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

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Females, too, may compete for mating opportunities. We show that the presence and quality of rivals impact female mate attraction success. In particular, by using artificial glow-worm females that attract flying males to mate by glowing during the night, we found that solitary females have more mates than clustered ones. Within groups, females benefit from having exclusively neighbours with dim glow. Hence, rival presence and attractiveness are important for female mating strategies.

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Abstract

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

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

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INTRODUCTION

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

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

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

To date, our understanding of the consequences of clustering or neighbour attractiveness on the distribution of matings has largely based on lekking species, in which large clusters of males gather together. In contrast, less is known about the role of clusters and signalling neighbourhoods in species that do not form leks and especially when females compete with other females for mate attraction. Such situation may arise especially when reproducing using only stored resources, i.e. in capital breeders (Houston et al. 2007). Capital breeding females may pay particularly high fecundity, or other fitness, costs from prolonged sexual signalling or self maintenance and hence are under time pressure to mate: mating quickly increases the expected number of offspring (in glow-worms: Hopkins 2018). Females may therefore need to actively attract mates, and even compete for matings, independent of whether female fitness increases with the number of matings. Indeed, capital breeding can result in increased variation in female reproductive success, with strong sexual selection on female traits related to mate attraction.

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

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

MATERIALS AND METHODS

Study site and model species

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

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

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

Study design

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

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~0.13 µW/nm). Each dummy female of the dimmer type (hereon: "D"), in turn, had its LED wired with four 1000 ohm resistors (peak glow intensity: ~0.02 µW/nm). Such a difference in relative brightness is easily visible to a human observer and reflects the range seen among wild females in the local population (personal observations).

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

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

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(pronotum) width of each male was later measured in the laboratory using a calliper. The males were then marked and released back to the wild.

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

Probability of attracting a mate

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

Potential to be choosy

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

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

Male size

With regard to male body size, we were particularly interested in whether clusters of females attract males of different of sizes compared to solitary females. For example, if multiple males arrive at the same time, small males might have higher chances of success when targeting a cluster rather than a solitary female. Overall, the female dummies captured 389 males. Of these, pronotum width data are missing for 9 individuals, 6 were recaptures from replicates run during previous nights and another 4 had been captured earlier (and then marked and released) in an unrelated experiment conducted near the research station. All available data points were included in the data analyses, and the exclusion of the recaptures does not change the conclusions. We applied a linear mixed effects model ('nlme' package) with male pronotum width as the response variable, and in other respects using the same variables and general approach as described above.

RESULTS

Probability of attracting a mate

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

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significant effect on the probability of attracting a mate (mixed model, overall neighbour effect: $\chi^2 = 15.50$, df = 3, $P = 0.0014$). In particular, mate attraction probability was the highest for solitary females (solitary: 63%, combined probability for clusters: 43%, a significant difference between solitary and clusters at $\alpha = 0.01$), and significantly lower than that in all other neighbourhood types, except for females having only D (dimmer) neighbours (Figure 2*b*, Table 1*a*). Indeed, within clusters, mating probability was the highest when the focal dummy female had only D neighbours (Figure 2*b*, Table 1*a*) and the lowest when both types of neighbours were present (Figure 2*b*, Table 1*a*).

Potential to be choosy

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

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Male size

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

DISCUSSION

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

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

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

In many systems, female reproductive success does not significantly increase with the number of matings (e.g. Parker 2006). This is also likely to be the case in capital breeders, such as glow-worms, which nevertheless are likely to benefit from mating quickly: in glow-worms mating delays can reduce fecundity, especially in small females (Hopkins 2018). The result of solitary females mating quicker also helps to explain why females in the wild are not more commonly clustered in smaller spatial scales. From the male perspective, our results imply that a solitary female is more likely to attract rival males arriving within a short timeframe, inducing higher potential for male-male competition and, hence, a higher probability of failure to mate after finding a female. After mating, the glow-worm male stays to guard the female (Tyler 2002; personal observations), but a cluster of females might nevertheless provide an approaching male higher potential for comparing females or for mating with additional females later. If some males are indeed able to remate later, without getting markedly sperm depleted, for females, the difference between signalling alone versus in a cluster may be smaller than our results suggest. However, the scope for male remating seems to be limited in

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this system (Tyler 2002; personal observations). Indeed, our results indicate that the system is female rather than male driven: females benefit from signalling separately, whereas males should benefit from arriving at clusters of signalling females.

