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1 **Soundscape of urban-tolerant crickets (Orthoptera: Gryllidae, Trigonidiidae) in a**  
2 **tropical Southeast Asia city, Singapore**

3

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5

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9

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11

## 12 **Abstract**

13

14 Urbanisation impact biodiversity tremendously, but a few species can still tolerate the harsh  
15 conditions of urban habitats. Studies regarding the impact of urbanisation on the soundscape  
16 and acoustic behaviours of sound-producing animals tend to overlook invertebrates, including  
17 the crickets. Almost nothing is known about their acoustic community in the urban  
18 environment, especially for Southeast Asia where rapid urbanisation is widespread. Grass  
19 verges in Singapore—characterised by complex mosaics of land-use types—were sampled as  
20 a microcosmic representation of the urban environment to address these questions: (i) What is  
21 the acoustic community of crickets in the urban environment? (ii) How do co-occurring  
22 species partition their calls? (iii) How do the call properties vary with environmental  
23 conditions and individuals? The calling songs of ten species were recorded and they generally  
24 have distinct call signatures in both the time and frequency domains. The acoustic community  
25 was dominated by *Polionemobius taprobanensis* and *Gryllodes sigillatus*. They also showed  
26 repeatabilities in their call properties with static properties being more repeatable than  
27 dynamic properties, but these call properties were not associated with environmental  
28 variables. The presence of these crickets is highly relevant for a biophilic city as they  
29 represent what most urban dwelling humans could frequently hear.

30

31 **Key words:** calling song, niche partitioning, noise pollution, repeatability, urbanisation

32

## 33 **Introduction**

34

35 Urbanisation represents an extreme form of environmental change and is a major driver of  
36 biodiversity loss (Sala 2000; McKinney 2006; Grimm et al. 2008). Nonetheless, a tiny

37 fraction of species can tolerate, exploit and persist in the novel environment created as a  
38 result of urbanisation (Newbold et al. 2015). Ability to communicate in the noisy urban  
39 soundscape—dominated by vehicular traffic, construction work among other human  
40 activities—is one of the few behavioural responses that help these species adapt to the novel  
41 environment.

42

43 The urban soundscape can have consequences on the wellbeing and quality of life for human  
44 city-dwellers, which accounts for more than half of global human populations (Stockfelt 1991;  
45 Raimbault and Dubois 2005). The study of urban soundscape since evolved from tackling  
46 noise pollution in urban areas to enhancing quality of the environment through improved  
47 urban development (Stockfelt 1991; Skanberg and Ohrstrom 2002). However, more recently,  
48 many city planners have attempted to make the cities more liveable by incorporating  
49 greeneries and improving soundscape (Irvine et al. 2009).

50

51 Likewise, anthropogenic noises also have effect on the animals in the city. One of the most  
52 distinct natural sounds that can still be present in an urban city belongs to that of birds.

53 Studies of avian acoustic ecology in urban context have drawn huge attention, including on  
54 how birds adapt their calling patterns to urban noises (e.g., Hu and Cardoso 2010; Nemeth  
55 and Brumm 2010; Slabbekoorn 2013; Gil and Brumm 2014). Likewise, bats use ultrasonic  
56 sounds to navigate and search for prey; and their activities and behaviours are also greatly  
57 altered in the urban environments compared to counterparts in the forest (Gehrt and Chelvig  
58 2004; Smith and Gehrt 2010; Coleman and Barclay 2012). Such urban studies are primarily  
59 focusing on vertebrates while overlooking the invertebrates.

60

61 One of the most notable sound-producing invertebrates is the crickets and their relatives.  
62 Many crickets and bush-crickets rub their forewings to produce sound during which the teeth  
63 of the stridulatory file on the left tegmen contact the scraper on the right tegmen (Elliot and  
64 Koch 1985; Bennet-Clark 1989). While bush-crickets of the superfamily Tettigonioidea with  
65 known calls generally produce ultrasonic songs (Montealegre-Z et al. 2006), crickets of the  
66 superfamily Grylloidea typically produce pure-tone calls that are audible to human (Otte  
67 1992). In contrast to birds and bats, relatively little is known about the orthopteran acoustics  
68 in urban areas, even though calls made by male orthopterans are one of the most dominant  
69 sounds in the natural habitats.

70

71 A main reason for the gap on the orthopteran acoustics in urban context is that very few  
72 orthopterans can survive the harsh environment of urban city landscape. The most well-  
73 known urban-tolerant species are probably the *Grylloides sigillatus* (Walker, 1869) and  
74 *Acheta domesticus* (Linnaeus, 1758) from the tropics and temperate respectively. At present,  
75 these species have established in urban ecosystems in many parts of the world (Weissman  
76 and Rentz 1977; Smith and Thomas 1988), but it is less clear what other species can also  
77 adapt to the urban environment. Therefore, the first objective of this study is to investigate  
78 what species can be heard in an urban habitat.

