

1 **Title**

2 A sensory ecological perspective on mate sampling strategies: simulation models and
3 an empirical test

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27 **Abstract**

28 Long-range communication signals play a central role in mate search and mate choice
29 across a wide range of taxa. Among the different aspects of mate choice, the strategy
30 an individual employ to search for potential mates (mate sampling) has been less
31 explored despite its significance. Although analytical models of mate sampling have
32 demonstrated significant differences in individual fitness returns for different
33 sampling strategies, these models have rarely incorporated relevant information on the
34 ecology of signalers and sensory physiology of receivers, both of which can
35 profoundly influence which sampling strategy is optimal. In this study, we used
36 simulation models to compare the costs and benefits of different female mate
37 sampling strategies in an acoustically communicating field cricket (*Plebeiogryllus*
38 *guttiventris*) by incorporating information on relative spacing of callers in natural
39 choruses, their signal intensity and the effect of signal intensity on female phonotaxis
40 behaviour. Mating with the louder caller that the female first approaches emerged as
41 the optimal strategy, thus reflecting the importance of physiological mechanisms of
42 sound signal localization (passive attraction) over active sampling. When tested
43 empirically in the field, female behaviour was consistent with passive attraction.

44

45 **Keywords**

46 Mate search, mate choice, acoustic communication, crickets, phonotaxis behaviour,
47 sexual selection, mate sampling strategies, behavioural simulations.

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53 **Introduction**

54 Searching for mates is a critical component of animal mating behaviour. Mate
55 sampling strategies are employed by individuals of the choosier sex (typically
56 females) in their search for potential mates (Andersson 1994). In systems where
57 sexual selection acts via the mechanism of mate choice, active mate sampling
58 strategies can directly influence the strength of sexual selection (Andersson 1994;
59 Reinhold and Schielzeth 2014). The kind of sampling strategy employed and the
60 number of potential mates sampled influence the extent to which mate choice affects
61 the evolution of sexual traits (Gibson and Langen 1996; Roff and Fairbairn 2015).
62 Despite the importance of sampling strategies for understanding sexual selection,
63 empirical studies have largely focused on measuring sexual trait variation, choosiness
64 for these traits and mating preferences (Reinhold and Schielzeth 2014).

65

66 A number of theoretical studies have, however, investigated mate sampling strategies
67 utilizing analytical models (Janetos 1980; Parker 1982; Wiegmann et al. 1996;
68 Johnstone 1997; Kokko et al. 2014). In the threshold or sequential sampling
69 strategies, females evaluate mates sequentially based on a certain threshold value of
70 the trait and decide to mate only if the mate quality is higher than the threshold
71 criterion that either remains constant or declines with increasing costs of sampling
72 (Janetos 1980; Real 1990; Dombrovsky and Perrin 1994; Wiegmann et al. 1996). In
73 the other category of models, mating decisions are based on a comparative assessment
74 of the previously sampled potential mates; either between the last pair of successively
75 sampled individuals ('Sequential-comparison'), or a fixed number of sampled
76 individuals ('best-of-n') (Janetos 1980; Wittenberger 1983). Unlike 'threshold'
77 strategies, the 'comparison' strategies allow for a potential mate to be revisited during
78 sampling and hence require the female to remember the location and/or the identity of

79 a previously sampled individual (Janetos 1980). Models with and without search costs
80 yielded maximum fitness returns for the ‘One-step decision’ and the ‘Best-of-n’
81 strategy strategies respectively (Janetos 1980; Real 1990). More recent models have
82 employed information theoretic approaches to reduce the uncertainty of information
83 gathered on mate quality by allowing for multiple revisits to potential mates (‘Bayes
84 tactic’, “threshold” strategy and ‘Random walk’: Luttbeg 1996; Wiegmann and
85 Angeloni 2007; Wiegmann et al. 2010; Castellano and Cermelli 2011).

86

87 A critical feature of all active mate sampling strategies is the ability of females to
88 reject mates or defer their mating decision until further sampling (Parker 1982). In
89 mating systems in which females localize mates using their sexual advertisement
90 signals, the potential mate with a more intense advertisement signal can, however,
91 attract more females due to a larger broadcast area (Parker 1982, 1983). This
92 phenomenon, referred to as ‘passive attraction’, may superficially appear like active
93 female choice (Parker 1983; Kotiaho and Puurtinen 2007). However, a female’s
94 attraction in this case is guided entirely by its physiological response to the relative
95 strengths of the perceived advertisement signal and does not involve active mate
96 sampling (Parker 1983). A distinction between active mate sampling strategy and
97 ‘passive attraction’ is critical especially because female ‘choosiness’, a component of
98 mate choice, has been defined as the extent of mate sampling that it engages in before
99 mating (Kokko et al. 2006; Kotiaho and Puurtinen 2007).

100

101 Empirical studies on mate sampling strategies demonstrate varied strategies being
102 used by animals belonging to different taxa, suggesting a role of the ecology of the
103 system in determining the optimal strategy. For instance, while some species of birds
104 have been reported to use either ‘best-of-n’ or the ‘Bayes tactic’ (Trail and Adams

105 1989; Dale et al. 1990, 1992; Petrie et al. 1991; Bensch and Hasselquist 1992; Hovi
106 and Rätti 1994; Rintamäki et al. 1995; Luttbeg 1996; Uy et al. 2001), others have
107 been found to employ ‘sequential comparison’ and ‘one step decision’ strategies
108 (Choudhury and Black 1993). Studies on mate sampling strategies in fishes and
109 invertebrates have generally provided evidence on the use of sequential threshold
110 strategies (Bakker and Milinski 1991; Milinski and Bakker 1992; Forsgren 1997; Reid
111 and Stamps 1997).

112

113 During mate search animals often utilize communication signals wherein, typically,
114 individuals of one sex use signals produced by the other sex to localize and evaluate
115 mates. Consequently, in long-range communication for mate attraction, the ecology of
116 signalers and the sensory physiology of receivers can profoundly affect mate
117 sampling strategies. The extent of time spent signaling and movement during
118 signaling can constrain the time window of female mate search, since some of the
119 ‘comparison-based’ strategies require the female to revisit an already sampled male.
120 Relative spacing of signalers determines the amount of movement involved in female
121 mate search. Therefore, the optimal mate sampling strategy will vary depending upon
122 the energetic and predation costs of female mate search, and the relative spacing of
123 males. Moreover, signal intensity determines the extent of broadcast of a signal and
124 its effect on receiver response to the signal can be critical (Parker 1983; Kotiaho and
125 Puurtinen 2007). The number of signalers that a female can simultaneously perceive
126 is determined by the degree of overlap between the broadcast areas, which in turn
127 depends on the relative signal intensities and spacing of signaling males (Forrest and
128 Raspet 1994; Murphy and Gerhardt 2002). Neither theoretical models nor empirical
129 research of mate sampling strategies, however, have incorporated relevant sensory
130 ecological information of the communication system.

131

132 Lack of simultaneous availability of information on the ecology of signalers in wild
133 populations and the sensory physiology of responders has severely constrained our
134 understanding of the ecological effects on mate sampling strategies. Elaborate
135 experimentation on the auditory sensory physiology of acoustic signal reception and
136 detailed characterization of structurally simple acoustic signals in orthopterans and
137 anurans provide potential model systems to explore the aforementioned questions
138 (Gerhardt and Huber 2002). Empirical studies on female mate sampling strategies in
139 some species of crickets have however been conducted under laboratory conditions
140 mainly using playback experiments, rendering them difficult to interpret in a natural
141 context since rejection of loudspeakers may not imply rejection of calling males
142 (Wiegmann 2000; Wagner Jr. et al. 2001; Beckers and Wagner Jr. 2011). More
143 conclusive are field studies in anurans, where females were observed to mate with the
144 first encountered male closest to the female position (Murphy and Gerhardt 2002;
145 Meuche et al. 2013). Since the closest males are also likely to be the loudest at the
146 female position, a lack of measurement of signal intensity in these studies limits the
147 interpretation of the role of acoustic signals in female mate sampling. Song intensity
148 is particularly pertinent because it is well established to play a critical role in female
149 phonotactic response, and can override female preferences for other call features
150 (Stout and McGhee 1988; Castellano et al. 2000; Nandi and Balakrishnan 2013).

151

152 Previous studies on the ecology of callers and the effect of sensory physiological
153 mechanisms on female phonotaxis behaviour, proffers the field cricket species
154 *Plebeigryllus guttiventris* as a suitable model system for exploring female mate
155 sampling (Mhatre and Balakrishnan 2006; Nandi and Balakrishnan 2013). *P.*
156 *guttiventris* males can form dense choruses where individual callers maintain their

157 calling site within a night (Mhatre and Balakrishnan 2006), but move frequently
158 across multiple nights of calling, with inconsistent calling activity across the calling
159 nights (Nandi and Balakrishnan 2016). Moreover, callers are also consistent in the
160 different acoustic features of their calling songs within a night of calling activity
161 (Nandi and Balakrishnan 2013). These facts suggest that the time window available to
162 females for sampling mates is more likely to be limited to the calling period of males
163 within a night. Results based on playback experiments in this species further
164 demonstrate that the calling song sound pressure level (SPL), a measure of signal
165 intensity, profoundly affects female phonotaxis behaviour and overrides female
166 preference for faster calls (Mhatre and Balakrishnan 2007; Nandi and Balakrishnan
167 2013). Females approach the sound source that is louder at the female position and
168 not at source (Mhatre and Balakrishnan 2008). Moreover, females do not approach
169 the closest sound source, demonstrating the dominant role of signal intensity over
170 source proximity in female evaluation of mates (Mhatre and Balakrishnan 2008).
171 Models based purely on the auditory physiology of females were able to accurately
172 predict phonotactic trajectories of female approach, further illustrating the dominant
173 role of calling song SPL in female phonotaxis behaviour (Mhatre and Balakrishnan
174 2007, 2008).

