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Hopkins, Juhani

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Research article

Beauty is in the eye of the beholder: mate choice in glow-worms depends on perceived, not emitted signals

Juhani Hopkins, Veijo Kaitala and Arja Kaitala

J. Hopkins (<https://orcid.org/0000-0003-4724-2755>) ✉ (juhani.hopkins@oulu.fi) and A. Kaitala, Ecology and Genetics Research Group, Univ. of Oulu, Oulu, Finland and Tvärminne Zoological Station, Univ. of Helsinki, Helsinki, Finland. – V. Kaitala, Organismal and Evolutionary Biology Research Programme, Univ. of Helsinki, Helsinki, Finland.

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While the strength of sexual signals is important in mate attraction, the ability to accurately compare signals may also have a major effect on mate choice. Large distances between competitors may reduce competition, as accurate comparison of signals becomes harder. This may be advantageous to weak signallers and detrimental to stronger signallers. We create a mathematical model examining optimal distance from stronger competitors for sexual signallers and test its predictions using the common glow-worm *Lampyris noctiluca*. Female glow-worms are flightless and attract males by glowing. Males prefer the brightest female if two females are close to each other. Our model gave different predictions depending on whether searchers fly or not. The model and experiment showed that weak signallers should move away from competitors and strong signallers should move closer to weaker competitors when searchers fly. In contrast, the model predicted that the distance between competing signallers has no effect when searchers do not fly. This reveals an unexpected spatial competition between strong and weak signallers. We conclude that, while signal strength is important in sexual selection, location in relation to others is similarly important as ornamentation in determining the result of mate attraction.

Keywords: aggregation, glow-worm, lampyrid, lek, mate choice

Introduction

Sexual ornaments and signals attract mates by providing information about quality. Several models exist explaining the linkage between signals and choice, both from a mechanical (how did this individual come to choose that one?) (Jennions and Petrie 1997) and an evolutionary (why is it better to choose that individual?) perspective (Fisher 1930, Zahavi 1975, Hamilton and Zuk 1982, Andersson and Iwasa 1994). The models agree that signal strength correlates with the evolutionary benefits of mating with the signal producer, and therefore stronger signals are better at attracting mates (Andersson and Iwasa 1994, Andersson and Simmons 2006). What is easily overlooked is that strength is a relative measure from the perspective of signal receivers (Endler 1992, Akre and Johnsen 2014). Mate choice models often implicitly assume



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that any individual comparing potential mates will have an accurate and comparable view of all signals.

Some signals/ornaments are assessed at close range (e.g. many displays, tactile signals), whereas others may be assessed at distance, particularly long-range visual and auditory signals. In the latter two cases, the distance to the signaller is an ecologically important determinant of the perceived intensity of the signal (Andersson and Iwasa 1994).

In reality, information received about signals is not as accurate as mate choice models often assume. For an individual searching for a mate, it is crucial to be able to compare signallers accurately, which is dependent on numerous factors in the signaller, receiver and environment (Guilford and Dawkins 1991, Endler 1992, 1993, 1999, Bateson and Healy 2005, Holman et al. 2014, Ronald et al. 2018). Distance to the observer will have an effect on the apparent size, volume or brightness, making comparison inaccurate. For example, instead of the absolutely largest ornament attracting the most mates, it may be that the largest signal as seen by receivers is most effective.

The easiest way to estimate the effect of distance to perceived signal strength is through the inverse square law, which states that the magnitude of a physical property such as volume or brightness is proportional to the inverse square of the distance. For example, if the distance to the signaller doubles, the strength of the received signal is quartered. Without some mechanism for assessing distance accurately, no ornaments or signals can be reliably compared to each other.

