

Leave me alone: solitary females attract more mates in a nocturnal insect

Short title: Lone females attract more males

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1 **Abstract**

2 Spatial distributions of sexual competitors and potential mating partners have a large
3 impact on sexual selection and mating systems. Typically, such effects are investigated
4 with regard to male aggregations. However, females may also need to compete for
5 mating opportunities. Here we investigated consequences of clustering and rival
6 attractiveness on female mate attraction success under field conditions in a nocturnal
7 beetle, the common glow-worm, *Lampyrus noctiluca*. We placed dummy females of
8 two glow intensity (attractiveness) levels either alone or in clusters of varying
9 attractiveness compositions. We found that by displaying alone rather than in a cluster,
10 females have a higher probability of mating and greater potential to exercise mate
11 choice. Within clusters, females of both attractiveness levels had the highest probability
12 of mating when having neighbours of only the less attractive type. These results show
13 that both the presence and attractiveness of rivals can strongly influence females' mate
14 attraction. The findings also suggest that the typical distribution of glowing females in
15 the wild is better explained by female than male benefits. Hence, the results highlight
16 the important links between spatial distribution of females, male mate searching and
17 sexual selection.

18

19 **Keywords:** aggregation, bioluminescence, female competition, neighbour effect, sex
20 role, sexual selection

21 INTRODUCTION

22 Spatial clustering of both potential mates and sexual competitors is a key factor in the
23 distribution of mating success within populations. In particular, spacing of individuals
24 impacts both the tactics for mate searching (and sampling) and the intensity of
25 interactions between rivals (Emlen and Oring 1977; Ims 1988; Andersson 1994). In this
26 respect, the consequences of spatial distribution of sexual signallers may differ
27 depending on their attractiveness. For example, some empirical studies suggest that
28 when mates are located farther apart (or otherwise in a lower density), their mating
29 success is distributed more evenly, which may benefit less ornamented sexual signallers
30 (Palokangas et al. 1992; Shelly and Bailey 1992; Berglund 1995; Kokko and Rankin
31 2006; Dougherty and Shuker 2015). However, under a different set of circumstances,
32 less attractive individuals may benefit from forming a cluster (see Adams and Morse
33 2014; van Wijk et al. 2017) for example due to attraction of potential mates by a cluster
34 being more important than attractiveness of individuals within the cluster. In males,
35 mating success benefits from clustering may result in impressive lek aggregations
36 (Beehler and Foster 1988; Gibson et al. 1990).

37 Within a cluster, an individual's success may also depend on the attractiveness of its
38 neighbours. For example, comparatively unattractive individuals might benefit from
39 close associations with more attractive signallers due to an increased number of visits
40 by members of the opposite sex (Beehler and Foster 1988; Partecke et al. 2002), which
41 also increases the potential of weaker signallers to "steal" matings from attractive rivals
42 (Gross 1996). An alternative hypothesis asserts that by associating with comparatively
43 unattractive rivals, an individual might benefit by increasing its relative attractiveness to
44 prospective mates (Bateson and Healy 2005). For instance, larger fiddler crab, *Uca*

45 *mjoeberti*, males may increase their mating success if managing to associate with
46 smaller neighbours (Callander et al. 2011).

47 To date, our understanding of the consequences of clustering or neighbour attractiveness
48 on the distribution of matings has largely been based on lekking species, in which large
49 clusters of males gather together. In contrast, less is known about the role of clusters
50 and signalling neighbourhoods in species that do not form leks and especially when
51 females compete with other females for mate attraction. Such situations may arise
52 especially when reproducing using only stored resources, i.e. in capital breeders
53 (Houston et al. 2007). Due to the finite resources being traded-off between different
54 aspects of reproduction, capital breeding females may pay particularly high fecundity or
55 other fitness costs from prolonged sexual signalling or self-maintenance. Indeed, mating
56 quickly can increase their expected number of offspring (in Lampyridae: Wing 1989;
57 Hopkins 2018) and they may therefore need to actively attract mates and even compete
58 for matings, independent of whether their fitness increases with the number of matings.
59 Hence, capital breeding can result in increased variation in female reproductive success
60 and strong sexual selection on female traits related to mate attraction.

