

1 **Title:**

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

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11 **Abstract**

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

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

27 **Introduction**

28 Male crickets make loud advertisement calls to attract females who use these calls to locate mates (Regen,  
29 1913). Louder calls travel further, cover more area, and attract more females (Deb et al., 2020; Farris et  
30 al., 1997; Römer et al., 1993). When faced with a choice, females prefer louder calls (Deb et al., 2020;  
31 Forrest, 1991). Being louder therefore has implications for mating success and evolutionary fitness in  
32 these singing insects. However, despite the apparent loudness of a nighttime chorus, cricket calls are  
33 acoustically constrained by a phenomenon known as ‘acoustic short-circuiting’ (Forrest, 1982; Mhatre et  
34 al., 2017). The smaller the wings of a cricket with respect to the wavelength of the sound it makes, the

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

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

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

45 ***Baffle use in crickets may be rare due to a “lack of utility”***

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

61 However, to truly test the lack of utility hypothesis, we must quantify tool utility and use of the tool must  
62 have implications for evolutionary fitness. It is often difficult to meet these two conditions. Work in  
63 chimpanzees has directly quantified tool utility by evaluating how much caloric value can be gained by  
64 using a tool to exploit an otherwise unexploitable resource (Boesch and Boesch, 1983). Other studies  
65 have made more indirect arguments about the utility of tools. Work in sea otters has shown that tools are  
66 employed more frequently in populations in which tough prey require tools to access them (Fujii et al.,  
67 2015). In capuchin monkeys, larger individuals who can more effectively use tools to crack nuts are more  
68 likely to use tools (Spagnoletti et al., 2011). However, few studies directly assess the lack of utility  
69 hypothesis, particularly outside the context of food.

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

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

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

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

## 104 **Results and Discussion**

### 105 *All crickets would benefit from baffle use in idealized conditions*

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

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

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

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

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

142 With baseline efficiencies measured above, we next calculated how much each species could gain by  
143 using a baffle, while singing at the same frequency. To do this, we used the optimal efficiency ridge, since  
144 optimal radiator efficiency is the same as optimal baffled efficiency (Hambric and Fahnline, 2007). If  
145 animals were to continue using the same call frequency, but used an ideal baffle, each species stood to  
146 gain between 1.7 – 35 times (5 – 30 dB) above their baseline SRE (mean:  $7.6 \pm 0.41$  times,  $16 \pm 0.37$  dB,  
147 n = 99). Among those who stood to gain the most included animals in clade B, specifically in the  
148 subfamily Mogoplistinae (scaly crickets). These animals have very small wings (mostly under 5 mm<sup>2</sup>),  
149 suggesting a poor match between radiator and wing size. On the other hand, the animal closest to the  
150 optimal efficiency ridge, was *Madasumma affinis*, belonging to the subfamily Podoscirtinae in clade F.  
151 This animal has the largest wing at 258 mm<sup>2</sup>, however, even this animal stood to gain 0.5 Pa/m/s (5 dB or  
152 1.6x increase) with the use of an ideal baffle. Taken together, these data suggest that all crickets could  
153 increase SRE, and therefore, stand to benefit from use of a baffle.

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

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

160 To address whether and how the efficiency landscape is changed by realistic calling conditions, we used  
161 boundary element modeling. Specifically, we use this model to add a "ground" component to our existing  
162 models, where the ground could have different characteristics including vegetation cover. In these  
163 models, sound can be reflected and dissipated by the ground. We model the effect of the vegetation by an  
164 excess attenuation term (see methods). We used empirical measurements of different types of ground so  
165 although our modeled ground is flat and smooth, these measures take realistic ground variability into  
166 account. We also varied the height of the caller above the ground (grounded calling: 0 m, elevated calling:  
167 1 m). We measured efficiency again by normalizing sound levels against radiator vibration levels (see  
168 methods). Sound levels were measured at two distances from the caller: near (averaged from 0.05 – 0.2 m  
169 away), and far (averaged from 0.8 – 0.9 m away). To simplify analysis, we always measured efficiency at  
170 the same height as the caller. To differentiate this measure of efficiency from SRE, we called it sound  
171 propagation efficiency or SPE (Pa/m/s).

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

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

190 ***Alternative strategies persist when ground properties and vegetation are varied***

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

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

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

#### 214 ***Alternative strategies are still viable when considering call directionality***

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

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

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

#### 240 *Alternative calling strategies are likely in use by some cricket species*

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

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

256 We turn first to clade F, consisting primarily of the Oecanthines, or tree crickets. Members of this group  
257 stand to gain efficiency on the order of about 4.5x, (13 dB) from grounded calling compared to unaided  
258 calling according to our data (figure 4). However, they could gain 9x, (19 dB) if they baffled. Indeed,  
259 Oecanthine natural history bears out our predictions; tree crickets are known to mostly call from  
260 vegetation, including vegetation that is suitable for baffle building and use (Deb and Balakrishnan, 2014;  
261 Forrest, 1982). In fact, all known cricket baffle users are in this clade, as predicted based on the lack of  
262 utility hypothesis. For clade G, on the other hand, consisting mostly of the Gryllinae, or field crickets, we  
263 predict the opposite. On average, grounded calling gives an advantage of 9x (19 dB) above unaided for  
264 species in this group, whereas baffling gives an advantage of about 8x (18 dB) above unaided. Again,  
265 behavioral data suggests that many field crickets indeed prefer to call from the open ground habitats that  
266 we predict would maximize their efficiency (Weissman and Gray, 2019).

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

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

278 high for all calling conditions, we therefore suggest that directionality does not preclude one alternative  
279 strategy over another.

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

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

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

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

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

## 313 **Materials and Methods**

### 314 *Specimen Data*

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



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

### 336 ***Finite Element Models for Sound Radiation Efficiency***

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

### 341 ***Model geometry, boundary conditions, symmetry, and vibration***

342 Animals were represented by two ellipses which modelled the forewings sitting next to each other along  
343 the long axis, in the same plane (Supplement to Figure 2-2). These ellipses should accurately approximate  
344 total radiated sound power and the true shape of the sound field, and it is the size and shape of the radiator  
345 and frequency of the call that determines radiation efficiency, and not the radiator's material properties  
346 (Hambric and Fahline, 2007). Surrounding the wings was a spherical acoustic domain consisting of air  
347 with a 20 cm radius. The acoustic domain was suspended inside a second spherical domain of 40 cm  
348 radius (Supplement to figure 2-2). A perfectly-matched layer (PML) was applied to the area between the  
349 acoustic domain and larger outer sphere. PMLs in finite element modelling are used to mimic an open and  
350 non-reflecting infinite acoustic domain, which absorbs all sound energy from the acoustic domain  
351 (Berenger, 1994). Thus PMLs mitigate modelling artefacts such as the effects of sound reflecting from the  
352 edges of the acoustic domain (Mhatre et al., 2017). To reduce computational time, our model was  
353 constructed using  $\frac{1}{4}$  symmetry. That is, we modeled  $\frac{1}{2}$  of one wing and  $\frac{1}{4}$  of the two spherical domains.  
354 We then mirrored this model twice, once about the short axis of the wing to create a whole wing and  $\frac{1}{2}$  of  
355 the spherical domains, and a second time about a line between and parallel to the long axis of the wings to  
356 create a second wing and the whole spherical domains. We applied a time- and space-averaged velocity  
357 normal to the entire surface of the wings at 0.13m/s. This was the value measured from the wings of  
358 singing *Oecanthus henryi* and is the only known estimate for crickets (Mhatre et al., 2017). However,  
359 given that we are calculating efficiency rather than reporting actual sound pressure levels, normalizing

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

#### 364 *Finite Elements*

365 3D tetrahedral elements were used in both the acoustic domain and PML. After undertaking a mesh size  
366 sensitivity study (Supplement to figure 2-3), we chose the “extra fine” mesh setting in COMSOL, with  
367 about 60000 elements in the acoustic domain. This number did vary somewhat with wing size, as fewer  
368 elements are used with very small wings.

#### 369 *Model Parameters*

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

#### 377 *Other Modeling Considerations*

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

#### 384 *Boundary Element Models for sound propagation efficiency*

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

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

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

#### 406 *Model geometry, forcing, and boundary conditions*

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

#### 418 *Model Parameters*

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

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

#### 435 *Sound propagation efficiency definition*

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

441 centre between the two elliptical ‘wings’. We divided this line into “near” and “far” from the caller: near  
442 = 0.05 – 0.2 m from wings, far = 0.8 – 0.9 m from wings. Efficiency was calculated as before, by dividing  
443 sound pressure level (Pa) by 0.13 m/s, the space and time averaged velocity applied to the wings. We also  
444 created an additional boundary element model with no ground, to allow for direct comparisons between  
445 ground and no ground and to sanity check the boundary element method compared with the previous  
446 finite element models.

#### 447 *Finite Elements*

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

#### 453 *Excess attenuation due to vegetation*

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

$$457 \frac{EA(Pa)}{FL} = 3[1 - \exp(0.3 - 0.5(ka))], ka > 0.6$$

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

#### 463 *Efficiency of individual species and how much they gain with baffle*

464 To test the lack of utility hypothesis, we used the output of our models to estimate the gains in efficiency  
465 that each species could attain if it used a baffle. We did this for both the idealized measure of efficiency  
466 (SRE) and the more realistic scenario involving a ground and vegetation (SPE). For each modeling  
467 scenario, we first estimated the efficiency of each cricket species in our dataset, given their wing area and  
468 call frequency. Next, we calculated the efficiency that each species would have if it used an ideal baffle.  
469 To do this, we first determined the size at which the wings and baffle working together as a single radiator  
470 would reach maximal efficiency. The optimal size is a function of the wavelength of that sound frequency  
471 in that medium. We calculated the quantity  $ka$  for each surface area-frequency combination in the model,  
472 where  $k$  is the wavenumber and  $a$  is the effective radius of the sound radiating plates (Hambric and  
473 Fahnline, 2007).  $ka$  is a dimensionless quantity often used in acoustics, as it helps define when a radiator  
474 of a particular size transitions from being inefficient sound radiator at low frequencies to an efficient high  
475 frequency radiator. For instance, an optimally sized circular piston has  $ka = 1$  (Hambric and Fahnline,  
476 2007).

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

480 a separate trace for each frequency (Supplement to Figure 4-1). We then identified the  $k_a$  at which  
481 maximal efficiency was reached for all frequencies. This value represents the size at which highest  
482 attainable efficiency is reached, consistent with an optimally baffled condition (Hambric and Fahline,  
483 2007) (Supplement to Figure 4-1). In our finite element models, we found optimal  $k_a$  to be about 1.3. For  
484 the boundary element models at the far distance, optimal  $k_a$  was approximately 1.55 (Figure 4-1).

485 Next, we performed a simple linear regression between frequency and maximal efficiency at optimal  $k_a$ ,  
486 then calculated the slope and y-intercept of this regression (Supplement to Figure 4-1). We used this  
487 equation to calculate optimal baffled efficiency for each species. The relationship between frequency and  
488 efficiency differed depending on condition (open ground vs ground + vegetation) (Supplement to figure  
489 4-1), so this regression was performed separately for each environmental condition when calculating  
490 optimal baffled efficiency for a given condition.

### 491 ***Directionality index***

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

### 512 **Acknowledgements**

513 We wish to acknowledge a number of undergraduate students who assisted with the collection and  
514 databasing of cricket acoustic and morphometric data: Morteza Al Rabya, Nancy Kim, Shanker  
515 (Matthew) Nadarajah, and Daniel Xie. Nancy Collins provided specimens for several of the wing  
516 measurements. Graduate students Hossein Asgari and Reese Gartly assisted with multiplexing dozens of  
517 model runs on multiple machines. Emine Celiker and Damian Elias provided feedback on an earlier  
518 version of this manuscript. This work would have not been possible without an extensive worldwide  
519 network of specimen databases. We especially wish to thank those who contribute to, curate, or maintain

520 Orthoptera Species File, Singing Insects of North America, Museum D’Historie Naturelle, and numerous  
521 university insect collections. We also wish to thank the photographers who graciously provided their  
522 images free of charge for inclusion in this manuscript.

523 We would also like to thank the following funding sources for their support of this research: NSERC  
524 Discovery (Grant no. 687216), and early career supplement (675248), and an NSERC Canada research  
525 chair (Grant no. 693206) to NM; the Western University Postdoctoral Fellowship to EEB; Western  
526 Undergraduate Work Study to SD and HW; Western Undergrad Summer Research Internship to HW.

