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How noise determines the evolution of communication

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This essay focuses on a dozen predictions from a previous analysis of the evolution of communication in the presence of noise. First of all, (1) noise creates an unavoidable trade-off between two kinds of error by receivers. Furthermore, (2) a receiver's optimal criterion for response depends on the level of signals and (3) a signaller's optimal level of signalling depends on the receiver's criterion. As a result, (4) communication in noise can evolve to a joint optimum. (5) Communication at a joint optimum is honest on average. (6) Joint optima for communication in noise do not eliminate noise. (7) Many parameters of communication in noise remain poorly studied. (8) Noise leads to strong predictions for the evolution of exaggeration and thresholds. (9) Signals for advertising and for warning are contrasts in probable costs of errors. (10) The evolution of new signals and responses encounters a hurdle. (11) New signals and responses can evolve by exploitation. (12) Joint evolution of signallers and receivers has a predictable direction. These predictions will remain untested hypotheses until communication in noise is studied more thoroughly than it has been previously.

Following Darwin's (1972) detailed argument that animals' displays, or ‘expressions’, served for conspecific communication, almost half a century elapsed before the idea took hold among field biologists (Huxley, 1914). On first investigation, these displays seemed to be whimsical. Although Darwin had suggested his ‘Principle of Antithesis,’ according to which expressions with opposite meanings often had contrasting forms, there was scant suggestion that signals evolved to fit environmental situations. They even seemed to provide direct access to the phylogeny of species, without contamination by environmental adaptations (Heinroth, 1911, pp. 598–702; Lorenz, 1941).

This view was first shaken by Peter Marler's (1955, 1957) studies of the species distinctiveness of birds' vocalizations. He emphasized that although species specificity had advantages in some circumstances, such as territorial advertisement, it had disadvantages in other situations, such as vigilance for predators by flocks of mixed species. Furthermore, he argued that alarm calls in the latter situation had converged on sounds that were especially effective in hindering localization by predators. The time seemed right for reconsidering the importance of adaptations in animal's signals. The crucial advance came when Eugene Morton's (1975) pioneering studies revealed that birds' songs included adaptations to improve transmission through their respective habitats. Since then reports of adaptations in animals' signals have multiplied steadily. Attention has been given especially to adaptations that reduce attenuation, degradation, and effects of background environmental noise. Recently, reports have focused on human activities as widespread sources of environmental noise. Noise is now recognized to have manifold consequences for the evolution of communication.

Nevertheless, the crucial characteristic of noise with deep implications for the evolution of communication is still not generally appreciated. Noise, as Shannon (1948a, 1948b) originally realized, is best measured by receivers' errors. These errors are often thought just to introduce additional variance in responses to signals. As a result, adaptations to noise are assumed to consist of adjustments by signallers to minimize this extra variance. Although noise must often increase the variance of responses, it has even wider significance for the evolution of communication, because noise produces *unavoidable trade-offs for any receiver*. A receiver cannot maximize its performance in the presence of noise; it can only optimize these trade-offs. Furthermore, not only does the optimal behaviour of receivers depend on the behaviour of signallers, but the optimal

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behaviour of signallers also depends on the behaviour of receivers. Neither the evolution of signallers nor the evolution of receivers can be convincingly explained without taking into account the full consequences of noise.

Previous efforts to explain the evolution of signalling include those that emphasize the evolution of honesty (Enquist, Plane, & Röed, 1985; Getty, 1998; Grafen, 1990; Hurd, 1995; Johnstone, 1995; Maynard Smith, 1991; Maynard Smith & Harper, 2003; Számado & Penn, 2015; Zahavi, 1977; Zahavi & Zahavi, 1997), those that focus on the dynamics of mate choice (for instance, Kirkpatrick, 1982; Lande, 1981; Servedio, 2011) and those that focus of the evolution of stable cooperative interactions (for instance, Scott-Phillips, Blythe, Gardner, & West, 2012; Scott-Phillips & Kirby, 2013). Some previous analyses include the effects of noise as additional variance in responses (Johnstone, 1994) and even emphasize the consequences of the receiver's trade-offs in noise (Johnstone, 1998; Wiley, 1994), but none includes these trade-offs in combination with full interdependence of the receiver's and signaller's performances.

