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2 forest katydids

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27
28 **Running title (40 character limit):** Temporal dynamics of katydid signaling

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45 **Abstract (400 word limit):**

46 Researchers have long examined the structure of animal advertisement signals, but
47 comparatively little is known about how often these signals are repeated and what factors
48 predict variation in signaling rate across species. Here, we focus on acoustic advertisement
49 signals to test the hypothesis that calling males experience a tradeoff between investment in
50 the duration or complexity of individual calls and investment in signaling over long time
51 periods. This hypothesis predicts that the number of signals that a male produces per 24 hours
52 will negatively correlate with 1) the duration of sound that is produced in each call (the sum of
53 all pulses) and 2) the number of sound pulses per call. To test this hypothesis, we measured call
54 parameters and the number of calls produced per 24 hours in 16 species of sympatric
55 phaneropterine katydids from the Panamanian rainforest. This assemblage also provided us
56 with the opportunity to test a second taxonomically-specific hypothesis about signaling rates in
57 taxa such as phaneropterine katydids that transition from advertisement calls to mating duets
58 to facilitate mate localization. To establish duets, male phaneropterine katydids call and
59 females produce a short acoustic reply. These duets facilitate searching by males, females, or
60 both sexes, depending on the species. We test the hypothesis that males invest either in calling
61 or in searching for females. This hypothesis predicts a negative relationship between how often
62 males signal over 24 hours and how much males move across the landscape relative to females.
63 For the first hypothesis, there was a strong negative relationship between the number of
64 signals and the duration of sound that is produced in each signal, but we find no relationship
65 between the number of signals produced per 24 hours and the number of pulses per signal.
66 This result suggests the presence of cross-taxa tradeoffs that limit signal production and
67 duration, but not the structure of individual signals. These tradeoffs could be driven by
68 energetic limitations, predation pressure, signal efficacy, or other signaling costs. For the
69 second hypothesis, we find a negative relationship between the number of signals produced
70 per day and proportion of the light trap catch that is male, likely reflecting males investing
71 either in calling or in searching. These cross-taxa relationships point to the presence of
72 pervasive trade-offs that fundamentally shape the spatial and temporal dynamics of
73 communication.

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76 **Total word count (excluding references, tables, and figure legends): 6481**

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90 **Introduction:**

91

92 Many animal species rely on long range acoustic advertisement signals to convey their location,
93 availability for mating, or quality to potential mates (Andersson 1994). Because these signals
94 are usually necessary to attract a mate and reproduce, signaling more often or with more
95 conspicuous signals can enhance reproductive success (Hedrick 1986; Ryan 1988; Ryan and
96 Keddy-Hector 1992; Sung and Handford 2020). However, various costs and constraints shape
97 signaling rate across animals. The energy expenditure associated with certain signals may limit
98 the rate at which they can be repeated (Mowles 2014; Oberweger and Goller 2001; Symes et al.
99 2015; Taigen and Wells 1985). For example, the energetic demands of calling appear to limit
100 both the amount of time in a single night and the total number of nights that male tree frogs
101 spend chorusing, even though increased calling time would increase reproductive success
102 (Murphy 1994; Ryan and Kime 2003; Wells and Taigen 1986). Likewise, eavesdropping
103 predators and competitors impose a fitness cost on signaling because they can more easily
104 home in on conspicuous and repetitive signals (Trillo et al. 2016; Zuk and Kolluru 1998).
105 Therefore, signalers must strike a balance between incurring these costs and providing key
106 information to potential mates.

107

108 Several interrelated factors can affect signaling rate (Endler 1993). Signal structure - here, the
109 spectral and temporal properties of individual acoustic calls - can affect signal rate due to
110 tradeoffs with the fitness costs associated with signal structure. A single signal that is
111 energetically expensive to produce or is highly conspicuous to predators or competitors might
112 be repeated infrequently compared to a less energetically expensive or less conspicuous signal.
113 Over short timescales, several taxa show evidence of tradeoffs between signal structure
114 (bandwidth or pulse duration) and temporal properties (pulse rate) within individual signals
115 (Clink et al. 2018; Pasch et al. 2011; Podos 1997; Symes et al. 2015; Wells and Taigen 1986). As
116 the costs and benefits of advertisement signals generally accrue over much longer timespans
117 than a single signal, it is important to consider the relationship between signal properties and
118 signal repetition rate over ecologically-relevant timescales. Historically, relatively few studies
119 have examined signaling strategy over long periods of time due to time and budget constraints
120 (Trillo and Vehrencamp 2005; Vehrencamp et al. 2013), but recent advances in monitoring
121 technology make collecting these data easier and allow for studies integrating signal structure
122 and production over longer time scales.

123

124 In this study, we use data from Neotropical phaneropterine katydids to identify behavioral correlates
125 of daily signal repetition rate that reflect ecological or physiological selective pressures. Male katydids
126 produce acoustic signals (calls) to advertise their location and mating status to females from a
127 distance. Katydid calls consist of one or more pulses of sound (Fig. 1), and usually each pulse is
128 produced by a wing closing movement that rubs together sound generating structures. The temporal
129 pattern of these pulses is highly species-specific (ter Hofstede et al. 2020). We first tested the
130 hypothesis that signaling costs generate phenotypic tradeoffs in signaling investment. This hypothesis
131 predicts a negative relationship between investment in individual calls, measured as call duration or
132 number of sound pulses per call, and investment in signaling over long time periods, measured as

133 number of calls per 24 hours. Call duration and complexity can impact fitness through energy balance
134 (Prestwich 1994; Symes et al. 2015), predation risk (Bernal and Page In review; Falk et al. 2015) or
135 signal efficacy (Bradbury and Vehrencamp 2011; Guilford and Dawkins 1991). Alternatively, the fitness
136 impacts of signaling might vary substantially across species due to the influence of an unrelated
137 behavioral or ecological trait, resulting in no relationship or possibly even a positive relationship
138 between daily signal rate and signal duration or complexity. For example, to find a female, males of
139 species that form aggregations around patchy food resources might not need to signal as often as
140 those of highly dispersed species, regardless of signal structure.

