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Cover Photograph: An *Idionycteris phyllotis* bat. © José G. Martínez-Fonseca.

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Species-specific Trills by New World Big-eared Bats

Donald I. Solick[1, 2, *], Nicholas D. Solick[1, 2], and Rogelio M. Rodriguez[3]

Resumen - Muchas especies de murciélagos usan sonidos ultrasónicos para la navegación y comunicación. Asociar estos sonidos durante el estudio de monitoreo acústico provee un entendimiento de su comportamiento y uso de su hábitat. En este estudio, describimos los trinos de murciélagos de tres especies de orejas grandes: *Corynorhinus rafinesquii* (Murciélago Orejudo de Rafinesque)*, Idionycteris phyllotis* (Murciélago Orejudo de Allen) y *Euderma maculatum* (Murciélago Orejudo Manchado). Estas especies representan a la única tribu existente de Plecotini (Chiroptera: Vespertilionidae), este sonido podría ser una característica basal de estos linajes. Estas tres especies produjeron tonos oscilantes de larga duración con un pulso terminal, pero difiere en la frecuencia y en el ritmo de repetición. *Euderma maculatum* también produce un sonido descontinuado "entre cortado" compuesto de un sonido rápido, alto y agudo justo antes del pulso terminal. Nosotros interpretamos los trinos de estas especies en el contexto de ecolocalización y vocalizaciones sociales producidas por otros murciélagos. Nuestra hipótesis es que los trinos de murciélagos están asociados con un comportamiento de canto.

Abstract - Many bat species produce ultrasonic sounds for navigation and communication. Linking these sounds to specific species enhances acoustic monitoring and provides insights into the bats' behavior and habitat use. In this study, we describe diagnostic trills produced by 3 North American species with large pinnae: *Corynorhinus rafinesquii* (Rafinesque's Big-eared Bat), *Idionycteris phyllotis* (Allen's Big-eared Bat), and *Euderma maculatum* (Spotted Bat). These species represent the only extant genera of the tribe Plecotini (Chiroptera: Vespertilionidae), suggesting that trilling may be a basal trait of this lineage. All 3 species produce long-duration oscillating tones ("continuous" trills) with a terminal pulse, differing in frequency and pulse-repetition rate. *Euderma maculatum* also emits a non-continuous "stutter" trill, composed of rapid, high-bandwidth pulses preceding a terminal pulse. We interpret these trills in the context of both echolocation and social vocalizations in bats, and we hypothesize that trilling is associated with singing behavior.

Most species of bat produce high-frequency calls that are primarily used for navigation and foraging. For North American bats, such calls typically have simple structure, are short duration (<20 milliseconds [msec]), have bandwidth dependent on whether the bat is flying in open (low bandwidth) or cluttered (high bandwidth) airspace, and are emitted at a rate dependent on whether the bat is commuting (<20 pulses/sec) or actively pursuing prey (up to 200 pulses/sec; Griffin et al. 1960, Schnitzler and Kalko 2001). Because echolocation calls are context-dependent and many bats fly in similar habitats, forage on similar foods, and share common ancestors, overlap in call characteristics can make identification of species difficult (Barclay 1999, Russo et al. 2018). Some species produce sounds for intraspecific communication (social vocalizations) to attract mates, defend territories, and locate roosts (Chaverri et al. 2010). Social vocalizations can be distinct and aid in identification of species during acoustic surveys (Bohn and Gillam 2018, Lausen et al. 2023).

Here, we describe species-specific trills made by 3 bat species that have similar body sizes (8–20 g), have large pinnae (27–50 mm), and feed primarily on moths: *Corynorhinus rafinesquii* (Lesson) (Rafinesque's Big-eared Bat), *Idionycteris phyllotis* (G.M. Allen) (Al-

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len's Big-eared Bat), and *Euderma maculatum* (J.A. Allen) (Spotted Bat) (Czaplewski 1983, Jones 1977, Watkins 1977). *Corynorhinus*, *Idionycteris*, and *Euderma* are the only extant genera of tribe Plecotini (Chiroptera: Vespertilionidae), or big-eared bats, that occur in the New World (Handley 1959). *Idionycteris* and *Euderma* are sister taxa (Jones et al. 2002), and *C. rafinesquii* likely diverged from other *Corynorhinus* during the Pliocene (Lack and van den Bussche 2009). Hereafter, we refer to these species by their generic name. The trills made by the 3 bats share a similar structure when viewed as a spectrogram (Fig. 1), but can be separated by minimum frequency (Table 1).