61 We assessed the roles of clustering and signalling neighbourhoods in mate attraction in
62 females of a nocturnal, capital breeding beetle, the common glow-worm, *Lampyrus*
63 *noctiluca*. In particular, we used dummy females in the field to assess the competing
64 hypotheses of benefits from clustering (as in leks: Beehler and Foster 1988; Gibson et
65 al. 1990) and the proximity of rivals impacting female mating success negatively (male
66 examples: Arak et al. 1990; Wong et al. 2018). In addition, we tested how attractiveness
67 of rivals affects the probability of attracting a mate and the potential for exercising mate
68 choice. We expected opportunities for mate choice to be highest for solitary females and

69 females with less attractive rivals. Finally, we hypothesised that if male body size
70 correlates with competitiveness (as in many species: Hunt et al. 2009), smaller males
71 may be more likely to target female clusters or less attractive females within such
72 clusters.

73

74 **MATERIALS AND METHODS**

75 **Study site and model species**

76 The study was conducted in the vicinity of Tvärminne Zoological Station, southern
77 Finland (59°50.7' N; 23°15.0' E), during the glow-worm breeding season (June - early
78 July) in 2019.

79 The common glow-worm is a nocturnal beetle species in which flightless females emit a
80 continuous greenish glow during calm summer nights to attract flying, non-glowing
81 males. Females that have a larger body size emit, on average, a brighter glow and are
82 also more fecund (Hopkins et al. 2015). A brighter glow, in turn, is expected to be more
83 efficient in attracting males (Hopkins et al. 2015). This is particularly relevant because
84 adult glow-worms do not eat (i.e. are capital breeders) and therefore need to use
85 resources gathered during the larval stage for reproduction. Any delays in mating
86 decrease female fecundity and are therefore likely to be highly costly to the female
87 reproductive success (Hopkins 2018). In other words, it should be advantageous for a
88 female to mate as soon as possible. While multiple males sometimes arrive within a
89 short period of time, and a majority of females succeed in attracting a mate during their
90 first or second night of displaying, considerably longer mating lags are not rare and
91 mating delays up to three weeks have been documented (Dreisig 1971; Tyler 2002;

92 Hickmott & Tyler 2011; personal observations). The female ceases to glow very soon
93 after succeeding to mate, typically with a single male, then lays her eggs and dies soon
94 after (Dreisig 1971; Tyler 2002; personal observations). Field observations suggest that
95 the successful male tends to guard the female until the morning (Tyler 2002; personal
96 observations), but it may potentially mate again at least during oncoming nights.
97 Glowing females are aggregated within good signalling habitats and areas, whereas
98 within such areas, their spatial distribution does not seem to be similarly aggregated. In
99 the local population, the distance between adjacent females was found to be an average
100 4 metres, >1 metre in 79% of the assessed cases, and ≤ 0.50 metres in slightly over 10%
101 of the cases (Borshagovski et al. 2019). The realised distances between signalling
102 females may be affected by e.g. the population size, behavioural interactions among
103 females, suitable spots for mate attraction, and egg-laying opportunities within the
104 habitat.

105 **Study design**

106 We tested female attractiveness with respect to different signalling neighbourhood
107 compositions in the field using dummy females that trapped males landing to mate. The
108 dummy females were constructed by slightly modifying the methods of Hopkins et al.
109 (2015). Briefly, each dummy female consisted of a plastic funnel trap (volume: ~1 litre)
110 that had a green 5 mm light emitting diode (LED) mounted on the top and in the centre
111 of the funnel's mouth (Figure 1a). The peak emission wavelength of the LED was ~560
112 nm, mimicking the glow of a live female common glow-worm (Tyler 2002; De Cock
113 2004), and it was powered by two standard AA dry batteries (Figure 1a). We
114 constructed dummy females of two brightness and hence expected attractiveness
115 (Hopkins et al. 2015) levels. The glow intensity of the brighter female type (hereon:
116 "B") was controlled by wiring the LED with one 1000 ohm resistor (resulting in the

