

Substrate-borne vibration in Pacific field cricket courtship displays

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Abstract

While thought to be widely used for animal communication, substrate-borne vibration is relatively unexplored compared to other modes of communication. Substrate-borne vibrations are important for mating decisions in many orthopteran species, yet substrate-borne vibration has not been documented in the Pacific field cricket *Teleogryllus oceanicus*. Male *T. oceanicus* use wing stridulation to produce airborne calling songs to attract females and courtship songs to entice females to mate. A new male morph has been discovered, purring crickets, which produce much quieter airborne calling and courtship songs than typical males. Purring males are largely protected from a deadly acoustically orienting parasitoid fly, and they are still able to attract female crickets for mating though typical calling song is more effective for attracting mates. Here, we document the first record of substrate-borne vibration in both typical and purring male morphs of *T. oceanicus*. We used a paired microphone and accelerometer to simultaneously record airborne and substrate-borne sounds produced during one-on-one courtship trials in the field. Both typical and purring males produced substrate-borne vibrations during courtship that temporally matched the airborne acoustic signal, suggesting that the same mechanism (wing movement) produces both sounds. As previously established, in the airborne channel, purring males produce lower amplitude but higher peak frequency songs than typical males. In the vibrational channel, purring crickets produce songs that are higher in peak frequency than typical males, but there is no difference in amplitude between morphs. Because louder songs (airborne) are preferred by females in this species, the lack of difference in amplitude between morphs in the substrate-borne channel could have implications for mating decisions. This work lays the groundwork for investigating variation in substrate-borne vibrations in *T. oceanicus*, intended and unintended receiver responses to these vibrations, and the evolution of substrate-borne vibrations over time in conjunction with rapid evolutionary shifts in the airborne acoustic signal.

Keywords

communication, purring crickets, *Teleogryllus oceanicus*

Introduction

Natural and sexual selection have created complex and beautiful signals through which organisms communicate. These signals

are presented in a broad spectrum of sensory modalities, ranging from visual, such as the colorful dances of male jumping spiders, to chemical, like the sweet scent flowers produce to attract pollinators. One of the oldest, yet least understood, modes of communication is substrate-borne vibration, in which vibrations are sent and carried through a substrate (e.g., the stem of a leaf or dirt) to a receiver (Hill 2009, Cocroft et al. 2014). The ubiquitous presence of vibrosensory systems, including campaniform sensilla, hair sensilla, and chordotonal organs, in nearly all insects supports the ancient origin of mechanosensory communication (Hoy and Robert 1996, Lakes-Harlan and Strouß 2014). Vibrational communication is part of the auditory mode of communication, but it is a discrete channel because of the difference in media through which, and types of waves by which, vibrations are propagated. Auditory signals are primarily sent through a fluid medium like air as longitudinal pressure waves and typically travel long distances, while vibrational signals are primarily sent through a solid medium, are often characterized by low-frequencies, and generally travel relatively short distances as boundary waves, specifically Rayleigh waves through the ground or boundary waves through plants (Čokl and Virant-Doberlet 2003, Caldwell 2014, Hill et al. 2019). Unlike sounds that travel through air, body size does not constrain pitch for vibrational signals (except for those produced via tremulation), meaning that a small animal can potentially produce a very lowfrequency substrate-borne vibration (Cocroft and Rodríguez 2005, Caldwell 2014).

Due to the human perceptual bias for airborne sound and technological limitations, we learned of the ubiquity of substrate-borne vibrations in animal communication relatively recently (Virant-Doberlet et al. 2019). It is estimated that upwards of 200,000 species of insects use substrate-borne vibrations in both inter- and intra-specific communication (Cocroft and Rodríguez 2005, Hill et al. 2019). Mechanisms by which such communicative vibrations are produced are diverse and include, but are not limited to, percussion, stridulation, and tremulation (Čokl and Virant-Doberlet 2003, Hill 2009). For example, tremulation—moving the whole body without touching the substrate—is common in orthopterans (e.g., in the bush cricket *Onomarchus uninotatus* (Serville, 1838),

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Rajaraman et al. 2015, 2018, and in katyids, Morris et al. 1994; reviewed in Stritih and Čokl 2014) and can be important for mate choice (e.g., in groundhopper *Tetix ceperoi* (Bolívar, 1887), Kočárek 2010; in katydid *Conocephalus nigropleurum* (Bruner, 1891), de Luca and Morris 1998). Adding further complexity, while many insect species rely exclusively on substrate-borne vibrations for communication, many others employ a combination of both substrate-borne vibrations and other signaling modalities, either with each individual component presenting unique information or with both components providing information relative to the other (Hebets and Papaj 2005, Higham and Hebets 2013, Caldwell 2014). Airborne sound is a likely modality to be paired with substrate-borne vibrations, as the production of airborne sound unavoidably excites energy in the substrate-borne vibrational channel, whether via direct coupling of the signaler's body to the substrate or induction of airborne waves to the substrate (e.g., Stölting et al. 2002, Caldwell 2014).