We recorded trills as part of acoustic surveys from 2019 to 2021 for a species inventory in Glynn County, coastal Georgia (31.26°N, 81.60°W), and for the North American Bat Monitoring program in the Manti-La Sal National Forest of southeastern Utah (37.84°N, 109.77°W) and in the Bureau of Land Management Southwest District of Colorado (37.35°N, 108.55°W). For all surveys, ultrasonic detectors (SM4BAT-FS, Wildlife Acoustics, Maynard, MA) were deployed for multiple nights (157 detector-nights total; Table 2) and were programmed to record from sunset to sunrise. We analyzed and manually reviewed full-spectrum recordings using acoustic software (SonoBat 30.0, Arcata, CA). We identified audio files containing trills by *Corynorhinus* in Georgia (*n* = 14 audio files), *Idionycteris* in Utah (73), and *Euderma* in Utah and Colorado (50; Fig. 1). We made species classifications based on the presence of diagnostic search phase echolocation calls (Szewczak 2022, 2024) that were recorded in the same files as trills.

All 3 species produced a long-duration oscillating tone ("continuous trill") with a terminal pulse that abruptly descended in frequency (Fig. 1). At 4 locations, *Euderma* also produced a non-continuous sound, or "stutter trill", composed of rapidly emitted broadband pulses ending with an abrupt terminal pulse (Fig. 1). In our sampling, *Euderma* produced stutter trills (45 audio files) more frequently than continuous trills (5 files). Typical search-phase calls (Fig. 1) were recorded much more often than trills for all 3 species. We used Kaleidoscope Pro software (Wildlife Acoustics) to measure parameters of the trills and terminal pulses for a subset of files (Table 1). Overall, continuous trills for all 3 species were long duration (46–148 msec), with oscillations across 5–8 kHz of bandwidth before descending 7–25 kHz to a terminal pulse (Table 1). The *Euderma* stutter trill was longer duration (mean ± *SD* = 175.2 ± 65.7 msec) but was composed of 16.4 ± 5.6 pulses emitted at a high rate (93.9 ± 6.9 pulses/sec). *Corynorhinus* produced trills of the highest frequency (minimum frequency [Fmin] = 40.3 ± 2.2 kHz), followed by *Idionycteris* (20.6 ± 1.3 kHz), and *Euderma* (13.5 ±1.2 kHz). Parameters for terminal pulses were comparable to search-phase echolocation calls for all 3 species (Szewczak 2022, 2024; Table 1). Within recordings, trills and terminal pulses were emitted repeatedly (Fig. 1). Often, trills were faint at the start and end of a recording and loudest in the middle, suggesting that bats were producing these sounds in flight as they moved towards and away from the stationary microphone. Pulse-repetition rate and pulse interval were variable among species. Both trills by *Euderma* had lower pulse-repetition rates with longer inter-pulse intervals than trills by *Corynorhinus* and *Idionycteris* (Table 1).

The function of these trills is unknown. Trills for *Corynorhinus* and *Idionycteris* have previously been described, but were thought to be echolocation calls, not social vocalizations (Simmons and O'Farrell 1977, Hayes et al. 2009, Loeb and Britzke 2010). *Euderma* has been known to make stutter trills (W. Rainey, University of California, Berkeley, CA; C. Corben, Titley Scientific, Columbia, MO; J. Szewczak, California Polytechnic State University, Arcata, CA, pers. comms.), but these have never been formally reported or described. To our knowledge, we are the first to describe a continuous trill by *Euderma*.

