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THE COSTS AND CONSEQUENCES OF FEMALE SEXUAL SIGNALS
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Abstract

Sexual ornaments have developed in a very wide variety of animal taxa to increase fitness by improving mating success. How increased mating rate improves fitness is obvious in the case of most males: each mating provides more offspring. Whether more matings benefit females, whose fecundity is limited by resources and not mates, is unclear. Mate choice is linked to ornamentation, when individuals of one sex choose who to mate with based on the ornamentation in members of the other sex. Ornaments may work as a basis for mate choice due to conveying information about the quality of the mate. Mate choice may then lead to intrasexual competition for mates in the chosen sex as animals try to outcompete their neighbours and attract more mates.

My aim in this thesis is to study the purpose and costs of female ornamentation as well as female competition for males. The main questions revolve around understanding what information female ornaments provide about the bearer and how males choose between females. I also examine how females compete against each other and what the costs of being ornamented are for a female. To study these questions I use the common glow-worm (Lampyris noctiluca Linnaeus, Lampyridae), whose females glow at night to attract flying males.

According to my results, a female’s glowing provides accurate information about fecundity and males base their choice of mate on the intensity of female glowing. I showed that the perceived strength of an ornament in comparison to others close by is more important than the actual strength of an ornament. In the glow-worm, the perceived strength of an ornament depends on distance to the observer, making the system open to exploitation. A mathematical model I developed suggested that dull females could outcompete brighter ones by choosing optimal locations, and experimentation showed this to be the case. Finally, my results show that glow-worm females lose eggs each day they remain unmated. This suggests that the evolution of female ornamentation may have been driven in part by the need to find a mate as soon as possible after eclosion. Which in turn means that female and male ornamentation may have fundamentally different purposes: for females mating soon may be important, while for males the total number of offspring fertilized is critical.

Keywords: female ornaments, glow-worm, male mate choice, sexual signals

Tässä väitöskirjassaan tarkoituksena on tutkia naaraiden ornamenttien tarkoitusta ja kustannuksia sekä tutkia miten naaraat voivat kilpailla toisiaan vastaan. Pääkysymykset liittyvät ornamenttien välillä käytettyihin informaatioihin ja siihen, miten naaraat valitsevat paritettujen ornamenteiden paristoa.

Lisäksi tarkastelen, miten naaraat voivat kilpailla keskenään ja mitä kindistänaaraiden ornamenteista naaraalle. Kysymystä on selvittää ornamenttien välillä käytetty informaatioja ja siihen, miten naaraat valitsevat paritettujen ornamenteidensa perusteella.

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To my family and friends
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If I forgot to thank anyone, I apologise and hope you are not too offended. As you can see, a lot of people have made this thesis possible, and seeing the number of names is a humbling experience. Please accept my deepest gratitude for being a part of my life.

Oulu, 6.9.2018

Juhani Hopkins
**List of original articles**

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:


III  Hopkins J, Kaitala V, Kaitala A: Beauty is in the eye of the beholder (Manuscript)

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Original articles
1 Introduction

Animals use signals to modify the behaviour of conspecifics (Smith & Harper, 2003). Sexual ornaments are signals that can be defined as any features which have evolved specifically to attract mates (Andersson, 1994). How they do this varies: ornaments may be conspicuous morphological features, such as peacocks’ tails, visual or acoustic signals, like bird calls, or any of a multitude of other features. As a rule larger, brighter, louder or more extravagant ornaments are better at attracting mating partners. Sexual ornaments commonly indicate the benefit of mating with the bearer. This may be as the indirect benefit of producing more attractive offspring (Fisher, 1930). Or the ornament may indicate genetic quality of the bearer by showing the ability of the bearer to cope with the costs of an ornament, which correlates with its, and potentially its offsprings’, ability to survive (Zahavi, 1975). This in turn means that ornaments can be used as a way to improve the genetic quality of offspring. Alternatively ornaments may also correlate with direct benefits, such as nuptial gifts, provided by the bearer (Price, Schluter, & Heckman, 1993).