79

80 Urban cricket populations can have different requirements as populations found in their  
81 natural habitats (Fartmann et al. 2008). For example, higher temperature owing to urban  
82 island heat effects can change voltinism in nemobines (Matsuda et al. 2018) as well as their  
83 calling properties (Walker, 1962; Bennet-Clark 1989; Martin et al. 2000). In addition to  
84 environmental-driven effects on cricket acoustics, urban crickets need to compete for acoustic  
85 space (both frequency and temporal domains) with males of the same and different species to

86 attract conspecific mates. It was previously demonstrated that presence of anthropogenic  
87 sound leads to increased pauses between calling and call durations (Orci et al. 2016; Duarte et  
88 al. 2019), increased amplitude of calls (which may make them more vulnerable to predation)  
89 (Erregger and Schmidt 2018) and increased difficulty for females to locate calling males  
90 (Bent et al. 2018; Gurule-Small and Tinghitella 2018). These selection pressures can also  
91 drive between- and within-individual variations that differ from that among individuals from  
92 the natural habitats. As such, the second objective of this study is to further investigate how  
93 the call properties of the urban-tolerant species vary and/or partition between different  
94 individuals, species and environmental conditions.

95

96 Studies on urban-tolerant crickets typically originate in temperate or New World tropics (e.g.,  
97 Orci et al. 2016; Bent et al. 2018; Duarte et al. 2019). There remains a dearth of information  
98 about orthopteran bioacoustics in tropical Asia, including Singapore situated in the biodiverse  
99 tropical Southeast Asia. Singapore is a highly urbanised, built-up and densely populated  
100 island city-state (Newman 2014). Self-proclaimed as a “City in a Garden”, Singapore has  
101 invested greatly on the streetscape management to create a ‘seamless green mantle’  
102 throughout the island (Newman 2014). This creates microhabitats along grass verges that  
103 some urban-tolerant orthopterans can potentially thrive in.

104

105 Research on the orthopterans from Singapore has caught up in the past decade, particularly  
106 on species diversity (e.g., Tan 2010, 2012, 2013), new species discovery (e.g., Gorochov and  
107 Tan 2012; Tan and Robillard 2014), ecology (e.g., Tan and Tan 2017; Tan et al. 2017a) and  
108 natural history (e.g., Tan 2011; Tan et al. 2017b, Fung et al. 2018). As many as 200 species  
109 of orthopterans can be found in the forest remnants of Singapore but studies incorporating  
110 bioacoustics data is relatively few (but see Gorochov and Tan 2012; Tan and Robillard 2014)

111 and concerted investigation on the orthopteran calls from Singapore is scanty (but see Tan et  
112 al. 2018, 2019). Furthermore, most of these studies were done in the forested and natural  
113 environment rather than the highly urbanised parts of Singapore (but see Tan 2010, 2012).  
114 Nonetheless, these ample resources have provided an important basis to facilitate urban  
115 studies.

116

117 In summary, the current gap on the urban species and acoustics of crickets in Singapore  
118 prompted me to address the following questions: (i) What is the acoustic community of  
119 crickets in the urban environment of Singapore? (ii) How do co-occurring urban-tolerant  
120 species partition their calls from each other? (iii) How do the call properties of the urban-  
121 tolerant species vary between environmental conditions and individuals?

122

123

## 124 **Materials and Methods**

125

### 126 *Study area*

127 I sampled the grass verges (approximately 5 m in width) bordering road and walkways  
128 around Kampong Ubi (N1.32857, E103.90238) (Singapore)—specifically along Ubi Avenue  
129 1, Ubi Road 3 and Ubi Avenue 2 (Fig. 1). The area within which the roads encircle comprises  
130 of two schools (Maha Bodhi School and Manjusri Secondary School), a Mass Rapid Transit  
131 train station (Ubi DT27) and a construction site for an upcoming housing estate. The grass  
132 verges are surrounded by dense public housing along Ubi Avenue 1 and light industry along  
133 Ubi Road 3 and Ubi Avenue 2. These make this study area a microcosmic representation of  
134 the urbanised environment of Singapore which is characterised by complex mosaics of land-  
135 use types.

136

137 I sampled over seven nights between 18 and 30 May 2020, commencing at around 2000  
138 hours for an average of 1 hour. This involved walking along the walkways and  
139 opportunistically recording songs of crickets *in situ* whenever they were encountered. I  
140 obtained from the Meteorological Service Singapore (MSS) (Meteorological Service  
141 Singapore undated) the daily temperature and rainfall data from the nearest weather station  
142 (i.e., Tai Seng, N1.3399, E103.8878, about 1.9 km from study site).

