

1 **Title**

2 The ground offers acoustic efficiency gains for crickets and other calling animals

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28 **Abstract**

29 Male crickets attract females by producing calls with their forewings. Louder calls travel  
30 further and are more effective at attracting mates. However, crickets are small, and  
31 therefore inefficient, dipole sound-sources. Only a small group called tree crickets make  
32 acoustic tools called baffles which reduce acoustic short-circuiting, a source of dipole  
33 inefficiency. Here, we ask why baffling is uncommon among crickets. We hypothesize  
34 that baffling may be rare, because like other tools they offer insufficient advantage for  
35 most species. To test this, we modelled the calling efficiencies of crickets within the full  
36 space of possible natural wing sizes and call frequencies, in multiple acoustic  
37 environments. We then generated efficiency landscapes, within which we plotted the  
38 positions of 111 cricket species across 7 phylogenetic clades. We found that all sampled

39 crickets, in all conditions, could gain efficiency from tool use. Surprisingly, however, we  
40 also found that calling from the ground significantly increased efficiency, with or without  
41 a baffle, by as much as an order of magnitude. We found that the ground provides some  
42 reduction of acoustic short-circuiting but also halves the air volume within which sound is  
43 radiated. It simultaneously reflects sound upwards, allowing recapture of a significant  
44 amount of acoustic energy through constructive interference. Thus, using the ground as  
45 a reflective baffle is a very effective strategy for increasing calling efficiency. Indeed,  
46 theory suggests that this increase in efficiency is accessible not just to crickets, but to all  
47 acoustically communicating animals whether they are dipole or monopole sound  
48 sources.

## 49 Significance Statement

50 Loudness is a crucial functional feature of calls in acoustically communicating animals.  
51 Animals attempting to reach prospective mates or ward off predators are expected to  
52 make themselves as loud as possible. Given the importance of loudness, there are two  
53 long-standing, seemingly unrelated paradoxes in acoustic communication. The first is  
54 the rarity of acoustic tool use. The second is the high number of animals that call from  
55 reflective surfaces, like the ground, known to be an impediment to sound propagation. We  
56 resolve both paradoxes and show them to be related. By refocusing analysis from sound  
57 propagation to sound radiation, we show that the ground is the opposite of an  
58 impediment and can, in fact, boost sound loudness more than tool use. Thus, we show  
59 that calling from a reflective surface is an alternative strategy for maximizing call  
60 loudness, and one that is available to all animals.

## 61 Introduction

62 Male crickets make loud advertisement calls to attract females who use these calls to  
63 locate mates (1). Louder calls travel further, cover more area, and attract more females  
64 (2–4). When faced with a choice, females prefer louder calls (2, 5). Being louder  
65 therefore has implications for mating success and evolutionary fitness in these singing  
66 insects. However, despite the apparent loudness of a nighttime chorus, cricket calls are  
67 acoustically constrained by a phenomenon known as ‘acoustic short-circuiting’ specific  
68 to dipole sound sources (6, 7). Cricket wings are sound radiators that vibrate back and  
69 forth in the air like pistons. As a wing moves in one direction, the air in front of the wing  
70 is compressed, and the air behind it is rarified. These two changes in pressure travel  
71 away as waves as the motion is periodically repeated. However, the waves on either  
72 side of the wing are of opposite phase and interfere destructively where they meet, at  
73 the edges of the wing. Thus, less sound is radiated, reducing sound radiation efficiency  
74 (6, 8). The smaller the wings of a cricket with respect to the wavelength of the sound it  
75 makes, the higher the short-circuiting and associated loss of efficiency. Indeed, the few  
76 crickets that have been studied are small and experience significant short-circuiting (9).

77 To reduce the efficiency lost to acoustic short-circuiting, a few tree cricket species build  
78 and use an acoustic tool known as a baffle (5–7, 10). A baffle consists of a leaf with a

79 hole chewed by the cricket near the middle of the leaf. When the size of the leaf and  
80 hole are optimal, such structures reduce acoustic short-circuiting and increase efficiency  
81 by as much as 10 dB compared to unbaffled calling, reflecting a tripling of sound  
82 pressure levels (7). However, despite their benefits, only a handful of species among  
83 thousands make baffles, all within the sub-family Oecanthinae (5, 7, 10, 11).

84 Given the obvious benefits, why is acoustic baffle use rare in crickets? Tree cricket  
85 baffles are tools, and tool use is generally rare (12–14). Indeed, few species use tools,  
86 whether crickets, other invertebrates or even vertebrates. Invertebrate tool use,  
87 however, seems especially rare. For example, 56 independent occurrences of tool use  
88 were found in mammals, whereas only 13 occurrences were found in the significantly  
89 more speciose insects (14). Two hypotheses from the tool use literature, the “cognitive  
90 capacity” and the “lack of utility” hypotheses offer two different reasons for this rarity.  
91 The “cognitive capacity” hypothesis suggests that complex tool use behaviors are less  
92 likely to evolve in animals with smaller brains and lower cognitive capacity. This is an  
93 unlikely explanation since many animals with relatively low cognitive capacities do use,  
94 and even make, tools which themselves are not necessarily complex objects. Small-  
95 brained animals are even known to make very complex and highly functionally optimized  
96 habitation structures which do not require high cognitive capacity (7, 15).

97 A competing hypothesis is the “lack of utility” hypothesis which posits that tool behavior  
98 can evolve regardless of cognitive capacity, but that its evolution requires an ecological  
99 context in which it confers sufficient selective advantage (15). Only species that can  
100 achieve higher gains from tool use than from other strategies (e.g., morphological  
101 features, site selection) are likely to evolve tool using behavior.

102 To test the lack of utility hypothesis, we must quantify tool utility and use of the tool must  
103 have implications for evolutionary fitness. It is often difficult to meet these two conditions.  
104 Work in chimpanzees has directly quantified tool utility by evaluating how much caloric  
105 value can be gained by using a tool to exploit an otherwise unexploitable resource (16).  
106 Other studies have made more indirect arguments; work in sea otters has shown that  
107 tools are employed more frequently in populations in which tough prey require tools to  
108 access them (17). In capuchin monkeys, larger individuals who can more effectively use  
109 tools to crack nuts are more likely to use tools (18). However, few studies quantitatively  
110 assess the lack of utility hypothesis, particularly outside the context of food.

111 Baffle use in crickets is an ideal system in which to test the lack of utility hypothesis.  
112 First, baffle use is rare and second, we can directly measure its acoustic utility in terms  
113 of increase in sound radiation efficiency (12). Finally, baffle use has been shown to have  
114 real fitness implications, by increasing the number of mates attracted to a given male,  
115 and also by increase mating duration, both processes likely to increase reproductive  
116 success (2).

117 Therefore, in this study, we tested the lack of utility hypothesis across a large group of  
118 singing insects, the true crickets or Grylloidea. We used finite element models to quantify  
119 baffle utility in two ways. First, we ascertained the range of sizes of the sound radiator  
120 (cricket wings) and frequency ranges of the calls used by 111 crickets, spread over the  
121 cricket phylogeny and used it to define an acoustic-morphospace (Fig 1). Then we  
122 quantified a volumetric sound radiation efficiency ( $SRE_v$ ), averaged across all positions  
123 in this space, specifically the relation between the radiator vibration amplitude, and the  
124 sound levels that are generated, similar to the previous study on tree cricket baffle  
125 efficiency (7). Since the amplitude of the radiator vibration would reflect the effort applied  
126 by the animal, this measure of efficiency captures a significant component of the  
127 relationship between singing effort and output. By plotting  $SRE_v$  over the complete  
128 acoustic-morphospace, we were able to generate efficiency landscapes, which  
129 encompassed baffled and unbaffled crickets and enabled us to fully investigate all  
130 possible crickets, even those that did not appear in our sample.

131 We also considered natural ecological conditions in which crickets call, such as, from  
132 close to the ground, and from within vegetation. In both these cases, the environment  
133 interacts with the sound radiator and the sound emanating from it across spatial scales,  
134 and may effectively remove any gains from baffling (19, 20). To capture spatial effects,  
135 we generated a second metric sound radiation efficiency, this time measured along a  
136 transect, ( $SRE_t$ ). Here we used the boundary element method and quantified the effect  
137 of interacting acoustic surfaces on acoustic efficiency as sound propagates away from  
138 the singer, under a range of environmental conditions.

139 Here we considered calling from the ground more carefully, in terms of its effect on  
140 efficiency. In the animal communication literature, typically the ground is considered  
141 during propagation and not in relation of sound radiator efficiency. In this context, it is  
142 typically seen as a severe impediment to sound propagation by causing significant  
143 amount of excess attenuation (21–24). Researchers also focus on the ground effect as  
144 degrading temporal structure (25) and directional information (26, 27). While we cannot  
145 address temporal structure in our examination of sound radiation efficiency, excess  
146 attenuation is accounted for. Additionally, using the same models, we also quantified  
147 directionality to test how efficiency might trade off with this biologically crucial feature.

148 Using these data, we asked whether the rarity of baffle use in crickets is explained by  
149 the lack of utility hypothesis. We examined the differences between baffled and  
150 unbaffled calling in different realistic scenarios. We expect that known baffle-users will  
151 be animals who benefit most from baffle use, and non baffle-users might not accrue as  
152 many benefits due to acoustic, morphological or environmental constraints.

## 153 Results

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

155 To capture the natural range of wing sizes and calling frequencies among true crickets,  
156 we collected wing surface area and call frequency data for 111 cricket species from a  
157 large range of sources (Fig 1, Tables S11, S12, Fig S1). Species were distributed across  
158 7 clades as described by the most recent phylogeny of the Grylloidea or “true cricket”  
159 super family (28) (Fig 1, SI 1).

160 We then constructed finite element models which predicted the sound fields produced by  
161 wings of different sizes at different call frequencies for 1086 different combinations which  
162 encompassed all the observed frequencies and wing sizes, i.e. the full acoustic-  
163 morphospace (Fig 2). In all conditions, wings were modelled as suspended in free  
164 space, vibrating with a uniform velocity perpendicular to the wing plane (SI 2). The  
165 model predicts the resulting sound field (see Supplementary methods for details). We  
166 then calculate sound radiation efficiency ( $SRE_v$  (Pa/m/s)), by taking a volumetric average  
167 of the sound pressure level generated (Pa), over a sphere of radius 20 cm around the  
168 wing, divided by the time-space average of the wing vibration velocity (m/s). This  
169 normalized measure of efficiency enables comparison between species, no matter their  
170 actual wing velocity or sound pressure level.

171 Next we plotted an  $SRE_v$  landscape (Fig 1) for the full acoustic-morphospace. On this  
172 landscape, we plotted the locations of the 111 species of crickets with known wing size  
173 and frequency allowing us to infer their  $SRE_v$  (Fig 1). These data therefore demonstrate  
174 precisely how suboptimal crickets are in terms of their efficiency (Fig 1F), and how much  
175 they could gain through use of an optimal baffle (Fig 1G).

176 Previous work examining four species of crickets and a small number of other insects  
177 determined that they each perform less efficiently than the theoretical optimal level for  
178 dipole sound sources (9). In our larger dataset, there is a clear ridge of high efficiency  
179 running through the  $SRE_v$  landscape (red line in Fig 1c, hereafter referred to as “optimal  
180 efficiency ridge”), which shows the optimal radiator size for every frequency. Despite  
181 sampling species with a wide range of wing areas (0.4 – 258 mm<sup>2</sup>) and call frequencies  
182 (1.6 – 27.9 kHz), all species lie below this optimal efficiency ridge. The efficiency  
183 distribution among crickets is somewhat bimodal (Fig 1F, G). The nine species with an  
184  $SRE_v$  above 1 Pa/m/s all had calling frequencies above 14 kHz and belonged to the  
185 subfamily Eneopterinae, in clade G. Given the difference in their song radiation  
186 mechanics (29) we excluded these individuals from subsequent analyses (see  
187 supplementary methods). After excluding these high frequency callers, we found that  
188  $SRE_v$  ranges from 0.02 to 0.67 Pa/m/s, mean:  $0.18 \pm 0.01$  SE,  $n = 101$ .

