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Exploring efficiency landscapes in the acoustic-morphospace of crickets reveals two alternative calling strategies

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Abstract

Male crickets attract females by rubbing forewings together to produce calls. Louder calls are more effective, as they travel further, and attract more mates. However, crickets are small and produce calls inefficiently. Tree crickets make baffles, which reduce acoustic short-circuiting and increase efficiency. Previous work showed that tree cricket baffles function optimally (Mhatre et al., 2017). Here, we ask why baffle use is uncommon in crickets despite its advantages. We hypothesize that baffling may be rare because it is advantageous only for certain species. To test this, we modelled the calling efficiencies of cricket wings within their acoustic-morphospace (ie: the complete space of natural wing sizes and call frequency range). Using finite and boundary element analysis we calculated cricket acoustic efficiency in multiple of acoustic environments, incorporating both reflective and scattering surfaces like the ground and vegetation into our analyses. Within the efficiency landscapes generated from these data, we plotted the positions of 111 species across 7 phylogenetic clades. Using landscape and clade level analyses, we found that calling from the ground and using a baffle represent effective alternate strategies that both maximize calling efficiency.

Keywords: insect sound production | crickets | tool use | finite element modeling | boundary element modeling | sound propagation | acoustic efficiency

Introduction

Male crickets make loud advertisement calls to attract females who use these calls to locate mates (Regen, 1913). Louder calls travel further, cover more area, and attract more females (Deb et al., 2020; Farris et al., 1997; Römer et al., 1993). When faced with a choice, females prefer louder calls (Deb et al., 2020; Forrest, 1991). Being louder therefore has implications for mating success and evolutionary fitness in these singing insects. However, despite the apparent loudness of a nighttime chorus, cricket calls are acoustically constrained by a phenomenon known as ‘acoustic short-circuiting’ (Forrest, 1982; Mhatre et al., 2017). The smaller the wings of a cricket with respect to the wavelength of the sound it makes, the

higher the short-circuiting and associated loss of efficiency. Indeed, the few crickets that have been studied are small and experience significant short-circuiting (Bennet-Clark, 1998).

Baffle use is an effective – but rare – means to overcome short-circuiting

To reduce the efficiency lost to acoustic short-circuiting, a few tree cricket species build and use baffles (Forrest, 1991, 1982; Mhatre et al., 2017; Prozesky-Schulze et al., 1975). A baffle consists of a leaf with a hole chewed by the cricket near the middle of the leaf. When the size of the leaf and hole are optimal, such structures reduce acoustic short-circuiting and increase efficiency by as much as 10 dB compared to unbaffled calling, reflecting a tripling of sound pressure levels (Mhatre et al., 2017). However, despite their obvious benefits, only a handful of species among thousands make baffles, all within the sub-family Oecanthinae (Collins, 2012; Forrest, 1991; Mhatre et al., 2017; Prozesky-Schulze et al., 1975).

Baffle use in crickets may be rare due to a "lack of utility"

Given the obvious benefits, why is acoustic baffle use rare in crickets? Some researchers believe that tree cricket baffles fit the criteria for manufactured tools (Mhatre, 2018; Pierce, 1986) and, two hypotheses from the tool use literature, the "cognitive capacity" and the "lack of utility" hypotheses offer two different reasons. The "cognitive capacity" hypothesis suggests that complex tool use behaviors are less likely to evolve in animals with smaller brains and lower cognitive capacity. This is an unlikely explanation since many animals with relatively low cognitive capacities do use, and even make, tools which themselves are not necessarily complex objects. A competing hypothesis is the "lack of utility" hypothesis. This posits that tool and building behavior generally can evolve regardless of cognitive capacity, but that its evolution requires an ecological context in which it confers sufficient selective advantage (Hansell and Ruxton, 2008). Stated another way, only species that can achieve higher gains from tool use than from other strategies (e.g., morphological features, site selection) are likely to evolve tool using behavior. Indeed, few species use tools, whether crickets, other invertebrates or even vertebrates (Hunt et al., 2013), but invertebrate tool use seems especially rare. For example, 56 independent occurrences of subsistence-related tool use were found in mammals, whereas only 13 occurrences were found in the significantly more speciose insects.

However, to truly test the lack of utility hypothesis, we must quantify tool utility and use of the tool must have implications for evolutionary fitness. It is often difficult to meet these two conditions. Work in chimpanzees has directly quantified tool utility by evaluating how much caloric value can be gained by using a tool to exploit an otherwise unexploitable resource (Boesch and Boesch, 1983). Other studies have made more indirect arguments about the utility of tools. Work in sea otters has shown that tools are employed more frequently in populations in which tough prey require tools to access them (Fujii et al., 2015). In capuchin monkeys, larger individuals who can more effectively use tools to crack nuts are more likely to use tools (Spagnoletti et al., 2011). However, few studies directly assess the lack of utility hypothesis, particularly outside the context of food.

Baffle use in crickets is an ideal system in which to test the lack of utility hypothesis. First, baffle use is rare and second, we can directly measure its acoustic utility in terms of increase in calling efficiency (ref Mhatre et al 2018). Finally, baffle use has been shown to have real fitness implications, by increasing the number of mates attracted to a given male, and also by increase mating duration, both processes likely to increase reproductive success (Deb et al., 2020).

Therefore, in this study, we tested the lack of utility hypothesis across this large group of singing insects, the true crickets or Grylloidea. We used mathematical models to quantify baffle utility in two ways. First, we ascertained the sizes of call radiator (cricket wings) and frequency ranges of the songs used by a large number of crickets, spread over the cricket phylogeny. Then we quantified sound radiation efficiency (SRE), with and without "perfect" baffles, for this complete parameter space which we call the acoustic-morphospace. SRE captured the efficiency of the singer, by calculating local losses due to acoustic short circuiting, similar to the previous study on tree cricket baffle efficiency (Mhatre et al., 2017). By plotting SRE over the acoustic-morphospace, we were able to generate efficiency landscapes to fully investigate the calling efficiency of crickets with and without baffles.

Finite element methods are known to be accurate at predicting sound levels and fields in acoustics modeling, and have been used previously to model sound fields in crickets (Garud et al., 2017; Godthi et al., 2022; Mhatre et al., 2017; Seybert et al., 1994). However, so far models have only considered very idealized physical conditions. However, crickets live in real environments populated by objects such as the ground and vegetation, which interact with sound and its radiator across spatial scales, which may form the basis of an alternative strategy (Erregger and Schmidt, 2018; Muñoz and Halfwerk, 2022). Therefore, we generated a second more ecological metric of utility, which we have called sound propagation efficiency (SPE). By using the boundary element method, we quantified the effect of such interacting acoustic surfaces and their effect on acoustic efficiency as sound propagates away from the singer, under a range of environmental conditions. Since we considered calling from the ground, this raised the issue of directionality. The spatial gradient of the sound field is also crucial to its utility, and may be degraded preventing mate finding when animals call from near the ground (Embleton, 1996; Kostarakos and Römer, 2010). Therefore, using the same models, we also quantified directionality to test how efficiency might trade off with this biologically crucial feature.

Using these data, we asked whether the rarity of baffle use in crickets is explained by the lack of utility hypothesis. We examined the differences between baffled and unbaffled calling in different realistic scenarios. If the lack of utility hypothesis is supported, we predict that there would be at least two alternative strategies to maximize calling efficiency. Known baffle-users will be animals who benefit more from baffle use than non baffle-users who might instead use a morphological or environmental means to maximize efficiency.

Results and Discussion

All crickets would benefit from baffle use in idealized conditions

To capture the natural range of wing sizes and calling frequencies among true crickets, we collected wing surface area and call frequency data for 111 cricket species from a large range of sources (Figure 1, Tables 1, 2, Supplement to Figure 1). Species were distributed across 7 clades as described by the most recent phylogeny of the Grylloidae or "true cricket" super family (Chintauan-Marquier et al., 2016) (Figure 1).

We then constructed finite element models which predicted the sound fields produced by wings of different sizes at different call frequencies for 1086 different combinations which encompassed all the observed frequencies and wing sizes , i.e. the full acoustic-morphospace (Figure 2). In all conditions, wings were modelled as suspended in free space, vibrating with a uniform velocity perpendicular to the

wing plane (Figure Supplement 2-1, 2-3). The model then predicts the resulting sound field (see methods for details). We then calculate sound radiation efficiency (SRE (Pa/m/s)), by taking a volumetric average of the sound pressure level generated (Pa), over a sphere of radius 20 cm around the wing, divided by the time-space average of the wing vibration velocity (m/s). Since we do not have data on wing vibration velocities for most cricket species, this normalized measure of efficiency enabled comparison between species. This method of applying a velocity across the entire wing and the resulting normalized metric has also been used previously for tree crickets (Mhatre et al., 2017), and does not generate substantially different prediction from only vibrating part of the wing (Supplement to figure 2-4).

Next we plotted an SRE landscape (Figure 2) for the full acoustic-morphospace. On this landscape, we plotted the locations of the 111 species of crickets with known wing size and frequency allowing us to infer their SRE (Figure 2). These data indicate how efficient each wing should be at radiating sound, reflecting the match between radiator size and the wavelength of the radiated sound frequency. These data therefore demonstrate precisely how suboptimal crickets are in terms of their efficiency (Figure 2D), and how much they could gain through use of an optimal baffle (Figure 2E).

Previous work examining four species of crickets and a small number of other insects determined that they each perform less efficiently than the theoretical optimal level for dipole sound sources (Bennet-Clark, 1998). However, our finite element methods model more realistic geometries than these previous methods, which were restricted to analytically tractable shapes like circular pistons. In our dataset, there is a clear ridge of high efficiency running through the SRE landscape (red line in figure 2A, hereafter referred to as “optimal efficiency ridge”), which shows the optimal radiator size for every frequency. Despite sampling a wide range of wing areas (0.4 – 258 mm^2) and call frequencies (1.6 – 27.9 kHz), all species in our dataset occupy a region of the SRE landscape below this optimal efficiency ridge. The efficiency distribution among crickets is somewhat bimodal. The nine species with an SRE above 1 Pa/m/s all had calling frequencies above 14 kHz and belonged to the paraphyletic subfamily Eneopterinae, in clades F or G. Given the difference in their song radiation mechanics (Robillard et al., 2007) we excluded these individuals from subsequent analyses (see methods). After excluding these high frequency callers, we found that SRE ranges from 0.02 to 0.67 Pa/m/s, mean: 0.18 ± 0.01 SE, n = 101.

With baseline efficiencies measured above, we next calculated how much each species could gain by using a baffle, while singing at the same frequency. To do this, we used the optimal efficiency ridge, since optimal radiator efficiency is the same as optimal baffled efficiency (Hambric and Fahnline, 2007). If animals were to continue using the same call frequency, but used an ideal baffle, each species stood to gain between 1.7 – 35 times (5 – 30 dB) above their baseline SRE (mean: 7.6 ± 0.41 times, 16 ± 0.37 dB, n = 99). Among those who stood to gain the most included animals in clade B, specifically in the subfamily Mogoplistinae (scaly crickets). These animals have very small wings (mostly under 5 mm^2), suggesting a poor match between radiator and wing size. On the other hand, the animal closest to the optimal efficiency ridge, was *Madasumma affinis*, belonging to the subfamily Podoscirtinae in clade F. This animal has the largest wing at 258 mm^2, however, even this animal stood to gain 0.5 Pa/m/s (5 dB or 1.6x increase) with the use of an ideal baffle. Taken together, these data suggest that all crickets could increase SRE, and therefore, stand to benefit from use of a baffle.

Grounded calling emerges as an alternative strategy to baffle use in complex environments

While analysis of SRE suggests that all crickets should use baffles, this prediction is based on sound fields travelling in free space and over short distances. It is possible that efficiency advantages from baffle use become negligible as sounds interact with objects in the cricket's local environment (such as the ground), or as the call propagates through space. Either of these scenarios would lend support to the lack of utility hypothesis.

To address whether and how the efficiency landscape is changed by realistic calling conditions, we used boundary element modeling. Specifically, we use this model to add a "ground" component to our existing models, where the ground could have different characteristics including vegetation cover. In these models, sound can be reflected and dissipated by the ground. We model the effect of the vegetation by an excess attenuation term (see methods). We used empirical measurements of different types of ground so although our modeled ground is flat and smooth, these measures take realistic ground variability into account. We also varied the height of the caller above the ground (grounded calling: 0 m, elevated calling: 1 m). We measured efficiency again by normalizing sound levels against radiator vibration levels (see methods). Sound levels were measured at two distances from the caller: near (averaged from 0.05 – 0.2 m away), and far (averaged from 0.8 – 0.9 m away). To simplify analysis, we always measured efficiency at the same height as the caller. To differentiate this measure of efficiency from SRE, we called it sound propagation efficiency or SPE (Pa/m/s).

The most striking result was that calling from the ground (Figure 3C, D) yielded much higher SPEs than calling from above it (Figure 3A, B). This is reflected in the efficiency landscapes by a general increase in efficiency values near the ground across the ranges of frequency and wing area that we measured (see scale bars). This is likely due to the ground effect, in which much of the sound energy that would propagate below the radiators is instead reflected upward from the ground, and significant constructive interference is responsible for increased SPE (Rossing, 2014). Indeed, the highest SPE observed with a grounded caller was 4 Pa/m/s (Figure 3C), two orders of magnitude higher than peak SPE with an elevated caller (0.06 Pa/m/s, Figure 3A). On the other hand, calling from far above the ground yields SPE values that are similar in level to SRE values calculated in the ideal free-field scenario modeled previously. At farther distances, the values decrease, as would be predicted by spreading in open air.

The SRE landscape for grounded calling was not smooth and became increasingly rougher as the distance from the caller increased. Whereas elevated calling yields landscapes with broad, smooth peaks and valleys, the landscapes of callers near the ground show high levels of variation in efficiency across small changes in frequency and radiator size. In fact, the irregularity of the landscapes for grounded calling did not allow us to calculate clean optimal efficiency ridges. However, given that grounded calling is generally much higher efficiency than elevated calling, grounded callers may not need to use a baffle in the first place. Taken together, our models incorporating the ground posit that grounded calling and elevated baffled calling are two potential alternative strategies to maximize efficiency.

Alternative strategies persist when ground properties and vegetation are varied

All grounds are not equivalent. For instance, soft grounds or those covered with vegetation would be much more dissipative and may eliminate the advantage accrued from ground calling. To test this possibility, we investigated whether this alternative strategy framework holds up when these properties of the environment are varied. We found few differences in SPE with different types of grounds.