141

142

143 We also tested the hypothesis that males invest either in calling or in searching for females.
144 Typically, in acoustically advertising insect species, females perform phonotaxis and males call
145 frequently and remain stationary to increase the chances of a female finding him (Greenfield
146 2016). In most katydid species, females perform phonotaxis to find the calling male, but almost
147 all species of phaneropterine katydid use duets to form mating pairs (Heller et al. 2015; Shaw et
148 al. 1990). Duetting is a relatively common mate-finding strategy across insects (Bailey 2003) and
149 makes it possible for either sex to engage in mate searching behavior. To establish duets, male
150 phaneropterine katydids call and females produce an acoustic reply that consists of a single tick
151 or short series of pulses at a species-specific time interval after the male call (Heller and von
152 Helversen 1986; Shaw et al. 1990). Depending on the species, the female remains stationary
153 while the male moves toward her, the female does the majority of the movement to the male,
154 or both males and females move toward each other (Spooner 1995; Zimmermann et al. 1989),
155 sometimes with variation within species depending on mating history (Bateman 2001).
156 Consequently, depending on the behavior of the females, males can enhance their fitness by
157 engaging in more calling or by engaging in more searching. Over evolutionary time, the
158 allocation of searching behavior between sexes is likely a product of the operational sex ratio,
159 which is determined by factors such as male energetic investment in spermatophores, sex-
160 specific mortality, and sex differences in refractory periods (reviewed in (Lehmann 2012)). In
161 duetting species, the sex that is overrepresented in the operational sex ratio over evolutionary
162 time is predicted to invest in searching for members of the limiting sex.

163

164 The duetting mating system and potential for mutual mate search enabled us to test the
165 hypothesis that males invest either in calling or in searching for females. This hypothesis
166 predicts a negative relationship between how often males signal over 24 hours and how much
167 males move across the landscape relative to females. For species in which males do most of the
168 searching, we would expect that males would change locations frequently and produce few
169 calls in each location. Given that females do not move to males in these species, calling
170 repeatedly from one location where no females reply would not be an optimal strategy. For
171 species in which females do most of the searching, we would expect males to move less and call
172 more often to increase the chances of a female hearing his signal and locating him.

173

174 To test these two hypotheses, we collected data on acoustic signaling behavior and relative
175 abundance of males and females at lights for 16 Neotropical phaneropterine katydid species.
176 We quantified the number of calls produced by males over 24 hours and measured two

177 acoustic parameters that are relevant to the fitness costs of signaling: the summed duration of
178 sound produced per call and the number of pulses in each call. Although longer calls should
179 impose higher energetic demands and greater predation risk from eavesdropping predators,
180 both consequences depend on how much sound is produced during the call. In katydids, total
181 call duration (time from the start of the first pulse to the end of the last pulse) does not
182 necessarily correspond well with energetic demands or conspicuousness to predators because
183 some katydids produce calls containing long pulses with little silence between them and other
184 katydids produce calls consisting of short pulses at long intervals. Therefore, we measured the
185 total duration of sound in each call by adding the durations of all the pulses in the call. To
186 assess the relative amount of movement between males and females of each species, we
187 quantified the sex ratio for individuals attracted to lights at night. In the Neotropics, there can
188 be substantial variation in the ratio of males and females caught at lights across species. In
189 some species, the catch is predominantly male, while other species have an even sex ratio or
190 one that is female biased. This variation in sex ratio likely reflects differences in the movement
191 patterns between sexes, with movement through the habitat increasing the likelihood of being
192 diverted to a light trap. The relationship between signaling investment, call characteristics and
193 male movement was assessed using Phylogenetic Generalized Least Squares Regression (PGLS)
194 to control for the effect of phylogenetic relationships between species.

195

196 **Methods:**

197 Insect collection: Katydids were captured at lights on Barro Colorado Island (9.1521° N,
198 79.8465° W), a research station located in the Panama Canal near Gamboa, Panama. Sampling
199 consisted of visiting a standardized set of locations around the lab clearing and capturing all
200 katydids that had been attracted to the building lights. This sampling protocol was conducted
201 twice per night, at approximately 23:00 and 04:30, and was repeated on 248 total nights
202 between December and March of 2015-2020. After each round of sampling, we recorded the
203 mass, sex, and species of each katydid. A subset of the males were used for focal 24-hour
204 recordings. We preserved 3-5 individuals of each species and sex in 95% ethanol for
205 phylogenetic analyses and as taxonomic vouchers. The remaining katydids were contributed to
206 the Museo de Invertebrados Fairchild de la Universidad de Panamá (MIUP) in Panama City,
207 used in additional experiments, or released in the forest at a site several kilometers away to
208 ensure that they were not recaptured at lights.

209

210 Signal rate and structure: To determine the daily signaling rate of individual species, we
211 recorded focal males for 24 hours and counted the number of calls the male produced
212 following the methods of Symes et al. (2020). In brief, each male was in a screen cage for 24
213 hours and sound from the cage was recorded as .wav files using a Tascam DR-40 digital
214 recorder that sampled at 96 kHz and 16 bit depth. Recording stations were located inside
215 screen greenhouses adjacent to the forest to preserve natural temperature and humidity
216 regimes and the acoustic background of the forest. By removing individuals from the acoustic
217 signals of potential mates, we isolated the baseline daily signaling rates of males outside of the
218 duetting context. Signal times were extracted from .wav files using a custom R script and
219 functions from the *tuneR* and *seewave* packages (Ligges et al. 2018; Sueur et al. 2008; Team
220 2017) to identify high amplitude events in the frequency range of the focal species. Detection

221 events were reviewed manually, and false positives were removed. A subset of the files were
222 reviewed in their entirety and no false negatives were detected. The daily signal rate data from
223 this study (N = 8 species) were integrated with the phaneropterine daily signal rate data from
224 the Symes et al. (2020) study (N = 8 species), resulting in a set of 16 species.