## 527 **References**

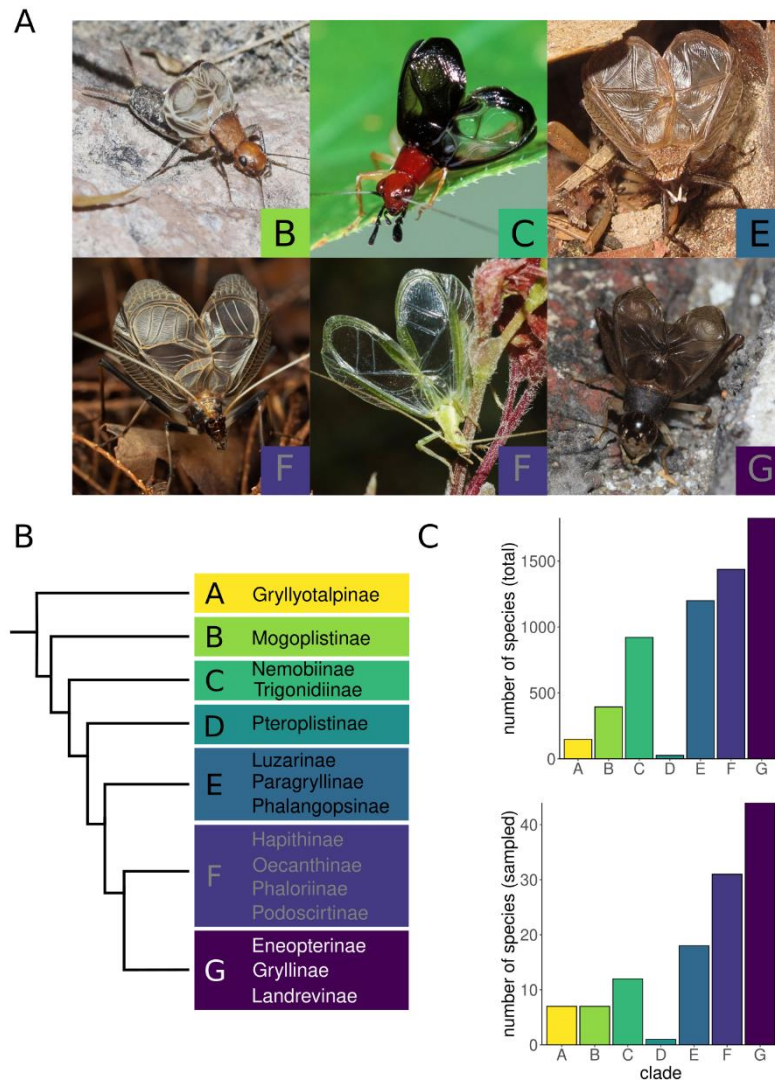
- 528 Attenborough K, Bashir I, Taherzadeh S. 2011. Outdoor ground impedance models. *The Journal of the*  
529 *Acoustical Society of America* **129**:2806–2819. doi:10.1121/1.3569740
- 530 Bashir I, Taherzadeh S, Shin H-C, Attenborough K. 2015. Sound propagation over soft ground without  
531 and with crops and potential for surface transport noise attenuation. *J Acoust Soc Am* **137**:12.
- 532 Bennet-Clark HC. 1998. Size and scale effects as constraints in insect sound communication. *Phil Trans*  
533 *R Soc Lond B* **353**:407–419. doi:10.1098/rstb.1998.0219
- 534 Bennet-Clark HC. 1987. The Tuned Singing Burrow of Mole Crickets. *Journal of Experimental Biology*  
535 **128**:383–409.
- 536 Berenger J-P. 1994. A perfectly matched layer for the absorption of electromagnetic waves. *Journal of*  
537 *Computational Physics* **114**:185–200. doi:10.1006/jcph.1994.1159
- 538 Boesch C, Boesch H. 1983. Optimisation of Nut-Cracking With Natural Hammers By Wild Chimpanzees.  
539 *Behaviour* **83**:265–286. doi:10.1163/156853983X00192
- 540 Bradbury JW, Vehrencamp SL. 1998. Principles of Animal Communication, First edition. ed.  
541 Sunderland: Sinauer Associates, Inc.
- 542 Chintauan-Marquier IC, Legendre F, Hugel S, Robillard T, Grandcolas P, Nel A, Zuccon D, Desutter-  
543 Grandcolas L. 2016. Laying the foundations of evolutionary and systematic studies in crickets  
544 (Insecta, Orthoptera): a multilocus phylogenetic analysis. *Cladistics* **32**:54–81.  
545 doi:10.1111/cla.12114
- 546 Cigliano, M. M., Braun, D. C., Eades, D. C., Otte, D. n.d. Orthoptera Species File. *Orthoptera Species*  
547 *File Version 50/50*. <http://orthoptera.speciesfile.org/HomePage/Orthoptera/HomePage.aspx>
- 548 Collins N. 2012. A Citizen Scientist’s Contributions to Tree Cricket Taxonomy. *American Entomologist*  
549 **58**:9–10. doi:10.1093/ae/58.1.0009
- 550 Deb R, Balakrishnan R. 2014. The opportunity for sampling: the ecological context of female mate  
551 choice. *Behavioral Ecology* **25**:967–974. doi:10.1093/beheco/aru072
- 552 Deb R, Modak S, Balakrishnan R. 2020. Baffling: a condition-dependent alternative mate attraction  
553 strategy using self-made tools in tree crickets. *Proceedings of the Royal Society B: Biological*  
554 *Sciences* **287**:20202229. doi:10.1098/rspb.2020.2229
- 555 Desutter-Grandcolas L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera  
556 (Insecta, Orthoptera). *Zoologica Scripta* **32**:525–561. doi:10.1046/j.1463-6409.2003.00142.x
- 557 Embleton TFW. 1996. Tutorial on sound propagation outdoors. *The Journal of the Acoustical Society of*  
558 *America* **100**:31–48. doi:10.1121/1.415879
- 559 Erregger B, Schmidt AKD. 2018. Anthropogenic calling sites boost the sound amplitude of advertisement  
560 calls produced by a tropical cricket. *Animal Behaviour* **142**:31–38.  
561 doi:10.1016/j.anbehav.2018.05.021
- 562 Farris HE, Forrest TG, Hoy RR. 1997. The effects of calling song spacing and intensity on the attraction  
563 of flying crickets (orthoptera: Goryllidae: Nemobiinae). *J Insect Behav* **10**:639–653.  
564 doi:10.1007/BF02765384
- 565 Forrest TG. 1991. Power output and efficiency of sound production by crickets. *Behav Ecol* **2**:327–338.  
566 doi:10.1093/beheco/2.4.327

- 567 Forrest TG. 1982. Acoustic Communication and Baffling Behaviors of Crickets. *The Florida*  
568 *Entomologist* **65**:33–44. doi:10.2307/3494144
- 569 Fujii JA, Ralls K, Tinker MT. 2015. Ecological drivers of variation in tool-use frequency across sea otter  
570 populations. *Behavioral Ecology* **26**:519–526. doi:10.1093/beheco/aru220
- 571 Garud M, Godthi V, Reddy J, Dangi A, Pratap R. 2017. Cricket Inspired High Efficiency MEMS  
572 Speakers. *Proceedings* **1**:345. doi:10.3390/proceedings1040345
- 573 Godthi V, Balakrishnan R, Pratap R. 2022. The mechanics of acoustic signal evolution in field crickets.  
574 *Journal of Experimental Biology* **225**:jeb243374. doi:10.1242/jeb.243374
- 575 Gu J-J, Montealegre-Z F, Robert D, Engel MS, Qiao G-X, Ren D. 2012. Wing stridulation in a Jurassic  
576 katydid (Insecta, Orthoptera) produced low-pitched musical calls to attract females. *Proceedings*  
577 *of the National Academy of Sciences* **109**:3868–3873. doi:10.1073/pnas.1118372109
- 578 Hambric SA, Fahline JB. 2007. Structural Acoustics Tutorial—Part 2: Sound—Structure Interaction.  
579 *Acou Today* **3**:9. doi:10.1121/1.2961152
- 580 Hansell M, Ruxton G. 2008. Setting tool use within the context of animal construction behaviour. *Trends*  
581 *in Ecology & Evolution* **23**:73–78. doi:10.1016/j.tree.2007.10.006
- 582 Hunt GR, Gray RD, Taylor AH. 2013. Why is tool use rare in animals? In: Boesch C, Sanz CM, Call J,  
583 editors. *Tool Use in Animals: Cognition and Ecology*. Cambridge: Cambridge University Press.  
584 pp. 89–118. doi:10.1017/CBO9780511894800.007
- 585 K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology. 2020. Raven Lite:  
586 Interactive Sound Analysis Software (Version 2.0).
- 587 Kostarakos K, Römer H. 2010. Sound transmission and directional hearing in field crickets:  
588 neurophysiological studies outdoors. *J Comp Physiol A* **196**:669–681. doi:10.1007/s00359-010-  
589 0557-x
- 590 Mhatre N. 2018. Tree cricket baffles are manufactured tools. *Ethology* **124**:691–693.  
591 doi:10.1111/eth.12773
- 592 Mhatre N, Balakrishnan R. 2007. Phonotactic walking paths of field crickets in closed-loop conditions  
593 and their simulation using a stochastic model. *Journal of Experimental Biology* **210**:3661–3676.  
594 doi:10.1242/jeb.003764
- 595 Mhatre N, Balakrishnan R. 2006. Male spacing behaviour and acoustic interactions in a field cricket:  
596 implications for female mate choice. *Animal Behaviour* **72**:1045–1058.  
597 doi:10.1016/j.anbehav.2006.02.022
- 598 Mhatre N, Malkin R, Deb R, Balakrishnan R, Robert D. 2017. Tree crickets optimize the acoustics of  
599 baffles to exaggerate their mate-attraction signal. *eLife* **6**:e32763. doi:10.7554/eLife.32763
- 600 Muñoz MI, Halfwerk W. 2022. Amplification of frog calls by reflective leaf substrates: implications for  
601 terrestrial and arboreal species. *Bioacoustics* **31**:490–503. doi:10.1080/09524622.2021.1978319
- 602 Pierce JD. 1986. A Review of Tool Use in Insects. *The Florida Entomologist* **69**:95–104.  
603 doi:10.2307/3494748
- 604 Prozesky-Schulze L, Prozesky OPM, Anderson F, Van Der Merwe GJJ. 1975. Use of a self-made sound  
605 baffle by a tree cricket. *Nature* **255**:142–143. doi:10.1038/255142a0
- 606 Regen J. 1913. Über die Anlockung des Weibchens von *Gryllus campestris* L. durch telephonisch  
607 übertragene Stridulationslaute des Männchens. *Pflügers Archiv European Journal of Physiology*  
608 **155**:193–200.
- 609 Robillard T, Grandcolas P, Desutter-Grandcolas L. 2007. A shift toward harmonics for high-frequency  
610 calling shown with phylogenetic study of frequency spectra in Eneopterinae crickets (Orthoptera,  
611 Grylloidea, Eneopteridae). *Can J Zool* **85**:1264–1275. doi:10.1139/Z07-106
- 612 Römer H. 2021. Neurophysiology goes wild: from exploring sensory coding in sound proof rooms to  
613 natural environments. *J Comp Physiol A* **207**:303–319. doi:10.1007/s00359-021-01482-6
- 614 Römer H. 2015. Directional hearing: from biophysical binaural cues to directional hearing outdoors. *J*  
615 *Comp Physiol A* **201**:87–97. doi:10.1007/s00359-014-0939-6
- 616 Römer H, Butlin RK, Guilford T, Krebs JR. 1993. Environmental and biological constraints for the  
617 evolution of long-range signalling and hearing in acoustic insects. *Philosophical Transactions of*