Stridulation, in which two body parts are rubbed together to produce sound, is the primary mechanism of both vibratory and airborne signal production in numerous insect and arachnid species and often functions in intersexual (e.g., Elias et al. 2010), intrasexual (e.g., Hill and Shadley 1997), and interspecific communication such as aposematic warnings (e.g., Masters 1979). Among orthopteran species, stridulation is typically associated with the production of an acoustic signal; however, in several species, stridulation has also been shown to simultaneously produce substrate-borne vibrations that function in signaler localization (in the field cricket *Gryllus bimaculatus* De Geer, 1773, Weidemann and Keuper 1987 and the bush cricket *Tettigonia cantans* (Fuessly, 1775), Latimer and Schatral 1983) and territory establishment among males (in bush crickets *Tettigonia viridissima* (Linnaeus, 1758), Schatral et al. 1985 and *T. cantans*, Keuper and Kühne 1983). Despite the increasing effort to document substrate-borne vibration in Orthoptera, we have just begun, and most species remain unexplored (Cocroft and Rodríguez 2005, Benediktov 2009).

Pacific field crickets, *Teleogryllus oceanicus* (Le Guillou, 1841), signal in multiple modalities, including using stridulation to produce an airborne signal, but substrate-borne vibration has not been documented. Male *T. oceanicus* use an airborne acoustic calling song to attract females from a distance and then produce a different airborne acoustic courtship song in close one-on-one encounters with females. Females use these courtship songs and chemical signals from cuticular hydrocarbons to make mate choice decisions (Balakrishnan and Pollack 1997, Pascoal et al. 2017). In the Hawaiian Islands, the typical airborne acoustic calling song also attracts an acoustically orienting predator, the parasitoid fly *Ormia ochracea* (Bigot, 1889). *O. ochracea* facilitated the evolution of an obligately silent male morph of *T. oceanicus* (Zuk and Kolluru 1998, Zuk et al. 2006) and is likely playing a role in the evolution of a newly discovered male morph, purring crickets (Tinghitella et al. 2018, Tinghitella et al. 2021). Purring crickets are a new acoustic morph in Hawaii in which males use wing stridulation to produce airborne acoustic signals that are lower in amplitude and more broadband than typical male songs. The mean peak frequency is higher for purring males than typical males, and there is more variation in peak frequency among purring males compared to typical males (Tinghitella et al. 2018). Phonotaxis experiments have revealed that female crickets use the purring song to locate mates, and the role of the purr in courtship is still uncertain (Tinghitella et al. 2018). Some female *O. ochracea* can also locate hosts using the purr,

but they overwhelmingly prefer typical males in field choice tests (Tinghitella et al. 2021).

The first objective of this study was to investigate the presence of substrate-borne vibrations in purring and typical *T. oceanicus* courtship songs. We hypothesized that *T. oceanicus* males generate substrate-borne vibrations during courtship as a result of the energy generated via stridulation propagating through both the air and substrate. Caldwell (2014) stated that any acoustic signaler that is in contact with a substrate will also produce a substrate-borne signal as a byproduct of the airborne signal. Since purring crickets were just discovered, this investigation is timely because shifts to substrate-borne communication channels have been previously associated with a reduction in airborne signals. In a famous example, it was hypothesized that Panamanian katyids evolved an attenuated song in response to acoustically orienting predators, and that this change in song was coupled with an increase in vibrational signals (Belwood and Morris 1987, Morris et al. 1994). There are also examples of animals shifting signals into vibrational channels in response to abiotic factors like darkness (Partan 2017). In our study system, the purring morph has reduced amplitude in the airborne channel (Tinghitella et al. 2018), likely due, in part, to selective pressure from an acoustically orienting parasitoid (Zuk and Kolluru 1998).

Our second objective was to compare the amplitude and peak frequency of substrate-borne vibrations between purring and typical males. Because airborne acoustic signals (both calling song and courtship song) differ in peak frequency and amplitude between typical and purring male morphs (Tinghitella et al. 2018), we hypothesized that substrate-borne vibrations produced via stridulation would also differ in frequency and amplitude between male morphs. Specifically, typical courtship song has a lower peak frequency (median = 5.0 kHz) than purring courtship song (median = 7.6 kHz) in the airborne channel (Tinghitella et al. 2018). Finally, we hypothesized that the mechanism of substrate-borne sound production was through wing movement during stridulation, as seen in other orthopterans (Keuper and Kühne 1983, Weidemann and Keuper 1987). If substrate-borne vibrations and airborne sounds are produced through the same mechanism (wing movement during stridulation), then the two sounds should have matching temporal patterns.

