit: T. Robillard); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 37. Call pulse parameters of *Cocconotus wheeleri* (6 individuals, 60 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (60)	5.4 ± 3.8		23.6 ± 1.7	20.2 ± 1.6	27.9 ± 1.3	7.7 ± 1.1
2 (60)	7.5 ± 2.9	17.1 ± 3.7	23.8 ± 1.3	20.7 ± 1.6	28.1 ± 1.2	7.5 ± 1.7
3 (60)	9.1 ± 2.7	20.8 ± 1.5	23.9 ± 1.4	21.0 ± 1.7	27.8 ± 1.0	6.9 ± 1.6
4 (60)	9.8 ± 2.1	21.8 ± 1.0	24.7 ± 0.9	21.2 ± 1.3	28.0 ± 1.3	6.9 ± 1.4
5 (60)	9.4 ± 1.8	23.8 ± 1.5	24.8 ± 0.8	21.4 ± 1.5	27.9 ± 1.2	6.5 ± 1.3
6 (58)	8.8 ± 2.2	23.4 ± 0.6	24.9 ± 0.8	21.4 ± 1.4	28.2 ± 1.5	6.8 ± 1.6
7 (55)	9.3 ± 1.7	23.2 ± 1.2	24.8 ± 0.7	21.3 ± 1.4	27.9 ± 0.9	6.7 ± 1.2
8 (47)	9.6 ± 0.9	22.8 ± 1.6	24.7 ± 1.0	21.4 ± 1.1	27.9 ± 1.0	6.5 ± 1.3
9 (42)	8.9 ± 2.1	22.9 ± 1.5	24.6 ± 0.8	20.9 ± 0.9	28.3 ± 1.2	7.3 ± 1.1
10 (37)	10.1 ± 1.8	23.0 ± 2.3	24.5 ± 0.7	20.9 ± 0.8	28.2 ± 1.5	7.2 ± 1.4
11 (36)	9.5 ± 1.7	24.7 ± 0.7	24.3 ± 0.6	21.0 ± 1.0	28.2 ± 1.5	7.2 ± 1.4
12 (31)	11.0 ± 2.6	23.7 ± 1.5	24.3 ± 0.8	21.0 ± 1.1	28.3 ± 1.7	7.2 ± 1.5
13 (27)	10.7 ± 1.7	24.5 ± 0.4	24.0 ± 0.7	20.9 ± 1.2	27.5 ± 0.7	6.5 ± 1.4
14 (16)	10.4 ± 2.2	25.3 ± 1.0	24.2 ± 0.8	20.7 ± 1.0	27.7 ± 0.9	6.9 ± 1.2
15 (9)	11.9 ± 2.5	25.8 ± 1.0	24.4 ± 0.8	20.8 ± 1.4	27.9 ± 0.9	7.1 ± 1.8

Docidocercus gigliotosi (Griffini, 1896)

Fig. 45 [MNHN-SO-2019-337, -338, -339, -340, -341, -342, -343]

Docidocercus gigliotosi is a medium-sized $(1.26 \pm 0.17 \text{ g}, \text{n} = 22)$, cylindrical, tan katydid with dark and light brown banding on the dorsal surface of the abdomen and a light blue face (Fig. 45A, B). Some individuals have shiny, greenish-yellow coloration on the dorsal surface of the pronotum. This species is only known from Panama (Cigliano et al. 2020).

The call consists of 1–3 (mean: 1.6) identical pulses (Fig. 45C, D) with a total call duration ranging from \sim 13 ms (single pulse) to 376 ms (3 pulses) and having a mean of \sim 118 ms (Ta-

ble 1). Each pulse has a sinusoidal shape (Fig. 45D) and a mean duration of ~20 ms (Table 38). Of the 140 calls measured, 77 were a single pulse, 48 were two pulses, and 15 were three pulses. The peak frequency of each pulse (Table 38) and the entire call is ~24 kHz with a -20 dB frequency range spanning ~23.5–26 kHz, giving a narrow bandwidth of ~2.5 kHz (Table 1). Pulse amplitudes are similar in calls with more than one pulse.

The calls of this species were previously described by Belwood and Morris (1987), Belwood (1988a), Morris et al. (1994), Römer et al. (2010), ter Hofstede et al. (2010), and Falk et al. (2015). In addition to acoustic signals, both males and females produce vibrational signals (described in Belwood 1988a, Römer et al. 2010).



