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Review

A receiver–signaler equilibrium in the evolution of communication in noise

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Abstract

Communication in noise differs in a fundamental way from communication without noise, because a receiver faces four possible outcomes every time it checks its input. These outcomes present inevitable trade-offs for a receiver in adjusting its threshold for response. A signaler also faces trade-offs, in this case between costs and benefits as the exaggeration of signals increases. Furthermore, a receiver's and signaler's performances are mutually interdependent. The utility of a receiver's threshold depends on the signaler's exaggeration (the level of the signal in relation to the level of noise), and the utility of a signaler's exaggeration depends on the receiver's threshold. Diminishing returns for both receiver and signaler suggest the possibility of a joint evolutionary equilibrium for a receiver's threshold and a signaler's exaggeration. The present analysis combines previous expressions for the utility of a receiver's threshold (U_{r}) and the utility of a signaler's exaggeration (U_{s}) in order to explore the possibility of this joint equilibrium. Utilities for both parties are expressed as survival $\times$ fecundity, an approximate measure of the spread of genes associated with a phenotype. Thus, U_{r} and U_{s}, as functions of both the receiver's threshold (t) and the signaler's exaggeration (e), represent the adaptive landscapes for each party, and the reciprocal partial derivatives of these utilities, $\partial U_{\mathrm{r}}/\partial e$ and $\partial U_{\mathrm{s}}/\partial t$, approximate the selection gradients for the receiver's threshold and the signaler's exaggeration. With parameters for both the receiver's and the signaler's performances set to plausible values for many cases of mate choice, the resulting analysis shows that there exists a joint optimum for the receiver's threshold and the signaler's exaggeration. This optimum is a Nash equilibrium at which neither party can do better by a unilateral change in behavior. In some conditions, the equilibrium for communication in mate choice occurs at a higher threshold and higher exaggeration than the equilibrium for communication with warning signals. In general, these results indicate that the normal situation for communication in noise is honesty with deception — honesty on average but with instances of disadvantageous outcomes for receivers or signalers. Furthermore, the relationship between honesty and costs is more complex than currently recognized. Most important, the joint optimum for receiver and signaler indicates that communi-

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cation in noise cannot escape the problems created by noise. Noise is an inevitable component of communication, and perfection in communication is not expected in natural conditions.

Keywords
signal detection, correct detection, false alarm, missed detection, signal exaggeration, mate choice, warning signal, signal costs, honesty, deception, sexual selection, evolution of communication.

1. Introduction

Questions about the evolution of communication have proliferated in recent decades, since Dawkins & Krebs (1978) emphasized that signalers and receivers often have conflicting interests. Since then theoretical, observational and experimental studies have dealt with questions such as, do signals communicate information?, what ensures honesty?, how do signaler and receiver converge on similar meanings of signals?, and how can communication evolve when signalers have no benefits in the absence of appropriate receivers and vice versa? During the same decades, investigations of mate choice and prey choice have also proliferated. These interactions consist primarily of communication, so some of the same questions arise in their study. In this welter of recent work on the evolution of communication, almost none has considered the consequences of noise.

Noise has featured more prominently in research on signal design, the properties of signals that minimize attenuation and degradation and maximize contrast with the background. The underlying objective of this research has been to explain how signals might evolve to increase the efficacy of communication in noise (Wiley & Richards, 1982; Endler, 1992; Brumm & Naguib, 2009). Theory has also addressed the consequences of noise for the evolution of communication. This work has identified the principal manifestation of noise — variable responses to a signal. It turns out, however, that statistical variance in responses does not change the equilibria of evolution (the evolutionarily stable states), so long as the mean response does not change (Grafen, 1990; Johnstone & Grafen, 1992).

In parallel with this work on the evolution of communication, the theory of signal detection in noise has developed in the past half century into a vast literature (Green & Swets, 1966; Macmillan & Creelman, 1991; Macmillan, 2002). Originally applied to procedures for evaluating the performance of receivers in psychophysical experiments, it now provides the rationale for analyzing responses in a wide range of psychological studies.

Signal detection theory has more recently been extended to the evolution of receivers (Wiley, 1994, 2006). This approach suggests that the performance of receivers should evolve in accordance with the payoffs for erroneous and correct responses. It becomes clear that parameters critical for evaluating a receiver's performance are rarely if ever measured in studies of communication. Yet even if the theory of signal detection can help to explain the behavior of receivers, it cannot provide a complete explanation for the evolution of communication, because the optimal behavior of receivers depends on the behavior of signalers. Signalers influence the relationship of signal to noise for receivers, by altering the intensity, attenuation, degradation, and contrast of signals. On the other hand, the behavior of receivers alters the probability of responses to signals. The question, thus, remains: How does the interaction of signaler and receiver evolve?

The purpose of this paper is to combine the theory of signal detection with a model of signal production to explore the co-evolution of signaler and receiver. Because the ramifications of this topic are so numerous, the analysis here focuses on a particular case — communication in mate choice. It assumes the prevalent situation in which males produce signals to induce females to mate with them, and females can respond to these signals. Males, the signalers, incur benefits and costs as a result of producing signals, and females, the receivers, incur benefits and costs as a result of their responses. Unlike previous treatments of this situation, the present approach assumes that females must make their decisions in the presence of noise. In other words, females sometimes make errors in their responses to signals.

In this approach a receiver's optimal threshold for response depends on the intensity of the signal in relation to noise, in other words, the signal/noise ratio or the exaggeration of the signal. Conversely, the signaler's optimal level of exaggeration depends on the receiver's criterion for response, in other words, its selectivity or choosiness or, in simple cases, its threshold for response. A search of these optima reveals a joint optimum, a Nash equilibrium, at which each party does the best it can, provided the other does the same. The location of this joint optimum depends on the payoffs for the receiver and the signaler and on the probabilities of signaling and paying attention, by the signaler and the receiver, respectively.

Under plausible conditions for mate choice, there is a joint optimum with a higher threshold for a receiver (greater choosiness) and a higher level of exaggeration for a signaler than in other examples of communication, such as warning calls in the presence of a predator. At the joint optimum, communication overall is honest, although in particular instances of communication receivers remain susceptible to deception by inappropriate signalers and signalers remain susceptible to exploitation by inappropriate receivers (such as eavesdroppers, predators, or parasites). The evolution of communication in noise, thus, reaches a joint optimum that falls short of perfection. The equilibrium is not a Pareto point, at which neither party can do better. Receivers sometimes make mistakes, and signalers are sometimes frustrated.

2. Methods

2.1. The signal detection paradigm

The feature of signal detection that makes a joint optimum of signaler and receiver possible is the inescapable trade-offs faced by a receiver in deciding whether or not to respond (Wiley & Richards, 1982; Wiley, 1994). The characteristic of noise is two distinct kinds of error by receivers, errors of commission and omission. Noise is not just an increase in variance of responses. On the contrary, it is impossible to minimize the two kinds of error simultaneously. Decreasing the probability of one increases the probability of the other.

This trade-off is apparent in a diagram of signal detection in noise (Figures 1 and 2). A signal in this case is any pattern of energy or matter that evokes a response more often than randomly but does not provide all of the power for the response. Because the receiver provides some, often most, of the power for the response, the receiver must decide when to respond. A receiver must, therefore, consist of three components: a sensory mechanism, a mechanism to associate activity in the sensor with a particular response, and a mechanism to amplify the response. A receiver's sensor has a mean level of activity (with a variance) in the absence of a signal. A signal provides enough power to raise this level of activity, so that during a signal the activity in the sensor has a higher mean level and (if the signal includes its own variation) a higher variance (for further discussion of these points, see Wiley, 1994, 2006, 2013a, b).

A receiver in this situation must adopt some criterion for a response. The simplest criterion is a threshold (Figure 1). If activity in the sensor exceeds the threshold, the receiver responds. Otherwise, it does not. Note

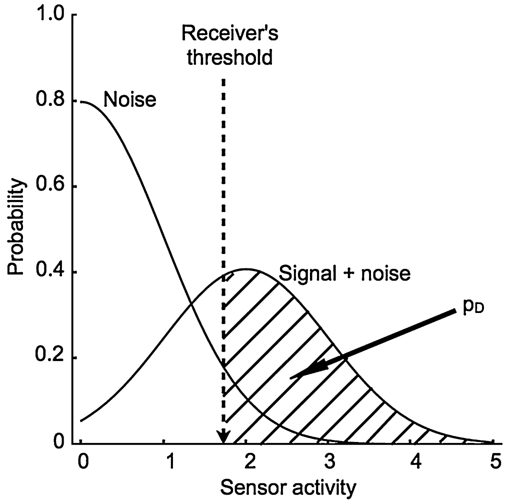


Figure 1. An example of signal detection in noise. The receiver's sensor has a probability distribution of activity for noise only and for noise plus a signal. In this example, these probability distribution functions (PDFs) have means = 0.0 and 2.0, respectively, and standard deviations = 1.0. The receiver sets a criterion for response, in this case a threshold level of activity in its sensor. This threshold in combination with the PDFs for noise and signal plus noise determine the probabilities of correct detection (p_{D}, the hatched area to the right of the threshold under the PDF for signal plus noise), false alarm (p_{F}, the area to the right of the threshold under the PDF for noise only), missed detection, and correct rejection (p_{M} and p_{R}, the areas to the left of the threshold under the PDFs for signal plus noise and for noise only, respectively). The hatched area, corresponding to p_{D}, provides an example of how one of these probabilities is calculated. If the receiver increases its threshold for response, p_{F} decreases but p_{M} increases (also p_{D} decreases and p_{R} increases). If it lowers its threshold, the consequences reverse.

that the receiver only 'knows' two states of the world — sensor-activity-above-threshold or not. It is reasonable to presume that receivers can evolve a threshold at any level of sensor activity. Wherever the threshold is located, a receiver faces four possible outcomes each time it checks the activity of its sensor (in other words, pays attention) and decides to respond or not (Figure 1). If a signal is present and activity in the sensor is above threshold, the receiver responds, an instance of a correct detection (D). If activity in the sensor at that moment is below the threshold, the receiver fails to respond, a missed detection (M). When a signal is not present, two corresponding possibilities arise, either a false alarm (response but no signal, F) or a correct rejection (no signal, no response, R). Provided the distribution of activity by the sensor in the presence of a signal overlaps the distribution in the absence

		Receiver's decision	
		Response	No response
Signal	Present	CORRECT DETECTION	MISSED DETECTION
	Absent	FALSE ALARM	CORRECT REJECTION

Figure 2. The exhaustive set of mutually exclusive outcomes each time a receiver samples its sensor and decides to respond or not. If the receiver benefits on average from its decisions (usually because a correct detection has advantages for the receiver), then two of the outcomes (false alarm and missed detection) are usually errors with disadvantages for the receiver.

of a signal, there are four possible outcomes every time a receiver checks its sensor (Figures 1 and 2).