117 peak glow intensity of $\sim 0.13 \mu\text{W}/\text{nm}$). Each dummy female of the dimmer type (hereon:
118 "D") had its LED wired with four 1000 ohm resistors (peak glow intensity: ~ 0.02
119 $\mu\text{W}/\text{nm}$). Such a difference in relative brightness is easily visible to a human observer
120 and reflects the range seen among wild females in the local population (personal
121 observations).

122 Each dummy female was placed either on its own (B: $n = 30$; D: $n = 30$) or in a cluster
123 of four dummy females that were placed in the formation of a quadrangle with 50 cm sides
124 (Figure 1b; $n = 57$ clusters that included 228 dummy females). To assess the effects of
125 different competitive neighbourhoods, we ran replicates with all possible combinations
126 of B and D dummy females. This allowed our female level analysis (see below for
127 details) to have the following four neighbourhood categories: no neighbours ($n = 60$),
128 all neighbours of the B type ($n = 56$), all neighbours of the D type ($n = 56$) and both
129 neighbour types present ($n = 116$; Figure 1).

130 There was no direct line of sight between any adjacent replicates and the minimum
131 distance between them was 100 metres. Each replicate lasted one night, and we ran ~ 1
132 replicate of each replicate type (range: 0 - 2) simultaneously, with the locations of
133 replicates relative to each other having been randomised using a random number
134 generator. The female dummies were set at 23:00 - 24:00 hours and then left out to
135 attract males for 130 - 180 minutes (depending on the night), which covered the entire
136 nightly glowing period of wild females and mate searching period of males at the
137 research site (personal observations). The surroundings of each replicate were checked
138 once or twice during the night to ensure that no other females were glowing in close
139 proximity. After a replicate was completed, the number of males trapped by the dummy
140 female was counted and, as a proxy of body size, the dorsal exoskeletal plate

141 (pronotum) width of each male was later measured in the laboratory using a calliper.

142 The males were then marked and released back to the wild.

143 The above data were used, as follows, to assess how clustering and competitive
144 neighbourhood affect females' probability of mate attraction (during their first night of
145 signalling), their potential to be choosy, and phenotypes (body sizes) of the attracted
146 males.

147 **Probability of attracting a mate**

148 We used R 3.3.2 software (R Development Core Team) for all statistical analyses. First,
149 we ran a generalised mixed models ('lme4' package) with a binomial distribution to
150 assess whether or not a dummy female had managed to attract at least 1 male, i.e. using
151 the presence of at least one trapped male (possible values: 0 / 1) as the response
152 variable. Dummy brightness (B / D) and neighbourhood category (solitary / all B
153 neighbours / all D neighbours / B and D neighbours present) were assigned as fixed
154 effects and "replicate ID" was added as a random effect to account for the non-
155 independence of dummy females within a replicate. We then proceeded with refitting
156 the model using χ^2 - tests (as per Crawley 2007). In this regard, if the interaction was
157 found to be non-significant, the main effects were assessed from a model fitted without
158 it.

159 **Potential to be choosy**

160 As a proxy of a (dummy) female's opportunity to be choosy, we used the number of
161 attracted males. This assessment was conducted among the subset of dummy females
162 that had attracted at least 1 male. Here we assumed a Poisson distribution ('lme4'
163 package) as appropriate for count data that is not overdispersed (assessed as per Zuur et

164 al. (2013)). We then applied the same fixed effects, a random effect, and refitting
165 procedure as described in the previous section.