Material and methods

We traveled to Hawaii to record substrate-borne vibration produced by wild-caught male *Teleogryllus oceanicus* during courtship. After discovering purring crickets on Moloka'i in 2016 and noting the presence of substrate-borne vibration at that time, we began measuring vibrations in the field in 2017. We refined our methods and began recording both vibrational and airborne acoustic songs simultaneously during field seasons in June 2018, December 2018, and June 2019. We conducted this study alongside a larger survey of courtship behavior across four islands (Hawaii, O'ahu, Moloka'i, and Kauai) that included many populations of both typical and purring male morphs (unpublished). For a subset of these courtship trials, we used a simultaneous recording technique to record both air-borne and substrate-borne songs from 13 typical males and 14 purring males.

The collection of animals and courtship trials were conducted identically on all islands and on all occasions. We collected adult males and females from grassy disturbed areas (lawns) and housed them, separated by sex, in 27 × 39 × 17 cm plastic containers. We provided rabbit food, egg cartons for shelter, and moist cotton for water. After at least 48 hours of isolation from the opposite sex, we randomly selected one male and one female for each courtship

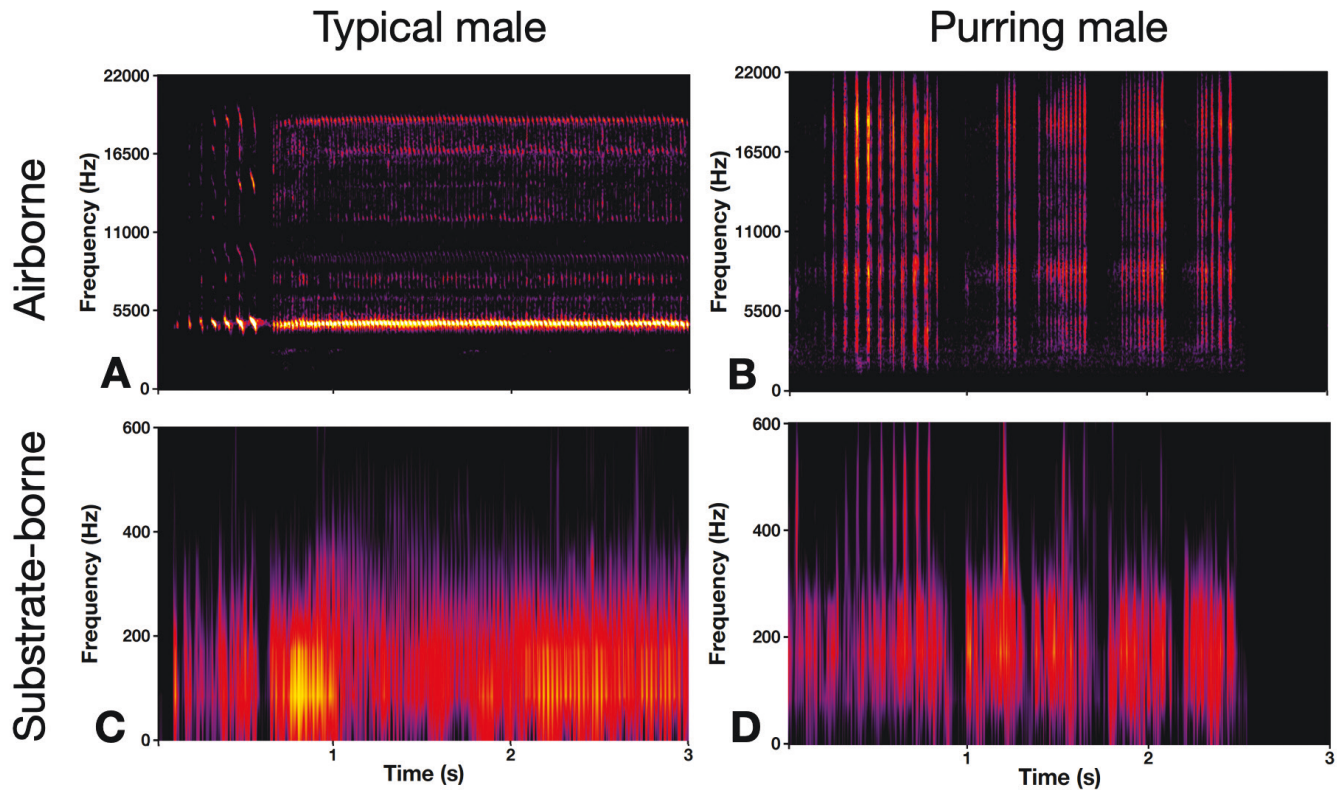


Fig. 1. Representative spectrograms showing the same song in an airborne channel (A and B) and a substrate-borne vibrational channel (C and D) for a typical male (A and C) and a purring male (B and D). Time is shown on the x-axis (seconds), and the colors (purple < orange < yellow) represent the power present at the various frequencies shown on the y-axis.

trial. The male and female paired in each courtship trial were always from the same population and were assayed on the island from which they were collected. We measured the width of the pronotum of each individual using digital calipers, and then placed both animals in a 1.5-L deli cup equipped with recording gear. Since some purring males produce very low-amplitude songs (Tinghitella et al. 2018), we began recording at the first visual observation of stridulation. The wing posture and motor behavior during stridulation is the same in the derived silent morph as it is in ancestral-typical males (Schneider et al. 2018) as well as in the purring morph (unpublished). Recordings lasted 10 minutes after the male began stridulating. If mounting occurred, we disrupted the copulation and returned animals to group housing separated by sex so as not to influence mating in the wild population. Females and males were never used more than once in courtship trials. After completing all trials, we released animals back into their natal grassy fields.