Inspection of Figure 1 shows that a receiver can reduce its probability of a missed detection by lowering its threshold, but it thereby increases its probability of a false alarm. Raising its threshold can decrease false alarms but inevitably increases missed detections. Whenever noise and signal cannot be completely separated by the receiver's sensor, the two kinds of error cannot be concurrently minimized.

This model incorporates the essential feature of signal detection, the inevitable trade-off faced by a receiver. There are several points that need emphasis. First, noise is pervasive in communication. It is likely that all communication in natural situations occurs in the presence of overlapping distributions of noise with and without a signal. This expectation is reinforced by a result of the present analysis, which indicates that the joint optimum for signaler and receiver is unlikely to result in perfect communication. Diminishing returns of the approach to perfection guarantee noisy communication.

Second, an error by a receiver, in any analysis of the evolution of communication, is a decision that does not increase as much as possible the spread of its genes. An approximate measure of the spread of genes is the expected number of individual's genes in the next generation (its survival $\times$ fecundity). If a correct detection of a signal increases the receiver's survival or fecundity, but a missed detection or false alarm decreases them, then the latter two decisions are errors by the receiver.

Third, a receiver's criterion for a response can vary in complexity. A criterion for response might be a simple threshold, or it might be sophisticated human cognition. A criterion can be a highly tuned filter for particular features of stimulation. The complexity or selectivity of a criterion does not, however, change the inevitability of noise nor the trade-off between false alarms and missed detections (for more discussion of these points see Wiley, 1994, 2006).

2.2. The receiver's optimal performance

The first step in understanding the evolution of communication in noise is to find the optimal location of the receiver's threshold. To do so, it is necessary to define the overall utility of any threshold in terms of the receiver's survival × fecundity, the expected number of an individual's genes passing to the next generation. If fecundity and survival vary with the location of the receiver's threshold, then this product is a measure of selection on the location of the threshold. Because the four possible outcomes whenever a receiver checks its sensor are an exhaustive classification of mutually exclusive alternatives, the expected utility of a particular threshold is the sum of the probabilities of each outcome and its payoff (with each payoff expressed as survival × fecundity). The receiver's expected utility is thus:

$$U_\mathrm{r} = p_\mathrm{s}(p_\mathrm{D}d_\mathrm{r} + (1 - p_\mathrm{D})m_\mathrm{r}) + (1 - p_\mathrm{s})(p_\mathrm{F}f_\mathrm{r} + (1 - p_\mathrm{F})r_\mathrm{r})$$

where p_s = probability of a signal in a (usually brief) interval of time, p_D = probability of a correct detection (D) provided a signal has occurred, $1 - p_\mathrm{D}$ = probability of a missed detection (M) provided a signal has occurred, p_F and $1 - p_\mathrm{F}$ are analogous probabilities for a false alarm (F) and a correct rejection (R), the two possible outcomes when a signal has not occurred. d_r, m_r, f_r and r_r are the payoffs for the four outcomes, D, M, F and R (Table 1).

A receiver must receive a net benefit on average as a result of participating in communication, otherwise selection would eliminate responding to the signal. Consequently, some of the four outcomes must provide a positive payoff. Normally a correct detection would have the highest payoff in comparison to a correct rejection. In contrast, the two kinds of error, false alarm and missed detection, would often have adverse consequences and, thus, low payoffs in comparison to a correct rejection.

The optimal threshold for a receiver is the one that maximizes its expected utility, U_r. A previous analysis of the receiver's operating characteristic

Table 1.
Parameters for the analysis of communication in noise (with default values for communication in mate choice when not otherwise specified in the text).

Properties of noise	
Mean level of noise in the receiver's sensor = 0	
Standard deviation of noise = 1.0	
Receiver's parameters	
U_{r}	Receiver's overall utility
d_{r}	Payoff for a correct detection (D) = 2.0
m_{r}	Payoff for a missed detection (M) = 1.0
f_{r}	Payoff for a false alarm (F) = 0.5
r_{r}	Payoff for a correct rejection (R) = 1.0
p_{D}	Probability of a correct detection
p_{M}	Probability of a missed detection ($= 1 - p_{\mathrm{D}}$)
p_{F}	Probability of a false alarm
p_{R}	Probability of a correct rejection ($= 1 - p_{\mathrm{F}}$)
t	Location of the receiver's threshold (level of activity in a sensor >0)
p_{s}	Probability of a signal occurring in any unit of time = 0.5 (see also below)
Signaler's parameters	
U_{s}	Signaler's overall utility
b_{s}	Benefit as a result of a correct detection by a receiver = 2.0
n_{s}	Benefit when a receiver does not respond to a signal = 1.0
s_0	Proportionate change in survival when no signal is produced = 1.0
c_{m}	Marginal change in survival as a result of producing a signal = −0.01
s_{s}	Survival as a result of producing a signal ($= s_0 + c_{\mathrm{m}}e$)
p_{s}	Probability of producing a signal in any unit of time = 0.5
e	Exaggeration (level or magnitude) of a signal > 0
Alteration of a signal during transmission (not included in the current analysis)	
Attenuation (relative reduction of signal level or exaggeration) = 1.0	
Degradation (relative increase in signal variance) = 1.0	

(ROC) showed that, for a particular signal/noise ratio, the optimal threshold depends on the slope of the indifference curve tangential to the ROC (Wiley, 1994):

$$(1 - p_{\mathrm{s}})(r_{\mathrm{r}} - f_{\mathrm{r}})/p_{\mathrm{s}}(d_{\mathrm{r}} - m_{\mathrm{r}}).$$

The optimal threshold is high when this slope is high and, thus, p_{s} and $(d_{\mathrm{r}} - m_{\mathrm{r}})/(r_{\mathrm{r}} - f_{\mathrm{r}})$ are low, and the optimal threshold is low when these parameters are low. A low threshold is termed 'adaptive choosiness', because missed detections are relatively frequent (but false alarms are infrequent).

A low threshold is 'adaptive gullability', because false alarms are frequent (but missed detections are not) (Wiley, 1994).

A more general analysis, presented below, calculates U_r as a function of both the receiver's threshold (t) and the level of the signal (its exaggeration, e) in relation to the noise in a receiver's sensor,

$$U_r = f(t, e).$$

For this analysis, the level of activity in a receiver's sensor in the presence of noise is assumed to have a truncated normal probability density function (PDF) with mean = 0 and standard deviation = 1.0 (Figure 3). Thus, levels of activity in the sensor when a signal is present are scaled with respect to a the standard deviation of noise in the sensor (a level of 2.0 in the presence of a signal means that the difference between the mean levels of noise and of signal plus noise is twice as great as the standard deviation of noise alone). The analysis assumes that a signal does not increase the variance (as opposed to the mean) of the activity of the receiver's sensor. In other words, it assumes

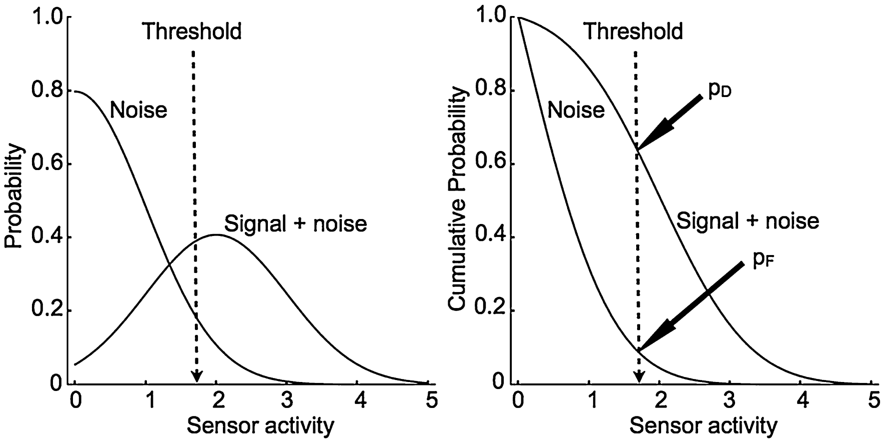


Figure 3. Examples of truncated normal distributions. The normal distribution (error function) expresses point probabilities for values between $-\infty$ and $+\infty$ and has a cumulative probability of all possible values = 1.0. Activity in any receiver's sensor, in contrast, only takes values $\geqslant 0$. These truncated normal distributions express probabilities in proportion to the cumulative probability for values $\geqslant 0$. This proportionality preserves the cumulative probability = 1.0 for all possible values of sensor activity. Possible probability density functions and cumulative density functions of activity in a receiver's sensor are shown for noise and for signal plus noise. An example of a receiver's threshold is also shown. The CDFs for a level of activity in the receiver's sensor at the threshold indicate p_F or p_D, in the cases of noise only or signal plus noise, respectively.

there is no additional variation introduced by the signaler, by transmission, or by transduction in the sensor. This assumption is discussed further below.

For any level of signal plus noise, it is possible to find the level of the receiver's threshold that maximizes its expected utility by solving the partial differential equation,

$$\partial U_{\mathrm{r}}/\partial t = 0, \quad e \text{ constant},$$

and checking the second derivative or inspecting $U_{\mathrm{r}} = f(t)$ for all relevant levels of signal plus noise, e. Note that for every level of activity in the receiver's sensor, e, the probabilities of the four outcomes require recalculation. As a consequence the equation above can only be solved with numerical methods. Mathematica 8.0.4 was used to find these solutions. A combination of procedures D, FindRoot and Max yields the same results as procedure FindMaximum.

2.3. *The signaler's optimal exaggeration*

The signaler can evoke a response from an appropriate receiver by producing a signal with enough power to affect activity of the receiver's sensor. It is plausible to assume a proportionality between the level of the signal produced by the signaler and the level of activity in the receiver's sensor. Although signals are normally affected by spherical spreading and attenuation during transmission, nevertheless the power arriving at a receiver at any distance remains proportional to the power at the source (despite the disproportionate decrease in power with distance). The level of the signal at the source is, therefore, called its exaggeration.