225

226 For characterizing differences in signal structure, we used published data from ter Hofstede et
227 al (2020). Table 1 in ter Hofstede et al. (2020) provides the mean number of pulses per call
228 directly. The mean total duration per call was calculated from the data set available in the
229 supplemental material of ter Hofstede et al. (2020). The pulse durations for all pulses in each
230 call were added together to give the duration of sound in each call. Values were then averaged
231 first by individual and then by species.

232

233 Phylogenetic tree: The phylogenetic relationships between the species under study were
234 reconstructed based on data from Mugleston et al. (2018) combined with newly generated
235 sequence data for katydid species from Panama (Table S1). We selected all 70 species belonging
236 to Phaneropterinae from Mugleston et al. (2018) and downloaded the corresponding
237 sequences from Genbank (Table S1). We added sequence data for 44 Panamanian
238 phaneropterine species and we selected three outgroup species from Mugleston et al. (2018)
239 belonging to the families Gryllacrididae and Rhabdophoridae.

240

241 We used DNA markers from six genes for tree construction: two from the mitochondrial
242 genome and four from the nuclear genome. The mitochondrial markers were partial sequences
243 of the *12S rRNA* gene (*12S*, amplicon ~ 400 bp; this study), and the *cytochrome c oxidase*
244 *subunit 2 (CO2)*, ~ 670 bp; (Mugleston et al. 2018)). Nuclear markers were partial sequences of
245 protein coding *histone H3* gene (*H3*, ~ 330 bp; this study and (Mugleston et al. 2018)), *Wingless*
246 (*WG*, ~ 370 bp; Mugleston et al. (2018)) and complete sequences of two non-protein-coding
247 genes corresponding to nuclear ribosomal subunits: *18S rRNA (18S)*, ~ 1800 bp; this study and
248 Mugleston et al. (2018)) and *28S rRNA (28S)*, ~ 2200 bp; (Mugleston et al. 2018)).

249 DNA extraction, PCR amplification, and sequencing for all newly generated sequences was
250 carried out at Service de Systématique Moléculaire of the MNHN, following the protocols
251 described in Dong *et al.* (2018), including primers and annealing temperatures for each DNA
252 marker. Sequences were cleaned and checked for sequencing errors in Geneious R9.0.2
253 (Biomatter Ltd., New Zealand, www.geneious.com, (Kearse et al. 2012)), and BioEdit v.7.0.5.3
254 (Hall 1999), then blasted with NCBI blast tools, and submitted to GenBank (Supplemental Table
255 S1). The sequences were aligned with MAFFT version 7 online (Kato and Standley 2013). The
256 complete combined dataset consists of 6,065 aligned base pairs (bp) for a total of 116 terminals
257 (see details in Table S1).

258 The concatenated dataset was then analyzed using maximum likelihood (ML) and Bayesian
259 inference (BI) analyses. ML analyses were run using the IQ-TREE 1.6.2 web portal:
260 <http://iqtree.cibiv.univie.ac.at/> with data partitioned by gene marker and the following options
261 selected: Edge-unlinked partitions, Substitution model: Auto (Kalyaanamoorthy et al. 2017;
262 Nguyen et al. 2015; Trifinopoulos et al. 2016). Clade support was assessed by conducting 1,000

263 bootstrap replicates (standard bootstrap). Nodes with bootstrap support values (BS) \geq 70%
264 were considered strongly supported. A clade with a posterior probability value higher than 0.95
265 was considered as well supported following Exicon et al. (2003).

266 BI phylogenetic analyses and divergence time estimation were run using Bayesian relaxed
267 clocks as implemented in BEAST 1.10.4. The partitions/clocks and substitution models were
268 selected under PartitionFinder 2.1.1 with the 'beast' set of models. BEAST analyses were
269 performed on the CIPRES Science Gateway using BEAGLE to improve and speed up the
270 likelihood calculation (Ayres et al. 2012; Miller et al. 2015). For each clock model/partitioning
271 scheme an uncorrelated lognormal relaxed clock was implemented. The Tree Model was set to
272 a birth-death speciation process (Gernhard 2008) to better account for extinct and missing
273 lineages. The ucl.d.mean prior of each clock model was set to an uninformative interval
274 (0.0001–1.0) with a uniform prior distribution. Based on the previous studies, two secondary
275 calibration points were enforced using lognormal distributions centered on previously
276 estimated median ages: we referred to the calibration time from Wolfe et al. (2016), Song et al.
277 (2015) and Mugleston et al. (2018), used for the root of the phylogenetic tree a time range of
278 251 to 272 Ma (Mean 261 – SD 6, normal distribution); a second calibration point is used for
279 family Gryllacrididae, at 56–65 Ma (Mean 60, SD 3, normal distribution). BEAST analyses
280 consisted of four runs of 100 million generations of MCMC with the parameters and trees
281 sampled every 10,000 generations. A burn-in of 25% was applied after checking the log-
282 likelihood curves. Trees obtained from distinct analyses were combined using LogCombiner
283 v1.8.4 (<http://beast.bio.ed.ac.uk/>). The maximum credibility tree, median ages and their 95%
284 highest posterior density (HPD) were generated with TreeAnnotator v1.8.4
285 (<https://github.com/beast-dev/beastmcmc/releases/tag/v1.8.4>).