175

176 Despite the considerable impact played by signal intensity across all the different
177 sensory modalities of communication, studies on mate sampling strategies have
178 seldom investigated their effects (Kotiaho and Puurtinen 2007). According to the
179 ‘passive attraction’ model, signal intensity directly affects the mating success of the
180 signaler by attracting more females (Parker 1983). However, the likelihood of
181 localizing high intensity signalers will depend on whether a female evaluates signal
182 intensity at the female position or at source and also on the extent of overlap between

183 the broadcast ranges of the signalers. Searchers may also increase their fitness by
184 mating with more intense signalers if signal intensity indicates male quality. For
185 instance, in *P. guttiventris* male calling song SPL in *P. guttiventris* has high
186 repeatability and is the only calling song feature that correlates positively with male
187 body size (Nandi and Balakrishnan 2013). Therefore searchers may adopt active
188 sampling strategies that maximize the likelihood of mating with high intensity
189 signalers, to overcome the constraints imposed by their sensory physiology and the
190 ecology of the communication system.

191

192 In this study, we investigated female mate sampling strategies, with a combination of
193 simulations based on natural distributions of male calling SPL and relative spacing,
194 and experiments on calling males and searching females in their natural habitat, using
195 *P. guttiventris* as a model system. In the simulations, we compared costs and benefits
196 of using passive attraction with those of active sampling strategies, under the sensory
197 ecological constraints of the communication system. In the experiments we
198 specifically asked whether females reject males based on their calling song SPL at
199 source in order to infer the possible mate sampling strategy that females use.

200

201 **Methods**

202 *Field site and animals*

203 All field work was conducted in privately-owned agricultural fields near the village
204 Ullodu, in the Chikballapur district of the southern Indian state of Karnataka
205 (13°38'48.81" N, 77°42'45.23" E), with consent and permission of the owners. In the
206 period between February and May from 2010 to 2013, all the observations and
207 experiments were conducted between 1900 and 2200 hours, the peak calling period of
208 male *P. guttiventris*. These were either collected from the field population as nymphs

209 close to their last instar (n =14) or were from a laboratory culture (n =19) that has
210 been maintained since 2008 and outbred with individuals from the wild population at
211 regular intervals of approximately a year (Nandi and Balakrishnan 2013).

212

213 *Male spacing and calling song SPL*

214 Data on spatial location of males and their calling song SPL measurements were
215 collected for a total of 11 choruses in the field. Choruses were identified by acoustic
216 sampling of the natural habitat, tracking individual callers and confirming calling
217 behaviour of males visually. Habitat patches were specifically selected where male
218 callers aggregate spatially for many nights. All calling males within a chorus were
219 identified and their calling sites were marked with caller ID-annotated flags. Calling
220 song SPL of all the callers was measured at 20 cm in front of the caller (referred to as
221 calling song SPL at source) at an angle of 90° with respect to the raised wings, using a
222 Brüel & Kjør ½" microphone, Type 4189 (20 Hz to 20 kHz) and a Sound Level
223 Meter, Type 2250 (Brüel & Kjør, Naerum, Denmark) set at fast root mean squared
224 (RMS) time weighting. Distances of the marked calling sites from a few centrally
225 located reference points and the angles subtended were measured using a meter tape
226 and survey precision compass mounted on a tripod (Survey Compass 17475780, error
227 ±0.5°, conceptualized by Francis Barker and Sons Ltd., sold and serviced by
228 Lawrence and Mayo, India). These distances and angles were used to generate the
229 Cartesian co-ordinates of individual calling sites for all the choruses using custom-
230 written scripts in Matlab version 7.11.0 (R2010B) (Math-Works, Natick, MA,
231 U.S.A.).

232

233 *Mate sampling simulations: General*

234 Simulations based on caller spacing in natural choruses, corresponding call SPL and
235 female phonotactic rules, were used to compare the performance of different mate
236 sampling strategies. All the simulations were performed in Matlab version 7.11.0
237 (R2010B) (Math-Works, Natick, MA, U.S.A.). Calling male spacing data from 11
238 natural choruses were used to generate chorus maps containing the Cartesian co-
239 ordinates of the callers and the corresponding call SPLs were used generate their
240 broadcast area (area around a calling male where the sound signal is audible to a
241 female). The broadcast area was estimated as a circle with the caller at the center and
242 the radius being determined by the distance at which the calling song SPL attenuates
243 to the mean female hearing threshold (40 dB SPL re 2×10^{-5} N/m²) in this species
244 (Mhatre and Balakrishnan 2006).

245

246 At the initiation of a simulation, virtual females were assigned positions randomly
247 within a circular area, with a radius of 20 m that was derived from the summation of
248 the maximum distance of callers from a central reference point across all the eleven
249 choruses and the maximum broadcast radius of the callers. The area of this circle,
250 encompassing all the callers within a chorus with their acoustic broadcast ranges, was
251 used as the sampling space for females (Fig. S1). Once assigned a position, it was
252 assessed whether the female could hear any of the callers by comparing the linear
253 distances (d_{fm}) between the female position and the callers with that of their
254 respective broadcast radii (br_m). If the linear distances were greater than the broadcast
255 radii of all the callers ($d_{fmi} > br_{mi}$ for all i), then the female was considered to be
256 outside the broadcast area of any caller. If $d_{fmi} < br_{mi}$ then the female could hear
257 the i^{th} male.

258

259 A female followed a random walk outside the signal broadcast area with a speed that
260 varied stochastically for every step within a run, with a mean movement of 0.1
261 m/minute and a standard deviation of 40 percent of the mean. After every five
262 seconds, the female position was assessed to check if it lay within the broadcast area
263 of any caller as described above. If the female was within the broadcast area of a
264 male, she approached that male (center of the circle) with a speed of 0.07 m/minute
265 (based on the mean time taken by a female to reach a male in the field phonotaxis
266 experiment).

267

268 A female could hear multiple males at certain spatial co-ordinates where the broadcast
269 areas of two callers overlapped. In such scenarios, a female approached the male that
270 was louder at its position if the difference in SPLs between the callers was more than
271 3 dB at the point of evaluation, or else the female chose randomly between the callers
272 that it could hear. The evaluation of louder callers was repeated four times while the
273 female was on its path towards the louder male to ensure that females had more than
274 one opportunity to evaluate the louder caller.

275

276 *Mate sampling simulations: Strategies*

277 A female was given a maximum of 180 minutes (3 hours) to sample males which was
278 based on previous observation of peak calling activity in wild populations of *P.*
279 *guttiventris* and low across-night calling site fidelity (Nandi 2016). In those 180
280 minutes a female evaluated male calls every five seconds, leading to 2160 evaluation
281 steps. After localizing a male, a female's mating decision was dependent on the
282 sampling strategy that it employed. In the simulations females were tested on five
283 different sampling strategies:

284

285 ‘*Random Sampling*’ (*RS*): A female mated with the first male encountered (spatial
286 proximity of less than 5 cm with the male) while moving randomly. In this strategy,
287 females did not evaluate males based on their calling song and hence did not show
288 phonotaxis and consequently the outcome is essentially based on random movement
289 of the females.

290

291 ‘*Fixed Threshold*’ (*FT*): Females sampled males based on their calling song SPL and
292 mated with a male only if its calling song SPL was greater than the threshold value,
293 which was set at the mean (77.2 dB) of the SPL distribution measured previously for
294 this *P. guttiventris* population (Nandi and Balakrishnan 2013). If the calling song SPL
295 was less than the threshold, the female continued its mate search either until it found a
296 caller with calling song SPL above the threshold or exhausted the maximum sampling
297 time.

298

299 ‘*One-step decision*’ (*OS*): This strategy was similar to the ‘fixed threshold’ strategy,
300 except the threshold declined as a function of increasing costs (time of searching).

301 The calling song SPL threshold (I_{th}) was assumed to be a function of time spent
302 searching (t) given by the equation $I_{th} = a + be^{-ct}$ where a , b and c are constants.

303 The starting threshold (at $t = 0$) was chosen to be the maximum SPL for the range of
304 calling song SPLs pooled across all the 11 choruses, instead of the population mean to
305 discount for the subsequent decay in mate quality (Real 1990). The slope of the curve
306 was selected such that the threshold declined steeply to the mean SPL value after
307 sampling for 22% of the time window available for sampling ($t = 0.22 \times 180$) to
308 ensure minimal rejection of mates based on the higher thresholds. The curve was
309 made to asymptote at the minimum value of the SPL range.

310

311 '*Best-of-n*' (BN): Females sampled a maximum of 5 males or for 180 minutes and
312 mated with the male with the highest calling song SPL at source. In this strategy a
313 female was allowed to mate only if it sampled more than one male ($n > 1$). Females
314 mating with a male after having sampled just that male ($n=1$), is similar to 'passive
315 attraction'. The minimum requirement of sampling more than one male in case of
316 'best-of-n' was therefore necessary to distinguish it from 'passive attraction'.

317

318 '*Passive attraction*' (PA): Females mated with the first male that they localized based
319 on the calling song SPL at female position and never rejected any male.

320

321 The number of females for a given run of the simulation was kept the same as the
322 number of calling males in the chorus (sex ratio = 1:1), for all the five sampling
323 strategies. The entire process was iterated a hundred times for each of the five
324 sampling strategies in 11 choruses. In every iteration, the initial co-ordinates of the
325 females were varied randomly.

326

327 Benefits to females employing each of the sampling strategies were assessed in terms
328 of the probability of mating and the probability of mating with a louder male. The
329 probability of mating was calculated by dividing the number of females that mated by
330 the total number of females used in the simulations using a particular strategy within a
331 chorus. The probability of mating with a louder male was calculated by dividing the
332 number of females that mated only with males which were louder than mean calling
333 song SPL by the total number of females. To compare the costs to females using
334 different sampling strategies, sampling time, defined as the time expended by a
335 female in finding a mate, was calculated for every female that found a mate in each of
336 the iterations. The number of males sampled before choosing a mate was also

337 calculated for each of the females that found a mate following the three active
338 sampling strategies (FT, OS, BN).

339

340 *Mate sampling simulations: exploring the input parameter space*

341 The initial conditions and values of different parameters in the simulation could affect
342 the relative performance of the females using different mate sampling strategies.

343 Increasing the rate of movement of females and time window available for sampling
344 and decreasing the area of sampling can enhance a female's likelihood of

345 encountering potential mates. Since different sampling strategies depend variably on

346 the encounter rates, the relative performance of the sampling strategies may vary in

347 consequence. Therefore, time available for sampling, rate of female movement and

348 the area of sampling were varied systematically to investigate the effect of these input

349 parameters. The simulations described above were repeated, increasing the sampling

350 time available for females from the initial 3 hours (180 minutes) to 6 hours (180×2

351 minutes) and 9 hours (180×3 minutes), separately. Simulations were also run for each

352 of these three sets, with a higher rate of female movement outside the broadcast areas

353 with a mean of 1 m/minute and a standard deviation of 40 percent of the mean.