189 Next, we calculated how much each species could gain simply by using a baffle. To  
190 calculate this gain, we used the optimal efficiency ridge, since optimal radiator efficiency  
191 is the same as optimal baffled efficiency (8). If animals were to continue using the same

192 call frequency, but used an ideal baffle, each species stood to gain between 1.7 – 35  
193 times (5 – 30 dB) above their baseline  $SRE_v$  (mean:  $7.6 \pm 0.41$  times,  $16 \pm 0.37$  dB,  $n =$   
194 99). Among those who stood to gain the most included animals in clade B, specifically in  
195 the subfamily Mogoplistinae (scaly crickets). These animals have very small wings  
196 (mostly under  $5 \text{ mm}^2$ ), suggesting a poor match between sound wavelength and wing  
197 size. On the other hand, the animal closest to the optimal efficiency ridge, was  
198 *Madasumma affinis*, belonging to the subfamily Podoscirtinae in clade F. This animal  
199 has the largest wing at  $258 \text{ mm}^2$ , however, even this animal stood to gain 0.5 Pa/m/s (5  
200 dB or 1.6x increase) with the use of an ideal baffle. Taken together, these data suggest  
201 that all crickets could increase  $SRE_v$ , and therefore, stand to benefit from use of a baffle.

### 202 **Ground calling emerges as an alternative strategy to baffle use in complex** 203 **environments**

204 While analysis of  $SRE_v$  suggests that all crickets should use baffles, this prediction is  
205 based on sound fields travelling in free space and over short distances. It is possible that  
206 efficiency advantages from baffle use become negligible as sounds interact with objects  
207 in the cricket's local environment such as the ground or the vegetation. Many baffle  
208 users are low frequency callers, and it is also possible that higher frequency crickets  
209 lose all advantage from baffling in complex acoustic conditions. Either of these scenarios  
210 would lend support to the lack of utility hypothesis.

211 To address whether and how the efficiency landscape is changed by realistic calling  
212 conditions, we used boundary element modeling. Specifically, we used this method to  
213 add a “ground” component to our existing models, where the ground could have different  
214 characteristics including vegetation cover. In these models, sound can be reflected and  
215 dissipated by the ground and the effect of the vegetation is captured by an excess  
216 attenuation term based on empirical data (see supplementary methods). We used  
217 empirical measurements of ground impedance and although our modeled ground is flat  
218 and smooth, these measures should take realistic ground variability into account. We  
219 also varied the height of the caller above the ground (ground calling: 0 m, elevated  
220 calling: 1 m). We measured efficiency again by normalizing sound levels against radiator  
221 vibration levels (see methods). Sound levels were measured at two distances from the  
222 caller: near (averaged from 0.05 – 0.2 m away), and far (averaged from 0.8 – 0.9 m  
223 away). To simplify analysis, we always measured efficiency at the same height as the  
224 caller. To differentiate this measure of efficiency from  $SRE_v$ , we call it sound radiation  
225 efficiency along a transect, or  $SRE_t$  (Pa/m/s).

226 The most striking and unexpected result from our analysis was that calling from the  
227 ground (Fig 2C, D) yielded much higher  $SRE_t$  than calling from one meter above it (Fig  
228 2A, B). This is reflected in the efficiency landscapes by an average increase of about 5x  
229 (14.5 dB) across the entire acoustic-morphospace that we measured. Indeed, the  
230 highest  $SRE_t$  observed with a ground caller was 4 Pa/m/s (Fig 2C), two orders of  
231 magnitude higher than peak  $SRE_t$  with an elevated caller (0.06 Pa/m/s, Fig 2A). This

232 increase in efficiency is likely due to two phenomena. The first is partial baffling offered  
233 by the ground, which will prevent some acoustic short-circuiting. A second phenomenon  
234 is likely the ground effect, in which the pressure field that would normally propagate  
235 below the radiator is instead reflected upward from the ground and mixes with the  
236 directly propagated field. Here, we see that the ground effect leads to constructive  
237 interference between the direct, and the reflected and the ground wave and an increase  
238 in sound pressure levels (30). We find that even optimally baffled animals could gain an  
239 average of 2.8x efficiency (9.2 dB) along the measurement transect, by calling from the  
240 ground compared to elevated calling.

241 On the other hand, calling from far above the ground yields  $SRE_t$  values that are similar  
242 in level to  $SRE_v$  values calculated in the ideal free-field scenario modeled previously. At  
243 further distances, the values decrease as predicted by spreading in open air. Taken  
244 together, our models posit that ground calling and elevated baffled calling are two  
245 potential alternative strategies to maximize efficiency.

#### 246 ***Calling from the ground is still efficient when ground properties and*** 247 ***vegetation are varied***

248 All grounds are not equivalent and the increase in the net increase  $SRE_t$  may depend on  
249 their properties. For instance, soft grounds or those covered with vegetation would be  
250 much more dissipative and may eliminate the advantage accrued from ground calling.  
251 To test this possibility, we investigated whether this alternative strategy framework holds  
252 up when these properties of the environment are varied. We found few differences in  
253  $SRE_t$  with different types of grounds (SI 7).  $SRE_t$  tends to be slightly higher with a “soft”  
254 ground, which is better at dissipating sound, similar to a freshly tilled agricultural field  
255 (see methods) and this effect is magnified further away from the caller. This suggests  
256 dissipation has a higher effect further from the source, and primarily on propagation,  
257 whereas here the phase shift is more appropriate for constructive interference near the  
258 source. With a harder, more reflective ground, similar to a tightly packed forest floor,  
259  $SRE_t$  is slightly lower. However, significant differences between these two ground types  
260 occur at wing sizes well outside the natural range for crickets. At close distances, and  
261 particularly above the ground, the differences between ground types are very small (SI  
262 7). Therefore, all future analyses assume a “hard” ground.

263 Finally, we tested whether vegetation would reduce the predicted  $SRE_t$  landscapes for  
264 ground calling. Vegetation does slightly decrease the magnitude of  $SRE_t$  overall and  
265 unsurprisingly, there is a slight frequency dependence where  $SRE_t$  is lowered slightly  
266 more at high frequencies (Fig SI 8). This suggests that high frequency callers may be at  
267 an increased disadvantage when calling in vegetation as suggested before (23), and will  
268 see diminishing returns when using a baffle. However, we found that excess attenuation  
269 due to vegetation does not significantly change the overall patterns of efficiency. By and  
270 large, it shifts the efficiency landscape to a lower point at most points within the  
271 parameter space (Fig 2, SI 8) (31). However, the efficiency near the ground remains

272 higher than the efficiency 1m above the ground (SI 9). Finally, the effects of vegetation  
273 on  $SRE_t$  are undoubtedly more complicated than an excess attenuation factor. Modeling  
274 plants explicitly, at a variety of shapes and sizes, would be a useful extension to this  
275 study. However, since the efficiency of ground calling remains higher than calling from  
276 1m above ground, we conclude that calling from the ground remains an effective  
277 alternative strategy, even if the ground is soft, or covered with some vegetation.

### 278 ***Ground calling does not significantly degrade call directionality***

279 So far, our analysis has used the loudness of calls to define efficiency. However, a call  
280 must be both loud and directional to be effective. That is, the call must present a spatial  
281 gradient that a potential mate can follow to the source. Previous data has suggested that  
282 such gradients are severely degraded in ground calling crickets (23, 27, 32, 33), but not  
283 in elevated calling (34). This suggests that  $SRE_t$  gains from ground calling may trade off  
284 against call directionality. To test this, we analyzed call directionality by designing a  
285 directionality metric that captured how difficult it would be for a female cricket to follow  
286 an acoustic gradient back to the call's source (see methods). A value of one indicates  
287 that the gradient along a transect perpendicular to the wing planes is always in the  
288 "correct" direction, that is, sound pressure level increases as the female moves toward  
289 the caller in steps of ~ 2 body lengths (2 cm). A lower value means that over some  
290 stretches of this transect, SPL increases and at other steps it decreases. A value of 0.5,  
291 for instance, means that the SPL decreases over 50% of the steps as the female moves  
292 closer.

293 We find that directionality varies with respect to frequency, radiator size, and height from  
294 ground (Fig SI 10). Although ground calling does experience a loss of directionality  
295 compared to elevated calling, these losses are small. Near a ground caller, calls are all  
296 strongly directional ( $> 0.9$ ) below about 5 kHz, except for very small wings. Further from  
297 the caller, calls are strongly directional below about 3.5 kHz. Therefore, high frequency  
298 callers would be most susceptible to the gradient effects. However, even below these  
299 cutoffs, directionality rarely drops below 0.5 in any condition, and ground calling remains  
300 a viable strategy. It should be noted that other studies have found more substantial  
301 degradations in call directionality in sounds traveling along the ground, but over greater  
302 distances than our current models (27). However, data for both field crickets and tree  
303 crickets suggest that the SPL of typical cricket calls drop below threshold at about 1 m  
304 from the caller (32, 34), and therefore we considered this a biologically relevant distance  
305 over which to measure directionality.

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

307 Based on the overall efficiency landscape, ground calling and baffled calling are  
308 potential alternative strategies to maximize efficiency. However, we have so far  
309 considered the full acoustic-morphospace, i.e. all possible combinations of radiator  
310 (wing) size and call frequency, but most of these combinations are not used by real  
311 crickets.



312 To shift our focus to the sampled crickets, we tested where alternate calling strategies  
313 may offer the largest advantage to actual crickets. We divided all sampled animals into  
314 their respective clades and calculated clade level  $SRE_t$  for each of three alternative  
315 strategies as measured far from the caller: calling from the open hard ground (ground  
316 calling), and from within vegetation 1 m off the ground with no baffle (unaided calling),  
317 and from within vegetation with a baffle (baffled calling) (Fig. 3). We compared both  
318 baffled calling and ground calling to unaided calling as a baseline. It would have been  
319 ideal to determine whether animals, in fact, use the strategy that we predict should  
320 maximize efficiency based on known calling preferences. Unfortunately, we do not have  
321 data on calling preferences of many sampled animals. However, some clade-level  
322 similarities have been observed in calling behaviors, and different clades show some  
323 clustering in the wing size-frequency space (Figs 3, SI 9). We give three examples below  
324 of clades with some known information about calling behavior.

325 We start with clade F, consisting primarily of the baffle making Oecanthines, or tree  
326 crickets. Members of this group stand to gain efficiency on the order of about 4.5x, (13  
327 dB) from ground calling compared to unaided calling according to our data (Fig 3).  
328 However, they could gain 9x, (19 dB) if they baffled. Indeed, what is known of  
329 Oecanthine natural history bears out our predictions; tree crickets are known to mostly  
330 call from vegetation, including vegetation that is suitable for baffle building and use (6,  
331 34). In fact, all known cricket baffle users are in this clade, as predicted based on the  
332 lack of utility hypothesis. For clade G, on the other hand, consisting mostly of the  
333 Gryllinae, or field crickets, we predict the opposite. On average, ground calling gives an  
334 advantage of 9x (19 dB) above unaided for species in this group, whereas baffling gives  
335 an advantage of about 8x (18 dB) above unaided. Again, behavioral data suggests that  
336 many field crickets indeed prefer to call from the open ground habitats that we predict  
337 would maximize their efficiency (35).

338 Clade A, the Gryllotalpidae or the mole crickets, represents an interesting exception to  
339 this alternative strategy framework. This group stands to gain the most from baffled calling  
340 of all clades (13x, 22 dB) compared to ground calling (2x, 6 dB). Yet, species in this  
341 group are all known to exclusively call from the ground and do not use baffles. However,  
342 they do use an acoustic aide. Mole crickets build and call from burrows which function as  
343 resonators and convert them into monopole sound sources, eliminating acoustic short-  
344 circuiting through a different mechanism than baffling (22, 36). Indeed, it is possible that  
345 other acoustic means of maximizing call efficiency exist and could in the future add  
346 further complexity to our hypotheses.

347 Finally, if an animal baffled, but its call propagated through vegetation compared with no  
348 vegetation, the gains would be relatively small in most cases (< 6 dB SPL) (SI 9). We  
349 also performed a similar analysis for call directionality (Fig 3C, D). However, since  
350 directionality was quite high for all calling conditions, we therefore suggest that  
351 directionality does not preclude one alternative strategy over another.

## 352 Discussion

### 353 ***Why would baffle use evolve among crickets in the first place?***

354 From our data, exploiting the ground effect by calling from the ground emerges as a  
355 viable alternative to tool use in crickets. This simple site selection strategy can even  
356 exceed the efficiency gains of tool use in some scenarios. Given that making and using  
357 tools like baffles requires a specialized behavioral repertoire, and precise execution of  
358 these behaviors (7, 12), the real question becomes why a species would ever use this  
359 strategy if simpler site selection preference for the ground could give similar increases in  
360 efficiency.