In order to record the substrate-borne vibrational and airborne components of the courtship song, we designed a courtship experimental container (deli cup) that used an accelerometer and a microphone to record both components simultaneously as separate audio tracks. This allowed us to determine whether the auditory signal and vibrational component were coupled and produced through the same mechanism of wing movement. Because these recordings took place in the field across islands, an accelerometer was the most portable and effective option for recording substrate-borne vibrations. To record vibrations, we attached an accelerometer (Knowles Acoustics, BU series 1771-000) to a piece of circular filter paper that fit perfectly in the bottom of the round 1.5-L deli cup (following Dierkes and Barth 1995). The cord from the accelerometer fit through

a small hole in the wall of the cup and traveled through a custom converter before entering a dual-input Roland Rubix 22 audio interface. The Roland Rubix audio interface box allows two inputs (in this case, the substrate-borne input and a simultaneously recorded audio track) and was attached to a laptop computer. For the airborne signal, we used a Rode NTG2 Multi-Powered Condenser Shotgun Microphone mounted 10 cm above the filter paper. The gain was set to 80% for both the microphone and accelerometer inputs. We recorded both tracks simultaneously. For a subset of observations, we also video-recorded trials to verify that the visual stridulation matched the audio and vibrational tracks we recorded. Because all trials took place with only red light in a dark room, we used a low-light action video camera (SiOnyx Aurora IR night vision camera).

After collecting recordings in the field, we uploaded WAV files into Audacity for analysis (version 2.3.0, <https://www.audacityteam.org>). To capture variation within each male's courtship song, we located and analyzed three songs within each male's recording: the first and second complete songs within the first continuous bout of calling and the last complete song within the final continuous bout of calling. For all song analyses, we used the same three songs from each male.

In order to test our hypothesis that males produce substrate-borne vibrations using the same mechanism—wing movement—that they use to produce airborne acoustic signals, we first measured the temporal components of both tracks. In Audacity, we visually identified the chirp and trill portions of the song; these two distinct sections of courtship song were visible in both the acoustic track and the vibrational track in both male typical and purring morphs (Fig. 1). Following Simmons et al. (2010), we

measured several features of each song in milliseconds: the total chirp length, the interval of silence between the chirp and the trill, the total trill length, and the trill/chirp interval. We also noted the start time within the recording for each song (three per male) for both the microphone track and the accelerometer track to verify that they matched.

We used Audacity to measure the peak frequency and amplitude of both the purring and typical songs. We analyzed the microphone tracks separately from the accelerometer tracks. One challenge in our data set was the fact that both males and females move nearly continuously for the duration of courtship interactions, producing broadband noise that overlapped the low-end frequencies visible in the accelerometer track. To ensure we did not disrupt normal male and female courtship behavior, we chose not to tether animals or have males court dead females; instead, we removed sections of the audio recordings that contained noise associated with locomotion after confirming that we could unambiguously identify these parts of the recordings using the video-recorded courtship trials. For audio tracks, we analyzed the entire trill portion of the three songs for each male after removing broadband noise associated with locomotion and applying a high-pass filter that removed all frequencies below 1500 Hz. For the accelerometer track, we used the same three songs for each male and selected the longest section of the trill portion of each song that was not interrupted by locomotor noise. For the accelerometer track, we applied a low-pass filter that removed all frequencies above 1000 Hz. We then used the plot spectrum function (settings: Hanning window, size = 2,048, log frequency axis) to extract peak frequency and the contrast function to extract the amplitude (values acquired as root mean squared (RMS) in dB) of each song relative to ambient noise. We used separately recorded background noise

in each recording space as a baseline of 0 dB. Decibels run on a logarithmic scale, so we converted dB to a linear scale (amplitude ratio) to accurately compare amplitude among songs. This amplitude measure is called linear amplitude, and it does not have a unit of measure (hereafter referred to as amplitude).

To analyze these data, we modeled the channels (airborne microphone track and substrate-borne accelerometer track) separately with morph (purring or typical) as the main effect in each model. Because we analyzed three songs per male, we included individual ID as a random effect nested within morph (typical or purring) in each two-way ANOVA. We ran repeated measures two-way ANOVAs for the four dependent variables: airborne peak frequency, airborne amplitude, substrate-borne peak frequency, and substrate-borne amplitude. We used the mean and standard deviation of the airborne and substrate-borne frequency and amplitude data sets to calculate effect sizes using Cohen's D (Cohen 1977). Next, to compare temporal patterns between channels (airborne and substrate-borne), we compared the two channels for a given male and a given song using paired t-tests for the three temporal measures: trill length, chirp length, and the interval between the chirp and trill. All analyses were conducted in JMP (JMP Version 14).

