1   **Title**

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

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25   Main Text
26   Figures 1 to 4
27   Supplementary figures and tables 1 to 12

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.

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 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.

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

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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.

Results

All crickets would benefit from baffle use in idealized conditions

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

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

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

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

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

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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 ± 0.41 times, 16 ± 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 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 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.

Ground calling emerges as an alternative strategy to baffle use in complex 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

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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.

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.

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.

8

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) it 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 alterative 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 though 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.

9

Discussion

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

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

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

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

Sound radiation efficiency in animal acoustic communication

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

11

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.

Materials and Methods

437

Specimen Data

438

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).

Finite Element Models for Sound Radiation Efficiency

462

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.

Model geometry, boundary conditions, symmetry, and vibration

468

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 ¼ symmetry. That is, we modeled ½ of one wing and ¼ 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 ½ 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^2,
501   scaled logarithmically by the equation 4×10^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 ± 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 ± 0.08 dB), except at wing sizes well outside the range
515   of the real wings that we measured (SI 4).

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).

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

14

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 kPa×s/m^2, porosity: 0.6) which is less reflective and a
572   "hard" ground (flow resistivity: 9 kPa×s/m^2, 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_t 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.

Finite Elements

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

Excess attenuation due to vegetation

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

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

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

Efficiency of individual species and how much they gain with baffle

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

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

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628 versus efficiency as measured from our models, with a separate trace for each
629 frequency (SI 6). We then identified the ka 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 ka to be about 1.3. For the boundary element models at the
633 far distance, optimal ka was approximately 1.55 (SI 6).

634 Next, we performed a simple linear regression between frequency and maximal
635 efficiency at optimal ka, 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 Δ SPL between each two adjacent points 2 cm apart (~ 2
655 body lengths for most animals in this analysis). Δ 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 Δ 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 Δ 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.

666 ## Acknowledgments
667

685

References

687

688 1.   J. Regen, Über die Anlockung des Weibchens von Gryllus campestris L. durch
689   telephonisch übertragene Stridulationslaute des Männchens. *Pflügers Archiv
690   European Journal of Physiology* **155**, 193–200 (1913).

691 2.   R. Deb, S. Modak, R. Balakrishnan, Baffling: a condition-dependent alternative
692   mate attraction strategy using self-made tools in tree crickets. *Proceedings of the
693   Royal Society B: Biological Sciences* **287**, 20202229 (2020).

694 3.   H. E. Farris, T. G. Forrest, R. R. Hoy, The effects of calling song spacing and
695   intensity on the attraction of flying crickets (orthoptera: Goryllidae: Nemobiinae). *J
696   Insect Behav* **10**, 639–653 (1997).

697 4.   H. Römer, R. K. Butlin, T. Guilford, J. R. Krebs, Environmental and biological
698   constraints for the evolution of long-range signalling and hearing in acoustic
699   insecs. *Philosophical Transactions of the Royal Society of London. Series B:
700   Biological Sciences* **340**, 179–185 (1993).

701 5.   T. G. Forrest, Power output and efficiency of sound production by crickets. *Behav
702   Ecol* **2**, 327–338 (1991).

703 6.   T. G. Forrest, Acoustic Communication and Baffling Behaviors of Crickets. *The
704   Florida Entomologist* **65**, 33–44 (1982).

705   7. N. Mhatre, R. Malkin, R. Deb, R. Balakrishnan, D. Robert, Tree crickets optimize
706   the acoustics of baffles to exaggerate their mate-attraction signal. *eLife* **6**, e32763
707   (2017).

708   8. S. A. Hambric, J. B. Fahnline, Structural Acoustics Tutorial—Part 2: Sound—
709   Structure Interaction. *Acou. Today* **3**, 9 (2007).

710   9. H. C. Bennet-Clark, Size and scale effects as constraints in insect sound
711   communication. *Phil. Trans. R. Soc. Lond. B* **353**, 407–419 (1998).

712   10. L. Prozesky-Schulze, O. P. M. Prozesky, F. Anderson, G. J. J. Van Der Merwe,
713   Use of a self-made sound baffle by a tree cricket. *Nature* **255**, 142–143 (1975).

714   11. N. Collins, A Citizen Scientist's Contributions to Tree Cricket Taxonomy. *American
715   Entomologist* **58**, 9–10 (2012).

716   12. N. Mhatre, Tree cricket baffles are manufactured tools. *Ethology* **124**, 691–693
717   (2018).

718   13. J. D. Pierce, A Review of Tool Use in Insects. *The Florida Entomologist* **69**, 95–104
719   (1986).

720   14. G. R. Hunt, R. D. Gray, A. H. Taylor, "Why is tool use rare in animals?" in *Tool Use
721   in Animals: Cognition and Ecology*, C. Boesch, C. M. Sanz, J. Call, Eds.
722   (Cambridge University Press, 2013), pp. 89–118.

723   15. M. Hansell, G. Ruxton, Setting tool use within the context of animal construction
724   behaviour. *Trends in Ecology & Evolution* **23**, 73–78 (2008).

725   16. C. Boesch, H. Boesch, Optimisation of Nut-Cracking With Natural Hammers By
726   Wild Chimpanzees. *Behaviour* **83**, 265–286 (1983).

727   17. J. A. Fujii, K. Ralls, M. T. Tinker, Ecological drivers of variation in tool-use
728   frequency across sea otter populations. *Behavioral Ecology* **26**, 519–526 (2015).

729   18. N. Spagnoletti, E. Visalberghi, E. Ottoni, P. Izar, D. Fragaszy, Stone tool use by
730   adult wild bearded capuchin monkeys (Cebus libidinosus). Frequency, efficiency
731   and tool selectivity. *Journal of Human Evolution* **61**, 97–107 (2011).

732   19. B. Erregger, A. K. D. Schmidt, Anthropogenic calling sites boost the sound
733   amplitude of advertisement calls produced by a tropical cricket. *Animal Behaviour*
734   **142**, 31–38 (2018).

735   20. M. I. Muñoz, W. Halfwerk, Amplification of frog calls by reflective leaf substrates:
736   implications for terrestrial and arboreal species. *Bioacoustics* **31**, 490–503 (2022).

737   21. J. W. Bradbury, S. L. Vehrencamp, *Principles of animal communication*, 2nd ed
738   (Sinauer Associates, 2011).

739   22.   H. C. Gerhardt, F. Huber, *Acoustic Communication in Insects and Anurans:*
740   *Common Problems and Diverse Solutions* (University of Chicago Press, 2002)
741   (February 17, 2023).

742   23.   H. Romer, J. Lewald, High-frequency sound transmission in natural habitats:
743   implications for the evolution of insect acoustic communication. *Behav Ecol*
744   *Sociobiol* **29**, 437–444 (1992).

745   24.   M. Van Staaden, H. Römer, Sexual signalling in bladder grasshoppers: tactical
746   design for maximizing calling range. *Journal of Experimental Biology* **200**, 2597–
747   2608 (1997).

748   25.   M. Jain, R. Balakrishnan, Does acoustic adaptation drive vertical stratification? A
749   test in a tropical cricket assemblage. *Behav. Ecol.* **23**, 343–354 (2012).

750   26.   T. F. W. Embleton, Tutorial on sound propagation outdoors. *The Journal of the*
751   *Acoustical Society of America* **100**, 31–48 (1996).

752   27.   K. Kostarakos, H. Römer, Sound transmission and directional hearing in field
753   crickets: neurophysiological studies outdoors. *J Comp Physiol A* **196**, 669–681
754   (2010).

755   28.   I. C. Chintauan-Marquier, *et al.*, Laying the foundations of evolutionary and
756   systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic
757   analysis. *Cladistics* **32**, 54–81 (2016).

758   29.   T. Robillard, P. Grandcolas, L. Desutter-Grandcolas, A shift toward harmonics for
759   high-frequency calling shown with phylogenetic study of frequency spectra in
760   Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae). *Can. J. Zool.* **85**,
761   1264–1275 (2007).

762   30.   K. M. Li, S. Taherzadeh, K. Attenborough, Sound propagation from a dipole source
763   near an impedance plane. *The Journal of the Acoustical Society of America* **101**,
764   3343–3352 (1997).

765   31.   I. Bashir, S. Taherzadeh, H.-C. Shin, K. Attenborough, Sound propagation over soft
766   ground without and with crops and potential for surface transport noise attenuation.
767   *J. Acoust. Soc. Am.* **137**, 12 (2015).

768   32.   N. Mhatre, R. Balakrishnan, Male spacing behaviour and acoustic interactions in a
769   field cricket: implications for female mate choice. *Animal Behaviour* **72**, 1045–1058
770   (2006).

771   33.   H. Römer, Directional hearing: from biophysical binaural cues to directional hearing
772   outdoors. *J Comp Physiol A* **201**, 87–97 (2015).

773   34.   R. Deb, R. Balakrishnan, The opportunity for sampling: the ecological context of
774   female mate choice. *Behavioral Ecology* **25**, 967–974 (2014).

775   35.   D. B. Weissman, D. A. Gray, Crickets of the genus Gryllus in the United States
776   (Orthoptera: Gryllidae: Gryllinae). *Zootaxa* **4705**, 1–277 (2019).

777   36.   H. C. Bennet-Clark, The Tuned Singing Burrow of Mole Crickets. *Journal of*
778   *Experimental Biology* **128**, 383–409 (1987).

779   37.   P. Senter, Voices of the past: a review of Paleozoic and Mesozoic animal sounds:
780   review. *Historical Biology* **20**, 255–287 (2008).

781   38.   H. Song, *et al.*, 300 million years of diversification: elucidating the patterns of
782   orthopteran evolution based on comprehensive taxon and gene sampling.
783   *Cladistics* **31**, 621–651 (2015).

784   39.   J.-J. Gu, *et al.*, Wing stridulation in a Jurassic katydid (Insecta, Orthoptera)
785   produced low-pitched musical calls to attract females. *Proceedings of the National*
786   *Academy of Sciences* **109**, 3868–3873 (2012).