Fig. 45. Photographs and calling song spectrograms of *Docidocercus gigliotosi*. A. Male (photo credit: C. Kernan); B. Female (photo credit: T. Robillard); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 38. Call p	oulse paramete	ers of Docidocercus	gigliotosi (7 individuals,	140 calls; mean	± SD); n =	= number of p	pulses measured
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Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (140)	20.0 ± 1.4		24.2 ± 0.5	23.6 ± 0.5	25.5 ± 0.7	1.9 ± 0.5
2 (63)	19.2 ± 2.7	190.6 ± 34.1	24.0 ± 0.6	23.5 ± 0.7	25.9 ± 1.0	2.4 ± 1.3
3 (15)	19.5 ± 0.6	159.0 ± 11.7	24.1 ± 0.7	23.7 ± 0.7	25.5 ± 0.4	1.8 ± 0.4

Eubliastes pollonerae (Griffini, 1896) Fig. 46 [MNHN-SO-2019-652, -653, -654, -655, -656]

Eubliastes pollonerae is a large $(1.9 \pm 0.37 \text{ g}, \text{n} = 15)$, cylindrical, tan-colored katydid with dark anterior and posterior edges of the pronotum, a uniformly pinkish-beige face, and bright green eyes (Fig. 46A, B). This species is known from Costa Rica, Panama, and Colombia (Cigliano et al. 2020).

The call consists of two main pulses with what appear to be relatively high-amplitude wing-opening sounds before each pulse (Fig. 46C, D). The total call duration is ~37 ms not including the first wing-opening sound (Table 1) and ~55 ms with the wing-

opening sound. The peak frequency of the entire call is \sim 24 kHz with a -20 dB range spanning \sim 21–25 kHz, giving a narrow bandwidth of 4 kHz (Table 1).

The two main pulses are very similar in duration and peak frequency (Table 39). The first wing-opening sound is longer, whereas the second wing-opening sound is shorter than the main pulses (Table 39). The peak frequency and low frequency of the wing-opening sounds are both lower than the main pulses, resulting in a greater bandwidth for the wing-opening sounds than the pulses (Table 39).

The calls of this species were previously described by Falk et al. (2015) and Symes et al. (2016).



Fig. 46. Photographs and calling song spectrograms of *Eubliastes pollonerae*. A. Male (photo credit: H. ter Hofstede); B. Female (photo credit: C. Kernan); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 39. Call pulse parameters of *Eubliastes pollonerae* (5 individuals, 100 calls; mean \pm SD); WO = wing-opening sound; n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
WO1 (100)	17.8 ± 0.6		20.9 ± 1.2	17.2 ± 1.5	26.6 ± 1.9	9.4 ± 1.6
1 (100)	13.2 ± 1.7	20.1 ± 0.6	24.2 ± 1.5	21.9 ± 1.7	26.5 ± 1.6	4.6 ± 1.6
WO2 (100)	7.7 ± 1.2	16.8 ± 1.6	21.3 ± 1.1	17.8 ± 1.6	26.9 ± 1.9	9.1 ± 1.7
2 (100)	12.9 ± 1.8	9.8 ± 1.2	24.3 ± 1.3	22.4 ± 1.2	26.4 ± 1.8	4.1 ± 0.8
Idiarthron majus Hebard, 1927 Fig. 47 [MNHN-SO-2019-1096, -1097, -1098]

Idiarthron majus is a very large $(2.38 \pm 0.7 \text{ g}, \text{ n} = 3)$, robust and dark brown katydid (Fig. 47A, B). This species is only known from Panama (Cigliano et al. 2020).

The call consists of two pulses (pulse duration $\sim 10-20$ ms) with a pulse period of ~25 ms and a mean call duration of ~45 ms (Table 1). The peak frequency of the call is ~24 kHz, with

a -20 dB range spanning ~20-30 kHz, giving a bandwidth of 10 kHz (Table 1). The first pulse is always shorter and much lower in amplitude than second pulse (Table 40). Both pulses are very similar in spectral properties to each other and the entire call (Table 40). Individual tooth strikes are visible on the spectrogram.

The calls of this species were previously described by Belwood and Morris (1987) and Belwood (1988a). In addition to acoustic signals, males produce vibrational signals (Belwood 1988a).