The common glow-worm *Lampyris noctiluca* is a species where flightless females attract flying males through nocturnal glowing (Tyler 2002). Males are more attracted to a brighter female if females are close to each other (Hopkins et al. 2015). Females actively avoid conspecifics by moving away from brighter glowing females (Borshagovski et al. 2019). In a field study, the median distance between conspecific females within the same patch (defined as within 10 m of each other) was 4 m and most females were more than 1 m apart (Borshagovski et al. 2019). Female–female competition is expected as females need to mate as soon as possible. Glow-worms are capital breeders and have limited energy for reproduction and maintenance. They may lose most of their eggs if they do not mate soon after eclosion (Wing 1989, Hopkins et al. 2021). Females generally mate once, lay all their eggs soon after mating and die soon after that. About 50% mate during their first night of glowing, but some do not attract a mate for more than 2 weeks (Hickmott and Tyler 2011). When a male finds a glowing female he seems not to leave her during that night even if there are other females around (Tyler 2002).

If females are in a tight group, most males select the brightest female (Hopkins et al. 2015, Lehtonen and Kaitala 2020), but perceived brightness is dependent on distance to the observer. Owing to female distribution the ability of males to compare females may be limited.

This study aimed to examine the role of distance to the nearest neighbour in determining the best mate attraction strategy. We did this theoretically using a mathematical model, and experimentally in the field. Our experiment tested how

many males dummy females attract when distances between dummy females and their relative brightnesses vary. We predicted that distance to a competitor affects the number of males attracted per dummy female.

Material and methods

Modelling male attraction

We modelled the optimal distance a dull female should maintain to its closest brighter neighbour. The model was based on the inverse-square law and allowed us to calculate what proportion of males heading for a bright female will be intercepted by a dull female. We assumed that males always fly towards the brightest female they can see. However, if a male flies close enough to a dull female, it will see the dull female as the brightest and change direction towards it. Based on this assumption and the inverse square law we could calculate the diameter of the area where the dull female appeared brighter. This, in turn, made it possible to calculate the proportion of males that a dull female intercepts from a brighter neighbour.

We present a model for the optimal distance to a stronger competitor a dull female glow-worm should maintain. Previous work shows that dull females are less attractive to males, as female brightness correlates strongly with attractiveness, fecundity and size (Hopkins et al. 2015). We studied how male behaviour is influenced by the location of the dull female in relation to the bright female. Optimal behaviour for brighter females is not modelled directly, but is discussed based on the results. We are interested in how large a proportion of males approaching from random directions are intercepted by a dull female near a brighter female; and how their relative brightnesses, the distance between them and how high males fly, affect the results.

The model considers two females of different brightness. We also assume that males appear far away from females and always head towards the brightest female they can see. As males pass dull females, they may change their preference as nearby females may appear brighter than those further away. We aim to first define the area within which the duller female appears brighter; and, second, to use the diameter of this area to calculate the proportion of males heading to the brighter female that the duller female will intercept (Fig. 1).

To make calculations easier, we define the brightness of the bright female to be 1 and that of the dull female to be b ($0 < b < 1$) (see Table 1 for a summary of symbols used). The distance between the two females is D . The system is located in an x,y -coordinate system. The bright female is at location $(0,0)$ and the dull female is at $(0,D)$. From any point (x,y) where a male might be, the distance to the bright and dull females is d_1 and d_2 , respectively (Eq. 1):

$$\begin{cases} d_1 = \sqrt{x^2 + y^2} \\ d_2 = \sqrt{x^2 + (y - D)^2} \end{cases} \quad (1)$$