166 **Male size**

167 With regard to male body size, we were interested in whether female clustering or
168 brightness affects the body size of attracted males. For example, if multiple males arrive
169 at the same time, small males might have higher chances of success when targeting less
170 attractive females or clusters of females (rather than solitary ones). Overall, the female
171 dummies captured 389 males. Of these, pronotum width data are missing for 9
172 individuals, 6 were recaptures from replicates run during previous nights and another 4
173 had been captured earlier (and then marked and released) in an unrelated experiment
174 conducted near the research station. All available data points were included in the data
175 analyses and the exclusion of the recaptures does not change the conclusions. We
176 applied a linear mixed effects model ('nlme' package) with male pronotum width as the
177 response variable and in other respects used the same variables and general approach as
178 described above.

179

180 **RESULTS**

181 **Probability of attracting a mate**

182 Overall, 47% (135 out of 288) of the dummy females, whether alone or in a cluster,
183 attracted at least 1 male. The interaction between female brightness and neighbourhood
184 type did not have a significant effect (mixed model, model comparison: $\chi^2 = 1.692$, $df =$
185 3 , $P = 0.64$). A dummy female was more likely to attract a male when it was brighter
186 (mixed model, $\chi^2 = 13.11$, $df = 1$, $P < 0.001$; Figure 2a). The neighbourhood also had a

187 significant effect on the probability of attracting a mate (mixed model, overall
188 neighbour effect: $\chi^2 = 15.50$, $df = 3$, $P = 0.0014$). In particular, mate attraction
189 probability was the highest for solitary females (solitary: 63% versus combined
190 probability for clusters: 43%, implying a significant difference at $\alpha = 0.01$), with the
191 probability being significantly lower in other neighbourhood types except for the one
192 with only D (dimmer) neighbours (Figure 2*b*, Table 1*a*). Within clusters, mating
193 probability was therefore the highest when the focal dummy female had only D
194 neighbours (Figure 2*b*, Table 1*a*) and it was the lowest when both types of neighbours
195 were present (Figure 2*b*, Table 1*a*).

196 **Potential to be choosy**

197 Regarding female dummies that attracted at least one male, the interaction effect
198 between brightness and neighbourhood category on the number of attracted males was
199 not significant (mixed model, model comparison, $\chi^2 = 3.084$, $df = 3$, $P = 0.38$). As with
200 the probability to mate, B dummy females attracted higher numbers of males than D
201 ones (mixed model, $\chi^2 = 7.763$, $df = 1$, $P = 0.0053$; Figure 3*a*). In addition,
202 neighbourhood had a significant effect on the number of attracted males (mixed model,
203 $\chi^2 = 32.33$, $df = 3$, $P < 0.001$; Figure 3*a*), with solitary females attracting a higher
204 number of males than any of the clustered neighbourhood types (Figure 3*b*, Table 1*b*)
205 and the different clustered neighbourhoods not significantly differing from each other
206 (Figure 3*b*, Table 1*b*). It is worth noting that the number of males attracted by clusters
207 of four with at least one successful dummy female (5.0 ± 0.6 [mean \pm SE], $n = 44$
208 clusters) was not significantly different from the number of males attracted by solitary
209 female dummies attracting at least one male (4.4 ± 0.6 , $n = 38$) (Wilcoxon rank sum test
210 with continuity correction, $W = 902$, $P = 0.54$). This conclusion remains the same if all
211 dummies (i.e. also non-successful ones) are included.

212 **Male size**

213 Body size of the attracted males did not significantly differ regarding any of the
214 assessed variables (Linear mixed model, all $P > 0.10$).

215

216 **DISCUSSION**

217 We found that, in accordance with the prior expectation (Hopkins et al. 2015), brighter
218 dummy females were more likely to attract males than dimmer ones. This effect was
219 independent of the neighbourhood types. Notably, independent of female brightness
220 (attractiveness), a higher percentage of solitary than clustered females attracted a mate,
221 with solitary females also attracting higher total numbers of males. The results also
222 show that when females are in clusters, their neighbourhood is important: female
223 success in attracting at least one mate was the highest when the neighbourhood only
224 consisted of females of the dimmer (D) category and it was the lowest when the
225 neighbourhood consisted of a mixture of both female types (B and D).