Fig. 47. Photographs and calling song spectrograms of Idiarthron majus. A. Male (photo credit: T. Robillard); B. Female (photo credit: H. ter Hofstede); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Table 40. Call pu	lse parameters of Idiarthron ma	jus (3	individuals, 26 calls;	mean ± SD)	; n = number of	pulses measured
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Pulse Number (n)	Pulse Duration	Pulse Period (ms)	Peak Frequency	Low Frequency	High Frequency	Bandwidth (kHz)
	(ms)		(kHz)	(kHz)	(kHz)	
1 (26)	10.8 ± 1.3		23.4 ± 0.7	18.4 ± 0.4	31.4 ± 1.3	13.1 ± 0.9
2 (26)	18.6 ± 1.9	27.2 ± 0.5	24.4 ± 0.7	20.3 ± 1.1	29.2 ± 1.9	8.9 ± 1.4

Ischnomela gracilis Stål, 1873 Fig. 48 [MNHN-SO-2019-1099, -1100, -1101, -1102]

Ischnomela gracilis is a large $(1.55 \pm 0.17 \text{ g}, \text{n} = 13)$ and very elongated tan-colored katydid with black knees, a yellow line along the anal margins of the tegmina, and conspicuous white ocelli on top of the head (Fig. 48A). This species is known from Costa Rica, Panama, Colombia, and Ecuador (Cigliano et al. 2020).

The call consists of a single pulse with a duration ranging from 8–14 ms and having a mean of ~11 ms (Table 1; Fig. 48B, C). The peak frequency of the call is ~74 kHz with a -20 dB range spanning 67–91 kHz, giving a broad bandwidth of ~24 kHz. The call also has significant energy at ~15 kHz, which is usually a lower amplitude than the peak frequency (Fig. 48C) but can also be equal in amplitude in some calls.

The calls of this species were previously described by ter Hofstede et al. (2010), Montealegre-Z (2012), and Jones et al. (2014).



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Ischnomela pulchripennis is a very large $(3.75 \pm 0.14 \text{ g}, \text{n} = 2)$ and cylindrical katydid with green wings, pronotum, and hind femurs and a tan body (Fig. 49A). This species is known from Panama (Nickle 1992) and Costa Rica (Cigliano et al. 2020).

The call consists of two pulses with a consistent call duration of 69 ms (Table 1; Fig. 49B, C). Calls can be produced individually, in small groups, or continuously with a period of ~200–250 ms for

long periods of time. The peak frequency of the entire call is ~14 kHz with a -20 dB range spanning ~12–15 kHz, giving a bandwidth of ~3 kHz (Table 1). The call has a significant harmonic structure, with energy at multiples of the fundamental/peak frequency, especially at ~60 kHz (Fig. 49C). The pulses are the same in amplitude, duration, and spectral properties (Table 41). Each pulse decreases slightly in frequency, starting at ~15 kHz and ending at ~12.5 kHz.

The calls of this species were previously described by Belwood (1988a). In addition to acoustic signals, males produce vibrational signals (Belwood 1988a).



Table 41. Call pulse parameters of *Ischnomela pulchripennis* (3 individuals, 15 calls; mean ± SD); n = number of pulses measured.

Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (15)	17.1 ± 0.9		13.7 ± 0.3	12.2 ± 0.3	15.3 ± 0.1	3.1 ± 0.2
2 (15)	16.5 ± 0.8	52.5 ± 1.4	13.5 ± 0.3	12.3 ± 0.2	15.3 ± 0.3	3.0 ± 0.2

Pristonotus tuberosus (Stål, 1875) Fig. 50 [MNHN-SO-2019-1794, -1795, -1796]

Pristonotus tuberosus is a very large $(5.24 \pm 0.48 \text{ g}, \text{n} = 5)$, brown katydid with two cream-colored stripes on the face and green mottling on the wings (Fig. 50A). It is very well-camouflaged when resting on lichen-covered bark (Fig. 50B). This species is known from Panama and Colombia (Cigliano et al. 2020).

The call consists of a single pulse with a duration ranging from 14–20 ms and having a mean of ~17.5 ms (Table 1; Fig. 50C, D). The peak frequency of the call is ~11 kHz with a -20 dB range spanning 8–17 kHz, giving a bandwidth of ~9 kHz. Individual tooth strikes are visible on the oscillogram (Fig. 50D).

The calls of this species were previously described by Belwood and Morris (1987) and Belwood (1988a). Females have been observed to produce vibrational signals (Belwood 1988a).