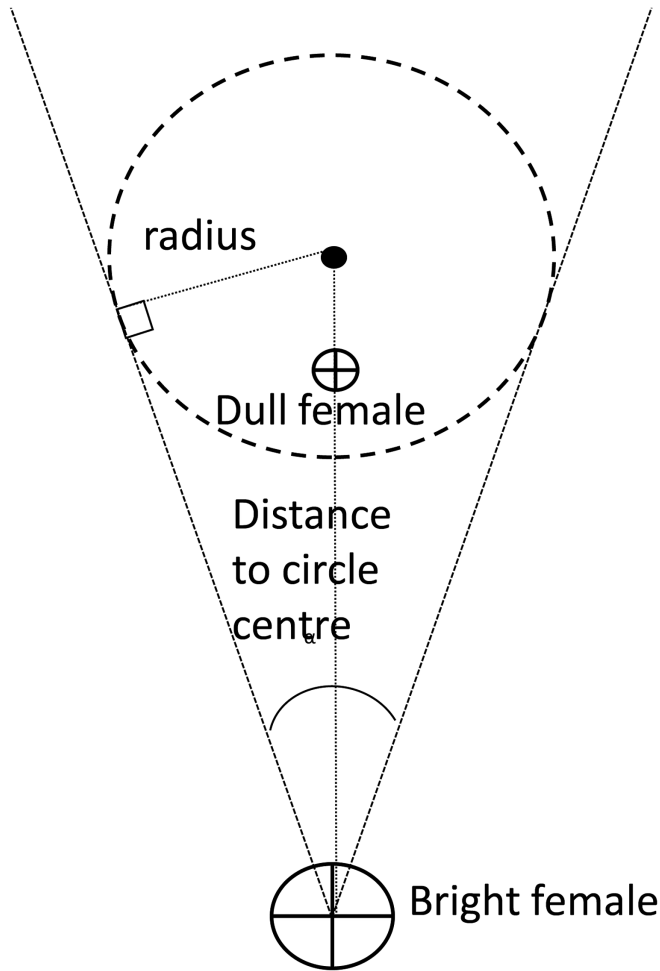


Figure 1. The dull female appears brighter within the dashed circle and any males approaching the bright female from within the marked sector will be intercepted by the dull female. By calculating the angle (α) from which the dull female intercepts males moving to the bright female we get the proportion ($\alpha/360$) of males heading to the bright female that opt to mate with the dull female. Lines for the radius of the circle and the distance from the bright female to the circle centre have been added to make the model easier to understand.

Owing to the power of any signal being proportionate to the inverse of the square of the distance (the inverse-square law) (Kepler 1604), the perceived strengths of light from the

bright and dull females at point (x,y) are proportional to $\frac{1}{d_1^2}$

and $\frac{b}{d_2^2}$, respectively. The border for the area within which the dull female seems stronger can be defined (Eq. 2) as:

$$\frac{b}{d_2^2} = \frac{1}{d_1^2} \quad (2)$$

The coordinates where both females appear equally bright are obtained by inserting d_1 and d_2 from Eq. 1 into Eq. 2 and simplifying (Eq. 3):

$$x^2 + \left(y - \frac{D}{1-b}\right)^2 = \left(\frac{D\sqrt{b}}{1-b}\right)^2 \quad (3)$$

The resulting border is a circle with the centre at $(0, D/(1-b))$ and a radius (r) equal to $D\sqrt{b}/(1-b)$. This means that the area is not centred on the dull female. Instead, the centre of the circle lies some distance behind it from the bright individual's point of view.

According to our assumptions, males appear from a different habitat patch than females and move towards the strongest signal they perceive. From far away, the bright female appears brighter than the dull one. However, any individual moving close enough to the dull female to enter the area defined above will perceive the duller female to be brighter, and change direction to head towards it.

We are interested in how large a proportion of males approaching from random directions are intercepted by the dull female. To do this we calculate the angle (α) from the bright female (Supporting information) within which the dull female seems stronger. As we know the radius of the sphere and its distance from the bright female, it is simple to calculate the angle. The angle allows easy estimation of how many males a dull female can intercept from the bright one. For example, if α is 90° then the dull female gets one-quarter of the mates attracted by the bright female.

The angle from which the dull female attracts all males (α) is given (Eq. 4) as:

$$\alpha = 2 \sin^{-1} \frac{\text{radius of the attraction circle}}{\text{distance to circle centre}} \quad (4)$$

Table 1. Summary of symbols used in the model.