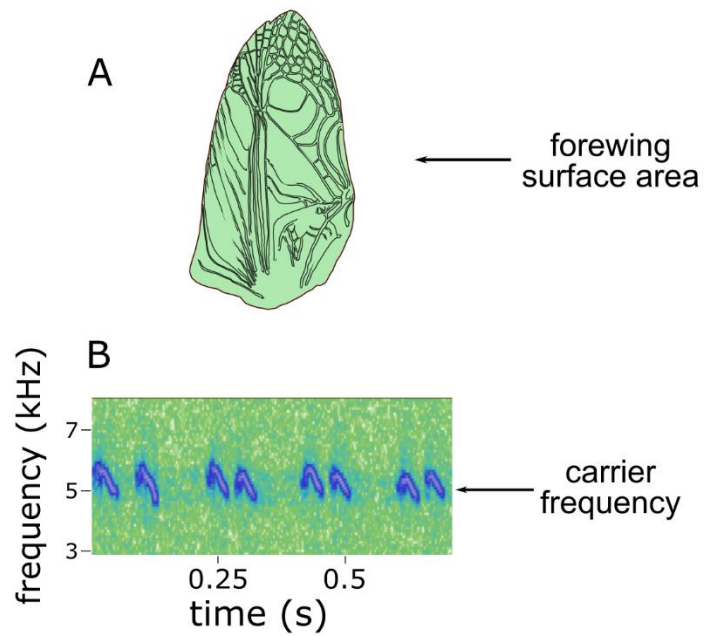
- 618 *the Royal Society of London Series B: Biological Sciences* **340**:179–185.  
619 doi:10.1098/rstb.1993.0056
- 620 Romer H, Lewald J. 1992. High-frequency sound transmission in natural habitats: implications for the  
621 evolution of insect acoustic communication. *Behav Ecol Sociobiol* **29**:437–444.  
622 doi:10.1007/BF00170174
- 623 Rossing TD, editor. 2014. Springer Handbook of Acoustics. New York, NY: Springer New York.  
624 doi:10.1007/978-1-4939-0755-7
- 625 Schindelin J, Rueden CT, Hiner MC, Eliceiri KW. 2015. The ImageJ ecosystem: An open platform for  
626 biomedical image analysis. *Molecular Reproduction and Development* **82**:518–529.  
627 doi:10.1002/mrd.22489
- 628 Senter P. 2008. Voices of the past: a review of Paleozoic and Mesozoic animal sounds: review. *Historical*  
629 *Biology* **20**:255–287. doi:10.1080/08912960903033327
- 630 Seybert AF, Wu TW, Wu XF. 1994. Experimental validation of finite element and boundary element  
631 methods for predicting structural vibration and radiated noise (No. NASA-CR-4561).
- 632 Song H, Amédégnato C, Cigliano MM, Desutter-Grandcolas L, Heads SW, Huang Y, Otte D, Whiting  
633 MF. 2015. 300 million years of diversification: elucidating the patterns of orthopteran evolution  
634 based on comprehensive taxon and gene sampling. *Cladistics* **31**:621–651. doi:10.1111/cla.12116
- 635 Spagnoletti N, Visalberghi E, Ottoni E, Izar P, Frigaszy D. 2011. Stone tool use by adult wild bearded  
636 capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *Journal of*  
637 *Human Evolution* **61**:97–107. doi:10.1016/j.jhevol.2011.02.010
- 638 Weissman DB, Gray DA. 2019. Crickets of the genus *Gryllus* in the United States (Orthoptera: Gryllidae:  
639 Gryllinae). *Zootaxa* **4705**:1–277. doi:10.11646/zootaxa.4705.1.1
- 640 Woodrow C, Baker E, Jonsson T, Montealegre-Z F. 2022. Reviving the sound of a 150-year-old insect:  
641 The bioacoustics of *Prophalangopsis obscura* (Ensifera: Hagloidea). *PLOS ONE* **17**:e0270498.  
642 doi:10.1371/journal.pone.0270498  
643
- 644



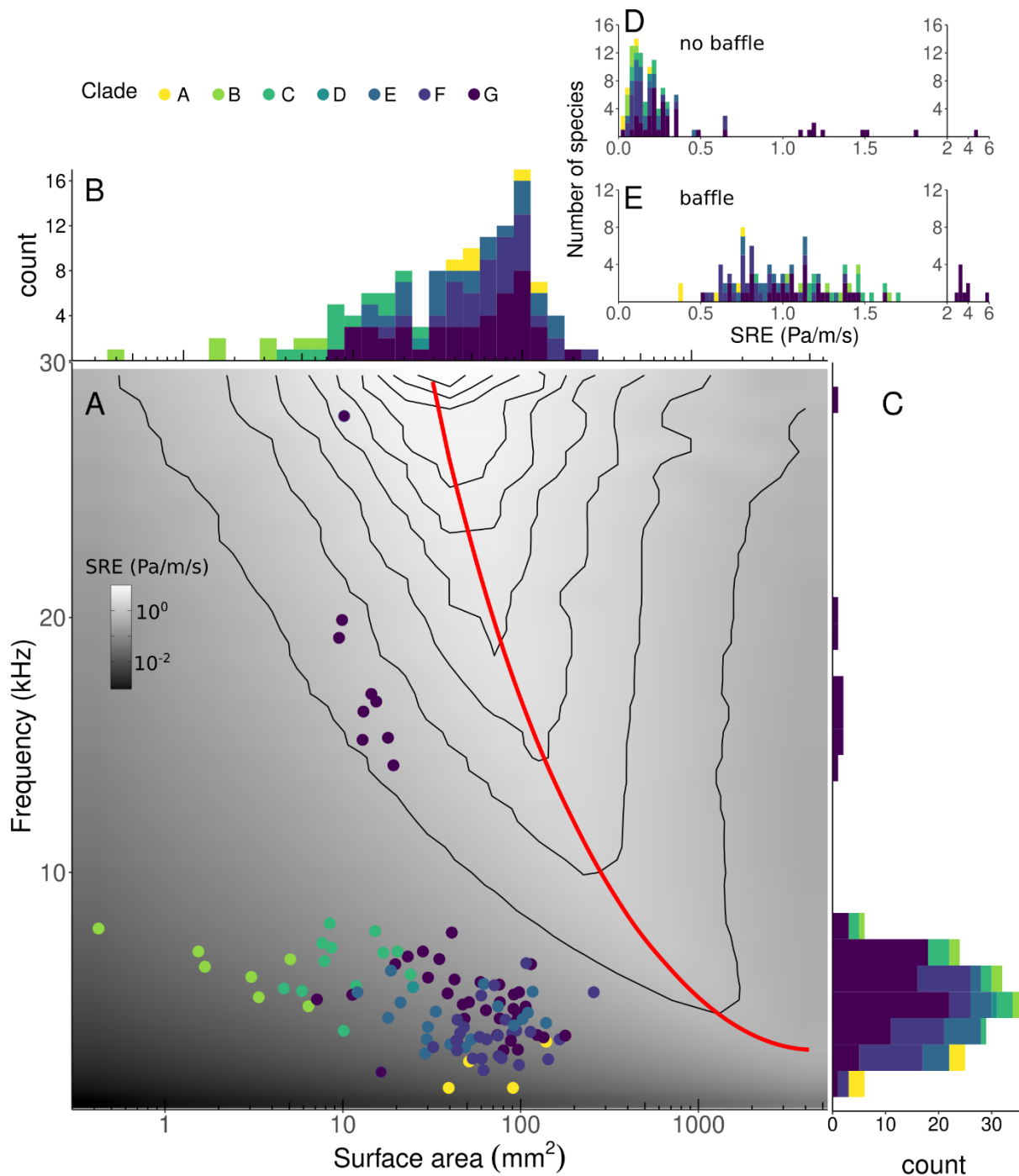
645 **Figures and Tables**



646 **Figure 1.** Crickets were sampled evenly across the cricket phylogeny covering most taxonomic groups  
 647 known to produce calls. **A.** Representative images of cricket males with wings raised in calling posture.  
 648 From upper left to lower right, species pictured are: *Hoplosphyrum boreale* (photo: James P. Bailey),  
 649 *Phyllopalpus pulchellus* (photo: Wilbur Hershberger), *Lerneca inalata* (photo: Richard C. Hoyer),  
 650 *Meloimorpha japonica* (photo: Ryosuke Kuwahara), *Oecanthus quadripunctatus* (photo: James P.  
 651 Bailey), and *Turanogryllus eous* (photo: Taewoo Kim). Boxes with letter indicate the clade to which each  
 652 species belongs. **B.** Phylogeny illustrating the seven clades defined by Chintauan-Marquier et al (2016)  
 653 along with subfamilies within each clade (branch lengths not to scale). Only subfamilies from which we  
 654 sampled for this study are included. Subfamilies with asterisks are polyphyletic between multiple clades.  
 655 **C.** Specimen sampling scheme. Top panel shows the distribution of all species described across each of  
 656 the seven clades in Grylloidea (according to Orthoptera Species File, as of February 16, 2022). Bottom  
 657 panel shows distribution of species that were sampled for this study.  
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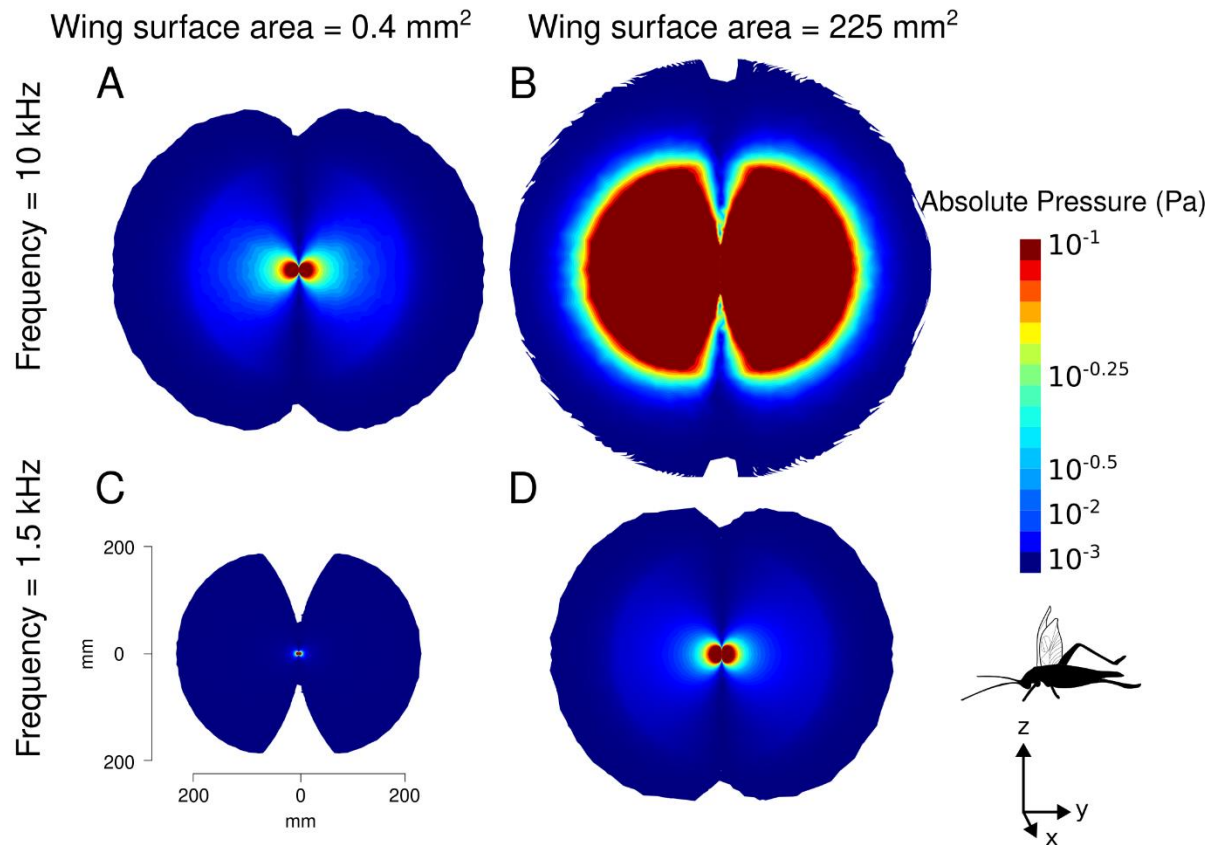
**Figure Supplement 1-1.** Measuring acoustic-morphospace of crickets. Wing area and call frequency were quantified. **A.** Wing surface area was calculated as the area of the entire forewing. **B.** The carrier frequency (sometimes called fundamental frequency) of the call was identified from spectrograms 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.

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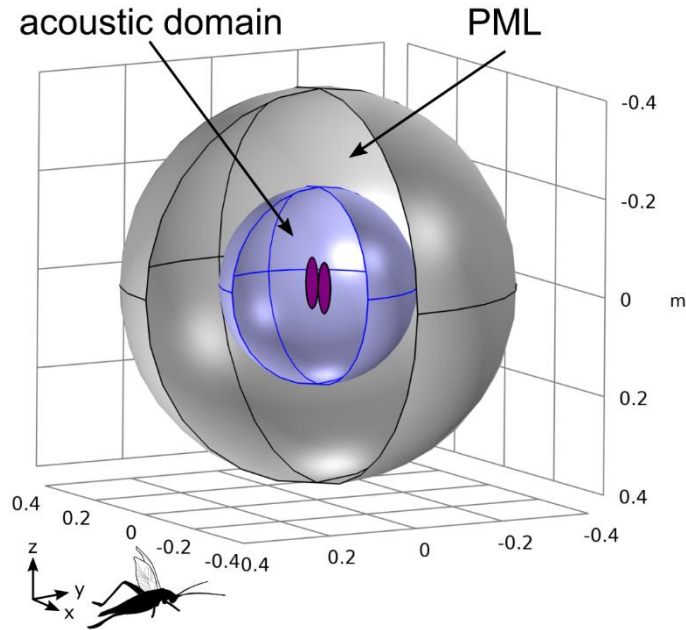
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**Figure Supplement 2-1.** Sound fields produced by modeled wings vary with respect to call frequency and wing size. Fields are oriented such that wings are perpendicular to page and vibrate left to right, as indicated by the silhouette cricket. Sound fields are given for the following combinations of wing size and frequency: **A.** wing size =  $0.04 \text{ mm}^2$ , frequency = 10 kHz; **B.** wing size =  $225 \text{ mm}^2$ , frequency = 10 kHz; **C.** wing size =  $0.4 \text{ mm}^2$ , frequency = 1.5 kHz; **D.** wing size =  $225 \text{ mm}^2$ , 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).