Results

As hypothesized, we detected substrate-borne vibrations in the courtship songs of male *T. oceanicus* (Fig. 1). We recorded substrate-borne vibrations in every male that we measured, including both typically singing males and purring males.

When comparing purring and typical males, the airborne acoustic signals differed in the ways previously demonstrated. As

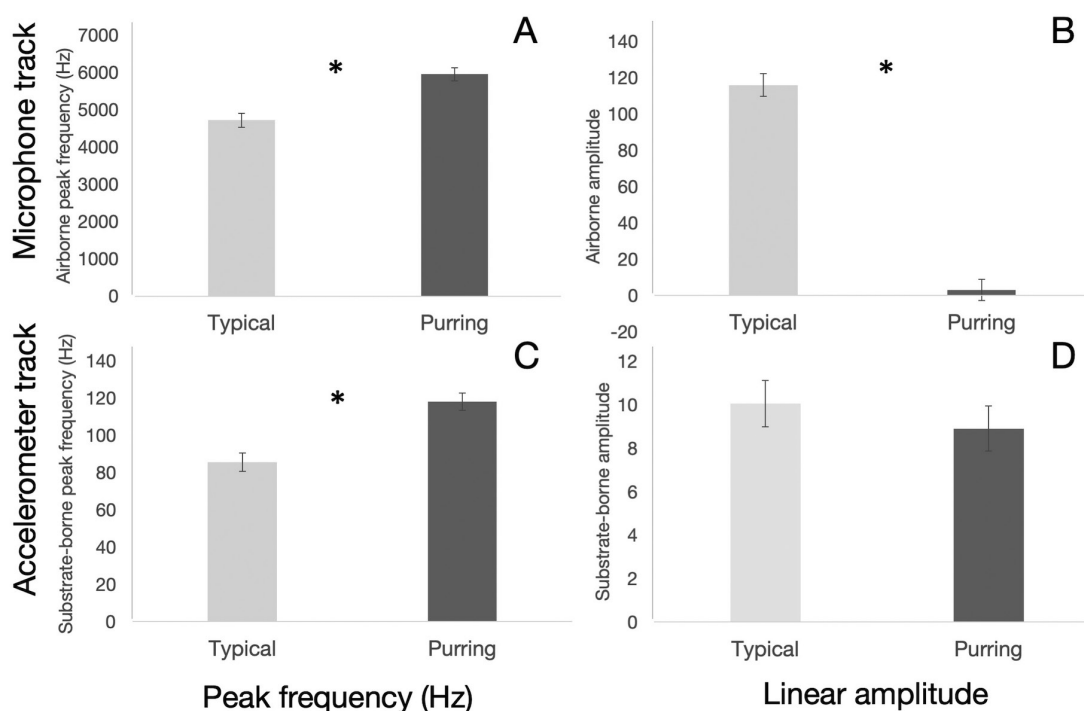


Fig. 2. Bar graphs showing the mean (equal to least squares means) and standard error (error bars) for different measures of song in typical (light gray) and purring (dark gray) male *T. oceanicus*. A. Peak frequency of airborne acoustic signals recorded with a microphone; B. Linear amplitude of airborne acoustic signals recorded with a microphone; C. Peak frequency of substrate-borne vibrations recorded with an accelerometer; D. Linear amplitude of substrate-borne vibrations recorded with an accelerometer. The asterisk indicates $p < 0.001$. Effect sizes (Cohen's D) are as follows: A. 1.83, B. 4.46, C. 1.05, and D. 0.27.

in Tinghitella et al. (2018), the average frequency was higher for purring males (mean \pm SE: 5955.8 ± 178.7 Hz) than typical males (4723.3 ± 185.4 Hz, $F_{25} = 22.9$, $p < 0.0001$; Fig. 2A), and the average amplitude was lower for purring males (3.1 ± 6.0) than typical males (115.9 ± 6.2 , $F_{25} = 172.32$, $p < 0.0001$; Fig. 2B). When we compared substrate-borne vibrations, we found a similar pattern for frequency, but not for amplitude. Substrate-borne vibrations in purring males were higher in peak frequency (118.0 ± 4.8 Hz) than typical males (85.5 ± 5.0 Hz, $F_{25} = 22.40$, $p < 0.0001$; Fig. 2C). There was no difference in amplitude between morphs in the substrate-borne channel (purring = 8.9 ± 1.0 , typical = 10.1 ± 1.1 ; $F_{25} = 0.601$, $p = 0.45$; Fig. 2D). The size of the effects between purring and typical males were as follows: airborne peak frequency = 1.83, airborne amplitude = 4.46, substrate-borne peak frequency = 1.05, and substrate-borne amplitude = 0.27.