143

#### 144 ***Recording of calls***

145 I recorded the male calls using a portable ultrasound recorder Echo Meter Touch Pro 2  
146 (Wildlife Acoustics, Inc. USA, Massachusetts), attached to a Samsung smart phone, and  
147 using a sampling frequency of 256 kHz-samples/s. The Echo Meter Touch Pro 2 (based on  
148 Knowles FG sensor, 16-bit WAV, mono channel, with frequency response of up to 128 kHz)  
149 was placed as close as possible to the cricket without disturbing the cricket, and to maximise  
150 amplitude without clipping the sound. Manual trigger was used. As temperature can influence  
151 the song parameters, a HOBO 8K Pendant® Temperature logger (model: UA-001-08, Onset,  
152 Bourne, MA) was used to track the ambient temperature once every 10 minutes. The GPS  
153 coordinates were also obtained using Google Earth Pro (Google Earth Pro 2020) so that  
154 recordings in the subsequent sampling nights were far apart enough to minimise the  
155 probability “double-counting” of the same cricket individual. Male crickets which were  
156 recorded are generally territorial and do not travel away from their burrow or territory during  
157 calling. Selected sound files were uploaded to the Orthoptera Species File Online Version  
158 5.0/5.0 (OSF) (Cigliano et al. 2020).

159

#### 160 ***Species examination and identification***



161 Whenever possible, I collected the singing crickets for vouchering. The male genitalia were  
162 dissected under stereo-zoom microscope, examined and the species were identified using  
163 taxonomic papers (Gorochov 1983; Otte 2006). When no specimen was available, I used Tan  
164 (2011, 2012, 2017) to narrow down possible candidate species that can occur in the grass  
165 verges and compared the calls with existing sound files deposited in the OSF and unpublished  
166 sound files of calls by Singaporean crickets.

167

### 168 *Acoustic analyses*

169 The basic cricket song terminology follows Ragge and Reynolds (1998). Calling song is the  
170 spontaneous song produced by an isolated male. One song unit is called a syllable and  
171 corresponds to one opening–closure cycle of the male forewings. A group of syllables  
172 constitutes an echeme, which corresponds to a call unit in terms of communication. I  
173 measured the call duration and syllable duration manually using Avisoft Lite 2.0.0. Power  
174 spectra using Fast Fourier Transformation (FFT) were generated using the ‘meanspec’  
175 function at 256,000 sampling frequency, using Hanning window of window length 512 from  
176 the R package *seewave* (Sueur et al. 2008) in the R software version 3.5.1 (R Development  
177 Core Team, 2018). Dominant frequency (frequency with the highest energy), second  
178 dominant frequency and fundamental frequency (lowest frequency of a harmonic series) were  
179 determined from the power spectra.

180

### 181 *Statistical analyses*

182 All statistical analyses were conducted with R version 3.5.1 (R Development Core Team  
183 2018). To obtain an indication of sample adequacy, I plotted an individual-based species  
184 rarefaction curve using the ‘specaccum’ function from the R package *vegan* (Oksanen et al.  
185 2015).

186

187 To examine how co-occurring urban species partition their calls from each other, I  
188 summarised the call properties (which were not mutually independent and likely to be highly  
189 intercorrelated) into major gradients of variation by performing a Principal Coordinates  
190 Analysis (PCoA) on the scaled call properties using the ‘cmdscale’ function. Gower  
191 dissimilarity was used as it can be calculated for a set of descriptors containing of continuous  
192 (bounded by zero) (i.e., echeme duration, syllable duration, dominant frequency, second  
193 dominant frequency, fundamental frequency) and categorical variables (i.e., call types—  
194 continuous trills or echemes consisting of a few syllables).

195

196 To investigate how the call properties of the urban-dwelling crickets correlate with  
197 environmental variables, I fitted univariate linear mixed effects models (LMMs) for  
198 fundamental frequency and syllable duration using the ‘lmer’ function from the R package  
199 *lme4* (Bates et al. 2014). I log-transformed both response variables. The ambient temperature  
200 at the time of recording (°C), mean daily temperature (°C) and daily rainfall total (mm)  
201 obtained from (MSS) were fitted as fixed effects. I checked for collinearity between the fixed  
202 effects, and all fixed effects were centred on their means to facilitate model fitting. Since I  
203 used multiple calls for each individual cricket, the ‘cricket identity’ was fitted as a random  
204 intercept. I fitted seven models containing different plausible combinations of the fixed  
205 effects as well as a null model without any fixed effect. The models were compared using  
206 AICc, which estimates the quality of each model by rewarding goodness of fit and penalizing  
207 overfitting (Burnham and Anderson 2002). Models with the differences between the values of  
208 the AICc of a particular model and that of the best model (delta) less than 2.0 (Burnham and  
209 Anderson 2002) were considered equally good and thus interpreted together. I used the  
210 Akaike weight of each model (which translates to the probability that the model is the best

211 model) and the marginal and conditional  $R^2$  values (i.e.,  $R^2_M$  and  $R^2_C$ , respectively) obtained  
212 using the ‘r.squaredGLMM’ function in the R package *MuMIn* (Barton and Barton 2015) to  
213 assess the quality of the models.