361 There is evidence that crickets have been singing as early as the Cretaceous period  
362 (37). These early calling crickets were likely ground dwellers, with some species  
363 subsequently moving up into vegetation as the group diversified (38). We therefore  
364 suggest that baffle-using crickets may have originally moved up into vegetation for non-  
365 acoustic reasons, whether it was to exploit additional food resources or avoid predators.  
366 Baffle use would have then evolved secondarily to recover some of the efficiency lost  
367 when abandoning ground calling. The biophysical modeling methods presented here  
368 open the door to testing such a hypothesis about baffle use.

369 It is also known that crickets call from other “ground” substrates such as tree trunks,  
370 cave walls, or artificial structures (19, 22), which our data suggest could also increase  
371 calling efficiency (35, Fig 4C, D). The efficiency effects of these substrates could be  
372 further investigated using biophysical models contributing to our knowledge of acoustic  
373 ecology. In principle, we could even model the wings of extinct crickets, and estimate  
374 calling frequency based on the stridulatory apparatus on the wing (39, 40). By bringing  
375 extinct crickets “back to life” in this way we could ask questions about the evolution of  
376 acoustic tool use and calling ecology more broadly. We suggest that biophysical  
377 modeling, grounded with data from real animals, can be a valuable tool for any biologist  
378 wishing to better characterize and understand tool use in the context of animal  
379 communication.

### 380 ***Sound radiation efficiency in animal acoustic communication***

381 In the field of animal acoustic communication, calling from the near the ground has been  
382 thought of as severely disadvantageous, whether in insects, birds or even primates (21,  
383 22, 41–46). One reason for this is that reflections from the ground degrade temporal  
384 cues in calls and songs (25). However, most animal calls are repetitive and redundant,  
385 since they are used for functions such as sexual or territorial signaling, or as contact or  
386 alarm calls. Here, fine temporal structure is not crucial and the primary functional factor  
387 is how loud the sound is (22). How then is loudness affected by the presence of a  
388 reflective surface such as the ground? In animal acoustics, it is widely believed that the  
389 ground generates high amounts of excess attenuation compared to simple spherical  
390 spreading of sound (21, 22, 41–46). Yet, paradoxically, many animals call from the

391 ground, tree trunks, or other vertical surfaces such as cave walls in many ecological  
392 contexts (22).

393 Previous acoustic analyses have typically measured excess attenuation as observed at  
394 two distances from the source. Thus, these analyses only account for propagation  
395 losses and fail to consider the first step in the process, sound radiation efficiency, i.e.,  
396 the relationship between the vibration amplitude of the radiator and the level of the  
397 sound field that is generated. Here we show that for dipole singers like crickets, calling  
398 from the ground can actually provide a substantial boost in sound radiation efficiency,  
399 outweighing propagation losses at distances and receiver positions relevant to cricket  
400 behavior. It is only when we take this first step in the process of sound generation into  
401 account, that it becomes clear that calling from the ground may be an advantage rather  
402 than an impediment.

403 In fact, this phenomenon may be much more general than currently appreciated;  
404 analytical findings from as far back as 1957 show that the acoustic power radiated by  
405 monopoles and horizontal dipoles (such as cricket wings) increases as they get closer to  
406 a perfectly reflecting surface, by as much as a factor of two (Fig 4) (47). When acoustic  
407 sources are close to the ground, the reflected sound field effectively sums with the direct  
408 sound field, and at very close distances, this summation is near perfect. In particular, the  
409 radiated field from dipoles becomes almost monopole like when the source is close to a  
410 reflective ground (Fig 4) (48).

411 Of course, real grounds are not perfectly reflective and do have a finite impedance; they  
412 absorb some sound energy (30, 49). However, this does not significantly alter the  
413 theoretical expectation of increased sound radiation, except that an additional ground  
414 wave is formed in addition to the reflected wave (30). Nonetheless, dipole and monopole  
415 sources near the ground are still theoretically expected to have higher sound radiation  
416 efficiencies compared to the free or direct field condition (30, 50). In our analyses, we  
417 considered dipole sound radiators of finite size, above realistically parametrized  
418 grounds. We found sound radiation efficiency increases considerably near the ground. In  
419 fact, in some cases efficiency increases by even more than a factor of 2, likely through  
420 the baffling effect offered by the ground against acoustic short circuiting.

421 These findings extend beyond crickets, as they are true for both horizontal dipoles and  
422 monopoles (Fig. 4). All acoustically communicating animals are considered to be either  
423 dipole or monopole-like sound sources. Among non-cricket invertebrates, both fruit flies  
424 and mosquitoes produce sounds with their wings, functioning as dipoles (9). Other  
425 invertebrates that use tymbal-based sound production like cicadas and wax moths  
426 behave like monopoles (9). Among vertebrates, the sound fields produced by bats are  
427 well captured by a baffled-dipole piston model (52, 53) and whales have a similarly  
428 directional sound field (54). Most acoustically active vertebrates such as fish, frogs,  
429 reptiles, birds and mammals are considered to be monopole sound sources (21, 51).  
430 Thus all these animals can exploit this mechanism for gaining efficiency (9, 21, 51). In

431 effect, by shifting the focus from sound propagation to sound radiation efficiency, we are  
432 able to posit an explanation for both the paradoxical rarity of tool use and paradoxically  
433 high number of animals that call from the ground. Indeed, our findings, and a  
434 reconsideration of established acoustics theory, leads us to the exciting discovery of a  
435 hitherto unknown mechanism for increasing calling efficiency available to all acoustically  
436 communicating animals.

## 437 **Materials and Methods**

### 438 ***Specimen Data***

439 We collected data on wing surface area and call frequency for each of 111 cricket  
440 species distributed across the 7 clades described by Chintauan-Marquier et al. (28) (Fig  
441 1, SI 1). We restrict our analysis to this group, since these species are known to raise  
442 their wings when singing (55). This behavior means that they are dipole sources of  
443 sound, and acutely affected by acoustic short-circuiting (5, 9). Each species was  
444 assigned to a clade based on the following two criteria: (1) the species itself was  
445 included in the Chintauan-Marquier et al (2016) dataset or (2) the subfamily of the  
446 species was included in the dataset and it was found to be monophyletic within one of  
447 the seven Chintauan-Marquier clades. Data were obtained from a variety of databases  
448 including Orthoptera Species File (56), Crickets North of Mexico, and numerous  
449 publications (all references are available in SI 11-12). For a few species of Oecanthines,  
450 wings were provided by Nancy Collins and photographed in the lab under a dissecting  
451 microscope. All specimens measured were adult males, identified by wing morphology  
452 and lack of ovipositor. We measured surface area of the entire left forewing including the  
453 lateral field. Fitting an ellipse to the wing, we calculated aspect ratio (length of  
454 ellipse/width of ellipse). All image data were gathered using ImageJ version 1.53 (57).  
455 We next calculated the fundamental frequency of cricket advertisement calls using  
456 Raven Lite version 2.0 (Cornell Lab of Ornithology, 2020). When multiple specimens of  
457 a single species were analyzed, averages were used for wing size and call variables. To  
458 better represent the full range of wing size and call frequency in our dataset, we included  
459 some specimens in the histograms showing wing size and frequency (Fig 1D, E) for  
460 which we had only one type of data. Twelve animals had only wing size, but not call  
461 data, and 57 animals had call, but not wing size data (see SI 11-12 for details).

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

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

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

469 Animals were represented by two ellipses which modelled the forewings sitting next to  
470 each other along the long axis, in the same plane (SI 2). These ellipses should

471 accurately approximate total radiated sound power and the true shape of the sound field,  
472 and it is the size and shape of the radiator and frequency of the call that determines  
473 radiation efficiency, and not the radiator's material properties (8). Surrounding the wings  
474 was a spherical acoustic domain consisting of air with a 20 cm radius. The acoustic  
475 domain was suspended inside a second spherical domain of 40 cm radius (SI 2. A  
476 perfectly-matched layer (PML) was applied to the area between the acoustic domain and  
477 larger outer sphere. PMLs in finite element modelling are used to mimic an open and  
478 non-reflecting infinite acoustic domain, which absorbs all sound energy from the acoustic  
479 domain (59). Thus PMLs mitigate modelling artefacts such as the effects of sound  
480 reflecting from the edges of the acoustic domain (7). To reduce computational time, our  
481 model was constructed using  $\frac{1}{4}$  symmetry. That is, we modeled  $\frac{1}{2}$  of one wing and  $\frac{1}{4}$  of  
482 the two spherical domains. We then mirrored this model twice, once about the short axis  
483 of the wing to create a whole wing and  $\frac{1}{2}$  of the spherical domains, and a second time  
484 about a line between and parallel to the long axis of the wings to create a second wing  
485 and the whole spherical domains. We applied a time- and space-averaged velocity  
486 normal to the entire surface of the wings at 0.13m/s. This was the value measured from  
487 the wings of singing *Oecanthus henryi* and is the only known estimate for crickets (7).  
488 However, given that we are calculating efficiency rather than reporting actual sound  
489 pressure levels, normalizing using this known value allows comparison between species.  
490 We vibrated the wings at a frequency range of 0.5 - 32 kHz, in increments of 0.25 kHz.  
491  $SRE_v$  was subsequently calculated from each of these model outputs as a volumetric  
492 average of the absolute pressure in the acoustic domain, divided by the time- and  
493 space-averaged velocity of 0.13 m/s, resulting in units of Pa/m/s.

#### 494 *Finite Elements*

495 3D tetrahedral elements were used in both the acoustic domain and PML. After  
496 undertaking a mesh size sensitivity study (SI 5), we chose the "extra fine" mesh setting  
497 in COMSOL, with about 60000 elements in the acoustic domain. This number did vary  
498 somewhat with wing size, as fewer elements are used with very small wings.

#### 499 *Model Parameters*

500 We ran the finite element model at a range of wing surface areas from 0.4 – 4000 mm<sup>2</sup>,  
501 scaled logarithmically by the equation  $4 \times 10^x$ , where x ranges from -1 to 3). We used an  
502 aspect ratio of 2 (wings are twice as long as they were wide). Our chosen aspect ratio of  
503 2 was well within the range of most cricket species (median: 1.6, range: 0.7 - 3.7).  
504 Aspect ratio did not play a large role in sound production, except at aspect ratios > 5  
505 (length of wing 5x the width), which were not observed in real wings (SI 4). For aspect  
506 ratios within the range of crickets, differences in  $SRE_v$  between aspect ratios at a given  
507 wing area and frequency never exceeded 3 dB.

#### 508 *Other Modeling Considerations*

509 The cricket body was not included in our models as it was found to have negligible  
510 effects on  $SRE_v$  at all wing sizes and frequencies (mean difference:  $0.05 \pm 0.01$  dB). We

511 also evaluated whether applying vibration to only a part of the wing (a “harp”) influenced  
512 sound production. Some cricket species (though not all) use this sound production  
513 method (60). We found only minor increases in  $SRE_v$  between vibrating only a harp or  
514 vibrating the entire wing (mean:  $4 \pm 0.08$  dB), except at wing sizes well outside the range  
515 of the real wings that we measured (SI 4).

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

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

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

535 We ran our boundary element models using the pressure acoustics, boundary elements  
536 module in COMSOL. All models were run in the frequency domain and assumed steady-  
537 state behavior. The Helmholtz equation does not take attenuation due to damping into  
538 account, which can become an issue at distances far from the source. However, at  
539 frequencies  $>500$  Hz, attenuation due to damping is only about 2 dB per kilometer (26),  
540 so we considered this effect to be negligible over the distances of interest for this study  
541 (0.2 – 1m).

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

543 Wings in the boundary element model were modeled the same way as in the finite  
544 element model (SI 2), with no material properties and one-way coupling between the  
545 wings and sound fields. Wings were positioned perpendicular to the top surface of the  
546 ground, with the flat surfaces of the wings aligned with the short axis of the ground. The  
547 wings were centered with respect to ground. The wings were placed above the ground at  
548 either 0 m, or 1 m. The same time- and space-averaged velocity was applied as above,  
549 and the same set of wing surface areas were used. The ground was modeled as a  
550 rectangular slab, 0.5 m wide, 2 m long, and 0.10 m thick. A sound-hard boundary was

551 applied to the bottom surface of the ground slab. Because we were interested in  
552 spatially-explicit measures of efficiency as sound propagates across ground, we did not  
553 use symmetry conditions to create this model. However, because the sound fields  
554 should be symmetric on either side of the wings, we only measured the sound field on  
555 one side.