Fig. 50. Photographs and calling song spectrograms of *Pristonotus tuberosus*. A. Male; B. Male resting on branch; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales. Photo credit: T. Robillard.

Scopiorinus fragilis (Hebard, 1927) Fig. 51 [MNHN-SO-2019-1800, -1801, -1802]

Scopiorinus fragilis is a mid-sized $(0.54 \pm 0.08 \text{ g}, \text{n} = 7)$, slender, and cylindrical green katydid (Fig. 51A, B). This species is only known from Panama (Cigliano et al. 2020).

The call consists of a "chirp" (groups of pulses; Fig. 51C, D) that is produced singly, in small groups, or every 0.5–2 s for long periods of time. Chirp durations range from 53-70 ms with a mean duration of ~60 ms (Table 1). The peak frequency of the call is ~26 kHz with a -20 dB range spanning ~22-32 kHz, giving a bandwidth of ~10 kHz.

The chirp consists of 6 pulses with the first two pulses being short (5-10 ms) and very low amplitude, and pulses 3-6 being longer and higher amplitude (8-20 ms; Fig. 51D). It looks like sound is produced both during the wing opening and wing closing movements resulting in pulses that vary in amplitude but have almost no silence between them (Fig. 51D). High-speed video of males singing would be helpful in confirming that this is the mechanism responsible for these chirps with very short silent periods between pulses.

The calls of this species were previously described by Belwood (1988a). In addition to acoustic signals, males produce vibrational signals (Belwood 1988a).



Fig. 51. Photographs and calling song spectrograms of Scopiorinus fragilis. A. Male (photo credit: C. Kernan); B. Female (photo credit: T. Robillard); C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of one call at different time scales.

Thamnobates subfalcata Saussure & Pictet, 1898 Fig. 52 [MNHN-SO-2019-1817, -1818, -1819]

Thamnobates subfalcata is a mid-size $(0.63 \pm 0.19 \text{ g}, n = 24)$, brown, cylindrical katydid with a darkened stridulatory area in males (Fig. 52A, B). This species is only known from Panama (Cigliano et al. 2020).

The call consists of 2 pulses (Fig. 52C, D) with a total call duration ranging from 21–33 ms and having a mean of 31 ms

(Table 1). The peak frequency of the entire call is ~19 kHz with a -20 dB frequency range spanning ~17.5–21 kHz, giving a bandwidth of ~3.5 kHz (Table 1). The two pulses are usually equal in amplitude (Fig. 52D). Wing-opening sounds are usually seen before the first pulse.

The first pulse is shorter in duration than the second pulse and the two pulses are similar in their spectral properties (Table 42).

An oscillogram of the call of this species is given in Lang et al. (2005).



Fig. 52. Photographs and calling song spectrograms of *Thamnobates subfalcata*. A. Male; B. Female; C. and D. Spectrogram (top panel) and oscillogram (bottom panel) of four calls (C) and one call (D) at different time scales. Photo credit: H. ter Hofstede.

Table 42. Call pulse parameters of Thamnobates subfalcata (3 individuals, 15 calls; mean ± SD); n = number	er of pulses measured
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Pulse Number (n)	Pulse Duration (ms)	Pulse Period (ms)	Peak Frequency (kHz)	Low Frequency (kHz)	High Frequency (kHz)	Bandwidth (kHz)
1 (15)	11.1 ± 0.3		18.7 ± 0.3	17.9 ± 0.5	20.7 ± 0.6	2.8 ± 0.4
2 (15)	14.1 ± 3.0	16.5 ± 0.4	19.0 ± 0.2	18.1 ± 0.4	20.9 ± 1.0	2.8 ± 0.6

Discussion

The data presented in this study demonstrate the incredible diversity of the acoustic signals of Neotropical katydids. In this discussion, we comment on overall patterns seen in these data and suggest topics for future studies, but we refrain from detailed statistical analyses until a suitable phylogenetic framework is available for these species. In general, calls varied enormously in duration, temporal patterning, peak frequency, and bandwidth both across and within subfamilies.