787   40.   C. Woodrow, E. Baker, T. Jonsson, F. Montealegre-Z, Reviving the sound of a 150-
788   year-old insect: The bioacoustics of Prophalangopsis obscura (Ensifera:
789   Hagloidea). *PLOS ONE* **17**, e0270498 (2022).

790   41.   H. Winkler, The Ecology of Avian Acoustical Signals in *Ecology of Sensing*, F. G.
791   Barth, A. Schmid, Eds. (Springer, 2001), pp. 79–104.

792   42.   E. S. Morton, Ecological Sources of Selection on Avian Sounds. *The American*
793   *Naturalist* **109**, 17–34 (1975).

794   43.   T. G. Forrest, From Sender to Receiver: Propagation and Environmental Effects on
795   Acoustic Signals. *Am Zool* **34**, 644–654 (1994).

796   44.   K. Marten, P. Marler, Sound transmission and its significance for animal
797   vocalization. *Behav Ecol Sociobiol* **2**, 271–290 (1977).

798   45.   K. Marten, D. Quine, P. Marler, Sound transmission and its significance for animal
799   vocalization. *Behav Ecol Sociobiol* **2**, 291–302 (1977).

800   46.   R. H. Wiley, "Signal Transmission in Natural Environments" in *Encyclopedia of*
801   *Neuroscience*, (Elsevier, 2009), pp. 817–822.

802   47.   U. Ingard, G. L. Lamb, Effect of a Reflecting Plane on the Power Output of Sound
803   Sources. *The Journal of the Acoustical Society of America* **29**, 743–744 (1957).

804   48.   G. W. Swenson, M. J. White, The Field of a Sound Source Reflected from a Hard
805   Ground (2004).

806   49.   K. Attenborough, I. Bashir, S. Taherzadeh, Outdoor ground impedance models.
807   *The Journal of the Acoustical Society of America* **129**, 2806–2819 (2011).

808 50. A. Putra, D. J. Thompson, Radiation efficiency of unbaffled and perforated plates
809   near a rigid reflecting surface. *Journal of Sound and Vibration* **330**, 5443–5459
810   (2011).

811 51. L. Jakobsen, J. Christensen-Dalsgaard, P. M. Juhl, C. P. H. Elemans, How Loud
812   Can you go? Physical and Physiological Constraints to Producing High Sound
813   Pressures in Animal Vocalizations. *Front. Ecol. Evol.* **9** (2021).

814 52. L. Jakobsen, J. M. Ratcliffe, A. Surlykke, Convergent acoustic field of view in
815   echolocating bats. *Nature* **493**, 93–96 (2013).

816 53. L. Jakobsen, A. Surlykke, Vespertilionid bats control the width of their biosonar
817   sound beam dynamically during prey pursuit. *PNAS* **107**, 13930–13935 (2010).

818 54. B. Møhl, M. Wahlberg, P. T. Madsen, A. Heerfordt, A. Lund, The monopulsed
819   nature of sperm whale clicks. *The Journal of the Acoustical Society of America* **114**,
820   1143–1154 (2003).

821 55. L. Desutter-Grandcolas, Phylogeny and the evolution of acoustic communication in
822   extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta* **32**, 525–561 (2003).

823 56. Cigliano, M. M., Braun, D. C., Eades, D. C., Otte, D., Orthoptera Species File.
824   *Orthoptera Species File. Version 5.0/5.0* (March 7, 2022).

825 57. J. Schindelin, C. T. Rueden, M. C. Hiner, K. W. Eliceiri, The ImageJ ecosystem: An
826   open platform for biomedical image analysis. *Molecular Reproduction and
827   Development* **82**, 518–529 (2015).

828 58. K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of
829   Ornithology, Raven Lite: Interactive Sound Analysis Software (Version 2.0) (2020).

830 59. J.-P. Berenger, A perfectly matched layer for the absorption of electromagnetic
831   waves. *Journal of Computational Physics* **114**, 185–200 (1994).

832 60. V. Godthi, R. Balakrishnan, R. Pratap, The mechanics of acoustic signal evolution
833   in field crickets. *Journal of Experimental Biology* **225**, jeb243374 (2022).

834 61. J. W. Bradbury, S. L. Vehrencamp, *Principles of Animal Communication*, First
835   edition (Sinauer Associates, Inc., 1998).

836 62. T. D. Rossing, Ed., *Springer Handbook of Acoustics* (Springer New York, 2014)
837   https:/doi.org/10.1007/978-1-4939-0755-7 (April 8, 2020).

838 63. H. Römer, Neurophysiology goes wild: from exploring sensory coding in sound
839   proof rooms to natural environments. *J Comp Physiol A* **207**, 303–319 (2021).

840 64. N. Mhatre, R. Balakrishnan, Phonotactic walking paths of field crickets in closed-
841   loop conditions and their simulation using a stochastic model. *Journal of
842   Experimental Biology* **210**, 3661–3676 (2007).
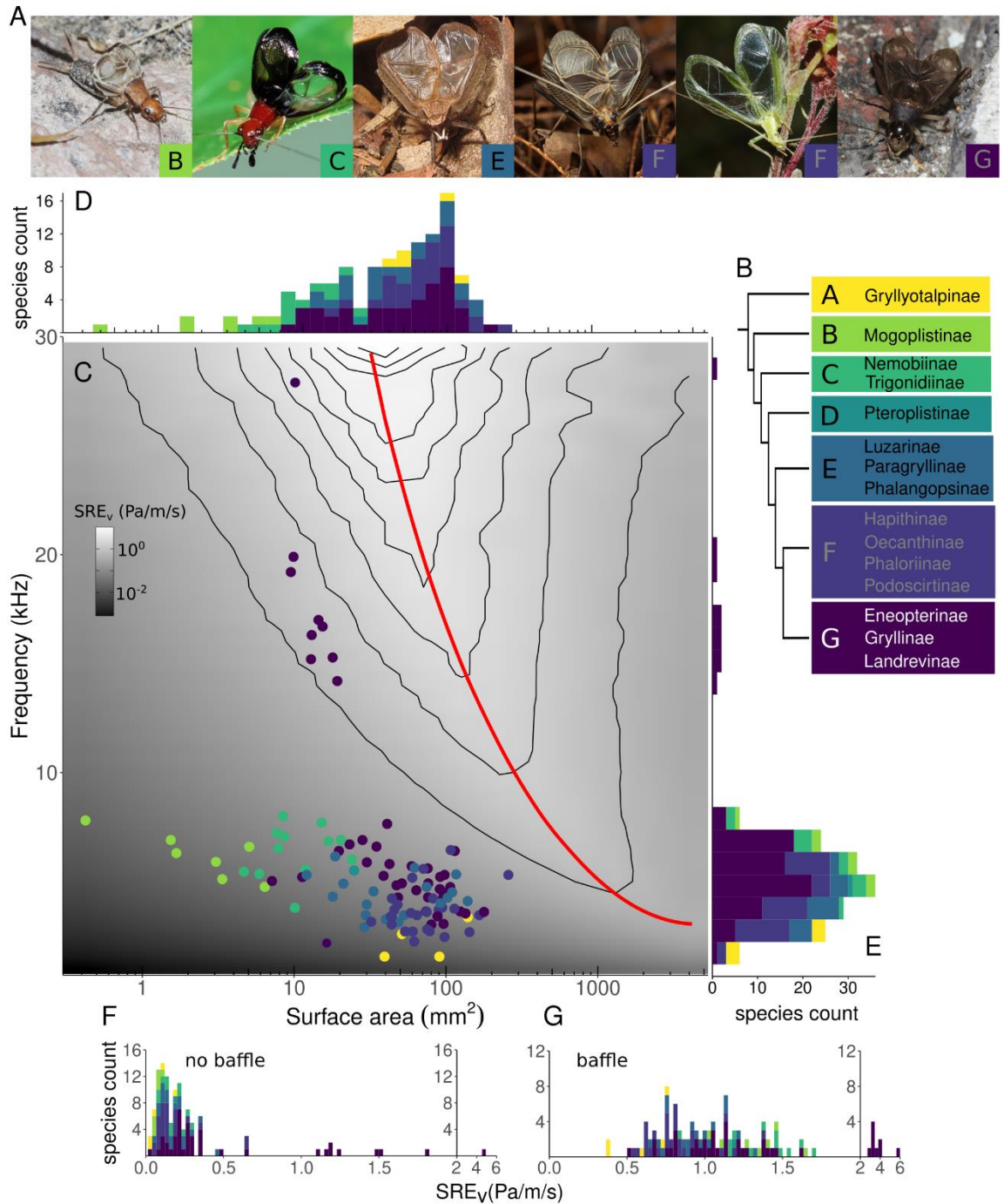
843
844 **Figures and Tables**