### 556 *Model Parameters*

557 We used a restricted frequency range for the boundary element models, ranging from of  
558 0.5 – 10 kHz, in increments of 0.25 kHz. We chose 10 kHz as the cutoff because very  
559 few of our measured animals call above this frequency, and those that do were  
560 Eneopterine species who were likely using a vibrational mode inconsistent with the  
561 piston mode that we have implemented (29). High frequency (> 10 kHz) callers were  
562 included in the finite element models to give a general sense of where they might fit in  
563 with the other animals, but in reality no animals occupy this space in the landscape and  
564 all analyses explicitly comparing species exclude them.

565 To model how a real ground interacts with sound, we applied an acoustic impedance to  
566 our modeled ground. Acoustic impedance quantitatively describes how much sound  
567 energy is dissipated by the ground, compared to the energy reflected. We used the  
568 Attenborough slit-pore model to implement ground impedance. This model uses three  
569 parameters to capture both dissipative and reflective properties: flow resistivity, pore  
570 density, and porous layer depth. We modeled two different types of ground, a “soft”  
571 ground (flow resistivity: 2000 kPaxs/m<sup>2</sup>, porosity: 0.6) which is less reflective and a  
572 “hard” ground (flow resistivity: 9 kPaxs/m<sup>2</sup>, porosity: 0.4), which is more dissipative.  
573 Porous layer depth was held constant for both treatments, at 0.04 m. Both ground  
574 parameters were taken from empirical measurements of a “soft” freshly-tilled field and a  
575 “hard” forest floor (49).

### 576 *Sound propagation efficiency definition*

577 In the finite element models, we calculated a volumetric average of absolute pressure  
578 within the acoustic domain. However, such a measure would not be appropriate to  
579 assess propagation efficiency, as the sound waves’ interactions with the ground would  
580 accumulate as distance from the source increases. Therefore, we calculated SRE<sub>t</sub> in a  
581 spatially-explicit manner. We measured absolute pressure at 50 points along a 1m long  
582 line parallel to the long axis of the ground, at the same height as the wings. The line  
583 originated at the center between the two elliptical ‘wings’. We divided this line into “near”  
584 and “far” from the caller: near = 0.05 – 0.2 m from wings, far = 0.8 – 0.9 m from wings.  
585 Efficiency was calculated as before, by dividing sound pressure level (Pa) by 0.13 m/s,  
586 the space and time averaged velocity applied to the wings. We also created an  
587 additional boundary element model with no ground, to allow for direct comparisons  
588 between ground and no ground and to sanity check the boundary element method  
589 compared with the previous finite element models.

## 590 *Finite Elements*

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

## 597 ***Excess attenuation due to vegetation***

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

$$602 \frac{EA(Pa)}{FL} = 3[1 - \exp(0.3 - 0.5(ka))], ka > 0.6$$

603 Where EA(Pa) represents excess attenuation due to foliage, F = foliage area per unit  
604 volume, L = path length, k = wavenumber, and a = average leaf size. We used values  
605 empirically derived for dense foliage with relatively large leaves (31), such as those used  
606 to construct baffles in known baffle-using species. To approximate the foliage area and  
607 leaf size that a typical baffle user would prefer, we used  $F = 6.3\text{m}^{-1}$  and  $a = 0.0784\text{m}$  in  
608 our measures of excess attenuation.

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

610 To test the lack of utility hypothesis, we used the output of our models to estimate the  
611 gains in efficiency that each species could attain if it used a baffle. We did this for both  
612 the idealized measure of efficiency ( $SRE_v$ ) and the more realistic scenario involving a  
613 ground and vegetation ( $SRE_t$ ). For each modeling scenario, we first estimated the  
614 efficiency of each cricket species in our dataset, given their wing area and call  
615 frequency. Next, we calculated the efficiency that each species would have if it used an  
616 ideal baffle. To do this, we first determined the size at which the wings and baffle  
617 working together as a single radiator would reach maximal efficiency. The optimal size is  
618 a function of the wavelength of that sound frequency in that medium. We calculated the  
619 quantity  $ka$  for each surface area-frequency combination in the model, where  $k$  is the  
620 wavenumber and  $a$  is the effective radius of the sound radiating plates (8).  $ka$  is a  
621 dimensionless quantity often used in acoustics, as it helps define when a radiator of a  
622 particular size transitions from being inefficient sound radiator at low frequencies to an  
623 efficient high frequency radiator. For instance, an optimally sized circular piston has  $ka =$   
624 1 (8).

625 However, the radiators being considered here are two aligned ellipses which not  
626 perfectly circular in shape. Hence the particular value of maximal efficiency  $ka$  will be  
627 different in this configuration. So, to estimate optimal  $ka$  for cricket wings, we plotted  $ka$



628 versus efficiency as measured from our models, with a separate trace for each  
629 frequency (SI 6). We then identified the  $k_a$  at which maximal efficiency was reached for  
630 all frequencies. This value represents the size at which highest attainable efficiency is  
631 reached, consistent with an optimally baffled condition (8) (SI 6). In our finite element  
632 models, we found optimal  $k_a$  to be about 1.3. For the boundary element models at the  
633 far distance, optimal  $k_a$  was approximately 1.55 (SI 6).

634 Next, we performed a simple linear regression between frequency and maximal  
635 efficiency at optimal  $k_a$ , then calculated the slope and y-intercept of this regression (SI  
636 6). We used this equation to calculate optimal baffled efficiency for each species. The  
637 relationship between frequency and efficiency differed depending on condition (open  
638 ground vs ground + vegetation) (SI 6), so this regression was performed separately for  
639 each environmental condition when calculating optimal baffled efficiency for a given  
640 condition. It should be noted that due to modelling constraints we were only able to  
641 calculate baffled efficiency on the ground for animals with a carrier frequency >3.5 kHz.

#### 642 ***Directionality index***

643 To address how difficult it would be for a female to localize a male call, we assessed the  
644 directionality of the call in each modeling scenario. In an open field with no ground, the  
645 sound level is expected to decrease smoothly following the inverse square law (61, 62).  
646 A cricket moving toward the source of a call should therefore always experience either  
647 an increase in loudness, or, if the increase is below the animal's difference threshold, no  
648 change in loudness. A cricket should always move in the direction of increasing SPL to  
649 locate the singing male and therefore a mating opportunity. However, in reality, sound  
650 fields become more complicated when they interact with the ground, resulting in a noisy  
651 relationship between SPL and distance (63). In such sound fields, female phonotaxis  
652 may fail as there is no clear acoustic gradient to follow to the source. To quantify this  
653 degree of potential "confusion", we calculated a directionality index for each modeling  
654 scenario. First, we calculated  $\Delta$  SPL between each two adjacent points 2 cm apart (~ 2  
655 body lengths for most animals in this analysis).  $\Delta$  SPL was calculated starting at 1 m  
656 away and moving toward the source. Next, we classified each of these values as either  
657 consistent with expected change in SPL or inconsistent. Consistent values represented  
658 either an increase, no change, or a decrease smaller than  $\Delta$  3dB SPL (a factor of about  
659 1.4), which is thought to be close to the detectable threshold for crickets (64). See  
660 Römer, 2021 for a more complex treatment of such thresholds. For our purposes,  
661 inconsistent values represented a decrease in SPL greater than 3 dB. For each  
662 modeling scenario, we calculated the proportion of  $\Delta$  SPLs classified as consistent. This  
663 resulting value we call "Directionality" ranging from 0 to 1 (SI 10). We calculated  
664 directionality for two different distance treatments, "near" was calculated from 0.05 – 0.2  
665 m from the wings, and "far" was calculated from 0.5 – 1m from the wings.

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667

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685

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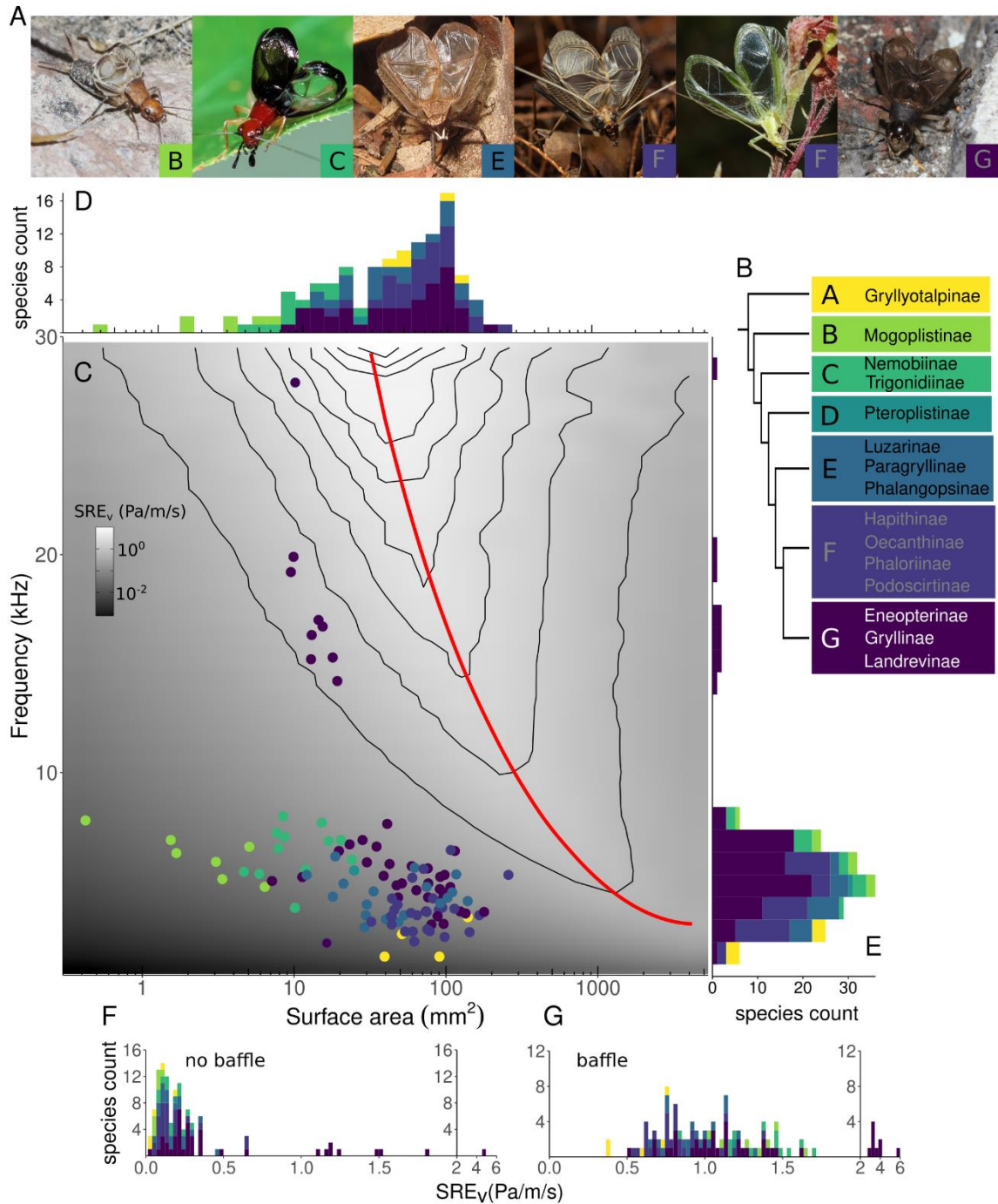
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Figures and Tables