286

287 Statistical analysis:

288 Statistical analyses were run in R version 4.0.3 (R Core Team, 2020). All variables used in
289 statistical analyses consisted of the mean values for each species or a proportion of count data
290 (Table 1). We tested whether the mean number of calls per 24 hours for each species ("*Mean*
291 *Calls*") could be predicted by four independent variables: the mean sum of the call pulse
292 durations in ms ("*Sum Sound*"), the mean number of pulses in a call ("*Pulses*"), the proportion
293 of the total captures for each species that were male individuals ("*Proportion Male*"), and the
294 mean male mass in grams ("*Male Mass*", from (ter Hofstede et al. 2020)). Although we do not
295 specify a hypothesis or prediction about how male mass might be related to daily signaling rate,
296 we included it as an independent variable because many physiological factors that could
297 influence calling rate, such as metabolic rate, scale with mass (Schmidt-Nielsen and Knut 1984;
298 West et al. 2000). Only Proportion Male was normally distributed, and the other four variables
299 were log transformed to achieve normality prior to analyses. We used the *pgls* function in the
300 *caper* package of R to test whether PGLS regression models were significant when controlling
301 for phylogenetic relationships (Orme et al. 2013). For the PGLS analyses, the complete
302 phylogenetic tree generated for the Phaneropterinae was pruned to include just the 16 species
303 for which we had data.

304

305 To identify the PGLS model that best explains variation in *Mean Calls*, we used a backward
306 selection approach. The complete model including all four independent variables was tested
307 first, and the variable with the lowest test statistic value was removed from the model for the
308 next test. This continued until the model only contained significant predictor variables. We used
309 sequential Bonferroni correction (Holm 1979) to adjust the alpha value of statistical tests to
310 correct for multiple tests on data collected from the same individuals. A scatterplot matrix of
311 the five variables suggested that many might be correlated, but variance inflation factors for
312 each model were low (<2.2 ; *vif* function, *car* package in R (Fox and Weisberg 2018)); therefore,
313 multicollinearity between independent variables was not an issue in the analyses. Hierarchical
314 partitioning was used to assess the relative contribution of each independent variable to
315 explaining variation in *Mean Calls* in the final model (*hier.part* function, *hier.part* package in R
316 (Mac Nally and Walsh 2004)). In addition to the test of significance for each independent
317 variable, we tested whether variables provided a significant improvement of fit using log
318 likelihood tests comparing models with or without the variable in question (*lrtest* function,
319 *lmtest* package in R (Zeileis and Hothorn 2002)). Pagel's lambda (λ) was estimated for each
320 model using maximum likelihood. Lambda is used to transform the variance-covariance matrix
321 of the regression model depending on the degree of phylogenetic signal in the residuals of the
322 relationship. It can range from zero, meaning no phylogenetic signal, to one, meaning a strong
323 phylogenetic signal following a Brownian motion model of evolution.

324

325 **Results:**

326 During 248 nights of light trap sampling over six years, we captured 6,324 katydids. Of these,
327 5,583 were in the subfamily Phaneropterinae and 3,399 were members of the 16 focal
328 phaneropterine species that we used in the analyses. In the focal phaneropterine species, the
329 mean number of calls produced per 24 hours varied substantially across species, ranging from
330 6.3 – 1302.9 calls per 24 hours (Table 1). In addition, the duration of sound per call ranged from
331 1.7 ms to 55.5 ms and the number of pulses per call ranged from one to 16 (Table 1).

332

333 **Table 1.**

334 Acoustic data, light catch data and mass for 16 species of Panamanian katydid. The sum of the
335 sound per call, number of pulses per calls and male mass are from ter Hofstede et al. (2020).
336 Mean call data for 8 species marked with asterisks are from Symes et al. (2020). Values are
337 mean \pm standard deviations with sample sizes in brackets. Names in single quotation marks are
338 names designated by the authors for identifiable morphotypes that could not be identified to
339 species.

340

Species	Number of calls/24 hrs	Call parameters			Proportion of individuals male	Male mass (g)
		Sum of sound in call (ms)	Pulses / call	N (individuals, calls)		
<i>Anaulacomera furcata</i>	1302.9 ± 1530.2 (7)	1.7 ± 0.2	2.0 ± 0.0	(3, 53)	0.31 (347)	0.14 ± 0.04 (43)
<i>Anaulacomera spatulata</i>	172.8 ± 133.8 (6)	2.8 ± 0.5	2.0 ± 0.0	(3, 59)	0.58 (309)	0.30 ± 0.08 (129)
<i>Anaulacomera 'wallace'</i>	1084.4 ± 1054.3 (5)	3.2 ± 0.4	3.1 ± 0.3	(4, 19)	0.3 (140)	0.22 ± 0.05 (28)
<i>Arota festae</i> *	82 ± 48.5 (13)	8.1 ± 1.2	8.0 ± 0.7	(10, 83)	0.69 (141)	0.98 ± 0.15 (34)
<i>Arota panama</i> *	181.8 ± 105.2 (8)	3.1 ± 0.4	4.9 ± 0.6	(10, 156)	0.88 (187)	0.57 ± 0.11 (68)
<i>Ceraia mytra</i>	13.5 ± 8 (6)	13.4 ± 1.1	9.7 ± 0.7	(9, 71)	0.46 (139)	1.30 ± 0.28 (31)
<i>Chloroscirtus discocercus</i> *	28.9 ± 19.1 (8)	55.5 ± 10.8	6.4 ± 0.5	(12, 157)	0.54 (362)	0.59 ± 0.22 (79)
<i>Dolichocercus latipennis</i>	6.3 ± 7.2 (4)	26.1 ± 5.4	15.6 ± 0.7	(3, 19)	0.77 (134)	0.21 ± 0.03 (40)
<i>Euceraia insignis</i>	11.6 ± 4.4 (5)	45.3 ± 8.2	16.3 ± 1.8	(3, 21)	0.75 (108)	0.58 ± 0.08 (37)
<i>Microcentrum 'polka'</i> *	86.1 ± 117.3 (12)	15.3 ± 5.5	7.6 ± 1.9	(8, 73)	0.71 (265)	1.2 ± 0.12 (117)
<i>Orophus conspersus</i> *	53 ± 42.7 (6)	36.5 ± 7.9	3.0 ± 0.7	(4, 40)	0.58 (40)	1.1 ± 0.13 (13)
<i>Philophyllia ingens</i>	21.1 ± 24.8 (11)	6.3 ± 2.2	1.0 ± 0.0	(9, 114)	0.94 (72)	3.42 ± 0.65 (38)
<i>Phylloptera dimidiata</i> *	124.2 ± 66 (11)	5.5 ± 0.9	7.7 ± 1.1	(12, 204)	0.74 (307)	0.54 ± 0.08 (115)
<i>Steirodon stalii</i> *	15.9 ± 14.4 (11)	14.4 ± 6.5	3.0 ± 0.0	(10, 92)	0.91 (47)	4.14 ± 0.49 (22)
<i>Viadana brunneri</i> *	374.9 ± 334.7 (9)	2.9 ± 0.3	2.0 ± 0.0	(11, 195)	0.57 (588)	0.38 ± 0.07 (70)
'Waxy' sp	148.6 ± 87.6 (8)	7.2 ± 1.9	6.5 ± 0.8	(3, 13)	0.61 (213)	0.735 ± 0.18 (73)