The production of a signal plausibly incurs a cost, in energy expended, risks taken, or opportunities lost. These costs are likely to be (and are here assumed to be) proportional to the level of a signal, at least within some range of signal level. For any analysis of the evolution of communication, the cost of a signal should be measured in units of survival × fecundity. Challenging, although feasible, this task remains an objective for the future.

The present analysis assumes that producing a signal reduces the signaler's survival in inverse proportion to the exaggeration of the signal (Figure 4, top):

$$s_{\mathrm{s}} = s_0 + c_{\mathrm{m}} e,$$

where s_0 = survival when no signaling occurs and c_{m} = the marginal cost of increased signaling ($\leqslant 0$). By setting $s_0 = 1$, the actual survival becomes

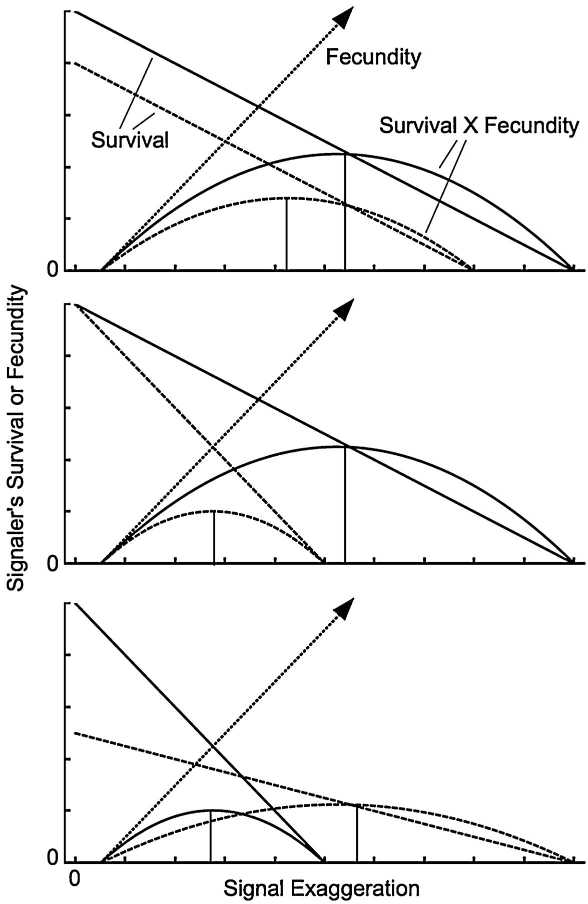


Figure 4. Honesty in advertising when signalers differ in intrinsic survival (survival in the absence of signaling, top) or in marginal costs of exaggeration (middle). Each plot shows survival as a function of exaggeration for each of two signalers (sloping lines) and also their survival × fecundity (convex lines). Vertical lines indicate the level of exaggeration that would maximize each signaler's survival × fecundity. Both signalers realize the same fecundity as a function of exaggeration of their signals, as would happen if receivers responded solely to signals and could not directly judge signalers' quality. The scales of the axes are linear but otherwise unspecified; the vertical scale would usually differ for survival and fecundity (survival is always $\leqslant 1.0$). Changes in scale do not affect the ranking of signalers' optimal levels of exaggeration. Signalers of lower quality (either intrinsic or marginal survival) always have lower optimal levels of exaggeration. The situation is more complicated (bottom) if the lines for signalers' survival cross or if signalers with lower intrinsic quality also have sufficiently lower marginal costs of exaggeration (see text for further discussion).

a proportion of the maximal survival in the absence of signaling ($s_s = s_0 = 1.0$ when $c_m = 0$). Because costs must also rise with the rate of signaling, the signaler's marginal cost of signaling is multiplied by his probability of signaling in any small interval of time, p_s. Recall that the probability of a signal also affects the receiver's performance.

A signaler receives a benefit (b_s) when an appropriate receiver responds in a way that raises the signaler's survival $\times$ fecundity. For instance, in the case of mate choice, a female's response might promote mating with a male signaler and, thus, an increase in the signaler's expected fecundity. In the absence of producing a signal, a male presumably would have a lower probability of mating and, thus, lower expected fecundity. Setting the signaler's survival $\times$ fecundity in the absence of a response (n_s) $= 1.0$ makes b_s proportional to the signaler's survival $\times$ fecundity in the absence of communication.

Note that the signaler's utility is not strictly proportional to the exaggeration of the signal. Instead it depends on the receiver's threshold in relation to the level of the signal, which fixes the probabilities of the four outcomes for the receiver. The higher the receiver's threshold, the lower the probability of a correct detection and, thus, the lower the probability of a response to the signal. The present approach, therefore, calculates the expected utility for a signaler as a function of the receiver's threshold and the level of exaggeration of the signal:

$$U_s = p_s s_s (p_D b_s + (1 - p_D) n_s) + (1 - p_s) s_0 n_s$$

where $s_s = s_0 + c_m e$, as above, p_D, p_F, d_r, m_r, f_r and r_r are the probabilities and payoffs of the receiver's outcomes, as described in the previous section, p_s is the probability of signaling in a small unit of time, b_s is the benefit received from a response by the receiver, and n_s is the benefit received when there is no response (Table 1). Notice that this formulation assumes that the signaler receives no benefit from a false alarm. In mate choice, a false alarm by a receiver would consist of mating with a partner other than signaler.

For any level of the receiver's threshold there exists an optimal level of signaling (exaggeration) by the signaler, the level that maximizes the signaler's expected utility. At lower levels of exaggeration, the signaler evokes too few responses, and at higher levels, it incurs too high a cost in survival. The optimal level of signaling (exaggeration) as a function of the receiver's threshold can be calculated by finding the solution to the partial differential equation,

$$\partial U_s/\partial e = 0, \quad t = \text{constant},$$

and checking the second derivative or inspecting the contour of $U_s = g(e)$ for constant t. This solution can only be found by numerical methods, again as implemented in Mathematica 8.0.4 (see above).

2.4. The receiver's and signaler's joint optimum

So far this extension of signal detection theory has derived the overall utilities for a signaler and an appropriate receiver. Each of these utilities is a unique function of both the receiver's threshold and the signaler's exaggeration:

$$U_r = f(t, e); \qquad U_s = g(t, e).$$

To find any joint optimum, it is necessary to search for points at which the receiver's optimal threshold and the signaler's optimal exaggeration coincide. These joint optima occur at the intersections of the two curves, $t^* = f(e)$ and $e^* = f(t)$, with an asterisk indicating an optimum. A joint optimum represents a particular combination of signaler's exaggeration and receiver's threshold that produce local maxima for both parties' utilities. A joint optimum is, thus, a Nash equilibrium for an interaction with the relevant parameters. Each party would do less well by unilaterally perturbing its behavior.

Depending on the receiver's and signaler's parameters, there were 0–2 such joint optima, as explained below. In all cases with two joint optima, one had lower utility for both sender and receiver and occurred at a combination of lower exaggeration of the signal and lower threshold by the receiver. To find the unique optimum (in cases with just one) or the more advantageous optimum (in cases with two optima), the present implementation in Mathematica 8.0.4 searched the level of exaggeration downwards to find the point at which (1) the two parties' optima coincided within a precision of $<1\%$ and (2) they both had higher utility than any second joint optimum.

Once a procedure was available for finding the most advantageous joint optimum for signaler and receiver, it was possible to explore the sensitivity of this optimum to perturbations of the parameters. This analysis explores in particular the relative magnitudes of the receiver's four payoffs and the signaler's cost and benefit. In each case, plots of a series of joint optima show how the joint optimum changes as each parameter changes. Because the possibilities are large, the present analysis focuses on situations that seem plausible for many cases of mate choice. For comparison, there is also briefer consideration of plausible cases of a warning call in the presence of a predator.

2.5. Parameters for communication during mate choice and warning calls

The receiver's parameters are predicted to differ contrastingly in these two situations. As described earlier (Wiley, 1994), mate choice is likely to result in a high threshold for response, adaptive choosiness, because false alarms by a receiver (choice of a suboptimal mate) have lower payoffs than missed detections (failing to respond to an optimal mate). A false alarm could result in a major reduction in a female's reproductive success, while a missed detection would result in continued searching, with some loss of time and exposure to risks, but with only a minor reduction in a female's reproductive success. In mate choice, the female's task is discriminating between optimal and suboptimal potential mates. The presence of the latter are the predominant forms of noise for this case of communication.

In contrast, warning signals are predicted to be associated with a low threshold for response and low exaggeration of signals, adaptive gullability (Wiley, 1994). In this case, a missed detection (failing to respond to a warning) would expose the receiver to a predator, while a false alarm (taking cover in the absence of a predator) would result in some loss of time, for instance for feeding or interacting with potential mates. The payoffs for missed detections and false alarms, therefore, contrast with the situation in mate choice.

Although mate choice and warnings illustrate contrasting payoffs for receivers, other forms of communication have their own relationships among the payoffs for the four possible outcomes a receiver faces. Figure 5 is a proposal for arranging plausible relationships of these payoffs in different situations. The payoff for a correct rejection (no response when no signal is present), r_r, is set to 1.0, so that the payoffs for the remaining three outcomes are scaled to the expected utility of this one. The utility of a correct rejection is presumably similar to the utility of life in the absence of communication (no signals, no responses). With this scaling, the relative payoffs for remaining outcomes, along with the probability of a signal, determine the receiver's utility of participating in communication, relative to the utility of life in the absence of communication.