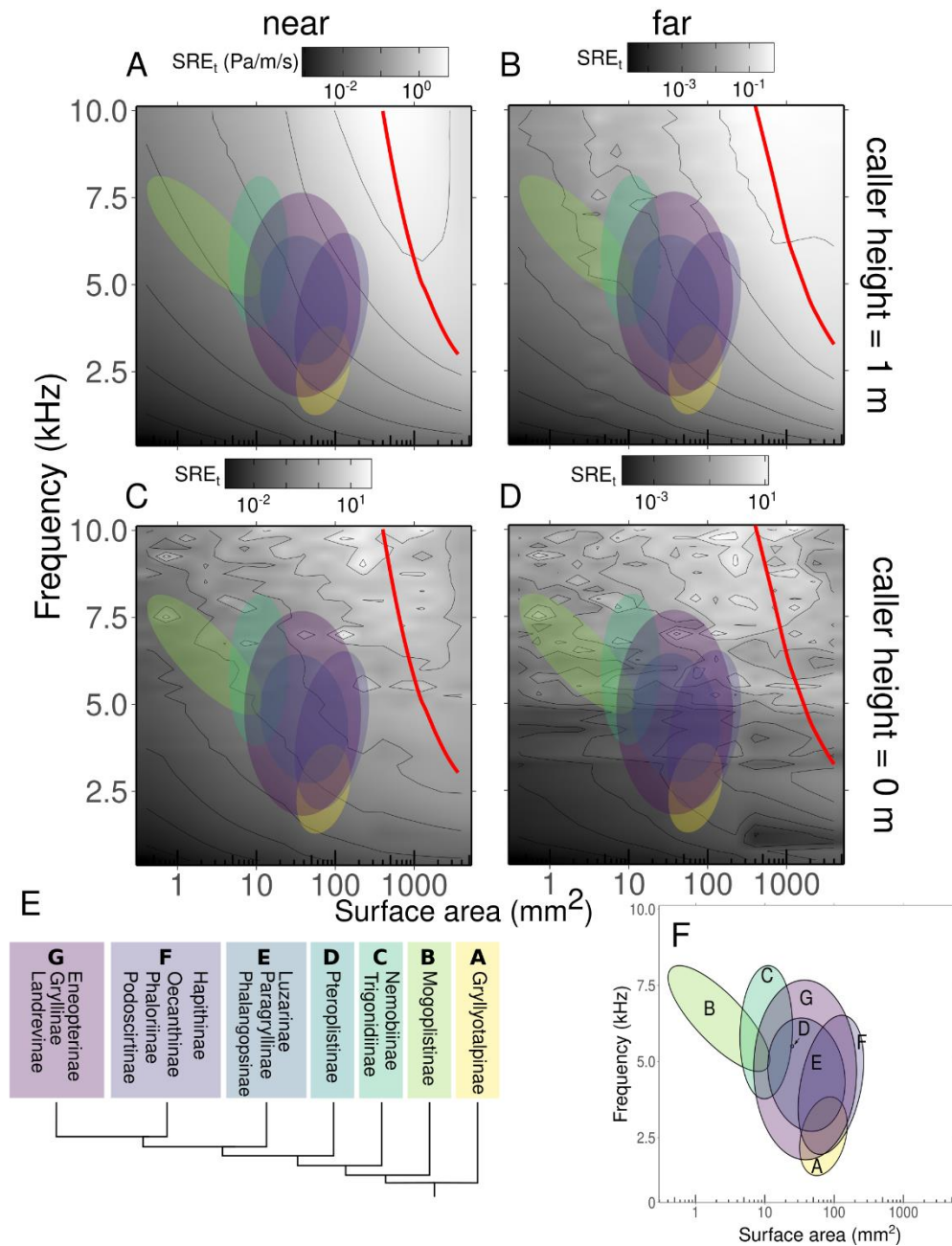
845

846 **Figure 1.** All crickets could increase efficiency by baffled calling. Sound radiation efficiency (SRE)  
 847 landscape across the acoustic-morphospace of crickets. **A.** Representative images of cricket  
 848 males with wings raised in calling posture. From upper left to lower right, species pictured are:  
 849 *Hoplosphyrum boreale* (photo: James P. Bailey), *Phyllopalpus pulchellus* (photo: Wilbur  
 850 Hershberger), *Lerneca inalata* (photo: Richard C. Hoyer), *Meloimorpha japonica* (photo: Ryosuke

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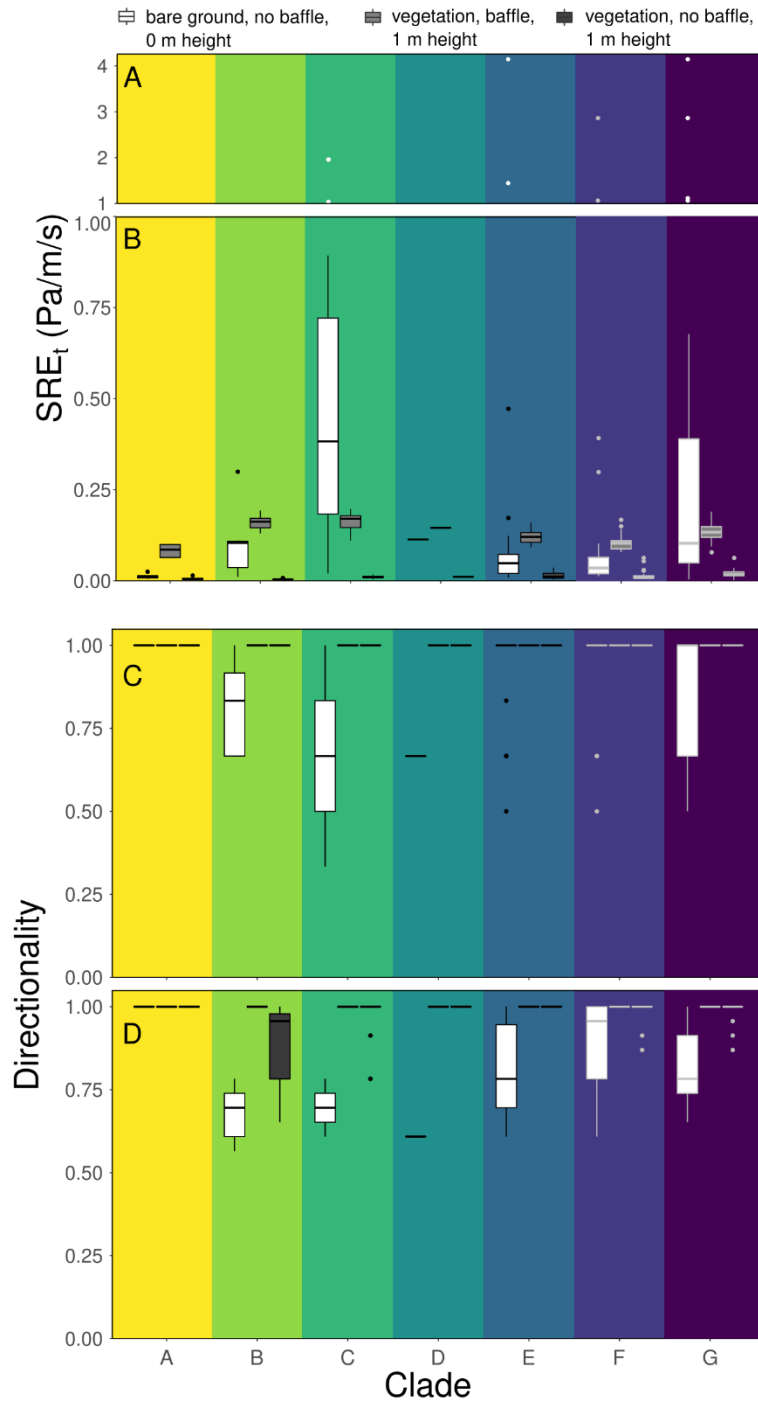
851 Kuwahara), *Oecanthus quadripunctatus* (photo: James P. Bailey), and *Turanogryllus eous* (photo:  
852 Taewoo Kim). Boxes with letter indicate the clade to which each species belongs. **B.** Phylogeny  
853 illustrating the seven clades defined by Chintauan-Marquier et al (2016) along with subfamilies  
854 within each clade (branch lengths not to scale). **C.**  $SRE_v$  achieved by different combinations of  
855 wings sizes vibrating at different frequencies. Within this space of possibilities the wing areas and  
856 call frequencies of all sampled animals are shown overlaid as points on the SRE landscape. This  
857  $SRE_v$  is calculated from finite element models. Red line indicates optimal efficiency ridge, or the  
858 size at each frequency that would produce an ideally baffled calling scenario. **D, E.** Distributions  
859 of the calling song frequency and wing size of different animals, respectively. Histograms include  
860 additional species for which only wing or call measurements were available. **F.**  $SRE_v$  of each  
861 species without use of a baffle. **G.**  $SRE_v$  of each species with use of an ideal baffle.  
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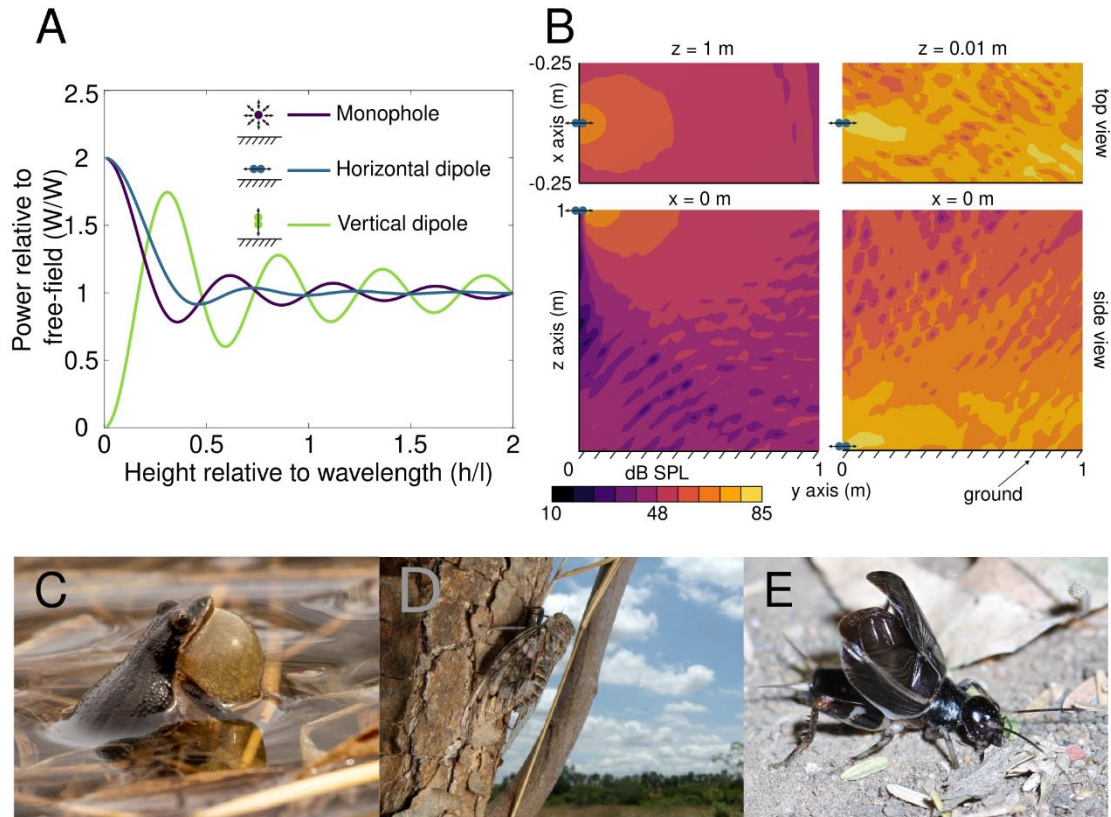
863

864 **Figure 2.** Sound propagation efficiency when the cricket sings near the bare hard ground is  
 865 orders of magnitude higher than in free space. Each panel represents a combination of caller  
 866 height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 0.2 m “near” and 0.8 –  
 867 0.9 m “far”). **A.** Distance = near, height = 1 m, **B.** Distance = far, height = 1 m; **C.** Distance = near,  
 868 height = 1 m, **D.** Distance = far, height = 0 m. Red lines indicate optimal efficiency ridge, or the  
 869 size at each frequency that would produce an ideally baffled calling scenario. Note that the  
 870 frequency range is reduced compared to figure 2, in order to exclude high frequency callers which  
 871 likely use alternative vibrational modes. Each clade of animals is represented by a colored ellipse.  
 872 **E.** Phylogeny representing each clade **F.** Key to clade represented by each ellipse.