Generally the individual with the largest, loudest, brightest or longest-lasting ornament is preferred as a mate (Andersson, 1994). Examples include the widowbird where females prefer males with longer tails (Andersson, 1982), many anurans where there is a preference for call pitch or volume (Arak, 1983), sticklebacks where the brightest colours win (Milinski & Bakker, 1990) and gray tree frogs, where males with the longest calls are preferred (Gerhardt, Tanner, Corrigan, & Walton, 2000). However, when comparing ornaments, it is important to recognize the difference between the absolute and relative differences between two or more potential ornaments. Animals are commonly more likely to be able to differentiate between large relative differences in signal strength rather than large absolute differences (Akre & Johnsen, 2014). For example, it is much easier to spot the difference between a 2 cm long tail and a 3 cm long tail than the difference between 102 cm and 103 cm tails despite both differences being the same absolute size: 1 cm.

What confounds comparing potential mates (usually via their signals) even more is the fact that signals change under transmission (Endler, 1993, 1999) and according to the social environment (M. Bateson & Healy, 2005). The medium a signal travels through, the sensory system of the receiver and even the psychology of the receiver will have an effect on how the signal is perceived (Akre & Johnsen, 2014; Guilford & Dawkins, 1991). One specific way that signal reception may vary
is with distance to the signaller varying. Many physical properties such as brightness and volume follow the inverse square law, which dictates that the magnitude of a received signal is proportional to the inverse of the square of the distance regardless of the medium the signal travels through (Kepler, 1604). For example, a singing bird will sound four times louder at two metres than at four. This may have implications on sexual signalling as distance between signallers and signal receivers may affect the outcome of mate choice by making accurate comparison of potential mates harder.

While males are more often the ornamented sex, there are also many examples of ornamented females among a wide range of taxa (reviewed in (Amundsen, 2000)). The main reason why female ornaments are less common than male ornaments lies in the differences in potential reproductive rates between males and females (Clutton-Brock & Vincent, 1991). Male fitness is generally limited mainly by access to females, while female fitness is usually limited by available resources (Bateman, 1948, though see Kokko & Jennions, 2008; Queller, 1997). This means that, in theory, males benefit from each mating with a different female so they are ornamented to increase mating rate and compete for females. Females on the other hand generally don’t benefit to the same extent from mating with multiple males (however, see (Arnvquist & Nilsson, 2000; Kvarnemo & Simmons, 2013) for discussion on the many cases where female multiple mating is common). Instead, females tend to have an overabundance of available males so they are choosy about which males they accept. In practice, most animals have various constraints making their mating systems more diverse than this general model.

Understanding the evolution of female ornamentation poses a problem: ornaments that increases mating rate use resources that could be used to increase fecundity (Fitzpatrick, Berglund, & Rosenqvist, 1995), but an increase in mating rate might not increase female fitness. Too many matings may even stress females and reduce fitness (Arnvquist & Rowe, 2005; Daly, 1978). For female ornamentation to evolve, the ornament must provide greater fitness benefits than investing the same resources into fecundity or increased survival to the next breeding episode.

Some mechanisms that let females ignore the cost of ornamentation have been suggested (Fitzpatrick et al., 1995). In some cases, female ornamentation is cheap and has very little effect on fecundity. For example pheromones are often cheap to produce in the amounts required to attract males, especially if the female is able to eat as an adult and compensate for the cost of mate attraction (Harari & Steinitz, 2013). It is also possible that ornamentation reduces survival, but not current
reproduction. In short-lived species survival past reproduction is unimportant as a second breeding opportunity is unlikely even with more resources available. Ornaments may also evolve to be efficient enough not to affect survival or fecundity. Finally, females may have a surplus of resources allowing them to be ornamented without losing any fitness.