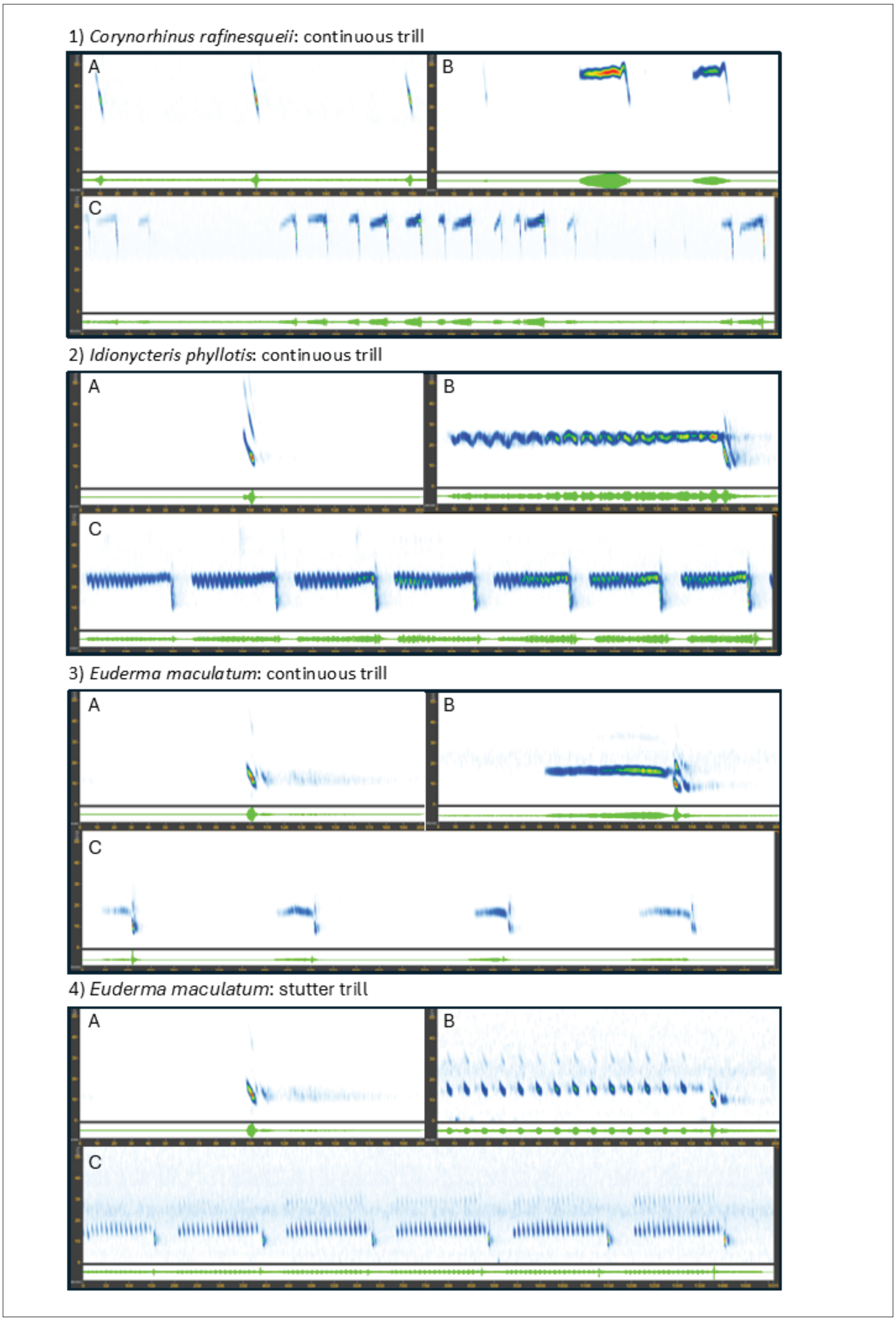

Figure 1. Full-spectrum recordings of *Corynorhinus rafinesquii* (1), *Idionycteris phyllotis* (2), and *Euderma maculatum* (3–4), rendered in SonoBat 30.2. In each panel, views of search-phase echolocation calls (A) and trills (B) are shown at a standardized 200-msec timescale, with fast Fourier transform size of 2048. The bottom panels are real-time views of sequences containing continuous (1–3) or stutter trills (4) and shown at a standardized 1.500-sec timescale, with fast Fourier transform size of 512. The *y*-axis for all views range between 0 and 55 kHz.

The similar morphology and diet of the 3 species (Czaplewski 1983, Jones 1977, Watkins 1977) suggest that trills may be related to foraging on moths, though we believe it is unlikely that continuous trills aid with echolocation of prey. Low-duty echolocators, such as these species, often couple echolocation with the downstroke of their wingbeats to reduce the energetic costs of producing sound (Speakman and Racey 1991). Yet, sounds of long duration, such as continuous trills, span multiple wingbeats and are energetically expensive. Also, the returning echoes of long-duration warbles and trills would overlap the outgoing sound, preventing the bat from hearing and interpreting the echoes (Kalko and Schnitzler 1993).