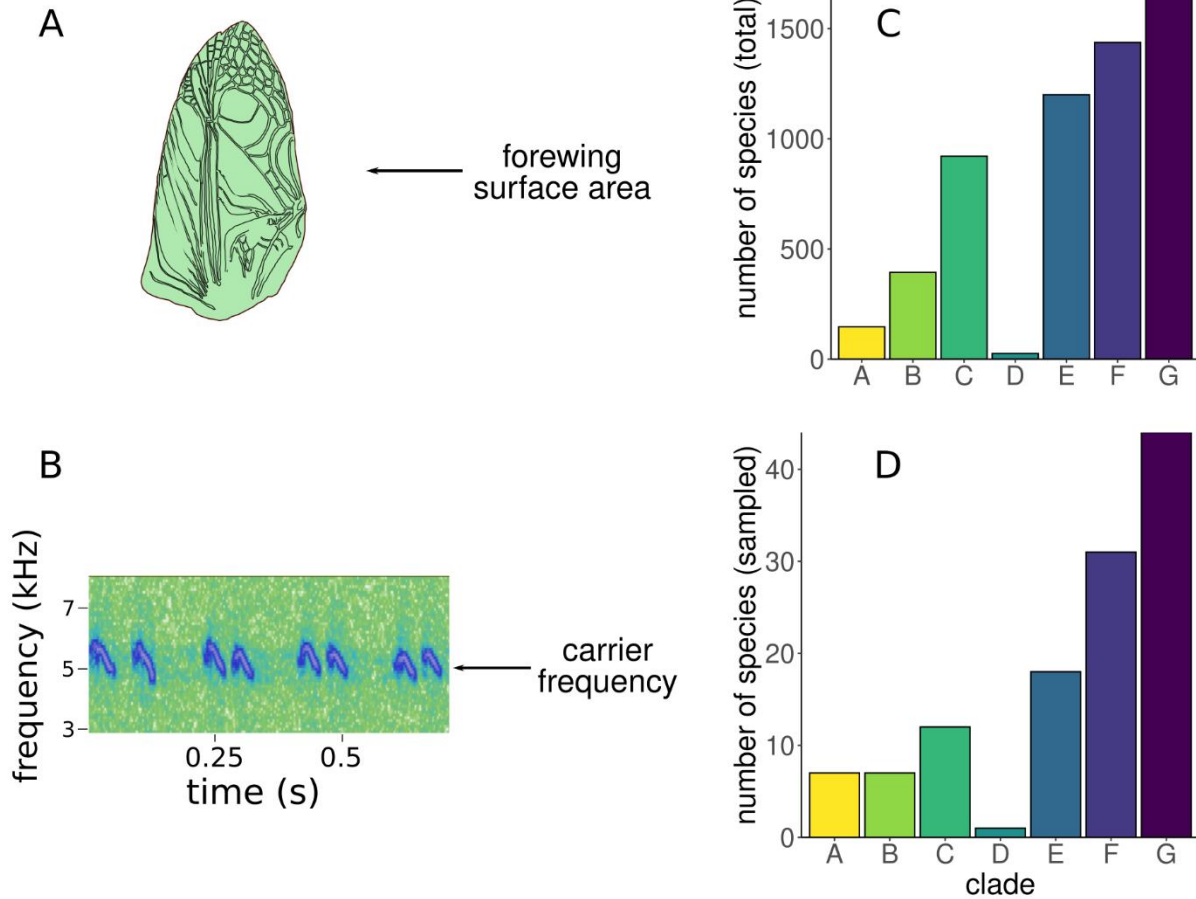
873 **Figure 3.** The most effective calling strategy (ground vs baffled) varies depending on clade,  
874 however directionality does not vary significantly. **A, B.** Comparison of SRE<sub>t</sub> on bare ground with  
875 no baffle, and 1 m in vegetation with and without an ideal baffle. These measurements were  
876 taken far from the caller, i.e. an average of the SPL at a distance of 0.8-0.9 m from wings, directly  
877 in front of the wings was used. A. indicates extreme outliers, which only occur when we consider  
878 animals calling from the bare ground. Baffled and ground calling do not substantially differ with

879 respect to directionality, although it does vary somewhat by clade. **C.** Directionality in near  
880 condition, **D.** Directionality in far condition.  
881



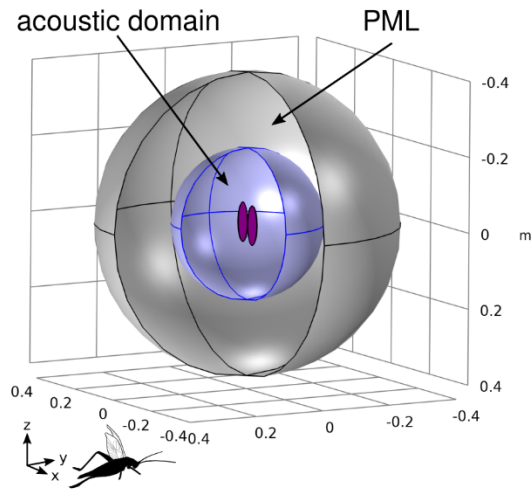
882 **Figure 4.** Hard reflective surfaces like the ground or water offer all acoustically active animals an  
 883 increase in sound radiation efficiency. **A.** The presence of a perfectly reflective surface near an  
 884 acoustic source can lead to an increase of the power radiated in the hemisphere above the  
 885 source, relative to the power that same source would radiate over a full spherical volume in free  
 886 space. Both monopole and horizontal dipole sources (whose vibration axis is parallel to the  
 887 reflective surface) can get a large boost in power when they are close to the reflective surface,  
 888 relative to the wavelength of sound being radiated. (Reproduced from equations in ref. 41). In  
 889 contrast, vertically oriented dipoles need to be further from the reflective surface to get an  
 890 equivalent gain in efficiency. **B.** In fact, near the ground, the sound field from a dipole source is  
 891 expected to become less directional and we observe this in our models. Data shown here are  
 892 from a radiator of surface area of 126 mm<sup>2</sup> and at frequency 5 kHz, which is seen to be  
 893 directional 1 m above the ground, but much less so when right next to the ground. **C-E.** Different  
 894 animals, especially small animals who have low sound radiation efficiency whether they are  
 895 monopole or dipole sources may call from near acoustically hard and reflective surfaces, like **C.**  
 896 water (photo: Doug Mills), **D.** tree trunks (photo: Natasha Mhatre), or even the **E.** ground (photo:  
 897 Brandon Woo) may be exploiting this effect. Animals that are monopole-like sources are likely to  
 898 orient themselves parallel to the surface since this is advantageous for camouflage as well.  
 899 However, crickets which are dipole-like acoustic sources, are constrained to expose themselves  
 900 by calling with their wings perpendicular to the ground surface to maintain the advantageous  
 901 horizontal dipole orientation.

## Supplementary Material

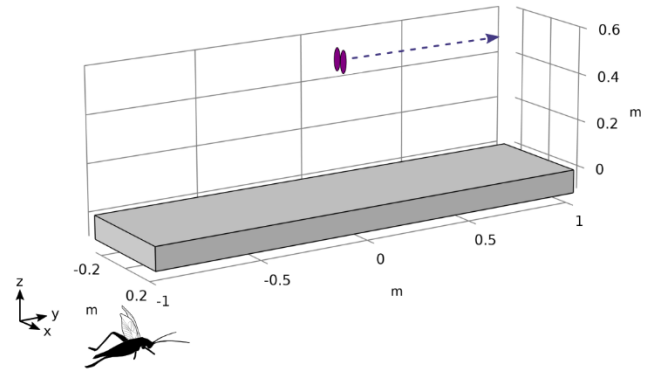


**SI 1.** Measuring acoustic-morphospace of crickets. Wing area and call frequency were quantified. **A.** Wing surface area was calculated as the area of the entire forewing. **B.** The carrier frequency (sometimes called fundamental frequency) of the call was identified from spectrograms and recorded. If the fundamental frequency occupied a sweep over a range of frequencies (as shown), an average was taken. **C.** Specimen sampling scheme. Distribution of all species described across each of the seven clades in Grylloidea (according to Orthoptera Species File, as of February 16, 2022). **D.** Distribution of species that were sampled for this study.

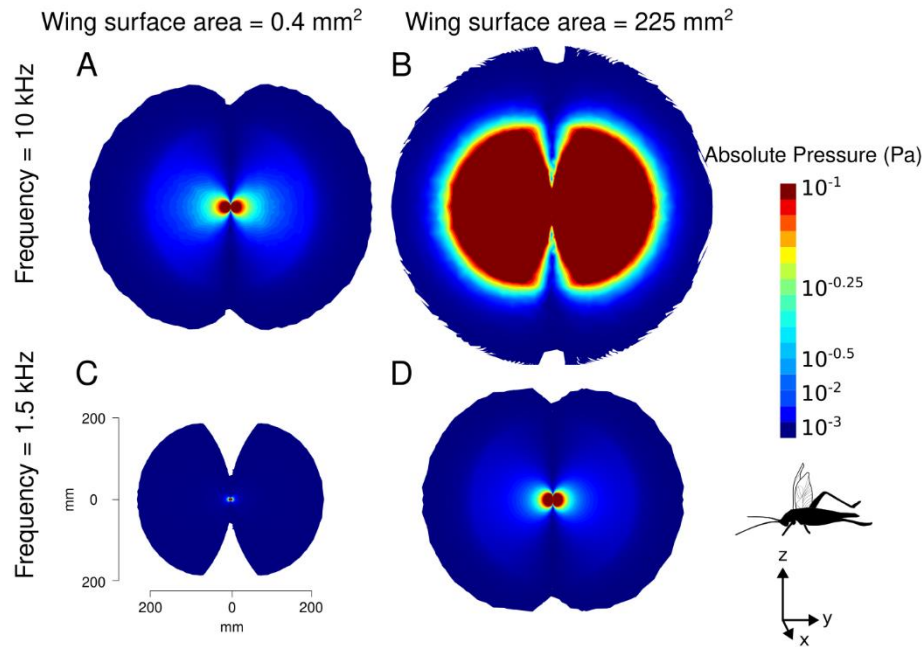
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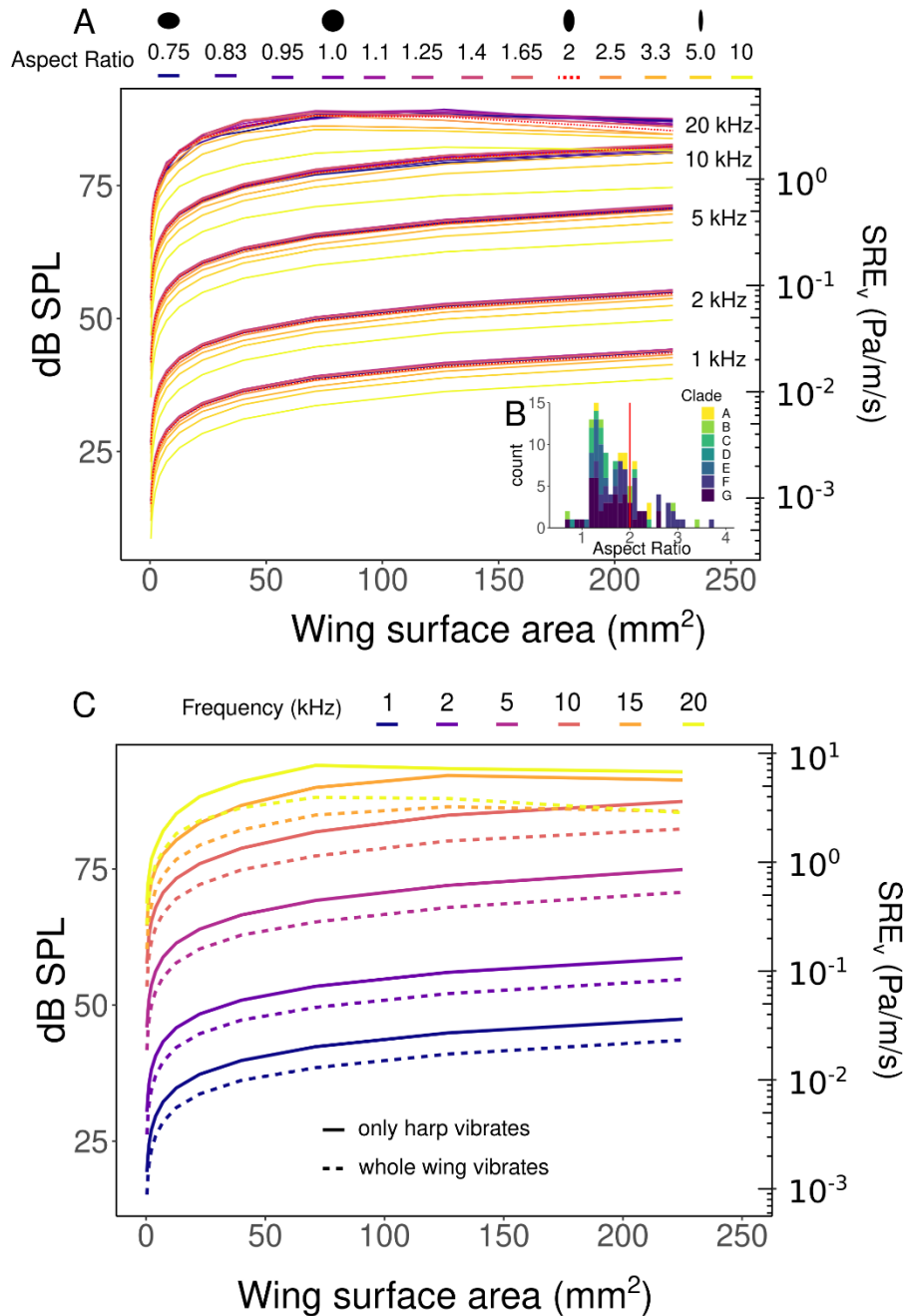
B



**SI 2. Geometry of biophysical models. A.** Geometry of finite element (FE) models. 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  $SRE_v$ . Wings vibrate along the y axis, as indicated by the cricket silhouette. **B.** Geometry of boundary element (BE) models. Grey shape represents a ground of defined acoustic impedance. Purple ellipses represent wings. Dotted line illustrates the line (transect) along which measurements were taken to assess  $SRE_t$ .