Finally, we predicted that wing movement produced both the airborne signals and substrate-borne vibrations. For all songs analyzed, the start time in milliseconds was a perfect match for the microphone and accelerometer recordings. The temporal pattern also matched when we compared simultaneously recorded airborne signals and substrate-borne vibrations (for example, see Fig. 1). Of the 81 songs analyzed, only two individuals were not an exact match for chirp length (0.001 and 0.002 milliseconds off). Similarly, only six individuals were not an exact match when we compared trill length and seven when we compared the interval between the trill and the chirp. In each case, the difference was less than 0.002 milliseconds. In paired t-tests, there was no difference between the airborne and substrate-borne vibrations in chirp length ($t_{79} = 0.44$, $p = 0.66$), trill length ($t_{79} = -0.80$, $p = 0.42$), and the interval between the trill and the chirp ($t_{79} = 0.76$, $p = 0.45$).

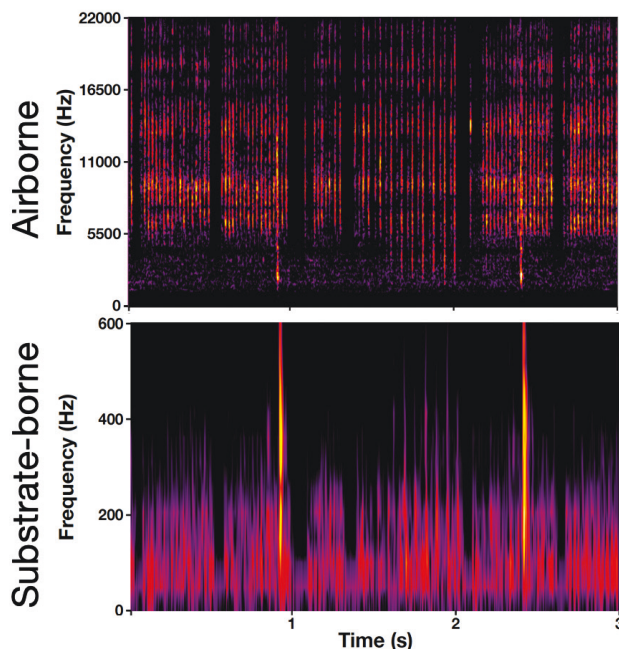


Fig. 3. Representative spectrograms from a microphone recording (airborne: top) and an accelerometer recording (substrate-borne: bottom) for a purring male that illustrates the broadband percussive sound present in many of our recordings. Percussive strikes (presumably with forelegs) appear as white vertical bars just before 1 second and at 2.5 seconds. The time is shown on the x-axis (seconds), and the colors (purple < red < orange < yellow < white) represent the power present at the various frequencies shown on the y-axis.

We also detected vibrations that were not associated with stridulation and were not associated with locomotion. These high-power broadband vibrations were present in 19 of the 27 field-recorded individuals (Fig. 3) and appear percussive. Video footage suggested that the percussive bursts were produced through foreleg drumming: males could be seen striking the substrate with either the right or left foreleg repeatedly, and all males used both legs (Suppl. material 1: video). For example, the male in the Suppl. material 1: video makes several drums with his left leg, followed by one drum with his right leg and then a pause. For the 19 males that exhibited drumming, we randomly selected one drum from the first song that contained drumming, one drum from the second song that contained drumming, and one drum from the last song that contained drumming. Following the methods described above to extract data from the accelerometer track (substrate), we analyzed the peak frequency and amplitude of the three drums per male. We also counted the number of drums during each of the three songs. The drumming sounds had an average peak frequency of 105 ± 19.5 kHz (mean \pm standard deviation) and an amplitude of 49 ± 54 (Fig. 3). There was an average of 5.6 ± 2.9 drums per song.

Discussion

This is the first documentation of substrate-borne vibration in *T. oceanicus*. We recorded vibrations in two different male morphs of *T. oceanicus* (typical and purring) that appear to be generated through the movement of the wings, as the pattern in the vibrational channel perfectly matches the airborne signal. When we compared typical and purring males, we found that typical males produced lower peak frequency sounds in both the airborne (Fig. 2a) and the vibrational channel (Fig. 2c). For amplitude, typical males produced sounds that were many times louder than purring males in the airborne channel (Fig. 2b), but there was no difference between morphs in amplitude in the vibrational channel (Fig. 2d).

As expected, purring males differed from typical males in the airborne channel, with a mean peak frequency of 4.7 kHz for typical males and 6.0 kHz for purring males. These values are similar to those of Tinghitella et al. (2018), who reported a median peak frequency of 5.0 kHz for typical males and 7.6 kHz for purring males. Amplitude also matched previous results, with typical males producing significantly louder songs than purring males in the airborne channel. Because we used linear amplitude instead of decibels, which are on a logarithmic scale, we can linearly compare values of amplitude across male morphs. Thus, in the airborne channel, the amplitude of the typical song was 38 times greater than that of the purring song (115 divided by 3).