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

23

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.
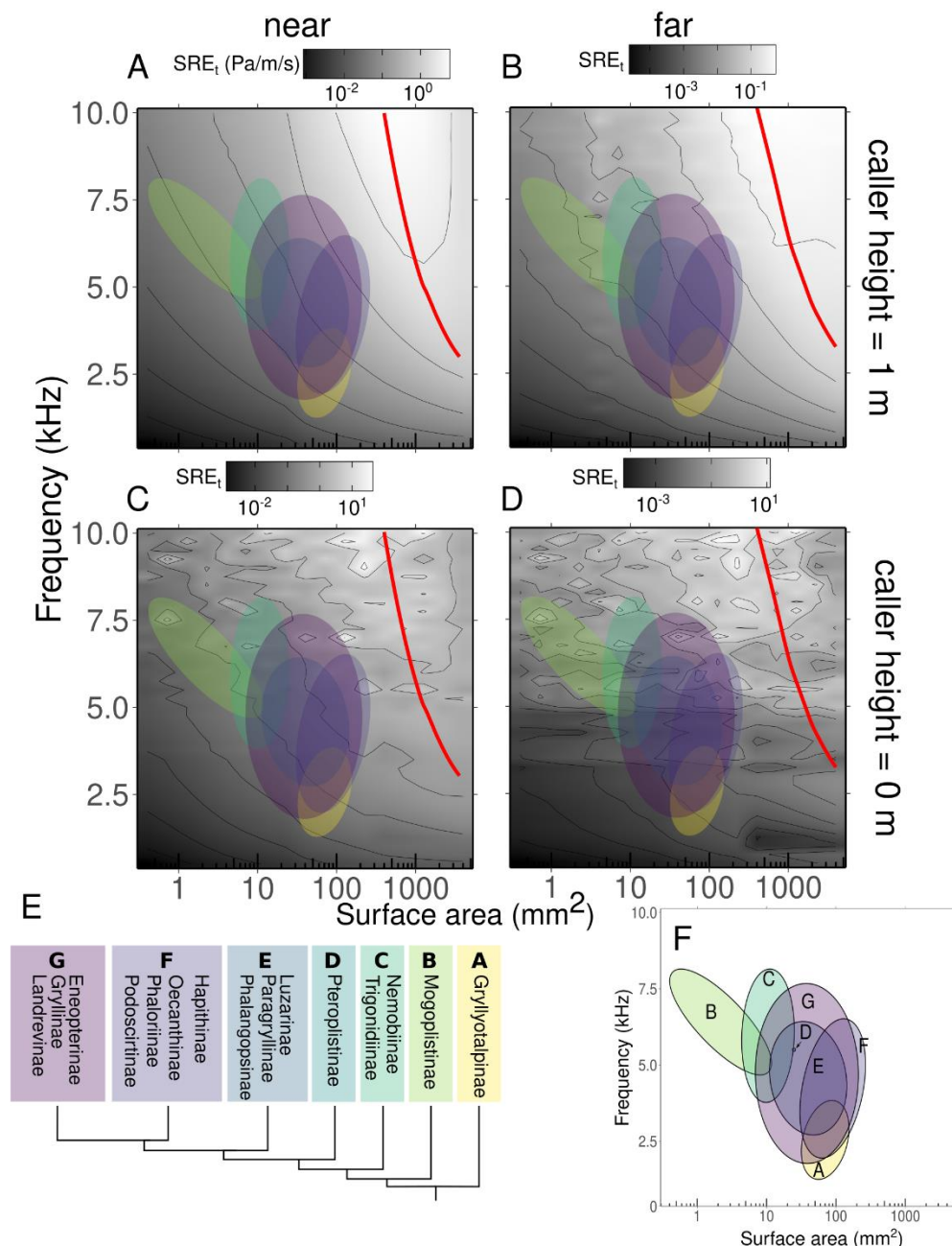862

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 – 02 m "near" and 0.8 –
867 0.9 m "far"). **A.** Distance = near, height = 1m, **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.
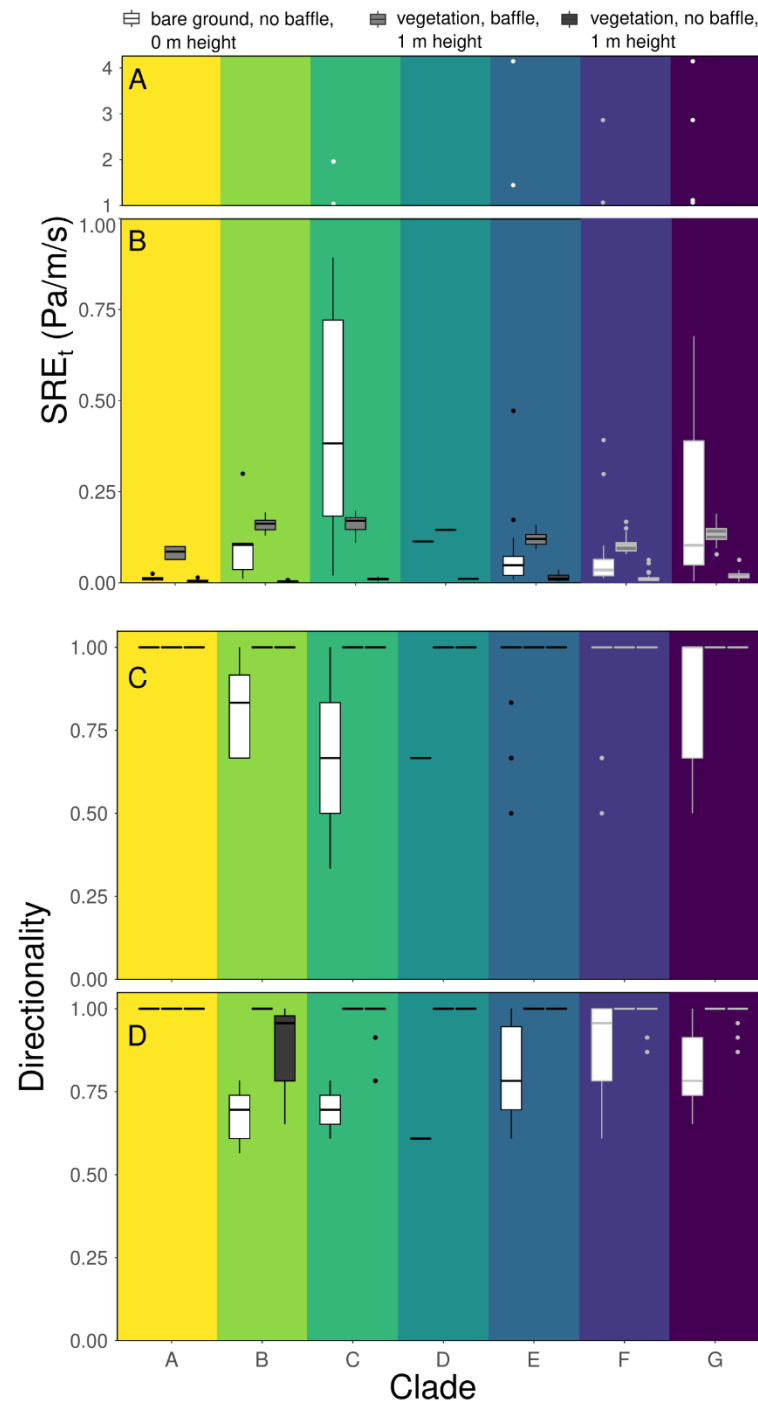
Figure 3. The most effective calling strategy (ground vs baffled) varies depending on clade, however directionality does not vary significantly. **A, B.** Comparison of SRE$_t$ on bare ground with no baffle, and 1 m in vegetation with and without an ideal baffle. These measurements were taken far from the caller, i.e. an average of the SPL at a distance of 0.8-0.9 m from wings, directly in front of the wings was used. A. indicates extreme outliers, which only occur when we consider 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.
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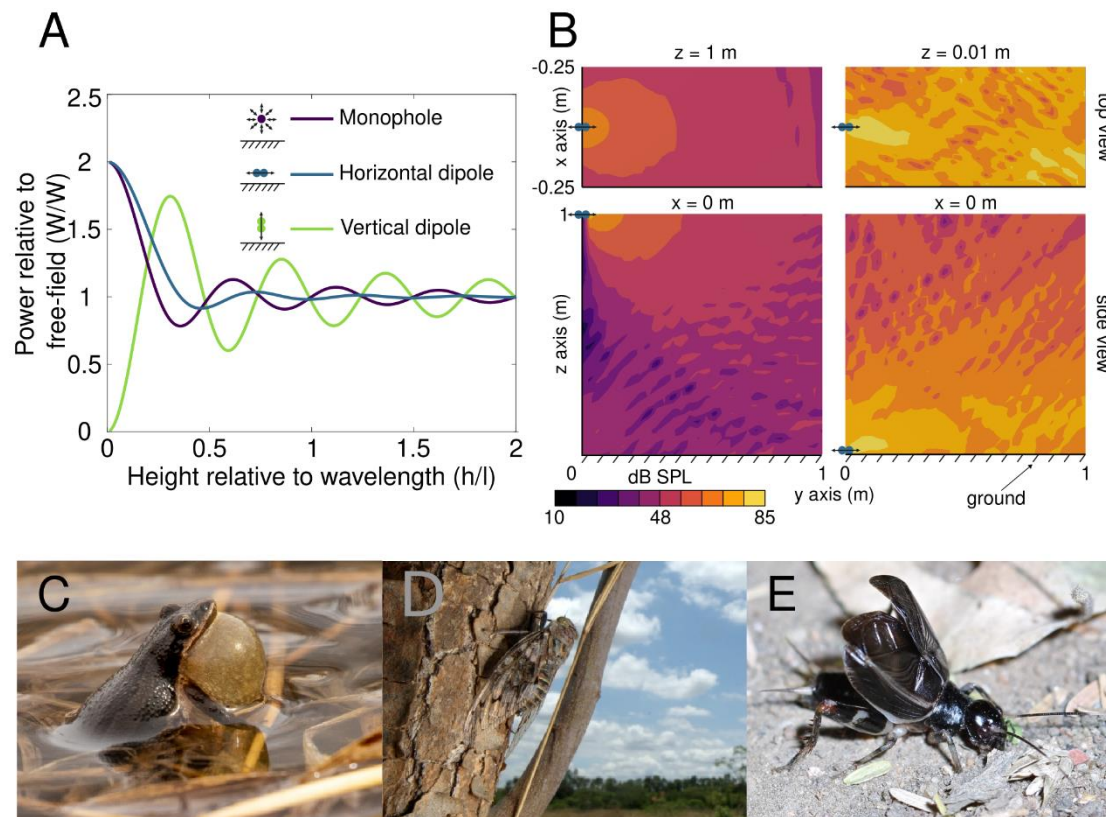
Figure 4. Hard reflective surfaces like the ground or water offer all acoustically active animals an increase in sound radiation efficiency. **A.** The presence of a perfectly reflective surface near an acoustic source can lead to an increase of the power radiated in the hemisphere above the source, relative to the power that same source would radiate over a full spherical volume in free space. Both monopole and horizontal dipole sources (whose vibration axis is parallel to the reflective surface) can get a large boost in power when they are close to the reflective surface, relative to the wavelength of sound being radiated. (Reproduced from equations in ref. 41). In contrast, vertically oriented dipoles need to be further from the reflective surface to get an equivalent gain in efficiency. **B.** In fact, near the ground, the sound field from a dipole source is expected to become less directional and we observe this in our models. Data shown here are from a radiator of surface area of 126 mm^2 and at frequency 5 kHz, which is seen to be directional 1 m above the ground, but much less so when right next to the ground. **C-E.** Different animals, especially small animals who have low sound radiation efficiency whether they are monopole or dipole sources may call from near acoustically hard and reflective surfaces, like **C.** water (photo: Doug Mills), **D.** tree trunks (photo: Natasha Mhatre), or even the **E.** ground (photo: Brandon Woo) may be exploiting this effect. Animals that are monopole-like sources are likely to orient themselves parallel to the surface since this is advantageous for camouflage as well. However, crickets which are dipole-like acoustic sources, are constrained to expose themselves by calling with their wings perpendicular to the ground surface to maintain the advantageous horizontal dipole orientation.