214

215 To assess repeatability of the call properties, I followed the mixed effect modelling approach  
216 by Nakagawa and Schielzeth (2010) and Dingemanse and Dochtermann (2013). Repeatability  
217 here is defined as the intraclass correlation coefficient (ICC), which is calculated as the ratio  
218 of inter- individual cricket variance and the sum of inter- and within-individual cricket  
219 variance (Nakagawa and Schielzeth, 2010). To calculate ICC after controlling for variation  
220 due to covariates, I used the functions ‘rpt’ function from the R package *rptR* (Stoffel et al.  
221 2017) for fundamental frequency and syllable duration with the fixed and random effects  
222 specified based on the final model after model selection by AICc described above.

223 Repeatability estimates larger than 0.1 were considered as weak evidence, even if the  
224 estimated CI included zero; and repeatability estimates smaller than 0.1 as not repeatable,  
225 even if the p-value suggested significance (Schuster et al. 2017).

226

227

## 228 **Results**

229

### 230 *(i) What is the acoustic community of crickets?*

231 I recorded the calls of 42 individuals from ten species of crickets and bush-cricket (Fig. 2,  
232 Table 1). These include five species from Gryllidae and four species from Trigonidiidae; and  
233 one species from Tettigoniidae.

234

235 The most commonly heard gryllid is the *Gryllodes sigillatus* (Walker, 1869) [Gryllidae:  
236 Gryllinae]. Commonly known as the decorated cricket, they can be heard calling in both  
237 vegetated and non-vegetated structures, including drains, and concrete crevices. The male call  
238 (echeme duration =  $55.6 \pm 5.8$  ms [45.6–68.2 ms]) consists of echemes with four syllables of  
239 increasing amplitudes and duration (Fig. 3a), and has a harmonic series with the dominant  
240 frequency (=  $7.3 \pm 0.4$  kHz [6.5–8.0 kHz]) typically peaking in the first harmonic (also the  
241 fundamental frequency) (Fig. 4a). The echemes are closely and more or less consistently  
242 spaced apart (Fig. 3a).

243

244 *Gryllus bimaculatus* De Geer, 1773 [Gryllidae: Gryllinae] call (echeme duration =  
245  $0.205 \pm 0.039$  s [0.145–0.265 s]) consists of echemes with four to five syllables (Fig. 3b), and  
246 has a harmonic series with a fundamental frequency of 4.5 kHz and a dominant frequency of  
247  $13.1 \pm 0.2$  kHz [13.0–13.5 kHz] (Fig. 4b). The echemes are more widely spaced apart and  
248 down times are less consistent (Fig. 3b). I did not encounter the cricket but was able to  
249 identify the calls using sound file uploaded in OSF [SoundID = 1295].

250

251 *Teleogryllus c.f. mitratus* (Burmeister, 1838) [Gryllidae: Gryllinae] call is loud and distinct  
252 from other gryllids, consisting of a relatively long trill (echeme duration =  $1.05 \pm 0.05$  s [0.97–  
253 1.10 s]) making up of around  $40 \pm 4$  (38–45) syllables (Fig. 3c), and has a harmonic series  
254 with the dominant frequency (=  $11.6 \pm 1.6$  kHz [10.0–13.0 kHz]) peaking in the second  
255 harmonic; and fundamental frequency of 3.5 kHz (Fig. 4c). I also did not encounter the  
256 cricket but identified the calls using unpublished sound files and sound file uploaded in OSF  
257 (SoundID = 1756, 1759).

258

259 An unknown species of Gryllinae can be heard fairly frequently, albeit not as frequent as *G.*  
260 *sigillatus*, and often a few individuals call in close proximity to each other. The call consists  
261 typically of syllables occurring in doublets (echeme duration =  $71.3 \pm 6.5$  ms [63.9–93.9 ms];  
262 syllable duration =  $30.3 \pm 3.8$  s [26.0–45.0 ms]) (Fig. 3d), and has a harmonic series with the  
263 dominant frequency either peaking in the first harmonic (i.e., = fundamental frequency of 5.5  
264 kHz) or peaking in the third harmonic of 17 kHz (16.5–17.5 kHz) (Fig. 4d). The second  
265 harmonic peaks at 11.5 kHz. The calls are drastically different from that of *Velarifictorus*  
266 *aspersus* (Walker, 1869) which is a common gryllid in Singapore but not recorded in this  
267 study.