High-duty echolocating bats, such as *Pteronotus mesoamericanus* Smith (Mesoamerican Mustached Bat), produce long-duration sounds of a constant frequency and detect the fluttering wings of moths as acoustic glints in single-tone echoes (Schnitzler et al. 1983). Flutter detection is not limited to bats using high-duty echolocation (Fenton et al. 2012), and it is possible that glints of a fluttering moth would be interspersed in the oscillations of a returning sinusoidal echo, although this would need to be verified by experimentation (H. Schnitzler and A. Denzinger, Universitat Tübingen, Germany, pers comm.). It is also possible that echoes from the trill and terminal pulse components provide different types of information and are processed separately (Simmons and O'Farrell 1977). However, unless the large ears of *Corynorhinus*, *Idionycteris*, and *Euderma* possess specialized structures to avoid pulse-echo overlap, it is unlikely the bats would be able to hear and interpret echoes

Table 1. Characteristics of trills for 3 bat species, measured using Kaleidoscope Pro software. Sample sizes provided as number of pulses (number of individuals). Data for search-phase pulses from Szewczak (2022, 2024). Recordings available on Xeno-canto (www.xeno-canto.org), for *Corynorhinus* (XC1025204–XC1025214, XC1025216), *Idionycteris* (XC1025245–XC1025252), and *Euderma* (XC1025219, XC1025231, XC1025233–XC1025239, XC1025241–XC1025244).

		Corynorhinus rafinesquii	*Idionycteris phyllotis*	*Euderma maculatum*	*Euderma maculatum*
		55 (11)	40 (8)	25 (5)	40 (8)
Syllable	Parameter		Continuous trills		Stutter trills
Trill	PRR (pulses/sec)	11.9 ± 2.6	5.5 ± 0.5	2.8 ± 0.4	2.9 ± 0.8
	IPI (msec)	45.5 ± 56.4	46.3 ± 31.0	343 ± 87.0	177.6 ± 95.4
	Duration (msec)	46.7 ± 34.0	148.6 ± 23.9	86.0 ± 30.0	175.2 ± 65.7
	Fmin (kHz)	40.3 ± 2.2	20.6 ± 1.3	13.5 ±1.2	12.5 ± 1.6
	Fmax (kHz)	48.8 ± 2.9	27.2 ± 1.6	18.8 ± 0.7	22.5 ± 1.4
Terminal pulse	Fmin (kHz)	24.0 ± 1.9	7.8 ± 0.8	6.4 ± 0.5	6.6 ± 1.2
	Fmax (kHz)	48.8 ± 2.9	22.7 ± 1.3	13.7 ± 0.7	15.8 ± 1.2
Search-phase pulse	Fmin (kHz)	22.5 ± 2.5	11.5 ± 1.5	8.7 ± 1.0	8.7 ± 1.0
	Fmax (kHz)	39.8 ± 2.2	26.1 ±5.9	14.0 ± 2.0	14.0 ± 2.0

PRR = pulse-repetition rate; IPI = inter-pulse interval; msec = milliseconds; Fmin = minimum frequency; Fmax = maximum frequency; kHz = kilohertz.

from long-duration, continuous trills. The *Euderma* stutter trill has a repetition rate similar to feeding buzzes (i.e., terminal phase echolocation; Griffin et al. 1960) and a long interpulse interval (Table 1), so this bat is more likely to produce echoes that could be heard. Yet the low bandwidth of stutter trills (~10 kHz; Table 1) would produce low-information echoes. The repetitive nature of the trills by all 3 species (Fig. 1), and the cost to produce them, suggest that these bats may instead use trills for communication.

Given the phylogenetic grouping and ancestry of *Corynorhinus*, *Idionycteris*, and *Euderma* (Bogdanowicz et al. 1998), it is possible that trilling behavior is a basal trait for the 3 lineages. Social vocalizations may be more conserved among closely related species, and less influenced by external factors, than echolocation calls, because the characteristics of vocalizations are more aligned with evolutionary relationships (Russo et al. 2025). Trills, also termed “warbles”, “vocal oscillations”, and “sinFM” calls, have been described for other species, often in the context of aggressive behaviors, such as chasing, aerial collisions, or physical contact (Fernandez et al. 2014, Gadziola et al. 2012, Knörnschild et al. 2010). However, these sounds are often shorter duration than the trills we describe, have greater bandwidth, are lower in frequency than their associated echolocation calls, and are emitted as part of a multisyllabic phrase. Corcoran and Conner (2014) describe sinFM calls used by *Tadarida brasiliensis* (I. Geoffroy) (Brazilian Free-tailed Bat) during the feeding buzz of conspecifics to jam their sonar and disrupt foraging. Leonard and Fenton (1984), Obrist (1995), and Storz (1995) all describe unique agonistic vocalizations by *Euderma* during close-range encounters while foraging. A *Euderma* would chase a conspecific when it came within 50 m and utter calls at an increased repetition rate (Storz 1995) or circle within 1–2

Table 2. Sampling effort during coustic monitoring surveys that detected trills by *Corynorhinus rafinesquii* (Georgia), *Idionycteris phyllotis* (Utah), and *Euderma maculatum* (Utah and Colorado).