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**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.

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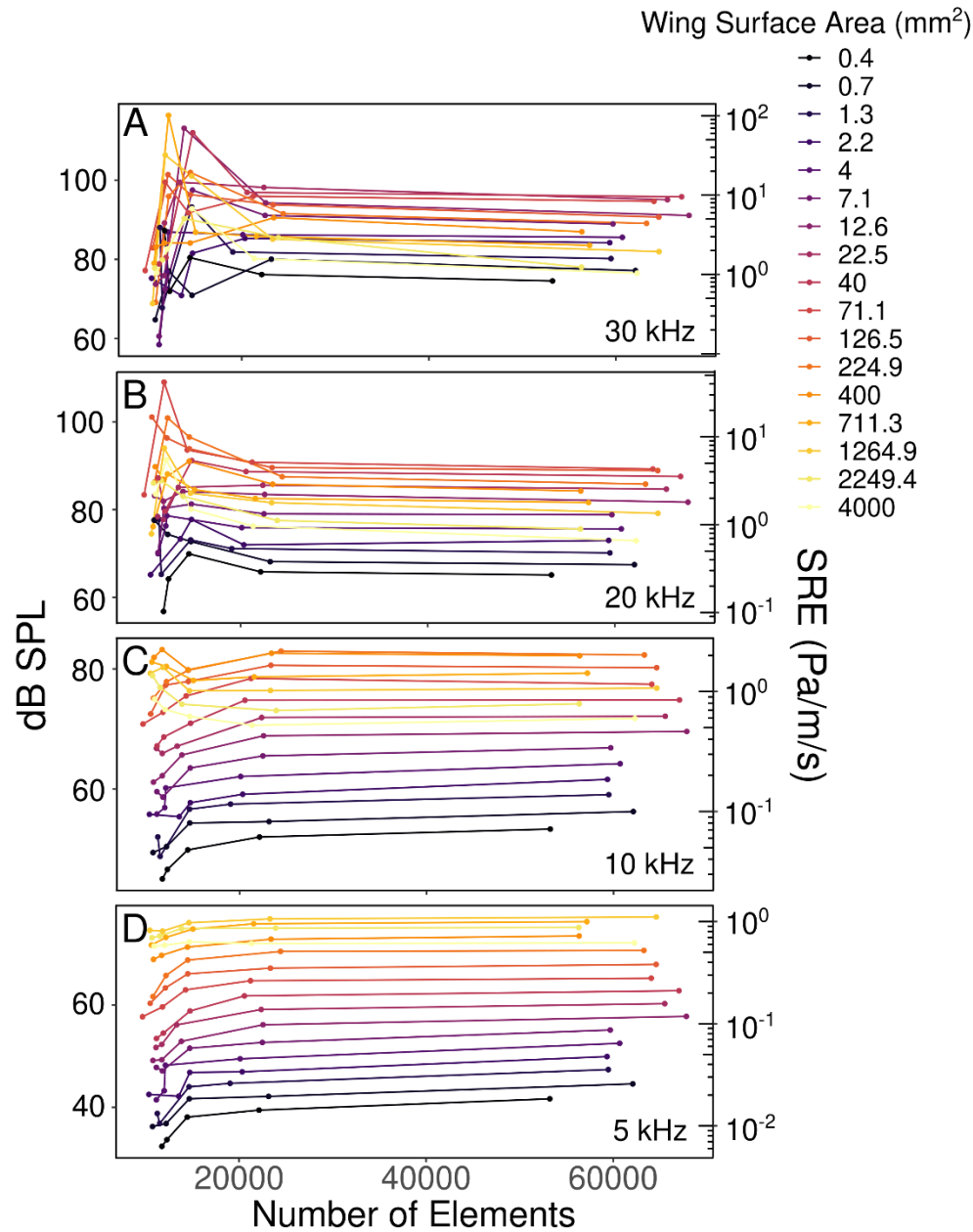
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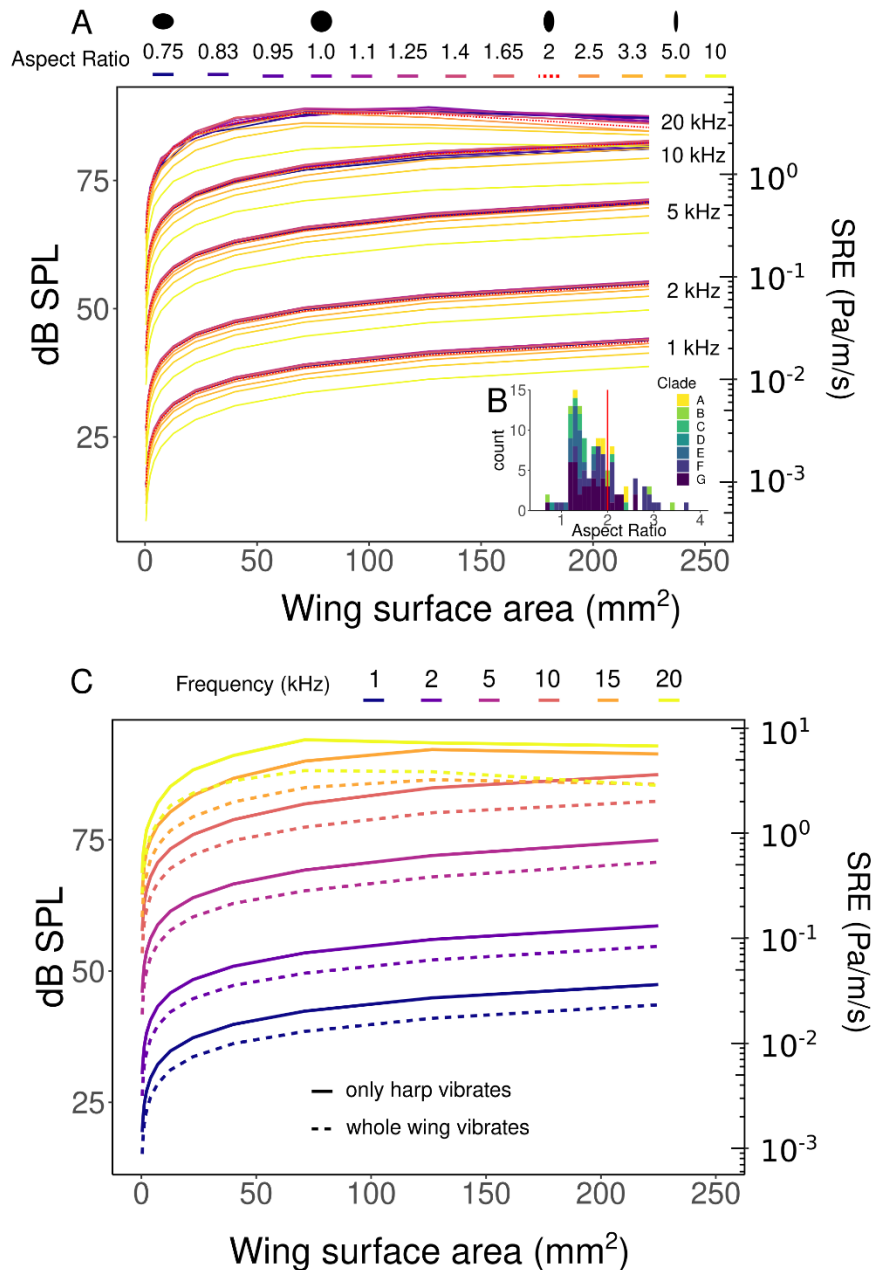
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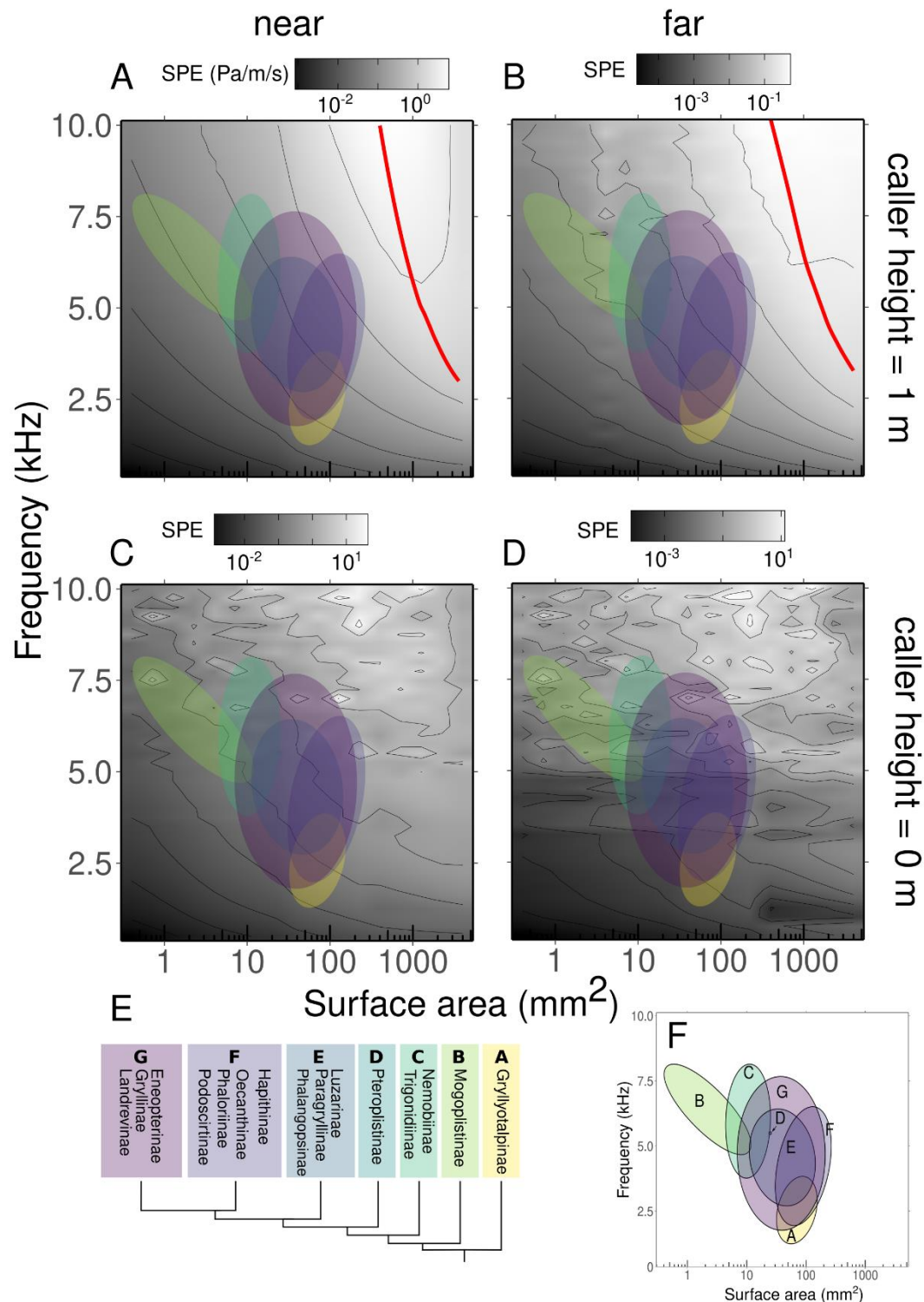
**Figure Supplement 2-3.** Mesh sensitivity analysis for models based on the finite element method. Each line represents the SPL of a single wing size with a different number of mesh elements. Each panel shows this analysis at a different frequency: A. 30 kHz, B. 20 kHz, C. 10 kHz, D. 5 kHz. As the difference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

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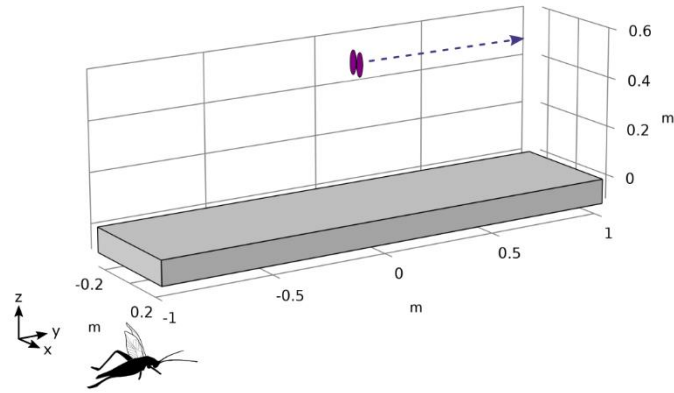
**Supplement to Figure 2-4.** Wing aspect ratio and use of a “harp” resonator do not significantly impact SRE within biologically-relevant ranges of wing size and call frequency. **A.** The effect of wing aspect ratio on SRE at six different call frequencies. The aspect ratio that was used on all models 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). **C.** 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.