Supplementary Material
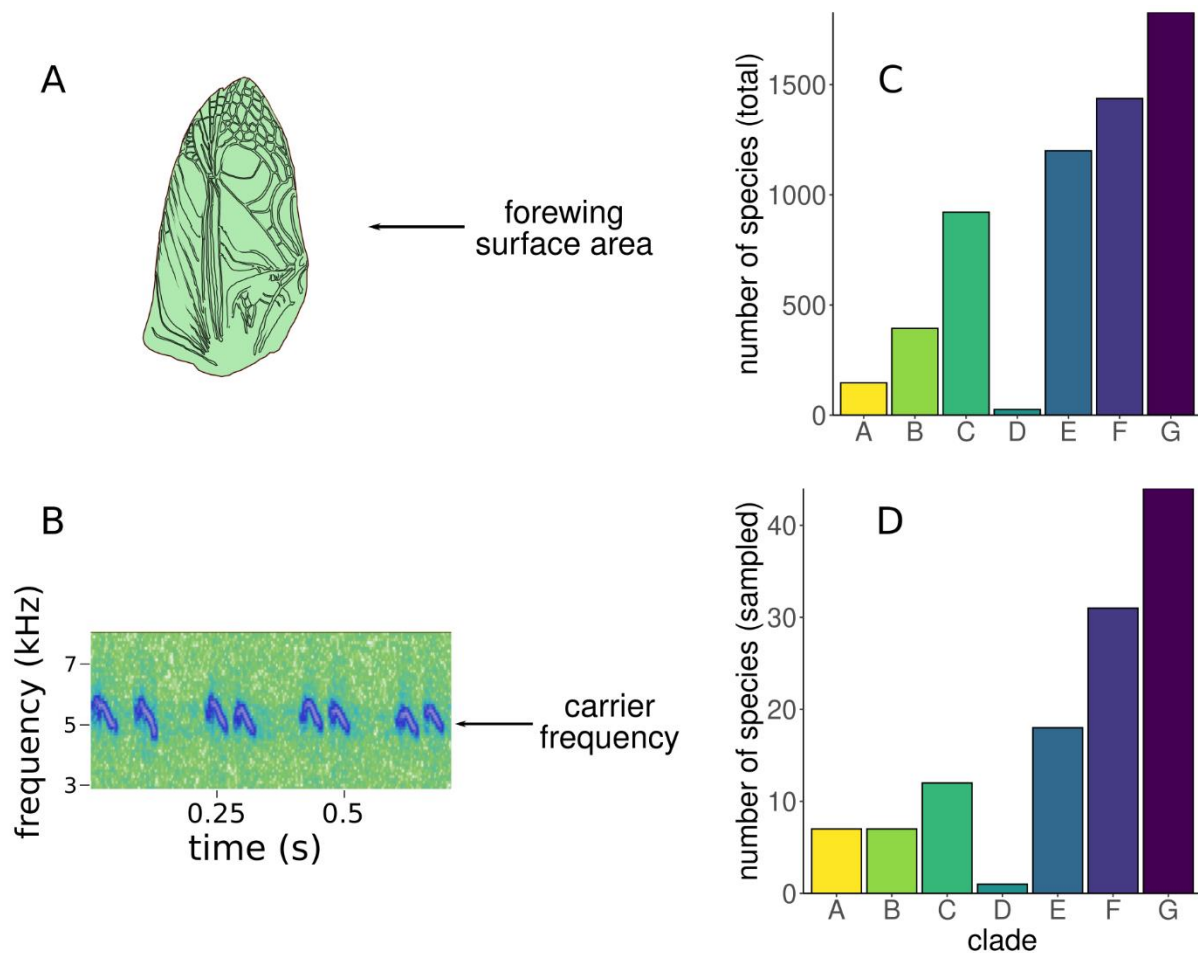
SI 1. Measuring acoustic-morphospace of crickets. Wing area and call frequency were quantified. **A.** Wing surface area was calculated as the area of the entire forewing. **B.** The carrier frequency (sometimes called fundamental frequency) of the call was identified from spectrograms and recorded. 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.