354 Therefore, there were two sets with different rates of female movement, 'slow

355 females' (0.1 m/minute) and 'fast females' (1 m/minute). The six sets of simulations

356 (3 time windows for sampling × 2 rates of female movement) were repeated with a

357 reduced area of sampling. In the 'Small' area sets, circles were constructed for each of

358 the choruses separately, with radii estimated as the sum of the maximum distance of a

359 caller from the centroid of the chorus and its corresponding broadcast radius for a

360 given chorus (range of area reduction: 10-95%, Fig. S1). Therefore, the simulations

361 were conducted separately for a total of 12 parameter combinations.

362

363 *Mate sampling simulations: Statistical analyses*

364 The main objective of our analyses was to compare and contrast the benefits and costs
365 between females using ‘passive attraction’ and the active sampling strategies. P-
366 values estimated under the frame-work of ‘null hypothesis tests’ can lead to biased
367 interpretations when the sample sizes are very high particularly in the context of
368 simulations (White et al. 2014). Instead, estimations of effect sizes and confidence
369 intervals have been argued as a more appropriate alternative to ‘null hypothesis
370 testing’ (Nakagawa and Cuthill 2007) and were consequently used to interpret our
371 simulation results. All statistical analyses were conducted using R version 3.3 (R
372 Development Core Team 2014). The effect sizes for the probability of mating and the
373 probability of mating with a louder male were estimated as the median of the
374 bootstrapped pairwise differences between the probabilities for females using ‘PA’
375 strategy and other active sampling strategies over 1000 iterations, for every chorus
376 separately. The effect sizes for the sampling time were estimated as the mean
377 difference between the bootstrapped means of sampling times across choruses for
378 females using ‘PA’ strategy and other strategies. 95 percent confidence intervals were
379 estimated using the bootstrapped distributions with 1000 iterations. Confidence
380 intervals not overlapping zero imply a less than 5 percent likelihood of observing the
381 difference by chance alone.

382

383 *Mate sampling experiment*

384 This experiment was designed to test whether female crickets actively reject some
385 callers in favor of others and if so, to distinguish between the mate sampling strategies
386 in use. The experimental design had to ensure that the female crickets be presented
387 with the best chance of rejecting a male i.e. scenarios where the females were most
388 likely to approach a male with a suboptimal trait value while simultaneously

389 perceiving the presence of another male. Pairs of male *P. guttiventris* calling males
390 were located in the field such that the distance between them was less than a meter to
391 ensure female's perception of both males simultaneously (Mhatre and Balakrishnan
392 2006). After measuring calling song SPL at source, a pair was selected for the
393 experimental trial only if one of the callers called at an SPL less than the mean SPL
394 (77.2 dB) of the population except in 4 trials (where both were higher). If multiple
395 pairs of callers were located within a night, the pair with the least distance between
396 the two callers or maximum relative SPL difference at source was selected for
397 experimentation. The relative SPL of male calling song at the female release position
398 was calculated using the known attenuation profile of *P. guttiventris* calling song in
399 the habitat (Mhatre and Balakrishnan 2006). Two CCTV cameras were deployed to
400 monitor the calling activity of males throughout the duration of the experiment, which
401 were connected to a laptop via a DVR system placed at a distance of more than 7 m
402 from the callers. The experiment was initiated 5-10 minutes after setting up the CCTV
403 cameras to ensure minimal disruption in calling activity.

404

405 Virgin females, aged 10 to 13 days after the final molt (see Supplementary Material
406 for details), were released approximately 40 cm from the caller with the lower calling
407 song SPL at source (1st male) such that the release point was collinear with the two
408 callers and the 1st male was louder at the female position than the 2nd male (louder at
409 source). Once released, the female was followed using either an IR-sensitive video-
410 camera or by eye under red light from a distance to ensure minimal disruption of its
411 movement. Female approach to a calling male was confirmed by two observers, one
412 directly observing the females and the other observing CCTV transmission of male
413 activity on the laptop. Female mating was confirmed either by female mounting
414 behaviour followed by male-female coupling and subsequent transfer of the male

415 spermatophore, when the mating behaviour took place outside the cracks in the
416 ground from which the males were found calling, or by relocating the female with a
417 spermatophore attached when matings took place inside the cracks. The experimental
418 observation was continued until the unmated male stopped calling or the mated
419 female walked away from the calling males. In trials where there was no mating after
420 phonotaxis, observations were continued until the males stopped calling or the female
421 walked away from the chorus.

422

423 *Remating experiment*

424 Laboratory experiments were conducted on *Plebeiogryllus guttiventris* females to
425 investigate the probability of remating and the time taken since the first mating to do
426 phonotaxis and remate. In the first set, single-speaker playback and mating trials were
427 conducted on the same females for at least five consecutive nights after the first
428 mating. In an independent second set, females were tested in the same experimental
429 paradigm with a latency of a week from the first mating for two weeks. Laboratory
430 bred females between the age of 11-17 days since the final moult were used for these
431 experiments. All experimental trials were conducted inside an anechoic chamber.

432 Phonotactic and mating behaviors were recorded using an IR sensitive video camera
433 (Sony, DCR TRV 17-E, Sony Corporation, Japan) under external infrared lights.

434

435 A female was released 50 cm from a speaker that played out a typical *P. guttiventris*
436 call with mean song parameter values appropriate for that temperature (25° C). The
437 SPL at the female release position was ensured to be at 61 dB (typical SPL value at 50
438 cm from the source in the field) using a Brüel & Kjær Sound Level Meter, Type 2250
439 with a ½" microphone, Type 4189. Females were presented with a conspecific male
440 after showing a phonotaxis response, defined as reaching within 5 cm from the

441 speaker or within 10 minutes from the initiation of the trial when phonotaxis response
442 was absent. The mating trials were conducted in a sponge cube of 35.5 cm x 35.5 cm
443 x 30 cm with a cylindrical hole of diameter 15 cm and depth 15 cm in the center. A
444 mating trial was scored as negative only if the male courted and the female did not
445 mount the male after 10 minutes from the start of the mating trial. A female was
446 exposed to a new male for the subsequent trials. Identical experimental methodology
447 was followed for the two different sets.

448

449 *Ethical Note*

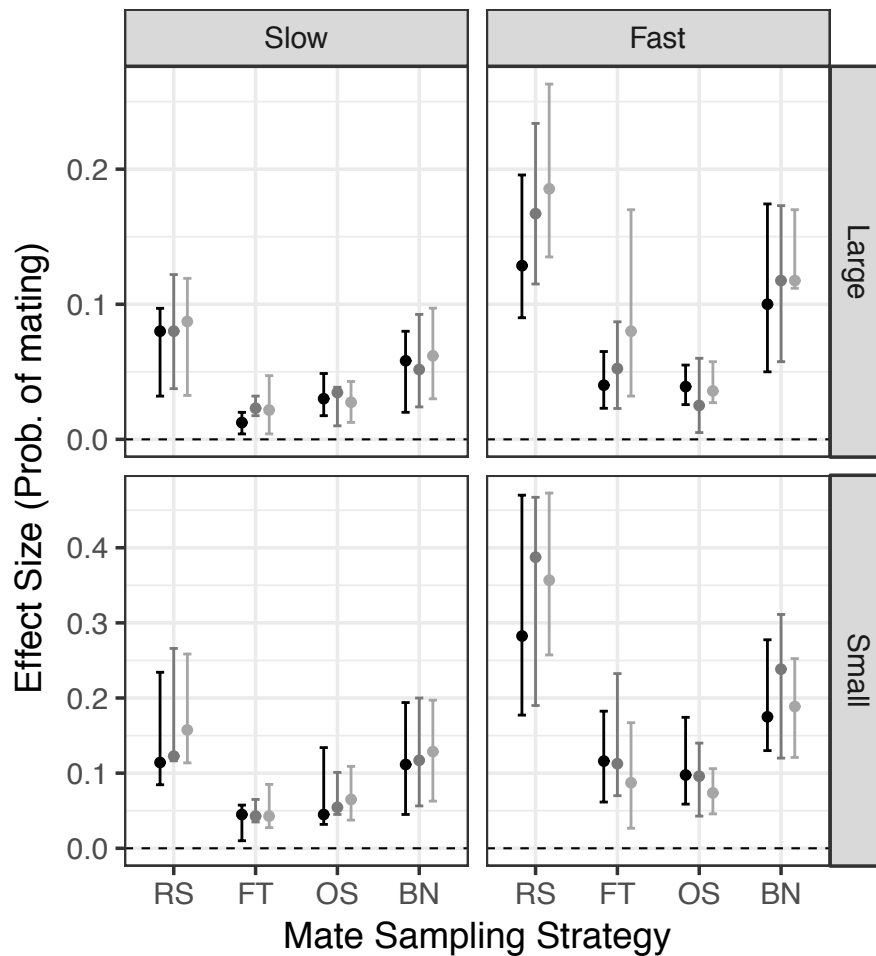
450 All the SPL measurements, spatial data collection and animal handling for the
451 behavioral experiments were as per the national guidelines for the ethical treatment of
452 animals.

453

454 **Results**

455 *Mate sampling simulations*

456 The choruses sampled in the field varied in the number of callers (4-13) and nearest
457 neighbour distances between callers (Fig. S2). The effect sizes for the probability of
458 mating was significantly greater than zero for all the comparisons across the different
459 simulation sets and therefore implies that the females using ‘passive attraction’ were
460 the most likely to mate (Fig. 1). Despite low magnitude of effect sizes, the percentage
461 change was considerable even for comparisons with the fixed-threshold strategy
462 (ranging from 15.6 % to 37.9 %) which yielded the least difference (Fig. 1 and Fig.
463 S3). The relative performance of different sampling strategies did not change across
464 the different treatments of time window for sampling and sampling area within the
465 ‘Fast’ and ‘Slow’ female sets (Fig. S3).