268

269 I tentatively identified the calls of this single specimen as *Mitius* sp. [Gryllidae: Gryllinae]  
270 based on the calls of *Mitius blennus* (Saussure, 1877) and *Mitius enatus* Gorochov, 1994 from  
271 OSF (SoundID = 1792, 1794, respectively), of which they are somewhat similar in the  
272 dominant frequency and syllable duration. The male call (echeme duration =  $69.4 \pm 1.6$  ms  
273 [67.1–71.0 ms]) consists of echemes with four syllables (syllable duration =  $12.3 \pm 1.1$  ms  
274 [11.4–13.8 ms]) (Fig. 3e), and has a harmonic series with the dominant frequency (= 9.5 kHz)  
275 peaking in the first harmonic (also the fundamental frequency) (Fig. 4e).

276

277 *Polionemobius taprobanensis* (Walker, 1869) [Trigonidiidae: Nemobiinae] is the most  
278 frequently recorded cricket. Males call both in the day and at night. Calling males were never  
279 encountered, as they appear to hide among leaf blades and sheaths of grasses. The males' call  
280 is a continuous trill of infinite number of syllables (syllable duration =  $5.7 \pm 0.9$  ms [3.6–7.8  
281 ms]) (Fig. 3f), comprising of a harmonic series with the dominant frequency (=  $10.8 \pm 0.7$  kHz  
282 [7.0–12.0 kHz]) peaking in the first harmonic (= fundamental frequency) (Fig. 4f).

283

284 *Pteronemobius* sp. [Trigonidiidae: Nemobiinae] has very similar niche and calls as *P.*  
285 *taprobanensis*. The male's call differs by echeme consisting of a short trill (echeme duration  
286 =  $0.84 \pm 0.11$  s [0.52–0.99 s]) with around  $110 \pm 17$  (81–150) syllables per echeme (syllable  
287 duration =  $7.6 \pm 0.6$  ms [6.4–8.9 ms]) (Fig. 3g). Each syllable increases in amplitude within  
288 each echeme (Fig. 3g). The call comprises of a harmonic series with the dominant frequency  
289 (=  $9.8 \pm 0.3$  kHz [9.5–10.0 kHz]) peaking in the first harmonic (= fundamental frequency) (Fig.  
290 4g).

291

292 Another distinct but unidentified species of Nemobiinae (owing to the lack of specimen) has  
293 call consisting of trills with varying duration (echeme duration =  $0.12 \pm 0.02$  s [0.08–0.14 s])  
294 with around  $13 \pm 3$  (7–17) syllables per echeme (syllable duration =  $9.3 \pm 0.8$  ms [8.5–10.1 ms])  
295 (Fig. 3h). The call comprises of a harmonic series with the dominant frequency (= 6.5 kHz)  
296 peaking in the first harmonic (= fundamental frequency) (Fig. 4h).

297

298 A single unidentified Trigonidiinae was also recorded. The specimen was not collected  
299 successfully. The male's call consists of continuous trills of infinite number of syllables  
300 (syllable duration =  $31.4 \pm 2.2$  ms [27.9–34.9 ms]) (Fig. 3i), comprising of a harmonic series  
301 with the dominant frequency (=  $8.0 \pm 0.3$  kHz [7.5–9.0 kHz]) peaking generally in the first  
302 harmonic (= fundamental frequency) (Fig. 4i). Compared to *P. taprobanensis*, the down time  
303 between syllables are also longer (Fig. 3i). The trigoniid was sighted, somewhat unicolorous  
304 pale yellow and resembling *Natula longipennis* (Serville, 1838) but differs in the call  
305 properties.

306

307 The only bush-cricket recorded was that of a *Euconocephalus* sp. (sensu Tan, 2011)  
308 [Tettigoniidae: Conocephalinae]. This bush-cricket could only be heard among taller grasses

309 and sedges when the grass verges were left unmanaged for considerable period. The call  
310 consists of a broad-band continuous trill of infinite number of syllables (syllable duration =  
311  $2.72 \pm 0.22$  ms [2.25–3.10 ms]) (Fig. 3j) with dominant frequency ( $11.8 \pm 0.6$  kHz [11.0–13.5  
312 kHz]) and another near-ultrasonic peak at  $20.7 \pm 0.9$  kHz (18.5–22.5 kHz) (Fig. 4j).