226 Some previous studies have suggested that males of non-lekking species should
227 advertise relatively far apart from their rivals. For instance in bushcrickets, *Tettigonia*
228 *viridissima*, males were less successful in attracting females when clustered than when
229 regularly spaced within an experimental arena (Arak et al. 1990). In the European tree
230 frog, *Hyla arborea*, the ability of mate sampling females to discriminate male acoustic
231 signals improved with increased separation of the speakers producing the male call
232 (Richardson and Lengagne 2010). These species, however, employ acoustic sexual
233 signals, which may be more prone to signal interference than species that rely mostly on
234 visual signals. Our results show that the benefit of physical distance from rivals does

235 apply also when females compete with other females for mating opportunities using a
236 visual signal. In particular, a larger proportion of glow-worm female dummies attracted
237 a male when alone than when in a cluster, with this effect being similar for females of
238 both brightness (attractiveness) levels. Among the females that succeeded in attracting a
239 male, solitary females attracted larger numbers of males than clustered females. Indeed,
240 the numbers of males attracted by four clustered female dummies together were not
241 significantly higher than those attracted by solitary female dummies, implying that the
242 benefits of solitary mate attraction are high in this system. We note the possibility that if
243 the local male density is exceptionally high, males might arrive in short enough
244 succession (before the female glow signal has faded) to sexually harass solitary females
245 especially.

246 In many systems, female reproductive success does not significantly increase with the
247 number of matings (e.g. Parker 2006). This is also likely to be the typical case in capital
248 breeders such as glow-worms, which nevertheless are likely to benefit from mating
249 quickly: mating delays can reduce their fecundity (Wing 1989; Hopkins 2018). The
250 result that solitary females mate quicker also helps to explain why females in the wild
251 are not more commonly clustered in smaller spatial scales. From the male perspective,
252 our results imply that a solitary female is more likely to attract rival males, inducing a
253 higher probability of failure to mate after finding a female due to male-male
254 competition. After mating, the glow-worm male usually guards the female (Tyler 2002;
255 personal observations), but a cluster of females might nonetheless provide the male
256 more opportunities to compare females or to mate with additional females later. If some
257 males are indeed able to remate later without getting markedly sperm depleted, for
258 females, the difference between signalling alone versus in a cluster may be smaller than
259 our results suggest. However, the scope for males to remate, at least during the same

260 night, seems to be limited in this system (Tyler 2002; personal observations). Therefore,
261 our results indicate that the system is female rather than male driven: females benefit
262 from signalling separately, whereas males should benefit from arriving at clusters of
263 signalling females.

264 In the competitive situation within a cluster, differences in individuals' mate attraction
265 abilities may be important. We found evidence for the cost of having neighbours being
266 the lowest (i.e. mating probability being the highest) when all neighbours were of the
267 lower attractiveness (brightness) category. By showing that the neighbourhood does
268 affect attractiveness of an individual, the results suggest that an active choice of the
269 social environment may pay off (see Laland et al. 1999; Ryder et al. 2009). Previous
270 studies have found, for instance, that less attractive male house finches, *Carpodacus*
271 *mexicanus*, can improve their pairing success by changing to a new social group (Oh
272 and Badyaev 2010). Glow-worm females, in turn, have been found to move away from
273 a particularly bright (dummy) rival (Borshagovski et al. 2019). Females of glow-worms
274 and other capital breeding species may also face a trade-off between mating as quickly
275 as possible (to optimise fecundity) and exercising mate choice, with larger (and hence
276 likely brighter) females being in a better position to pay the costs of any mating delays
277 (Hopkins 2018). In the current study, a neighbourhood consisting of both bright and dim
278 rivals was the least favourable. Such a pattern could be due to, for example, a
279 heterogeneous female cluster being less detectable or attractive to males, providing an
280 interesting avenue for future research. Furthermore, clusters of four consisting solely of
281 bright (B) females attracted more males than clusters with only dim (D) females, which
282 increases the observed success of females in the "B neighbours only" category and
283 decreases the detected benefit of having only D neighbours.

