Amplifiers and the origin of animal signals

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In 1989, Hasson introduced the concept of an ‘amplifier’ within animal communication. This display reduces errors in the assessment of traits for which there is direct selection and renders differences in quality among animals more obvious. Amplifiers can evolve to fixation via the benefit they confer on high-quality animals. However, they also impose a cost on low-quality animals by revealing their lower quality, potentially leading these to refrain from amplifying. Hence, it was suggested that, if the level of amplification correlates with quality, direct choice for the amplifying display might emerge. Using the framework of signal detection theory, this article shows that, if the use of an amplifier is observable, direct choice for the amplifying display can indeed evolve. Consequently, low-quality animals may choose to amplify to some extent as well, even though this reveals their lower quality. In effect, the amplifier evolves to become a signal in its own right. We show that, as amplifiers can evolve without direct female choice and are likely to become correlated with male quality, selection for quality-dependent amplification provides a simple explanation for the origin of reliable signals in the absence of pre-existing preferences.

1. Introduction

Within sexual selection, the evolution of male displays is driven by female mating preferences [1,2]. The cost that a display confers on male viability is overcompensated for by the increase in the reproductive success of displaying males. In 1989, Hasson presented a population genetic model which showed that particular male displays can evolve as a consequence of female mating preferences without the need for direct choice for those displays [3]. This may occur when females initially base their preferences on a cue that is correlated with some quality trait of the male, such as viability, health or foraging ability [4]. If a display amplifies the differences between the cues of the males in the population, it can evolve to fixation. Hasson’s idea is that such a display, or amplifier, reduces the error in the perception of the cue by females and makes differences in male quality more obvious. Specifically, it improves the correlation between the perceived cue and the male’s true quality [5]. This will then allow high-quality males to benefit more from their high-quality cue. On the other hand, a low-quality male may do better not to amplify his cue at all. He stands to gain by concealing his low quality.

The names originally given to displays that either increase or decrease the perception of quality differences among males were ‘amplifiers’ and ‘attenuators’ [6]. We may also speak of ‘revealers’ and ‘concealers’. An amplifier of a signal does not increase the size, strength or impact of that signal, but merely reduces the error in its perception on the receiving end. It reveals, as opposed to conceals, true quality. Certain patterns that reveal body size by making the assessment of size easier have been suggested as examples of amplifiers [7–10]. It is important to remember that, although the discussion of amplifiers is often placed in a sexual selection context, amplification can also occur in parent–offspring conflicts, predator–prey interactions and intraspecific rivalry.

In his article, Hasson describes a two-locus, two-allele, haploid model of amplifiers [3]. The first locus controls the viability of the male, assumed to be a binary component indicating high or low quality. The second determines whether or not it amplifies. Hasson initially assumes that males are able to amplify their
quality cue, but do so independently of their quality. He showed that amplifying displays increase mating success of the more viable males and decrease mating success of the less viable males. Such an unconditional amplifier can evolve if the total benefit to the more viable amplifying males is higher than the total cost to the less viable amplifying males. It follows that the higher the frequency of the more viable males, the more likely it is that the amplifier evolves to fixation.

Hasson argues that, due to the negative effect on low-quality males, selection will favour the evolution of a modifier which reduces the expression of the amplifier in these males [3]. He adds a coefficient to his model which determines the degree of conditional expression of the amplifier in low-quality males. When this coefficient has a positive value, the requirements for the fixation of the amplifier are less restricted by its negative effect on these males. For the extreme case in which low-quality males do not amplify at all, it is shown that the sole requirement for the evolution of the amplifier is that it benefits high-quality males. Although the modelling method in this article is different, a replication of Hasson’s model gives similar qualitative results, described in electronic supplementary material, appendix D.