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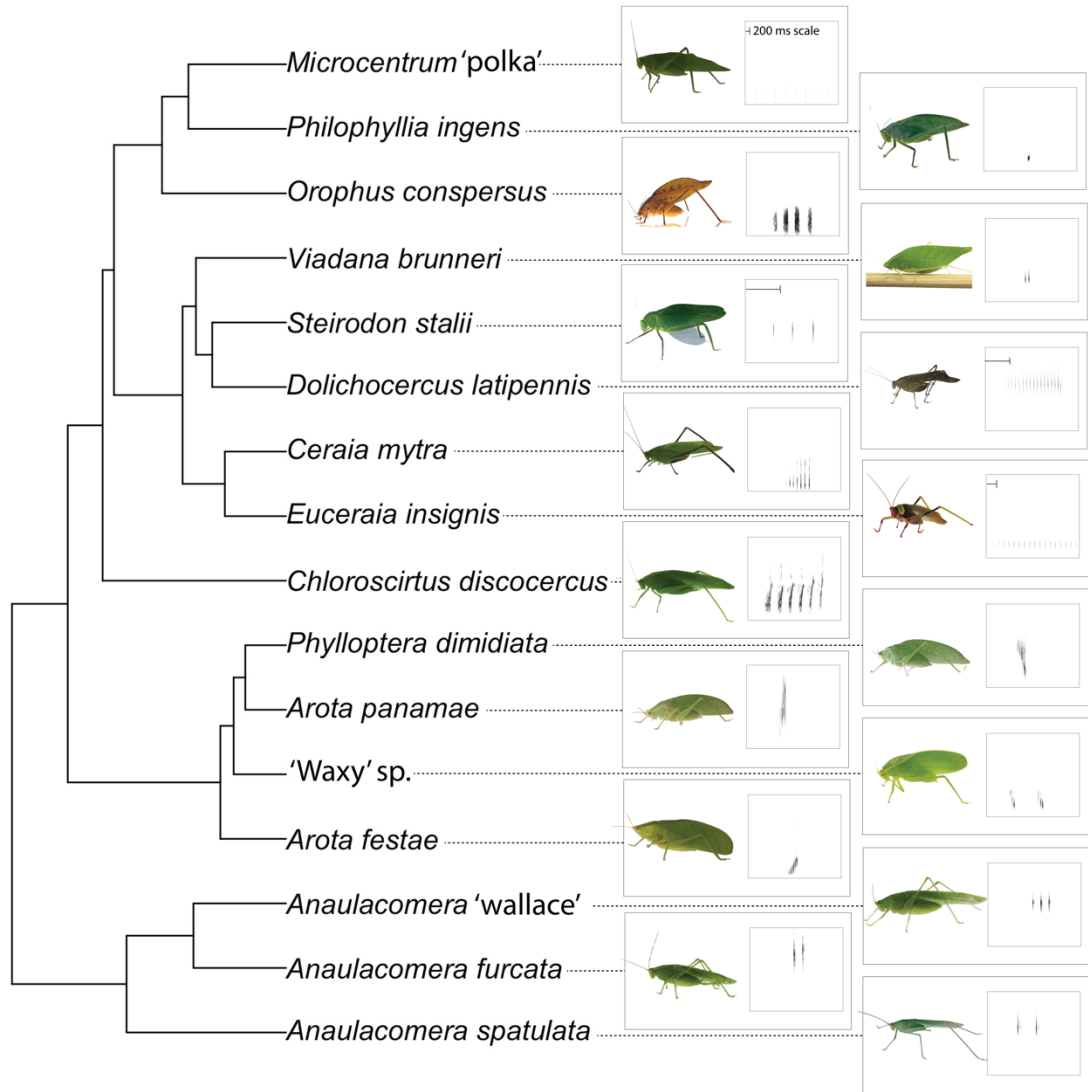
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348

For inferring the phaneropterine phylogeny, the best-fit partition scheme and substitution models used in BEAST analyses consisted of two partitions corresponding to mitochondrial and nuclear gene markers (partition 1: *CO2*, *12S*; partition 2: *18S*, *28S*, *WG*, *H3*) both with a best-fit model GTR+I+G. The topology recovered by BEAST analysis relying on these partitions /clocks converged with all parameters showing ESS values ≥ 200 . The analysis yielded a topology congruent with ML analysis (Fig S1).

349



350
351

352 **Fig. 1:** Phylogenetic relationships among 16 paneropterine katydid species from Panama, with
 353 male photos and spectrograms of the male call. Call length varies dramatically across species.
 354 All spectrograms have a frequency range (y-axis) of 7-40 kHz and a time axis of 200 ms, except
 355 for *Euceraia insignis* (2000 ms), *Microcentrum 'polka'* (9000 ms), *Steirodon stalii* (500 ms), and
 356 *Dolichocercus latipennis* (600 ms). Species vary substantially in size and photos are scaled to
 357 maximize the visibility of each species. Comparative mass data are given in Table 1.