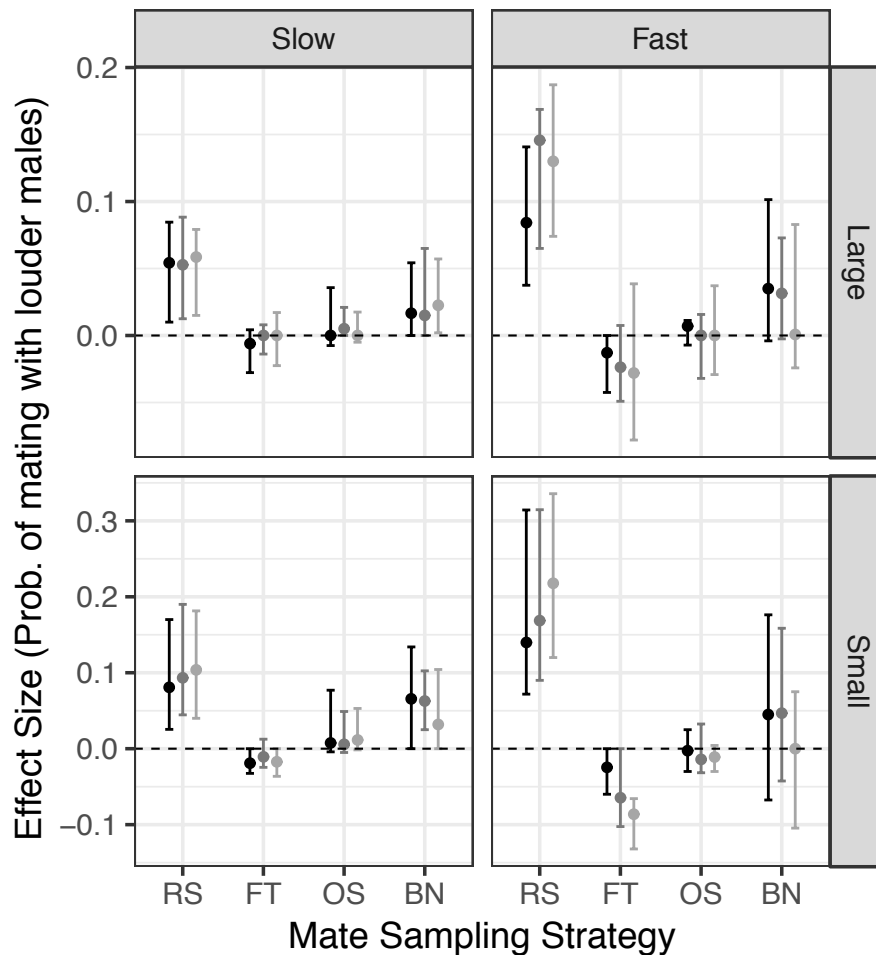
466

467 Figure 1. Effect sizes of the probability of mating. The circles and the error-bars
 468 represent the medians and confidence intervals of the bootstrapped distributions of the
 469 pairwise differences (choruswise) in the probability of mating between ‘passive
 470 attraction’ and the other sampling strategies. Black = 3 hours, Grey = 6 hours, Light
 471 grey = 9 hours time window available for sampling. RS = Random sampling; FT =
 472 Fixed-threshold; OS = One-step decision, BN= Best-of-n. ‘Large’ = Large Area,
 473 ‘Small’= Small Area.

474

475 The probability of mating with a louder male for females using the ‘passive attraction’
 476 strategy did not significantly differ from those using the active sampling strategies
 477 (Fig. 2). Only the ‘Fast’ females with 9 hours sampling time window in ‘Large’ area
 478 using ‘Fixed-threshold’ strategy yielded significantly higher values than ‘passive

479 attraction' (Fig. 2). Comparisons with the 'best-of-n' strategy yielded significantly
480 positive effect sizes only in 2 out of 12 scenarios, despite higher magnitudes in the
481 rest of the sets (Fig. 2 and Fig. S4).



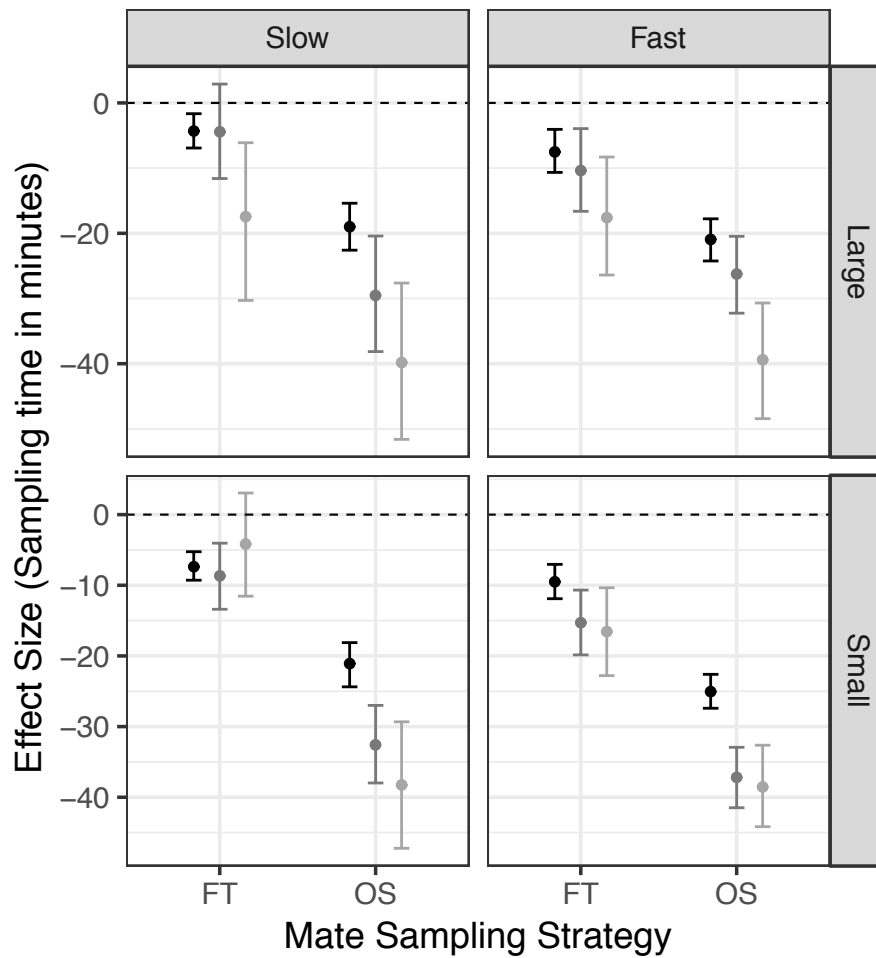
482

483 Figure 2. Effect sizes of the probability of mating with a louder male. The circles and
484 the error-bars represent the medians and confidence intervals of the bootstrapped
485 distributions of the median pairwise differences (choruswise) in the probability of
486 mating with louder males between 'passive attraction' and the other sampling
487 strategies. Black = 3 hours, Grey = 6 hours, Light grey = 9 hours time window
488 available for sampling. RS = Random sampling; FT = Fixed-threshold; OS = One-
489 step decision, BN= Best-of-n. 'Large' = Large Area, 'Small'= Small Area.

490

491 Females using the ‘best-of-n’ strategy utilized the entire time window available for
492 sampling, consequently spending the maximum time searching for mates across all
493 the sets (Fig. S5). In absence of acoustic cues, females that searched for mates
494 randomly (“RS”) also spent more time searching for mates compared to other
495 strategies (Fig. S5). Effect sizes significantly lower than zero in comparisons between
496 the ‘passive attraction’ and the threshold strategies (‘FS’ and ‘OS’) in most of the
497 simulation sets implies that females spent the least time searching for mates while
498 using ‘passive attraction’ (Fig. 3). Only in 2 out of 12 scenarios, the time spent
499 sampling for females using the ‘fixed-threshold’ strategy did not significantly differ
500 from that of ‘passive attraction’ (Fig. 3). Females using ‘passive attraction’ could
501 reduce their sampling time by a minimum of 10 % when compared to the threshold
502 strategies. Most of the ‘Slow’ and ‘Fast’ females (> 75%) sampled only one male
503 before mating while using ‘fixed-threshold’ and ‘one-step decision’ strategies (Fig. 4
504 and Fig. S6). Females using the ‘best-of-n’ strategy could sample more males with
505 increasing the rate of movement, time window for sampling and in the smaller
506 sampling area (Fig. S6).

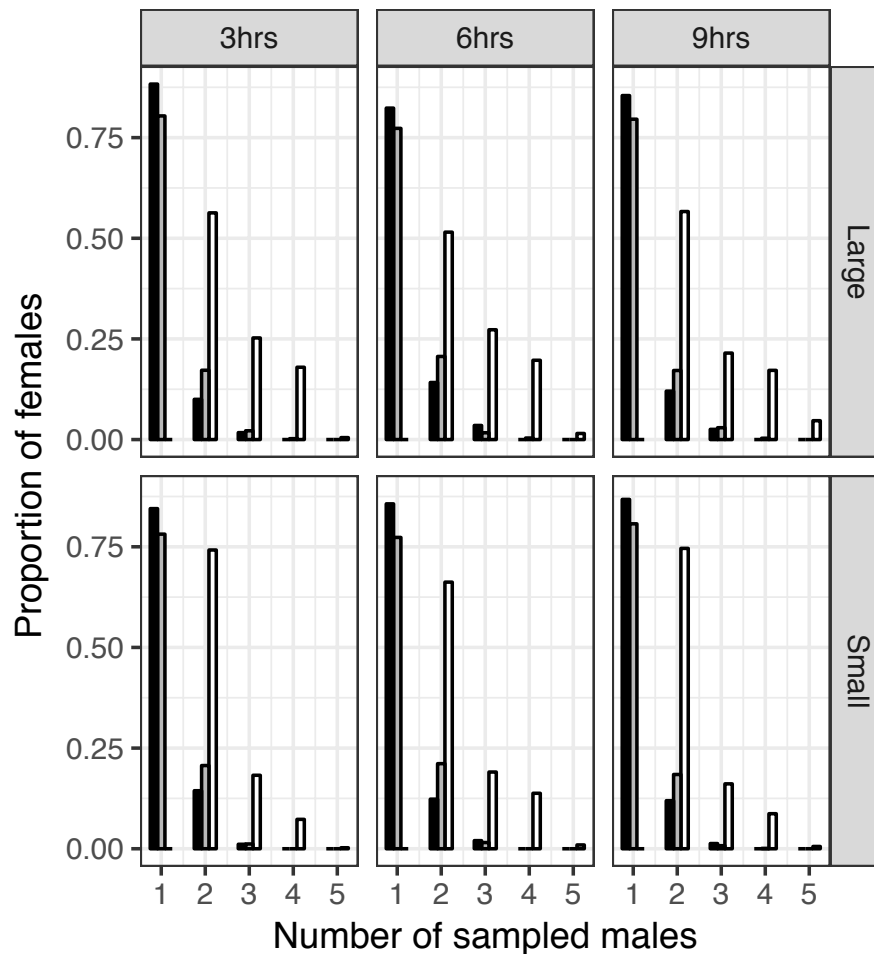
507



508

509 Figure 3. Effect sizes of the time spent sampling for females that mated. The circles
510 and the error-bars represent the means and confidence intervals of the distributions of
511 the mean differences in the time spent sampling between ‘passive attraction’ and the
512 threshold strategies, as estimated by bootstrap sampling. FT = Fixed-threshold; OS =
513 One-step decision. ‘Large’ = Large Area, ‘Small’= Small Area.