284 We cannot rule out a completely passive mate attraction (Arak 1988) taking place in this
285 system, with males simply mating with the first female they happen to detect. Such a
286 mating pattern may result in an overall advantage for B females and within groups an
287 advantage to females that have only D neighbours. Neither is the scenario in direct odds
288 with our finding that a greater brightness did not always ensure an advantage, with D
289 females attracting some (albeit on average a lower number of) males even when in the
290 same cluster with one or multiple B rivals. Regardless of whether males exert active or
291 passive mate choice, our results suggest that selection favours females that glow alone
292 rather than in groups and within a group females should be better off signalling in the
293 absence of any attractive neighbours.

294 To conclude, in this study we have shown that by displaying alone rather than in
295 clusters, females, independent of their attractiveness, have a higher probability of
296 mating quickly and have a greater potential to be choosy. The results also show that
297 within clusters, the most favourable neighbourhood may be the one that exclusively has
298 neighbours of lower level of attractiveness. Hence, the results strengthen our
299 understanding of the relationships between spatial distribution, sexual competition and
300 mating success, showing their importance even when females compete with other
301 females.

302

303 **Funding**

304 The work was supported by the Academy of Finland [grant number 294664 to AK].

305

306 **Acknowledgements**

307 We are grateful to Anna-Maria Borshagovski, Christina Elgert, Juhani Hopkins, Timo
308 Piepponen and Otso Valkeeniemi for their help with the fieldwork preparations, to
309 Natarsha Babic and Timo Piepponen for assistance with data gathering, Ulrika
310 Candolin, Juhani Hopkins and anonymous reviewers for insightful comments on earlier
311 versions of the text, Maria-Elena Bernal for checking the grammar, and the staff of
312 Tvärminne Zoological Station for logistic support.

313

314 **Data Accessibility:** Analyses reported in this article can be reproduced using the data
315 provided by Lehtonen and Kaitala (2020).

316

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394 **Tables**

395 Table 1. Pair-wise differences between neighbourhood types. B and D refer to the two
 396 brightness levels. In both panels, (a) and (b), the upper right part gives *z* values
 397 (provided by a mixed model described in the methods) and the lower left part gives the
 398 matching *P* values

		Solitary	Only B	Only D	Both B and D
(a) Mating probability	Solitary		2.243	0.442	3.262
	Only B	<i>0.025</i>		1.665	0.734
	Only D	0.66	0.096		2.576
	Both B and D	<i>0.0011</i>	0.46	<i>0.010</i>	
		Solitary	Only B	Only D	Both B and D
(b) Number of males	Solitary		3.638	3.672	5.929
	Only B	<i><0.001</i>		0.197	1.397
	Only D	<i><0.001</i>	0.84		1.756
	Both B and D	<i><0.001</i>	0.16	0.079	

399 **Figure legends**

400

401 **Figure 1**

402 (a) A female dummy, i.e. a funnel trap equipped with a green LED on top, as a
403 schematic presentation (left panel) and as seen during night time from above (right
404 panel). (b) Dummy females were placed either in clusters of four or singly. (c) Within a
405 cluster, the neighbours were either all of the brighter type (darker orbs, left cluster) all
406 dim (paler orbs, right cluster) or a mix of the two neighbour types (lower middle
407 cluster). In these examples, the focal dummy female, denoted with a dashed ring, was of
408 the brighter type

409

410 **Figure 2**

411 The percentage of dummy females that attracted at least 1 male with regard to (a)
412 brightness and (b) neighbourhood categories. In (b), columns without a letter in
413 common are significantly different (mixed model, $\alpha = 0.05$; Table 1a), and the clustered
414 neighbourhood categories are coloured. The error bars show 95% confidence intervals.
415 Sample size are given above each column

416

417 **Figure 3**

418 The number of males attracted by those female dummies that attracted at least 1 male,
419 with regard to (a) female dummy brightness and (b) neighbourhood categories (those
420 without a letter in common are significantly different; mixed model, $\alpha = 0.05$, Table
421 1b). Sample size are given above each column