	Symbol	Possible values
Distance between signallers	D	>0
Strength of weaker signal	b	$0 \leq b \leq 1$ relative to stronger signal
Strength of stronger signal	None	1
Distance from point (x,y) to signaller i	d_i	>0
Male flight altitude	h	≥ 0
Female attraction radius at altitude h	r_h	≥ 0
Distance from bright female to centre of dull female's attraction circle at altitude h	C_h	>0
Angle from which dull female attracts male flying at altitude h	α_h	$0 \leq \alpha_h < 180$

In terms of our model we get (Eq. 5):

$$\alpha = 2 \sin^{-1} \frac{\frac{D\sqrt{b}}{1-b}}{\frac{D}{1-b}} = 2 \sin^{-1} \sqrt{b} \quad (5)$$

Signalling in a 3-D world

Given that glow-worm males fly some distance above ground level, we extend the model into three dimensions. We made the simplifying assumptions that 1) males fly at an even altitude until they are directly above a female and then drop down onto it; and 2) females are at the same height. In nature it is likely that male altitude fluctuates and that they dive towards females at an angle rather than dropping straight down. However, to avoid vegetation the angle is likely to be somewhat steep, and it is unlikely that male altitude varies by too much as that would waste energy. While females can climb onto vegetation, and are known to do so, our observations show that this does not lead to great differences in their altitude. Therefore, we feel that these assumptions (while simplifications) are not unreasonable.

In contrast to the 2-D case, instead of an attraction circle, there is an attraction sphere. The radius of the sphere is the same as of the circle. Moreover, we have to take male flight height (h) into account. The radius (r_b) of the attraction sphere's cross-section at altitude h is given (Eq. 6) as:

$$r_b = \sqrt[2]{r^2 - h^2} = \sqrt[2]{\left(\frac{D\sqrt{b}}{1-b}\right)^2 - h^2} \quad (6)$$

Similarly, the distance from the brighter female to the centre of the cross-section at altitude h (Eq. 7) is:

$$C_b = \sqrt[2]{\left(\frac{D}{1-b}\right)^2 + h^2} \quad (7)$$

So the angle of attraction at a male's flight height (Eq. 8) is:

$$\alpha_b = 2 \sin^{-1} \left(\frac{r_b}{C_b} \right) = 2 \sin^{-1} \left(\frac{\sqrt[2]{\left(\frac{D\sqrt{b}}{1-b}\right)^2 - h^2}}{\sqrt[2]{\left(\frac{D}{1-b}\right)^2 + h^2}} \right) \quad (8)$$

Results of the model

If males do not fly, the distance between females is cancelled out in the equation for the angle (α) of the sector dominated by the dull female. In this situation, distance to a stronger competitor has no effect on how many males a dull female

can intercept from a bright female. Consequently, there is no lower or upper limit to where the dull female should position herself with respect to the bright female. Only brightness will have an effect: as b increases from zero to 1 the angle α increases from zero to 180 degrees. An analogy would be walking along a line with a rock concert at the other end and a person playing the guitar somewhere along the line. Whatever the distance between the concert and the guitarist, anyone walking along the line will at some point experience the guitar as louder than the concert, but the point where this happens may be very close to the guitar and depends on the loudness of the concert and guitar.

A second interpretation does arise. If males approach the stronger signaller from one direction only, then dull females should attempt to position themselves on the path males travel along to get to bright females. Distance between females would have no effect on the fraction of males intercepted by the dull female, but position would. For example, if most potential mates approach from the west, then there is a strong advantage in being the westernmost signaller. The same is equally valid for bright and dull females, as both benefit from being closer to males.

When males fly above ground level ($h > 0$), two things happen (Fig. 2):

- 1) Unlike when flying at ground level, a dull female is more likely to intercept males, if the distance between the two females is high. However, the benefits to the dull female of increasing distance past a certain point are negligible. This is because the system begins to resemble the 2-D model when the distance between females increases. For example, if males fly at 1 m and the females are 1 m apart, the system is obviously in 3-D, but what if males fly at 1 m and the females are 50 m apart?
- 2) As males move higher, the attraction angle decreases (i.e. the duller females attracts fewer males) because the attraction sphere gets narrower at greater height. As the sphere's sides become more horizontal towards the top, the decrease accelerates as males move higher. If males fly higher than the radius of the attraction sphere, the dull female will never appear brighter. In this situation, a dull female should try to move further away to increase the altitude from which it can attract males or attempt to climb upwards itself.