(Supplement to figure 3-2). SPE tends to be slightly higher with a “soft” ground, which is better at dissipating sound, similar to a freshly tilled agricultural field (see methods) and this effect is magnified further away from the caller. With a harder, more reflective ground, similar to a tightly packed forest floor, SPE is slightly lower. However, the differences between these two ground types occur at wing sizes well outside the natural range for crickets. At close distances, and particularly above the ground, the differences between ground types are very small. Therefore, all future analyses assume a “hard” ground.

Finally, we tested whether vegetation would reduce the predicted SPE landscapes for grounded calling. Vegetation does slightly decrease the magnitude of SPE overall. However, we found that excess attenuation due to vegetation does not significantly change the overall patterns of efficiency, by and large shifting the efficiency landscape to a lower point at most points within the parameter space (Supplement to figure 3-3 C, D) (Bashir et al., 2015). Therefore, it turns out baffled calling would be less efficient with vegetation than without. This shift in efficiency is also not perfectly equal at all frequencies, and SPE is lowered slightly more at high frequencies (Supplement to Figure 3-3). This suggests that high frequency callers may be at an increased disadvantage when calling in vegetation as suggested before (Romer and Lewald, 1992), and will also see diminishing returns when using a baffle. This effect is relatively small, however (< 6 dB). Additionally, the effects of vegetation on SPE are undoubtedly more complicated than an excess attenuation factor, so modeling plants explicitly, at a variety of shapes and sizes, would be a useful extension to this study. However, overall, we conclude that calling from the ground remains an effective alternative strategy, even if the ground is soft, or covered with some vegetation.

Alternative strategies are still viable when considering call directionality

So far, our analysis has used the loudness of calls to define efficiency. However, a call must be both loud and directional to be effective. That is, the call must present a spatial gradient that a potential mate can follow to the source. Previous data has suggested that such gradients are severely degraded in ground calling crickets (Kostarakos and Römer, 2010; Mhatre and Balakrishnan, 2006; Römer, 2015; Romer and Lewald, 1992), but not in elevated calling (Deb and Balakrishnan, 2014). This suggests that SPE gains from grounded calling may trade off against call directionality. Since our models generate spatially explicit predictions of sound fields, we can address this possibility. We analyzed call directionality by measuring how difficult it would be for a female cricket to follow an acoustic gradient back to the call’s source. A value of one indicates that the gradient along a chosen transect perpendicular to the wing planes is always in the “correct” direction, that is, sound pressure level increases as the female moves toward the call in steps of ~ 2 body lengths (2 cm). A lower value means that over some stretches over this transect, SPL increases and at other steps it decreases. A value of 0.5, for instance, means that the SPL decreases over 50% of the steps as the female moves closer (see methods).

Directionality varies with respect to frequency, radiator size, and height from ground (Supplement to Figure 3-4). Although grounded calling does experience a loss of directionality compared to elevated calling, these losses are mostly minimal. Near a grounded caller, there is a strong cutoff at about 5 kHz, below which all are strongly directional (> 0.9) except for very small wings. This cutoff decreases to about 3.5 kHz far from the caller. Therefore, high frequency callers would be most susceptible to the gradient effects. However, even below these cutoffs, directionality rarely drops below 0.5 in any condition, and grounded calling remains a viable alternative. It should be noted that other studies have found more substantial degradations in call directionality in sounds traveling along the ground, but over greater distances than our current models (Kostarakos and Römer, 2010). However, data for both field

crickets and tree crickets suggest that the SPL of typical cricket calls drop below threshold at about 1 m from the caller (Deb and Balakrishnan, 2014; Mhatre and Balakrishnan, 2006), and therefore we consider this a biologically relevant distance over which to measure directionality.

Alternative calling strategies are likely in use by some cricket species

Based on the overall propagation efficiency landscape, grounded calling and baffled calling are potential alternative strategies to maximize efficiency. However, these landscapes cover the full acoustic-morphospace, i.e. all possible combinations of radiator (wing) size and call frequency, but most of these combinations are not used by real crickets.

To shift our focus from the acoustics, and to make it more biologically relevant, we performed an analysis to determine whether alternate calling strategies are in use by actual crickets. We divided all sampled animals into their respective clades and calculated clade level SPE for each of three alternative strategies as measured far from the caller: calling from the open hard ground (grounded calling), from within vegetation 1 m off the ground with no baffle (unaided calling), and 1 m off the ground with a baffle (baffled calling). We compared both baffled calling and grounded calling to unaided calling as a baseline. It would then be ideal to determine whether the animals in fact use the strategy that we predict should maximize efficiency based on known calling preferences. Unfortunately, we do not have data on calling preferences of many sampled animals, however, some clade-level similarities have been observed in calling behaviors, and different clades show some clustering in the wing size-frequency space (figures 2 and 3). We give three examples below of clades with some known information about calling behavior.

We turn first to clade F, consisting primarily of the Oecanthines, or tree crickets. Members of this group stand to gain on average about 12 dB from grounded calling compared to unaided calling according to our data (figure 4). However, they could gain ~19 dB it they baffled. Indeed, Oecanthine natural history bears out our predictions; tree crickets are known to mostly call from vegetation, including vegetation that is suitable for baffle building and use (Deb and Balakrishnan, 2014; Forrest, 1982). In fact, all known cricket baffle users are in this clade, as predicted based on the lack of utility hypothesis. For clade G, on the other hand, consisting mostly of the Gryllinae, or field crickets, we predict the opposite. On average, grounded calling gives an advantage of 7x or 17 dB above unaided for species in this group, whereas baffling only gives an advantage of 10x or 20 dB above unaided. Again, behavioral data suggests that many field crickets indeed prefer to call from the open ground habitats that we predict would maximize their efficiency (Weissman and Gray, 2019).

Clade A, the Gryllotalpidae or the mole crickets, represents an interesting exception to this alterative strategy framework. This group stands to gain the most from baffled calling of all clades (13x, 22 dB) compared to grounded calling (2x, 6 dB). Yet, species in this group are all known to exclusively call from the ground and do not use baffles. However, they do use an acoustic aide. Mole crickets build and call from burrows which function as resonators and convert them into monopole sound sources, eliminating acoustic short-circuiting through a different mechanism than baffling (Bennet-Clark, 1987). Indeed, it is possible that other acoustic means of maximizing call efficiency exist and could in the future add further complexity to our hypotheses.

Finally, if an animal baffled, but its call propagated though vegetation compared with no vegetation, the gains would be relatively small in most cases (< 6 dB) (Supplement to figure 4-2), We also performed a similar analysis for call directionality (Figure 5). However, since directionality was quite high for all

calling conditions, we therefore suggest that directionality does not preclude one alternative strategy over another.

Ideas and Speculation – why would baffle use evolve in the first place?

From our data, exploiting the ground effect with grounded calling emerges as a viable alternative to baffle use. Grounded calling even exceeds the efficiency gains of baffled calling in some scenarios. Given that baffle creation and use requires a combination of site selection preferences, a specialized behavioral repertoire, and precise execution of these behaviors (Mhatre, 2018; Mhatre et al., 2017), the real question becomes why a species would ever use this strategy if a fairly simple site selection preference for the ground could give similar increases in efficiency.

Crickets have been calling for a long time. There is evidence that crickets with stridulatory mechanisms (and therefore the ability to produce sound) existed as early as the Cretaceous period (Senter, 2008). These early calling crickets were likely ground dwellers, with some species subsequently moving up into vegetation as the group diversified (Song et al., 2015). We therefore suggest that baffle-using crickets may have originally moved up into vegetation for non-acoustic reasons, whether it was to exploit additional food resources or avoid predators. Baffle use would have then evolved secondarily to recover some of the efficiency lost when abandoning grounded calling. Our biophysical modeling methods open the door to testing such a hypothesis about baffle use.

Additionally, there are almost certainly undescribed instances of baffle use in crickets, but identifying baffled calling involves careful observation of a species' calling behavior, followed by subsequent measurements to confirm that a structure indeed has acoustic properties consistent with a baffle. Using our biophysical models, we can help narrow the search for baffle-using crickets by identifying the clades which would stand to benefit the most in terms of calling efficiency given their call frequency and wing size. Boundary element models are particularly flexible in this regard, as their computational efficiency allows the construction of larger, more complex habitats that can test a wide range of variables within habitats. It is known, for example, that crickets use other acoustic aides to increase calling efficiency. Some crickets call from burrows or cracks in the ground, from tree trunks or the walls of caves or even use structures that have some baffling capability but do not function as fully optimal baffles (Weissman and Gray, 2019). We show here that biophysical models can both test and generate hypotheses about such rare behaviors in animals.

Another advantage of our modeling approach is that it does not require live, or even extant, animals. In principle, we could model the wings of extinct crickets, and estimate their calling frequency based on the stridulatory apparatus on the wing (Gu et al., 2012; Woodrow et al., 2022). By bringing extinct crickets "back to life" in this way we could ask questions about the evolution of acoustic aides more broadly. We suggest that biophysical modeling, grounded with data from real animals, can be a valuable tool for any biologist wishing to better characterize and understand the diversity of animal communication.

Materials and Methods

Specimen Data

We collected data on wing surface area and call frequency for each of 111 cricket species distributed across the 7 clades described by Chintauan-Marquier et al. (Chintauan-Marquier et al., 2016) (Figure 1).

We restrict our analysis to this group, since these species are known to raise their wings when singing (Desutter-Grandcolas, 2003). This behavior means that they are dipole sources of sound, and acutely affected by acoustic short-circuiting (Bennet-Clark, 1998; Forrest, 1991). Each species was assigned to a clade based on the following two criteria: (1) the species itself was included in the Chintauan-Marquier et al (2016) dataset or (2) the subfamily of the species was included in the dataset and it was found to be monophyletic within one of the seven Chintauan-Marquier clades. Data were obtained from a variety of databases including Orthoptera Species File (Cigliano, M. M. et al.), Crickets North of Mexico, and numerous publications (all references are available in tables 1-2). For a few species of Oecanthines, wings were provided by Nancy Collins and photographed in the lab under a dissecting microscope. All specimens measured were adult males, identified by wing morphology and lack of ovipositor. We measured surface area of the entire left forewing including the lateral field. Fitting an ellipse to the wing, we calculated aspect ratio (length of ellipse/width of ellipse). All image data were gathered using ImageJ version 1.53 (Schindelin et al., 2015). We next calculated the fundamental frequency of cricket advertisement calls using Raven Lite version 2.0 (Cornell Lab of Ornithology, 2020). When multiple specimens of a single species were analyzed, averages were used for wing size and call variables. To better represent the full range of wing size and call frequency in our dataset, we included some specimens in the histograms showing wing size and frequency (Figure 2) for which we had only one type of data. Twelve animals had only wing size, but not call data, and 57 animals had call, but not wing size data (see tables 1-2 for details).

Finite Element Models for Sound Radiation Efficiency

We first estimated the sound radiation efficiency of crickets calling in open air using finite element (FE) analysis (Supplement to Figure 2-2). We built this model and all subsequent models in COMSOL Multiphysics version 5.5. All models used the pressure acoustics module and were solved in the frequency domain assuming a steady state. The Helmholtz equation was the governing equation.

Model geometry, boundary conditions, symmetry, and vibration

Animals were represented by two ellipses which modelled the forewings sitting next to each other along the long axis, in the same plane (Supplement to Figure 2-2). These ellipses should accurately approximate total radiated sound power and the true shape of the sound field, and it is the size and shape of the radiator and frequency of the call that determines radiation efficiency, and not the radiator's material properties (Hambric and Fahnline, 2007). Surrounding the wings was a spherical acoustic domain consisting of air with a 20 cm radius. The acoustic domain was suspended inside a second spherical domain of 40 cm radius (Supplement to figure 2-2. A perfectly-matched layer (PML) was applied to the area between the acoustic domain and larger outer sphere. PMLs in finite element modelling are used to mimic an open and non-reflecting infinite acoustic domain, which absorbs all sound energy from the acoustic domain (Berenger, 1994). Thus PMLs mitigate modelling artefacts such as the effects of sound reflecting from the edges of the acoustic domain (Mhatre et al., 2017). To reduce computational time, our model was constructed using ¼ symmetry. That is, we modeled ½ of one wing and ¼ of the two spherical domains. We then mirrored this model twice, once about the short axis of the wing to create a whole wing and ½ of the spherical domains, and a second time about a line between and parallel to the long axis of the wings to create a second wing and the whole spherical domains. We applied a time- and space-averaged velocity normal to the entire surface of the wings at 0.13m/s. This was the value measured from the wings of singing *Oecanthus henryi* and is the only known estimate for crickets (Mhatre et al., 2017). However, given that we are calculating efficiency rather than reporting actual sound pressure levels, normalizing

using this known value allows comparison between species. We vibrated the wings at a frequency range of 0.5 - 32 kHz, in increments of 0.25 kHz. SRE was subsequently calculated from each of these model outputs as a volumetric average of the absolute pressure in the acoustic domain, divided by the time- and space-averaged velocity of 0.13 m/s, resulting in units of Pa/m/s.

Finite Elements

3D tetrahedral elements were used in both the acoustic domain and PML. After undertaking a mesh size sensitivity study (Supplement to figure 2-3), we chose the "extra fine" mesh setting in COMSOL, with about 60000 elements in the acoustic domain. This number did vary somewhat with wing size, as fewer elements are used with very small wings.

Model Parameters

We ran the finite element model at a range of wing surface areas from 0.4 – 4000 mm^2, scaled logarithmically by the equation 4×10^x, where x ranges from -1 to 3). We used an aspect ratio of 2 (wings are twice as long as they were wide). Our chosen aspect ratio of 2 was well within the range of most cricket species (median: 1.6, range: 0.7 - 3.7). Aspect ratio did not play a large role in sound production, except at aspect ratios > 5 (length of wing 5x the width), which were not observed in real wings (Supplement to Figure 2-4). For aspect ratios within the range of crickets, differences in SRE between aspect ratios at a given wing area and frequency never exceeded 3 dB.

Other Modeling Considerations

The cricket body was not included in our models as it was found to have negligible effects on SRE at all wing sizes and frequencies (mean difference: 0.05 ± 0.01 dB). We also evaluated whether applying vibration to only a part of the wing (a "harp") influenced sound production. Some cricket species (though not all) use this sound production method (Godthi et al., 2022). We found only minor increases in SRE between vibrating only a harp or vibrating the entire wing (mean: 4 ± 0.08 dB), except at wing sizes well outside the range of the real wings that we measured (Supplement to figure 2-4).