514



515

516 **Figure 4:** Proportion of sampled males. Relative frequency distribution of the number
517 of males sampled by females that were successful in mating, using each of the three
518 active sampling strategies for ‘Slow’ females. Black = 3 hours, Grey = 6 hours, White
519 = 9 hours of time window available for sampling.

520

521 The probability of mating while using ‘passive attraction’ was higher than both the
522 ‘fixed-threshold’ and ‘one-step decision’ strategies despite lowering the thresholds
523 (Fig. S7a). The magnitude of the difference (effect size) however diminished on
524 reducing the threshold. The difference in the probabilities of mating with a louder
525 male between ‘passive attraction’ and ‘fixed-threshold’ strategies remained
526 insignificant even after lowering the threshold (Fig. S7b). However, on reducing the

527 starting threshold, ‘Slow’ females using ‘one-step decision’ strategy were more likely
528 to mate with a louder male than females using ‘Passive Attraction’ (Fig. S7b).

529

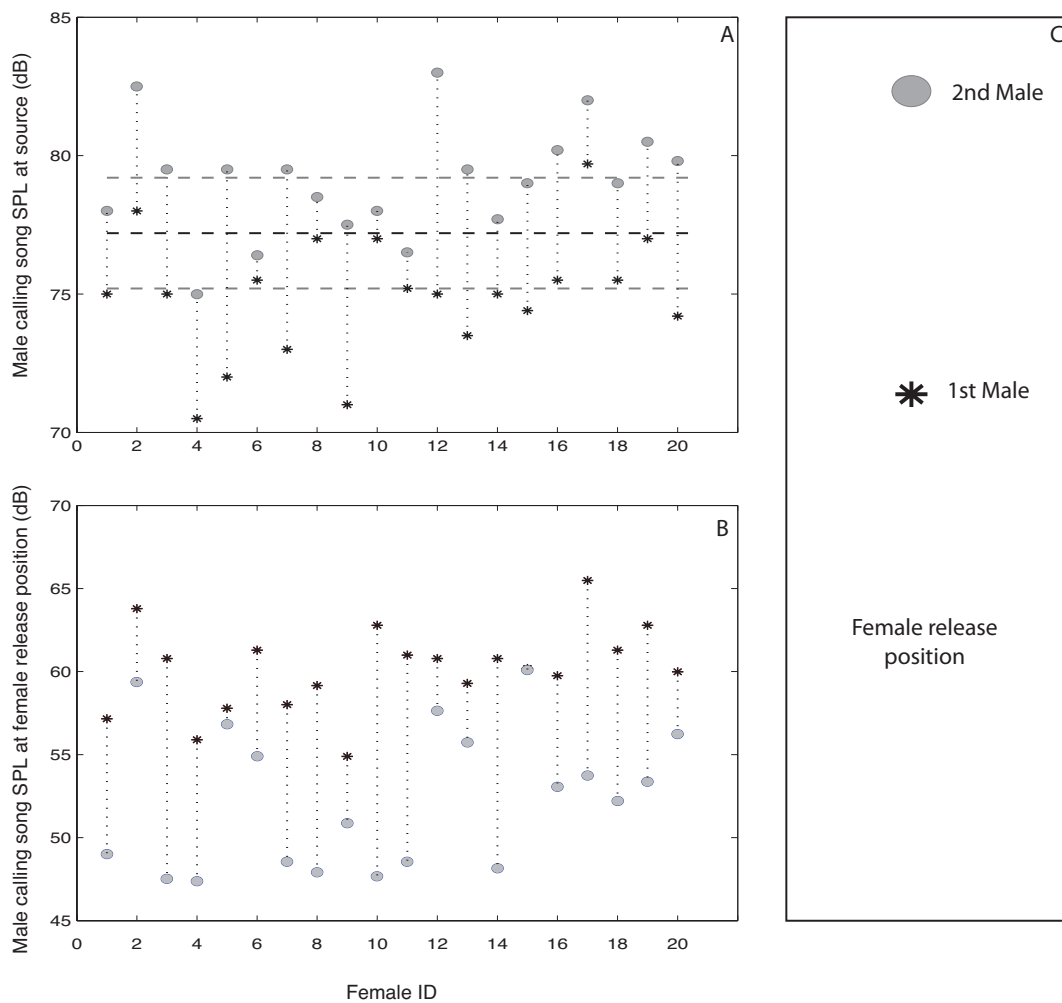
530 *Mate sampling experiment*

531 Ten out of 33 trials were dropped because in five of them the females did not show
532 phonotaxis, in two trials the second male had stopped calling by the time of first
533 mating and in three trials matings could not be confirmed. In the remaining 23 trials,
534 a significant majority (20) of the females mated with a male after showing phonotaxis
535 (Chi square test: $\chi^2 = 12.56$, $P = 0.0004$). None of the females approached the second
536 male after localizing the first male, even in cases where they did not mate with the
537 first male (3/23 trials). Thus, females predominantly mated with the first male they
538 localized and never approached the second caller. Both the laboratory bred ($n = 11$)
539 and wild caught females ($n = 9$) followed the same strategy of mating with the first
540 male approached irrespective of their nymphal growth conditions.

541

542 Out of the 20 trials in which matings were observed, all females mated with the first
543 male approached despite their calling at a lower SPL (at source) than the second male
544 (Fig. 5a) (*Exact binomial test*: $P < 0.0001$). Only in two out of 20 trials was the male
545 that the female mated with the one that called at an SPL higher than the population
546 mean of the SPL distribution (Fig. 5a) (*Exact binomial test*: $P = 0.0004$). In ten out of
547 the 18 trials where the first male called at an SPL below the population mean, the
548 calling song SPL was even lower than one standard deviation below the mean (Fig.
549 5a). Both the males were audible to females in all the 20 trials as their calling song
550 SPL at the female position was higher than the phonotactic hearing threshold of 40 dB
551 (Fig. 5b). Moreover, the first male was louder than the second male at the female
552 release position in all the trials (Fig. 5b).

553



554

555 **Figure 5:** Female mating in relation to male calling song SPL. Calling song SPL of
556 the pair of males per trial (A) at source and (B) at the female release position, in each
557 of the 20 trials where matings were observed. Within a trial, the 1st male is denoted by
558 a star and the 2nd male by a filled circle. The mated males are denoted by an asterisk.
559 The pair of males tested in a trial is joined by a vertical dotted line. The horizontal
560 black dashed line marks the mean call SPL of the population with the standard
561 deviation on either side represented by gray dashed lines. (C) A diagrammatic
562 representation illustrating the positions of first and second males relative to the female
563 release position

564

565 *Remating experiment*

566 In the first set, out of the 27 females that mated as virgins, 11 (40.7 %) remated at
567 least once when tested on six consecutive days. In the second set, out of 21 females
568 that mated as virgins, 11 (52.4 %) remated at least once when tested on two
569 consecutive weeks. The modal value of latency between the first and the second
570 mating (refractory period) across days was one day (Table S1). In the second set,
571 females remated after a week's refractory period (Table S1). Only 1 (9.1 %) and 2
572 (18.2 %) out of independent sets of 11 mated females showed phonotaxis before
573 remating. Therefore, the probability of showing phonotaxis prior to remating was
574 significantly lower than that of a virgin and does not increase with increasing time
575 since the last mating (1/11 mated versus 14/27 virgin in the first set: $\chi^2 = 4.33$, $P =$
576 0.038; 2/11 mated versus 14/21 virgin in the second set: $\chi^2 = 4.99$, $P = 0.026$).

577

578 **Discussion**

579 *'Passive attraction' as an optimal search strategy: simulations*

580 Among all the different sets of simulations, 'Slow' females with a sampling window
581 of 3 hours in a 'Large' area of sampling is the ecologically most relevant scenario in
582 the case of our study system, the field cricket *P. guttiventris*. Females responding to
583 an acoustic signal in the field moved at a speed comparable with the 'Slow' females.
584 Hence, females are unlikely to move faster outside the signal broadcast area unless
585 they fly (which is rarely observed). Calling activity within a night is usually limited to
586 a peak period in most acoustically communicating species and callers may change
587 their calling site across multiple nights as has been demonstrated in certain species of
588 crickets (Ritz and Köhler 2007; Nandi and Balakrishnan 2016). In such scenarios the
589 sampling period of females is likely to be limited by the calling activity period within
590 a night.