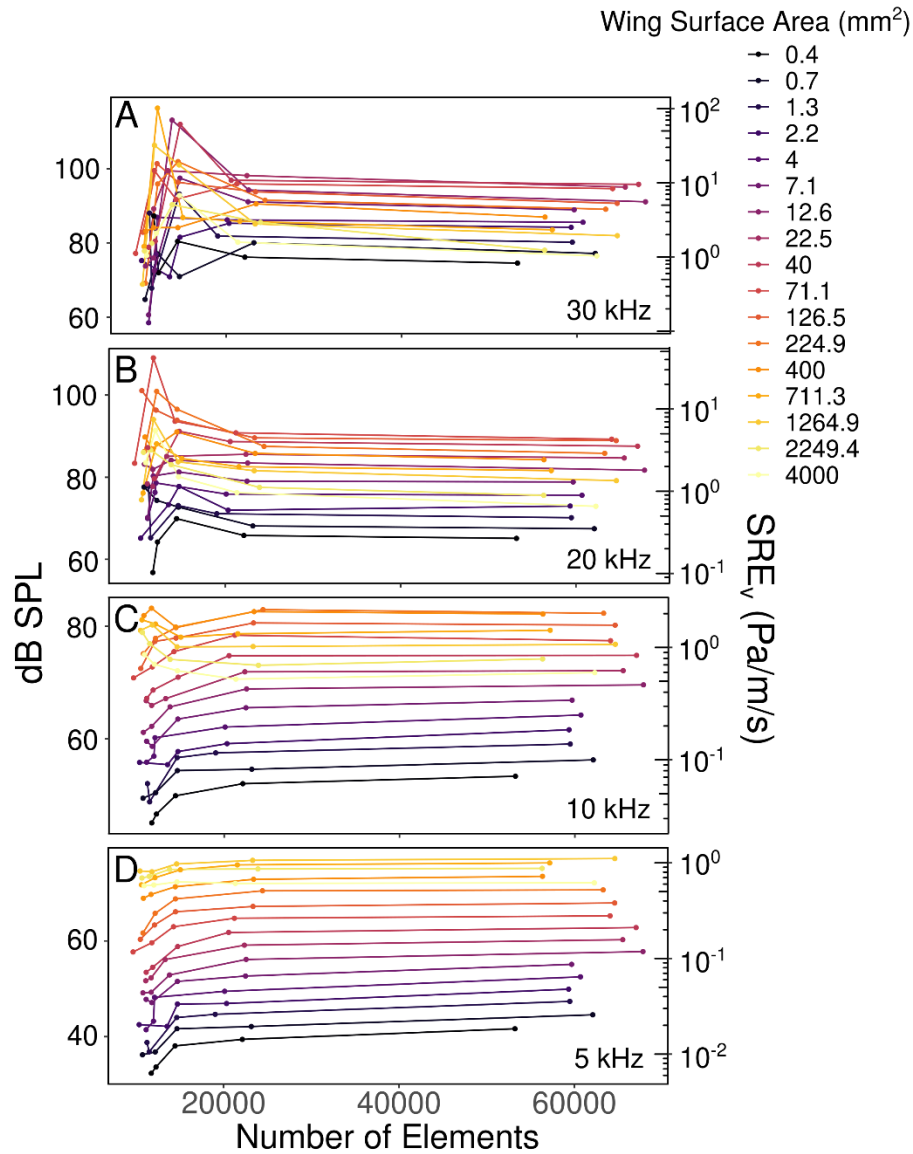


**SI 3.** Sound fields produced by modeled wings vary with respect to call frequency and wing size. Fields are oriented such that wings are perpendicular to page and vibrate left to right, as indicated by the silhouette cricket. Sound fields are given for the following combinations of wing size and frequency: **A.** wing size = 0.04 mm<sup>2</sup>, frequency = 10 kHz; **B.** wing size = 225 mm<sup>2</sup>, frequency = 10 kHz; **C.** wing size = 0.4 mm<sup>2</sup>, frequency = 1.5 kHz; **D.** wing size = 225 mm<sup>2</sup>, 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).

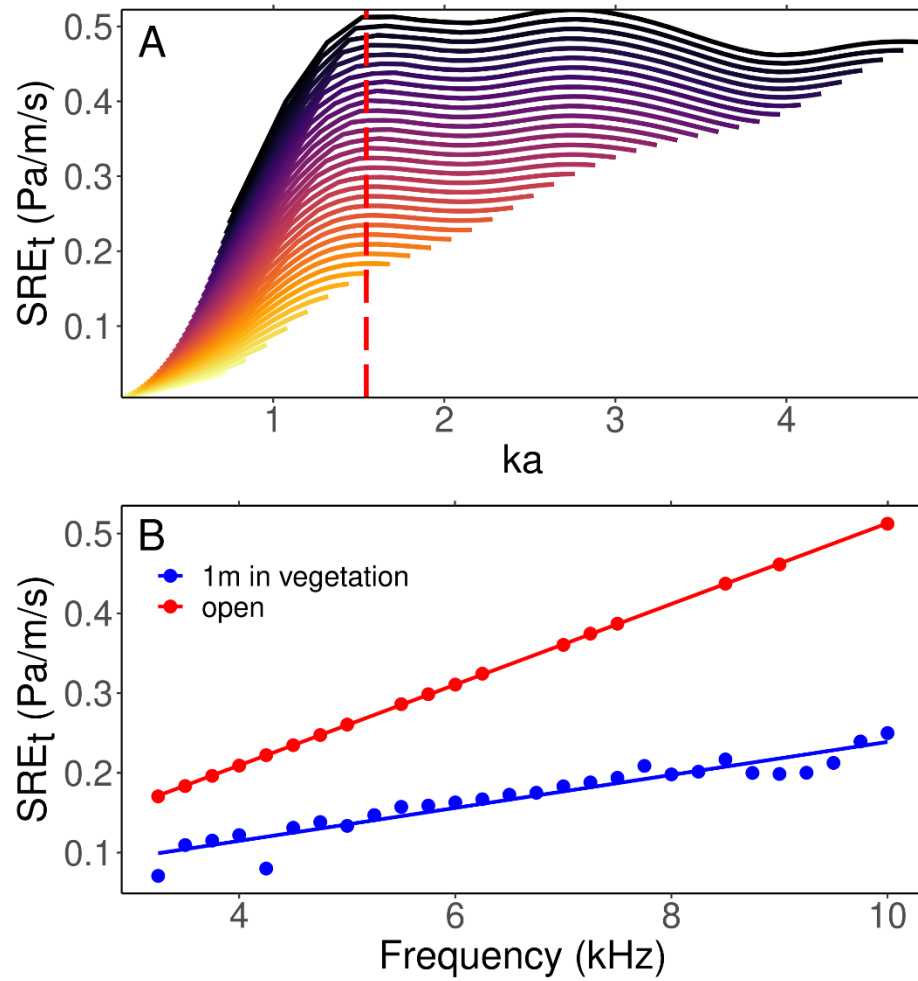


**SI 4.** Wing aspect ratio and use of a “harp” resonator do not significantly impact  $SRE_v$  within biologically-relevant ranges of wing size and call frequency. **A.** The effect of wing aspect ratio on  $SRE_v$  at six different call frequencies. The aspect ratio that was used on all models in this study (2) is shown by 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  $SRE_v$ , 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  $SRE_v$  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.