A recent effort to understand the interaction of receiver and signaller in noise has produced some unexpected results (Wiley, 2013a, 2013b, 2015). Some long-standing problems, such as conditions for the evolution of honesty and for evolutionarily stable signalling, appear in an entirely new light. The evolution of mate choice takes on a new dimension. Furthermore, it also becomes apparent that some critical features of communication have so far not received much, or any, investigation. The mathematical analysis of the optimal behaviour for receiver and signaller in noise has been described elsewhere (Wiley, 2013a, 2015). This essay instead isolates a dozen principles, or distinctive predictions, of the evolution of communication in noise. They reveal that noise is an essential factor in the evolution of all communication.

NOISE CREATES AN UNAVOIDABLE TRADE-OFF BETWEEN TWO KINDS OF ERROR BY RECEIVERS

In the presence of noise, there are exactly four possible outcomes each time a receiver makes a decision to respond or not: correct detection, correct rejection, false alarm and missed detection. These four possibilities are the logical combinations of two possible external conditions (noise only or noise plus signal) and two possible decisions by a receiver (respond or not). Two of the four are errors: false alarm and missed detection. In an analysis of the evolution of communication, these two would result in lower survival or reproduction. These two kinds of error are conceptually the same as type I and type II errors in analyses of statistical significance, or errors of commission and errors of omission. The probabilities of the four possible outcomes define a receiver's performance in any particular situation, a situation thoroughly analysed by signal detection theory (Green & Swets, 1966; Macmillan, 2002; Macmillan & Creelman, 2005).

These four outcomes are also a direct consequence of the defining feature of communication – responses (changes in behaviour) by one party (a receiver) to signals by another party (a signaller). A signal in this context is any pattern of energy and matter that can evoke a response *without providing all of the power for the response* (Wiley, 1994, 2006, 2013c). As a consequence, a receiver must make the decision to respond. To do so, it must include sensors (to detect impinging energy and matter), gates (switches to determine which inputs elicit a response), and amplifiers (to provide the additional power for the response). A receiver's gate for a particular response might take the form of a threshold (a minimal level of activation of the sensor) or a filter (an optimal level of activation) – or complex combinations of these two to produce a cognitive criterion for response.

The four possible outcomes each time a receiver checks its sensor are an exhaustive and mutually exclusive categorization of possibilities. Whenever a receiver's sensor cannot absolutely eliminate noise, these four possibilities recur. Furthermore, the two kinds of error cannot be simultaneously minimized. Adjusting a threshold or filter to reduce one inevitably augments the other (Wiley, 1994, 2006). False alarms and missed detections are therefore an inevitable trade-off for any receiver in noise. Noise does not just create extra variance in responses; it puts every receiver in a double bind.

A RECEIVER'S OPTIMAL CRITERION FOR RESPONSE DEPENDS ON THE LEVEL OF SIGNALS

Because of the inevitable trade-off between two kinds of errors, a receiver cannot minimize its errors overall; the best it can do is to choose a criterion for response that optimizes the trade-off. The criterion for an evolutionary optimum depends on (1) the probabilities of the four possible outcomes and (2) the consequences of each outcome for the receiver's survival and reproduction (the evolutionary payoff for each outcome). The probability of a correct detection, for instance, is a product of the probability that a signal actually occurs at the moment a receiver checks its sensor and the probability that the receiver responds in this situation. The probability that the receiver responds when a signal occurs depends in turn on its criterion for responses (the location of its threshold, for instance) and on the level of the signal in relation to any noise (the signal/noise ratio). In general, the probability of each of the four possible outcomes depends on (1) the probability that a signal occurs, (2) the receiver's criterion for response and (3) the level of the signal in relation to noise. A linear combination of these probabilities and payoffs for the four possible outcomes specifies the utility of a receiver's criterion for response (Wiley, 1994, 2013a, 2015). This approach is the basis of decision theory (van Neumann & Morgenstern, 1953).

Maximizing this utility depends on the trade-offs between the two possible errors and between the two possible correct responses. It also depends on the level of the signal in relation to the noise (the signal/noise ratio). Consequently, the receiver's optimal criterion for response depends in part on the level of signal produced by the signaller.