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**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 – 0.2 m “near” and 0.8 – 0.9 m “far”). **A.** Distance = near, height = 1 m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 0 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.

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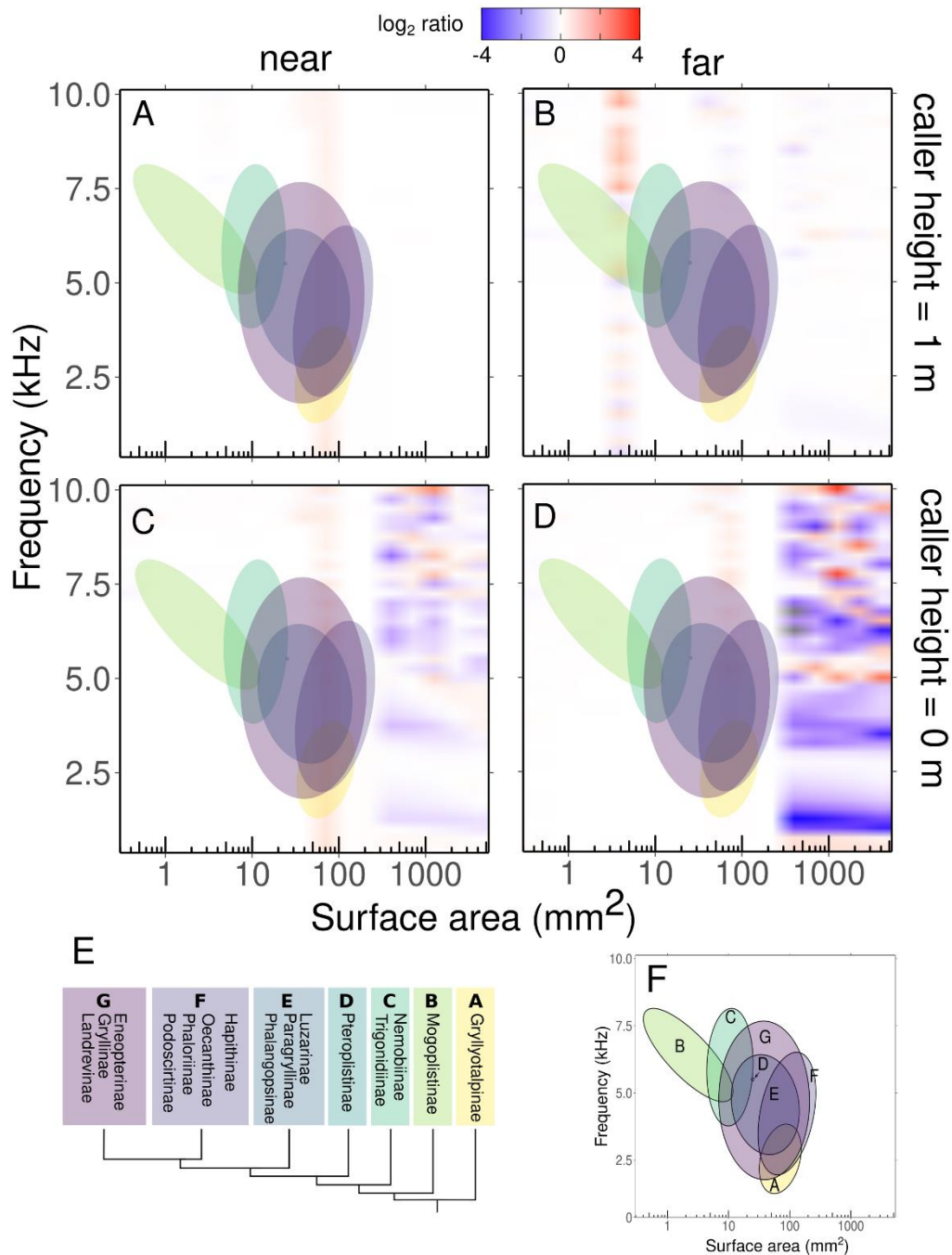
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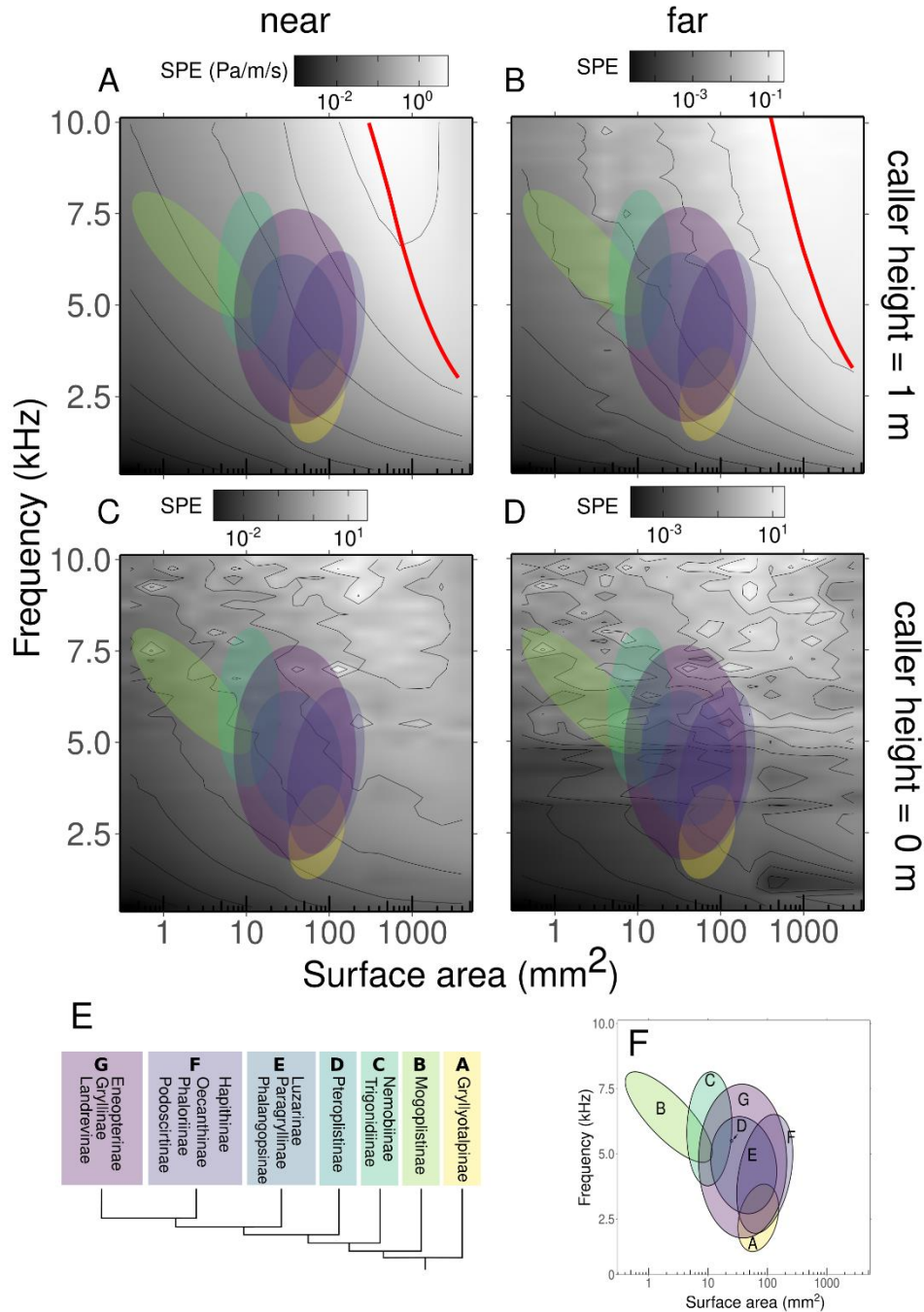
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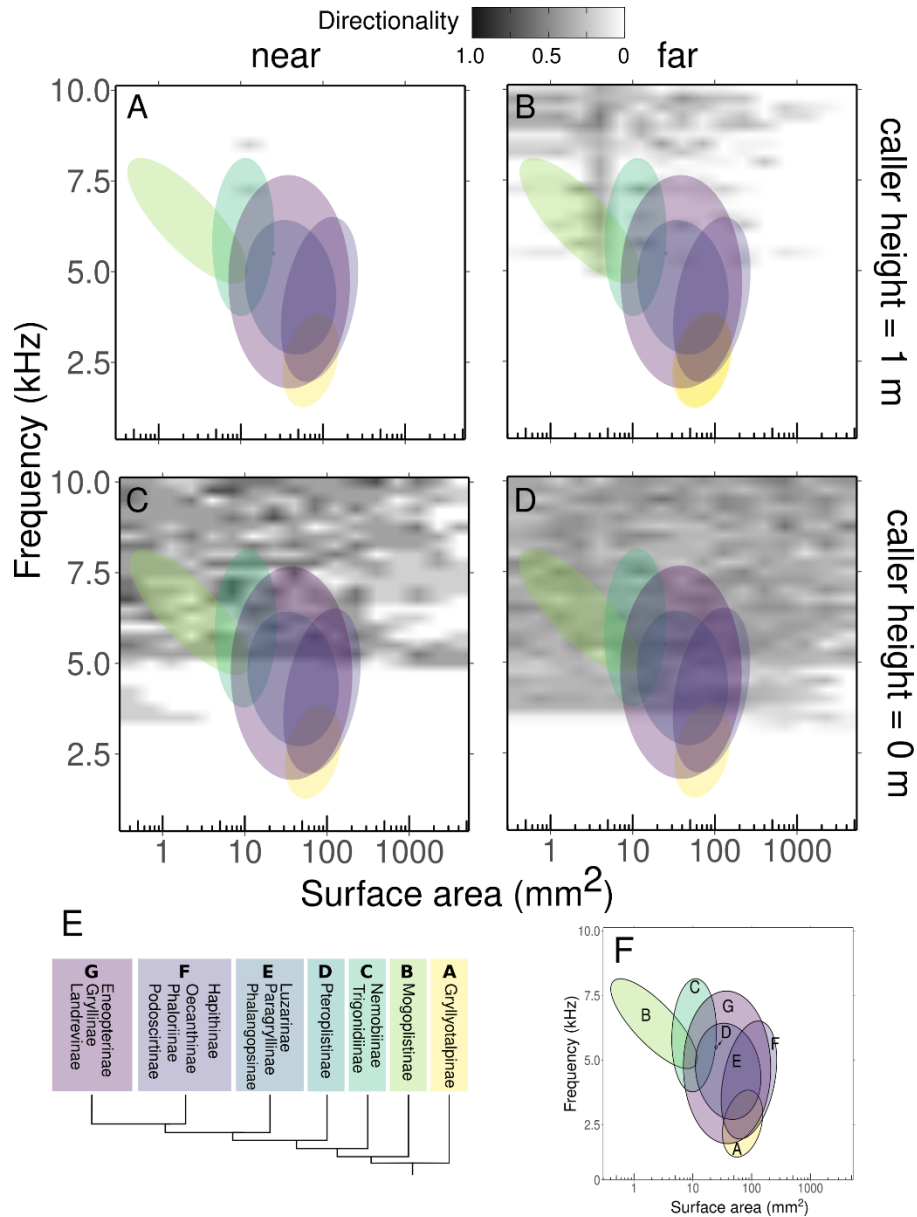


**Supplement to figure 3-2.** Acoustic hardness of ground does not significantly influence SPE at biologically relevant ranges of wing size and call frequency. Comparison of SPE over hard vs soft ground. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 0.2 m “near” and 0.8 – 0.9 m “far”). **A.** Distance = near, height = 1 m, **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<sub>2</sub> ratio instead of a straight proportion. Log<sub>2</sub> 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