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

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

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

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Tables

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

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

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Figure legends

Figure 1

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

Figure 2

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

Figure 3

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

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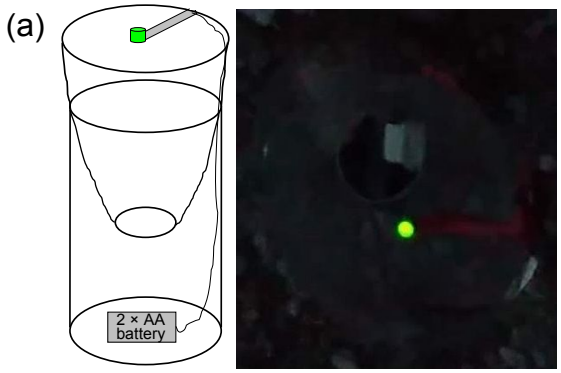

Figure 1a

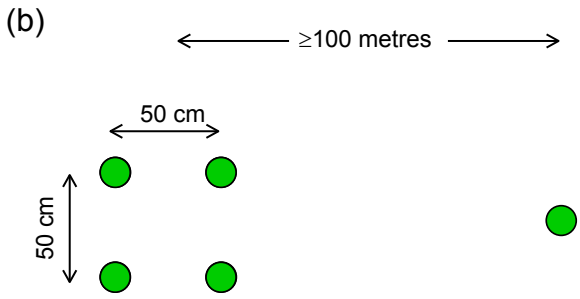

Figure 1b

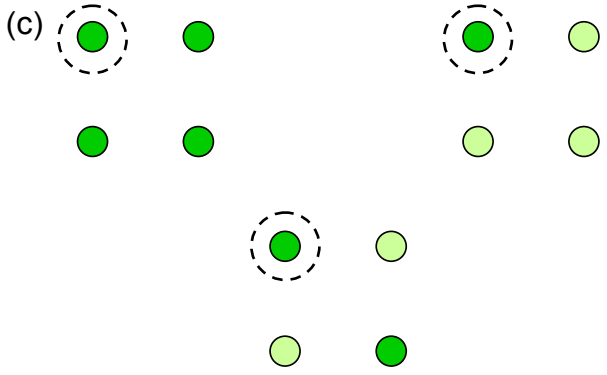

Figure 1c

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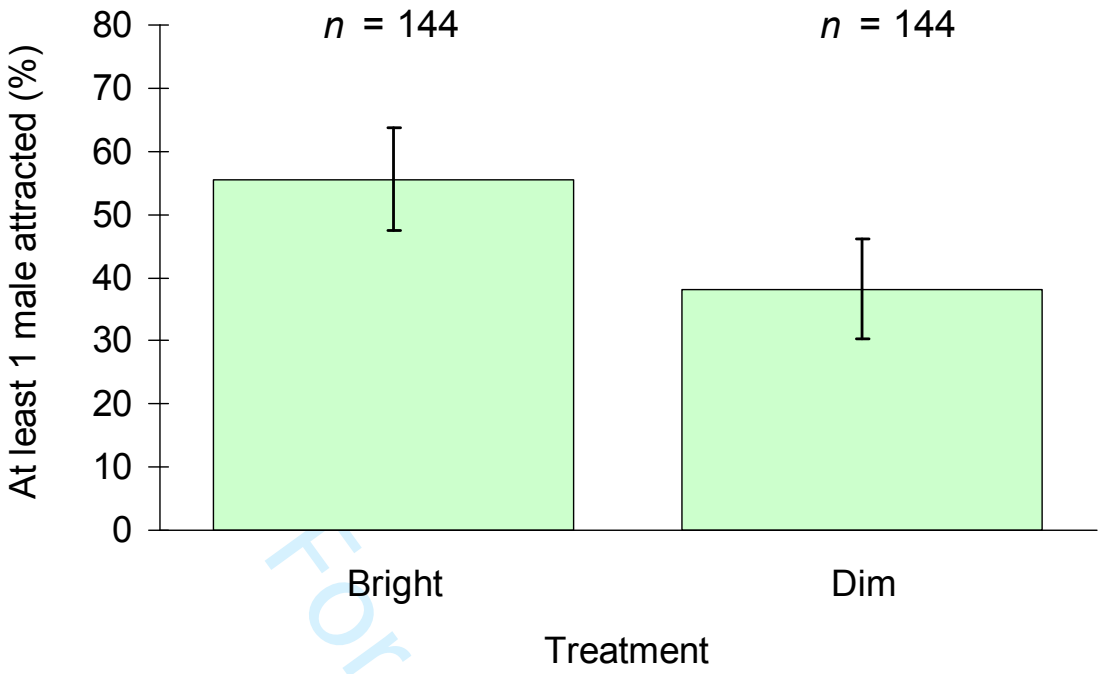