A SIGNALLER'S OPTIMAL LEVEL OF SIGNALLING DEPENDS ON THE RECEIVER'S CRITERION

Often, perhaps always, a higher level of signalling (greater intensity, size or saturation, or in general greater ‘exaggeration’) comes with costs, as a result of greater expenditure of energy, commitment of time, opportunities lost, or exposure to inappropriate receivers (such as predators, parasites or competitors). There have previously been two lessons drawn from these costs of signalling: (1) costs are necessary for the evolution of honest signalling (sometimes with a provision that the costs must be ‘wanton’ or ‘excessive’) (Maynard Smith & Harper, 2003; Zahavi & Zahavi, 1997); and (2) increasing costs multiplied by increasing benefits can produce evolutionarily stable signals, which in turn are honest (Getty, 1998; Nur & Hasson, 1984; Wiley, 2000, 2015).

It is easy to show that combinations of benefits and costs can produce equilibrial levels of signalling (including signals for advertisement and for solicitation; see Appendix and Wiley, 2000, 2015). These treatments however ignore the interdependent evolution of the signaller and receiver. The benefit for the signaller comes from responses (correct detections) by appropriate receivers, and the probability of these responses depends on the optimal criterion for response by these receivers.

Thus the optimal level of signals by a signaller cannot be determined without reference to the performance of the appropriate receivers. At the same time, as introduced in the preceding section, a receiver's optimal criterion cannot be determined without reference to the signaller's level of signalling. It is not possible for either party to optimize its behaviour on the basis of fixed costs and benefits. So no argument that honesty (or any other feature of communication) depends only on a signaller's costs can be complete. Instead, the only way to understand the evolution of communication in the presence of noise is to consider the possibility of a joint optimum, one at which the receiver's criterion is optimal provided the signaller's exaggeration is optimal and vice versa.

Notice that the preceding definition of a signal differs from previous ones especially in lacking any qualification that signals (as opposed to cues) must have evolved for the purpose of communication. This qualification, which has the unfortunate consequence of making the definition of signals and communication circular, is unnecessary (Wiley, 2013c, 2015). On the other hand, it is apparent that when signallers, as well as receivers, are living organisms, then each can evolve in relation to the other.

COMMUNICATION IN NOISE CAN EVOLVE TO A JOINT OPTIMUM

By proposing utility functions for both the receiver's threshold for response and for the signaller's level of exaggeration, it is possible to derive optimal thresholds for every level of exaggeration and, conversely, optimal exaggerations for every level of threshold. It then becomes possible to search for points of coincidence between these optima for threshold and for exaggeration (Wiley, 2013a, 2015).

The result depends on the payoffs for the possible outcomes of a receiver's decisions and on the cost of exaggeration and the benefit to a signaller from a receiver's correct detection of a signal. The result also depends on the frequency of signals, both overall (which affects the signaller's overall cost) and at times when receivers are monitoring their sensors (which affects the probabilities of a receiver's four possible outcomes). It turns out that communication in noise, with reasonable conjectures for these parameters, often leads to evolutionarily stable levels of a receiver's threshold and a signaller's exaggeration (Wiley, 2013a, 2015).

Calculation of the adaptive landscapes around these joint optima show that they are Nash equilibria: joint optima at which each party does the best it can provided the other does also. On the other hand, there are often loci in the adaptive landscapes where evolution can diverge, either towards a joint optimum or towards a collapse of communication. Such a collapse occurs when the optimal exaggeration $= 0$, indicating no signal, or the optimal threshold $= 0$, indicating no discrimination and thus no association of responses with signals.

Evolution through the adaptive landscape defined by levels of receivers' thresholds and levels of signallers' exaggeration is a process that involves continual adjustments of both thresholds for response and exaggeration of signals. The exact course of evolution towards a joint optimum depends on the starting conditions and on the payoffs, costs, benefits and probabilities already mentioned, but in no case does either receiver or signaller evolve in relation to a fixed level of performance by the other party.