313

314 ***(ii) How do co-occurring urban-tolerant species partition their calls from each other?***

315 By summarising echeme duration, syllable duration, dominant frequency, second dominant  
316 frequency, fundamental frequency and call types (continuous trills or echemes consisting of a  
317 few syllables), the first two axes of the PCoA explained about 85.2 % (73.6 + 11.5 %) and  
318 showed that the calls of ten urban-tolerant species generally partition across both time and  
319 frequency domains (Fig. 5). This can be evident from the non-overlapping ellipses and data  
320 points between species. There are however two exceptions. The call of *Euconocephalus* sp. is  
321 very similar to that of *P. taprobanensis* based on the call properties, as shown by the  
322 overlapping ellipses in the PCoA plot (Fig. 5), but *P. taprobanensis* is more tonal with a  
323 distinct harmonic series whereas *Euconocephalus* sp. is more broadband (Fig. 4). The PCoA  
324 also suggests that the call properties of *G. sigillatus* and *Nemobiinae* sp. are very similar (Fig.  
325 5) but examination of the oscillograms (Fig. 3) and power spectra (Fig. 4) reveal clear-cut  
326 differences.

327

328 ***(iii) How do the call properties of the urban-tolerant species vary between environmental***  
329 ***conditions and individuals?***

330 The model with  $\Delta < 2.0$  were found to be the null models for both *P. taprobanensis* (n =  
331 169, 20 individuals) and *G. sigillatus* (n = 64 echemes, nine individuals) and for both syllable  
332 duration and fundamental frequency. These indicate that ambient temperature, mean daily

333 temperature and daily rainfall total did not correlate strongly with both syllable duration and  
334 fundamental frequency (Table 2).

335

336 I found that syllable duration showed high repeatabilities, thus indicating consistent inter-  
337 individual differences in both *P. taprobanensis* (ICC =  $0.45 \pm 0.10$ , p-value  $< 0.001$ , 95 % CI  
338 [0.24, 0.62]) and *G. sigillatus* (ICC =  $0.59 \pm 0.15$ , p-value  $< 0.001$ , 95 % CI [0.23, 0.78]). The  
339 same is also observed for fundamental frequency in both *P. taprobanensis* (ICC =  $0.97 \pm 0.01$ ,  
340 p-value  $< 0.001$ , 95 % CI [0.93, 0.98]) and *G. sigillatus* (ICC =  $0.96 \pm 0.03$ , p-value  $< 0.001$ ,  
341 95 % CI [0.85, 0.98]).

342

343

## 344 **Discussion**

345

### 346 *(i) What is the acoustic community of crickets?*

347 The acoustic community of crickets in the urban environment differs vastly from that of the  
348 forested or grassy habitats in Singapore. The acoustic community is dominated by the calls of  
349 *P. taprobanensis* and *G. sigillatus*. *Gryllodes sigillatus* is the most frequently heard gryllids  
350 in the urban environment but has not been recently encountered in Singapore's natural  
351 habitats. In contrast, other gryllids which are typically forest-edge or grassland species are  
352 only sparsely heard (Tan, 2017). Moreover, the acoustic community in the urban environment  
353 is limited to calls peaking at non-ultrasonic to near-ultrasonic frequencies ranging from 5.5 to  
354 23.5 kHz, while the forests harbour more species which calls at ultrasonic frequencies (Tan et  
355 al. 2019). This suggests that the harsh urban conditions can only permit a very limited groups  
356 of crickets to exist.

357



358 Numerous factors favour these urban-tolerant species to establish in the highly isolated grass  
359 verges (Møller 2009). Firstly, these often-flightless crickets need to be able to disperse into  
360 the urban areas which are isolated from natural habitats by road networks and human  
361 constructs. It is very likely that many of these species are transported through the grasses and  
362 soil by human. Small species like *P. taprobanensis* and other nemobine lawn crickets can  
363 hitch-hike among the grasses occasionally brought in by human to replenish the exposed  
364 surfaces. Other species, especially the less frequently encountered gryllids, may have been  
365 brought in through the soil where the eggs are laid along with the grasses. This begs the  
366 question whether how sustainable these cricket populations are, since nothing is known about  
367 their population dynamics and the dependence on new propagules in these grass verges, and  
368 that I did not encounter females of many species during the survey.

369

370 Secondly, low threshold for fear to human and anthropogenic noises is crucial for the males  
371 to continuing calling in the highly disturbed environment and for the females to be bold  
372 enough to travel and search for mates (Møller 2009; Lowry et al. 2011; Gallego-Abenza et al.  
373 2019). This appears to be the case for most species recorded here, as noises generated by  
374 passing vehicles did not stop or modify the calling of many species. It is plausible that these  
375 crickets are already habituated to the anthropogenic noises (Bejder et al. 2009), a  
376 phenomenon which is also observed in some urban birds (e.g., Lowry et al. 2011; Payne et al.  
377 2012).

378

379 Thirdly, the ability to utilise non-natural microhabitats and adapt to periodic human-induced  
380 microhabitat changes favours the establishment of species in urban areas. The greater  
381 presence of impervious surfaces can limit gryllids to make burrows but *G. sigillatus* are  
382 observed to exploit crevices of hard structures. I also observed that after the grass verges

383 were mowed, *P. taprobanensis* continued calling on the same day and nearly as frequently as  
384 before the mowing occurred. This in turn can be attributed to the bolder nature of these  
385 urban-tolerant nemobines.