Costly female ornaments have received multiple explanations. Females may need to fight against conspecifics for resources needed to rear offspring (LeBas, 2006; Lyon & Montgomerie, 2012; Roughgarden, 2012; Tobias, Montgomerie, & Lyon, 2012). Ornaments may aid in competition for males in polyandrous species (Clutton-Brock, 2009), help to gain more nuptial gifts from males (Arnqvist & Nilsson, 2000; Clutton-Brock, 2009) or signal mating status or fecundity (Clutton-Brock, 2007). In many species, female size correlates with fecundity, fighting ability and other critical functions (Honěk, 1993; Rosenqvist & Berglund, 2011). Therefore, males should prefer larger females when given a choice. Sexual signals or ornaments in females may sometimes exist to accentuate female size (Rosenqvist & Berglund, 2011).

While competition for mates is more common in males than females, female-female mate competition is well documented in a range of taxa (Andersson & Iwasa, 1996; Tobias et al., 2012). Females are likely to compete against each other for mating opportunities when every female is not guaranteed to gain a mate, when males dominate a critical resource, when males vary in quality or when females are in a hurry to mate (Clutton-Brock, 2007, 2009; Rosvall, 2011; Tobias et al., 2012). In addition, males may become choosy about which females to mate with if there is great variation in female quality (Bonduriansky, 2001; Edward & Chapman, 2011), leading to increased female competition. Intrasexual competition may in turn lead to females developing sexual ornaments to improve their chances of attracting males (Clutton-Brock, 2007; Kokko & Mappes, 2005) or weaker competitors may develop novel behaviours to outcompete their stronger rivals (Oliveira & Taborsky, 2008).

Female-female mating competition commonly occurs together with male mate choice. Male mate choice is common, but intuitively unexpected as choosiness requires rejecting one or more potential mates and males generally benefit from each mating (Barry & Kokko, 2010). Males may become choosy, i.e. not mate with all potential mates, if females are superabundant, males have limited capacity to mate or mating is highly costly (Candolin & Salesto, 2009; Kokko & Monaghan, 2001). Males will prefer females that provide the greatest fitness benefits, which usually means mating with the largest female available (Honěk, 1993). Exactly how
individuals choose their mates varies greatly, but usually involves comparing one or more potential mates to each other or an internal threshold and making a choice based on collected information about their quality (Jennions & Petrie, 1997). Female ornamentation may aid males in identifying the best females, especially where direct observation of size is not possible or size does not correlate with fecundity (Chenoweth, Doughty, & Kokko, 2006).

1.1 Aims of the study

This thesis aims to study female sexual signalling and male ability to detect a female. I examine the purpose and function of female ornamentation, the possibility of female-female signalling competition through choosing optimal locations in relation to others and the costs of female ornaments. The main research questions and the papers they are presented in (I-IV) are:

1. Do males choose females based on female ornamentation? (Paper I) I used dummy females with varying levels of ornamentation to study how well they attracted males in the wild. I expected that males would be more likely to choose females with more intense ornamentation.

2. How do attractive females differ from less attractive ones? If males systematically prefer certain females over others, what traits do these females have and do they correlate with female ornamentation? (I) I measured the level of female ornamentation, lifetime fecundity and size to see whether preferred females were more ornamented and provided males with larger fitness benefits. My hypothesis was that there would be a positive correlation between the level of female ornamentation and fecundity.

3. Can less attractive females use alternative tactics to compete successfully for males? (Papers II & III) I examined whether distance to neighbouring females had an effect on perceived attractiveness using mathematical modelling and a field experiment. Female response to other females was tested in a controlled laboratory experiment. I expected females to move close to competitors that are more attractive to intercept males approaching the other female.