The following sections consider conditions for mate choice in which the payoff for a correct detection, d_r, takes values of 1.5, 2 and 3, while the

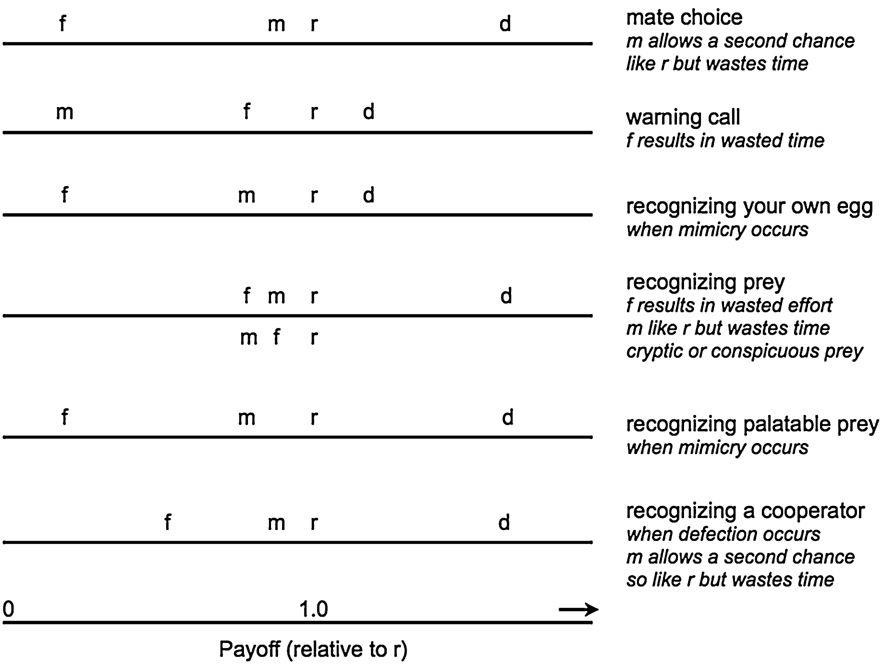


Figure 5. Plausible values for the relative payoffs for the four possible outcomes for a receiver in a variety of situations for communication. The four outcomes (see Figure 2) are represented by d, m, f and r, and their relative payoffs in each situation are indicated by their positions on separate scales. Each payoff (advantage minus disadvantage for the receiver's survival × fecundity) is proportional to the payoff for a correct rejection in the relevant situation. This payoff for no response when there is no signal is tantamount to life's payoff in the absence of communication in this situation. With $p_R = 1$, then usually $p_D > 1$, $0 < p_F < 1$, and $0 < p_M < 1$. Within these limits, the magnitudes of plausible payoffs vary with the situation. Because only two points (0 and 1.0) are stipulated on these scales, the scales need not be linear. There are no measurements for all four payoffs in any case of communication that I know of, so the values suggested here are no more than plausible hypotheses.

payoff for a false alarm, f_r, takes values of 0.1, 0.5 and 0.9 (all payoffs relative to the payoff for R, as just explained). The payoff for a missed detection, m_r, is set at 0.9 (a 10% reduction compared to r_r as a result of lost time and increased risk of further searching). In contrast, conditions for warning signals have payoffs for correct detections of 0.8, 1.0 and 1.5, and for missed detections of 0.1, 0.5 and 0.9. The payoff for a false alarm in this case is set at 0.95.

This approach makes no attempt to justify these values because none has ever been measured. It is unlikely that all cases of mate choice or of warning signals would have relative parameters matching these figures. Nevertheless, these parameters seem plausible for at least some cases of mate choice and warning signals.

The signaler's parameters also have a large influence on the nature of communication. The present analysis considers a range of costs for producing a signal and benefits received by a signaler if an appropriate receiver responds. For mate choice, the signaler's benefit from a response, b_s, takes values from 1.5 to 8. The marginal cost of producing a signal, c_m, takes values of -0.001, -0.01 and -0.05. For warning signals, the signaler's benefit is set at 1.5 and its marginal cost of exaggeration at -0.01. The receiver's payoff for a false alarm, f_r, in this case is set at 0.99. The payoff for a correct detection (avoiding contact with a predator), d_r, takes values of 0.8, 1.0 and 1.5, and the payoff for a missed detection (lost time), m_r, takes values of 0.1, 0.5 and 0.9. The payoffs for a false alarm and for a missed detection, therefore, contrast with the case of mate choice.

Another potentially critical difference between these two situations is the probability (1/frequency) of a signal, p_s. In this analysis, this parameter is set at 0.5 for mate choice (Table 1) and takes values of 0.01 and 0.001 for warning signals.

Default values for other parameters are presented in Table 1. In the cases of mate choice and warning signals considered here, it is assumed that a signaler does not benefit from a false alarm by a receiver (although in some cases of communication this possibility could arise). The analyses here also assume that the appropriate receiver is paying attention all of the time and is within range of the signaler.

Note that these models for noisy communication address the consequences for each instance of communication (each time a receiver checks its sensor or a signaler produces a signal). Depending on what constitutes a signal, many forms of communication can consist of hundreds or thousands of such instances in the life of an individual. On the other hand, some signals might occur once in a lifetime (constructing a display court, for instance).

3. Results

The first sections below present the utilities and optima for a receiver's threshold and a signaler's exaggeration for parameters that seem plausible for mate choice (Table 1). Then a comparison is made with plausible situations for warning signals.

3.1. Mate choice: the receiver's utility

For any set of parameters for the payoffs of the four possible outcomes for a receiver and for the probability of a signal, the receiver's utility is a function of its threshold for a response, t, and the signal level in relation to the noise, also called the exaggeration of the signal, e. U_r as a function of t and e is the adaptive landscape for a receiver's performance (Figure 6).

For any mean level of the signal (exaggeration), the utility of the receiver's threshold depends on its location (Figure 7). For a threshold close to 0 (the mean level of noise), the receiver's utility is usually low ($\approx$1). A low threshold does a poor job of separating signal and noise, so many false alarms result. As the threshold increases, the receiver's utility increases to a maximum at some value below the level (exaggeration) of the signal. Higher thresholds result in a drop in the receiver's utility, because these thresholds exclude many correct detections. Nevertheless, at high levels of the receiver's threshold, the receiver's utility changes only slightly with changes in the location of its threshold. The increased discrimination between signal and noise is offset by the decreased probability of correct detections. The drop is more pronounced the higher the payoff for a correct detection (Figure 6). It is also slightly more pronounced the higher the payoff for a false alarm, because then the cost of a mistake is less. Recall that all payoffs in these analyses are scaled in relation to $r_r = 1.0$, so $f_r < 1$ and $d_r > 1$.

A striking feature of the receiver's utility are the large domains in which it changes little with either the location of the threshold or the mean exaggeration of the signal. In these domains the trade-off faced by the receiver each time it decides to respond or not dominates its utility. Small changes in threshold or exaggeration result in counteracting changes in the probabilities of correct detections and false alarms. When the threshold < signal exaggeration, p_D decreases with increasing t less rapidly than does p_F ($\partial p_D/\partial t$ is less negative than $\partial p_F/\partial t$). When the threshold > exaggeration, this relationship reverses. The receiver's utility, thus, increases slowly as the threshold approaches the mean level of the signal, drops near this level, and then continues to drop slowly beyond the mean level of the signal. Overall the surface of U_r is relatively flat on either side of a locus of points along a diagonal line with a slope approximately equal to 1. Figure 7 shows the optimal threshold for three levels of exaggeration (mean level of signal), when payoffs $d_r = 2$ and $f_r = 0.5$ (see Table 1 for default values of other parameters for mate choice).

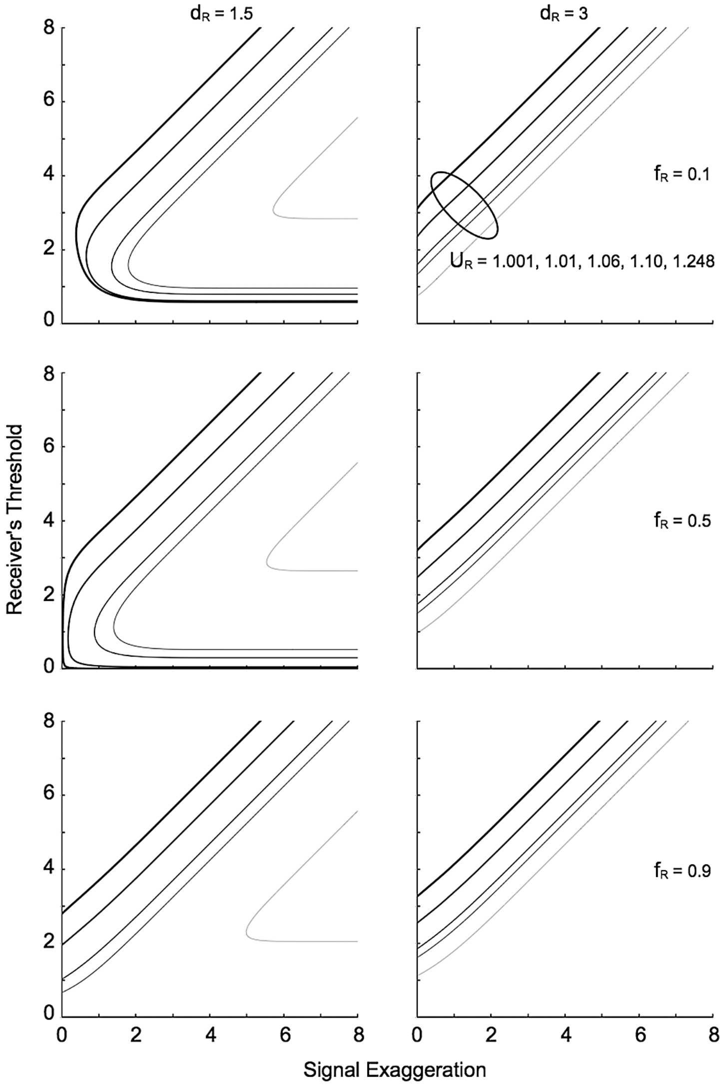


Figure 6. Contours of the receiver's utility, U_R, as a function of signal exaggeration and the receiver's threshold. The five contours represent (from thickest to thinnest) $U_R = 1.001$, 1.01, 1.06, 1.10 and 1.248, respectively. The highest value is close to the maximum for the conditions represented. The lowest value is set just above 1.0, because $U_R > 1.0$ over the entire plot in each case. The two columns show contours with $d_R = 1.5$ and 3.0; the three rows show them with $f_R = 0.1$, 0.5, and 0.9. The contours show the relatively steep rise diagonally across each plot (with a slope ≈ 1) and in some cases also with very low thresholds. With $d_R = 1.5$ there is also an indication of a diagonal ridge of maxima. A similar ridge is much weaker with $d_R = 3.0$.