Boundary Element Models for sound propagation efficiency

To test hypotheses about how cricket calls interact with objects in the environment, we needed to include an additional domain in the model: a "ground" with realistic parameterized acoustic impedance. To make this model as realistic as possible and to minimize boundary effects, we needed to make the ground element as large as possible relative to the size of the wings. The combination of the large size of ground and the high sound frequencies of interest resulted in finite element models that were too computationally intensive to run. We therefore turned to boundary element (BE) modeling as an alternative means of assessing sound propagation efficiency.

Both acoustic boundary element models and finite element models are numerical methods for solving the Helmholtz equation to capture a developing sound field within a medium. However, they differ in how they discretize space within the model. Finite element models discretize volumes by partitioning into a 3-dimensional mesh of finite elements. This allows detailed descriptions of the medium in which the field develops. Boundary element models on the other hand reduce computational cost by discretizing only the boundaries of the acoustic domain and assume a linear homogenous medium in all other spaces. The boundary element formulation therefore trades off some specificity in exchange for computational efficiency, allowing us to make relatively large, more biologically relevant models to assess sound

propagation in a spatially explicit manner. We ran our boundary element models using the pressure acoustics, boundary elements module in COMSOL. All models were run in the frequency domain and assumed steady-state behavior. The Helmholtz equation does not take attenuation due to damping into account, which can become an issue at distances far from the source. However, at frequencies >500 Hz, attenuation due to damping is only about 2 dB per kilometer (Embleton, 1996), so we considered this effect to be negligible over the distances of interest for this study (0.2 – 1m).

Model geometry, forcing, and boundary conditions

Wings in the boundary element model were modeled the same way as in the finite element model (Supplement to Figure 3-1), with no material properties and one-way coupling between the wings and sound fields. Wings were positioned perpendicular to the top surface of the ground, with the flat surfaces of the wings aligned with the short axis of the ground. The wings were centered with respect to ground. The wings were placed above the ground at either 0 m, or 1 m. The same time- and space-averaged velocity was applied as above, and the same set of wing surface areas were used. The ground was modeled as a rectangular slab, 0.5 m wide, 2 m long, and 0.10 m thick. A sound-hard boundary was applied to the bottom surface of the ground slab. Because we were interested in spatially-explicit measures of efficiency as sound propagates across ground, we did not use symmetry conditions to create this model. However, because the sound fields should be symmetric on either side of the wings, we only measured the sound field on one side.

Model Parameters

We used a restricted frequency range for the boundary element models, ranging from of 0.5 – 10 kHz, in increments of 0.25 kHz. We chose 10 kHz as the cutoff because very few of our measured animals call above this frequency, and those that do were Eneopterine species who were likely using a vibrational mode inconsistent with the piston mode that we have implemented (Robillard et al., 2007). High frequency (> 10 kHz) callers were included in the finite element models to give a general sense of where they might fit in with the other animals, but in reality no animals occupy this space in the landscape and all analyses explicitly comparing species exclude them.

To model how a real ground interacts with sound, we applied an acoustic impedance to our modeled ground. Acoustic impedance quantitatively describes how much sound energy is dissipated by the ground, compared to the energy reflected. We used the Attenborough slit-pore model to implement ground impedance. This model uses three parameters to capture both dissipative and reflective properties: flow resistivity, pore density, and porous layer depth. We modeled two different types of ground, a “soft” ground (flow resistivity: 2000 kPa×s/m^2, porosity: 0.6) which is less reflective and a “hard” ground (flow resistivity: 9 kPa×s/m^2, porosity: 0.4), which is more dissipative. Porous layer depth was held constant for both treatments, at 0.04 m. Both ground parameters were taken from empirical measurements of a “soft” freshly-tilled field and a “hard” forest floor (Attenborough et al., 2011).

Sound propagation efficiency definition

In the finite element models, we calculated a volumetric average of absolute pressure within the acoustic domain. However, such a measure would not be appropriate to assess propagation efficiency, as the sound waves’ interactions with the ground would accumulate as distance from the source increases. Therefore, we calculated SPE in a spatially-explicit manner. We measured absolute pressure at 50 points along a 1m long line parallel to the long axis of the ground, at the same height as the wings. The line originated at the

centre between the two elliptical ‘wings’. We divided this line into “near” and “far” from the caller: near = 0.05 – 0.2 m from wings, far = 0.8 – 0.9 m from wings. Efficiency was calculated as before, by dividing sound pressure level (Pa) by 0.13 m/s, the space and time averaged velocity applied to the wings. We also created an additional boundary element model with no ground, to allow for direct comparisons between ground and no ground and to sanity check the boundary element method compared with the previous finite element models.

Finite Elements

Tetrahedral elements were used on the surface of the ground and 2D triangular elements on the wings. After performing a similar sensitivity study as with the finite element models, we decided on a maximum element size for the wing surfaces of 0.5 cm and 1 cm for the surface of the ground. Since the sound wave is not explicitly modelled, this element size is not related to sound frequency, and instead captures boundary conditions and hence can be larger than in the finite element models.

Excess attenuation due to vegetation

To calculate the effect of vegetation, we used existing models to calculate how standing vegetation is expected to impact call efficiency. We then subtracted this excess attenuation from the COMSOL result. We calculated excess attenuation using the following empirically derived equation from Bashir et al 2015:

$$\frac{EA(Pa)}{FL} = 3\left[1 - \exp\left(0.3 - 0.5(ka)\right)\right], ka > 0.6$$

Where EA(Pa) represents excess attenuation due to foliage, F = foliage area per unit volume, L = path length, k = wavenumber, and a = average leaf size. We used values empirically derived for dense foliage with relatively large leaves (Bashir et al., 2015), such as those used to construct baffles in known baffle-using species. To approximate the foliage area and leaf size that a typical baffle user would prefer, we used F = 6.3m^{-1} and a = 0.0784m in our measures of excess attenuation.

Efficiency of individual species and how much they gain with baffle

To test the lack of utility hypothesis, we used the output of our models to estimate the gains in efficiency that each species could attain if it used a baffle. We did this for both the idealized measure of efficiency (SRE) and the more realistic scenario involving a ground and vegetation (SPE). For each modeling scenario, we first estimated the efficiency of each cricket species in our dataset, given their wing area and call frequency. Next, we calculated the efficiency that each species would have if it used an ideal baffle. To do this, we first determined the size at which the wings and baffle working together as a single radiator would reach maximal efficiency. The optimal size is a function of the wavelength of that sound frequency in that medium. We calculated the quantity ka for each surface area-frequency combination in the model, where k is the wavenumber and a is the effective radius of the sound radiating plates (Hambric and Fahnline, 2007). ka is a dimensionless quantity often used in acoustics, as it helps define when a radiator of a particular size transitions from being inefficient sound radiator at low frequencies to an efficient high frequency radiator. For instance, an optimally sized circular piston has ka = 1 (Hambric and Fahnline, 2007).

However, the radiators being considered here are two aligned ellipses which not perfectly circular in shape. Hence the particular value of maximal efficiency ka will be different in this configuration. So, to estimate optimal ka for cricket wings, we plotted ka versus efficiency as measured from our models, with

a separate trace for each frequency (Supplement to Figure 4-1). We then identified the ka at which maximal efficiency was reached for all frequencies. This value represents the size at which highest attainable efficiency is reached, consistent with an optimally baffled condition (Hambric and Fahnline, 2007) (Supplement to Figure 4-1). In our finite element models, we found optimal ka to be about 1.3. For the boundary element models at the far distance, optimal ka was approximately 1.55 (Figure 4-1).

Next, we performed a simple linear regression between frequency and maximal efficiency at optimal ka, then calculated the slope and y-intercept of this regression (Supplement to Figure 4-1). We used this equation to calculate optimal baffled efficiency for each species. The relationship between frequency and efficiency differed depending on condition (open ground vs ground + vegetation) (Supplement to figure 4-1), so this regression was performed separately for each environmental condition when calculating optimal baffled efficiency for a given condition.

Directionality index

To address how difficult it would be for a female to localize a male call, we assessed the directionality of the call in each modeling scenario. In an open field with no ground, the sound level is expected to decrease smoothly following the inverse square law (Bradbury and Vehrencamp, 1998; Rossing, 2014). A cricket moving toward the source of a call should therefore always experience either an increase in loudness, or, if the increase is below the animal's difference threshold, no change in loudness. A cricket should always move in the direction of increasing SPL to locate the singing male and therefore a mating opportunity. However, in reality, sound fields become more complicated when they interact with the ground, resulting in a noisy relationship between SPL and distance (Römer, 2021). In such sound fields, female phonotaxis may fail as there is no clear acoustic gradient to follow to the source. To quantify this degree of potential "confusion", we calculated a directionality index for each modeling scenario. First, we calculated Δ SPL between each two adjacent points 2 cm apart (~ 2 body lengths for most animals in this analysis). Δ SPL was calculated starting at 1 m away and moving toward the source. Next, we classified each of these values as either consistent with expected change in SPL or inconsistent. Consistent values represented either an increase, no change, or a decrease smaller than Δ 3dB (a factor of about 1.4), which is thought to be close to the detectable threshold for crickets (Mhatre and Balakrishnan, 2007). See Römer, 2021 for a more complex treatment of such thresholds. For our purposes, inconsistent values represented a decrease in SPL greater than 3 dB. For each modeling scenario, we calculated the proportion of Δ SPLs classified as consistent. This resulting value we call "Directionality" ranging from 0 to 1 (Supplement to figure 3-4). We calculated directionality for two different distance treatments, "near" was calculated from 0.05 – 0.2 m from the wings, and "far" was calculated from 0.5 – 1m from the wings.

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Figures

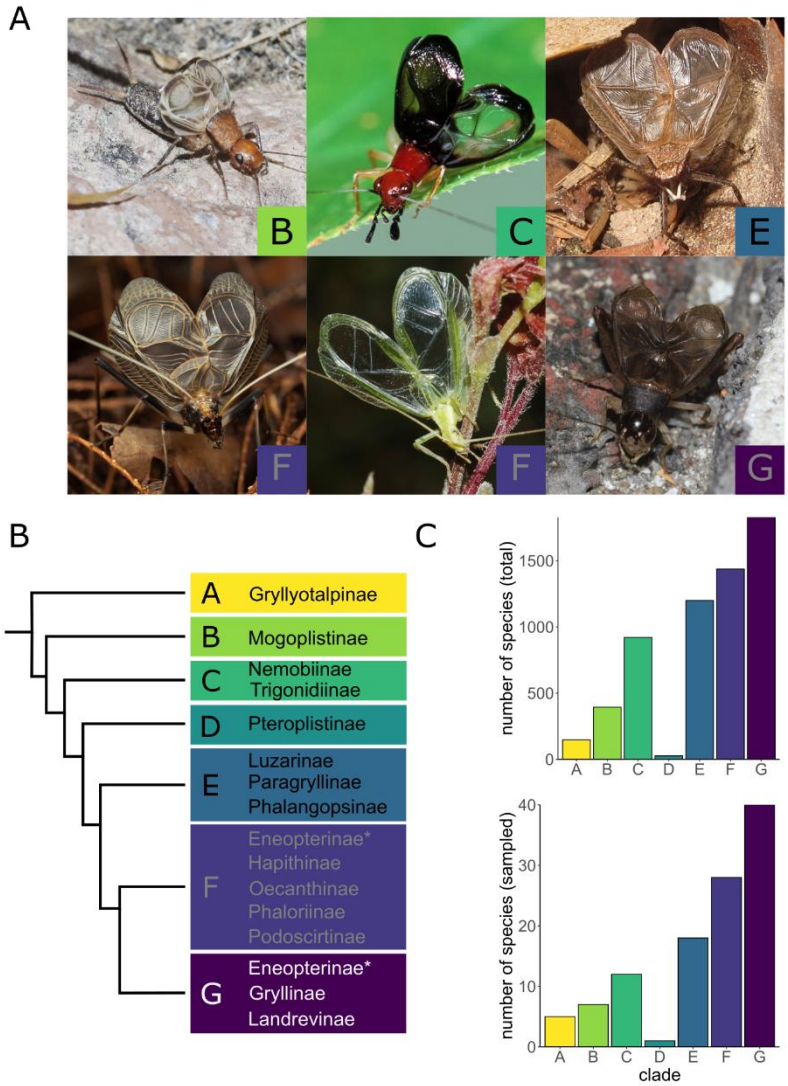


Figure 1. Crickets were sampled evenly across the cricket phylogeny covering most taxonomic groups known to produce calls. **A.** Representative images of cricket males with wings raised in calling posture. From upper left to lower right, species pictured are: *Hoplosphyrum boreale* (photo: James P. Bailey), *Phyllopalpus pulchellus* (photo: Wilbur Hershberger), *Lerneca inalata* (photo: Richard C. Hoyer), *Meloimorpha japonica* (photo: Ryosuke Kuwahara), *Oecanthus quadripunctatus* (photo: James P. Bailey), and *Turanogryllus eous* (photo: Taewoo Kim). Boxes with letter indicate the clade to which each species belongs. **B.** Phylogeny illustrating the seven clades defined by Chintauan-Marquier et al (2016) along with subfamilies within each clade (branch lengths not to scale). Only subfamilies from which we sampled for this study are included. Subfamilies with asterisks are polyphyletic between multiple clades. **C.** Specimen sampling scheme. Top panel shows the distribution of all species described across each of the seven clades in Grylloidea (according to Orthoptera Species File, as of February 16, 2022). Bottom panel shows distribution of species that were sampled for this study.

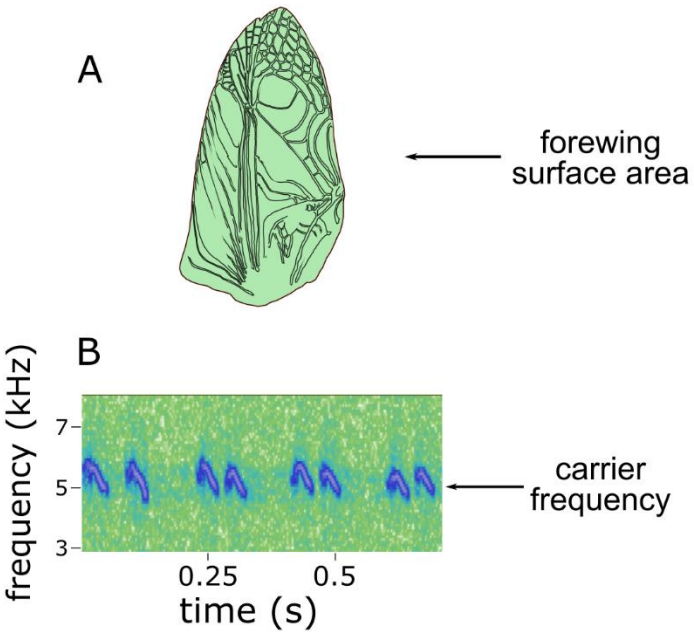


Figure Supplement 1-1. Measuring acoustic-morphospace of crickets. Wing area and call frequency were quantified. **A.** Wing surface area was calculated as the area of the entire forewing. **B.** The carrier frequency (sometimes called fundamental frequency) of the call was identified from spectrograms and recorded. If the fundamental frequency occupied a sweep over a range of frequencies (as shown), an average was taken.