591

592 In the ecologically relevant simulation set ('Slow' females with 3 hours sampling
593 window in 'Large' area), females using 'passive attraction' were most likely to mate.
594 The probability of mating depends on the rate of encounters between the searching
595 female and the signaling male. Performance of active sampling strategies depends
596 more heavily on encounter rates as they rely on sampling more males. However, even
597 after relaxing the values of parameters such as rate of female movement, sampling
598 window and sampling area, to increase encounter rates, females using 'passive
599 attraction' performed significantly better than other active sampling strategies in
600 terms of mating probability. Moreover, even after a reduction of the threshold
601 criterion for 'fixed-threshold' and 'one-step decision' strategy, females following
602 those strategies failed to match the performance of 'passive attraction'

603

604 While probability of mating indicates the efficiency of finding mates, probability of
605 mating with louder males indicates fitness benefits, as call SPL is assumed to be
606 correlated with fitness (Nandi and Balakrishnan 2013). By definition, active sampling
607 strategies are expected to yield higher probability of mating with louder males, due to
608 the threshold criterion for selection or comparison of SPLs at source (Janetos 1980;
609 Real 1990; Gibson and Langen 1996). In the simulations, however, active sampling
610 strategies could not outcompete 'passive attraction' with respect to mating with a
611 louder male. Increasing the encounter rates by relaxing the values of the input
612 parameters, such as 'Fast' females or longer sampling durations (9 hours) or lower
613 initial threshold, did lead to an enhanced performance of active sampling strategies
614 but still failed to perform better than 'passive attraction' in most cases. In burrowing
615 field crickets, callers are known to maintain their calling site across multiple nights
616 and therefore allow females to sample for longer durations (Forrest and Green 1991;

617 Rodríguez-Muñoz et al. 2010, 2011). Dense choruses can also provide a smaller area
618 of sampling. However, our simulations demonstrate that, even after reducing the
619 ecological constraints, active sampling strategies based on acoustic cues rarely
620 outperform ‘passive attraction’ in finding a mate with higher fitness.
621
622 In the simulations, among the active sampling strategies, ‘best-of- n ’ was severely
623 affected by the ecological constraints. Females using the ‘best-of- n ’ strategy could not
624 sample more than 4 males, the optimal n , due to the constrained time window
625 available for sampling and restricted female movement relative to the spatial
626 separation between callers. The suboptimal sampling opportunity led to diminished
627 performance. This result mirrors the consequences of incorporating costs into the
628 analytical models of active mate sampling, leading to suboptimal performance of the
629 ‘best-of- n ’ sampling strategy (Real 1990; Dombrovsky and Perrin 1994; Wiegmann et
630 al. 1996).
631
632 Females that succeeded in mating using ‘passive attraction’ took the least time to find
633 mates since any encounter with a mate always guaranteed a mating, unlike in active
634 sampling strategies. Time optimization can be critical to a sampling strategy,
635 considering the possible costs such as energetic expenditure, time investment and
636 increased exposure to predation (Real 1990). Search costs have been empirically
637 shown to play an important role in mate sampling behaviour in both vertebrates and
638 invertebrates (Milinski and Bakker 1992; Wickman and Jansson 1997; Byers et al.
639 2005; Kasumovic et al. 2007; Berger-Tal and Lubin 2011). The costs of mate
640 searching could thus lead to the use of a strategy that not only maximizes the
641 probability of finding mates with better quality, but also reduces the time spent
642 searching.

643

644 In the simulations, females using either an active sampling strategy or ‘passive
645 attraction’ always approached a caller guided by their auditory physiology.
646 Furthermore, females using the ‘fixed-threshold’ and ‘one-step decision’ strategies
647 were as likely to mate with a louder male as while using ‘passive attraction’, thus
648 suggesting a mechanistic similarity. This similarity is corroborated by the fact that
649 even in the threshold strategies, females predominantly mated with the first
650 approached male, thereby reducing the requirement of their behavioural rules. Thus
651 our simulations demonstrate that the physiological rule of approaching males louder
652 at the female position can be sufficiently beneficial to females without employing
653 active mate sampling strategies. Therefore, females using ‘passive attraction’ based
654 purely on well-established physiological rules of sound localization (Mhatre &
655 Balakrishnan, 2008) performed optimally across all the different sets of the
656 simulations.

657

658 *Female mate sampling strategies: experimental results*

659 The fact that females approached only one of the males in all experimental trials and
660 never rejected a male in favour of the other male, indicates that they were not using a
661 ‘best-of-n’ strategy, which requires a certain number of males to be sampled before
662 choosing a mate (Janetos 1980; Real 1990; Gibson and Langen 1996; Wiegmann et
663 al. 1996). If females were using male calling song SPL at source as thresholds to
664 evaluate potential mates, then mated males should have called at an SPL higher than
665 the population mean (Janetos 1980; Real 1990). However, 90% of the males that the
666 females mated with called at SPLs lower than the mean population SPL and 50% of
667 the males called at SPLs even lower than one standard deviation below the mean SPL.
668 Thus, virgin females of *P. guttiventris* are unlikely to be using either of the threshold

669 strategies. The results of our experiments instead suggest that female mating decisions
670 are dictated by evaluation of male calling song SPL at female position and not at
671 source, that is, females are using the ‘passive attraction’ strategy. A critical distinction
672 between active mate sampling strategies and ‘passive attraction’ is the rejection of
673 some potential mates over others (Parker 1982, 1983). In this study, a small
674 proportion (13.6%) of females did not mate with the first male they approached, but,
675 importantly, these females never approached the second male. Theoretical models of
676 female phonotaxis as well as empirical studies of phonotaxis, particularly in this
677 species, have demonstrated the importance of relative SPL difference at the female
678 position in determining female approach to sound sources (crickets and anurans:
679 Forrest and Green 1991; Forrest and Raspet 1994; *P. guttiventris*: Mhatre and
680 Balakrishnan 2007, 2008). In this study we show that virgin females not only localize
681 males that are louder at the female position but also mate with them, and do not
682 actively sample calling males before deciding to mate.

683

684 Mating status could potentially affect the mate sampling strategy employed by
685 females by making them choosier after the first mating. A mated female would invest
686 in mate search only when the benefits of a second mating exceed the costs incurred by
687 searching for males. In the laboratory experiments, *P. guttiventris* females remated, at
688 times, when males were offered in close proximity, but rarely responded
689 phonotactically. This implies that mated females, despite their motivation to remate,
690 are rarely using male acoustic signals to search for potential mates. Moreover,
691 latencies after mating, which were more than sufficient to induce remating, did not
692 increase the likelihood of phonotaxis. The lack of phonotaxis prior to mating therefore
693 raises pertinent questions regarding the importance of male calling song for mated
694 females. In a few pilot trials (n =5) of the mate sampling experiment in the field with

695 mated females, females did not approach either of the callers, despite being tested
696 after the latency period from their first mating. Our results, therefore, suggest that
697 mated females are unlikely to use a mate sampling strategy based on acoustic
698 sampling of potential mates and points to differences in mating strategies between
699 virgin and mated females that merit further investigation.

700

701 **Conclusion**

702 A simulation framework incorporating information on natural distributions of calling
703 song SPL and male spacing, and the physiology of female phonotaxis behavior,
704 enabled an ecologically relevant comparison of female sampling strategies. ‘Passive
705 attraction’ to the advertisement signal emerged as an optimal solution to mate search
706 when ecological factors such as male spacing, female movement and total time
707 available for sampling constrained sampling strategies. Moreover, in experiments
708 using calling males in the wild, we demonstrate that virgin *P. guttiventris* females use
709 passive attraction rather than an active sampling strategy to search for mates. ‘Passive
710 attraction’ could possibly be a general female mating strategy in acoustically
711 communicating animals considering the sensory ecological constraints of the
712 communication system (Murphy and Gerhardt 2002; Meuche et al. 2013). Future
713 studies on mate sampling, both theoretical and experimental, should therefore
714 consider incorporating information on the sensory physiology of receivers and the
715 ecology of signalers.

716

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857

858 **Appendix**

859 *Materials*

860 *Animal maintenance*

861 The collected nymphs were maintained individually in plastic boxes (14 × 10 × 5 cm)
862 with moistened cotton wads and fed *ad libitum* with juvenile dog food (Pedigree,
863 Mars India Pvt Ltd.) and Calcium Sandoz (Novartis India Ltd.). The date of their final
864 moult was noted down and the adult was maintained in the same container till the end
865 of the experimental trial. For the set from the culture, male and female nymphs were

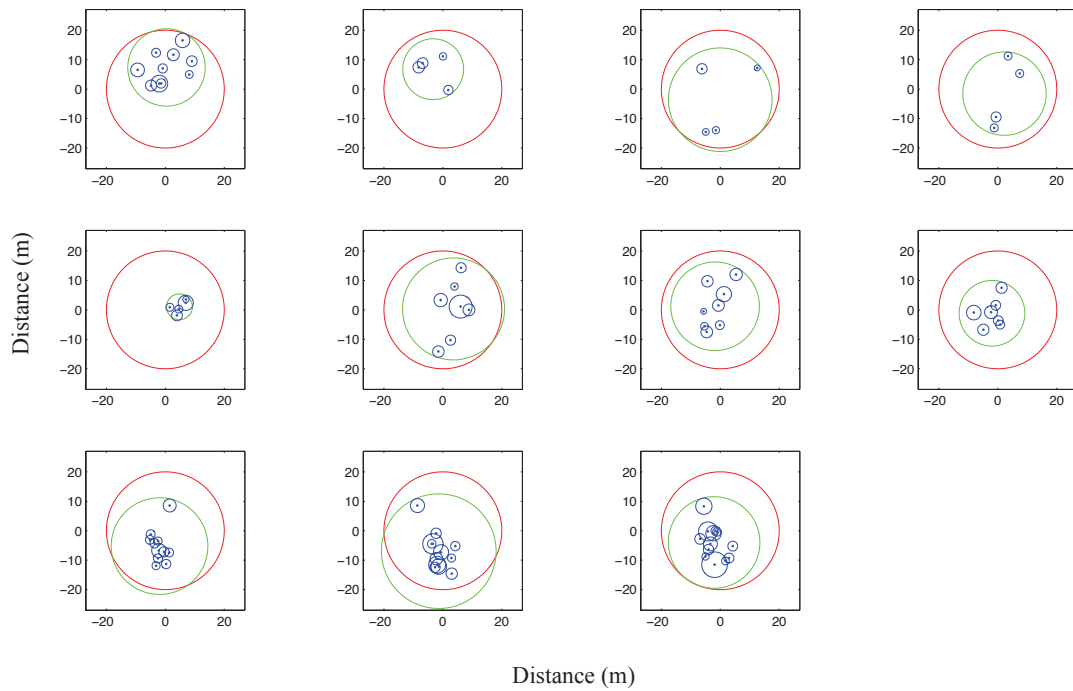
866 maintained separately in 50-litre plastic barrels. Female nymphs were transferred to
867 similar plastic boxes as described above on the day of their moulting into adults. All
868 the females were marked on their pronotum with unique colour codes using a
869 nontoxic paint marker (Edding 780, Edding, St Albans, U.K.) for individual
870 identification.