4. Are there costs of female ornamentation? (Paper IV) I examined the effect of female signalling effort on lifetime fecundity and compared it to the effect of not attracting males soon. I hypothesised that excessive female sexual signalling would reduce fecundity.
2 Material and methods

2.1 Study species and collection of animals

This study was conducted using the common glow-worm (*Lampyris noctiluca*), a nocturnal capital breeding beetle. Females are sedentary and glow to attract flying males. Males and females differ greatly: females are larviformous, have small eyes and are usually much larger than males. Males resemble normal beetles and have very large eyes. The glow is a green (546-570 nm) light produced in the lantern on the ventral side of the abdomen (Bird & Parker, 2014; De Cock, 2004). The light is produced through bioluminescence and requires the glow-worm to increase energy use to power the process (Woods, Hendrickson, Mason, & Lewis, 2007). Larvae can also glow, but their lanterns are considerably smaller and thought to be aposematic signals (De Cock & Matthysen, 2003). Female glowing has probably evolved from larval glowing to act as a sexual signal (Branham & Wenzel, 2001).

Adults live for at most a few weeks (Tyler, 2002). During adulthood, glow-worms cannot feed so all energy required for reproduction and maintenance must be collected prior to pupation. Females generally glow for up to several hours every night until mating after which they stop glowing, lay all their eggs in one clutch and die soon after (Tyler, 2002). Clutches vary between 20 and 200 eggs (Tyler, 2002). Most females gain a mate within the first two nights of glowing, but some continue to glow for over two weeks (Hickmott & Tyler, 2011). In the field, females are found in open habitats such as fields, edges of forests, clearings and meadows. It remains unknown if females regularly mate multiply, but some field observations of females accompanied by multiple males do exist (Tyler, 2002). Whether males mate singly or multiple remains unstudied, as does possible male-male competition for females and female mate choice.

I conducted my experimental studies at Tvärminne Zoological station in Hanko, Southern Finland during June and July 2014-2016. Females for the experiments were collected at night by one or more people walking through known glow-worm habitats and picking all the glowing females they could see. Known areas were spread throughout the Hanko peninsula as well as Lohja, Kemiō, Särkisalo and Salo in Southwestern Finland. Males were collected using traps made out of 1.5 litre lemonade bottles. The bottles were cut in half horizontally with the neck section inserted into the lower half to create a funnel trap (fig. 1). Each trap was baited with a single green (562nm) 3mm through-hole LED that closely imitates a female glow-
worm (I). All collected individuals were kept indoors in separate jars without being allowed to see each other until mating. After mating, eggs were collected, counted and either released into the places the females were collected from or taken to the University of Oulu to start a laboratory population for other studies.

All statistical analyses were conducted using R 2.12.1, 3.1.1 and 3.3.2 (R Development Core Team, 2008) using the MASS, pscl, nlme and Barnard packages (Erguler, 2016; Jackman, 2017; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016; Venables & Ripley, 2002; Zeileis & Kleiber, 2008).

Fig. 1. Example of the traps used to collect males (I & II).

2.2 Do males choose females based on ornamentation?

The aim was to see if males choose females based on female ornamentation and if they do, why (I). We used pairs of traps set out in the field to capture males. In each pair, one trap was noticeably (2.7x or 18x) brighter than the other while brightnesses were similar to the human eye to what we observed among females in
the field. The hypothesis was that the brighter trap (resembling a brighter female) would attract more males than the duller trap. This was tested using a nested ANOVA.

2.3 How do attractive females differ from less attractive ones?

To see how attractive females differed from less attractive females, I collected 26 females from the field and kept them in captivity. While captive, female brightness was monitored and the females were allowed to mate. After mating and death, we measured female size and counted the number of eggs laid. I expected female size, brightness and fecundity to correlate, which I tested using Spearman’s rank correlation.

2.4 Is there evidence of weaker females using better tactics?

When individuals differ greatly in their ability to attract mates, alternative reproductive strategies, such as sexual parasitism, may occur. I used a laboratory experiment to test whether female glow-worms parasitize each other by individually placing field collected females (n=80) in the centre of a long arena with a green LED identical to the ones used in the traps at one end. If females behaved as predicted, they should have moved towards the LED. A linear mixed effects model was used to test if females moved as predicted.