COMMUNICATION AT A JOINT OPTIMUM IS HONEST ON AVERAGE

Communication is honest because at these joint optima receivers benefit (utility > 0). It has been recognized previously that receivers must benefit ‘on average’ or overall for communication to evolve, otherwise it would not pay for receivers to attend to signals (Grafen, 1990; Guilford & Dawkins, 1991). Any costs of deception or manipulation of receivers (or exploitation of signallers) must be more than balanced by benefits. Nevertheless, the emphasis has often been placed on the costs for the signaller (Lachmann, Számado, & Bergstrom, 2001; Szamadó, 2011). In contrast, the evolution of communication in noise shows that receivers and signallers evolve to a joint optimum at which each party benefits on average and each optimizes its behaviour provided the other does also. Despite adaptations to reduce the effects of noise, possibilities for deception, manipulation and exploitation persist. So do benefits on average for both parties. Communication in noise predicts the evolution of both honesty on average and residual manipulation.

JOINT OPTIMA FOR COMMUNICATION IN NOISE DOES NOT ELIMINATE NOISE

The joint optima for receiver and signaller in noise never reach a level at which noise is eliminated. Both parties face diminishing benefits and augmenting costs as thresholds and exaggeration rise. As a result communication evolves to optimize performance in noise by *reducing* the consequences of noise but not by *eliminating* noise. In high levels of noise, communication can evolve high thresholds and high exaggeration yet always retain the possibility of errors by receivers and signals without responses. Likewise, in low levels of noise, communication can evolve low thresholds and low exaggeration, yet still retain possibilities for errors and frustration. In both situations, the optimal performances of receiver and signaller scale to the level of noise.

MANY PARAMETERS OF COMMUNICATION IN NOISE REMAIN POORLY STUDIED

This new analysis indicates that most of the parameters that influence the evolution of communication in noise are not well known. For instance, the probabilities of the four possible outcomes and the relative frequencies of signals have received little or no attention. Some of the costs, benefits and payoffs, in particular the payoffs for false alarms or missed detections, are also often neglected. On the other hand, the costs of signals and the benefits of correct detections are better known.

There are many reports of the costs of signals (displays), well summarized by Bill Searcy and Steve Nowicki (2005). Møller's (1994) pioneering studies of the costs of tail streamers in barn swallows, *Hirundo rustica*, provided a model for demonstrating that individuals of higher quality could produce larger displays with less overall cost than could individuals of lower quality. Yet this study did not estimate the *marginal* cost of exaggeration. The available data suggest that the costs are not linear with exaggeration in this case (see Wiley, 2015). There seems to be no reason why future studies of this or other displays could not estimate marginal costs of exaggeration as well as intrinsic quality of signallers (for instance, by extrapolation to survival in the absence of any signalling). Overall costs of a signal do not alone provide a way to deduce either of these other parameters.

Benefits of responding to optimal signals have also received attention, especially in the case of choosing an optimal as opposed to a suboptimal mate (again Searcy & Nowicki, 2005). These comparisons, however, have never considered the payoffs for all four possible outcomes for a receiver (or at least the relative payoffs for three of them in comparison to the fourth). There have also been estimates of the risks of signals for predation and parasitism. Studies of mimicry have estimated nearly all the costs and benefits of signals, and even their relative frequencies (Kikuchi & Pfennig, 2013), but we know less about the payoffs for the four possible outcomes for receivers.

These examples are enough to suggest that all of the parameters relevant to understanding the evolution of communication in noise can be estimated in natural conditions – like those in which the signals and responses evolved. Because, as emphasized above, escape from noise is not expected, a full understanding of the evolution of communication must include more attention to these neglected or ignored parameters.

NOISE LEADS TO STRONG PREDICTIONS FOR THE EVOLUTION OF EXAGGERATION AND THRESHOLDS

This new analysis permits an analysis of the sensitivity of the evolution of communication in noise to variation in each of the parameters. An important caveat is that a predicted effect of changing any one parameter requires that all other parameters remain constant. Foremost among these analyses is the prediction that (1) high marginal costs of exaggeration (the cost of each unit of exaggeration) result in lower levels of exaggeration and lower thresholds for response. Perhaps contrary to current expectations, exaggerated signals are predicted to have low marginal costs (all else equal). Furthermore, the payoffs for each of the four possible outcomes of a receiver's decision to respond or not affect *both* its optimal threshold and the signaller's optimal level of exaggeration. As a result, there are two more predictions to make. (2) Higher costs (lower payoffs) of false alarms for *receivers* lead to higher levels of exaggeration by *signallers*. (3) Higher benefits of correct detections (higher payoffs) for *receivers* lead to lower levels of exaggeration by *signallers*. Lower exaggeration also results from higher costs (lower payoffs) of missed detections.