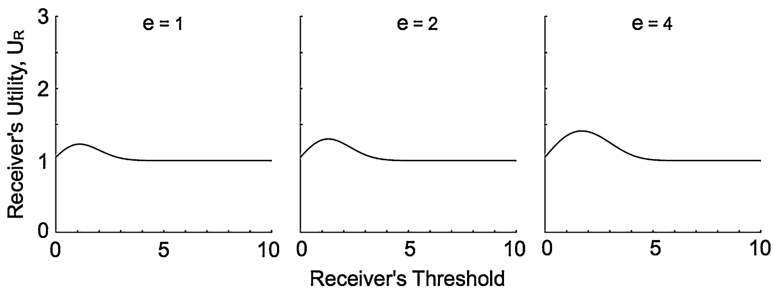


Figure 7. The receiver's utility, U_R, as a function of its threshold for three levels of signal exaggeration. For all plots, $d_R = 2$, $f_R = 0.5$, and other parameters have default values for mate choice (Table 1). In each of these cases there is a single maximum for the receiver's utility.

For some sets of parameters, $U_r = f(t, e)$ has only a weak maximum (Figure 6, right), but in other cases, especially with d_r and f_r both small, there is a clear diagonal locus of maxima with $t < e$ (Figure 6, left).

3.2. Mate choice: the signaler's utility

For the signaler, the parameters affecting its performance (the marginal cost of producing a signal, the payoffs when an appropriate receiver responds or does not, and the probability of producing a signal) define its expected utility as a function of the exaggeration of its signal and the receiver's threshold. For any exaggeration (mean level of the signal), the receiver's threshold determines the probability of a response to the signal. The signaler's utility, $U_s = g(t, e)$, like the receiver's utility, $U_r = f(t, e)$, is a diagonal locus of maxima with e approximately equal to t (Figures 8 and 9).

For any level of the receiver's threshold, increasing the mean level of the signal at first increases the probability of responses (correct detections) by the receiver (Figure 9). The increased probability of responses is, however, balanced by the increased cost of producing a signal with a higher mean level. Near the point $t = e$, the increase in the probability of a response is greatest. A maximum is reached a point where $e \approx t$. Further increases in e result in a slow decline in the signaler's utility, as progressively less increase in responses is outweighed by a steadily increasing cost. Figure 9 shows the signaler's optimal exaggeration for three different levels of the receiver's threshold, when $d_r = 2$ and $f_r = 0.5$ (other parameters have default values for mate choice, Table 1).

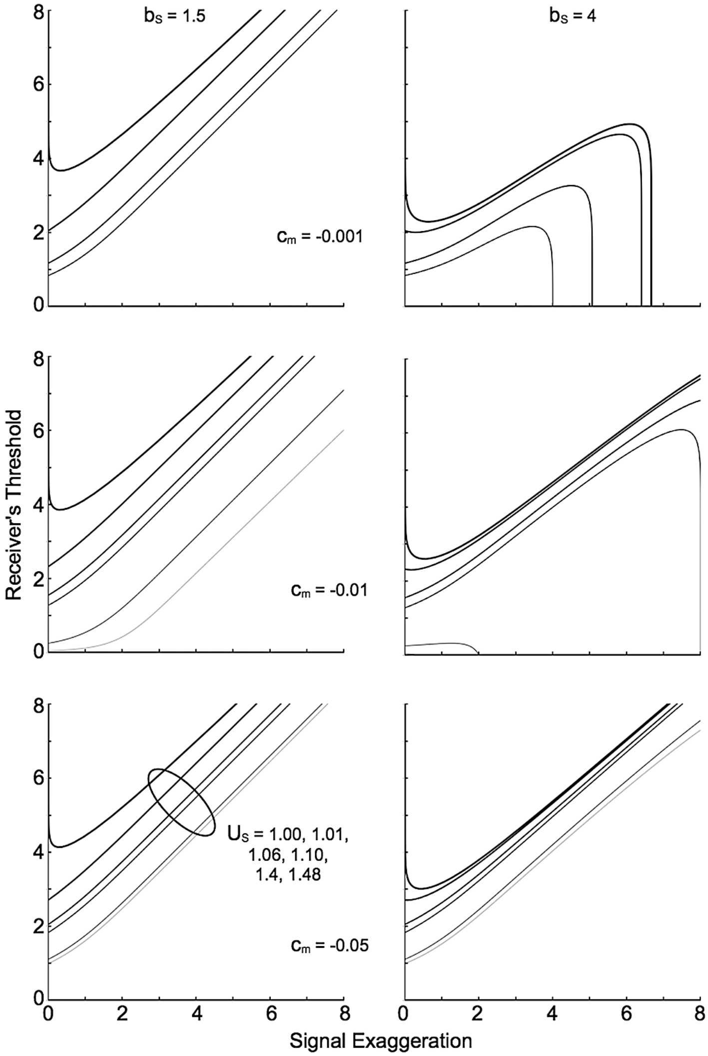


Figure 8. Contours of the signaler's utility, U_S, as a function of signal exaggeration and the receiver's threshold. The six contours represent (from thickest to thinnest) $U_R = 1.00$, 1.01, 1.06, 1.10, 1.4 and 1.48, respectively. The highest value is close to the maximum for the conditions represented. The lowest value at 1.0 indicates that in the upper left corner of each plot it does not pay for a potential signaler to produce signals ($U_S < 1.0$). The two columns show contours with $b_S = 1.5$ and 4.0; the three rows show them with c_m -0.001, -0.01 and -0.05. The contours show the relatively steep rise diagonally across each plot (with a slope ≈ 1) and the limit beyond which further exaggeration does not pay.

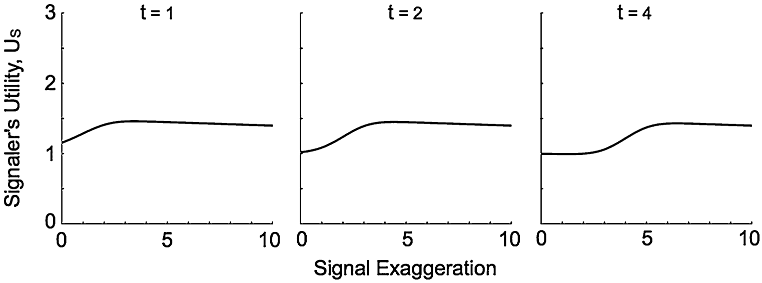


Figure 9. The signaler's utility, U_S, as a function of its exaggeration for three levels of the receiver's threshold. For all plots, $d_R = 2$, $f_R = 0.5$, and other parameters have default values for mate choice (Table 1). In each of these cases there is a single maximum for the receiver's utility, although the shoulders have low slopes. At high levels of the receiver's threshold, low levels of exaggeration do not pay ($U_S < 0$ with a slight negative slope).

Like the receiver's utility, the signaler's utility includes large domains in which changes in t or e result in relatively little change in utility, as a result of trade-offs between costs and benefits. The locus of maxima is again a diagonal line with a slope approximately equal to 1. Note that the signaler's utility and its maxima do not depend on the payoffs for the four possible outcomes a receiver faces. It does depend on the probabilities of these outcomes, which are determined by the mean level of the signal (exaggeration) in relation to the noise.

3.3. Mate choice: the optima for receiver and signaler

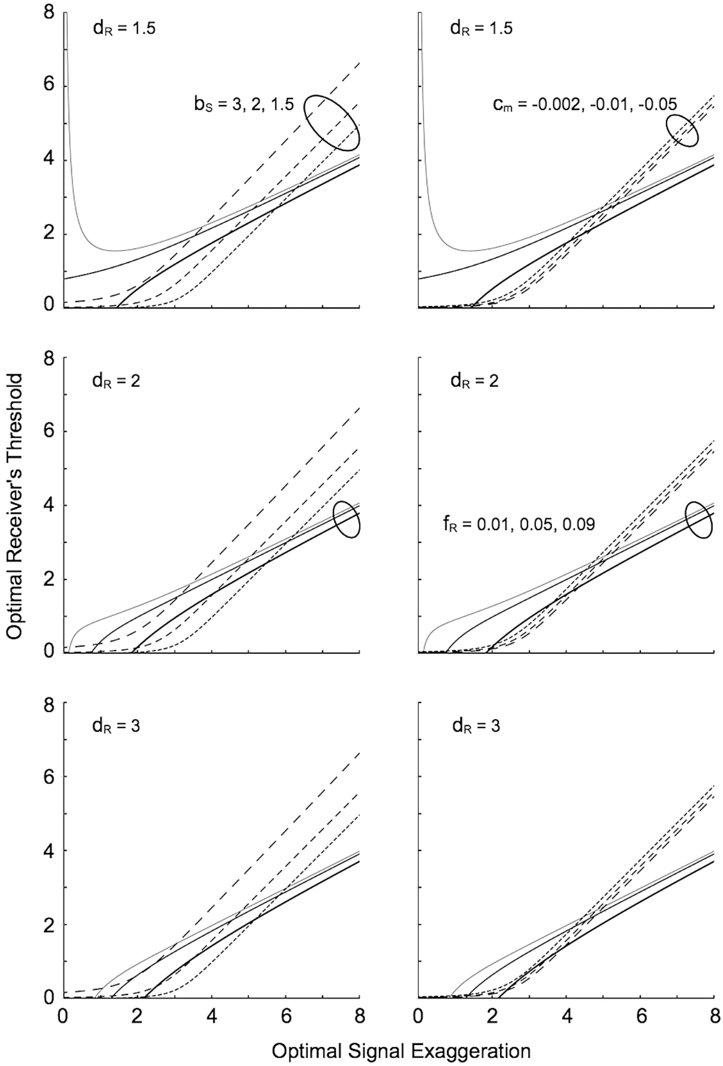
Differentiating $U_r = f(t, e)$ with respect to e and solving for $\partial U_r / \partial e = 0$ yields the locus of optimal thresholds for any set of parameters for the payoffs of the receiver's four possible outcomes and the probability of a signal (Figure 10, solid lines). These optimal thresholds either increase monotonically with exaggeration of the signal or in some cases have an abrupt concave shape as a result of a sharp rise in the optimal threshold for $e < 1$. As the figure shows, this concave shape arises when the payoffs for both false alarms and correct detections (f_r and d_r) are relatively low (Figure 10, top), so a high threshold at low levels of signal exaggeration avoids the high costs of false alarms. With a relatively high payoff (low cost) for false alarms, the optimal threshold remains 0 until signal exaggeration exceeds a minimal value near $e \approx (1, 2)$. Below this minimal exaggeration, it does not pay for the receiver to discriminate between signal and noise, because a threshold < 1 results in too many missed detections. Note that when the optimal threshold $= 0$ it does not pay for a receiver to participate in communication. Instead, in these cases, it is better to respond regardless of the presence or absence of a signal.