871

872 *Varying threshold parameters in the simulations*

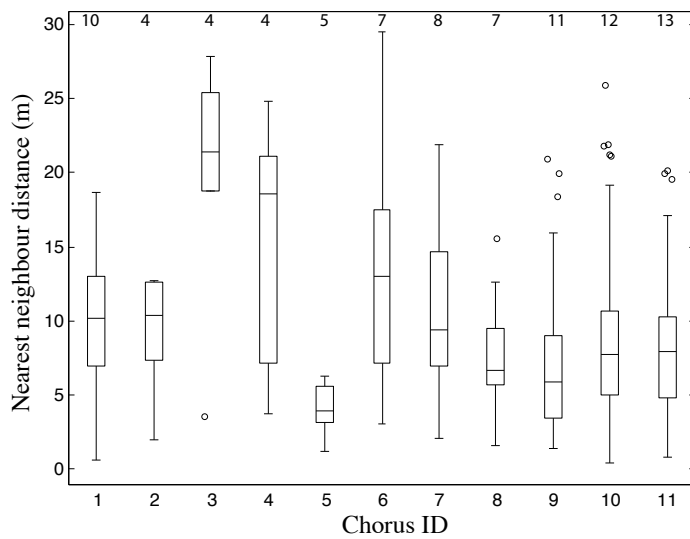
873 A lowering of the threshold SPL for females following the threshold strategies could
874 increase the probability of mating for active sampling strategies relative to passive
875 attraction. To investigate the effect of varying thresholds on the performance of
876 females using threshold strategies, two sets of simulations were conducted separately.
877 In the first set, the threshold criterion for females using the fixed-threshold strategy
878 was reduced from mean SPL to 1 SD below the mean SPL for simulations with both
879 ‘Fast’ and ‘Slow’ females with 3 hours time window for sampling in the ‘Large’
880 sampling area. In the second set, the initial threshold for females using one-step
881 decision strategy was reduced to the mean SPL for simulations with both ‘Fast’ and
882 ‘Slow’ females with 3 hours time window for sampling and in the ‘Small’ area of
883 sampling.

884 *Figures*



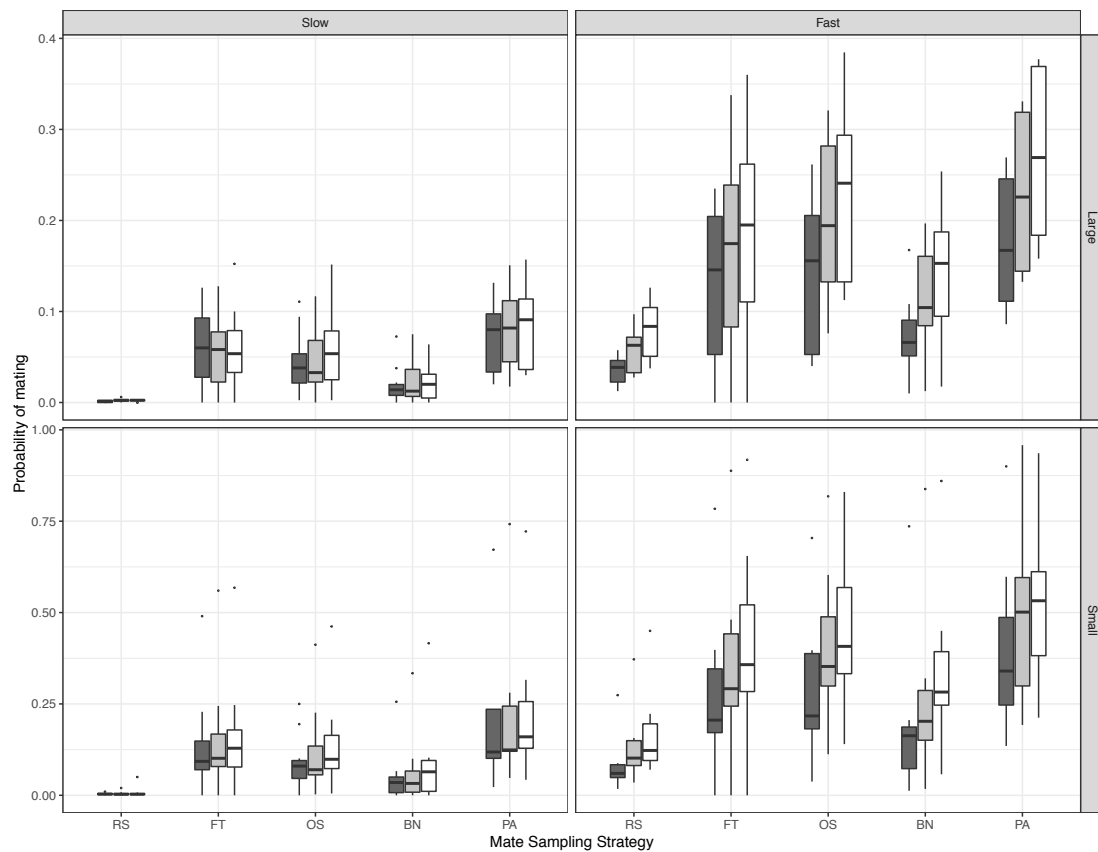
885

886 **Figure A1.** Chorus maps and sampling area. The red and the green circles represent
887 'Large' and 'Small' sampling area respectively for each of the 11 choruses. The blue
888 dots and circles represent the position and broadcast area of callers.



889

890 **Figure A2.** Distributions of nearest neighbor distances of the 11 choruses which were
891 used in the simulations. The number at the top of each boxplot corresponds to the
892 number of callers in the chorus.
893

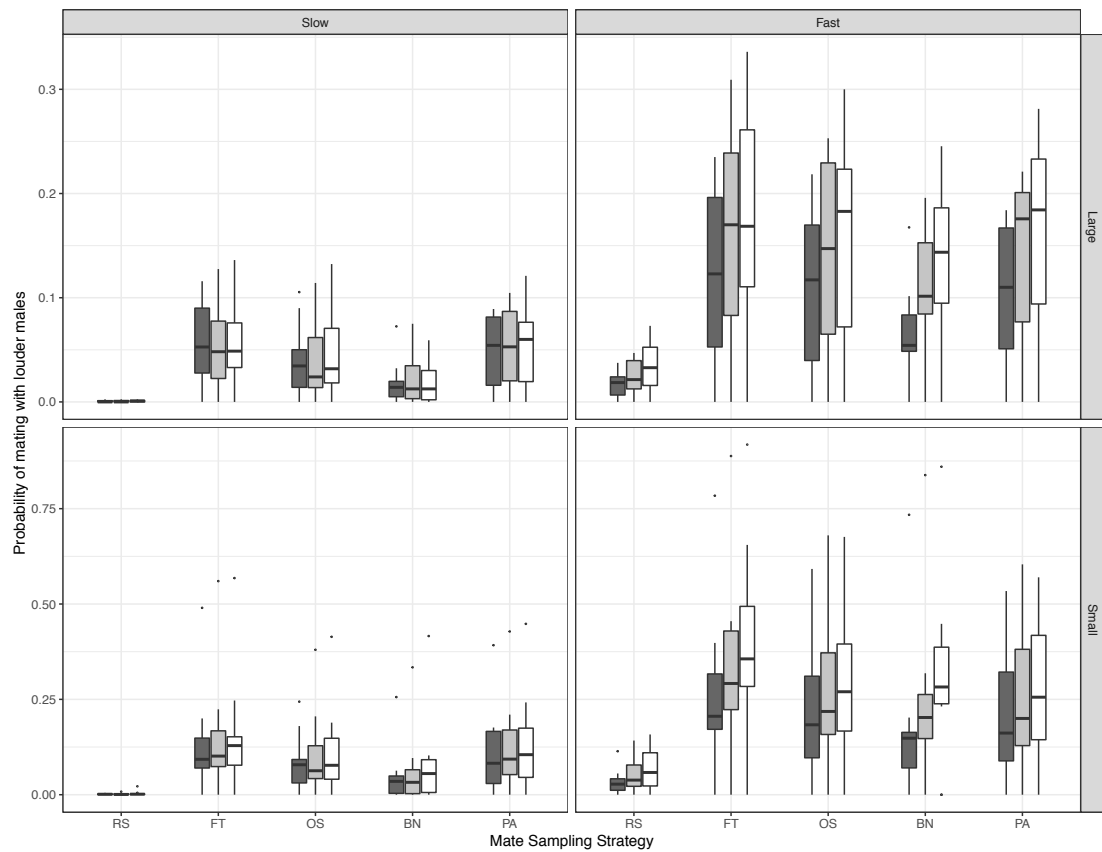


894
895 **Figure A3:** Probability of mating for different mate sampling strategies. The
896 probability of mating for a female using each of the different mate sampling strategies
897 across all the simulation sets. Grey = 3 hours, Light grey = 6 hours, White = 9 hours
898 time window available for sampling. RS = Random sampling; FT = Fixed-threshold;
899 OS = One-step decision, BN= Best-of-n, PA= Passive attraction. 'Large' = Large
900 Area, 'Small'= Small Area