358

359 The PGLS model that best explained variation in *Mean Calls* contained two significant
 360 independent variables: *Sum Sound* and *Proportion Males* (Table 2, Fig. 2). *Male Mass* and *Pulses*
 361 were not significant variables when included in PGLS regression models. It was not possible to
 362 estimate lambda using maximum likelihood for a PGLS with only Sum Sound as a predictor.
 363 Therefore, two PGLS models were run, one setting lambda to 0.001 and the other setting
 364 lambda to one (Table 2, model 4). A log likelihood ratio test confirmed that a model containing
 365 both Sum Sound and Proportion Males had a significantly better fit than either of the models

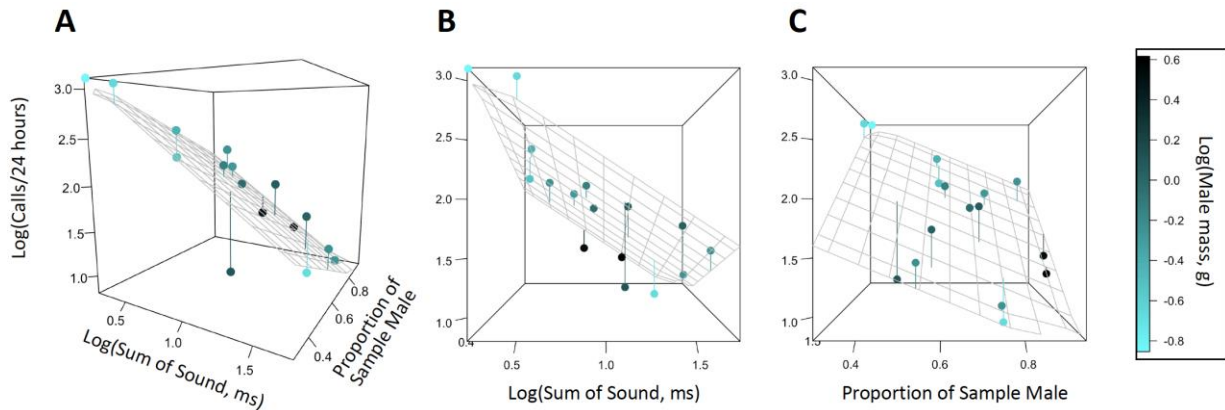
366 containing only Sum Sound ($\lambda = 0.001$: $\chi^2 = 9.1$, $P = 0.003$; $\lambda = 1$: $\chi^2 = 9.4$, $P = 0.002$).
 367 Of the total variance explained by the best fitting model (adjusted $R^2 = 0.75$), hierarchical
 368 partitioning analysis showed that 68% was explained by *Sum Sound* and 32% by *Proportion*
 369 *Male*. All significant statistical tests remained significant after using the sequential Bonferroni
 370 method to adjust P-values for multiple tests.

371
 372 Lambda was estimated to be zero for all models, except model 4 mentioned above (Table 2).
 373 Therefore, there was no phylogenetic signal in the residuals of these models, and they give the
 374 same results as regular linear multiple regression analysis. Confidence intervals for λ , however,
 375 could not be estimated for model 1 and they were large for models 2 and 3 (Table 2). For the
 376 best fitting PGLS model (Table 2, model 3), we ran the PGLS analysis again but set λ to the
 377 upper confidence interval limit to test whether the model was significant across the full range
 378 of potential λ values. Even at the highest λ value of 0.95, the overall relationship remained
 379 significant ($F_{2,13} = 9.9$, $P = 0.002$, adjusted $R^2 = 0.54$) and both predictor variables remained
 380 significant (Sum Sound: $P = 0.003$; Proportion Male: $P = 0.036$).

381
 382 **Table 2:** PGLS model results. CI: confidence interval for estimate of Pagel's lambda (λ).
 383

PGLS Model	Significant predictor(s)	P-value predictor	P-value model	Adjusted R ²	Pagel's λ (CI)
1 Log(Mean calls) ~ Log(Sum Sound) + Log(Pulses) + Proportion Male + Log(Male mass)	Log(Sum Sound)	0.011	< 0.001	0.72	0 (0-1)
2 Log(Mean calls) ~ Log(Sum Sound) + Log(Pulses) + Proportion Male	Log(Sum Sound) Proportion Male	0.002 0.010	< 0.001	0.74	0 (0-0.95)
3 Log(Mean calls) ~ Log(Sum Sound) + Proportion Male	Log(Sum Sound) Proportion Male	< 0.001 0.008	< 0.001	0.75	0 (0-0.95)
4 Log(Mean calls) ~ Log(Sum Sound)	Log(Sum Sound) Log(Sum Sound)	< 0.001 0.006	< 0.001 0.006	0.60 0.39	= 0.001 = 1

384
 385
 386
 387



388
389

390 **Fig. 2:** The number of acoustic signals (calls) produced by male katydids per 24 hours can be
391 predicted by the total duration of sound in each call and the proportion of all individuals
392 captured at lights that are male. Points are individual species (16), the grey grid is the plane
393 predicted by PGLS (Table 2, model 3), vertical lines are residuals, and color of the points
394 represents male mass (color legend on right). **A)** Graph tilted to maximize visibility of all axes. **B)**
395 Graph tilted to show relationship between calls per 24 hours and the amount of sound per call.
396 **C)** Graph tilted to show relationship between calls per 24 hours and the proportion of light
397 captures that are male.

398

399 **Discussion:**

400 Despite a long history of research on animal signals, researchers have rarely quantified a key
401 property of these signals – how often they are repeated. We tested the hypothesis that fitness
402 costs associated with different aspects of signaling generate tradeoffs in signaling investment
403 over long time scales. A key prediction of this hypothesis is a negative relationship between
404 investment in individual calls, measured as the duration of sound or number of sound pulses
405 per call, and investment in signaling over long time periods, measured as number of calls per 24
406 hours. There was a strong negative relationship between the number of calls produced per 24
407 hours and the duration of sound per call, indicating that some species called often, producing
408 short durations of sound each time, and other species called rarely, but produced sound for
409 longer with each call. There was, however, no relationship between the number of calls
410 produced and the number of pulses produced in each call. The fact that there is a tradeoff
411 between the number of signals produced and the duration of sound per signal is notable given
412 the substantial ecological and morphological variation across these species (Fig. 1). The
413 selective pressures giving rise to these tradeoffs are less-well understood and could include
414 energetic constraints, the efficacy of signals, the predation risks, and the mate finding strategy
415 of a species.