State	Location	Year	Nights	Detector-nights
Georgia	Altama Plantation Wildlife Management Area	2019	9–10 Oct	2
Georgia	Altama Plantation Wildlife Management Area	2020	15 Mar	1
Georgia	Altama Plantation Wildlife Management Area	2020	18–19 Oct	2
Georgia	Altama Plantation Wildlife Management Area	2020	21–25 Dec	5
Georgia	Altama Plantation Wildlife Management Area	2020	21–24 Dec	4
Georgia	Altama Plantation Wildlife Management Area	2021	31 Aug–1 Sept	2
Utah	Manti-La Sal National Forest (Big Flat)	2019	15–18 July	4
Utah	Manti-La Sal National Forest (Big Flat)	2020	20–25 July	5
Utah	Manti-La Sal National Forest (Gooseberry)	2020	20–25 July	5
Utah	Manti-La Sal National Forest (Redd Pasture)	2020	20–25 July	5
Utah	Manti-La Sal National Forest (Polar Mine)	2020	13 May–2 June	21
Utah	Manti-La Sal National Forest (Valley View Mine HO)	2020	27 July–11 Sept	47
Utah	Manti-La Sal National Forest (Valley View Mine VO)	2020	27 July–8 Sept	44
Colorado	Bureau of Land Management Tres Rios District	2022	11–14 Aug	4
Colorado	Bureau of Land Management Uncompahgre District	2023	5–11 July	6

m of a speaker playing conspecific calls and emit an "interaction buzz" (Leonard and Fenton, 1984). These observations may be examples of our *Euderma* stutter trill, but the earlier authors do not provide spectrograms for comparison. Only 2 of the files we examined in Table 1 included echolocation calls of other individuals, and none included feeding buzzes, which suggests the use of trills by these 3 species are unlikely to be agonistic or involved in foraging behavior.

Smotherman et al. (2016:538) define bat songs as, "longer, more complex stereotyped call sequences [than echolocation] that are repeated frequently . . . over extended periods of time". This definition seems to best describe the trills we observed for *Corynorhinus*, *Idionycteris*, and *Euderma*. Male *Saccopteryx bilineata* (Temmink) (Greater White-lined Bat) include a high proportion of long-duration (~150 msec) trills during sedentary courtship songs (Behr and von Helversen 2004). Male *Rhinolophus ferrumequinum* (Schreber) (Greater Horseshoe Bat) produce long duration (150–300 msec) oscillating trills in autumn that are thought to be advertisement vocalizations (Middleton et al. 2022). The repetitive bouts of songflight by male *Pipistrellus nathusii* (Keyserling and Blasius) (Nathusius's Pipistrelle) and *Vespertilio murinus* Linneaues (Particolored Bat) (Middleton et al. 2022) and of in-flight songs by *Lasionycteris noctivagans* (Le Conte) (Silver-haired Bat) (Lausen et al. 2023) and *T. brasiliensis* (Bohn et al. 2016) are evocative of the repeated trills reported here (Fig. 1). Repeated bouts of song may increase the likelihood of detection (Morton 1986) and can balance the energetic costs of signaling with the potential benefits of attracting a mate or defending a mating territory. If trills are used for mating by *Corynorhinus*, *Idionycteris*, and *Euderma*, we predict that they will be recorded most frequently during the fall mating period. Most of our sampling occurred outside the fall mating period, so we were unable to test this prediction. Yet, other bats that sing to attract mates in the fall sing at other times of year, and the songs may perform other functions, such as defense of feeding territories (Bohn and Gillam 2018, Corcoran and Conner 2014).

Songs and social vocalizations have been documented for few bats, though this is likely due to sampling bias and the technical constraints of recording ultrasound (Smotherman et al. 2016, Springall et al. 2019). Advances in technology now provide opportunities for naturalists to view spectrograms of free-flying bats in real time, using affordable devices that transform smartphones or electronic tablets into ultrasonic, active bat detectors (e.g., Echo Meter Touch 2, Wildlife Acoustics; Metcalfe et al. 2025). Trills produced by *Corynorhinus*, *Idionycteris*, and *Euderma* are diagnostic for these species when recorded during passive acoustic monitoring. The functions of these trills remain elusive, but direct observations of bats by active bat detectors, possibly coupled with thermal videography (e.g., Corcoran 2022), could help shed light on the behavioral context of trills and other ultrasonic sounds, unlocking new discoveries in the young field of bat acoustics.

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