For the species studied here, call duration ranged from a single 1.7 ms pulse by Anaulacomera "goat" to the continuous calls of some of the conocephaline katydids, such as *Eppia truncatipennis*, which calls repeatedly for 20 seconds at a time. Species in the Conocephalinae tend to produce longer calls than those in the Phaneropterinae and Pseudophyllinae, mostly due to repetition of the base call or pulse many times over a long period of time. However, several conocephaline species produce very short calls at long intervals (Copiphora brevirostris, Subria sylvestris, and Vestria punctata). The Pseudophyllinae that we recorded all produce short calls, ranging from a single pulse of 10 ms (Ischnomela gracilis) to a call of 11 pulses over 250 ms (Cocconotus wheeleri), consistent with previous reports of short and sporadic calling in this subfamily in the Neotropics (Rentz 1975, Belwood and Morris 1987, Belwood 1988a, Morris et al. 1994). However, some Neotropical pseudophyllines are known to produce longer calls (e.g., Mimetica mortuifolia from Panama, 1.2-2.1 s: Belwood 1988a; Ottotettix smaragdopoda from Ecuador, 600 ms: Braun 2011b). Within the Phaneropterinae, call durations varied from a single pulse of 1.7 ms (Anaulacomera "goat") to a call of 8 pulses over 6 seconds (Microcentrum "polka"), but many combinations of pulse numbers and call durations are found across the species in this subfamily (Table 1). Heller et al. (2015) reviewed the acoustic characteristics of 330 phaneropterine katydid species and reported a median call duration of 1 second, whereas the median call duration in our sample of 31 species was only 70 ms. In addition, although *Microcentrum* "polka" produces a long duration call (~6 s), it consists of very short pulses (2 ms) produced at long intervals (~1 s), making the duty cycle of the call (the proportion of time occupied by sound) very low. Our data suggest that, similar to Neotropical forest pseudophyllines, Neotropical phaneropterines have short calls compared to phaneropterine species from other parts of the world.

In the Neotropics, continuously calling katydid species are generally found in dense secondary growth in clearings or fields, whereas species with short and sporadic calls are more commonly found in forest habitats (Belwood and Morris 1987, Greenfield 1990), although there are some nocturnal Neotropical forest species that also call frequently (e.g., Ischnomela pulchripennis from Panama, Belwood and Morris 1987; Typophyllum erosifolium from Ecuador, Braun 2015b). There are several factors that might contribute to this general pattern: predation, habitat structure, and reproductive strategy. One family of bats that is endemic to the Neotropics (the Phyllostomidae) has diversified to include species with a wide range of foraging strategies, including species that specialize on locating prev by eavesdropping on their acoustic signals (Belwood 1988b, Kalko et al. 1996, Falk et al. 2015, Denzinger et al. 2018). Katydids comprise a large proportion of the diet of these bat species (Belwood 1988a, Römer et al. 2010, ter Hofstede et al. 2017). Katydids that call sporadically are more difficult for eavesdropping bats to locate than those that call frequently (Belwood and Morris 1987, ter Hofstede et al. 2008). Bat species that use this eavesdropping foraging strategy are captured in mistnets in forest habitats but not

in fields or clearings (Belwood 1988a). These patterns of bat and katydid activity led to the hypothesis that eavesdropping by phyllostomid bats in the Neotropics selected for reduced acoustic signaling in forest-dwelling Neotropical katydid species (Rentz 1975, Belwood and Morris 1987, Belwood 1988a, Morris et al. 1994) compared to tropical forests in other parts of the world, where bats with this foraging strategy are either absent or rare (Heller 1995).

The structure of a habitat can influence the transmission of acoustic signals (Römer and Lewald 1992, Römer 1998) and might also contribute to differences in katydid calls between habitats. Highly repetitive signals appear adapted to allow receivers to locate the source of the sound in densely structured habitats, such as tall grasses in fields, where signal can be lost and gained as the receiver moves through the vegetation (Römer and Lewald 1992, Römer 1998, Kostarakos and Römer 2010), whereas mature forests with open spaces might facilitate communication with short and infrequent acoustic signals.