In the substrate-borne channel, purring males produced vibrations that were higher in frequency than typical males, but the difference was not as dramatic as in the airborne channel; the effect size was 1.05 for substrate-borne compared to 1.83 in the airborne channel. As expected, the peak frequencies were much lower in the substrate-borne channel, ranging from 32 to 176 Hz. Because higher frequencies attenuate more quickly in soil, we would expect substrate-borne vibrations to be lower in frequency (Čokl and Virant-Doberlet 2003, Caldwell 2014), and small-bodied species can produce low-frequency vibrations through stridulation (Cocroft and Rodríguez 2005). The frequency range measured for *T. oceanicus* matches that of other known species of Orthoptera that send airborne and substrate-borne vibrations through wing stridulation: *G. bimaculatus* at 30–500 Hz (Weidemann and Keuper 1987) and *T. cantans* at 0–800 Hz (Keuper and Kühne 1983). We did not

detect a difference in amplitude between morphs in the substrate-borne channel. This suggests that the differences in wing morphology between morphs only affect amplitude in the airborne channel and not the substrate-borne channel. Purring males have a reduction in the size of the harp and mirror (resonating structures) compared to typical males (Tinghitella et al. 2018 and unpublished). Thus, resonating structures on the wings (harp and mirror) play a key role in amplifying sound in the airborne channel but do not seem to affect the transfer of the vibration to the substrate.

We found support for our hypothesis that wing movement produces both airborne signals and substrate-borne vibrations. Temporal components of song matched when we compared the microphone track to the accelerometer track, and these included start time, chirp length, trill length, and the interval between the chirp and the trill. These values were almost a perfect match in every category except for a few that differed by 0.001 milliseconds, which can be attributed to human and equipment error. We were unable to distinguish between substrate-borne vibrations produced via coupling of the male to the substrate (through the legs or abdomen) or induction of airborne waves to the substrate. Future work could make this distinction by not allowing the stridulating male to come in contact with the substrate or by adapting methods from Keuper and Kühne (1983) where different substrates were tested. Regardless of the mechanism (direct coupling or induction of waves to the substrate), our results support the claim that the production of an acoustic signal unavoidably excites vibrations in the substrate on which a signaler is resting (Caldwell 2014), and our work adds to the growing literature documenting coupled airborne and substrate-borne sound produced by stridulation in Orthopterans (e.g., *T. cantans*, Latimer and Schatral 1983; *T. viridissima*, Schatral et al. 1985; *G. bimaculatus*, Weidemann and Keuper 1987).

The big question remaining is whether female *T. oceanicus* can sense the substrate-borne vibrations and whether they affect mate choice. First, the ability to detect, receive, and translate vibrations is ancient and ubiquitous, found throughout vertebrates and arthropods (Hoy and Robert 1996, Cocroft and Rodríguez 2005, Hill 2009, Lakes-Harlan and Straub 2014). In *T. oceanicus*, males and females use cerci to detect sounds between 0 and 1000 Hz (Hoy et al. 1982, Pollack et al. 1998). Air flow and air currents produced by wing movements rather than stridulation can produce low-frequency (<70 Hz) air vibrations that are detectable through cerci up to a few centimeters away in *Gryllus bimaculatus* (Kämpfer and Dambach 1985). Similarly, it has been suggested that air currents produced by stridulating *T. oceanicus* males can be perceived by females, but substrate-borne vibration was not measured in that study (Pollack et al. 1998). The subgenual organ in the tibia is also a likely candidate for the detection of low-frequency vibrations in *T. oceanicus* (Lakes-Harlan and Strauß 2014), as it is used to detect substrate-borne vibrations as low as 50 Hz in related species (e.g., *Gryllus bimaculatus* and *Gryllus campestris*; Dambach 1989), and the substrate-borne vibrations we measured are above that 50 Hz threshold (85.5 Hz for typical and 118.0 Hz for purring).

When discussing the detectability of these substrate-borne vibrations for *T. oceanicus*, we should consider amplitude and the average distance that vibrations travel through soil. While we did not measure female response to substrate-borne vibration in this study, Pollack et al. (1998) used electrodes inserted into abdominal interneurons from the cerci to show that female *T. oceanicus* can “hear” low-frequency sounds produced by male wing movement from 2 cm away. We measured vibrations in a courtship context where females are a few centimeters from a signaling male,

well within the range of perception for *T. oceanicus*, and our amplitude measurements were adjusted for background noise (e.g., 9.5 represents a signal that exceeded background noise, 0). In other Orthopterans that produce both airborne and substrate-borne vibrations via stridulation, *G. major* vibrations travel up to a meter through the soil from a signalling male’s burrow (Hill and Shadley 1997), *T. cantans* vibrations travel about a meter through plant stems (Keuper and Kühne 1983), and *G. bimaculatus* vibrations are detectable 20 cm away in dry soil (Weidemann and Keuper 1987). Additionally, while the amplitudes we measured (purring = 8.9 ± 1.0 , typical = 10.1 ± 1.1) should be detectable over the short distances associated with courtship (1–2 cm), it is possible that the percussive sounds we detected may travel further since the amplitude was much greater (49 ± 54). Following methods described by Hill and Shadley (2001), we plan to measure the distance over which substrate-borne vibrations are detectable in *T. oceanicus* in a future study.