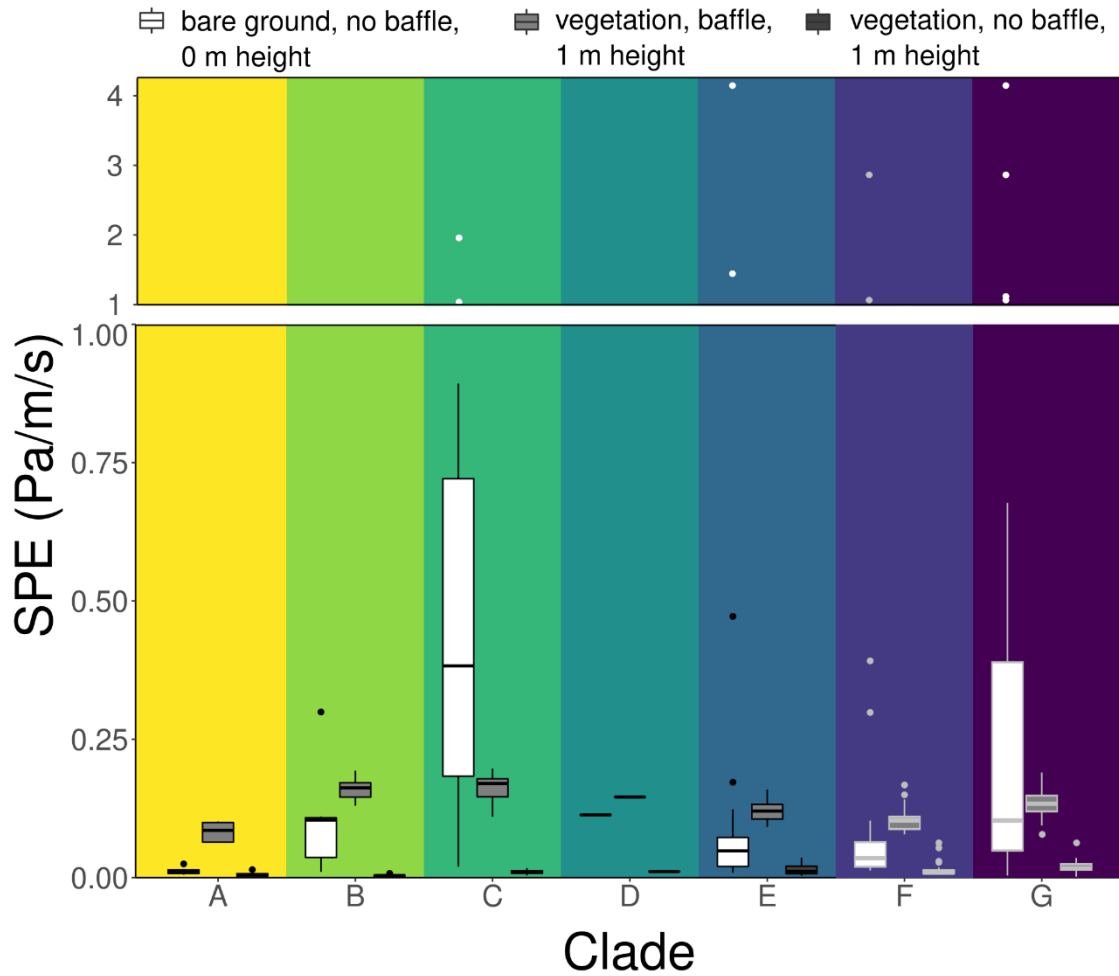


**Supplement to figure 3-3.** Vegetation decreases efficiency overall but does not substantially change the landscape pattern of efficiency. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 0.2 m “near” and 0.8 – 0.9 m “far”). In each height and distance scenario, an excess attenuation factor due to vegetation was also applied. **A.** Distance = near, height = 1 m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 0 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.

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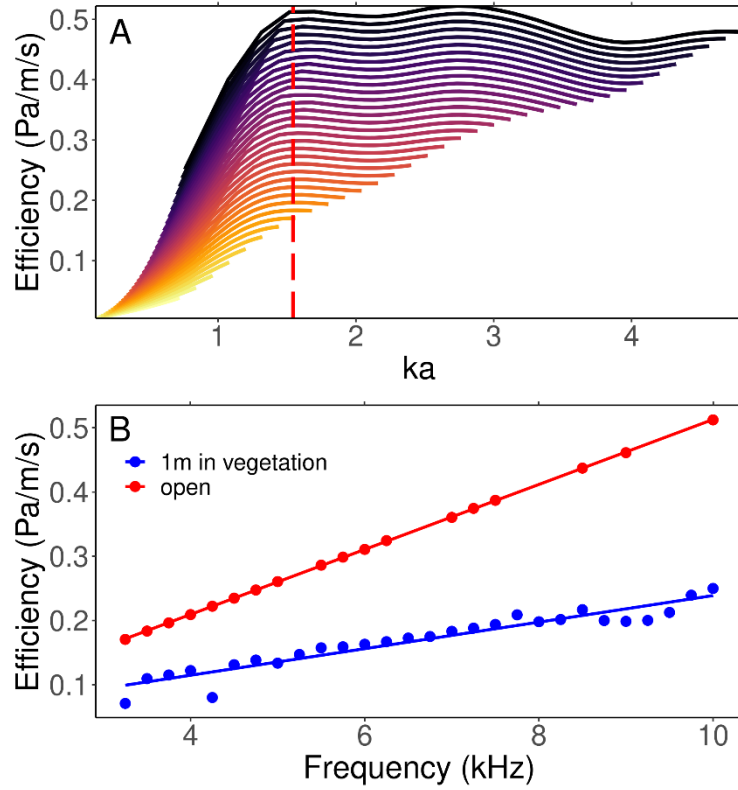
**Supplement to figure 3-4.** Call directionality decreases at higher frequencies, particularly with grounded calling. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 0.2 m “near” and 0.8 – 0.9 m “far”). **A.** Distance = near, 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.

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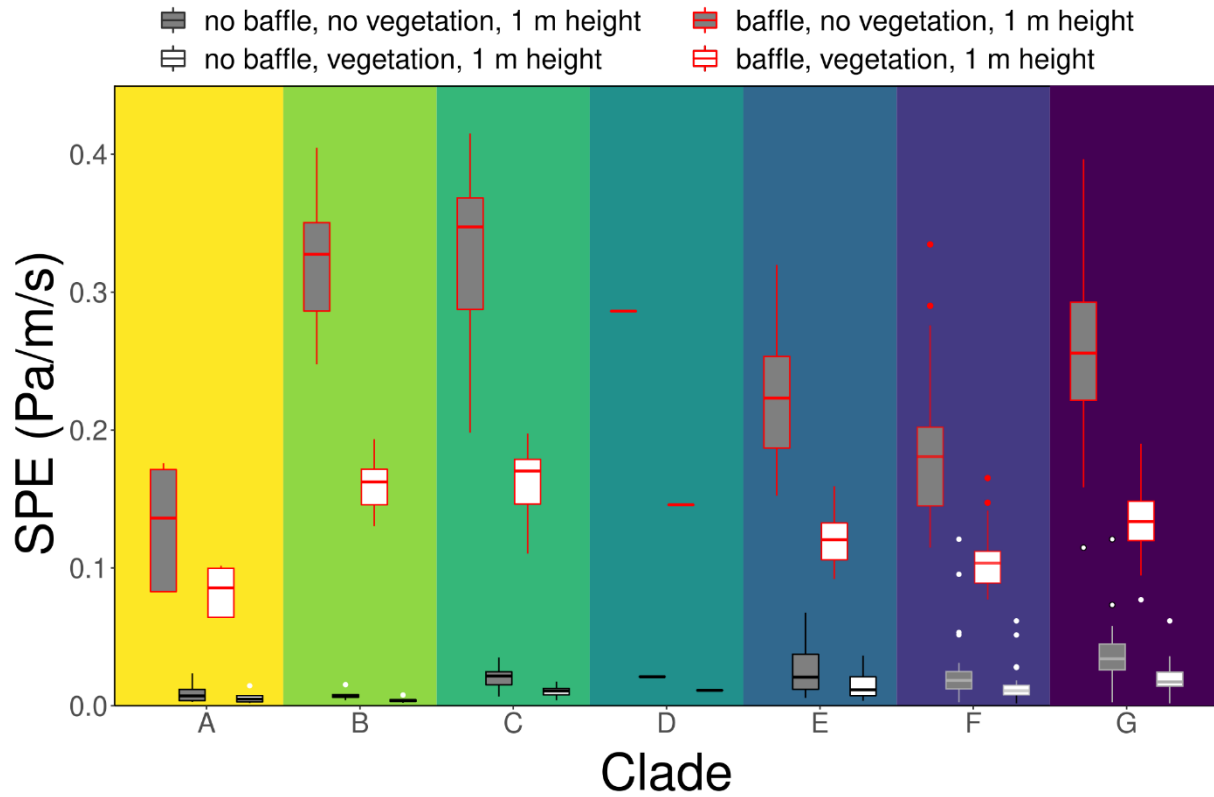
**Supplement to Figure 4-1.** Calculating efficiency with optimal baffle. **A.**  $ka$  at which optimal efficiency occurs for each frequency. Each frequency is represented by a different line. Line at which efficiency is maximized for each frequency (maximum efficiency ridge) is shown by red dashed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

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**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.

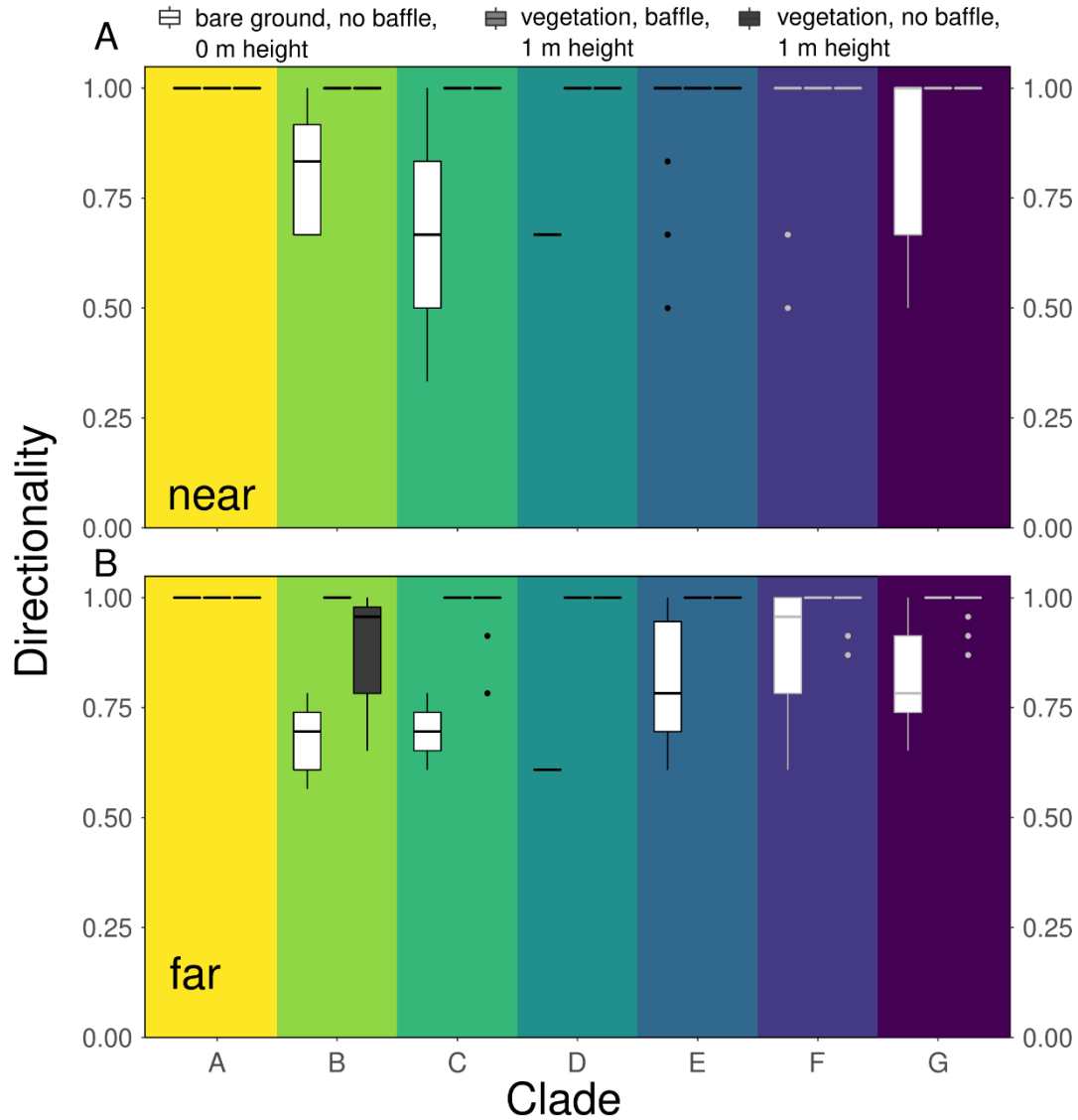
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**Figure 5.** Baffled and grounded calling do not substantially differ with respect to directionality, although it does vary somewhat by clade. **A.** Directionality in near condition, **B.** Directionality in far condition.