2.5 Can less attractive females outcompete stronger neighbours by using better tactics?

The previous study showed that males were more likely to mate with brighter females (I) and that females moved away from stronger competitors (II). I aimed to discover if and how duller females could gain matings despite this. I created a mathematical model describing the effect of distance to brighter females on how many males a dull female can attract (III). The model predicted that dull females should move away from brighter neighbours to maximise their chance of attracting males.

I conducted a field experiment using a set of seven traps to see whether distance to stronger neighbours had any effect on the proportion of males split between dull and bright traps. The trap set was made using traps similar to the ones used in study I. However, this time the set consisted of one bright trap in the middle surrounded
by six identical duller traps at a distance of one or three metres (in the field around half of all females are closer than 3m to their nearest neighbour, II). We expected to see a difference in the proportion of males in the central bright trap and outer dull traps between the one and three metre setups. Again, a nested ANOVA was the statistical method of choice to test for differences in the number of males caught by central and outer traps between the two treatments.

Fig. 2. Diagram of the experimental setup using traps to study how distance to neighbours affects the number of males each female attracts.

2.6 What is the cost of attracting males?

Glowing is energetically costly (Woods et al., 2007), but how females allocate energy between glowing maintenance and eggs is unknown. Adult glow-worms cannot feed, so they may have to trade-off resource use between reproduction and maintenance. How many eggs a female would lose to excessive glowing or waiting too long to mate is an important question for understanding the evolution of glow-worm signals (IV).

To study if signalling (glowing) reduced female fecundity I collected 47 females from the field and kept them in the laboratory until they died. Half the females were allowed to mate immediately after collection and half after five days. The five-day wait was to increase the amount of time females glowed. While in captivity, the females were kept in 6 hours of darkness and 18 hours of light a day
and their glowing duration and intensity were monitored at approximately 5-minute intervals. Two different rhythms of light were used. In the first, the six hours of darkness were continuous and in the second, there were three two-hour dark periods with 2 hours of light in between before 14 hours of light. Two light rhythms were used because in the field females appear to glow most commonly for a short period after sunset. By providing three “sunsets” in the course of a day, I aimed to triple the glowing output of each female. During the dark periods, females were monitored at five-minute intervals and their brightness was estimated to measure total glowing effort over the course of the experiment. The number of eggs each female laid was counted after the female died. The data was analysed to see if delaying mating by five days or total glowing effort had an effect on the number of eggs a female produced. I used Barnard’s exact test to see if delays had an effect on the likelihood of reproductive failure and logistic regression to see if glowing effort affected fecundity.

Glowing may also have non-energetic costs, for example the light may make females easier to find for predators or parasites (Engqvist, Cordes, & Reinhold, 2015; Zuk & Kolluru, 1998). However, glowing first developed in the glow-worm as an aposematic signal for larvae (De Cock & Matthisen, 2003; Moosman, Cratsley, Lehto, & Thomas, 2009), and only later evolved additional use as a female sexual signal (Branham & Wenzel, 2001). Given that female glowing is the same as larval, but brighter, the same aposematic function may well remain among females. This dual-use shows that studying the costs of ornamentation is much more complicated than is commonly thought as it may be impossible to differentiate between sexual and aposematic signals at times. Whether the glow attracts parasites is unknown. Potential costs of glowing from non-energetic factors are beyond the scope of this thesis.
3 Results

3.1 Do males choose females based on ornamentation and if they do, why?

When testing if males prefer brighter females, the main results were that males did prefer brighter females when given a choice of two dummy females of different brightness and that naturally brighter females were also more fecund and larger (fig. 3 & fig. 4, I). Female size and fecundity varied greatly: between 25 and almost 200 eggs per female. The strength of male preference towards brighter females correlated positively with the magnitude of brightness difference between them (I). This meant that female brightness acted as a reliable signal of fecundity that males utilised.