Figure 2a

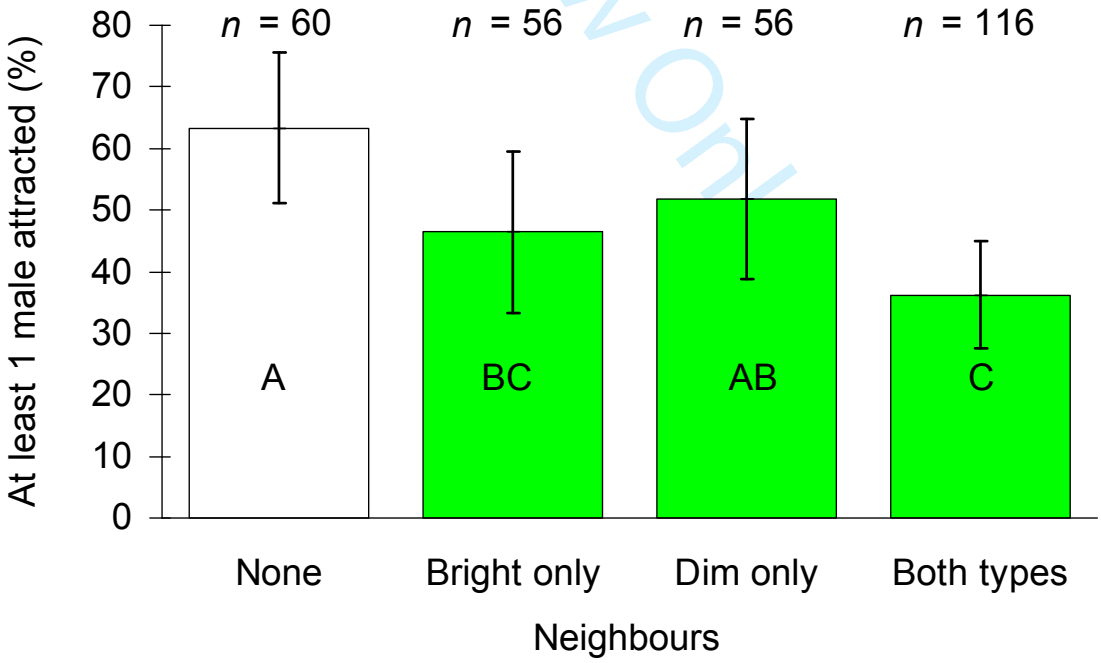

Figure 2b

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