Both reproductive strategies and habitat use differ between the subfamilies of katydids (Gwynne 2001). Male katydids produce a spermatophore that is transferred to the female during mating (Gwynne 1990). Female katydids can gain nutritional benefits by eating the gelatinous, non-sperm-containing component of the spermatophore after mating (Gwynne 1988, Simmons 1994). The size of the spermatophore varies enormously between katydid species and is typically very small in conocephalines compared to phaneropterines and pseudophyllines (Gwynne 1977, Gwynne 1990, Vahed and Gilbert 1996). A large spermatophore can benefit males by acting as parental investment in offspring and protecting the sperm from female consumption (Gwynne 1990, Vahed and Gilbert 1996, McCartney et al. 2008). In some katydid species, the spermatophore is so large that it can even lead to sex role reversal due to the large male investment in reproduction, with males becoming choosy about mates and females competing for matings (Gwynne 1981, Simmons 1992, Ritchie et al. 1998). Since conocephalines are usually found in secondary growth and fields and phaneropterines and pseudophyllines are usually found in forests, some of the difference in acoustic signaling investment might be due to trade-offs in male reproductive investment (calling activity vs. spermatophore size) and sexual selection (male choosiness related to spermatophore size) (Gwynne 2001, del Castillo and Gwynne 2007 and corrigendum). However, exceptions to these taxonomic habitat associations support the additional role of predation and acoustic transmission in shaping Neotropical katydid calls. For example, the forest-dwelling conocephaline Copiphora *brevirostris* has a short call, sporadic sound production, and a large spermatophore (Belwood and Morris 1987, Belwood 1988a). Likewise, the forest-dwelling pseudophylline Ischnomela pulchripennis calls frequently, but does so from the protection of a spiny bromeliad in the forest (Belwood and Morris 1987).

Peak frequencies of the calls recorded in this study ranged from 10 kHz (many species) to 74 kHz (*Ischnomela gracilis*) (Table 1, Fig. 2), although most katydid species (86%) had peak frequencies between 10 and 30 kHz. We did not record any species with unusually low frequency calls, as have been documented for tropical forests in Southeast Asia (Malaysia: *Tympanophyllum arcufolium*, 0.6 kHz; Heller 1995), India (*Onomarchus uninotatus*, 3 kHz: Diwakar and Balakrishnan 2007a; Rajaraman et al. 2013), Africa (Tanzania: *Aerotegmina megaloptera* and *A. vociferator*, 2 kHz: Heller and Hemp 2019), the Caribbean (Guadeloupe: *Xerophyllopteryx fumosa*, 3 kHz: Stumpner et al. 2013), and South America (Brazil: *Paracycloptera grandifolia*, 3 kHz: Dias et al. 2017). It is possible that we are missing data on katydid species with low frequency calls in **Fig. 53.** Relationships between call peak frequency (kHz) and mean mass (mg) for 49 katydid species from Panama. **A.** All data for each subfamily. Points surrounded by grey dashed circles appear to be outliers for each subfamily (green circle at 74 kHz = *lschnomela gracilis;* red triangle at 3.4 g = *Philophyllia ingens;* red triangle at 4.2 g = *Steirodon stalii*); **B.** Data for families Phaneropterinae (red triangles) and Pseudophyllinae (green circles) with outliers removed. Lines are linear regression lines.



Central America, but it is interesting to speculate if the absence of low frequency calling species could be related to predation pressure as well. Morris et al. (1994) suggested that very high frequency calls in Neotropical katydids could be a defense against eavesdropping bats since high frequency sounds do not travel as far as low frequency sounds due to higher attenuation. Perhaps there is also selection against low-frequency calls in Neotropical regions where eavesdropping bat species specialize on low-frequency calling prey. Although most bats have very poor hearing in the range of 2-6 kHz (Neuweiler 1984), eavesdropping gleaning bat species for which data are available appear to be more sensitive to lower frequencies than other bat species (Neuweiler 1990). In particular, the Neotropical bat species Trachops cirrhosus is especially sensitive to frequencies between 0.5-3 kHz, corresponding with the frequencies of sympatric frog calls, one of their favorite prey (Ryan et al. 1983). Interestingly, two pseudophylline species with low frequency calls were documented for the Caribbean island of Guadeloupe (Stumpner et al. 2013), which has frugivorous phyllostomid bat species but no eavesdropping gleaning bat species (Baker et al. 1978).

Previous studies have documented a negative relationship between call frequency and measures of body size, i.e., smaller katydids produce higher frequency calls than larger katydids (Heller et al. 2006, Montealegre-Z 2009, Montealegre-Z et al. 2017). Montealegre-Z et al. (2017) found strong relationships between call frequency and both body size metrics (pronotum and mid-femur length) and specific sound generating structures on the wings (file and mirrors) for 94 katydid species with phylogenetic controls. Measures of sound generating structures were better at predicting call frequency than body size measures in general (Montealegre-Z et al. 2017). For the species in our study, there was no significant re-