Fig. 3. Number of males (mean ±SE) attracted by green LED-lights differing in brightness. In treatment a the difference in brightness was 18x and b 2.7x (I).
3.2 Can and do weaker females use alternative tactics to outcompete their neighbours?

I developed a mathematical model and a field experiment to test whether distance between females had an effect on how males chose females (III). The model showed that increasing distance to stronger neighbours increases the number of males a dull female is likely to attract (fig. 5, III). This is due to received signal strength decreasing as distance increases, so by being far away from a stronger female, a dull female appears brighter over a wider area. The field experiment showed that the model’s predictions were valid in nature (fig. 6). When the outer traps were three metres away from the brighter central trap, they caught all the males, leaving the bright central trap without any males, but when the distance was one metre, the central trap also caught a sizeable portion of all males (III). Combined, the model and experiment showed that while signal strength is
important, optimal location can be more important in determining the outcome of sexual competition and that comparison of signals is a vital part of mate choice.

The laboratory experiment (II) showed that females behave according to the model’s predictions and increase distance to brighter dummy females, but remain stationary when there is no competition (Fig. 7.).

Fig. 5. The effect of distance between females on how large a percentage of approaching flying males a dull female can potentially intercept from a brighter female.
Fig. 6. Female distribution between bright central trap and dull outer traps (six outer traps combined) when distance between the traps was varied.
3.3 Costs of signalling

I studied how many eggs a female loses to five days of waiting and how many eggs it loses to glowing to attract males (IV). The main results were: 1. Glowing has such a small effect on energy use that it caused no discernible change to female fecundity and 2. Waiting had a negative effect on fecundity, but only for small females (fig. 8). Small females had a greatly increased risk of complete or near complete reproductive failure if they did not mate very soon after becoming adults leading to a decrease in the average number of eggs produced by small waiting females. In large females, there was no noticeable effect of waiting.
Fig. 8. Body size and number of eggs laid for females that waited for five days for a mate (triangle, dashed line) and females that mated without delay (circle, solid line). Note how only waiting females produced fewer than 20 eggs.
4 Discussion

The main findings of this thesis are: 1. The ability to accurately compare sexual competitors is a key factor of mate choice. If the chosen sex can reduce the accuracy of this comparison, it may have a large effect on mate choice for both males and females (II & III). 2. When competing for mates by using signals, emitted signal strength may be less important than perceived signal strength compared to others in the same population (II). These results are equally valid for both males and females, as they are based on the physical properties of the signals. 3. Female sexual signals provide information on female fecundity and males can choose their preferred mates based on this information (I). 4. The development of sexual ornaments in females may be influenced by the need to reduce time spent unmated instead of as is common in males, increasing the number of matings (IV).

The first field experiment showed that males are more attracted to brighter and thereby larger and more fecund females as mates if given an opportunity to choose (I). As female fecundity varied almost tenfold between the largest and smallest females, males have considerable benefits from preferring larger females. As body size dictates lantern size and thereby brightness, the signal is resistant to dishonesty by small females trying to appear larger than they are. The ornaments signal female size and therefore fecundity to males (Honěk, 1993; Rosenqvist & Berglund, 2011). This shows a contrast to male ornaments. Male ornamentation usually indicates a male’s direct or genetic quality and in some cases quality of parental care (Andersson, 1994; Andersson & Iwasa, 1996).

In my field experiment (III) the bright trap failed to attract any males when it was surrounded by dull traps at a distance of 3 metres, but attracted a decent number when the dull traps were closer. When distances between competitors increased, the chances of a brighter female to be visited first by males declined. This was because the duller female appears brighter to more and more males the further away it is from the brighter female. This in turn may explain why glow-worms are often several metres apart in the field (II): dull females do not benefit from being too close to their neighbours.