901

902

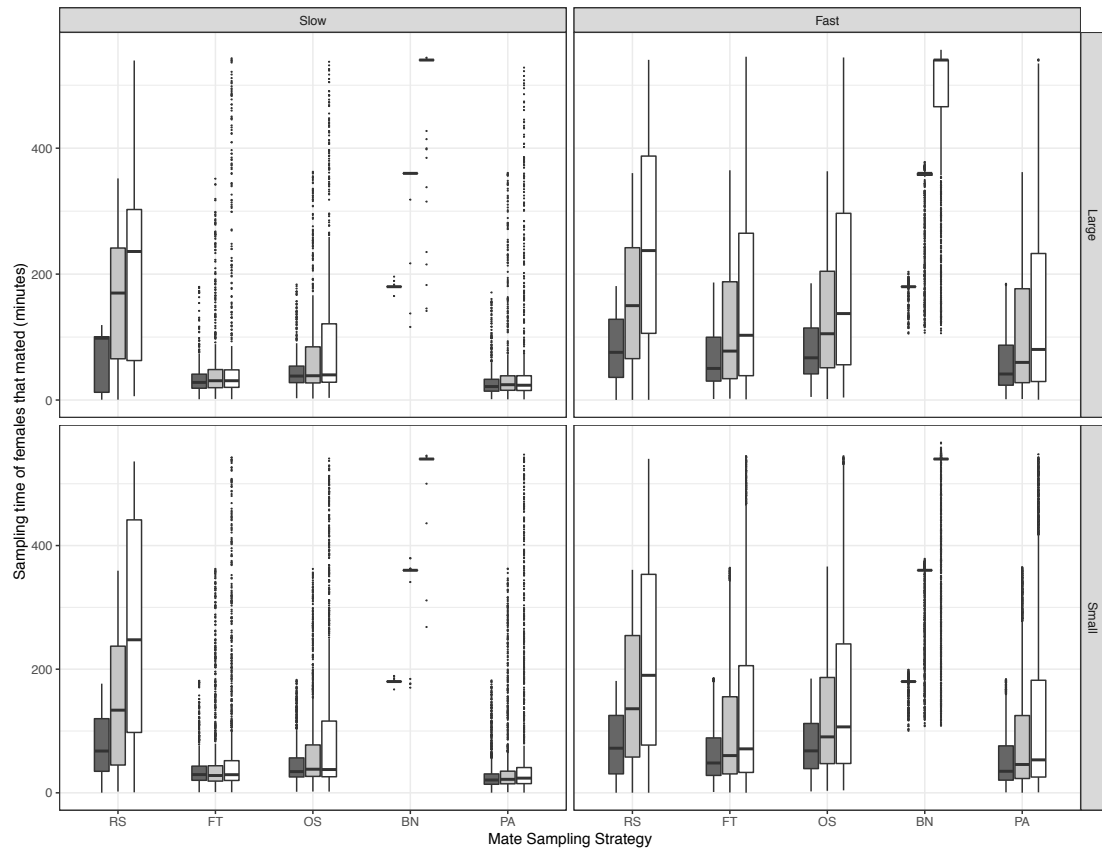
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904

905 **Figure A4:** Probability of mating with a louder male for different mate sampling
906 strategies. The probability of mating with a louder male for a female using each of the
907 different mate sampling strategies across all the simulation sets. Grey = 3 hours, Light
908 grey = 6 hours, White = 9 hours time window available for sampling. RS = Random
909 sampling; FT = Fixed-threshold; OS = One-step decision, BN= Best-of-n, PA=
910 Passive attraction. 'Large' = Large Area, 'Small'=Small Area

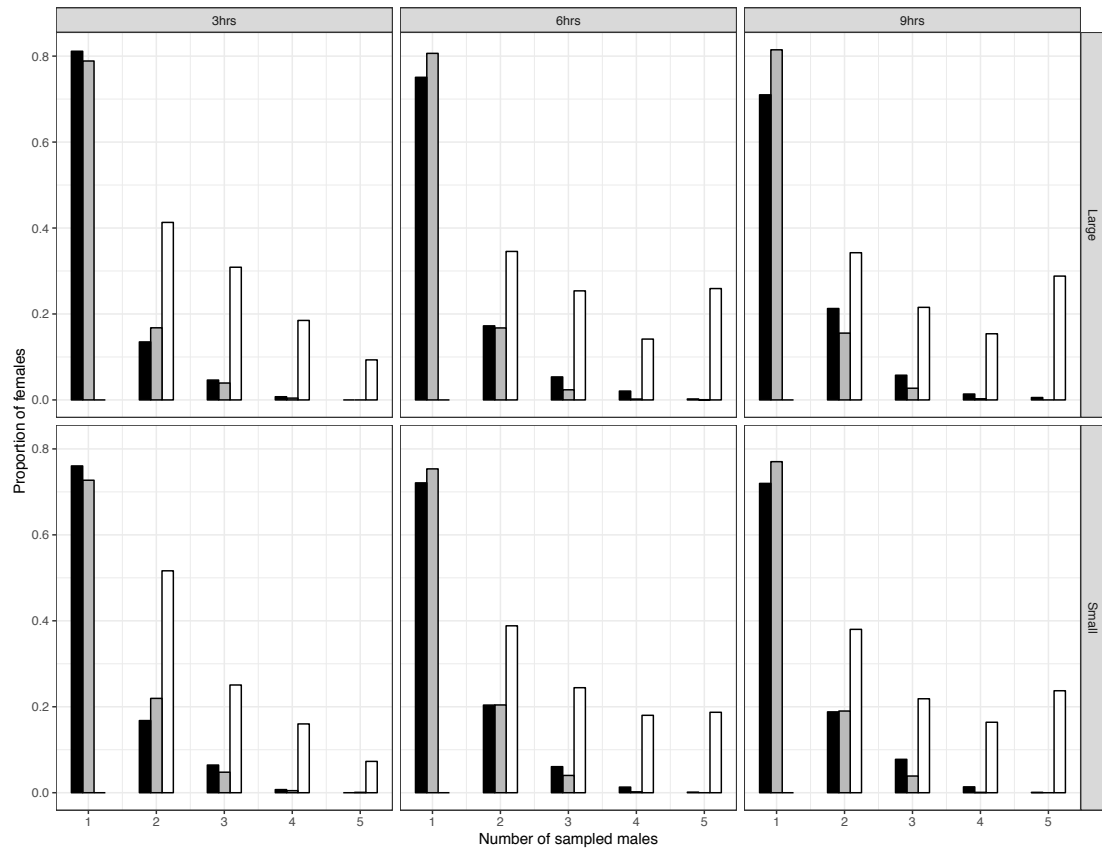
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912

913 **Figure A5:** Costs of different sampling strategies. Distribution of sampling time of
914 females successful in mating within the sampling window, using each of the five mate
915 sampling strategies across all the simulation sets. Grey = 3 hours, Light grey = 6
916 hours, White = 9 hours time window available for sampling. 'Large' = Large Area,
917 'Small' = Small Area

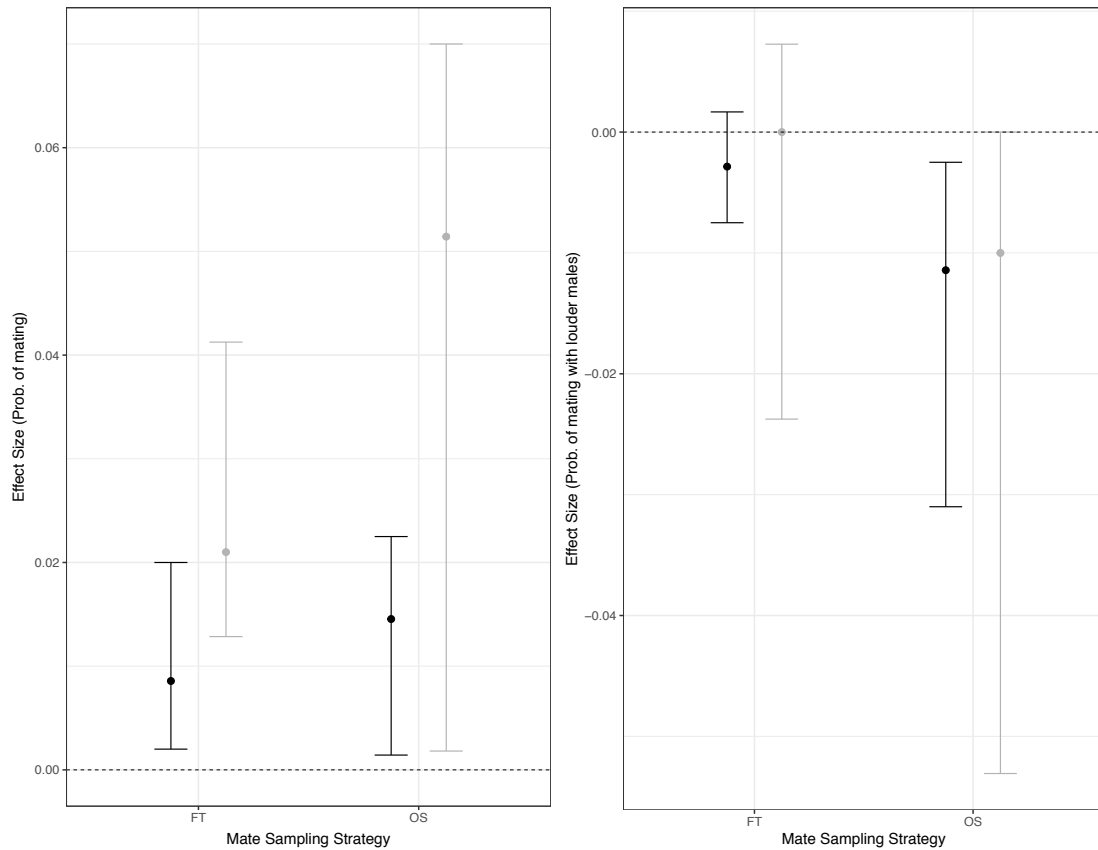
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919

920 **Figure A6:** Number of sampled males. Relative frequency distribution of the number
921 of males sampled by females that mated using each of the three active sampling
922 strategies (FT = Fixed-threshold; OS = One-step decision, BN= Best-of-n), for 'Fast'
923 females across the different simulation sets. Black = 3 hours, Grey = 6 hours, White =
924 9 hours of time window available for sampling. 'Large' = Large Area, 'Small'= Small
925 Area.

926



927

928 **Figure A7:** Effects of reducing the threshold criterion. The circles and the error-bars
 929 represent the medians and confidence intervals of the bootstrapped distributions of the
 930 median pairwise differences (choruswise) in the (a) probability of mating and (b)
 931 probability of mating with louder males between ‘passive attraction’ and the threshold
 932 strategies with reduced thresholds. The black and grey colours represent ‘Slow’ and
 933 ‘Fast’ females respectively. FT = Fixed-threshold; OS = One-step decision.

934

935 **Table A1.** Latency of second matings across the two sets of remating experiments. In
 936 the first set 4 females were followed only for 5 days.

1 st Set		2 nd set	
Latency (in days)	Number of females	Latency (in weeks)	Number of females
1	5	1	11
2	1	2	0

3	2
4	2
5	1
6	0

937