Based on the model, we predict four possible routes for location and ornamentation to be intertwined for weak signallers. 1) In taxa that fly while searching for mates, increasing distance to stronger competitors correlates with attracting mates from a wider angle. In nature, this would lead to weak signallers dispersing far from strong neighbours and a scattered pattern of signaller location. 2) In taxa where mate searchers travel along the ground, distance to stronger competitors has no effect on the likelihood of being chosen as a mate. However, 3) in taxa where potential mates arrive from one predictable direction the critical factor is to choose a location that any mates attracted by stronger neighbours will move through. In nature, this would be visible as competition

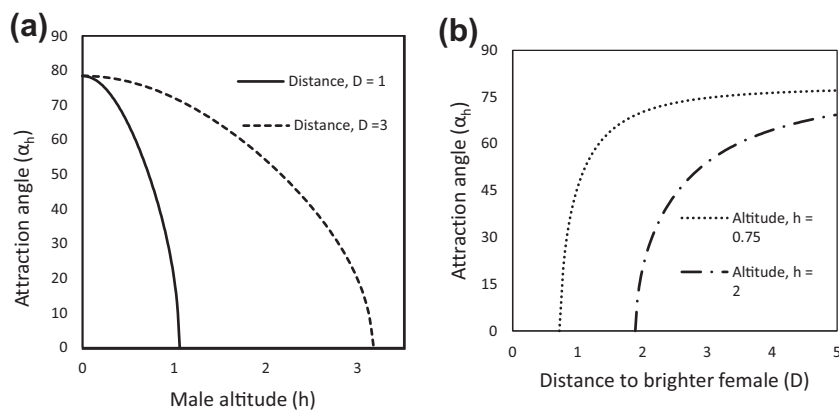


Figure 2. Plotting the results of the 3-D model to show how (a) male flight altitude affects the attraction angle α_b (i.e. the number of males attracted by a dull female) at two different distances between females and (b) distance between females affects the attraction angle α_h (i.e. the number of males attracted by a dull female) at two different male flight altitudes. Both figures drawn with $b=0.4$.

for display sites rather than females. (However, it must be noted that competition for breeding sites may also be due to other factors (Clutton-Brock and Huchard 2013).) 4) In taxa where mate choice is based on longer observation, location may be unimportant, as potential mates could observe multiple signallers closely before making a choice.

Testing the model

We tested the effect of distance on mate attraction in the glow-worm by using a set of one bright glow-worm trap surrounded by six equidistant dull traps. The traps imitate females closely and attract glow-worm males (Hopkins et al. 2015). We predicted that the greater distance to brighter females would increase the number of males attracted by a dull female. The distance between the central trap and its neighbours was either 1 m or 3 m (Fig. 3). The traps were deployed in glow-worm habitats around Tvärminne Zoological Station (59°51'N, 23°14'E) in Finland. We set the traps approximately 1 h before sunset and collected them the following morning.

From previous work in the area, we know that glow-worm females appear patchily, but do not seem to aggregate. It is normal to find a number of females in an open patch or scattered along the edge of a road or other geographical feature. Previous work has shown that females in these patches are normally several metres apart (Borshagovski et al. 2019).

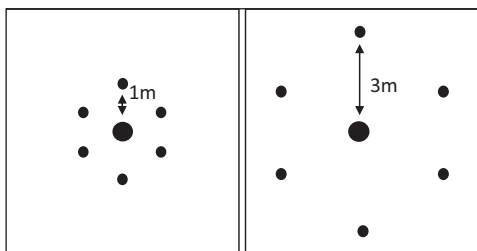


Figure 3. Diagram of the experimental setup using traps to study how distance to neighbours affects the number of males each female attracts. Small circles represent dull traps and large circles bright traps.

The traps were placed in locations where we had previously encountered glowing females, but we saw no females in the trap locations during the experiment. Trapping started 4 June 2016 and ended 2 August 2016. Traps were not placed during nights with rain or high wind as these have caused problems in earlier years (traps knocked over, filled with water or electronics damaged). Males were only caught between 7 June and 4 July. During most nights, we had three sets of traps out simultaneously. Exceptions were situations when one or more set broke when being placed. A total of 96 trap-nights was conducted (one trap night = one set of traps out for one night). The minimum distance between the sets was approximately 120 m and there was always thick forest between the sets.