When an amplifier has a conditional expression, there is a correlation with the male’s true quality. Then, the observation of such an amplifier provides information about the male. Hasson goes on to suggest that this might cause selection to favour the evolution of female choice based on the amplifying display itself, but he does not model this possibility explicitly. Gualla et al. [11] model the evolution of an attractive amplifier that directly appeals to female preferences and show that this attractiveness can benefit females. However, they do not allow for the evolution of those preferences themselves. In their formulation, the amplifier adds a fixed quantity to the perceived attractiveness of a male, with no scope for evolutionary change in female response to the level of amplification.

Here, we use an approach based on signal detection theory to analyse the evolution of amplifiers when females have some ability to assess the use of an amplifying display and can integrate information from both the direct quality cue, possibly amplified, and the level of amplification itself. In other words, we model the process whereby an amplifier is observable and becomes a signal in its own right. Assuming females can assess the level of amplification, do they take it into account? And, if so, how does this change the behaviour of males? Our analysis is an extension of the standard signal detection model to two dimensions of perceived variation, in which a receiver perceives both an error-prone cue indicating the quality of a sender and a second error-prone cue concerning the level of amplification used by the sender. This mathematical framework can also be applied to study handicap signalling combined with a quality cue [12].

The receiver stands to gain by correctly identifying the quality of the sender and by responding appropriately. Let us assume there are two possible responses, $G$ for good and $B$ for bad. The resulting payoff depends on the four possible outcomes within signal detection theory, which are a true positive, a false negative, a false positive and a true negative. For example, a true positive occurs when the receiver responds with $G$ to a truly high-quality sender. The associated payoffs are $b_{TP}$, $b_{FN}$, $b_{TN}$ and $b_{FP}$. Obviously, $b_{TP} > b_{FN}$ and $b_{TN} > b_{FP}$.

The receiver, however, cannot assess the sender’s quality with complete accuracy. Instead, it must rely on an error-prone cue, $P_q$, which stands for the perception of quality. This may take on any value. Let us assume that the perception of quality follows a normal distribution which is centred around the sender’s true quality, but has a variance $\sigma_q^2$ reflecting error in perception. The parameter $\alpha_q$ is a measure of how precisely the receiver can evaluate the quality of the sender.

The sender always stands to gain by eliciting the favourable response $G$ from the receiver. The associated payoff to the sender, $b_{H1}$ or $b_{L1}$, may depend on the quality of the sender. Here, $b_{H1}$ stands for benefit high and $b_{L1}$ for benefit low. If the response from the receiver is $B$, the sender obtains a payoff of zero, regardless of its quality.

The sender will be able to amplify its cue conditional on its type. This means the sender has influence over the receiver’s ability to assess its quality. By increasing the level of amplification, $a$, the sender can reduce the error in the receiver’s perception of its quality, resulting in a lower variance. More precisely, $\alpha_q(a)$ is a function of $a$ and is decreasing in $a$. Equation (2.1) gives the simplest of this type of function.

$$\alpha_q(a) = \frac{\sigma_q}{a}. \quad (2.1)$$

In this model, the level of amplification chosen by the sender is observable to the receiver. However, the receiver’s perception of the chosen level, $P_a$, is error prone, and the observed value for $a$ is randomly taken from a normal distribution with mean equal to the true value of $a$ and variance $\sigma^2_q$. Combining this with the error-prone quality cue, the probability distribution associated with the receiver’s perception follows a bivariate normal distribution, given in equation (2.2).

$$N(P_q, P_a, \sigma_q, \alpha_q) = \frac{1}{2\pi \sigma_q \sigma_a} e^{-\frac{(P_q - \mu_q)^2}{2\sigma^2_q} - \frac{(P_a - \mu_a)^2}{2\sigma^2_a}}. \quad (2.2)$$

The parameter $\sigma_a$ is a measure of the observability of the level of amplification used by the sender. The observability of a trait depends on the trait itself and on the psychology of the receiver [13]. Some types of amplifier, such as colours or patterns, are by nature obvious, efficacious and observable. In these cases, $\sigma_a$ is relatively small and the level of amplification can, in principle, be assessed. Furthermore, as our model will show, receivers benefit from the additional information the amplifier provides, so selection would favour improvements in the psychological aspect of its perception [11]. This may lead $\sigma_a$ to gradually decrease further. The observability of an amplifier need not automatically make it attractive, but it is a requirement for the evolution of preferences for the trait.