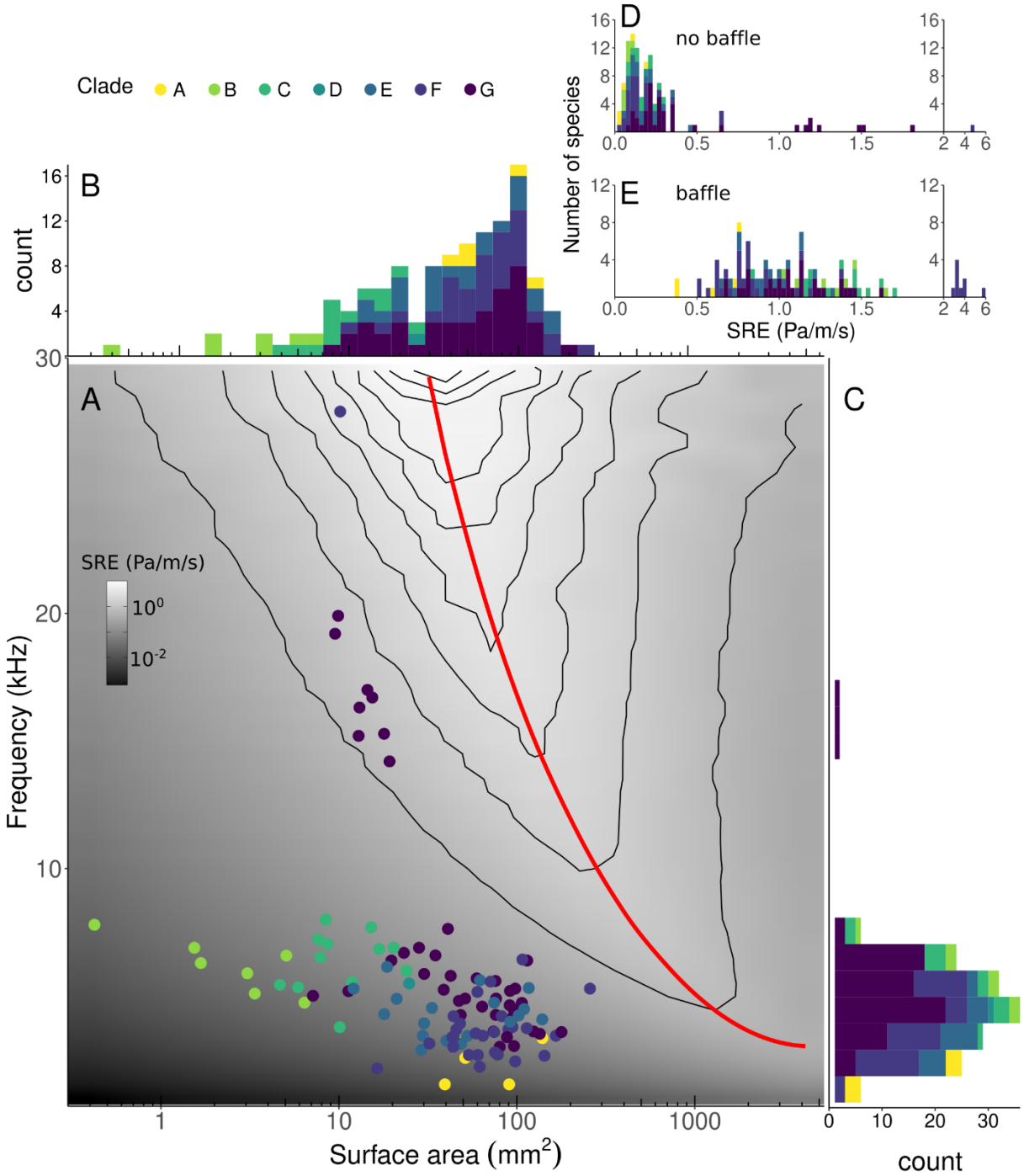


Figure 2. All crickets could increase efficiency by baffled calling. Sound radiation efficiency (SRE) landscape across the acoustic-morphospace of crickets. **A.** SRE achieved by different combinations of wings sizes vibrating at different frequencies. Within this space of possibilities the wing areas and call frequencies of all sampled animals are shown overlaid as points on the SRE landscape. This SRE is calculated from finite element models. Red line indicates optimal efficiency ridge, or the size at each frequency that would produce an ideally baffled calling scenario. **B, C.** Distributions of the calling song frequency and wing size of different animals, respectively. Histograms include additional species for which only wing or call measurements were available. **D.** SRE of each species without use of a baffle. **E.** SRE of each species with use of an ideal baffle.

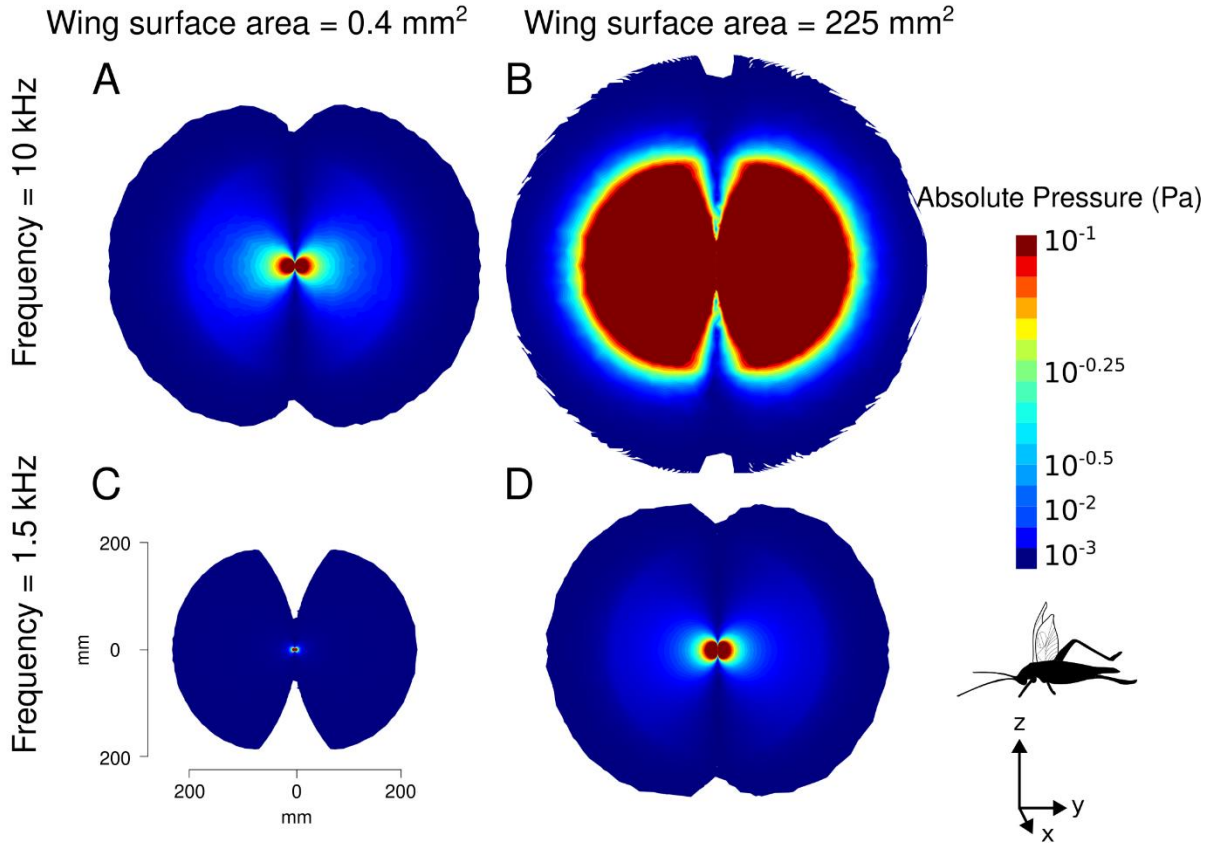


Figure Supplement 2-1. Sound fields produced by modeled wings vary with respect to call frequency and wing size. Fields are oriented such that wings are perpendicular to page and vibrate left to right, as indicated by the silhouette cricket. Sound fields are given for the following combinations of wing size and frequency: **A.** wing size = 0.04 mm^2, frequency = 10 kHz; **B.** wing size = 225 mm^2, frequency = 10 kHz; **C.** wing size = 0.4 mm^2, frequency = 1.5 kHz; **D.** wing size = 225 mm^2, frequency = 1.5 kHz. Spatial scale given in C applies to all sound fields. Efficiency (here, size and color of sound field) increases with improved match between wavelength of sound and size of radiator (wing). Cricket wings in general are small so this match is poor except at the extreme high end of radiator size and call frequency (B).

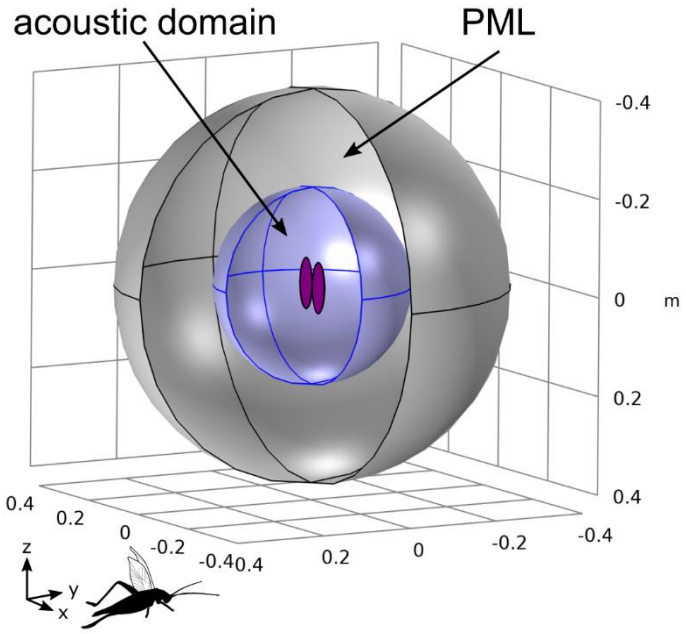


Figure Supplement 2-2. Geometry of finite element model. Inner blue sphere is the acoustic domain. The wings are represented by purple ellipses in the center. Outer sphere is a perfectly-matched layer, to mitigate boundary effects caused by the finite acoustic domain. SPL is averaged over the inner sphere for the calculation of SRE. Wings vibrate along the y axis, as indicated by the cricket silhouette.