The results were analysed in R ver. 3.2.4 for Windows (<www.r-project.org>) using a nested ANOVA where position within each trap set (middle/outer) was nested within distance. If a set of traps caught no males it was excluded from the analysis.

Results

The traps captured 34 males : 22 in the 1-m setup and 12 in the 3-m setup. After excluding sets that caught nothing, data remained from twelve 1-m sets and four 3-m sets. Distance between traps did not affect the number of males caught per trap set ($F=1.30$, $df=1,28$, $p=0.26$), but the interaction between distance and position was significant ($F=5.55$, $df=2,28$, $p < 0.01$), meaning that, in the 3-m sets, outer traps collected proportionately more males than were collected in the 1-m sets (Fig. 4). In the 3-m sets, the central traps failed to catch males at all.

We had no previous knowledge about the altitude at which males fly, but assumed that it must be more than the height of the tallest grass at the glow-worm sites (approx. 75 cm) and probably less than 2 m to avoid gusts of wind. Therefore, we estimated that α_b was between 0° and 43° when traps were 1 m apart and between 50° and 74° when traps were 3 m

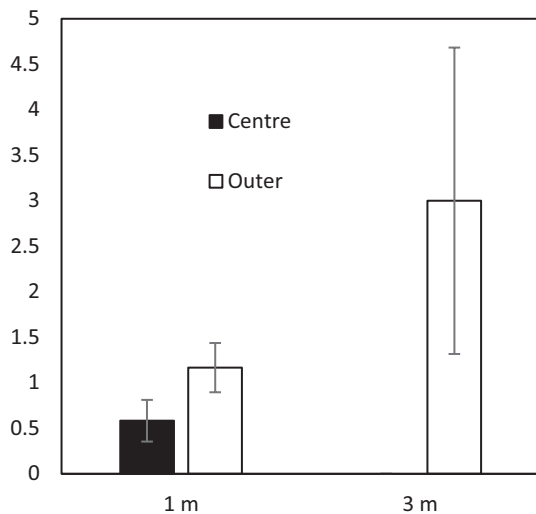


Figure 4. The number of males (mean \pm 1 SE) attracted by the centre and outside traps in the experiment. Note that centre traps in the 3-m setup caught no males.

apart. If these figures and our model were correct, the central trap in the 3-m setup should have collected no or very few males, due to there being no or a very narrow corridor along which a male could fly to it without getting intercepted. In the 1-m setup, the central trap would capture between about 72% and all of the males (72% because the outer traps would capture males from $6 \times 43^\circ/360^\circ = 258^\circ/360^\circ = 0.716$). The results of our experiment fit these predictions well.

Discussion

We examined how distance to neighbouring signallers affected the number of attracted mates in a species where females use visual signalling from a long distance. Our results showed that mate attraction is based on the comparison of received rather than emitted signals, which in turn means that, in mate attraction, location is as important as signalling. The results of the model and the experiment showed that weak signallers may outcompete stronger rivals by signalling from optimal locations. As the model predicted for the glow-worm, increasing distance to brighter traps allowed dull traps to capture more males. Dull dummy females appeared brighter to more flying males the further they were from competitors. Therefore, stronger signallers should attempt to be close to their weaker competitors to reduce the level of mating competition, while weak signallers should move far from stronger competitors.

Female glow-worms may use optimal distancing to manipulate signal perception. For females, any delays in mating may cause severe fitness losses (Wing 1989, Hopkins et al. 2021), and staying far from competitors may increase reproductive success, especially among small dull females, as supported by our experiment. This is supported by the fact that, in a field study, the mean distance between neighbouring females was 4 m and that female glow-worms actively move

away from brighter neighbours (Borshagovski et al. 2019). Female brightness depends on size and therefore is resistant to manipulation (as females cannot change their size). As a result, female signals accurately indicate female size (Hopkins et al. 2015), and males' choice for the brightest female is adaptive as the brightest females are more fecund. However, as we show, even when the signals themselves cannot be manipulated it is possible for signals to be inaccurate owing to failures in signal reception.