lationship between mean call peak frequency and mass when testing all species together (Fig. 53; Supplemental material). However, there was a significant relationship between these two variables for species in the family Phaneropterinae ($R^2 = 0.22$, $F_{1,28} = 8.0$, P = 0.008). Two phaneropterine species (Philophyllia ingens and Steirodon stalii) were more than twice the mass of the next heaviest phaneropterine species and appear to be outliers (Fig. 53A). When these two species were excluded from analysis, the variance in call frequency explained by mass increased ($R^2 = 0.70$, $F_{1,26} = 61.8$, P < 0.001; Fig. 53B). Call frequency was not significantly related to mass in the Pseudophyllinae, but one species (Ischnomela gracilis) produces calls that are three times higher in frequency than the next highest pseudophylline species and appears to be an outlier (Fig. 53A). When this species was excluded from analysis, there was a significant relationship between call frequency and mass for the Pseudophyllinae as well ($R^2 = 0.70$, $F_{1,8} = 18.5$, P = 0.003; Fig. 53B). Our results support previous studies showing a relationship between size and call frequency, but the nature of this relationship, i.e., the slope, might be different between subfamilies.

Both temporal and spectral properties of calls are important for identifying a potential mate of the same species in katydids (Bailey and Robinson 1971, Tauber and Pener 2000, Guerra and Morris 2002, Deily and Schul 2004, 2006, Bush and Schul 2006, Bush et al. 2009, Triblehorn and Schul 2009, Cole 2010, Hartbauer and Römer 2014). Most of the species we recorded produce broadband calls (-20 dB bandwidth of ~10 kHz or greater), but several species in the Phaneropterinae and Pseudophyllinae produce a tonal call, meaning it is a very narrowband signal (e.g., species with -20 bandwidths <4.4 kHz; Phaneropterinae: *Hyperphrona irregularis* = 3.9 kHz, *Philophyllia ingens* = 3.7 kHz, *Viadana*

brunneri = 4.2 kHz; Pseudophyllinae: Docidocercus gigliotosi = 2.6 kHz, Eubliastes pollonerae = 4.3 kHz, Ischnomela pulchripennis = 3.2 kHz, Thamnobates subfalcata = 3.4 kHz; Table 1). Chivers et al. (2017) found that a shorter stridulatory file and higher tooth density in the file corresponds with more tonal calls in katydids, providing predictions for the morphology of the sound generating structures in the species recorded here. Interestingly, the species that we recorded with narrowband calls are also species that produce very short calls of only one or two pulses. Two other species produce calls of only a single pulse but have greater bandwidth calls (Phaneropterinae: Anaulacomera "goat" = 9.9 kHz; Pseudophyllinae: *Ischnomela gracilis* = 24.1 kHz; Table 1). How these insects detect and recognize this short signal lacking a strong temporal pattern within the noise of a tropical forest is a fascinating question for future investigation (Lang et al. 2005). That these short and indistinct calls are usually narrowband might be adaptive. Within the auditory system of crickets and katydids, interneurons tuned to specific frequencies of biological importance can be found (Kostarakos et al. 2008, Stumpner and Nowotny 2014). These neurons are more narrowly tuned when species live in habitats with higher levels of background noise in the frequency range of the signal (Schmidt et al. 2011). We might predict that the katydid species with short and narrowband calls have an auditory interneuron that is narrowly tuned to the call of the male and acts as a matched filter to allow these species to detect the call in background noise (Schmidt and Balakrishnan 2015, Römer 2016). Ischnomela gracilis, on the other hand, has a short and broadband signal, but calls at an extremely high frequency (74 kHz) that is otherwise only produced by bats for echolocation in this community. It is also possible that these species compensate for their short signals by simultaneously signaling in other modalities. For example, males of many Neotropical pseudophylline species, including Docidocercus gigliotosi and Ischnomela pulchripennis, are known to alternate between acoustic and vibrational signaling (Belwood 1988a, Römer et al. 2010). Future studies could also investigate whether a combination of temporal, spatial, and frequency partitioning of acoustic space occurs in this community, as has been found in other insect communities (Sueur 2002, Diwakar and Balakrishnan 2007a,b, Schmidt et al. 2012, Montealegre-Z et al. 2014)