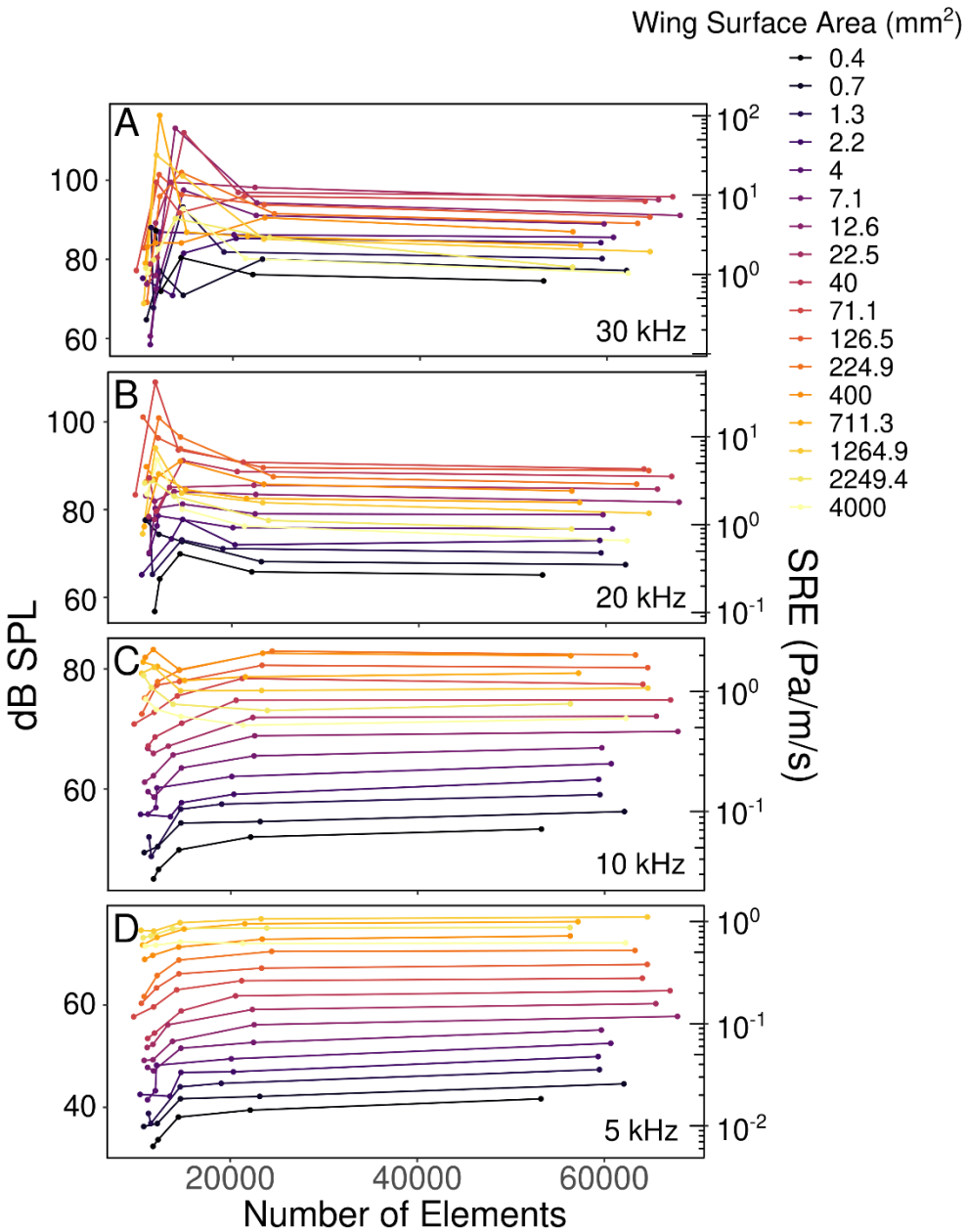
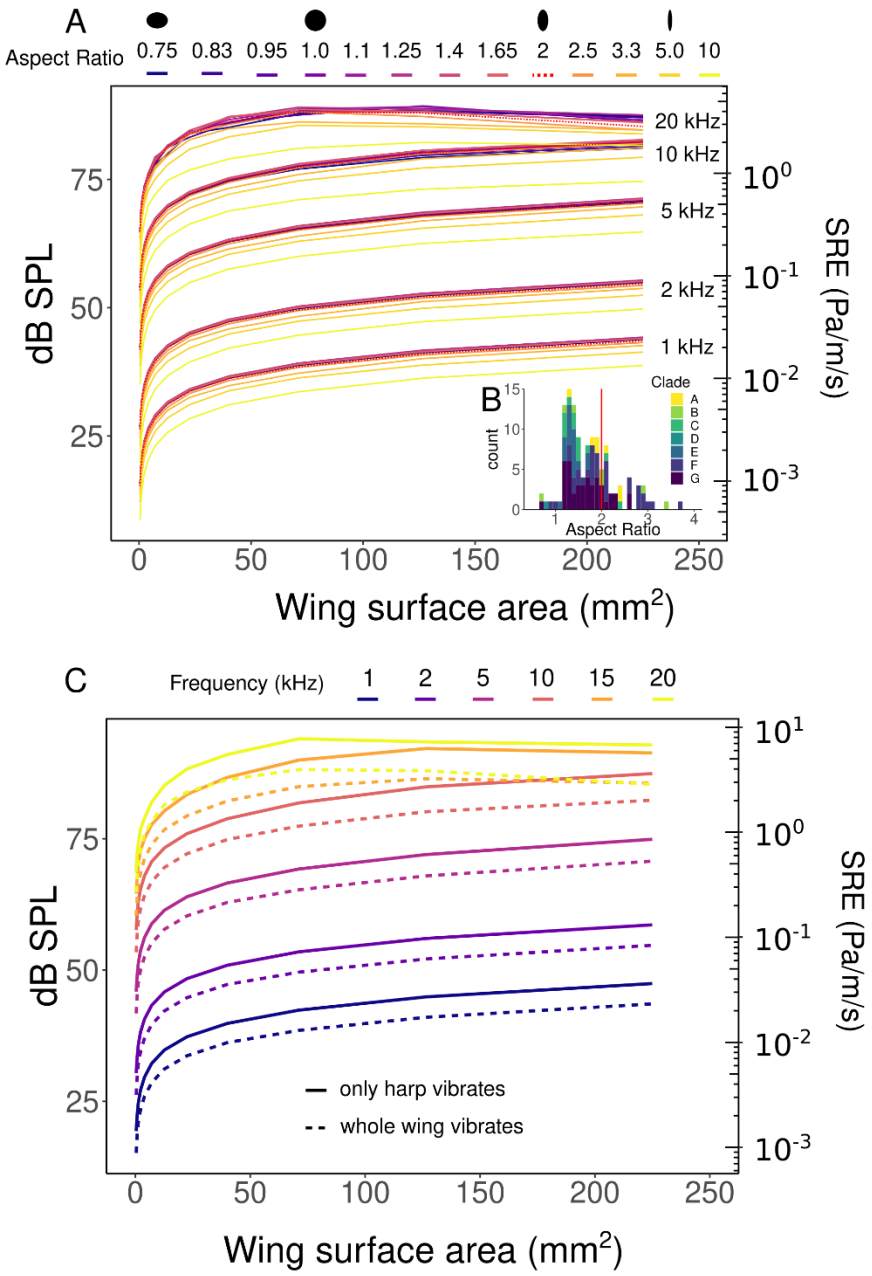


Figure Supplement 2-3. Mesh sensitivity analysis for models based on the finite element method. Each line represents the SPL of a single wing size with a different number of mesh elements. Each panel shows this analysis at a different frequency: A. 30 kHz, B. 20 kHz, C. 10 kHz, D. 5 kHz. As the difference between the second-largest and largest number of elements was small, we proceeded with the largest number of elements shown here for the analysis.



Supplement to Figure 2-4. Wing aspect ratio and use of a "harp" resonator do not significantly impact SRE within biologically-relevant ranges of wing size and call frequency. **A.** The effect of wing aspect ratio on SRE at six different call frequencies. The aspect ratio that was used on all models in this study (2) is shown in red dotted line. **B.** Actual distribution of aspect ratios among species. Red line indicates aspect ratio that was used in our models (2). We see that while aspect ratio influences SRE, this effect is minor within the realistic range of aspect ratios (typically <3 dB for ARs from 1 to 3.3). **B.** The effect on SRE of vibration spread over a small area (harp) compared with the whole wing. Some species of crickets restrict the vibrating portion of the wing to a "harp" region. However, we find that this does not strongly affect SRE at any frequency within our range of interest.

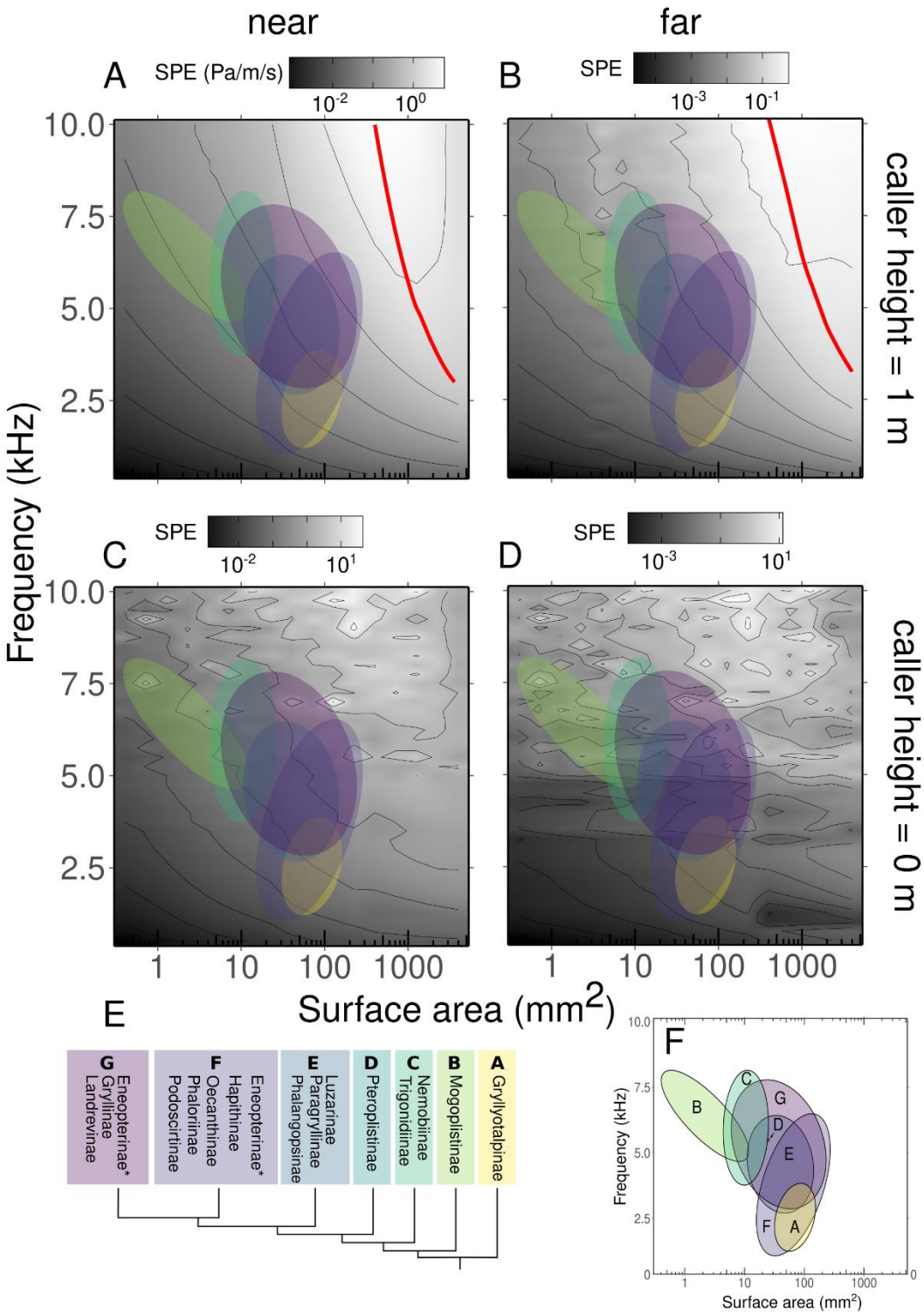
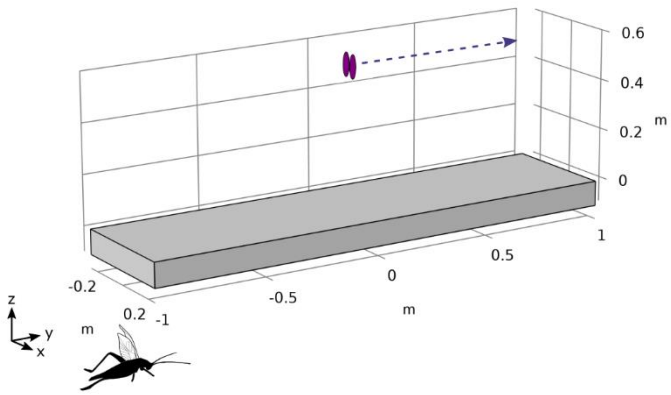
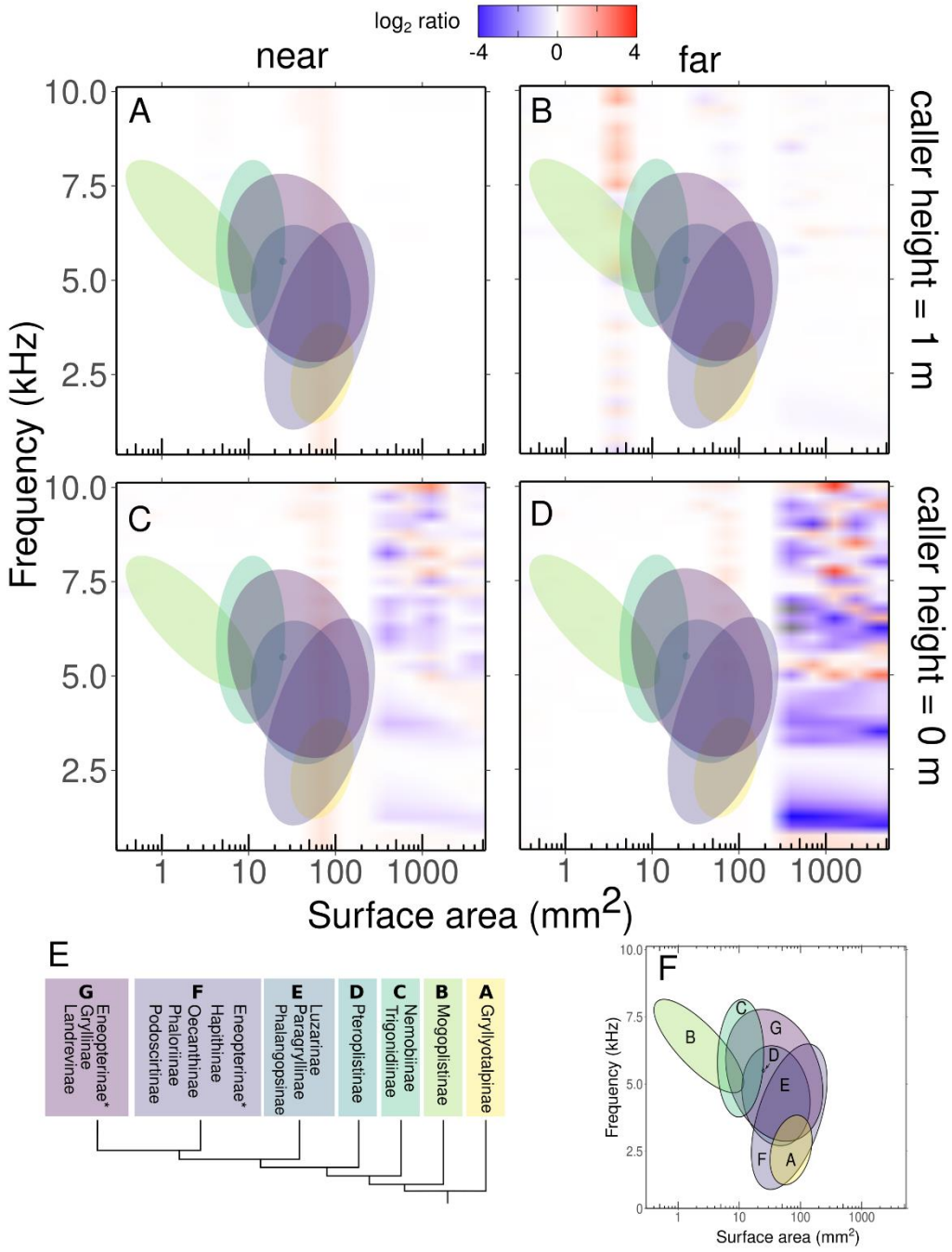