A
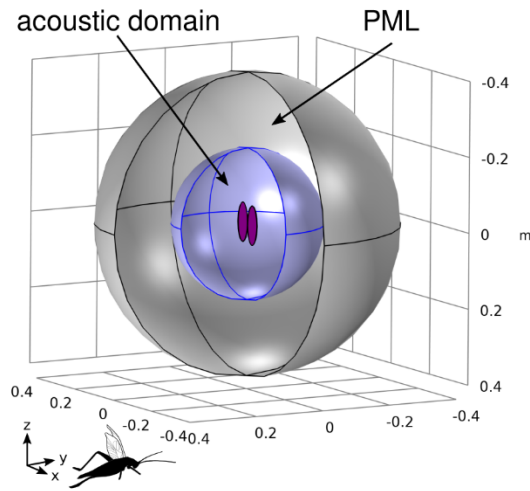
B
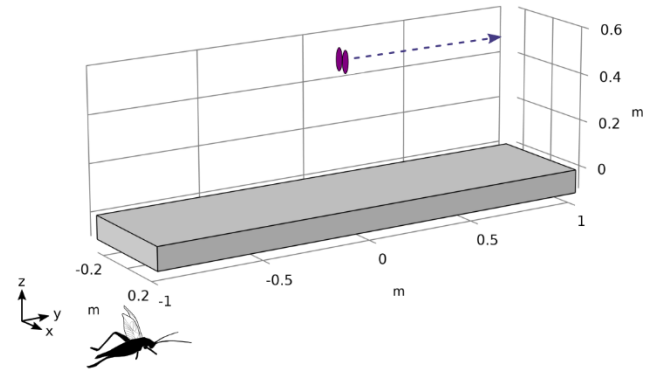
SI 2. Geometry of biophysical models. **A.** Geometry of finite element (FE) models. Inner blue sphere is the acoustic domain. The wings are represented by purple ellipses in the center. Outer sphere is a perfectly-matched layer, to mitigate boundary effects caused by the finite acoustic domain. SPL 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.
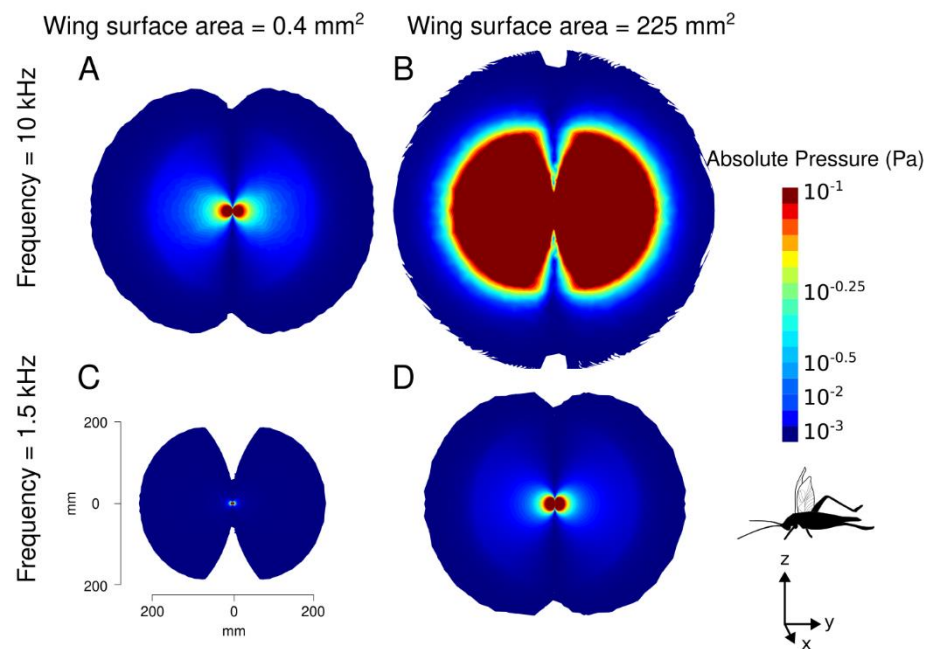
SI 3. Sound fields produced by modeled wings vary with respect to call frequency and wing size. Fields are oriented such that wings are perpendicular to page and vibrate left to right, as indicated by the silhouette cricket. Sound fields are given for the following combinations of wing size and frequency: **A.** wing size = 0.04 mm^2, frequency = 10 kHz; **B.** wing size = 225 mm^2, frequency = 10 kHz; **C.** wing size = 0.4 mm^2, frequency = 1.5 kHz; **D.** wing size = 225 mm^2, frequency = 1.5 kHz. Spatial scale given in C applies to all sound fields. Efficiency (here, size and color of sound field) increases with improved match between wavelength of sound and size of radiator (wing). Cricket wings in general are small so this match is poor except at the extreme high end of radiator size and call frequency (B).
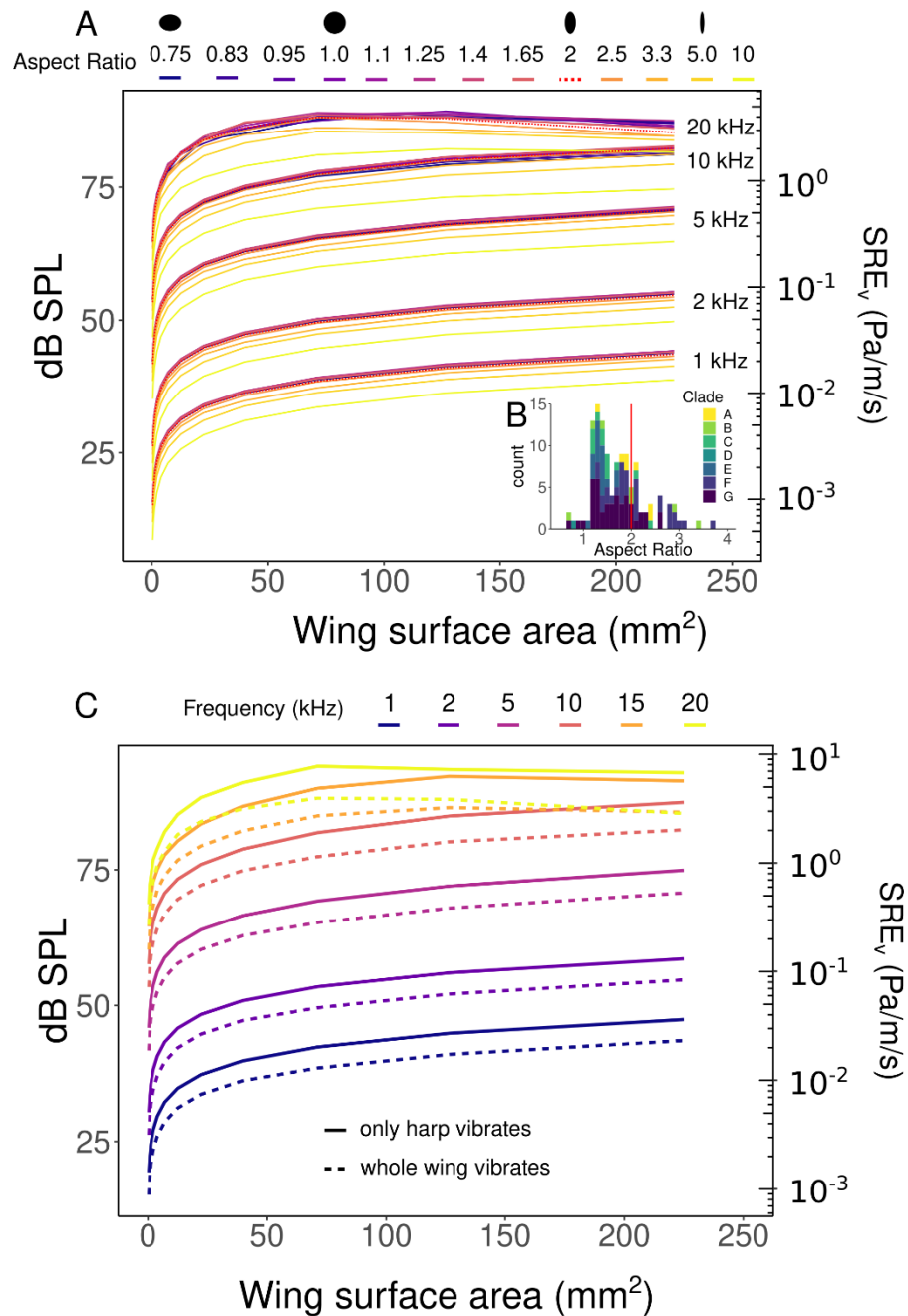
SI 4. Wing aspect ratio and use of a "harp" resonator do not significantly impact SRE_v within biologically-relevant ranges of wing size and call frequency. **A.** The effect of wing aspect ratio on SRE_v at six different call frequencies. The aspect ratio that was used on all models in this study (2) 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). **B.** 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.
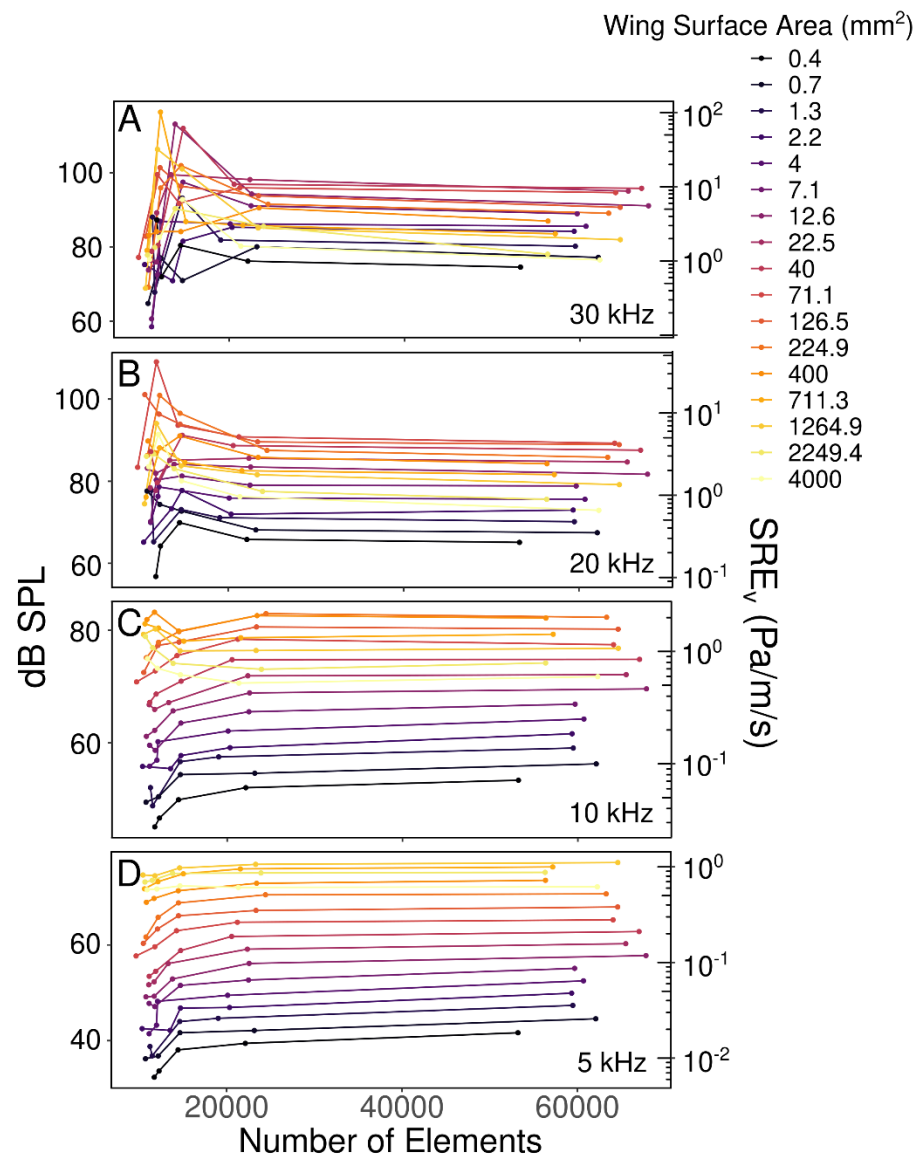
SI 5. Mesh sensitivity analysis for models based on the finite element method. Each line represents the SPL of a single wing size with a different number of mesh elements. Each panel shows this analysis at a different frequency: **A.** 30 kHz, **B.** 20 kHz, **C.** 10 kHz, **D.** 5 kHz. As the difference between the second-largest and largest number of elements was small, we proceeded with the largest number of elements shown here for the analysis.
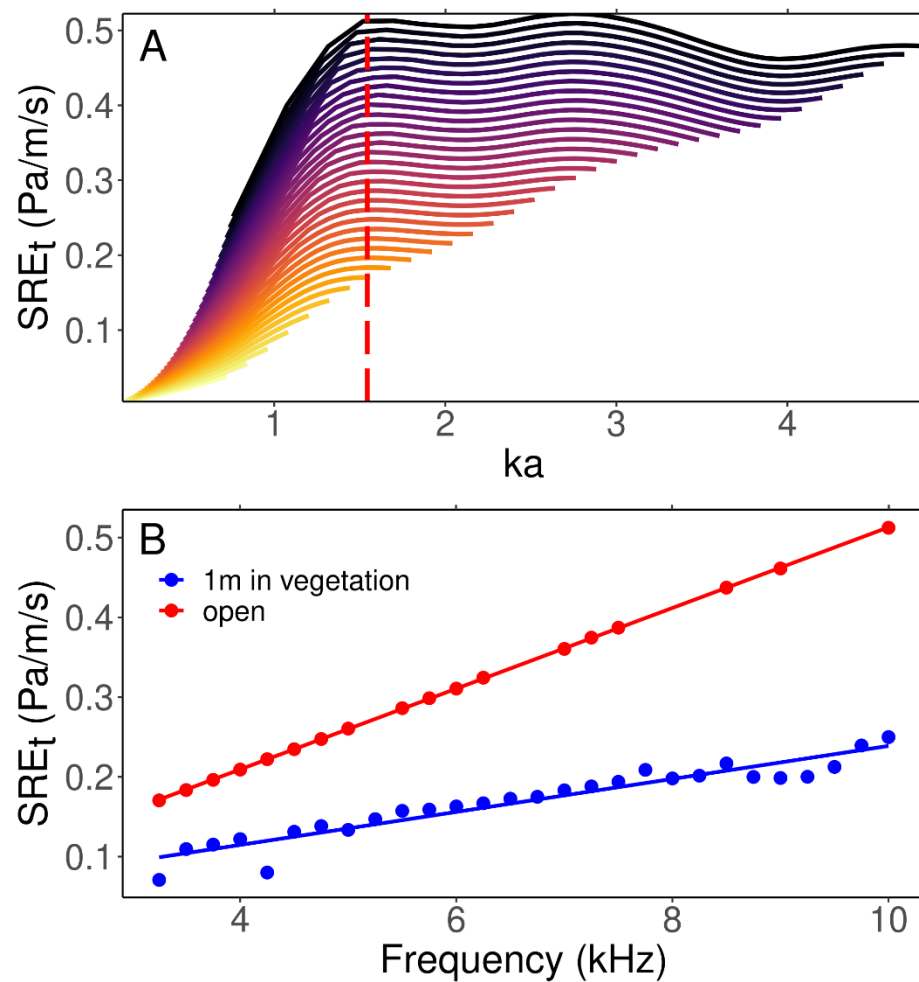
SI 6. Calculating efficiency with optimal baffle. **A.** ka at which optimal efficiency occurs for each frequency. Each frequency is represented by a different line. Line at which efficiency is maximized for each frequency (maximum efficiency ridge) is shown by red dashed line. **B.** Efficiency at this optimal ka (1.55) in open and vegetation conditions.