416

417 Energetic demands represent a substantial constraint on signaling in many animal species, with
418 calling often increasing energy expenditure to several times basal metabolic rate (Prestwich
419 1994; Symes et al. 2015; Taigen and Wells 1985). The metabolic cost of calling has not been
420 quantified for these Neotropical forest katydid species. Most studies of energetics of calling in
421 orthopteran insects have been on species that call multiple times per second for long periods of

422 time (Hoback and Wagner 1997; Prestwich 1994). Both within and across tested species, there
423 is a clear positive relationship between call rate and metabolic rate (Doubell et al. 2017;
424 Prestwich 1994). Interestingly, Hoback and Wagner (1997) found that the metabolic rate of
425 crickets increased with call rate, but not the duration of the call. Energy expenditure is,
426 however, unlikely to be a major factor driving the tradeoff between the number of signals and
427 the duration of sound produced per signal in the Neotropical phaneropterine forest katydids
428 studied here, which produce a total of only 0.13-3.43 seconds of sound per 24 hours (mean
429 number of calls / 24 hrs * sum of duration of sound pulses). This signaling output is incredibly
430 low compared to phaneropterines in many other parts of the world, where in a 24 hour
431 window, species with acoustically similar signals produce minutes or hours of sound (Heller et
432 al. 2015; Korsunovskaya 2008).

433
434 Even if energy availability is limited, the energy required for calling will be miniscule compared
435 to other energetic expenditures associated with reproduction in these katydids. Male katydids
436 produce a spermatophore, part of which the female will eat and gain direct nutritional benefits
437 that can go toward increased reproductive success (reviewed in (Lehmann 2012). The
438 spermatophore size and composition, and therefore paternal investment, varies enormously
439 between species, and males of some species invest so much energy in the spermatophore (30%
440 or more of their body weight; (McCartney et al. 2012) that sex role reversal can occur, with
441 males becoming the choosy sex (Gwynne 1990; Simmons et al. 1992). This investment in a very
442 large spermatophore can result in a female-biased operational sex ratio because males require
443 significant time between matings to produce the large spermatophore, whereas females
444 benefit nutritionally from multiple matings (Gwynne 1990). Correspondingly, species in which
445 females search for males produce larger spermatophores than those in which males search for
446 females (McCartney et al. 2012). Experiments have also shown that investment in calling,
447 investment in searching and sex-role reversal can be flexible and both density and resource-
448 dependent (Bateman 2001; Gwynne 1985; 1990). Given how little sound the species in our
449 study produce compared to other katydid species (ter Hofstede et al. 2020), energy expended
450 during calling would be minimal compared to the high energetic expenditures associated with
451 spermatophore production and flight (Doubell et al. 2017; Stevens and Josephson 1977).
452 Therefore, we suggest that energetic constraints are unlikely to be the primary factor driving
453 the tradeoff relationships seen in our study.

454
455 The efficacy of a signal refers to the ability of receivers to detect and recognize it despite the
456 effects of signal distortion or masking as it propagates through the environment (Bradbury and
457 Vehrencamp 2011; Endler 1993). For acoustic signals, habitat features such as background
458 noise and vegetation structure, can impact the amplitude and structure of a signal as it travels
459 from the sender to the receiver (Römer 2020). Both high repetition rates and longer calls have
460 the potential to increase signal efficacy. High repetition rates are an example of redundant
461 signaling, which can be effective at overcoming signal interference and improving detectability
462 (Kostarakos and Römer 2010; Luther and Gentry 2013). Likewise, a longer call or more pulses
463 per call could help improve detectability if noise interferes with part of the signal (Potash 1972).
464 Signal recognition is a separate and equally important part of signal efficacy. The number of
465 pulses per call did not explain the observed variation in daily signaling rate in this study.

466 Although more pulses might improve detectability, pulse number and structure are highly
467 stereotyped and species-specific in Orthoptera, likely due to unimodal female preference for
468 mate recognition (Blankers et al. 2015; Schöneich et al. 2015; Schul 1998; Symes 2014).
469 However, the information provided by a call could be greater if the signal contains a longer sum
470 duration of sound. Species with many pulses generally had higher sound durations, while
471 species with few pulses could have short or long pulses, resulting in a range of sum sound
472 durations (Fig S2). Among the many sounds in a tropical rainforest, a signal that contains more
473 sound might be easier to discriminate from background noise than one with little sound.
474 Therefore, very short calls, such as the double-pulse calls of *Anaulacomera furcata* with only 1.7
475 ms of sound, might need to be repeated much more often than the long calls of *Euceraia*
476 *insignis* (Table 1) to increase the probability of both signal detection and recognition by
477 prospective mates.

478
479 Conspicuous signaling can increase the chances of being detected by a mate, but it can also
480 increase the risk of predation from eavesdropping predators (Bernal and Page In review; Zuk
481 and Kolluru 1998). These two conflicting selection pressures, i.e mates selecting for more
482 conspicuous signals and predators selecting for less conspicuous signals, are likely to drive the
483 patterns observed in this study. Neotropical forests contain a guild of predatory gleaning bats
484 that eavesdrop on prey advertisement signals to locate their food (Belwood and Morris 1987;
485 Denzinger et al. 2018). Playback experiments demonstrate that these bats respond
486 preferentially to longer and more complex acoustic signals (Falk et al. 2015; Page and Ryan
487 2008) and also to signals produced at a higher repetition rate (Belwood and Morris 1987). Diet
488 analyses show that some of these bat species in Panama are katydid specialists, but
489 phaneropterines make up a relatively small proportion of the katydids in their diet (Belwood
490 and Morris 1987; ter Hofstede et al. 2017). Symes et al. (2020) found that eight phaneropterine
491 species from this study did not reduce their calling rate when exposed to bat echolocation calls,
492 whereas one pseudophylline katydid with a much higher calling rate did reduce calling in
493 response to bat calls. This suggests that phaneropterine katydids rely on their very low sound
494 output, either through short calls or low repetition rate, as a proactive defense against
495 eavesdropping bats. Phenotypes that do not trade-off signal sound duration and daily
496 repetition rate are likely selected against because of higher fitness costs, either reduced
497 probability of survival due to predation for individuals that produce long calls at a high rate or
498 reduced reproductive success for individuals that produce very few, short calls.