We assume amplification is cost free. In electronic supplementary material, appendix B, we speculate what would change if amplification were costly. Here, instead, we assume amplification is restricted to a value between $a_{\text{Min}}$ and $a_{\text{Max}}$. The fact that there is a maximum level of amplification

2. Model and assumptions

In our model, there are two individuals: a sender and a receiver. These two players are drawn at random from large populations. The sender may be either of high quality or of low quality. More precisely, let the value $q$ of the two types of quality be $q_H$ and $q_L$. The proportion of senders with high quality is $0 < p < 1$, whereas the proportion of low-quality senders is equal to $1 - p$. Electronic supplementary material, appendix A includes the extensive form of the model.
makes sense, for example, a pattern can only improve
perception by so much. Similarly, contrasting colours functioning
as amplifiers are restricted by the maximum possible level of
contrast [7]. If we fix \( \alpha_{\text{Min}} = 1 \) and \( \alpha_{\text{Max}} = 2 \), then \( \alpha_q \) is the free parameter which defines the receiver’s ability to assess the level of amplification used by the sender. For the quality axis, the scale is set by \( \alpha_q \). Let us take \( q_1 = 1 \) and \( q_1 = 0 \), and allow \( \alpha_q \) to be the free parameter which defines the receiver’s ability to assess the quality of the sender.

Figure 1 shows the two perception axes that describe the two
cues, \( P_q \) and \( P_p \), assessed by the receiver. It includes two bivariate normal distributions representing a high- and a low-quality sender. The \( z \)-axis in this figure represents the probability density and describes the relative likelihood for these cues to take on a given value. An interactive version is available in the MATLAB notebook which is part of the electronic supplementary material. If the high-quality sender amplifies its quality cue, the error in the quality perception is reduced, resulting in a distribution that is narrower along the \( P_q \) axis. Now, the main question is how the receiver distinguishes between a high- and a low-quality sender.

When the receiver comes across a sender, it tries to assess that
sender’s quality and its level of amplification. Based on the values of the two perceived cues, it has to make a choice of how to respond. The receiver’s strategy consists of a range of values for which it responds with \( G \) and a complementary range of values for which it responds with \( B \). This is expressed in equation (2.3). Let us define the region on the two-dimensional perception space for which it responds with \( G \) as \( R_G \), for region good. Its complement, \( R_B \), stands for region bad.

\[
R_G = R_B^c. \tag{2.3}
\]

Figure 1 shows region \( R_G \) meshed with diagonal lines and bounded by a parabola. All other values on this plane result in the response \( B \). In the next section, we will try to find out what the receiver’s optimal strategy is (i.e. where \( R_G \) and \( R_B \) lie). We will find out that, indeed, these regions are separated by a parabola-shaped boundary dependent on the model’s parameters and on the senders’ chosen levels of amplification. A simpler model with unobservable amplification is presented in electronic supplementary material, appendix D and may illuminate some of the mathematics of the following section.

### 3. Methods

The payoff the receiver obtains when it correctly identifies a high-
quality sender, by responding with \( G \), is \( b_{TP} \). The probability of a perceived sender being of high quality is given by the appropriate bivariate normal distribution, multiplied by the proportion of high-quality senders, \( p \). Therefore, the expected payoff of correctly identifying a high-quality sender is equal to \( b_{TP} \) weighted by its probability; the double integral of the bivariate normal distribution over region \( R_G \) multiplied by \( p \). Similar calculations follow for the incorrect identification of a high-quality sender and for the identification of a low-quality sender, leading to the receiver’s expected payoff, \( E_p \), as described in equation (3.1).