Above this minimal exaggeration, the receiver's optimal threshold increases approximately linearly with signal exaggeration with a slope < 1 and $t < e$, as previous inspection of the adaptive landscape for $U_r = f(t, e)$ suggested (Figure 8). At higher exaggeration of a signal, the receiver's optimal threshold diverges progressively from $t = e$. The lower tail of the PDF for the level of the signal always exceeds the upper tail of the PDF for the level of noise. In this region, $\partial t/\partial e < 1$ means that more of the signal is captured in relation to noise as exaggeration increases.

The signaler's optimal exaggeration for any set of its benefits and costs and the probability of a signal is obtained by differentiating $U_s = g(t, e)$ with respect to t and solving for $\partial U_s/\partial t = 0$ (Figure 10, dashed lines). At very low thresholds for the receiver, it pays a signaler to increase the exaggeration of its signal rapidly. Above a value of the receiver's threshold near $t \approx (2, 3)$, the signaler's optimal exaggeration increases linearly with the receiver's threshold with a slope ≈ 1 but with $t < e$, as previous examination of the surface $U_s = g(t, e)$ suggested (Figure 8).

For any set of parameters, the joint optima for receiver and signaler occur where the lines of optima for each party intersect. By switching the axes for the signaler's optimal exaggeration, $e^* = f(t) \rightarrow t = f(e^*)$, and plotting the result with the receiver's optimal threshold $t^* = f(e)$, it is possible to visualize the joint optima where the lines cross at points ($t = t^*$, $e = e^*$).

Figure 10. The receiver's optimal threshold in relation to the signaler's optimal exaggeration. Each plot shows the locus of the signaler's optimal exaggeration as a function of a receiver's threshold (dashed lines) and the converse, the locus of the receiver's optimal threshold as a function of the exaggeration of a signal (solid lines). In each plot the three solid lines show the receiver's optima for three values of the payoff for a false alarm ($f_R = 0.01$, 0.05 and 0.09 with thinner to thicker lines, respectively). The three rows show optima for three values of the payoff for a correct detection ($d_R = 1.5$, 2 and 3, respectively), the left column shows the signaler's optima for three values of the signaler's benefit from responses by the receiver ($b_S = 3$, 2 and 1.5 with thicker to thinner lines, respectively), and the right column shows the signaler's optima for three values of the marginal cost of exaggeration ($c_m = -0.002$, -0.01 and -0.05, respectively). In many cases the loci for the receiver's optima and for the signaler's optima cross. These intersections indicate the Nash equilibria for a signaler and receiver under the respective conditions. In some cases, the loci for optima do not cross, although they converge and diverge near points of attraction (see Figure 11). There are also intersections at very low values of thresholds and low values of exaggeration (see Figure 11 and discussion in the text).



These plots (Figure 10) reveal three possible cases for these joint optima: either 0, 1, or 2 optima, depending on the parameters for the receiver's and signaler's performance.

A single joint optimum occurs in those cases in which the locus of the receiver's optima is concave. As explained above, this case occurs when the payoffs for correct detections and false alarms, d_r and f_r, are both relatively low (low benefit for correct detection, high cost for false alarm).

Two joint optima occur with many sets of parameters, as a result of the upward curvature of the signaler's optima at thresholds near 0. One of the joint optima, thus, occurs with a low threshold and low exaggeration. The second joint optimum occurs at a much higher level of threshold and exaggeration, as a result of the steeper slope of the locus of optimal exaggeration. At each of these two points, neither party can improve its utility by perturbing its behavior (altering its threshold or the exaggeration of its signals, respectively). The lower point is often close to $t = 0$, so the receiver is close to no participation in communication at all (responding without regard to the presence or absence of a signal).

With some sets of parameters, the loci of optima for the receiver and the signaler do not intersect, and there is no joint optimum, although the lines of optima for the two parties converge and diverge as t or e increase. Figure 10 suggests that this eventuality occurs when the receiver's payoffs for false alarms and correct detections are high (cost of a false alarm is low) and the signaler's benefit from a response is high (high d_r and f_r, low b_s).

The course of evolution through these joint adaptive landscapes as functions of t and e is best revealed by a plot of streamlines and vectors for the partial derivatives $\partial U_r/\partial e$ and $\partial U_s/\partial t$ (procedures VectorPlot and StreamPlot in Mathematica 8.0.4 produce Figure 11). The vectors in this plot (short arrows with the magnitude of the vector indicated by the size of the arrow) are the joint selection gradients on the behavior of receivers and signalers, as determined by the parameters of their performances (costs, benefits, probability of signals). The streamlines (long arrows that sum the vectors over longer trajectories) are, therefore, the expected trajectories of evolution. Notice that in all cases analyzed the arrows of evolution converge at a joint optimum corresponding to the upper optima in Figure 10. In some

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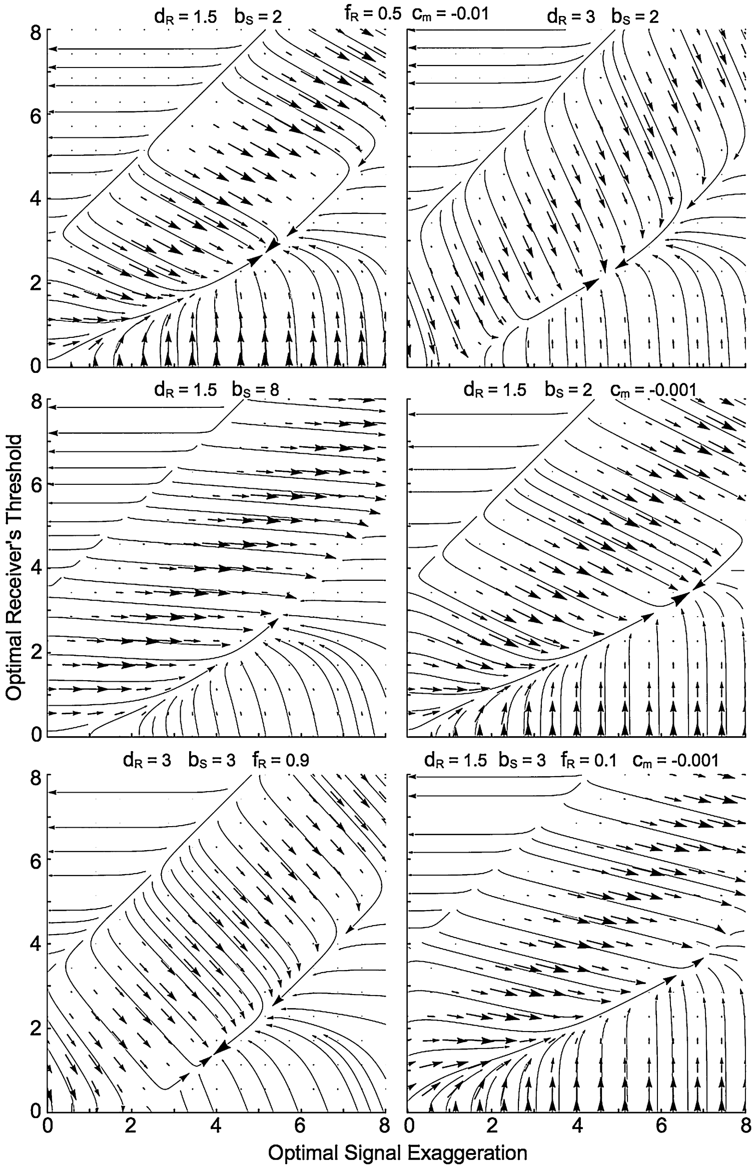
Figure 11. Streamlines and vectors for the gradients of the signaler's and receiver's utilities as functions of the receiver's threshold and signal exaggeration. The vectors (short arrows) show the gradients ($\partial U_r/\partial e$, $\partial U_s/\partial t$), with larger arrows for steeper gradients. The streamlines (longer arrows) result from sums of vectors. The vectors, thus, indicate the joint selection gradients on receivers and signalers under the conditions specified. The streamlines suggest the trajectories of evolution. For all plots, the payoff for a false alarm, $f_r = 0.5$ and the marginal cost of exaggeration, $c_m = -0.01$. Other parameters are specified in the headings for each plot or have default values (Table 1). Points of convergence are joint optima for the receiver's threshold and signal exaggeration in each condition. Compare these optima with the same ones displayed differently in Figure 10.



cases (Figure 11, upper right, lower left) at levels of t and $e < 2$, communication collapses as $t^* \to 0$. Notice that when the lines of optima do not cross (Figure 10, lower left, $b_\mathrm{s} = 3$, $f_\mathrm{r} = 0.9$), there is nevertheless an attraction point in the joint adaptive landscape (Figure 11, lower left), at a point above closest approach of the lines for the two parties' optima.

In all cases, the joint optima have asymmetrical slopes, with weak selective gradients on one side and strong ones on the other, a result of the large domains of nearly flat landscape for the functions, $U_r = f(t, e)$ and $U_s = g(e, t)$ (Figures 6 and 8). Nevertheless, from all directions around these joint optima, perturbations of either party's behavior would lower their utilities so that the selection gradients would tend to move their interaction back to the joint optimum. These points are, therefore, Nash equilibria for the interaction. A comparison of Figures 6, 8 and 11 reveals that these equilibria are not necessarily Pareto optima, the points of maximal utility for either party alone.

3.4. Mate choice: influences of the receiver's and signaler's parameters on the joint optimum

This initial analysis of noisy communication in mate choice explores the consequences of variation in four parameters: the receiver's payoffs for correct detections and false alarms and the signaler's marginal cost of signaling and benefit from a response by an appropriate receiver. The remaining parameters are set to default values (Table 1).

3.4.1. Receiver's payoffs

Recall that in communication for mate choice, a female receiver makes a correct detection when she responds to an optimal male and a false alarm when she responds to a suboptimal one. For simplicity the present analysis assumes only two categories of males, which produce two varieties of signals that are not always separated by females. The suboptimal males' signals, therefore, are the noise in communication between females and optimal males.