386

387 That other potential factors which can buffer individuals against the risks associated with an  
388 urban life, such as the tolerance to pesticide (from fogging of mosquito and cockroach) and  
389 toxic fumes from vehicles and constructions, are not known indicates that much remains  
390 unstudied about these urban-tolerant crickets and how urbanisation affects their behaviours  
391 (including acoustics). Rapidly expanding urbanisation in many other parts of Southeast Asia  
392 warrants the urgency of such studies to apprehend holistically the effect of urbanisation on  
393 wildlife and that invertebrates should receive more attention owing to their higher potential to  
394 respond to urban noises (Morley et al. 2015).

395

396 The rarefaction curve revealed that the sampling may be incomplete. But this may also be an  
397 artefact of the vegetation succession that occurred over the course of this study, leading to the  
398 colonisation of more species. For example, *Euconocephalus* sp. was recorded only towards  
399 the end of the study when the grasses grew taller and weeds flourished; and these katydid are  
400 known to prefer tall grasses over lawns (Tan 2011). However, such succession is atypical of  
401 Singapore's urban environment, if not for the Covid-19 pandemic during which grass  
402 mowing was halted during the national lockdown (Asher 2020; Hicks 2020). Increased in  
403 activity, acoustic diversity and complexity owing to vegetation succession have been reported  
404 in birds and insects (Fischer et al. 1997; Gasc et al. 2018; Wilson and Bayne 2019), but a  
405 future study on how the acoustic community of crickets respond to disturbances and  
406 successions may reveal interesting insights unique to urban environment.

407

408 ***(ii) How do co-occurring urban-tolerant species partition their calls from each other?***

409 It was clear that the co-occurring urban-tolerant species partition their calls from each other,  
410 as predicted, since the partitioning of call properties between closely related sympatric  
411 species is crucial for reproductive isolation (Tan et al. 2018, 2019). The distinct differences in  
412 both the frequency and time domains of the call properties (even within closely related  
413 crickets) reduce interspecific acoustic competition (Sueur 2002; Chek et al. 2003), especially  
414 since these crickets must also compete with anthropogenic noises (e.g., vehicles and  
415 construction) in addition to singing hetero- and conspecific males.

416

417 However, I did not observe clear-cut temporal partitioning among the urban-tolerant crickets,  
418 although *Teleogryllus* were generally heard towards the later hour of the surveys. This is  
419 unlike the *Gryllotalpa* in Singapore's forest, where *Gryllotalpa fulvipes* Saussure, 1877  
420 would call at around 6.30 pm followed by *Gryllotalpa nymphicus* Tan, 2012 at around 7.00  
421 pm (Tan 2017). This may be because unlike the *Gryllotalpa*, the call properties of the urban-  
422 tolerant crickets are already sufficiently different. Furthermore, much fewer species occurring  
423 in the grass verges perhaps also reduce the need to segregate their calling times and that  
424 competition with constant anthropogenic noises may drive these crickets to call more  
425 consistently throughout the night to maximise detection by conspecific females.

426

427 ***(iii) How do the call properties of the urban-tolerant species vary between environmental***  
428 ***conditions and individuals?***

429 Consistent inter-individual differences in the call properties signifies that some individuals  
430 consistently call at higher fundamental frequency and with longer syllable duration than other  
431 individuals, thus implying a form of partitioning between conspecific individuals.

432 Repeatability in the call properties has been reported in a few crickets, including

433 *Plebeiogryllus guttiventris* (Walker, 1871) and *G. bimaculatus* (Popov and Shuvalov 1977;  
434 Nandi and Balakrishnan 2013), but not in other species (see Deb et al. 2012). I also found that  
435 repeatabilities for fundamental frequency are higher than for syllable duration in both *P.*  
436 *taprobanensis* and *G. sigillatus*. This is in line with the current literature in which static  
437 properties (including fundamental frequency) tend to exhibit higher repeatability than  
438 dynamic properties (such as syllable duration) (Gerhardt 1991; Nandi and Balakrishnan  
439 2013).

440

441 Such consistent inter-individual differences can be attributed to the environment and/or the  
442 male conditions, which in turns have consequences on the mating success of the males  
443 (Nandi and Balakrishnan 2013). Body size, which can be indicative of the age, fecundity and  
444 fitness, is also known to correlate with call properties in some but not crickets (e.g., *G.*  
445 *sigillatus* and *G. bimaculatus*) (Simmons and Zuk 1992; Champagnon and Castillo 2008). As  
446 it was nearly impossible to collect the calling crickets, how the call properties are associated  
447 with body size could not be examined here. Trigonids tend to hide among leave sheath of  
448 grasses, whereas many gryllids quickly retreat into their burrows or crevices when their  
449 surrounding grasses were disturbed.