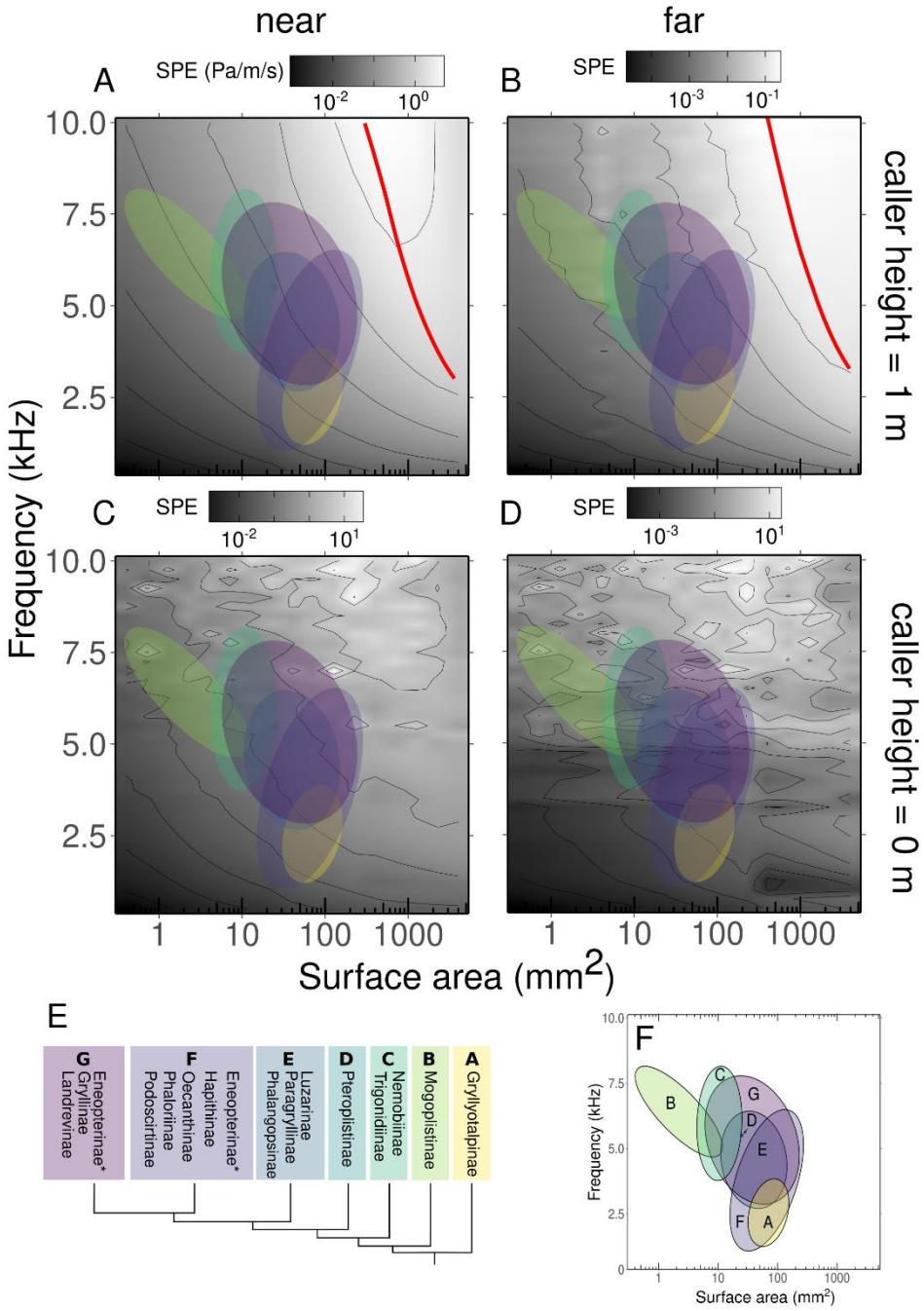
Figure 3. Sound propagation efficiency when the cricket sings near the bare hard ground is orders of magnitude higher than in free space. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 02 m "near" and 0.8 – 0.9 m "far"). **A.** Distance = near, height = 1m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 1 m, **D.** Distance = far, height = 0 m. Red lines indicate optimal efficiency ridge, or the size at each frequency that would produce an ideally baffled calling scenario. Note that the frequency range is reduced compared to figure 2, in order to exclude high frequency callers which likely use alternative vibrational modes. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F**. Key to clade represented by each ellipse.



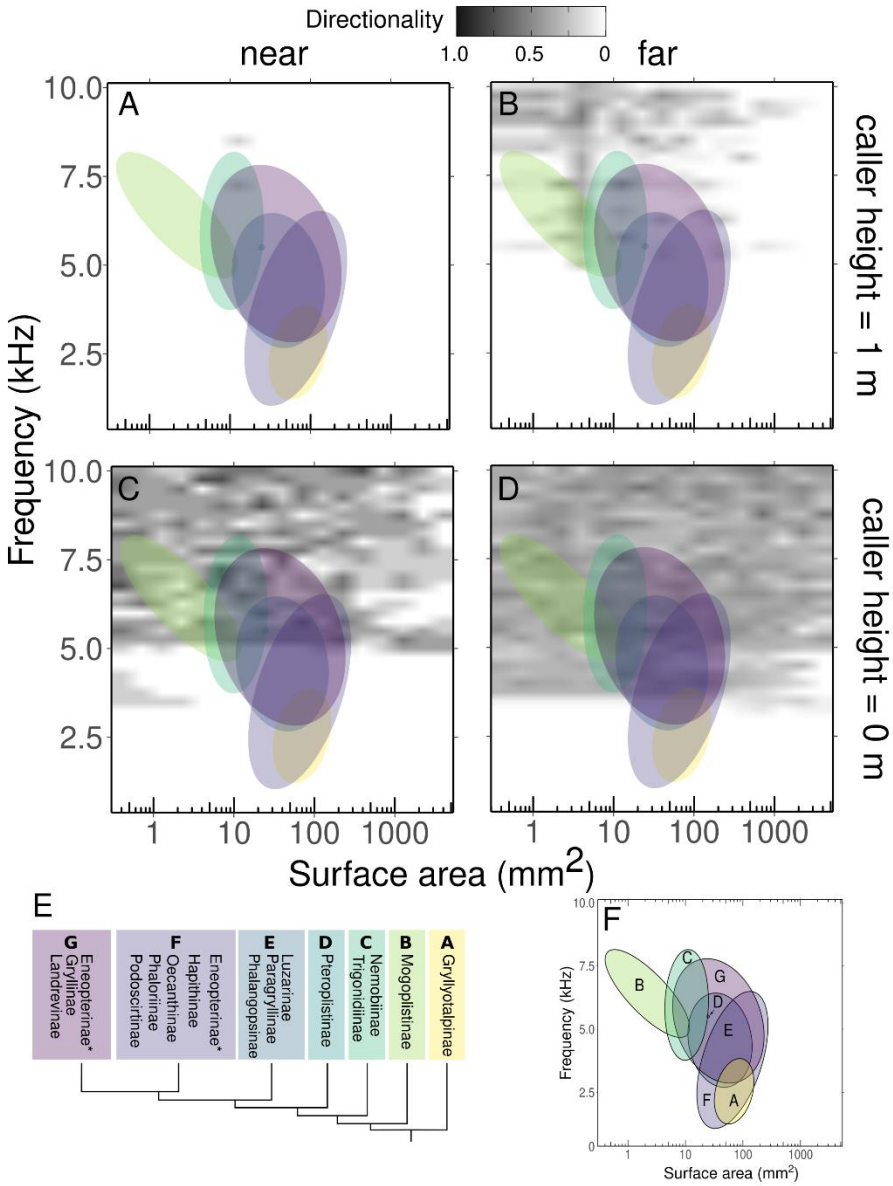
Supplement to figure 3-1. Geometry of boundary element models. Grey shape represents a ground of defined acoustic impedance. Purple ellipses represent wings. Dotted line illustrates the line along which measurements were taken to assess SPE.



Supplement to figure 3-2. Acoustic hardness of ground does not significantly influence SPE at biologically relevant ranges of wing size and call frequency. Comparison of SPE over hard vs soft ground. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 02 m "near" and 0.8 – 0.9 m "far"). **A.** Distance = near, height = 1m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 1 m, **D.** Distance = far, height = 0 m. Color indicates whether higher SRE is found with hard ground (red shades), soft ground (blue shades) or no difference (white). Data are presented as a $\log_2$ ratio instead of a straight proportion. Log_2 ratios are scaled such that the ranges above and below 1 are proportional, rather than values below 1 being compressed between 0 and 1. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny



Supplement to figure 3-3. Vegetation decreases efficiency overall but does not substantially change the landscape pattern of efficiency. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 02 m "near" and 0.8 – 0.9 m "far"). In each height and distance scenario, an excess attenuation factor due to vegetation was also applied. **A.** Distance = near, height = 1m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 1 m, **D.** Distance = far, height = 0 m. Red lines indicate optimal efficiency ridge, or the size at each frequency that would produce an ideally baffled calling scenario. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F**. Key to clade represented by each ellipse.



Supplement to figure 3-4. Call directionality decreases at higher frequencies, particularly with grounded calling. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 02 m "near" and 0.8 – 0.9 m "far"). **A.** Distance = near, height = 1m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 1 m, **D.** Distance = far, height = 0 m. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F**. Key to clade represented by each ellipse.

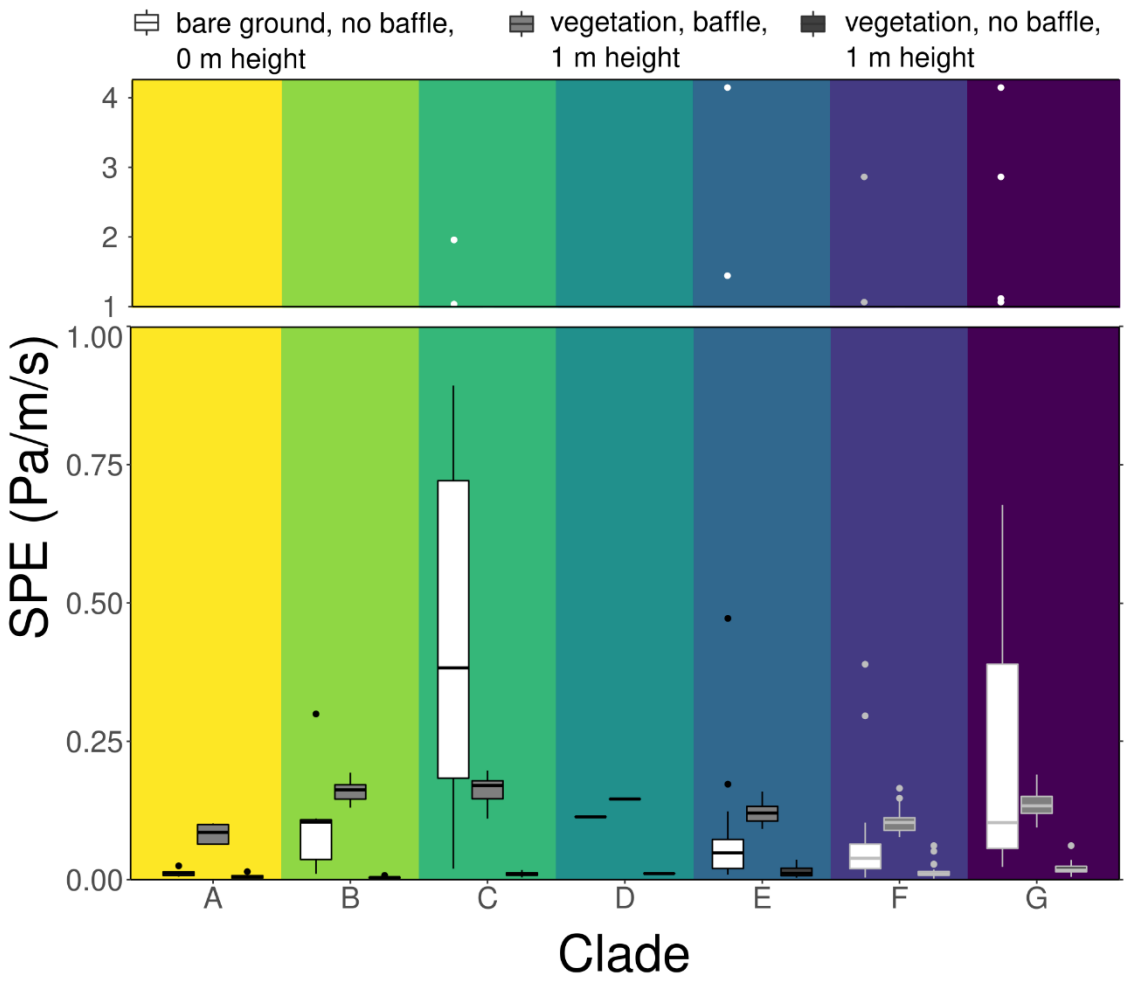
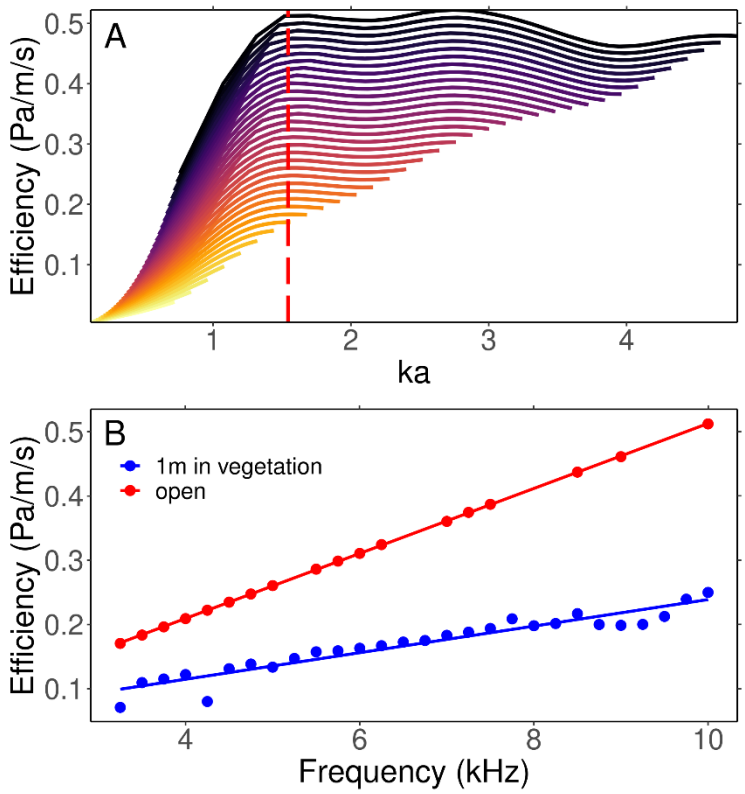
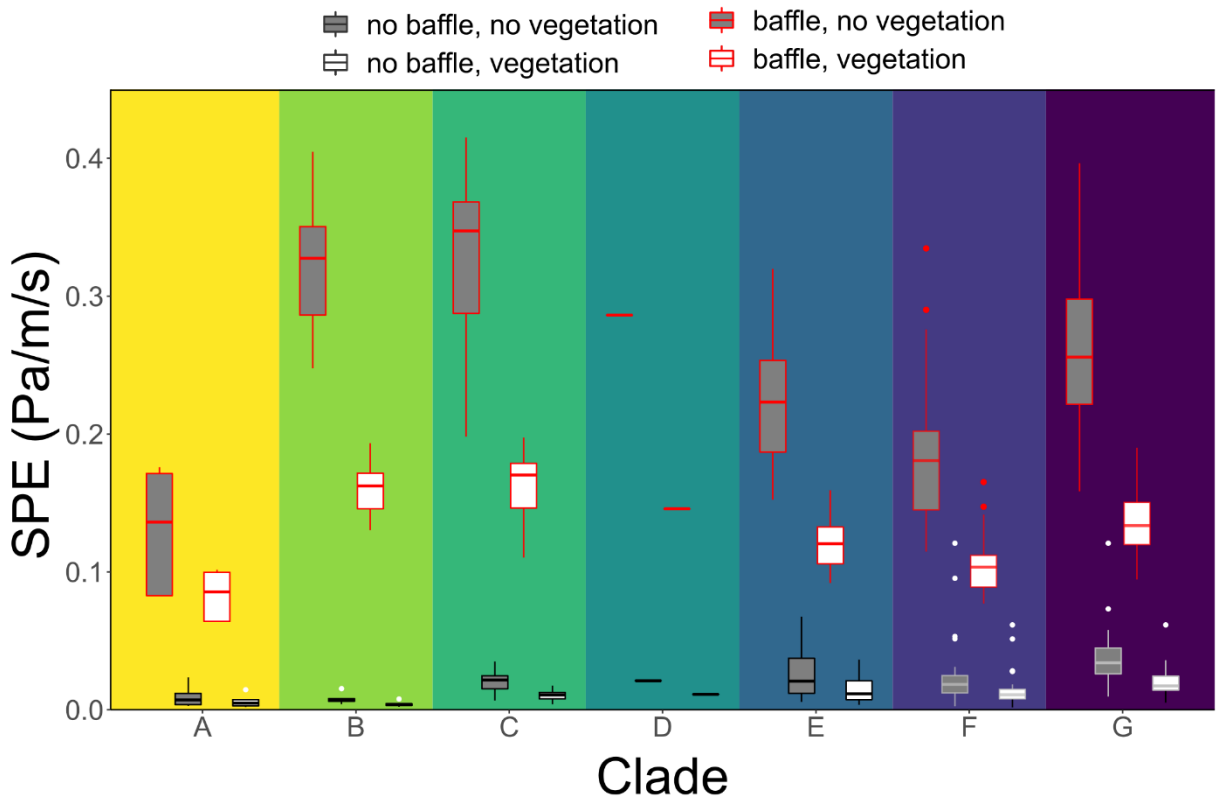