This analysis considered the following possibilities for the receiver's payoffs: $d_r = \{1.5, 2, 3\}$ and $p_F = \{0.1, 0.5, 0.9\}$. As explained above, by setting the payoff for a correct rejection, $r_r = 1.0$, the remaining payoffs are scaled in relation to this one. By choosing an optimal mate, a female's payoff (her survival $\times$ fecundity) is 1.5, 2, or 3 times her payoff if she kept searching. By choosing a suboptimal mate, her payoff is 0.1 (high cost), 0.5, or 0.9 (low cost) times her payoff otherwise.

Inspection of the plots in Figures 10 and 11 shows that, when a receiver's payoff for a correct detection increases, the upper joint optimum for communication moves to a lower threshold by the receiver and a lower exaggeration of the signal (summarized in Figure 12). Likewise, when a receiver's payoff for a false alarm increases (cost decreases), the joint optimum also moves to

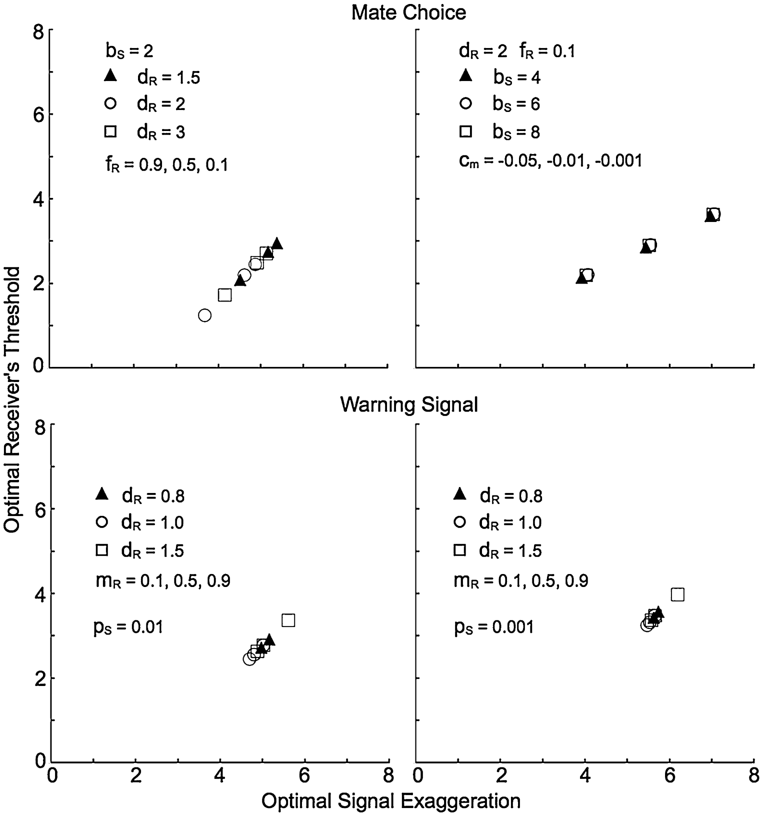


Figure 12. The Nash equilibria (upper equilibrial points in Figure 10) for the receiver's threshold and the signaler's exaggeration for representative combinations of parameters for mate choice (upper two plots) and warning signals (lower two plots). Relevant parameters are specified in the legends; all other parameters have default values for the relevant situation (Table 1).

a lower threshold and a lower exaggeration. When the payoff for a correct detection is high and the cost of a false alarm is low, it pays for receivers to use low thresholds in order to increase the number of correct responses, despite a concomitant increase in the number of false alarms. Thus, the greatest exaggeration of signals and highest threshold for response occurs with a low payoff for correct detection and a high payoff for false alarm, in other words a situation in which the consequences of mate choice for a female are the least pronounced (little difference between the benefit of choosing an optimal mate and the cost of choosing a suboptimal one).

3.4.2. Signaler's benefit and cost

The analysis considered the following possibilities for the signaler's cost and benefit: $c_{\mathrm{m}} = \{-0.001, -0.01, -0.05\}$ and $b_{\mathrm{s}} = \{2, 4, 6, 8\}$. The cost of producing a signal reduces the signaler's survival × fecundity by the marginal cost of exaggeration times the exaggeration of the signal, $c_{\mathrm{m}}e$. The benefit a signaler receives when an appropriate receiver responds increases its survival × fecundity by the factor b_{s}. Recall that this analysis applies to each instance of communication, each time a receiver samples its sensor or a signaler produces a signal. Depending on what a signal is taken to represent, some of the marginal costs of signaling are unlikely. A signal, such as a bird's song, produced hundreds or thousands of times in an individual's life can hardly have a marginal cost of -0.05. On the other hand, constructing and maintaining a display court might represent a single signal with a marginal cost far greater than -0.002.

Inspection of the upper optima in Figures 10 and 11 reveals that, not surprisingly, decreasing the marginal costs of signals or increasing the benefits of a response by a receiver increase both the optimal exaggeration of signals and the receiver's optimal threshold.

3.5. Comparison of mate choice and warning signals

The interest of this comparison, as explained above, comes from the contrasting relationship of the payoffs for the two possible errors by receivers, false alarms and missed detections. For warning signals, it is a missed detection that might have serious consequences, rather than a false alarm, as in the case of mate choice. In addition, the probability of a signal is often much lower for warning signals than for advertising signals. Finally, it is often difficult to identify the signaler's benefit from a response to a warning signal. In some cases, it might consist entirely of indirect benefits from kin selection. It is also possible that there is some direct benefit from notifying a predator that the signaler has spotted it.

For this analysis, it was assumed that a false alarm would cost little (have relatively high payoff) as a result of some time or opportunity lost for feeding or interacting with a mate ($f_{\mathrm{r}} = 0.95$). The analysis then considered different payoffs for correct detections and missed detections by the receiver: $d_{\mathrm{r}} = \{0.8, 1.0, 1.5\}$ and $m_{\mathrm{r}} = \{0.1, 0.4, 0.7\}$. A correct detection of a warning in the presence of a predator might have a payoff less than a correct rejection in the absence of a warning. Alternatively, it might have no effect or, if predators could strike without warning, it might increase survival.

The consequence of a missed detection consists of exposure to a predator, so $m_r = 0.1$ would indicate dire consequences and 0.7 more modest ones. Also investigated were the benefit for the signaler provided the receiver responded, $b_s = \{1.2, 1.4, 1.8\}$, and levels of the marginal cost of exaggeration, $c_m = \{-0.001, -0.01, -0.05\}$.

Increases in d_r produced upper joint optima with lower exaggeration of the signal and lower thresholds for the receiver, just as in the case of mate choice above (Figure 12). Increases in m_r (higher payoff, lower cost) produced the opposite effect, upper joint optima with higher exaggeration and thresholds. Just as in the case of mate choice, a low payoff for a correct detection and a high one (low cost) for a missed detection resulted in the greatest exaggeration and highest thresholds. The plausible values for these parameters were less dispersed than for mate choice and, thus, resulted in smaller differences in the joint optima.

Again, not surprisingly, higher benefits for the signaler from responses by the receiver (b_s) and lower marginal costs of exaggeration (c_m) resulted in joint optima with higher exaggeration and higher thresholds. A lower probability of signals (p_s) also resulted in optima with higher exaggeration and higher thresholds.

The highest exaggeration of signals for mate choice occurred with {low d_r, low f_r, low c_m, high b_s} and for warning signals with {low d_r, low m_r, low c_m, high b_s, low p_s}.

The actual values for optimal exaggeration and threshold in mate choice and warning signals were comparable in many cases. In both situations the highest joint optima were close to $e^* = 6$ and $t^* = 3$. These values, as explained earlier, are scaled to the standard deviation of noise in the receiver's sensor. Exaggeration $= 6$ is, thus, six times the standard deviation of the receiver's noise. The lowest upper optima have exaggeration and thresholds near $e^* = 4$ and $t^* = 2$. Two situations produced exceptionally high joint optima: mate choice when the marginal cost of exaggeration was low; and warning signals when the probability of a signal in the presence of a threat was low. Exaggeration of signals, according to this analysis, should be greatest under conditions that make measuring the marginal cost of signals most difficult.

4. Discussion

This analysis was intended to explore the consequences of noise for the evolution of communication. The inevitable trade-offs faced by both signalers and receivers during noisy communication frustrate simple intuitions. Do the trade-offs for receivers as well as signalers result in optimal thresholds for receivers and optimal exaggeration of signals? Do these individual optima ever coincide to produce joint optima for the interaction of signaler and receiver? Can noise explain differences in the exaggeration of signals in different circumstances? Can it explain the stability of honesty in communication? In the process of the investigation other issues arose as well. How are costs related to honesty in communication? What are the differences between mate choice and other forms of communication?

One result is clear. There is much more to learn about the evolution of communication in noise. The present model included only the minimal number of parameters to characterize signal detection in noise. Nevertheless, few of these parameters have ever been considered in studies of natural communication. The benefits to receivers of responding to signals have received some attention, but not the probability of correct detection. The costs and benefits to signalers have been addressed, but as discussed below it is clear that the potential complexities require much more investigation. Other parameters, the probabilities of the four possible outcomes for receivers, the payoffs for false alarms and missed detections, the probabilities of signals, have not been considered in studies of adaptations in communication.

It is just as surprising that these issues have never arisen in engineering applications either. There is a large body of work on optimal encoding of signals, but none that I know of on the costs and benefits of signal production and detection and their relationship. Yet the implications of noise for the evolution of communication apply just as well to the human design of communication. Most of the conclusions below apply to both evolutionary and economic scenarios.

As for the present model, although the number of parameters is minimal, it is nevertheless large. This report has only just begun exploring the consequences of variation in these parameters. The following sections address some of the questions raised above. They start with two old questions about the evolution of communication: the role of the signaler's costs and the stability of honesty.

4.1. Costs and benefits of signals and the stability of honesty

By formulating the costs and benefits of signals, the present analysis has clarified and also complicated previous conclusions about the role of costs in the evolution of honesty in signaling. If receivers cannot directly assess signalers' qualities and, therefore, only respond to the level (exaggeration) of their signals, and if signalers differ in intrinsic survival or marginal costs of exaggeration, signals can honestly indicate these aspects of quality. Figure 4 (top and middle) plots these relationships in a way that makes it clear that, if each signaler optimizes its level of exaggeration, by maximizing its survival $\times$ fecundity, then signals can honestly indicate each signaler's quality.