One potential criticism of the field experiment (III) is that it is hard to differentiate two possible forms of male behaviour from each other. Males may have preferred the dull traps or they may have opted to visit dull traps first and then fly on to the bright trap, but not been able to due to being trapped. However, if this were the case, the same behaviour would have been expected in all the trapping experiments I did (I&III). Instead, in the experiment with only two traps (I) and
the one-metre set of seven traps (III) males showed a strong tendency to first go to the brightest trap. Only in the three-metre set of seven traps was the result opposite. This does not mean that males were not aiming to visit more than one female before making a choice, but it does show that the order of choice, and therefore, most likely, preference, did change based on signal perception. My results showed that less attractive individuals may increase their chances of attracting a mate relative to more attractive individuals through better positioning simply because the strength of an emitted signal is not the most important aspect of signalling (III). What dictated the outcome of signalling competition is how strong a signal is perceived to be and how it compares to other received signals. Signal perception is affected by the environment that the signal is produced in, the physical properties of the signal and the signal receivers senses (Akre & Johnsen, 2014; Guilford & Dawkins, 1991; Ronald, Fernández-Juricic, & Lucas, 2018). In the case of the glow-worm the inverse square law (Kepler, 1604) dictates how light intensity diminishes over distance. The same law is applicable to many auditory or visual signals that rely on signal strength to relay information. For example, bird calls, frog croaks and possibly lepidopteran pheromone plumes may operate this way.

Comparison of two or more received signals is dependent on both the social environment and the perception of all produced signals in the population. Being able to accurately compare received signals is known to be critical to making behavioural decisions (Akre & Johnsen, 2014). The point that my results make clear is that signal receivers make behavioural choices based on how they perceive the signal in relation to its neighbours. For example, male glow-worms in my experiments quite happily chose a female of medium or even low brightness if there were no brighter females around, but ignored it if they believed another female to be brighter, regardless of which was actually brighter (I&III).

As long as distance cannot be judged accurately (often it can via relative size and comparison to nearby objects), a signal is open to exploitation in the manner of the glow-worms glow. Glow-worms may have problems judging distance to females accurately as the signal is a point source of light in an otherwise dark environment where landmarks may be hard to see. Signals that relay information via other means than signal strength will not be affected this way. For example, the pitch, complexity or duration of a bird’s song remain the same regardless of how far away it is heard from, though signal degradation will also affect these making distance estimates possible.

It is unclear how common taking advantage of the physical properties of signalling systems is. This study only presents one example, but if my results are
general, similar behaviour might be expected in a wide variety of taxa that use any signalling systems that obey the inverse square law. For example, some anuran and bird calls may well be similarly affected. Similarly, the physics of the signals remain the same regardless of whether the signaller is male or female, meaning that this result may be applicable regardless of the direction of mate choice. There are some recorded cases of males gaining mates easier if they maintain more distance to their neighbours (Arak, Eiriksson, & Radesäter, 1990; Telford, 1985). The predicted behaviour in each particular case would depend on the form of signal and whether the animals are capable of moving somewhat freely in three dimensions or not (III).

The field studies on males (I and III) provided contradictory results to the laboratory studies on males (II). In the field, males preferred what they perceived as the brighter, and thereby more fecund, of two females, but in the laboratory no mating preference was visible. There are a number of possible explanations. Firstly, in the field we used artificial females that provided no other signal than their brightness, whereas in the laboratory we used real females. Also, in the laboratory males were placed close enough to females that they may have been able to see other features than female brightness. It is likely that the males in the laboratory based their choice of mate on multiple factors, whereas in the field they made an initial choice based purely on brightness. Use of multiple sequential cues on mate choice has been documented in other taxa (Jennions & Petrie, 1997).