Figure 4. The most effective calling strategy (grounded vs baffled) varies depending on clade. Shown is a comparison of SPE on bare ground with no baffle, and 1 m in vegetation with and without an ideal baffle. These measurements were taken far from the caller, i.e. an average of the SPL at a distance of 0.8-0.9 m from wings, directly in front of the wings was used. Upper panel indicates extreme outliers, which only occur when we consider animals calling from the bare ground.



Supplement to Figure 4-1. Calculating efficiency with optimal baffle. **A.** ka at which optimal efficiency occurs for each frequency. Each frequency is represented by a different line. Line at which efficiency is maximized for each frequency (maximum efficiency ridge) is shown by red dashed line. **B.** efficiency at this optimal ka (1.55) in open and vegetation conditions.



Supplement to figure 4-2. Vegetation somewhat decreases efficiency in baffled and grounded calling conditions. Differences in SPE by clade depending on vegetation and baffle use. For each clade, bars with black outline represent SPE without baffle and bars with red outline represent SPE with ideal baffle. Background color of the bars indicate vegetation or no vegetation.

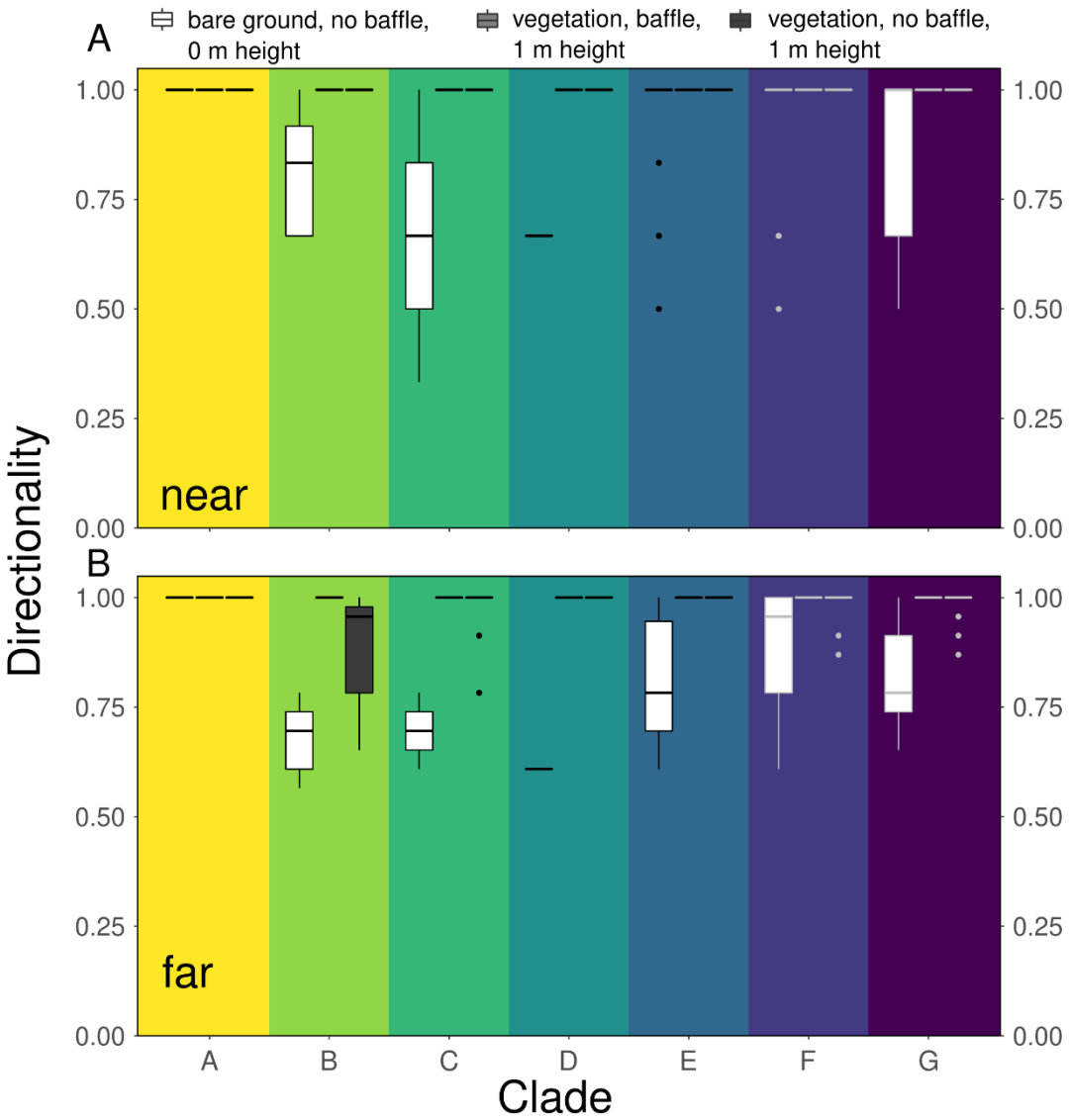


Figure 5. Baffled and grounded calling do not substantially differ with respect to directionality, although it does vary somewhat by clade. **A.** Directionality in near condition, **B.** Directionality in far condition.

Table 1. Sources for morphological data. Asterisk after species name indicates species is represented in both frequency and wing size datasets

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number
A	Gryllotalpinae	*Gryllotalpa*	*australis**	1	Orthoptera Species File Specimen ID: 45466
			*gryllotalpa**	1	Linnean Collection Specimen ID: LINN 8925
			*orientalis**	1	Orthoptera Species File Taxon ID: 1128860
			*permai**	1	(Tan and Kamaruddin, 2016)
			*vineae**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF4425
				2	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF4425
				3	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF4425
B	Mogoplistinae	*Cycloptiloides*	*canariensis**	1	(Dambach and Gras, 1995)
		Cycloptilum	*irregularis**	1	(Love and Walker, 1979)
			*slossoni**	1	(Love and Walker, 1979)
			*tardum**	1	(Love and Walker, 1979)
		Hoplosphyrum	*boreale**	1	(Love and Walker, 1979)
		Ornebius	*bimaculatus**	1	(Kim, 2011)
			*kanetataki**	1	(Kim, 2011)
C	Nemobiinae	*Allonemobius*	*allardi**	1	Orthoptera Species File Specimen ID: 40715
		Bobilla	*gullanae**	1	(Su and Rentz, 2000)
			*neobivittata**	1	(Su and Rentz, 2000)
		Hygronemobius	*guriri*	1	(Pereira et al., 2013)
			*indaia**	1	(Pereira et al., 2013)
			*iperoigae**	1	(Pereira et al., 2013)
		Nemobius	*sylvestris**	1	(Barranco et al., 2013)
		Pteronemobius	*nigrovus**	1	(McIntyre, 1977)
	Trigonidiinae	*Anaxipha*	*bradephona**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF6482

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number
			*hyalicetra**	1	(Cole and Funk, 2019)
			*tachephona**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF6486
		Cranistus	*colliurides**	1	(Martins et al., 2012)
		Phylloscirtus	*amoenus**	1	(Martins et al., 2012)
D	Pteroplistinae	*Singapuriola*	*separata**	1	(Gorochov and Tan, 2012)
E	Luzarinae	*Lerneca*	*inalata**	1	(Lima et al., 2018)
		Luzaridella	*susurra**	1	(Martins et al., 2013)
		Vanzoliniella	*sambophila**	1	(Mello and Reis, 1994)
	Paragryllinae	*Alcodes*	*chamocoru*	1	Orthoptera Species File Specimen ID: 65179
			mococharu	1	Orthoptera Species File Specimen ID: 65181
		Aclogryllus	*crybelos**	1	(Nischk and Otte, 2000)
		Escondacla	*thymodes**	1	Orthoptera Species File Specimen ID: 65198
		Neoacla	*clandestina**	1	Orthoptera Species File Specimen ID: 65199
		Silvastella	*epiplatys**	1	Orthoptera Species File Specimen ID: 65196
	Phalangopsinae	*Ceyloria*	*latissima*	1	Orthoptera Species File Specimen ID: 2983
		Endecous	*betariensis**	1	(Mello and Pellegatti-Franco, 1998)
			*chape**	1	(Souza-Dias et al., 2017)
			*didymus**	1	(Desutter-Grandcolas, 2009)
			*itatibensis**	1	(Mello and Pellegatti-Franco, 1998)
			naipi	1	(Souza-Dias et al., 2017)
			*troglobius**	1	(Castro-Souza et al., 2020)
		Lernecella	*trinitatis*	1	Orthoptera Species File Taxon ID: 1125930
		Pseudotrigonidium	*personatum*	1	(Desutter-Grandcolas, 2009)

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number
E	Phalangopsinae	*Tremellia*	*timah**	1	(Gorochov and Tan, 2012)
	Phaloriinae	*Phaloria*	*anapina**	1	(Otte, 2007)
			*chopardi**	1	(Desutter-Grandcolas, 2009)
			*jerelynae**	1	(Gorochov and Tan, 2012)
		Trellius	*neesoon*	1	(Gorochov and Tan, 2012)
F	Eneopterinae	*Gnominthus*	*baitabagus**	1	(Robillard and Su, 2018)
		Pixibinthus	*sonicus**	1	(Anso et al., 2016)
	Hapithinae	*Hapithus*	*agitator**	1	Orthoptera Species File Specimen ID: 138599
			*vagus**	1	Orthoptera Species File Specimen ID: 65035
	Oecanthinae	*Neoxabea*	*bipunctata**	1	Image captured for present study in lab
			*brevipes**	1	(Zefa et al., 2018)
			*cerrojesusensis**	1	Image captured for present study in lab
			*oltei**	1	Image captured for present study in lab
		Oecanthus	*alexanderi**	1	Image captured for present study in lab
			*angustus**	1	PaDILspecies ID: *Oecanthus angustus*
			*argentinus**	1	University of British Columbia Insect Collection, Specimen: SEM-UBC GRY-0951
			*forbsei**	1	Image captured for present study in lab
			*fultoni**	1	Orthoptera Species File Specimen ID: 40710
			*latipennis**	1	University of Guelph Insect Collection: Specimen BIOUG44550-E07
				2	University of Guelph Insect Collection: Specimen BIOUG44550-E08
			*lineolatus**	1	(Zefa et al., 2012)
			major	1	Orthoptera Species File Specimen ID: 40712
		Oecanthus	*nigricornis**	1	Orthoptera Species File Taxon ID: 345166

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number
F	Oecanthinae	*Oecanthus*	*niveus**	1	Orthoptera Species File Taxon ID: 345151
			*pallidus**	1	(Zefa et al., 2012)
			*pictus**	1	(Milach et al., 2015)
			*pini**	1	Image captured for present study in lab
			*quadripunctatus**	1	https://www.insectimages.org/browse/subthumb.cfm?sub=9113
				2	UBC Database ID: SEM-UBC GRY-0918
			*rileyi**	1	Orthoptera Species File Taxon ID: 1128127
			*rufescens**	1	NHM Specimen ID: 012497644
				2	NHM Specimen ID: 012497645
				3	NHM Specimen ID: 012497646
				4	PaDIL species ID: *Oecanthus rufescens*
			*texensis**	1	Image captured for present study in lab
			valensis	1	(Milach et al., 2016)
			*varicornis**	1	Image captured for present study in lab
	Podoscirtinae	*Madasumma*	*affinis**	1	(Otte, 2007)
		Truljalia	*formosa**	1	(He, 2012)
	Podoscirtinae	*Varitrella*	*suikei**	1	(Tan et al., 2020)
G	Eneopterinae	*Agnotecous*	*azurensis**	1	(Desutter-Grandcolas and Robillard, 2006)
			*brachypterus**	1	(Robillard et al., 2010)
			*meridionalis**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF1775
			*pinsula**	1	(Robillard et al., 2010)
			*sarramea**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF988
			*yahoue**	1	(Desutter-Grandcolas and Robillard, 2006)