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

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

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number
E	Phalangopsinae	<i>Tremellia</i>	<i>timah</i> *	1	(Gorochov and Tan, 2012)
	Phaloriinae	<i>Phaloria</i>	<i>anapina</i> *	1	(Otte, 2007)
			<i>chopardi</i> *	1	(Desutter-Grandcolas, 2009)
			<i>jerelynae</i> *	1	(Gorochov and Tan, 2012)
		<i>Trellius</i>	<i>neesoon</i>	1	(Gorochov and Tan, 2012)
F	Hapithinae	<i>Hapithus</i>	<i>agitator</i> *	1	Orthoptera Species File Specimen ID: 138599
			<i>vagus</i> *	1	Orthoptera Species File Specimen ID: 65035
	Oecanthinae	<i>Neoxabea</i>	<i>bipunctata</i> *	1	Image captured for present study in lab
			<i>brevipes</i> *	1	(Zefa et al., 2018)
			<i>cerrojesusensis</i> *	1	Image captured for present study in lab
			<i>oltei</i> *	1	Image captured for present study in lab
		<i>Oecanthus</i>	<i>alexanderi</i> *	1	Image captured for present study in lab
			<i>angustus</i> *	1	PaDILspecies ID: <i>Oecanthus angustus</i>
			<i>argentinus</i> *	1	University of British Columbia Insect Collection, Specimen: SEM-UBC GRY-0951
			<i>forbsei</i> *	1	Image captured for present study in lab
			<i>fultoni</i> *	1	Orthoptera Species File Specimen ID: 40710
			<i>latipennis</i> *	1	University of Guelph Insect Collection: Specimen BIOUG44550-E07
				2	University of Guelph Insect Collection: Specimen BIOUG44550-E08
			<i>lineolatus</i> *	1	(Zefa et al., 2012)
			<i>major</i>	1	Orthoptera Species File Specimen ID: 40712
			<i>nigricornis</i> *	1	Orthoptera Species File Taxon ID: 345166
<i>niveus</i> *	1	Orthoptera Species File Taxon ID: 345151			
<i>pallidus</i> *	1	(Zefa et al., 2012)			

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

Clade	Subfamily	Genus	Species	Specimen	Relevant reference and/or collection specimen number	
G	Eneopterinae	<i>Cardiodactylus</i>	<i>guttulus</i> *	1	(Robillard and Ichikawa, 2009)	
			<i>novaeguinea</i> *	1	(Robillard and Ichikawa, 2009)	
		<i>Eurepa</i>	<i>bifasciata</i> *	1	(Robillard and Su, 2018)	
		<i>Gnominthus</i>	<i>baitabagus</i> *	1	(Robillard and Su, 2018)	
		<i>Lebinthus</i>	<i>bitaeniatus</i> *	1	(Robillard et al., 2013)	
			<i>luae</i> *	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF3208	
		<i>Myara</i>	<i>pakaria</i> *	1	(Otte, 2007)	
			<i>wintrena</i> *	1	(Otte, 2007)	
		<i>Pixibinthus</i>	<i>sonicus</i> *	1	(Anso et al., 2016)	
		<i>Salmanites</i>	<i>peekara</i> *	1	(Otte, 2007)	
		<i>Xenogryllus</i>	<i>eneopteroides</i> *	1	(Jaiswara et al., 2019)	
			<i>transversus</i> *	1	(Jaiswara et al., 2019)	
	Gryllinae	<i>Eurepella</i>	<i>mjobergi</i> *	1	PaDIL species ID: <i>Eurepella mjobergi</i>	
		<i>Gryllus</i>	<i>amarensis</i>	1	Museum D'Historie Naturelle ID: 7031	
			<i>assimilis</i> *	1	SINA species ID: <i>Gryllus assimilis</i>	
			<i>bimaculatus</i> *	1	Orthoptera Species File Taxon ID: 1122377	
			<i>brevicaudus</i> *	1	SINA species ID: <i>Gryllus brevicaudus</i>	
			<i>campestris</i> *	1	Need to figure out specific specimen	
				2	Need to figure out specific specimen	
<i>carvalhoi</i>			1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF7242		
<i>chaldeus</i>			1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF7192		
<i>chappuisi</i> *	1	Museum D'Historie Naturelle ID: MNHN-EO-ENSIF7046				

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

Table 2. Sources for call frequency data. Asterisk after species name indicates species is represented in both frequency and wing size datasets

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

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



Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
E	Phalangopsinae	Endecous	<i>didymus</i> *	1	(Castro-Souza et al., 2020)
			<i>itatibensis</i> *	1	(Mello and Pellegatti-Franco, 1998)
			<i>troglobius</i> *	1	(Castro-Souza et al., 2020)
			<i>timah</i> *	1	(Gorochov and Tan, 2012)
		<i>Tremellia</i>	<i>anapina</i> *	1	(Su and Rentz, 2000)
	Phaloriinae	<i>Phaloria</i>	<i>chopardi</i> *	1	(Desutter-Grandcolas, 2009)
			<i>jerelynae</i> *	1	(Gorochov and Tan, 2012)
			<i>baitabagus</i> *	1	(Vicente et al., 2015)
	F	Hapithinae	<i>Hapithus</i>	<i>melodius</i>	1
<i>vagus</i> *				1	Macaulay Library asset: 114470
<i>diplastes</i>				1	Handbook of crickets and katydids
<i>Orocharis</i>			<i>gryllodes</i>	1	Handbook of crickets and katydids
			<i>luteolira</i>	1	Handbook of crickets and katydids
			<i>nigrifrons</i>	1	Handbook of crickets and katydids
			<i>saltator</i>	1	Handbook of crickets and katydids
			<i>tricornis</i>	1	Handbook of crickets and katydids
			<i>bipunctata</i> *	1	Crickets north of Mexico species ID: <i>Neoxabea bipunctata</i>
			<i>brevipes</i> *	1	(Zefa et al., 2018)
Oecanthinae		<i>Neoxabea</i>	<i>brevipes</i> *	1	(Zefa et al., 2018)

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
F	<i>Oecanthinae</i>	<i>Oecanthus</i>	<i>cerrojesusensis</i> *	1	Orthoptera Species File Sound ID: 2345
			<i>ottei</i> *	1	Orthoptera Species File Sound ID: 2346
			<i>alexanderi</i> *	1	Crickets North of Mexico Species ID: <i>Oecanthus alexanderi</i>
			<i>angustus</i> *	1	(Otte, 2007)
			<i>argentinus</i> *	1	Crickets North of Mexico Species ID: <i>Oecanthus argentinus</i>
			<i>argentinus</i> * <i>californicus</i>	2	Orthoptera Species File Sound ID: 1535
				1	Crickets North of Mexico Species ID: <i>Oecanthus californicus</i>
			<i>californicus</i> <i>forbsei</i> *	2	Orthoptera Species File Sound ID: 1536
				1	Crickets North of Mexico Species ID: <i>Oecanthus forbsei</i>
			<i>fultoni</i> *	1	Crickets North of Mexico Species ID: <i>Oecanthus fultoni</i>
			<i>latipennis</i> *	1	Crickets North of Mexico Species ID: <i>Oecanthus latipennis</i>
			<i>latipennis</i> *	2	Orthoptera Species File Sound ID: 1002
			<i>lineolatus</i> *	1	(Zefa et al., 2012)
			<i>nigricornis</i> *	1	Crickets North of Mexico Species ID: <i>Oecanthus nigricornis</i>
			<i>niveus</i> *	1	Crickets North of Mexico Species ID: <i>Oecanthus niveus</i>
			<i>pallidus</i> *	1	(Zefa et al., 2012)
			<i>pictus</i> *	1-9	Orthoptera Species File Taxon ID: 1223417 (9 songs from different temperatures)
<i>pini</i> *	1	Crickets North of Mexico Sound File: 587sl			

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
F	Oecanthinae	<i>Oecanthus</i>	<i>quadripunctatus*</i>	1	Orthoptera Species File Sound File 1531
			<i>rileyi*</i>	1	Orthoptera Species File Sound File: 1540
			<i>rufescens*</i>	1	(Otte, 2007)
			<i>texensis*</i>	1	(Symes and Collins, 2013)
			<i>varicornis*</i>	1	Crickets North of Mexico Sound File: 593sl
			<i>walker</i>	1	Crickets North of Mexico Species ID: <i>Oecanthus walkeri</i>
			<i>affinis*</i>	1	(Otte, 2007)
	Podoscirtinae	<i>Madasumma</i>	<i>jirranda</i>	1	(Otte, 2007)
			<i>kanina</i>	1	(Otte, 2007)
			<i>loorea</i>	1	(Otte, 2007)
			<i>formosa*</i>	1	(He, 2012)
		<i>Truljalia</i>	<i>suikei*</i>	1	(Tan et al., 2020)
		<i>Varitrella</i>	<i>azurensis*</i>	1	Museum D’Histoire Naturelle ID: MNHN-SO-2018-100
	G	Eneopterinae	<i>Agnotecous</i>	<i>brachypterus*</i>	1
<i>clarus</i>				1	Museum D’Histoire Naturelle ID: MNHN-SO-2018-102
<i>meridionalis*</i>				1	Museum D’Histoire Naturelle ID: MNHN-SO-2018-99
<i>Agnotecous</i>			<i>pinsula*</i>	1	(Robillard et al., 2010)
			<i>sarramea*</i>	1	(Robillard and Desutter-Grandcolas, 2004)

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
G	Eneopterinae	<i>Agnotecous</i>	<i>yahoue</i> *	1	(Robillard and Desutter-Grandcolas, 2004)
			<i>binderia</i> *	1	(Otte, 2007)
		<i>Arilpa</i>	<i>gidya</i> *	1	(Otte, 2007)
			<i>wirrilla</i>	1	(Otte, 2007)
			<i>guttulus</i> *	1	(Robillard and Ichikawa, 2009)
		<i>Cardiodactylus</i>	<i>novaeguinea</i> *	1	(Otte, 2007)
			<i>bifasciata</i> *	1	(Otte, 2007)
		<i>Eurepa</i>	<i>eeboolaga</i>	1	(Otte, 2007)
			<i>marginipennis</i>	1	(Otte, 2007)
			<i>noarana</i>	1	(Otte, 2007)
			<i>nurdina</i>	1	(Otte, 2007)
			<i>wirkutta</i>	1-2	(Otte, 2007) (range of values given in publication)
			<i>woortooa</i>	1	(Otte, 2007)
			<i>yumbena</i>	1	(Otte, 2007)
			<i>bitaeniatus</i> *	1	(Robillard and Tan, 2013)
		<i>Gnominthus</i>	<i>baitabagus</i> *	1	(Anso et al., 2016)
		<i>Lebinthus</i>	<i>luae</i> *	1	(Robillard and Tan, 2013)
<i>aperta</i>	1		(Otte, 2007)		

Clade	Subfamily	Genus	Species	Recording	Relevant reference and/or collection specimen number
G	Eneopterinae	<i>Myara</i>	<i>marimbula</i>	1	(Otte, 2007)
			<i>muttaburra</i>	1	(Otte, 2007)
			<i>pakaria</i> *	1	(Otte, 2007)
			<i>sordida</i>	1	(Otte, 2007)
			<i>unicolor</i>	1-2	(Otte, 2007) (range of values given in publication)
			<i>wintrena</i> *	1	(Robillard and Desutter-Grandcolas, 2004)
			<i>yurgama</i>	1	(Otte, 2007)
			<i>vittatus</i>	1	(Robillard and Desutter-Grandcolas, 2004)
		<i>Nisitrus</i>	<i>allaris</i>	1	(Otte, 2007)
		<i>Pixibinthus</i>	<i>sonicus</i> *	1	(Anso et al., 2016)
		<i>Salmanites</i>	<i>ninbella</i>	1	(Otte, 2007)
			<i>noccundris</i>	1	(Otte, 2007)
			<i>noonamina</i>	1	(Otte, 2007)
			<i>peekara</i> *	1	(Otte, 2007)
			<i>poene</i>	1	(Otte, 2007)
			<i>taltantris</i>	1	(Otte, 2007)
			<i>terba</i>	1-2	(Otte, 2007) (range of values given in publication)
			<i>wittilliko</i>	1	(Otte, 2007)

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

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

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

Full citations for Specimen data:

- Anso J, Barrabé L, Desutter-Grandcolas L, Jourdan H, Grandcolas P, Dong J, Robillard T. 2016. Old Lineage on an Old Island: Pixibinthus, a New Cricket Genus Endemic to New Caledonia Shed Light on Gryllid Diversification in a Hotspot of Biodiversity. *PLOS ONE* **11**:e0150920. doi:10.1371/journal.pone.0150920
- Barranco P, Gilgado JD, Ortuño VM. 2013. A new mute species of the genus Nemobius Serville (Orthoptera, Gryllidae, Nemobiinae) discovered in colluvial, stony debris in the Iberian Peninsula: A biological, phenological and biometric study. *Zootaxa* **3691**:201–219. doi:10.11646/zootaxa.3691.2.1
- Castro-Souza RA, Zefa E, Ferreira RL. 2020. New troglobitic and troglophilic syntopic species of Endecous (Orthoptera, Grylloidea, Phalangopsidae) from a Brazilian cave: a case of sympatric speciation? *Zootaxa* **4810**:271–304. doi:10.11646/zootaxa.4810.2.3



- Cole JA, Funk DH. 2019. *Anaxipha hyalictetra* sp. n. (Gryllidae: Trigonidiinae), a new sword-tailed cricket species from Arizona. *Journal of Orthoptera Research* **28**:3–9.
- Dambach M, Gras A. 1995. Bioacoustics of a miniature cricket, *Cycloptiloides canariensis* (Orthoptera: Gryllidae: Mogoplistinae). *Journal of Experimental Biology* **198**:721–728. doi:10.1242/jeb.198.3.721
- Desutter-Grandcolas L. 2009. New and little known crickets from Espiritu Santo Island, Vanuatu (Insecta, Orthoptera, Grylloidea, Pseudotrigonidium Chopard, 1915, Phaloriinae and Nemobiinae p.p.). *zoos* **31**:619–659. doi:10.5252/z2009n3a12
- Desutter-Grandcolas L, Robillard T. 2006. Phylogenetic systematics and evolution of Agnotecous in New Caledonia (Orthoptera: Grylloidea, Eneopteridae). *Systematic Entomology* **31**:65–92. doi:10.1111/j.1365-3113.2005.00299.x
- Gorochov AV, Tan MK. 2012. New crickets of the subfamilies Phaloriinae and Pteroplistinae (Orthoptera: Gryllidae) from Singapore. *Zootaxa* **3525**:18–34. doi:10.11646/zootaxa.3525.1.2
- He Z. 2012. A new species of *Truljalia* Gorochov 1985 from Taiwan (Orthoptera: Gryllidae; Podoscirtinae; Podoscirtini). *Zootaxa* **3591**:79–83. doi:10.11646/zootaxa.3591.1.5
- He Z, Lu H, Liu Y, Li K. 2017. A new species of *Ornebius* Guérin-Méneville, 1844 from East China (Orthoptera: Mogoplistidae: Mogoplistinae). *Zootaxa* **4303**:445–450. doi:10.11646/zootaxa.4303.3.10
- Hugel S. 2009. New Landrevinae from Mascarene islands and little known Landrevinae from Africa and Comoros (Grylloidea: Landrevinae). *Annales de la Société entomologique de France (NS)* **45**:193–215. doi:10.1080/00379271.2009.10697602
- Jaiswara R, Dong J, Ma L, Yin H, Robillard T. 2019. Taxonomic revision of the genus *Xenogryllus* Bolívar, 1890 (Orthoptera, Gryllidae, Eneopterinae, Xenogryllini). *Zootaxa* **4545**:301–338. doi:10.11646/zootaxa.4545.3.1
- Kavanagh MW, Young D. 1989. Bilateral symmetry of sound production in the mole cricket, *Gryllotalpa australis*. *J Comp Physiol A* **166**:43–49. doi:10.1007/BF00190208
- Kim T. 2011. A Taxonomic Study of the Scaly Cricket Family Mogoplistidae (Orthoptera: Ensifera: Grylloidea) in Korea. *Zootaxa* **2928**:41–48. doi:10.11646/zootaxa.2928.1.4
- Lima RM, Schuchmann K-L, Tissiani AS, Nunes LA, Jahn O, Ganchev TD, Lhano MG, Marques MI. 2018. Tegmina-size variation in a Neotropical cricket with implications on spectral song properties. *Journal of Natural History* **52**:1225–1241. doi:10.1080/00222933.2018.1457728
- Love RE, Walker TJ. 1979. Systematics and Acoustic Behavior of Scaly Crickets (Orthoptera: Gryllidae: Mogoplistinae) of Eastern United States. *Transactions of the American Entomological Society (1890-)* **105**:1–66.
- Martins L de P, Redü DR, Oliveira GL de, Zefa E. 2012. Recognition characters and new records of two species of Phylloscyrtini (Orthoptera, Gryllidae, Trigonidiinae) from southern Brazil. *Iheringia, Sér Zool* **102**:95–98. doi:10.1590/S0073-47212012000100013
- Martins LDP, Silva LGD, Henriques AL, Zefa E. 2013. First record of the genera *Luzarida* Hebard, 1928 and *Luzaridella* Desutter-Grandcolas, 1992 (Orthoptera, Gryllidae, Phalangopsinae) from Brazil, including a new species and description of the female of *Luzarida lata* Gorochov, 2011. *Zootaxa* **3609**:421–430. doi:10.11646/zootaxa.3609.4.4
- McIntyre ME. 1977. Acoustical communication in the field crickets *Pteronemobius nigrovus* and *P. bigelowi* (Orthoptera: Gryllidae). *New Zealand Journal of Zoology* **4**:63–72. doi:10.1080/03014223.1977.9517937
- Mello F de AG de, Pellegatti-Franco F. 1998. A New Cave Cricket of the Genus *Endecous* from Southeastern Brazil and Characterization of Male and Female Genitalia of *E. itatibensis* Rehn, 1918 (Orthoptera: Grylloidea: Phalangopsidae: Luzarinae). *Journal of Orthoptera Research* **185**–188. doi:10.2307/3503517
- Mello F de AG de, Reis JC dos. 1994. Substrate Drumming and Wing Stridulation Performed during Courtship by a New Brazilian Cricket (Orthoptera: Grylloidea: Phalangopsidae). *Journal of Orthoptera Research* **21**–24. doi:10.2307/3503603
- Milach EM, Costa MKMD, Martins LDP, Nunes LA, Silva DSM, Garcia FRM, Oliveira ECD, Zefa E. 2016. New species of tree cricket *Oecanthus* Serville, 1831 (Orthoptera: Gryllidae: Oecanthinae) from Reserva Natural Vale, Espírito Santo, Brazil, with chromosome complement. *Zootaxa* **4173**:137–146. doi:10.11646/zootaxa.4173.2.4

- Milach EM, Martins LDP, Costa MKMD, Gottschalk MS, Oliveira GLD, Redü DR, Neutzling AS, Dornelles JEF, Vasconcellos LA, Zefa E. 2015. A new species of tree crickets *Oecanthus* (Orthoptera, Gryllidae, Oecanthinae) in tobacco plantation from Southern Brazil, with body color variation. *Zootaxa* **4018**:266–278. doi:10.11646/zootaxa.4018.2.6
- Nischk F, Otte D. 2000. Bioacoustics, Ecology and Systematics of Ecuadorian Rainforest Crickets (Orthoptera: Gryllidae: Phalangopsinae), with a Description of Four New Genera and Ten New Species. *Journal of Orthoptera Research* 229–254. doi:10.2307/3503651
- Orsini MP, Costa MKMD, Szinwelski N, Martins LDP, Corrêa RC, Timm VF, Zefa E. 2017. A new species of *Miogryllus* Saussure, 1877 and new record of *Miogryllus* *piracicabensis* Piza, 1960 (Orthoptera: Gryllidae) from State of Rio Grande do Sul, Brazil, with calling song and chromosome complement. *Zootaxa* **4291**:361–372. doi:10.11646/zootaxa.4291.2.8
- Otte D. 2007. Australian Crickets (Orthoptera: Gryllidae). Academy of Natural Sciences.
- Pereira MR, Miyoshi AR, Martins LDP, Fernandes ML, Sperber CF, Mesa A. 2013. New Neotropical species of *Hygronemobius* Hebard, 1913 (Orthoptera: Grylloidea: Nemobiinae), including a brief discussion of male genitalia morphology and preliminary biogeographic considerations of the genus. *Zootaxa* **3641**:1–20. doi:10.11646/zootaxa.3641.1.1
- Robillard T, Desutter-Grandcolas L. 2004. High-frequency calling in Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae): adaptive radiation revealed by phylogenetic analysis. *Biological Journal of the Linnean Society* **83**:577–584. doi:10.1111/j.1095-8312.2004.00417.x
- Robillard T, Ichikawa A. 2009. Redescription of Two *Cardiodactylus* Species (Orthoptera, Grylloidea, Eneopterinae): The Supposedly Well-Known *C. novaeguineae* (Haan, 1842), and the Semi-Forgotten *C. guttulus* (Matsumura, 1913) from Japan. *jzoo* **26**:878–891. doi:10.2108/zsj.26.878
- Robillard T, Nattier R, Desutter-Grandcolas L. 2010. New species of the New Caledonian endemic genus *Agnotecous* (Orthoptera, Grylloidea, Eneopterinae, Lebinthini). *Zootaxa* **2559**:17–35. doi:10.11646/zootaxa.2559.1.2
- Robillard T, Su YN. 2018. New lineages of Lebinthini from Australia (Orthoptera: Gryllidae: Eneopterinae). *Zootaxa* **4392**:241–266. doi:10.11646/zootaxa.4392.2.2
- Robillard T, Tan MK. 2013. A taxonomic review of common but little known crickets from Singapore and the Philippines (Insecta: Orthoptera: Eneoptera: Eneopterinae) 21.
- Robillard T, Yap S, Yngente MV. 2013. Systematics of cryptic species of *Lebinthus* crickets in Mount Makiling (Grylloidea, Eneopterinae). *Zootaxa* **3693**:49–63. doi:10.11646/zootaxa.3693.1.3
- Souza-Dias PGB, Szinwelski N, Fianco M, Oliveira ECD, Mello FD a. GD, Zefa E. 2017. New species of *Endecous* (Grylloidea, Phalangopsidae, Luzarinae) from the Iguaçu National Park (Brazil), including bioacoustics, cytogenetic and distribution data. *Zootaxa* **4237**:454–470. doi:10.11646/zootaxa.4237.3.2
- Su YN, Rentz DCF. 2000. Australian Nemobiine Crickets: Behavioral Observations and New Species of *Bobilla* Otte & Alexander (Orthoptera: Gryllidae: Nemobiinae). *Journal of Orthoptera Research* 5–20. doi:10.2307/3503626
- Symes LB, Collins N. 2013. *Oecanthus Texensis*: A New Species of Tree Cricket from the Western United States. *orth* **22**:87–91. doi:10.1665/034.022.0203
- Tan MK, Japir R, Chung AYC, Wahab RBHA. 2020. New taxa of crickets (Orthoptera: Grylloidea: Phaloriinae, Phalangopsinae, Itarinae and Podoscirtinae) from Borneo (Brunei Darussalam and Sandakan). *Zootaxa* **4810**:244–270. doi:10.11646/zootaxa.4810.2.2
- Tan MK, Kamaruddin KN. 2016. A new species of *Gryllotalpa* mole cricket (Orthoptera: Gryllotalpidae: (Gryllotalpinae) from Peninsular Malaysia. *Zootaxa* **4066**:552–560. doi:10.11646/zootaxa.4066.5.3
- Vicente NM, Olivero P, Lafond A, Dong J, Robillard T. 2015. *Gnominthus* gen. nov., a new genus of crickets endemic to Papua New Guinea with novel acoustic and behavioral diversity (Insecta, Orthoptera, Gryllidae, Eneopterinae). *Zoologischer Anzeiger - A Journal of Comparative Zoology* **258**:82–91. doi:10.1016/j.jcz.2015.06.005
- Weissman DB, Gray DA. 2019. Crickets of the genus *Gryllus* in the United States (Orthoptera: Gryllidae: Gryllinae). *Zootaxa* **4705**:1–277. doi:10.11646/zootaxa.4705.1.1
- Zefa E, Acosta RC, Timm VF, Szinwelski N, Marinho MAT, Costa MKMD. 2018. The Tree Cricket *Neoxabea brevipes* Rehn, 1913 (Orthoptera: Gryllidae: Oecanthinae) from the Brazilian southern Atlantic Forest: morphology, bioacoustics and cytogenetics. *Zootaxa* **4531**:554–566. doi:10.11646/zootaxa.4531.4.6

Zefa E, Neutzling AS, Redü DR, Oliveira GLD, Martins LDP. 2012. A new species of *Oecanthus* and *Oecanthus lineolatus* Saussure, 1897 from Southern Brazil: species description, including phallic sclerites, metanotal glands and calling song (Orthoptera: Gryllidae: Oecanthinae). *Zootaxa* **3360**:53–67.  
doi:10.11646/zootaxa.3360.1.2