450

451 However, there was no evidence from this study that temperature or rainfall are associated  
452 with the static and dynamic call properties of both *P. taprobanensis* and *G. sigillatus*. This is  
453 contrary to my prediction and previous studies, in which temperature affects most aspects of  
454 calling songs, including syllable duration and frequency in other crickets (e.g., Walker, 1962;  
455 Martin et al. 2000). Temperature influences the speed at which the cricket open and close its  
456 wings, which directly affects the syllable duration and rate. Additionally, increased wing  
457 closure also imply a faster passage of scraper across the teeth on the stridulatory file, thus

458 leading to an increased frequency (Walker, 1962), although this is also not necessarily true  
459 for all crickets (Bennet-Clark 1989).

460

#### 461 ***Conclusions***

462 Urban animals can have a potentially disproportionate impact on the health and well-being of  
463 city-dwelling human beings (Newbold et al. 2015). As a “City in a Garden”, the calls of  
464 crickets at night should be an indispensable part of the overall natural soundscape in the  
465 urban Singapore landscape. This study also demonstrates that the very few urban-tolerant  
466 species may represent what most people would frequently hear. This is particularly relevant  
467 since the crickets call among grass verges along walkways frequented by students from  
468 schools, workers from the light industry and people from the surrounding housing  
469 neighbourhood.

470

471

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473

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478

479

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663

664

665 **Table:**

666

667 **Table 1.** Number of individuals recorded (n ID) and echemes (N echemes) analysed for each

668 species.

<b>Family: Subfamily</b>	<b>Taxon names</b>	<b>n ID</b>	<b>N echemes</b>
Gryllidae: Gryllinae	<i>Grylloides sigillatus</i> (Walker, 1869)	9	64
Gryllidae: Gryllinae	<i>Gryllus bimaculatus</i> De Geer, 1773	1	11
Gryllidae: Gryllinae	<i>Teleogryllus c.f. mitratus</i> (Burmeister, 1838)	1	4
Gryllidae: Gryllinae	Gryllinae	4	40
Gryllidae: Gryllinae	? <i>Mitius</i> sp.	1	4
Trigonidiidae:	<i>Polionemobius taprobanensis</i> (Walker,	20	169
Nemobiinae	1869)		
Trigonidiidae:	<i>Pteronemobius</i> sp.	2	22
Nemobiinae			
Trigonidiidae:	Nemobiinae	1	6
Nemobiinae			
Trigonidiidae:	Trigonidiinae	1	17
Trigonidiinae			
Tettigoniidae:	<i>Euconocephalus</i> sp.	2	18
Conocephalinae			

669

670

671

672 **Table 2.** Results from models with delta <2.0 examining how environmental conditions  
 673 predicts syllable duration and fundamental frequency. ID refers to individual cricket identity

	Model with delta <0.20	AICc	Weight	R <sup>2</sup> <sub>M</sub>	R <sup>2</sup> <sub>C</sub>
<b><i>Syllable duration</i></b>					
<i>Polionemobius</i>	~ 1 + (1 ID)	-418.8	0.90	0.00	0.45
<i>taprobanensis</i>					
<i>Gryllodes sigillatus</i>	~ 1 + (1 ID)	-198.3	0.95	0.00	0.59
<b><i>Fundamental frequency</i></b>					
<i>Polionemobius</i>	~ 1 + (1 ID)	-1017.9	0.97	0.00	0.97
<i>taprobanensis</i>					
<i>Gryllodes sigillatus</i>	~ 1 + (1 ID)	-443.5	0.97	0.00	0.96

674

675

676 **Figure captions:**

677

678 **Figure 1.** Map of Singapore (a) with the arrow indicating the location of the study site. The  
 679 inset photographs (b–d) illustrate the grass verges that were sampled at the time of sampling  
 680 (b) and during the day (c, d).

681

682 **Figure 2.** Individual-based rarefaction curve showing the cumulative number of species  
 683 recorded.

684

685 **Figure 3.** Oscillograms of the crickets and bush-cricket calls.

686

687 **Figure 4.** Power spectra of the crickets and bush-cricket calls based on a single echeme using  
688 Hamming window of window length 512.

689

690 **Figure 5.** PCoA plot showing the partitioning in the call properties of the cricket species. The  
691 ellipses represent the standard deviations for each species.

692

693 **Figure 6.** Spectrogram showing the partitioning in the call properties (both time and  
694 frequency domains) between *Polionemobius taprobanensis* (a), *Grylloides sigillatus* (b) and  
695 *Pteronemobius* (c).