The present analysis adopted this approach for a signaler's cost as a function of the exaggeration of its signals. If intrinsic survival is the signaler's survival in the absence of signaling (s_0, survival when exaggeration $= 0$), then a constant marginal cost of exaggeration (c_m) results in a signaler's survival that decreases linearly with the exaggeration of signals: $s_\mathrm{s} = s_0 + c_\mathrm{m} e$.

Although this graphical approach can clarify the relationship between a signaler's costs and honesty in signaling, it also raises some neglected questions. The absolute cost, relative cost, and marginal cost of signals differ in every case in Figure 4 yet are rarely distinguished in discussions of the costs of signaling. In addition, there has been much discussion of different forms of 'handicaps', with an emphasis on whether or not costs of signaling are paid up front or not (Maynard Smith & Harper, 2003). This distinction can be captured by supposing that survival is a nonlinear function of signal exaggeration, concave either upward or downward. In addition, intrinsic survival and signaling costs might not vary independently.

Arguments about honesty also assume that the signaler's benefit is a monotonically increasing function of signal exaggeration. The analysis of noisy communication has shown how the probability of a receiver's response can increase monotonically with the signal's exaggeration, as a result of the receiver's adjusting its trade-off between missed detections and false alarms. Noise in communication is, thus, sufficient to explain a monotonic relationship between a signaler's benefit and the exaggeration of its signals.

Nevertheless, this relationship is not simple. A signaler benefits from a receiver's response, but the probability of a response depends on the location of the receiver's threshold as well as the exaggeration of the signal. The probability of a response, therefore, does not depend in any simple way on the exaggeration of the signal. For instance, as the level of a signal increases, the probability of correct detection falls more steeply than the probability of false alarm (see Figure 1). Thus, the proportionate change in correct responses, $p_D/(p_D + p_F)$, for any constant change in the level of a signal decreases with the level of the signal. In other words, a constant proportionate change in this ratio requires a larger proportionate change in signal level at higher signal levels, a result qualitatively similar to Weber's Law. More work is needed to examine the precise correspondence between the present model of a receiver's decisions in noise and other models of discrimination or decision (for instance, Kacelnik & Brito e Abreu, 1998).

Extending the graphical model of signaling suggests more complexity in the relationship between costs and honesty than previously supposed (Figure 4, bottom). For instance, honesty can result whether males differ in intrinsic (s_0) or in marginal survival (c_m) (see Getty, 1998; Wiley, 2000). A sufficient condition for this conclusion is that the functions for survival of signalers cannot cross. Yet this is not a necessary condition (Figure 4, bottom) when signalers with low intrinsic survival also have low marginal costs of exaggeration. This situation might arise if there were a developmental trade-off between intrinsic survival and exaggerated signals. How to interpret this situation would then depend on whether a signaler's quality was more accurately indicated by high intrinsic survival or low marginal costs of signaling. Furthermore, males of different quality might accrue benefits at different rates. Suppose for instance, as a result of another developmental trade-off, that males with low intrinsic survival fertilize more eggs of females they attract. Their benefits of signaling would have a higher slope than that of males with high intrinsic survival. The interpretation of this situation would depend on whether quality was more accurately indicated by intrinsic survival or ability to fertilize eggs. The best indicator of quality, in every case, might instead be a male's expected survival × fecundity. So far as I know, none of these possibilities has received attention previously. Costs of signaling are related to honesty in communication in complex ways because of the interacting effects of a signaler's innate survival, marginal costs of exaggeration, and benefits of signaling.

An important conclusion from these suggestions and from the analysis of noisy communication is that the receiver's behavior is at least as important for explaining the exaggeration of signals and honesty in communication as are the signaler's costs. Indeed, the receiver's threshold, optimized in relation to the probabilities and payoffs of the four possible outcomes of any decision to respond or not, sets the conditions that determine the optimal exaggeration of signals and, thus, how much they cost.

The process of optimizing the individual parties' utilities during communication in noise often results in joint optima at which both parties benefit overall (with expected relative utilities > 1). These are Nash equilibria, combinations of behavior which neither receiver nor signaler can unilaterally perturb without decreasing its utility. They, therefore, represent stable conditions for communication with both parties benefiting. Nevertheless, at these equilibria receivers make errors, both false alarms and missed detections, and signalers do not always evoke responses from appropriate receivers. Such communication is, therefore, stable and honest on average, despite instances in which receiver or signaler or both do not benefit.

4.2. De novo evolution of signals

The plots of streamlines also clarify the selection gradients in the upper left corners, where the receiver's threshold is high and exaggeration approaches 0 (Figure 11). This is the situation for the initial evolution of a new signal. Presumably an incipient signal would have low exaggeration, and receivers would have little tendency to respond to it. Under these conditions, the selection gradients, although weak, uniformly stream to exaggeration $= 0$, or a collapse of communication.

The evolution of a new signal, therefore, has a hurdle to overcome. It requires either a preadaption or exaptation of a low threshold for response to the new signal, or it requires a behavior with an initial condition that already has a high contrast with noise. The first precondition might result from a sensory bias evolved in another behavioral context (Ryan & Keddy-Hector, 1992); the latter precondition might result from a previously irrelevant but conspicuous behavior, such as a displacement activity (Tinbergen, 1952). Either way it has long been recognized that the evolution of communication de novo must surmount a hurdle (for instance, Lande, 1981; Kirkpatrick, 1982, see Wiley, 2002, for further discussion).

4.3. Exaggeration of signals

This analysis of noisy communication has shown that the exaggeration of signals depends on the parameters affecting both the receiver's and the signaler's behavior. For both mate choice and warning signals different combinations of plausible parameters can produce at least 4-fold differences in exaggeration of signals and reach levels at least 6 times the standard deviation of noise in the receiver's sensor.

It is important to realize that this analysis did not include parameters for attenuation of a signal during transmission, nor for variation in the signal either at the source or as a consequence of propagation to the receiver. A parameter for attenuation would multiply the exaggeration of a signal at the source required to achieve any exaggeration at the receiver. The consequence of attenuation is, therefore, to raise the cost of signals for signalers, in order to achieve the optimal exaggeration at the receiver.

This analysis of noisy communication did not confirm the degree of contrast expected between levels of thresholds and exaggeration in signals in mate choice and warning signals (Wiley, 1994). Some cases of mate choice analyzed here do involve high levels of exaggeration and thresholds, but in many cases these levels broadly overlap those predicted for warning signals (Figure 12). This situation remains a conundrum for future analyses. If the relevant parameters were actually measured, would there be less contrast than we intuitively expect between such radically different situations for communication? Or are the parameters selected for this initial analysis in fact not realistic? Would other parameters produce greater contrast between mate choice and warning signals in noisy communication?

One result of including noise in any analysis of the evolution of communication is a clear prediction of the form that exaggeration should take. Relevant exaggeration consists of changes in a signal's properties that increase contrast with noise. Unlike other explanations for the spread of a receiver's responses to signals, noisy communication makes the prediction that receiver's responses favor the evolution of signals that contrast with noise from the position of the receiver. Investigation of adaptive signal design has suggested ways that signals can evolve to enhance contrast with noise (Wiley & Richards, 1982; Endler, 1993; Brumm & Naguib, 2009).

Theories of sexual selection do not usually include such predictions about which properties of signals should evolve. A few mathematical analyses have indicated that traits with greater advantages (or lesser disadvantages) for males should evolve preferentially (Heisler, 1984). Others have shown that traits promoting mate choice have evolved to increase contrast with the environmental background (Endler & Théry, 1996). An analysis of the evolution of communication in noise makes it clear that the exaggeration of preferred traits should usually follow this pattern.

The evolution of arbitrary preferences (responses to signals with no advantages for male or female) is the only exception to this rule. Such preferences cannot evolve if they have net costs (Pomiankowski, 1987). Any costs of searching must be balanced by benefits of mate choice. Considering the multiple payoffs and trade-offs for receivers in noisy communication, it seems unlikely that the effects of all the relevant parameters would exactly balance to yield no net cost nor gain ($U_r = 0$). Communication in noise, thus, makes it even less likely than otherwise that arbitrary responses and signals could evolve.

Although this analysis of noisy communication differs from sexual selection in predicting the direction of evolution for signals, it concurs with sexual selection in an important way. Despite the much fuller description of the interaction between a signaling male and a responding female, in the end this analysis shows how males with certain features mate with females with complementary features. This nonrandom mating generates a genetic correlation between any alleles associated with features of male signaling and those associated with features of female responding. This genetic correlation between signaler's and receiver's features can in certain circumstances generate accelerating (run-away) evolution of communication (Lande, 1981; Kirkpatrick, 1982). It is not clear whether or not Fisher had genetic correlation in mind when he described sexual selection. Nor is it clear whether or not he had frequency-dependent selection in mind, such as would apply to the evolution of all signals and corresponding responses, regardless of mating between signaler and receiver (Wiley, 2000). It is clear now that genetic correlation and accelerating evolution should apply to all cases of mate choice that meet certain initial conditions, regardless of whether or not signals are arbitrary or adaptive.

4.4. No perfection in communication

A fundamental conclusion from this analysis is that noisy communication is never perfect. Receivers and signalers instead evolve to joint optima, at which both parties benefit on average but at which both parties also fall short of perfection. Receivers remain susceptible to false alarms and, thus, to deception. Signalers remain incapable of evoking responses to every signal. Responding falls short of perfection and so does signaling. The system of communication is honest and stable, despite the occurrence of instances of communication disadvantageous to signaler or receiver.

From this point of view, the evolution of honesty in systems of communication is not surprising, but neither is the evolution of prevalent dishonesty and deception. This conclusion should apply to economic as well as evolutionary situations. We should not expect communication, of any sort, including systems designed by humans with costs and benefits in mind, ever to achieve perfection. The equilibrial condition for communication in noise is honesty with errors.

Noise is therefore an inevitable part of communication. By assuming that communication evolves in noise, this analysis shows that the evolution of communication cannot escape it. Evolution does not lead to signalers and receivers that perform ideally. Noise is inescapable.

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