\[
E_p(R_G) = b_{TP} \int R_G N(p_f, p_e, 1, \alpha_q, \sigma_q, \sigma_p) dP_p dP_q + b_{TN} \int R_G N(p_f, p_e, 1, \alpha_q, \sigma_q, \sigma_p) dP_p dP_q + b_{TP}(1 - p) \int R_G N(p_f, p_e, 0, \alpha_q, \sigma_q, \sigma_p) dP_p dP_q + b_{TN}(1 - p) \int R_G N(p_f, p_e, 0, \alpha_q, \sigma_q, \sigma_p) dP_p dP_q. \tag{3.1}
\]

To find out how the receiver should best respond (i.e. what \( R_G \) is optimal) let us define \( t = \partial R_G \) as the boundary of the region. Using differentiation under the integral sign, we can see how changes in this boundary affect the receiver’s payoff. This is described in more detail in electronic supplementary material, appendix B. In this two-dimensional signal detection model, the optimal \( t \) can be described as a function of \( P_q \), as in equation (3.2).

\[
t(P_q) = \frac{\alpha_{\text{Hi}} + \alpha_l}{2} + \frac{\alpha_{\text{Hi}}^2 \sigma_q^2}{2(\alpha_{\text{Hi}} - \alpha_l) \sigma_q^2} \log |K| - \frac{\alpha_{\text{Hi}}}{\alpha_{\text{Hi}} - \alpha_l} \frac{\sigma_q^2}{\sigma_q^2} p + \frac{\alpha_{\text{Hi}} + \alpha_l}{2} \frac{\sigma_p^2}{\sigma_q^2} q. \tag{3.2}
\]

Here, we made use of a new parameter, \( K \), defined in equation (3.3). Following Johnstone, the parameter \( K \) represents the receiver’s incentive to respond and is a measure of the relative costs and risks of false positives and false negatives [14]. The parameter \( K \) is an ‘amplified’ version of \( K \).

\[
K = \frac{\alpha_{\text{Hi}}}{\alpha_l} p b_{TP} - b_{TN} \tag{3.3}
\]

The optimal strategy for the receiver consists of a region \( R_G \) for which it responds to the sender with \( G \) and a complementary region \( R_B \) for which it responds with \( B \). These are defined by the optimal threshold \( t(P_q) \), as shown in equation (3.4).

\[
R_G = \{P_q, P_e \in \mathbb{R}^2 | P_q > t(P_q)\}. \tag{3.4}
\]

Whenever the perceived quality of the sender falls below the threshold value \( t \), when it falls in region \( R_B \), the receiver responds with \( B \). If \( K \) increases, threshold \( t \) moves to lower values. This means the receiver will respond more favourably to the sender by associating a wider range of values with a high-quality individual. The parameter \( K \) can increase if the proportion of high-quality senders, \( p \), increases or when the payoffs change such that the receiver has a larger incentive to respond favourably. Figure 1 shows this threshold for \( K = 1 \).

To find out how the sender should best respond (i.e. what level of amplification is optimal), let us examine its expected payoff, \( E_s \). Given the receiver’s strategy, this payoff is a function of the chosen level of \( a \), shown in equation (3.5).
Here, the integral is again performed over two variables, where $b_L \in \{b_L, b_h\}$ and $q \in \{1, 0\}$.

$$E_3(a) = b_L \int_{R^2} \mathcal{N}(P_q, P_q, q, a, \frac{a_0}{d}, a_0) \, dP_q \, dP_0.$$  \hspace{1cm} (3.5)

The best response of the sender to the receiver’s strategy is to increase its level of amplification if this increases its expected payoff and decrease it otherwise. Looking at figure 1, this coincides with getting as much probability density within region $R_2$ as possible. At equilibrium, the sender maximizes its payoff, holding the receiver’s strategy constant. We cannot obtain a closed form for the integral in equation (3.5); however, we can use it to numerically estimate the optimal strategy of the sender. This is described more fully in electronic supplementary material, appendix B. The optimal level of amplification is independent of $b_L$ and $b_h$.