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number
G	Eneopterinae	*Arilpa*	*binderia**	1	(Otte, 2007)
			*gidya**	1	(Otte, 2007)
		Cardiodactylus	*guttulus**	1	(Robillard and Ichikawa, 2009)
			*novaeguinea**	1	(Robillard and Ichikawa, 2009)
		Eurepa	*bifasciata**	1	(Robillard and Su, 2018)
		Lebinthus	*bitaeniatus**	1	(Robillard et al., 2013)
			*luae**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF3208
		Myara	*pakaria**	1	(Otte, 2007)
			*wintrena**	1	(Otte, 2007)
		Salmanites	*peekara**	1	(Otte, 2007)
		Xenogryllus	*eneopteroides**	1	(Jaiswara et al., 2019)
			*transversus**	1	(Jaiswara et al., 2019)
	Gryllinae	Eurepella	*mjobergi**	1	PaDIL species ID: *Eurepella mjobergi*
		Gryllus	*amarensis*	1	Museum D'Historie Naturelle ID: 7031
			*assimilis**	1	SINA species ID: *Gryllus assimilis*
			*bimaculatus**	1	Orthoptera Species File Taxon ID: 1122377
			*brevicaudus**	1	SINA species ID: *Gryllus brevicaudus*
			*campestris**	1	Need to figure out specific specimen
				2	Need to figure out specific specimen
			carvalhoi	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF7242
			chaldeus	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF7192
			*chappuisi**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF7046
			*cohni**	1	(Weissman and Gray, 2019)

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number
G	Gryllinae	*Gryllus*	*firmus**	1	(Weissman and Gray, 2019)
			*fultoni**	1	Orthoptera Species File Specimen ID: 40672
			*lineaticeps**	1	(Weissman and Gray, 2019)
			*multipulsator**	1	(Weissman and Gray, 2019)
			*pennsylvanicus**	2	Orthoptera Species File Specimen ID: 43773
				3	UBC Database ID: SEM-UBC GRY-0542
			*veletis**	1	Orthoptera Species File Specimen ID: 40674
				2	UBC Database ID: SEM-UBC GRY-0643
			*vocalis**	1	Orthoptera Species File Specimen ID: 64224
		Miogryllus	*itaquiensis**	1	(Orsini et al., 2017)
			*piracicabensis**	1	(Orsini et al., 2017)
		Teleogryllus	*commodus**	1	(Otte, 2007)
			*marini**	1	(Otte, 2007)
			*oceanicus**	1	(Otte, 2007)
	Itarinae	*Itara*	*kirejtshuki**	1	NMHUK 012497661
			*minor**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF8162
	Landrevinae	*Striduleva*	*crepitans**	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF2059

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
A	Gryllotalpa	*Gryllotalpa*	*australis**	1-47	(Kavanagh and Young, 1989) (range of values given in publication)
			*fulvipes**	1	(Tan and Kamaruddin, 2016)
			*gryllotalpa**	1	Orthoptera Species File Sound ID: 1176
			*permai**	1	(Tan and Kamaruddin, 2016)
			*vineae**	1	Orthoptera Species File Sound ID: 1198
			*canariensis**	1	(Dambach and Gras, 1995)
B	Mogoplistinae	*Cycloptiloides*	*irregularis**	1	Crickets north of Mexico species Id: Key's scaly cricket
		Cycloptilum	*slossoni**	1	Crickets north of Mexico species Id: Slosson's scaly cricket
			*tardum**	1	(Otte, 2007)
			*boreale**	1	Crickets north of Mexico species Id: long-winged scaly cricket
		Hoplosphyrum	*bimaculatus**	1	(He et al., 2017)
		Ornebius	*kanetataki**	1	(He et al., 2017)
			*allardi**	1	Crickets north of Mexico species Id: Allard's ground cricket
C	Nemobiinae	*Allonemobius*	*gullanae**	1	(Su and Rentz, 2000)
		Bobilla	*neobivittata**	1	(Su and Rentz, 2000)
			*indaia**	1	(Pereira et al., 2013)
		Hygronemobius	*iperoigae**	1	(Pereira et al., 2013)
			*sylvestris**	1	Orthoptera Species File Sound ID: 1045

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
C	Nemobiinae	*Nemobius*	*nigrovus**	1	(McIntyre, 1977)
		Pteronemobius	*bradephona**	1	Orthoptera Species File Sound ID: 1832
	Trigonidiinae	*Anaxipha*	*hyalicetra**	1	(Cole and Funk, 2019)
			*tachephona**	1	Orthoptera Species File Sound ID: 1833
			*colliurides**	1	(Martins et al., 2012)
		Cranistus	*amoenus**	1	(Martins et al., 2012)
		Phylloscirtus	*separata**	1	(Gorochov and Tan, 2012)
D	Pteroplistinae	*Singapuriola*	*inalata**	1	(Lima et al., 2018)
E	Luzarinae	*Lerneca*	*susurra**	1	(Martins et al., 2013)
		Luzaridella	*sambophila**	1	(Mello and Reis, 1994)
		Vanzoliniella	*chamocoru**	1	(Nischk and Otte, 2000)
	Paragryllinae	Aclodes	*mococharu**	1	(Nischk and Otte, 2000)
			*crybelos**	1	(Nischk and Otte, 2000)
		Aclogryllus	*thymodes**	1	(Nischk and Otte, 2000)
		Escondacla	*clandestine**	1	(Nischk and Otte, 2000)
		Neoacla	*epiplatys**	1	(Nischk and Otte, 2000)
		Silvastella	*betariensis**	1	(He, 2012)
	Phalangopsinae	Endecous	*chape**	1	(Souza-Dias et al., 2017)

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
			*didymus**	1	(Castro-Souza et al., 2020)
E	Phalangopsinae	*Endecous*	*itatibensis**	1	(Mello and Pellegatti-Franco, 1998)
			*troglobius**	1	(Castro-Souza et al., 2020)
			*timah**	1	(Gorochov and Tan, 2012)
		Tremellia	*anapina**	1	(Su and Rentz, 2000)
	Phaloriinae	*Phaloria*	*chopardi**	1	(Desutter-Grandcolas, 2009)
			*jerelynae**	1	(Gorochov and Tan, 2012)
			*baitabagus**	1	(Vicente et al., 2015)
F	Eneopterinae	*Gnominthus*	*sonicus**	1	(Anso et al., 2016)
		Pixibinthus	*agitator**	1	Crickets north of Mexico species ID: *Hapithus agitator*
	Hapithinae	*Hapithus*	*melodius*	1	Handbook of crickets and katydids
			*vagus**	1	Macaulay Library asset: 114470
			diplastes	1	Handbook of crickets and katydids
		Orocharis	*gryllodes*	1	Handbook of crickets and katydids
			luteolira	1	Handbook of crickets and katydids
			nigrifrons	1	Handbook of crickets and katydids
			saltator	1	Handbook of crickets and katydids
			tricornis	1	Handbook of crickets and katydids

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
F	Hapithinae	*Orocharis*	*bipunctata**	1	Crickets north of Mexico species ID: *Neoxabea bipunctata*
	Oecanthinae	*Neoxabea*	*brevipes* *	1	(Zefa et al., 2018)
			*cerrojesusensis**	1	Orthoptera Species File Sound ID: 2345
			*ottei**	1	Orthoptera Species File Sound ID: 2346
			*alexanderi**	1	Crickets North of Mexico Species ID: *Oecanthus alexanderi*
		Oecanthus	*angustus**	1	(Otte, 2007)
			*argentinus**	1	Crickets North of Mexico Species ID: *Oecanthus argentinus*
			*argentinus** *californicus*	2	Orthoptera Species File Sound ID: 1535
				1	Crickets North of Mexico Species ID: *Oecanthus californicus*
			*californicus forbsei**	2	Orthoptera Species File Sound ID: 1536
				1	Crickets North of Mexico Species ID: *Oecanthus forbsei*
			*fultoni**	1	Crickets North of Mexico Species ID: *Oecanthus fultoni*
			*latipennis**	1	Crickets North of Mexico Species ID: *Oecanthus latipennis*
			*latipennis**	2	Orthoptera Species File Sound ID: 1002
			*lineolatus**	1	(Zefa et al., 2012)
			*nigricornis**	1	Crickets North of Mexico Species ID: *Oecanthus nigricornis*
			*niveus**	1	Crickets North of Mexico Species ID: *Oecanthus niveus*
			*pallidus**	1	(Zefa et al., 2012)

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
F	Oecanthinae	*Oecanthus*	*pictus**	1-9	Orthoptera Species File Taxon ID: 1223417 (9 songs from different temperatures)
			*pini**	1	Crickets North of Mexico Sound File: 587sl
			*quadripunctatus**	1	Orthoptera Species File Sound File 1531
			*rileyi**	1	Orthoptera Species File Sound File: 1540
			*rufescens**	1	(Otte, 2007)
			*texensis**	1	(Symes and Collins, 2013)
			*varicornis**	1	Crickets North of Mexico Sound File: 593sl
			walker	1	Crickets North of Mexico Species ID: *Oecanthus walkeri*
			*affinis**	1	(Otte, 2007)
	Podoscirtinae	*Madasumma*	*jirranda*	1	(Otte, 2007)
			kanina	1	(Otte, 2007)
			loorea	1	(Otte, 2007)
			*formosa**	1	(He, 2012)
		Truljalia	*suikei**	1	(Tan et al., 2020)
		Varitrella	*azurensis**	1	Museum D'Historie Naturelle ID: MNHN-SO-2018-100
G	Eneopterinae	*Agnotecous*	*brachypterus**	1	(Robillard et al., 2010)
			clarus	1	Museum D'Historie Naturelle ID: MNHN-SO-2018-102
			*meridionalis**	1	Museum D'Historie Naturelle ID: MNHN-SO-2018-99

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
G	Eneopterinae	*Agnotecous*	*pinsula**	1	(Robillard et al., 2010)
			*sarramea**	1	(Robillard and Desutter-Grandcolas, 2004)
			*yahoue**	1	(Robillard and Desutter-Grandcolas, 2004)
			*binderia**	1	(Otte, 2007)
		Arilpa	*gidya**	1	(Otte, 2007)
			wirrilla	1	(Otte, 2007)
			*guttulus**	1	(Robillard and Ichikawa, 2009)
		Cardiodactylus	*novaeguinea**	1	(Otte, 2007)
			*bifasciata**	1	(Otte, 2007)
		Eurepa	*eeboolaga*	1	(Otte, 2007)
			marginipennis	1	(Otte, 2007)
			noarana	1	(Otte, 2007)
			nurndina	1	(Otte, 2007)
			wirkutta	1-2	(Otte, 2007) (range of values given in publication)
			woortooa	1	(Otte, 2007)
			yumbena	1	(Otte, 2007)
			*bitaeniatus**	1	(Robillard and Tan, 2013)
		Lebinthus	*luae**	1	(Robillard and Tan, 2013)

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
G	Eneopterinae	*Lebinthus*	*aperta*	1	(Otte, 2007)
		Myara	*marimbula*	1	(Otte, 2007)
			muttaburra	1	(Otte, 2007)
			*pakaria**	1	(Otte, 2007)
			sordida	1	(Otte, 2007)
			unicolor	1-2	(Otte, 2007) (range of values given in publication)
			*wintrena**	1	(Robillard and Desutter-Grandcolas, 2004)
			yurgama	1	(Otte, 2007)
			vittatus	1	(Robillard and Desutter-Grandcolas, 2004)
		Nisitrus	*allaris*	1	(Otte, 2007)
		Salmanites	*ninbella*	1	(Otte, 2007)
			noccundris	1	(Otte, 2007)
			noonamina	1	(Otte, 2007)
			*peekara**	1	(Otte, 2007)
			poene	1	(Otte, 2007)
			taltantris	1	(Otte, 2007)
			terba	1-2	(Otte, 2007) (range of values given in publication)
			wittilliko	1	(Otte, 2007)

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
G	Eneopterinae	*Salmanites*	*eneopteroides**	1	(Jaiswara et al., 2019)
		Xenogryllus	*maichauensis*	1	(Jaiswara et al., 2019)
			marmoratus	1	(Jaiswara et al., 2019)
			mozambicus	1	(Jaiswara et al., 2019)
			*transversus**	1	Database found within http://www.biologie.uni-ulm.de, no longer exists
				2	Database found within http://www.biologie.uni-ulm.de, no longer exists
			ululiu	1	Database found within http://www.biologie.uni-ulm.de, no longer exists
			ballina	1	(Otte, 2007)
	Gryllinae	*Eurepella*	*iando*	1	(Otte, 2007)
			jillangolo	1	(Otte, 2007)
			kulkawirra	1	(Otte, 2007)
			lewara	1	(Otte, 2007)
			mataranka	1	(Otte, 2007)
			meda	1	(Otte, 2007)
			*mjobergi**	1-2	(Otte, 2007) (range of values given in publication)
			moojerra	1	(Otte, 2007)
			oana	1	(Otte, 2007)
			quarriana	1	(Otte, 2007)

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
G	Gryllinae	*Eurepella*	*tinga*	1	(Otte, 2007)
			tjairaia	1	(Otte, 2007)
			torowatta	1	(Otte, 2007)
			wanga	1	(Otte, 2007)
			waninga	1	(Otte, 2007)
		Gryllus	*assimilis**	1	Crickets North of Mexico sound file: 483sl
				2	Crickets North of Mexico sound file: 483ss2
			*bimaculatus**	1	Orthoptera Species File Sound ID: 1295
			*brevicaudus**	1	Crickets North of Mexico sound file: 465sldw
				2	Crickets North of Mexico sound file: 465ss2wg
			*campestris**	1	Orthoptera Species File sound ID: 1741
			*chappuisi**	1	Orthoptera Species File sound ID: 1739
			*cohni**	1	Crickets North of Mexico sound file: 722sl
			*firmus**	1	Crickets North of Mexico sound file: 481sl
			*fultoni**	1	Crickets North of Mexico sound file: 484sl
				2	Crickets North of Mexico sound file: 484slc
			*lineaticeps**	1	Crickets North of Mexico sound file: 467sldw
			*multipulsator**	1	Crickets North of Mexico sound file: 499sl

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
G	Gryllinae	*Gryllus*	*multipulsator**	2	Crickets North of Mexico sound file: 499slwg
			*pennsylvanicus**	1	Orthoptera Species File sound ID: 1258
			texensis	1	Crickets North of Mexico sound file: 479sl
			*veletis**	1	Crickets North of Mexico sound file: 488sl
			*vocalis**	1	Crickets North of Mexico sound file: 466sldw
			*itaquiensis**	1	(Otte, 2007)
		Miogryllus	*piracicabensis**	1-30	(Orsini et al., 2017) (range of values given in publication)
			*commodus**	1	(Otte, 2007)
		Teleogryllus	*marini**	1-2	(Otte, 2007) (range of values given in publication)
			*oceanicus**	1	(Otte, 2007)
		Itara	*kirejtshuki**	1	Orthoptera Species File sound ID: 1796
			*minor**	1	Database found within http://www.biologie.uni-ulm.de, no longer exists
		Striduleva	*crepitans**	1-2	(Hugel, 2009) (range of values given in publication)

Full citations for Specimen data:

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