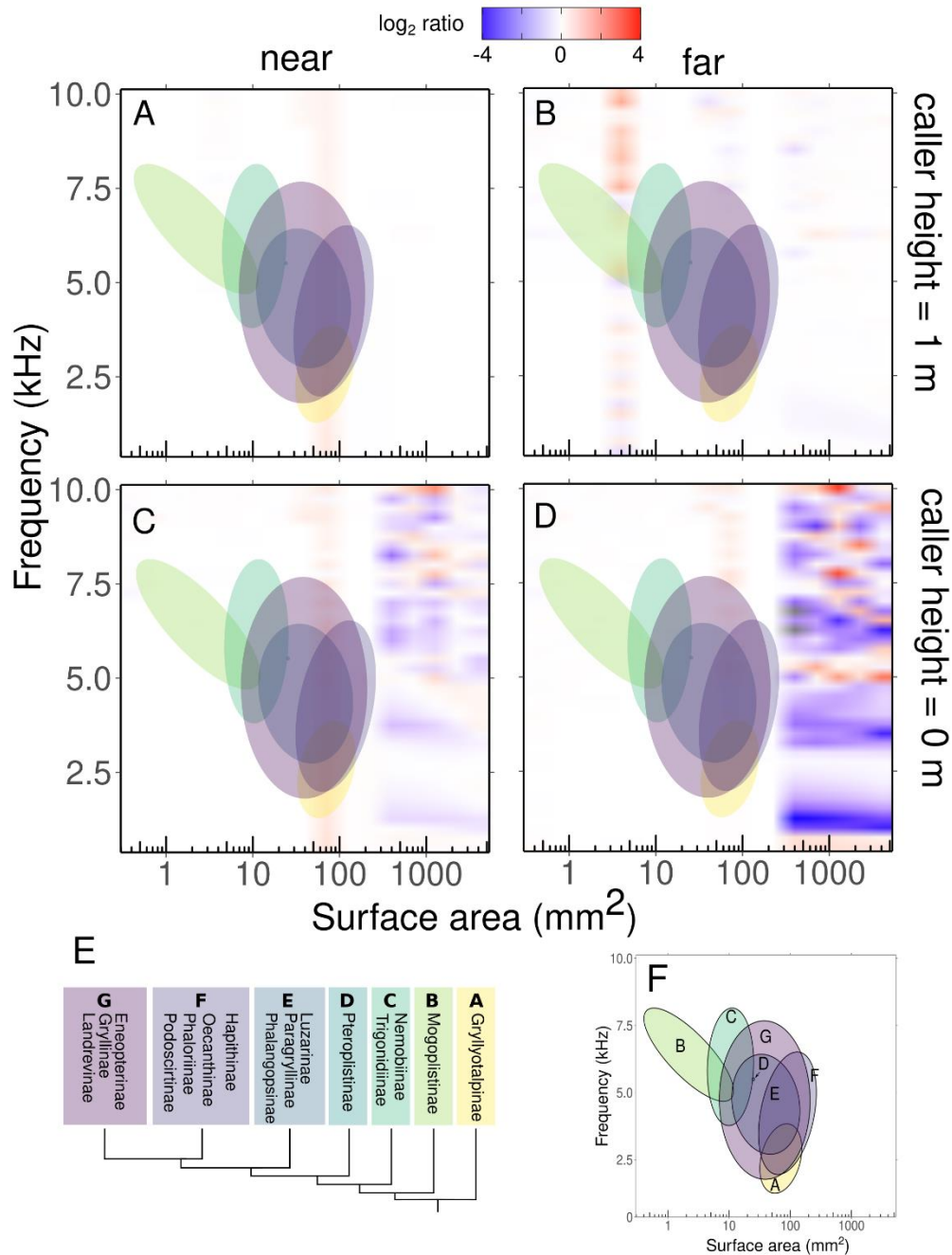




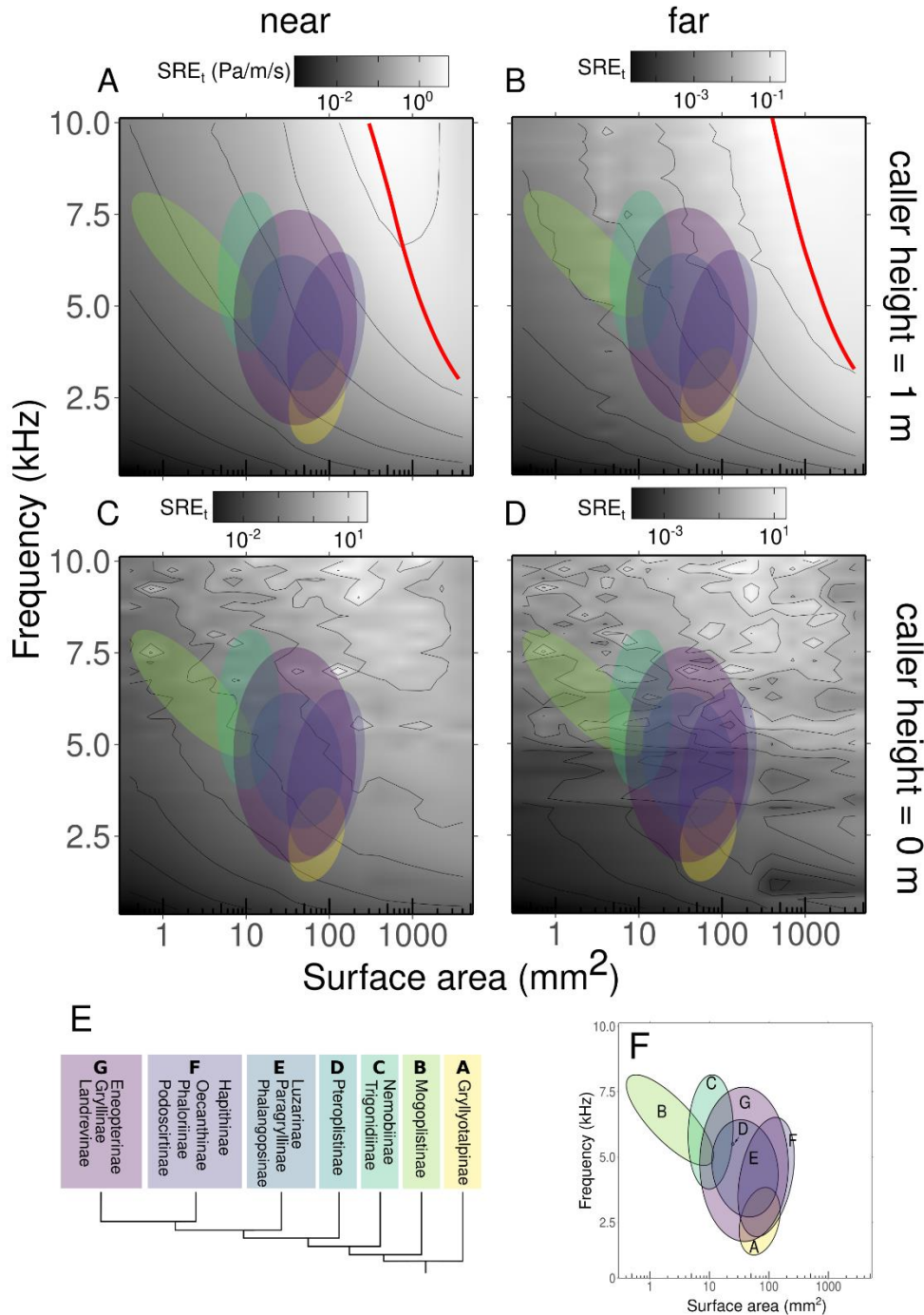
**SI 5.** Mesh sensitivity analysis for models based on the finite element method. Each line represents the SPL of a single wing size with a different number of mesh elements. Each panel shows this analysis at a different frequency: **A.** 30 kHz, **B.** 20 kHz, **C.** 10 kHz, **D.** 5 kHz. As the difference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



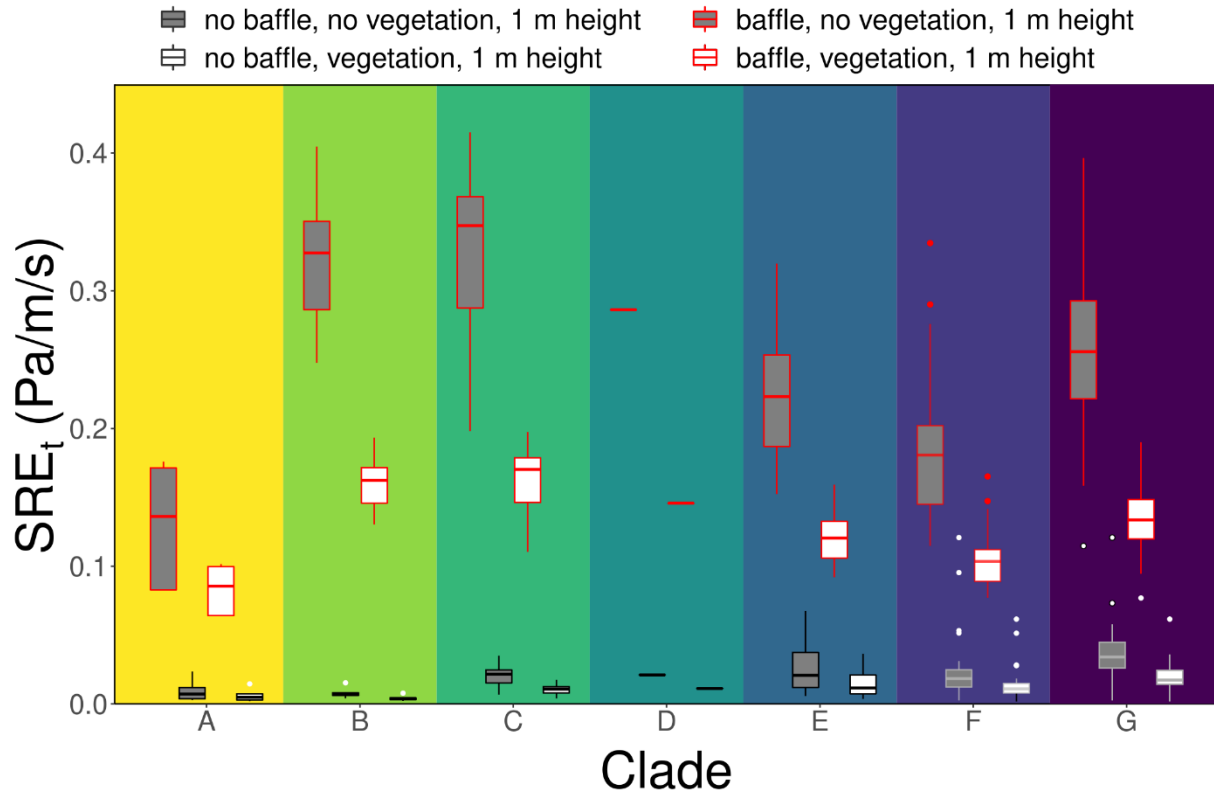
**SI 6.** Calculating efficiency with optimal baffle. **A.**  $ka$  at which optimal efficiency occurs for each frequency. Each frequency is represented by a different line. Line at which efficiency is maximized for each frequency (maximum efficiency ridge) is shown by red dashed line. **B.** Efficiency at this optimal  $ka$  (1.55) in open and vegetation conditions.



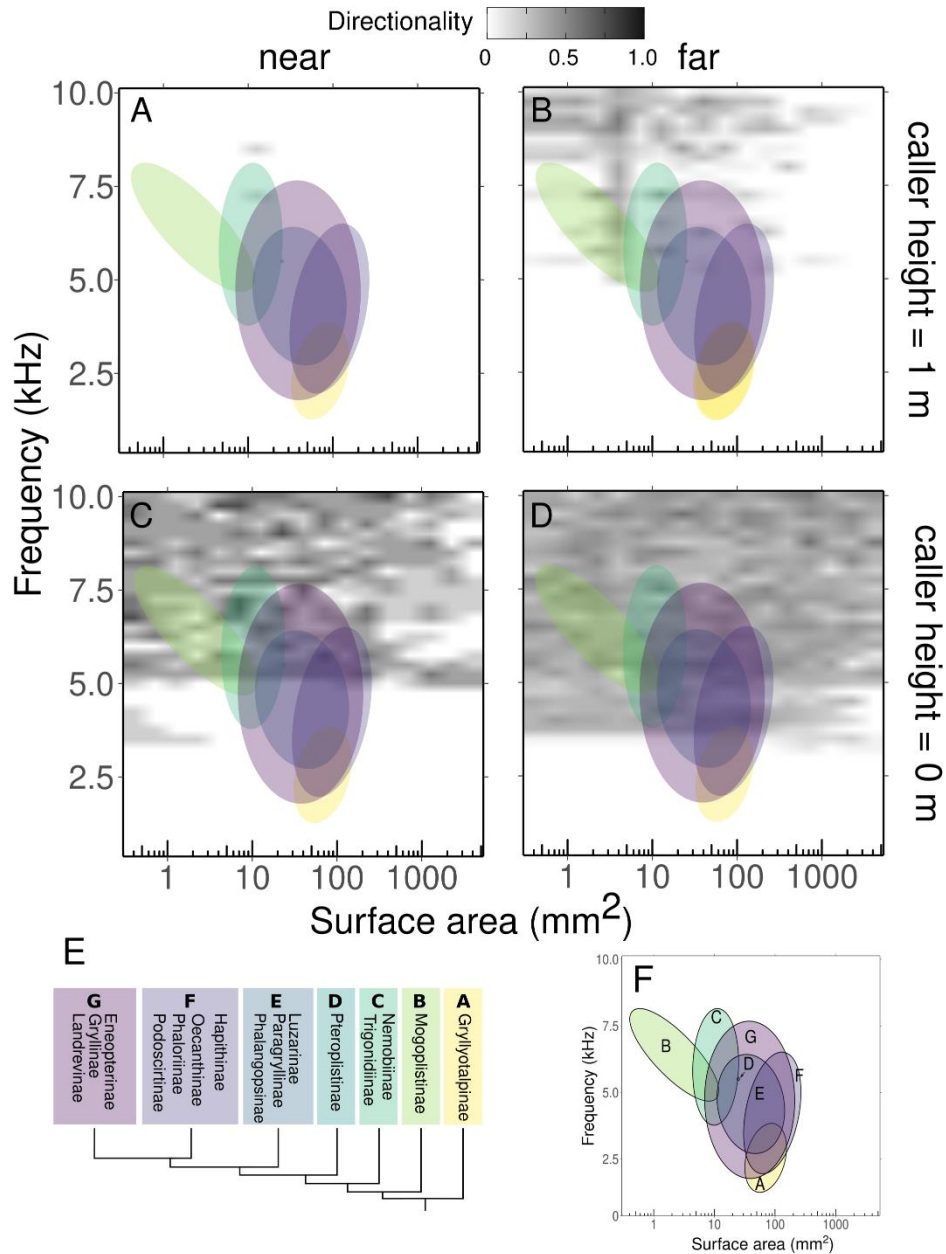
**SI 7.** Acoustic hardness of ground does not significantly influence SRE<sub>t</sub> at biologically relevant ranges of wing size and call frequency. Comparison of SRE<sub>t</sub> over hard vs soft ground. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance 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  $\log_2$  ratio instead of a straight proportion.  $\log_2$  ratios are scaled such that the ranges above and below 1 are proportional, rather than values below 1 being compressed between 0 and 1. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F.** Key to clade represented by each ellipse.



**SI 8.** 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 = 1 m, **D.** Distance = far, height = 0 m. Red lines indicate optimal efficiency ridge, or the size at each frequency that would produce an ideally baffled calling scenario. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F.** Key to clade represented by each ellipse.



**SI 9.** Vegetation somewhat decreases efficiency in baffled and grounded calling conditions. Differences in  $SRE_t$  by clade depending on vegetation and baffle use. For each clade, bars with black outline represent  $SRE_t$  without baffle and bars with red outline represent  $SRE_t$  with ideal baffle. Background color of the bars indicate vegetation or no vegetation.



**SI 10.** 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 = 1 m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 0 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.

**S1 11.** 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    |

SI 12. 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                     | Crickets north of Mexico species Id: Slosson's scaly cricket      |
|       |               |                       | <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   |
|       |               |                       | <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> *<br><i>californicus</i> | 2         | Orthoptera Species File Sound ID: 1535                             |
|                 |                    |   |  | 1         | Crickets North of Mexico Species ID: <i>Oecanthus californicus</i> |
|                 |                    |   | <i>californicus</i><br><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'Historie Naturelle ID: MNHN-SO-2018-100              |
|                      | G             | Eneopterinae      | <i>Agnotecous</i>       | <i>brachypterus*</i> | 1   |
| <i>clarus</i>        |               |                   |                         | 1                    | Museum D'Historie Naturelle ID: MNHN-SO-2018-102              |
| <i>meridionalis*</i> |               |                   |                         | 1                    | Museum D'Historie 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 |
|----------|--------------|--------------------|-------------------|-----------|--|
| <b>G</b> | 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)   |

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