4. Results

The behaviour predicted by our model depends on the values of the model’s parameters. We describe optimal behaviour as a pair $(a_L, a_h)$ where $a_L$ is the level of amplification chosen by a high-quality sender and $a_h$ is the level chosen by a low-quality sender. Figure 2 depicts part of parameter space and shows the various zones that result in qualitatively different behaviour. A detailed description of the methods leading up to this figure is presented in electronic supplementary material, appendix C. It can be seen that, at equilibrium, the high-quality sender amplifies either at the maximum or at the minimum level, $a_{Max}$ or $a_{Min}$. The low-quality sender chooses a level of amplification along this range, $a_{Min} \leq a_L \leq a_{Max}$ depending on the model’s parameters. As $k$ always enters the equations inside a log, it is most useful to depict parameter space as a function of $\sigma_0$, $\sigma_a$ and $\log[K]$. By setting $a_L = 6$, we can show part of parameter space in two dimensions.

There are three numbered lines in figure 2 which carve out different zones in parameter space. Line 1 separates a zone for which the low-quality sender does not amplify at all, $a_L = a_{Min}$, and a zone for which it amplifies at least partially, $a_L > a_{Min}$. This line is the only one dependent on $\sigma_a$ and moves upwards for higher values of $\sigma_a$. Below this line, $\sigma_a$ is low and $\sigma_a$ is high, and the receiver pays relatively more attention to the quality cue than to its assessment of the level of amplification. In this case, for the low-quality sender, the cost of amplifying in terms of revealing its low quality is higher than the benefit of amplifying in terms of resembling a high-quality sender. Therefore, the low-quality sender will not want to amplify and equilibria for which $a_L = a_{Min}$ are stable. Above this line, the balance changes and the low-quality sender will benefit by amplifying at least partially.

Line 2 of figure 2 separates a zone for which the low-quality sender amplifies maximally, $a_L = a_{Max}$, and a zone for which it amplifies below this level, $a_L < a_{Max}$. If both types of sender amplify at the same maximum level, the receiver cannot use this level to discriminate between the two types. It will solely pay attention to the quality cue. With identical levels of amplification, the behaviour of the receiver is the same as predicted by our model with unobservable amplification, described in electronic supplementary material, appendix D. When $\log[K]$ and $\sigma_a$ are high, the receiver is very lenient. It then responds favourably to perceived quality cues below the mean of the low-quality sender. This results in an incentive for the low-quality sender to increase its level of amplification. Therefore, to the right of this line, the $(a_{Max}, a_{Max})$ equilibrium is stable. On the left side of this line, the low-quality sender will amplify at a lower level.

Finally, line 3 of figure 2 separates a zone for which the high-quality sender always amplifies maximally, $a_H = a_{Max}$, and a zone for which not amplifying, $a_H = a_{Min}$, becomes a second, stable equilibrium. Which one the model ends up in depends on the starting point of the dynamics and on the basins of attraction of the equilibria. If both types of sender amplify at the same, minimum level, the receiver cannot use this level to discriminate between the two types. It will solely pay attention to the quality cue. Furthermore, when $\log[K]$ is negative and $\sigma_a$ is high, the receiver is fairly cautious. Without any amplification, it only responds favourably to perceived quality cues above the mean of the high-quality sender. This results in an incentive for the high-quality sender to decrease its level of amplification. Therefore, the $(a_{Max}, a_{Min})$ equilibrium is stable. With some amplification, the receiver’s strategy changes and it takes into account the sender’s level of amplification. This results in an incentive for the high-quality sender to decrease its level of amplification. Therefore, the $(a_{Max}, a_{Min})$ equilibrium is also stable. On the right side of this line, the high-quality sender will always increase its amplification up to the maximum level.