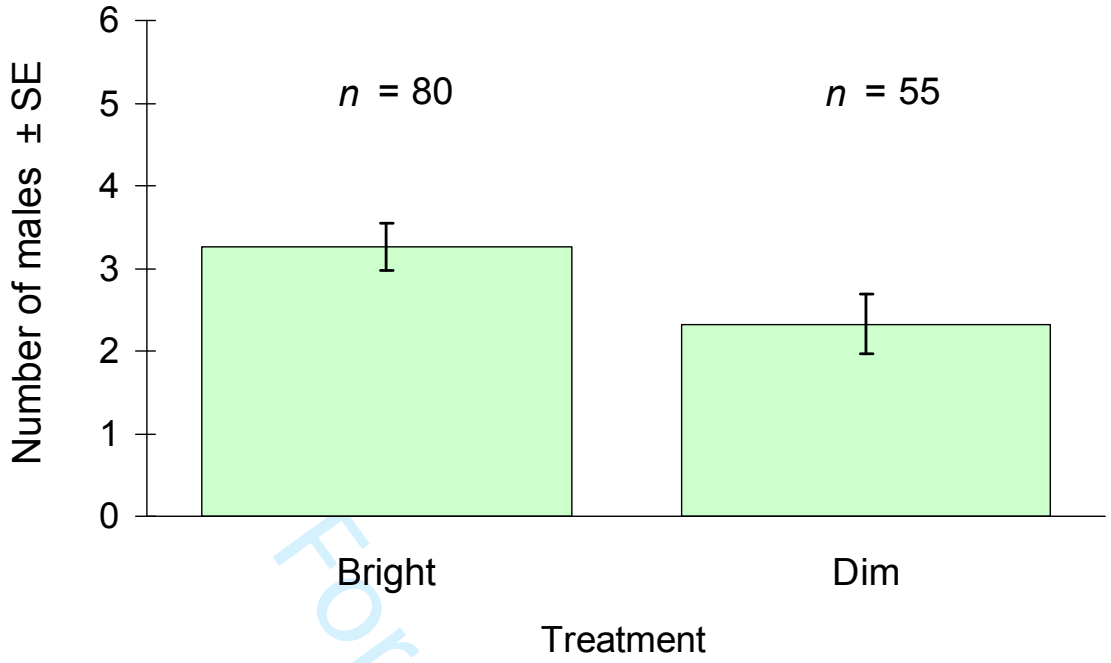

Figure 3a

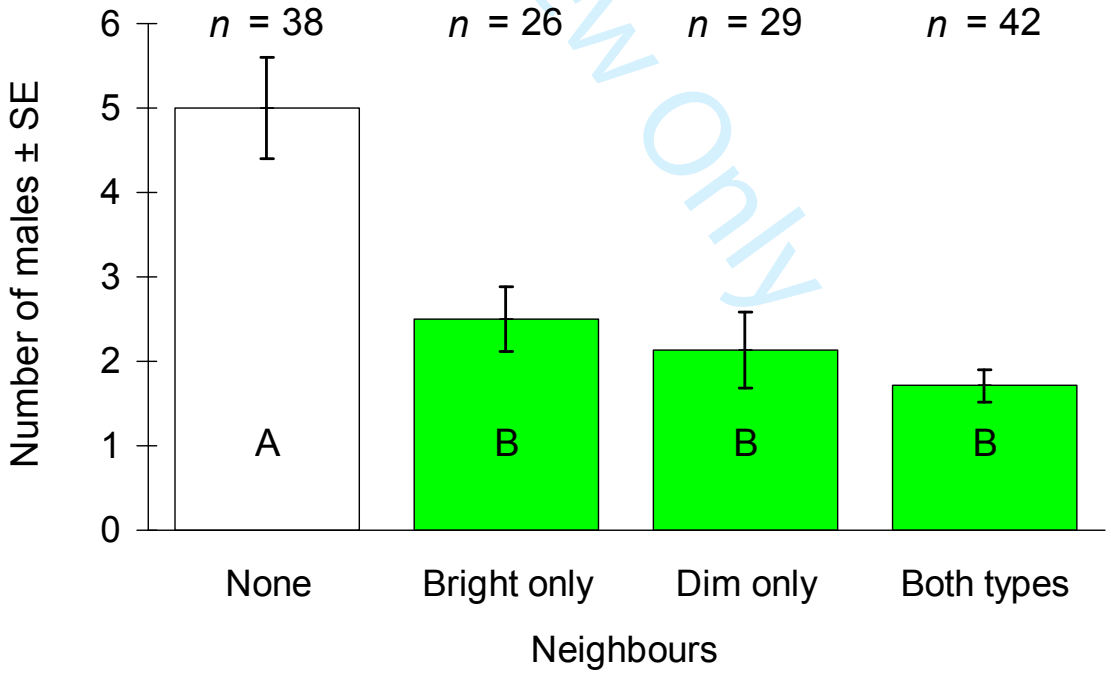

Figure 3b

For Review Only