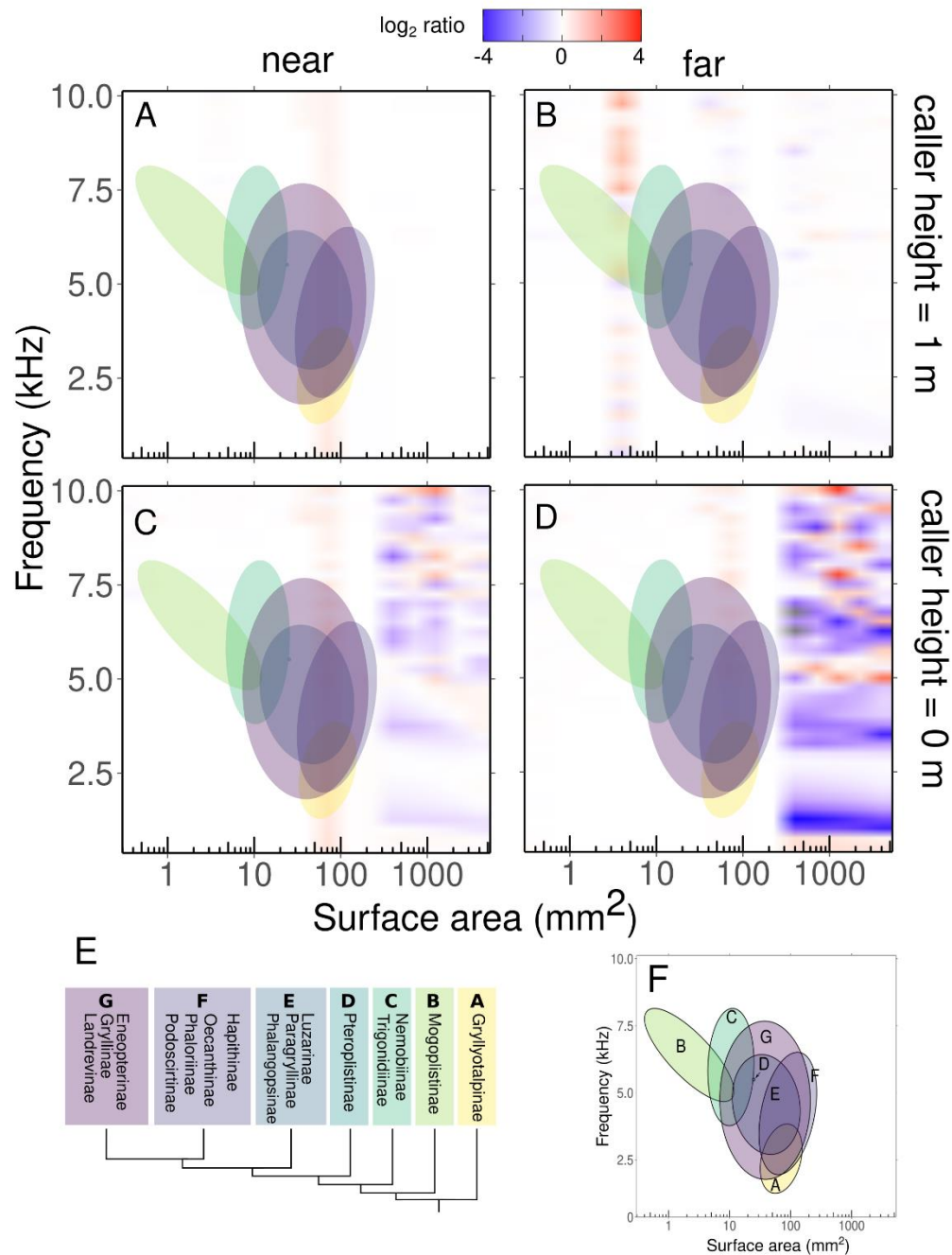
SI 7. Acoustic hardness of ground does not significantly influence SRE_t at biologically relevant ranges of wing size and call frequency. Comparison of SRE_t over hard vs soft ground. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 02 m "near" and 0.8 – 0.9 m "far"). **A.** Distance = near, height = 1m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 1 m, **D.** Distance = far, height = 0 m. Color indicates whether higher SRE is found with hard ground (red shades), soft ground (blue shades) or no difference (white). Data are presented as a $\log_2$ ratio instead of a straight proportion. $\log_2$ ratios are scaled such that the ranges above and below 1 are proportional, rather than values below 1 being compressed between 0 and 1. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F.** Key to clade represented by each ellipse.
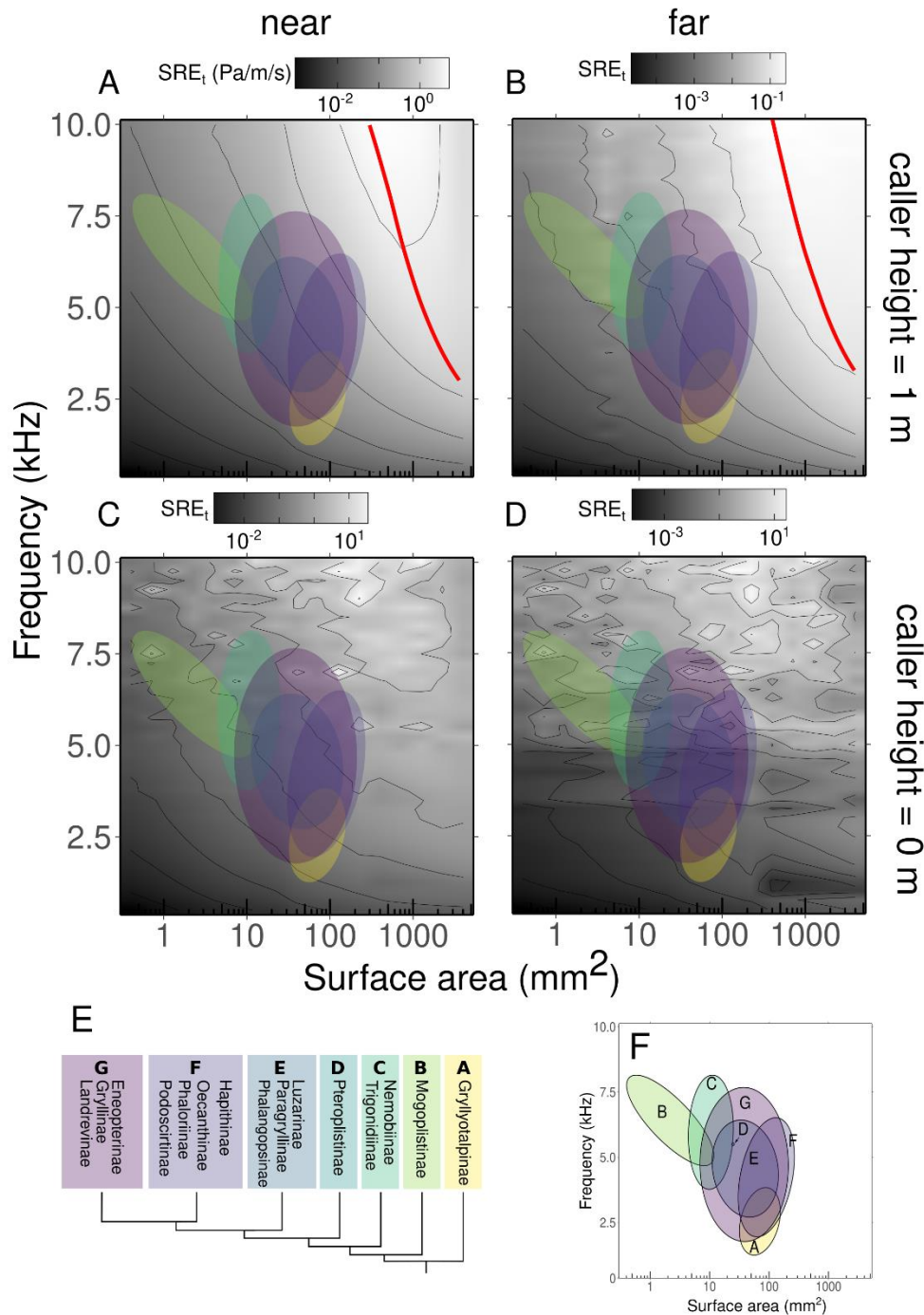
SI 8. Vegetation decreases efficiency overall but does not substantially change the landscape pattern of efficiency. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 02 m "near" and 0.8 – 0.9 m "far"). In each height and distance scenario, an excess attenuation factor due to vegetation was also applied. **A.** Distance = near, height = 1m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 1 m, **D.** Distance = far, height = 0 m. Red lines indicate optimal efficiency ridge, or the size at each frequency that would produce an ideally baffled calling scenario. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F**. Key to clade represented by each ellipse.
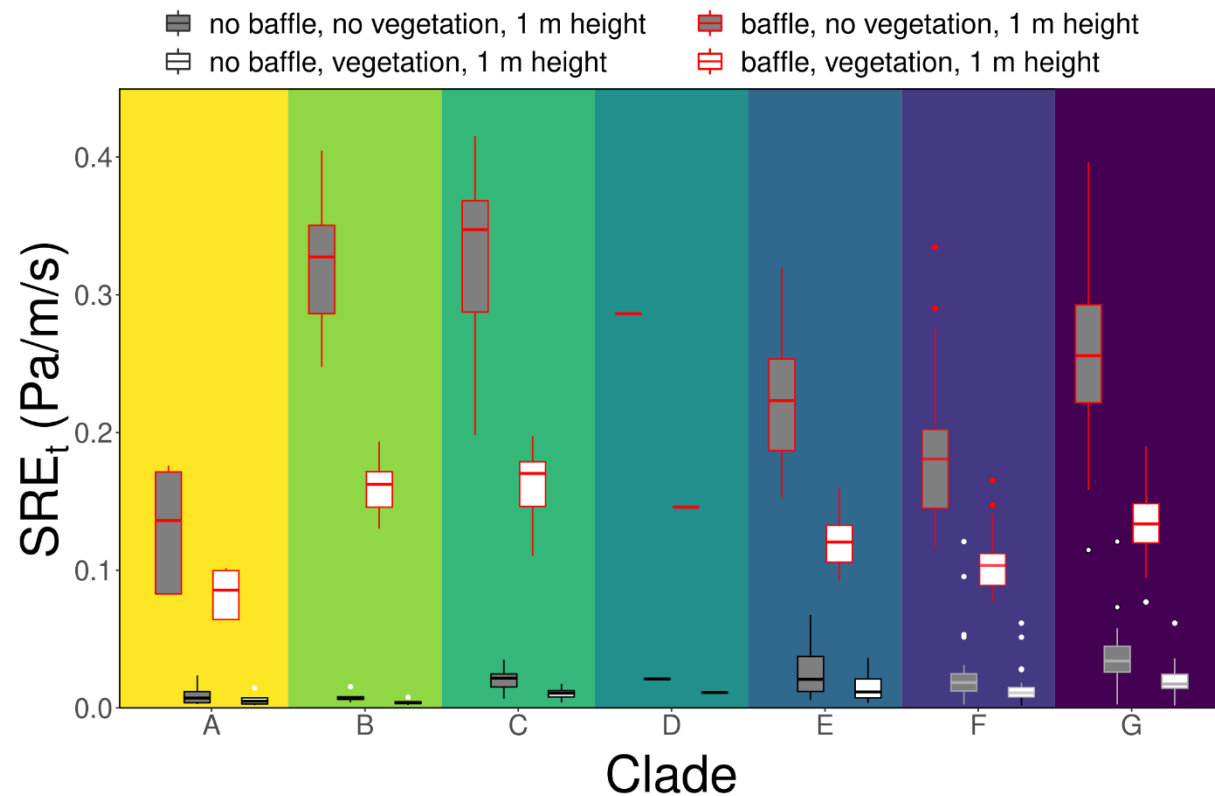
SI 9. Vegetation somewhat decreases efficiency in baffled and grounded calling conditions. Differences in SRE_t by clade depending on vegetation and baffle use. For each clade, bars with black outline represent SRE_t without baffle and bars with red outline represent SRE_t with ideal baffle. Background color of the bars indicate vegetation or no vegetation.
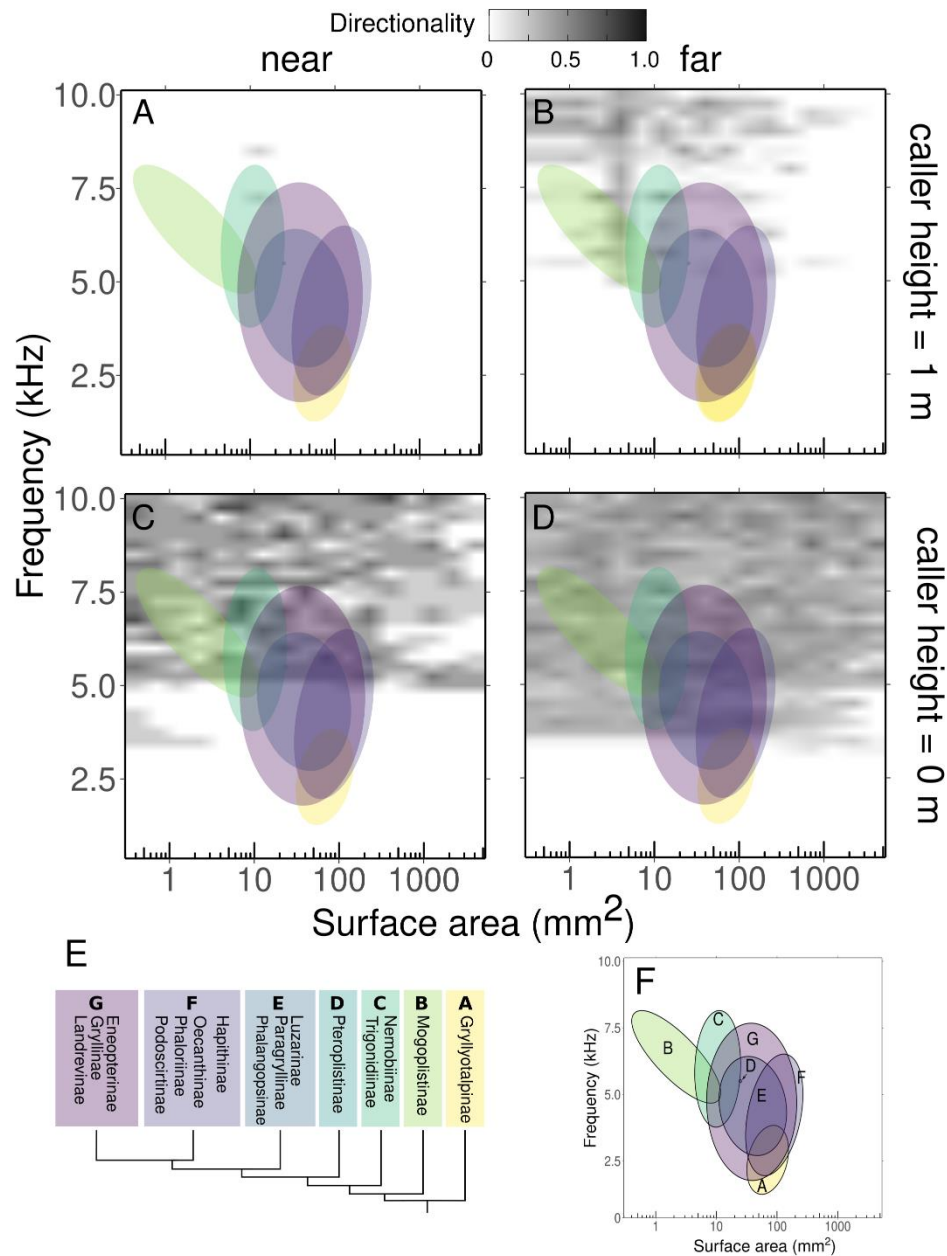
SI 10. Call directionality decreases at higher frequencies, particularly with grounded calling. Each panel represents a combination of caller height above ground (0 m or 1 m) and receiver distance from caller (0.05 – 02 m "near" and 0.8 – 0.9 m "far"). **A.** Distance = near, height = 1m, **B.** Distance = far, height = 1 m; **C.** Distance = near, height = 1 m, **D.** Distance = far, height = 0 m. Each clade of animals is represented by a colored ellipse. **E.** Phylogeny representing each clade **F**. Key to clade represented by each ellipse.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Full citations for Specimen data:

Anso J, Barrabé L, Desutter-Grandcolas L, Jourdan H, Grandcolas P, Dong J, Robillard T. 2016. Old Lineage on an Old Island: Pixibinthus, a New Cricket Genus Endemic to New Caledonia Shed Light on Gryllid Diversification in a Hotspot of Biodiversity. *PLOS ONE* **11**:e0150920. doi:10.1371/journal.pone.0150920

Barranco P, Gilgado JD, Ortuño VM. 2013. A new mute species of the genus Nemobius Serville (Orthoptera, Gryllidae, Nemobiinae) discovered in colluvial, stony debris in the Iberian Peninsula: A biological, phenological and biometric study. *Zootaxa* **3691**:201–219. doi:10.11646/zootaxa.3691.2.1

Castro-Souza RA, Zefa E, Ferreira RL. 2020. New troglobitic and troglophilic syntopic species of Endecous (Orthoptera, Grylloidea, Phalangopsidae) from a Brazilian cave: a case of sympatric speciation? *Zootaxa* **4810**:271–304. doi:10.11646/zootaxa.4810.2.3

Cole JA, Funk DH. 2019. Anaxipha hyalicetra sp. n. (Gryllidae: Trigonidiinae), a new sword-tailed cricket species from Arizona. *Journal of Orthoptera Research* **28**:3–9.