It is interesting to see how the optimal levels of amplification change as $\sigma_a$ decreases. The parameter $\sigma_a$ is a measure of the receiver's ability to assess the level of amplification used by the sender. Starting from unobservable amplification, which is equivalent to a very high $\sigma_a$, receivers may evolve the ability to assess the senders’ quality via their use of an amplifying display. Figure 3 plots the relative difference, $\Delta a$, between the level of amplification of the high and the low-quality sender. The variable $\Delta a$ is defined in equation (4.1). It is assumed that the model is always in an equilibrium where the high-quality sender amplifies maximally (i.e. the separating equilibrium).

$$\Delta a = a_{Max} - a_L. \hspace{1cm} (4.1)$$

Figure 3 shows that, as $\sigma_a$ decreases, the low-quality sender will amplify at a higher level and the difference with the high-quality sender, $\Delta a$, decreases. Electronic supplementary material, figure C.2 extends this for various values of $\sigma_a$ and $\log[K]$, and shows that, as $\log[K]$ increases, the receiver has a higher incentive to respond favourably and the low-quality sender is generally likely to amplify its cue more. Furthermore, when $\sigma_a$ increases, the receiver pays relatively more attention to the use of the amplifier, resulting in the low-quality sender choosing a higher level of amplification.

Figure 2. Zones of equilibria for $\sigma_a = 6$, $a_{Min} = 1$ and $a_{Max} = 2$. 

<table>
<thead>
<tr>
<th>Zone</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>$a_L = a_{Min}$</td>
</tr>
<tr>
<td>2</td>
<td>$a_L &lt; a_{Max}$</td>
</tr>
<tr>
<td>3</td>
<td>$a_L = a_{Max}$</td>
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that female choice that is based on variance in a display’s expression must be sufficiently common before the onset of the display [16,17]. High initial frequency of choice is usually explained by pleiotropy, genetic drift or sensory biases [16–21]. The evolution of amplifiers provides another route for the evolution of preferences. Direct female choice for any display can evolve more easily after the display already exists and after the degree of its expression is correlated with quality. As amplifiers can evolve without direct female choice and are likely to become correlated with male quality, they can set off the evolution of sexual displays.

Whether females have evolved a preference for amplifiers can be seen from the shape of the threshold boundary. As shown in figure 1, senders with higher levels of amplification are responded to more favourably. Once direct female choice for an amplifier has been established, the conditions may lead to a Fisher runaway process or to handicap signalling [22]. Handicap signalling was first described in economics in Spence’s signalling model [23]. Within biology, it was independently suggested by Zahavi using verbal arguments and modelled by Grafen [24–27]. Although the concept is a well-established theory of conspicuous male display, like the Fisher runaway process, it requires direct female choice well before it pays males to produce such a display. One of the main contributions this article hopes to make is to provide a formal description of a route to the origin of preferences (i.e. to show how female choice for a display can evolve).

The classification of displays has been the subject of many works [1,11,28,29]. Understanding the various types of displays is not easy and drawing clear boundaries is often unnatural [11]. M. Maynard Smith [29] suggested defining terms in relation to models and their assumptions. In this sense, there would seem to be a clear distinction between signals, which are the focus of direct receiver preference, and amplifiers, which are not themselves assessed or chosen, but influence the assessment of other traits. Even in terms of abstract modelling, however, our present analysis suggests that it is hard to distinguish clearly between signals and amplifiers, as the same trait may come to play both roles. Moreover, in the real world, it will probably often prove difficult to separate the amplifying aspect of a display from the signalling component. It is an open challenge to empiricists to determine whether amplifiers are actually applied in any type of animal interaction and whether there is direct choice for these displays. The specific predictions of our model may help focus such empirical investigation.

First, we predict that, at equilibrium, there will be a direct correlation between the amplifier and female preference. There are also correlations between the quality cue and female preference, and between male quality and the amplifier. Note that heteroscedasticity should be expected due to the effect of the amplifier on quality assessment. As the amplifier itself is attractive, manipulating its expression in an experiment should both positively affect the average attractiveness of the manipulated individuals and the correlation between the quality cue and female preference in the population. It is likely that low-quality males become less attractive with increased levels of amplification as their quality cue then better reveals their low quality. They may, however, become more attractive if females place emphasis on the use of the amplifier. In fact, a combination of both these effects takes place, possibly having a neutral impact on overall attractiveness. This is not the case when amplification is unobservable; higher levels of amplification then unambiguously leads to a lower attractiveness for