While the first step is to explore the ability of *T. oceanicus* to detect the vibrations that courting males are producing, the next step is to assess the use of vibrations in mate choice. This could be explored using playback experiments with an electrodynamic shaker played alone or in combination with an airborne signal (Cocroft and Rodríguez 2005). There are numerous examples of substrate-borne vibrational signals playing a key role in mate choice in Orthoptera (e.g., de Luca and Morris 1998, Cocroft and Rodríguez 2005, Kočárek et al. 2010). In *T. oceanicus*, it has been suggested that the cerci detection system evolved to detect terrestrial predators like frogs (Hoy et al. 1982). It is possible that this predator detection system has been co-opted for use in mate choice. Other studies have used phylogenetic approaches to demonstrate that vibrational communication evolved from existing responses like locomotion (Scott et al. 2010) and a startle response (ter Hofstede et al. 2015). We might expect the rapid evolution of acoustic song (silent morph, Zuk et al. 2006; purring morph, Tinghitella et al. 2018) and the evolution of relaxed female preferences (Tinghitella and Zuk 2009) in *T. oceanicus* to shape both the substrate-borne vibrations and the sensory capabilities of and preference for those vibrations. Additionally, selection may differ between the airborne and substrate-borne channels; louder airborne songs are preferred by *T. oceanicus* females, but there is no difference in amplitude between morphs in the substrate-borne channel. Thus, investigations of whether substrate-borne vibrations play a role in *T. oceanicus* courtship should compare populations with different morphs, simultaneously measure airborne song, and monitor both detection and preference over time in this rapidly evolving system.

While valuable, this work has limitations. First, we used filter paper as our substrate, which was appropriate for our question since we compared morphs measured on an identical substrate. However, because the composition of any substrate imposes frequency filters on substrate-borne vibrations, we expect the spectral characteristics found in this study to differ from those recorded on natural substrates. Future works should measure and characterize these substrate-borne vibrations on natural and variable substrates (e.g., following Hill 2001). Second, while our interindividual variation was low, suggesting that our sample size adequately captured the patterns between morphs, a larger sample across more populations would give a more holistic view of substrate-born vibration in Hawaiian *T. oceanicus*. More-advanced equipment, such as a high-speed video camera and a laser vibrometer, would also allow us to tease apart the way in which wing movement translates to substrate-borne vibrations (air movement or contact between file and scraper traveling through the legs).

As with most discoveries, this work lays the groundwork for future questions. In addition to exploring how *T. oceanicus* females detect and use substrate-borne vibrations, we must also recognize that communication happens in a network (Virant-Doberlet et al. 2014, 2019). Our network has multiple senders (signaling males), intended receivers (female crickets), and unintended receivers that are conspecifics (satellite males) and heterospecifics (parasitoid flies). The eavesdropping predators, *O. ochracea*, are an important driver of the rapid evolution of airborne signals in *T. oceanicus*, and because they are airborne aerial predators, vibration may be hidden from this natural selection. However, vibrations are likely susceptible to a different set of unintended predatory receivers, such as spiders (Virant-Doberlet et al. 2019). Eavesdropping male crickets may also be able to use vibration to locate singing males for satellite behavior. Finally, future work should also explore other parts of substrate-borne vibrations, such as the broadband percussive taps produced by the forelegs. RMT has conducted courtship trials in the field for the past 15 years and did not observe this behavior until 2017. To date, no literature has been published documenting this behavior in *T. oceanicus*, but drumming (percussive) behavior is a commonly utilized mechanism of vibrational signal production among diverse arthropods (e.g., fiddler crabs, Aicher and Tautz 1990; termites, Röhrig et al. 1999; wetas, Gwynne 2004; mole crickets, Hayashi et al. 2018; reviewed in Hill 2012), and drumming may be important even when there are other mechanisms producing substrate-borne vibrations (in our case, wing stridulation), as seen in a stink bug that uses tremulation, buzzing, abdomen vibration, and drumming (Kavčič et al. 2013). Finally, drumming may function in both the substrate-borne and airborne channels (Hill 2012).

This work is a first look at substrate-borne vibration in *T. oceanicus* and answers calls by many to explore communication in the vibrational channel (e.g., Hill 2001, Cocroft and Rodríguez 2005). This work lays the foundation for future research on variation in substrate-borne vibration in *T. oceanicus*, intended and unintended receiver responses to these vibrations, and the coevolution of substrate-borne vibrations with other courtship signals, such as airborne and chemical signals.

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Supplementary material 1

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Data type: multimedia

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