The model describes a perfect situation with only two signallers, but in nature nearly all signallers will have both stronger and weaker neighbours. The actual behaviour of natural animals is likely to be influenced by a need to balance between optimal distances towards several neighbours of varying brightness. Also, many species breed in leks, which may lead to very different optimal location strategies (Fiske et al. 2017). Factors such as predation and female preference lead to lekking systems (reviewed in Jiguet and Bretagnolle 2006). However, recent results show that glow-worm females attract more males when alone than when in a group (Lehtonen and Kaitala 2020), suggesting that, in glow-worms, females would not aggregate in leks to increase their chances of mating. The results of this study also support this conclusion: there was no difference between the treatments in the number of males attracted, meaning that tighter clusters of females will not attract more males than a more spread out set of females.

Our main result is that, with the aid of proper positioning, individuals with weak signals can outcompete even the strongest signallers. While stronger signals improve mating rates in most, if not all, sexually reproducing taxa (Andersson and Iwasa 1994, Andersson and Simmons 2006, Clutton-Brock 2009), the strength of a signal is relative, not absolute. How one individual is perceived depends on how it compares to its competitors (Jennions and Petrie 1997, Bateson and Healy 2005, Gasparini et al. 2013). This, and previous work showing the importance of location to mate choice (Apollonio et al. 1989, Gibson et al. 1991, Rintamäki et al. 2001), suggests that there may be a hitherto unacknowledged selection pressure involved in the evolution of mate choice: the pressure to be able to identify and move to optimal locations.

While our model is based on glow-worms, it may well be applicable to other signalling systems. Any system where the perceived signal strength follows the inverse square law and distance to the signaller cannot be accurately judged would fit this model. Examples could include other lampyrids, singing birds and even radio signals. The model predictions vary depending on whether the signallers and receivers are on the same plane (2-D) or not (3-D). The exact applicability of the model to each system must be judged on a case-by-case basis, as a wide range of factors may confound the predictions. For example, complex bird songs may degrade over distance, allowing for more accurate distance estimation than for simpler songs (see Speculations).

It is clear from our results and previous work that comparison of sexual ornaments and signals is more complicated than simply finding the individual with the largest ornament.

Any animal that is searching for a mate will receive signals from several potential mates and base its choice of mate on these signals. However, the signals that the chooser receives are not necessarily the same as the signals that were sent to it (Guilford and Dawkins 1991). If a signal attracts a mate from a long range, such as vocal and visual signals, distance is important. We show that distance affects signal strength enough to skew any mate choice preference. Similarly, signalling honesty, receiver biases, limits to perception, the social environment and the psychology of choosers will all have an effect on how signals are perceived (Dawkins and Guilford 1991, Endler and Basolo 1998, Bateson and Healy 2005). Without understanding how signals are perceived and the physics behind their transmission it is impossible to make any conclusions on how animals choose their mates based on signals.

In conclusion, how sexual signals are received and interpreted is not necessarily the same as how they are produced, and this discrepancy is enough to change the outcome of mate choice. Our experiment and model show that choosing an optimal distance to a stronger signaller greatly affects a weak signaller's chances of being chosen as a mate. Any weaker competitor that is able to take advantage of this will be able to compensate for its weakness and even outcompete much stronger competitors.

Speculations

We suspect that the model is not valid among animals that use pheromones to attract mates. Pheromones do not follow the inverse square law as they spread by diffusion. They may, however, follow the 'inverse cube law' which would potentially take diffusion into account. We encourage pheromone researchers to modify our equations and see whether moths or other pheromone users spread out accordingly.

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Author contributions

Juhani Hopkins: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Investigation (lead); Methodology (equal); Writing – original draft (lead). **Veijo Kaitala:** Formal analysis (equal); Methodology (supporting); Writing – review and editing (supporting). **Arja Kaitala:** Conceptualization (equal); Funding acquisition (equal); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.s4mw6m991>> (Hopkins et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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