Dambach M, Gras A. 1995. Bioacoustics of a miniature cricket, Cycloptiloides canariensis (Orthoptera: Gryllidae: Mogoplistinae). *Journal of Experimental Biology* **198**:721–728. doi:10.1242/jeb.198.3.721

Desutter-Grandcolas L. 2009. New and little known crickets from Espiritu Santo Island, Vanuatu (Insecta, Orthoptera, Grylloidea, Pseudotrigonidium Chopard, 1915, Phaloriinae and Nemobiinae p.p.). *zoos* **31**:619–659. doi:10.5252/z2009n3a12

Desutter-Grandcolas L, Robillard T. 2006. Phylogenetic systematics and evolution of Agnotecous in New Caledonia (Orthoptera: Grylloidea, Eneopteridae). *Systematic Entomology* **31**:65–92. doi:10.1111/j.1365-3113.2005.00299.x

Gorochov AV, Tan MK. 2012. New crickets of the subfamilies Phaloriinae and Pteroplistinae (Orthoptera: Gryllidae) from Singapore. *Zootaxa* **3525**:18–34. doi:10.11646/zootaxa.3525.1.2

He Z. 2012. A new species of Truljalia Gorochov 1985 from Taiwan (Orthoptera: Gryllidae; Podoscirtinae; Podoscirtini). *Zootaxa* **3591**:79–83. doi:10.11646/zootaxa.3591.1.5

He Z, Lu H, Liu Y, Li K. 2017. A new species of Ornebius Guérin-Méneville, 1844 from East China (Orthoptera: Mogoplistidae: Mogoplistinae). *Zootaxa* **4303**:445–450. doi:10.11646/zootaxa.4303.3.10

Hugel S. 2009. New Landrevinae from Mascarene islands and little known Landrevinae from Africa and Comoros (Grylloidea: Landrevinae). *Annales de la Société entomologique de France (NS)* **45**:193–215. doi:10.1080/00379271.2009.10697602

Jaiswara R, Dong J, Ma L, Yin H, Robillard T. 2019. Taxonomic revision of the genus Xenogryllus Bolívar, 1890 (Orthoptera, Gryllidae, Eneopterinae, Xenogryllini). *Zootaxa* **4545**:301–338. doi:10.11646/zootaxa.4545.3.1

Kavanagh MW, Young D. 1989. Bilateral symmetry of sound production in the mole cricket, Gryllotalpa australis. *J Comp Physiol A* **166**:43–49. doi:10.1007/BF00190208

Kim T. 2011. A Taxonomic Study of the Scaly Cricket Family Mogoplistidae (Orthoptera: Ensifera: Grylloidea) in Korea. *Zootaxa* **2928**:41–48. doi:10.11646/zootaxa.2928.1.4

Lima RM, Schuchmann K-L, Tissiani AS, Nunes LA, Jahn O, Ganchev TD, Lhano MG, Marques MI. 2018. Tegmina-size variation in a Neotropical cricket with implications on spectral song properties. *Journal of Natural History* **52**:1225–1241. doi:10.1080/00222933.2018.1457728

Love RE, Walker TJ. 1979. Systematics and Acoustic Behavior of Scaly Crickets (Orthoptera: Gryllidae: Mogoplistinae) of Eastern United States. *Transactions of the American Entomological Society (1890-)* **105**:1–66.

Martins L de P, Redü DR, Oliveira GL de, Zefa E. 2012. Recognition characters and new records of two species of Phylloscyrtini (Orthoptera, Gryllidae, Trigonidiinae) from southern Brazil. *Iheringia, Sér Zool* **102**:95–98. doi:10.1590/S0073-47212012000100013

Martins LDP, Silva LGD, Henriques AL, Zefa E. 2013. First record of the genera Luzarida Hebard, 1928 and Luzaridella Desutter-Grandcolas, 1992 (Orthoptera, Gryllidae, Phalangopsinae) from Brazil, including a new species and description of the female of Luzarida lata Gorochov, 2011. *Zootaxa* **3609**:421–430. doi:10.11646/zootaxa.3609.4.4

McIntyre ME. 1977. Acoustical communication in the field crickets Pteronemobius nigrovus and P. bigelowi (Orthoptera: Gryllidae). *New Zealand Journal of Zoology* **4**:63–72. doi:10.1080/03014223.1977.9517937

Mello F de AG de, Pellegatti-Franco F. 1998. A New Cave Cricket of the Genus Endecous from Southeastern Brazil and Characterization of Male and Female Genitalia of E. itatibensis Rehn, 1918 (Orthoptera: Grylloidea: Phalangopsidae: Luzarinae). *Journal of Orthoptera Research* 185–188. doi:10.2307/3503517

Mello F de AG de, Reis JC dos. 1994. Substrate Drumming and Wing Stridulation Performed during Courtship by a New Brazilian Cricket (Orthoptera: Grylloidea: Phalangopsidae). *Journal of Orthoptera Research* 21–24. doi:10.2307/3503603

Milach EM, Costa MKMD, Martins LDP, Nunes LA, Silva DSM, Garcia FRM, Oliveira ECD, Zefa E. 2016. New species of tree cricket Oecanthus Serville, 1831 (Orthoptera: Gryllidae: Oecanthinae) from Reserva Natural Vale, Espírito Santo, Brazil, with chromosome complement. *Zootaxa* **4173**:137–146. doi:10.11646/zootaxa.4173.2.4

Milach EM, Martins LDP, Costa MKMD, Gottschalk MS, Oliveira GLD, Redü DR, Neutzling AS, Dornelles JEF, Vasconcellos LA, Zefa E. 2015. A new species of tree crickets Oecanthus (Orthoptera, Gryllidae, Oecanthinae) in tobacco plantation from Southern Brazil, with body color variation. *Zootaxa* **4018**:266–278. doi:10.11646/zootaxa.4018.2.6

Nischk F, Otte D. 2000. Bioacoustics, Ecology and Systematics of Ecuadorian Rainforest Crickets (Orthoptera: Gryllidae: Phalangopsinae), with a Description of Four New Genera and Ten New Species. *Journal of Orthoptera Research* 229–254. doi:10.2307/3503651

Orsini MP, Costa MKMD, Szinwelski N, Martins LDP, Corrêa RC, Timm VF, Zefa E. 2017. A new species of Miogryllus Saussure, 1877 and new record of Miogryllus piracicabensis Piza, 1960 (Orthoptera: Gryllidae) from State of Rio Grande do Sul, Brazil, with calling song and chromosome complement. *Zootaxa* **4291**:361–372. doi:10.11646/zootaxa.4291.2.8

Otte D. 2007. Australian Crickets (Orthoptera: Gryllidae). Academy of Natural Sciences.

Pereira MR, Miyoshi AR, Martins LDP, Fernandes ML, Sperber CF, Mesa A. 2013. New Neotropical species of Hygronemobius Hebard, 1913 (Orthoptera: Grylloidea: Nemobiinae), including a brief discussion of male genitalia morphology and preliminary biogeographic considerations of the genus. *Zootaxa* **3641**:1–20. doi:10.11646/zootaxa.3641.1.1

Robillard T, Desutter-Grandcolas L. 2004. High-frequency calling in Eneopterinae crickets (Orthoptera, Grylloidea, Eneopteridae): adaptive radiation revealed by phylogenetic analysis. *Biological Journal of the Linnean Society* **83**:577–584. doi:10.1111/j.1095-8312.2004.00417.x

Robillard T, Ichikawa A. 2009. Redescription of Two Cardiodactylus Species (Orthoptera, Grylloidea, Eneopterinae): The Supposedly Well-Known C. novaeguineae (Haan, 1842), and the Semi-Forgotten C. guttulus (Matsumura, 1913) from Japan. *jzoo* **26**:878–891. doi:10.2108/zsj.26.878

Robillard T, Nattier R, Desutter-Grandcolas L. 2010. New species of the New Caledonian endemic genus Agnotecous (Orthoptera, Grylloidea, Eneopterinae, Lebinthini). *Zootaxa* **2559**:17–35. doi:10.11646/zootaxa.2559.1.2

Robillard T, Su YN. 2018. New lineages of Lebinthini from Australia (Orthoptera: Gryllidae: Eneopterinae). *Zootaxa* **4392**:241–266. doi:10.11646/zootaxa.4392.2.2

Robillard T, Tan MK. 2013. A taxonomic review of common but little knwon crickets from Singapore and the Philippines (Insecta: Orthoptera: Eneoptera: Eneopterinae) 21.

Robillard T, Yap S, Yngente MV. 2013. Systematics of cryptic species of Lebinthus crickets in Mount Makiling (Grylloidea, Eneopterinae). *Zootaxa* **3693**:49–63. doi:10.11646/zootaxa.3693.1.3

Souza-Dias PGB, Szinwelski N, Fianco M, Oliveira ECD, Mello FD a. GD, Zefa E. 2017. New species of Endecous (Grylloidea, Phalangopsidae, Luzarinae) from the Iguaçu National Park (Brazil), including bioacoustics, cytogenetic and distribution data. *Zootaxa* **4237**:454–470. doi:10.11646/zootaxa.4237.3.2

Su YN, Rentz DCF. 2000. Australian Nemobiine Crickets: Behavioral Observations and New Species of Bobilla Otte & Alexander (Orthoptera: Gryllidae: Nemobiinae). *Journal of Orthoptera Research* 5–20. doi:10.2307/3503626

Symes LB, Collins N. 2013. Oecanthus Texensis: A New Species of Tree Cricket from the Western United States. *orth* **22**:87–91. doi:10.1665/034.022.0203

Tan MK, Japir R, Chung AYC, Wahab RBHA. 2020. New taxa of crickets (Orthoptera: Grylloidea: Phaloriinae, Phalangopsinae, Itarinae and Podoscirtinae) from Borneo (Brunei Darussalam and Sandakan). *Zootaxa* **4810**:244–270. doi:10.11646/zootaxa.4810.2.2

Tan MK, Kamaruddin KN. 2016. A new species of Gryllotalpa mole cricket (Orthoptera: Gryllotalpidae: (Gryllotalpinae) from Peninsular Malaysia. *Zootaxa* **4066**:552–560. doi:10.11646/zootaxa.4066.5.3

Vicente NM, Olivero P, Lafond A, Dong J, Robillard T. 2015. Gnominthus gen. nov., a new genus of crickets endemic to Papua New Guinea with novel acoustic and behavioral diversity (Insecta, Orthoptera, Gryllidae, Eneopterinae). *Zoologischer Anzeiger - A Journal of Comparative Zoology* **258**:82–91. doi:10.1016/j.jcz.2015.06.005

Weissman DB, Gray DA. 2019. Crickets of the genus Gryllus in the United States (Orthoptera: Gryllidae: Gryllinae). *Zootaxa* **4705**:1–277. doi:10.11646/zootaxa.4705.1.1

Zefa E, Acosta RC, Timm VF, Szinwelski N, Marinho MAT, Costa MKMD. 2018. The Tree Cricket Neoxabea brevipes Rehn, 1913 (Orthoptera: Gryllidae: Oecanthinae) from the Brazilian southern Atlantic Forest: morphology, bioacoustics and cytogenetics. *Zootaxa* **4531**:554–566. doi:10.11646/zootaxa.4531.4.6

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