5. Discussion

Within sexual selection, our model can be interpreted to show that males will display an amplifier even when there is no direct female choice for that display. When there is conditional expression of the amplifier, and it thus correlates with male quality, it pays females to be able to assess the use of the amplifier. The observability of the amplifier need not automatically make it attractive [5,11]. However, as a consequence of the correlation with quality, it allows for direct choice to evolve. With increased precision of the amplifier assessment, females may not only base their mating decisions on the quality cue they perceive but also on the sender’s chosen level of amplification. In a sense, the amplifier thus becomes a signal in its own right.

One consequence of amplifiers evolving a conditional expression is that this can potentially remove the theoretical difficulty of explaining the origin of direct female choice for a male display. Previous models of sexual selection show how the amplifier information decreases for very low \( s_a \) level of amplification decreases. Figure 3 shows, as a dashed line, how the amplifier information decreases for very low \( s_a \).

The information conveyed by the quality cue is independent of \( s_a \). However, the dotted line in figure 3, representing its information content, does go up as receivers evolve the ability to assess the senders’ level of amplification. This is because senders will amplify their cue more as \( s_a \) becomes smaller. By definition, the effect of amplification is that the error in the perception of quality goes down. As such, the information content of the quality cue tends to go up with lower values of \( s_a \).

Figure 3. As \( s_a \) decreases, the receiver becomes better at assessing the level of amplification chosen by the sender. The figure shows, for \( \log(1+K) = 0 \) and \( s_a = 1 \), the equilibrium of the relative difference in these levels for the high- and the low-quality sender, \( \Delta \sigma \), as a function of \( s_a \) (solid), as well as the information content in bits of the two cues obtained by the receiver: quality information (dotted), amplifier information (dashed) and both cues combined (dot dashed).
low-quality males. In practice, it may prove hard to distinguish between these two cases.

To illustrate the type of amplification described by our signal detection model with observable sex differences, let us look at a speculative example. In pipefish, Syngnathus typhle, sex roles are reversed and it is the males who select females [8]. Female body size is an important measure for males, as larger females can produce large, energy-rich eggs. Females have a sexual display, a crosswise striped pattern along their body. They can increase or decrease the contrast of this pattern within a minute, allowing for quality-dependent expression of the trait. In a psychological experiment, using human students as observers, it has been shown that this pattern can facilitate the assessment of width of a rectangle [8]. If the same applies to pipefish, males will find it easier to assess body size of females who show this amplifying display. In an experiment manipulating the display by painting females and by controlling for sexual dance movements by sedating them and moving them in a dance-like fashion by a motor, males preferred the painted females over the control group [9]. This suggests that if the pattern indeed functions as an amplifier, it is an easily observable trait for which there is direct preference.

Female choice is not the only selection mechanism conceivable which may be responsible for the evolution of amplifiers. Amplifiers can emerge in any communication interaction in which one player wishes to obtain information about another player. It may even occur in economics [30]. Situations other than sexual selection in which animal communication is important are, for example, parent–offspring conflicts, predator–prey interactions or intraspecific rivalry. Consequently, there may be driving forces other than female preferences behind the evolution of amplifiers. We conclude that the obervability of amplifying displays can be an important feature for the evolution of the preferences of predators and rivals as well as those of mates, and may help us better understand the origin of many types of animal signals.

Data accessibility. The Mathematica calculations supporting this article have been uploaded as part of the electronic supplementary material.

Authors’ contributions. L.B. performed the calculations and wrote the majority of this article. R.A.J. came up with the idea of analysing observable amplification using signal detection theory, oversaw the modelling work and wrote part of this article.

Competing interests. We have no competing interests.

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Authors’ contributions. L.B. performed the calculations and wrote the majority of this article. R.A.J. came up with the idea of analysing observable amplification using signal detection theory, oversaw the modelling work and wrote part of this article.

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