499
500 We used the ratio of males to female katydids at lights as a proxy for differences in movement
501 between the sexes. Although it is possible that these ratios reflect actual adult sex ratios
502 instead of differences in movement, we consider this unlikely. At least one study has
503 documented a 50:50 sex ratio in a species of katydid (Gwynne 1985), and while many of the
504 species in our study had a male-biased light catch ratio, the sex ratio of katydid remains found
505 in bat roosts are typically even (ter Hofstede et al. 2017). In our study, phaneropterine species
506 with high male daily signaling rate had light trap sex ratios that were stable across years (Table
507 S2) and more strongly female-biased, likely reflecting a situation where females move through
508 the landscape, listening for signaling males. When males signal rarely, males represent a
509 greater proportion of the light catch for that species, likely reflecting a situation where males

510 are moving through the landscape to advertise, producing occasional calls to test for the
511 presence of receptive females that they can approach. These scenarios represent extremes of a
512 behavioral continuum and it is conceivable that some or many of these species engage in
513 mutual mate searching behavior, even if movement costs are not evenly distributed between
514 sexes. In addition to direct observations of movement patterns in these species, empirical data
515 on the relative size of the males' spermatophores could help estimate operational sex ratios for
516 each species, providing an explanation for differences in movement between sexes.

517
518 Hypotheses about sex-specific movement and searching strategies can be further tested by
519 collecting additional data about the structure of the sensory system. Strauß et al. (2014) noted
520 that in *Poecilimon* katydid species where stationary calling males were approached by searching
521 females, there was a reduction in the relative size of the auditory spiracle, a structure for which
522 size is positively correlated with auditory sensitivity. The relatively small size of the auditory
523 spiracle in species where females search is presumed to be a result of the fact that females can
524 localize males based on the comparatively long male call, permitting smaller auditory spiracles
525 than when males need to localize the short acoustic replies of females. If relative spiracle size is
526 connected to searching strategy in Neotropical forest katydids, we predict that, for species in
527 which males search for females, auditory spiracles will be relatively large, allowing searching
528 males to localize short female replies. **In contrast, auditory spiracles would be relatively small in**
529 **species where females search for the comparatively repetitive male calls.** Searching for the
530 source of signals can carry substantial costs (Geipel et al. 2020; Raghuram et al. 2015), and in
531 species with low male daily signaling rates and high female movement, we may also see
532 comparatively high male investment in the size and composition of spermatophores,
533 incentivizing female search behavior.

534
535 This phaneropterine assemblage is characterized by broad tradeoff relationships, and yet is
536 comprised of ecologically, morphologically, and acoustically heterogeneous species (Nickle
537 1992; ter Hofstede et al. 2020). The fact that different species fall at different points along the
538 tradeoff relationships raises the question of whether there are ecological correlates that predict
539 the strategies used by different species. For example, a species that calls from within dense
540 canopy vegetation may experience substantial degradation of call structure and use fewer
541 longer calls to find mates. Population density may also be an important correlate of signaling
542 and mate search strategy (Hartley et al. 1974). For example, low density species may evolve
543 mutual mate-searching and produce short signals in many locations to test for the presence of a
544 mate.

545
546 As discussed above, the findings of this study highlight multiple promising directions for future
547 research. This research has focused exclusively on acoustic signals, but similar tradeoffs may be
548 seen in other modalities as well. Related katydid subfamilies use vibration signals and duets in
549 addition to acoustic communication (Belwood 1990; Morris 1980; Rajaraman et al. 2018; Velilla
550 et al. 2020). In species that use multiple modalities to establish duets and attract mates,
551 comparative analyses may demonstrate similar tradeoffs between the daily repetition rate of
552 signals and the duration of the signal emission, within or across modalities. In addition,

553 amplitude remains an important and rarely measured aspect of acoustic communication that
554 may further contribute to explaining signaling strategy and risk exposure across species.

555

556 This research raises intriguing questions about the role of costs, constraints, and tradeoffs in
557 structuring the short- and long-term dynamics of animal signals. Constraints are well-
558 documented in the bandwidth-trill rate tradeoffs of birds (Podos 1997), gibbons (Clink et al.
559 2018), singing mice (Pasch et al. 2011), bowhead whales (Erbs et al. 2021), and other
560 organisms. Across taxa, previous comparative work on *Oecanthus* tree crickets (Symes et al.
561 2015) has shown that signals diverge via counterbalanced changes in pulse rate and pulse
562 duration: as pulse rate increases, pulse duration decreases, resulting in calls that have
563 comparable sound duration across species. Here, we see similar tradeoffs in acoustic signals,
564 but over 24 hour timescales and across a subfamily rather than within a genus. Interestingly,
565 closely related Phaneropterinae that occupy other habitats produce substantially more sound
566 (Heller and von Helversen 1993; Zhantiev and Korsunovskaya 2005), indicating that the
567 tradeoffs seen in this study are likely a property of the habitat, not the entire taxonomic group,
568 and that species have conformed to this relationship through multiple instances of colonization
569 and evolution. The pervasiveness of tradeoff relationships across species highlights the
570 potential existence of broad structuring principles that shape the spatial and temporal
571 dynamics of communication across taxa.

572

573 **Data availability statement**

574 The data used in these analyses are available in the paper and as supplemental material.

575

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580

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