Female glow-worms in my study could lose a large portion of their eggs each day they remained unmated (IV). Glowing proved to have no measurable effect on female fecundity. Using data on energy use during different actions in a closely related species (Woods et al., 2007) and information on the daily life of females allowed me to calculate the relative costs of glowing and waiting. This showed that during the course of a day glowing has a very minor impact on total energy use, while over the course of a day waiting uses at least an order of magnitude more energy than glowing. This provides a novel suggestion for understanding the evolution of female ornamentation: they may have evolved to reduce the time unmated, as waiting is very costly.

A specific set of factors in the glow-worm made it likely for signalling to evolve as a means to reduce time unmated. Firstly, glow-worms are capital breeders, meaning they breed using only resources gathered before the breeding season (Tyler, 2002). Therefore, any costs from signalling or waiting will be highly noticeable, as the animals cannot compensate for the loss of resources. Waiting costs in particular may be high as there is a minimum level of energy use required just to keep an
animal alive, whereas signalling is optional and controllable. This in turn means that anything that reduces waiting time will mean more resources available for reproduction. Secondly, glow-worm males invest heavily into actively searching for females. Previous work has suggested that even a very cheap ornament or signal can have a major effect on reducing waiting time if it makes the bearer easier to find (Kokko & Wong, 2007). This is because if one sex invests heavily into actively searching for the other, anything that makes the searched sex easier to find is going to have a large effect. For example, in the glow-worm males fly in search of mates in the dark. By glowing, females become much easier to find. Thirdly, female glow-worms have evolved greater maximum fecundity by losing their ability to fly in search of males (Lewis & Cratsley, 2008), requiring an alternative way to increase mate encounter rate. As glowing already existed as an aposematic signal for larvae (De Cock & Matthysen, 2003), it probably developed further in parallel with flightlessness to become a sexual signal in larviformous adult females. Females may have greatly benefited from these developments, as losing the ability to fly led to greater maximum fitness and in the process they developed a much cheaper way to attract males than before, glowing.

Female glow-worms developing ornamentation to potentially reduce waiting times before mating suggests a general trend in sexually signalling animals: when signalling costs are low compared to the price of insufficient signalling, signals should evolve to be as powerful as they possibly can. In glow-worm terms, this would mean growing to be as large as possible, which would also lead to a higher total fecundity. However, female size varies greatly and seems to follow the normal distribution suggesting that there are other factors stabilising selection on size. For example there may be variation in the duration of the larval stage leading to differences in adult size (Horne, Horne, & Tyler, 2017). My results on female-to-female competition (II&III) also show that small females have a decent likelihood of attracting males despite their size.

While, by definition, the purpose of sexual ornaments is to attract mates, the evolution female sexual ornaments has often been ignored, explained through male ornamentation, explained by social selection or assumed to have an identical evolutionary basis to male ornaments (Tobias et al., 2012). These views hold true in a number of taxa, but my results (IV) show that, at least in the glow-worm, female ornamentation may have evolved in part to reduce the length of time a female has to wait before mating for the first and often only time.
5 Concluding remarks

My results provide a number of wider conclusions for understanding the development of female sexual signalling. Firstly, unlike male signals, female signals may provide concrete information about a female fecundity allowing males to select the most fecund females first.

Secondly, certain forms of ornamentation are open to exploitation by taking advantage of the physical properties of the signal. This allows weaker individuals to potentially outcompete their stronger rivals potentially allowing a wider range of signal strengths to persist in a population. Variation in ornament quality has been explained before (for example the handicap principle (Zahavi, 1975)), but this study shows that variation may be maintained simply because having a poor ornament is not necessarily going to prevent breeding if the bearer is able to use better tactics than its neighbours.

Thirdly, female signals may have developed not to increase the number of mates a female has, but rather to speed up the arrival of the first mate. While male ornaments have usually evolved through sexual selection to indicate genetic benefits to females, female ornaments may have evolved to reduce waiting time before mating and to compensate for losing the ability to actively search for mates.
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