The majority of calls described here consist of a sequence of broadband pulses with stereotypical pulse durations and periods that do not overlap with other recorded species. These temporal differences provide a mechanism by which individuals can identify a potential mate. The most subtle difference in call structure between two species is that of the congeneric species Euceraia atryx and E. insignis. Males of these species both produce calls with overlapping ranges of the number of pulses, pulse durations, and spectral properties (Table 1), but pulse periods range from 80-90 ms in E. atryx (Table 21) compared to 100–110 ms in E. insignis (Table 22), providing a temporal mechanism for discrimination. Interestingly, these Euceraia species are also among the most diversely colorful katydid species on Barro Colorado Island, Panama (Figs 24A, B, 25A, B). The role of visual cues or chemical cues in mating is unknown for the species described here and is understudied in katydids in general. Chemical cues appear to play a role in mate recognition in the Mecopoda elongata species complex in India (Dutta et al. 2018), suggesting that they might also play a role in mate recognition in Neotropical species with similar acoustic or visual cues. Studies on katydid acoustic signals have revealed the presence of cryptic species that are morphologically very similar but can be distinguished by acoustic signals (Walker 1964, Walker

et al. 2003, Montealegre-Z et al. 2011, Heller et al. 2017) and also cases of morphologically distinct species that have extremely similar acoustic signals (Çiplak et al. 2009, Şirin et al. 2014, Grzywacz et al. 2017), emphasizing the importance of documenting acoustic signals for taxonomic and phylogenetic studies.

Bioacoustic monitoring is becoming an important tool for tracking and assessing habitats (Klingbeil and Willig 2015, Gibb et al. 2019, Hill et al. 2019), and a detailed knowledge of the acoustic signals of the species in a community is essential for this. Monitoring acoustic insects provides valuable and rapidly accessible information because these insects have specific habitat associations, rapid population changes, and are centrally located in food webs. In addition, the relatively low intraspecific variation in insect calls makes them tractable for machine learning approaches to sound detection and classification. However, the ability to employ machine learning is constrained by the availability of high quality, well-curated training data. Currently, when insects are represented in acoustic monitoring, they are often represented as a composite 'insects' class or as unique but unidentified sonospecies (Aide et al. 2013, Campos-Cerqueira et al. 2019). The lack of connection between the recorded sounds and the species of insect makes it difficult to connect the dynamics of individual insect species with the rich natural history of these species. Careful taxonomic work and call descriptions are essential to developing acoustic monitoring capabilities.

Conclusions

Our goals in publishing these data are to provide detailed descriptions and recordings of the acoustic signals of many Neotropical katydid species for studies on the evolution and ecology of katydid communication and for future acoustic monitoring projects. Our research group is currently developing a phylogeny of the species in this study to assess the evolution of acoustic and vibrational signaling in Neotropical katydids. In addition, we are developing artificial intelligence approaches to automate the detection of signals in field recordings for acoustic monitoring and conservation projects. We hope that making these recordings freely available will allow other researchers to incorporate these data in additional studies and accelerate our understanding of the evolution, ecology, and conservation of these amazing insects.

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Supplementary material 1

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Data type: XLSX file

Explanation note: Excel spreadsheet with all call measurements described in the manuscript.

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Link: https://doi.org/10.3897/jor.29.46371.suppl1

Supplementary material 2

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Data type: XLSX file

- Explanation note: Excel spreadsheet with the mean mass for each species reported in the manuscript and the statistical analysis of the relationship between mass and call peak frequency.
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Corrigendum of Masson MV, Tavares WS, Alves JM, Ferreira-Filho PJ, Barbosa LR, Wilcken CF, Zanuncio JC (2020) Bioecological aspects of the common black field cricket, *Gryllus assimilis* (Orthoptera: Gryllidae) in the laboratory and in Eucalyptus (Myrtaceae) plantations. Journal of Orthoptera Research 29(1): 83–89. https://doi.org/10.3897/jor.29.48966

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Although this article refers to the species under study as *Gryllus assimilis*, given the evidence presented, we cannot be certain of this identification. *G. assimilis* is a species that cannot reliably be identified based on morphology alone (Weissman and Gray 2019). For example, there are many species of *Gryllus* in Mexico with morphological characters similar to *G. assimilis* but with notably different calling songs (Weissman et al. 2009). The species of *Gryllus* in Brazil have not specifically been investigated, but, based on the diversity of Brazilian habitats, there are likely to be several species of *Gryllus* there (Weissman and Gray 2009). Without presenting a sonogram, characters of the file, and comparing DNA barcodes of cytochrome oxidase I (COI) with those in Weissman and Gray (2009), we cannot be certain that the species in question is in fact *G. assimilis*.

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