Furthermore, higher relative frequencies of signalling result in both higher overall costs for signallers and lower thresholds for receivers (because correct detections become inherently more likely than false alarms). For both reasons, (4) higher relative frequencies of signalling lead to lower levels of exaggeration. In the limit, when signals always occur whenever a receiver checks its threshold, it no longer pays for the receiver to bother; instead it pays to respond at any time, and the evolution of communication collapses.

The parameters that are the basis for these predictions – the marginal cost of signals, the payoff for a false alarm in comparison to that for a correct detections and the relative frequency of a signal – are all poorly known. Yet they have strong influences on the predicted evolution of communication in noise.

SIGNALS FOR ADVERTISING AND FOR WARNING ARE CONTRASTS IN PROBABLE COSTS OF ERRORS

Advertising for mates is the classical case for exaggerated signals. In this case the receiver (an individual of the choosy sex) encounters signals (displays by high-quality potential mates) as well as noise (displays by low-quality potential mates). The choosy sex is often supposed to have coy behaviour (frequent failures to respond to high-quality prospects). In other words, receivers (choosers) accept many missed detections (passing optimal mates). They would thereby minimize false alarms (accepting suboptimal mates). Coy behaviour thus corresponds to a high threshold for response – adaptive fastidiousness (Wiley, 1994).

In contrast, signals for warning presumably have the converse relationship between the costs of false alarms and missed detections. Receivers that miss a warning risk exposure to a dangerous predator. A false alarm, by responding for instance to a deceptive warning signal, might often entail only a brief interruption of feeding or courtship. A high cost for missed detections, in comparison to false alarms, would result in a low threshold for response. It would be manifest as jumpy receivers that often responded to deceptive signals – adaptive gullability (Wiley, 1994).

High thresholds for coy receivers choosing mates and low thresholds for jumpy receivers attending to warnings suggest that signals for advertisement should have high exaggeration and those for warning should have low exaggeration (Wiley, 1994). Yet analyses of the evolution of noisy communication with some hypothetical payoffs for the four possible outcomes of a receiver's decisions to respond have not confirmed that the contrast in payoffs for false alarms and missed detections produce the expected contrast in exaggeration of signals (Wiley, 2015, contra Wiley, 2013a). Instead a contrast in frequency of signals counteracts the contrast in costs of errors so that both warning and advertising signals are expected to evolve exaggeration. Warning signals in this analysis evolve high exaggeration, despite high costs of missed detection, because they are relatively infrequent; advertising signals evolve high exaggeration, despite high frequency, because false alarms are relatively costly.

THE EVOLUTION OF NEW SIGNALS AND RESPONSES ENCOUNTERS A HURDLE

The adaptive landscapes for the evolution of signaller and receiver in noise illustrate an intuitive conclusion about the origin of new signals. New signals cannot evolve in the absence of appropriate responses; and responses cannot evolve in the absence of suitable signals. The evolution of new signals and responses corresponds to initial conditions with high thresholds and low exaggeration. No response corresponds to an infinite threshold, so an incipient response would correspond to a high threshold. No signal is zero exaggeration, so an incipient one would have low exaggeration. The corresponding quadrant of the adaptive landscapes in noise epitomizes this problematic condition for the evolution of new signals or new responses *ab initio*. The recent analysis shows that selection gradients in these conditions move signallers and receivers towards a collapse of communication, towards no exaggeration of signals and no lower thresholds (Wiley, 2013a, 2015). This analysis is more precise than the intuitive adage, because it shows that the collapse of incipient communication is a result of signallers and receivers jointly optimizing their behaviour.

A similar situation has long been recognized for the evolution of signals for mate attraction in quantitative genetic models of sexual selection. The strength or prevalence of females' preferences (in the prevalent situation with female choice) must exceed a threshold before the evolution of males' traits begins to accelerate. The new analysis of communication in noise shows, in a quantitative phenotypic analysis, that a similar condition applies to the evolution of all communication. The evolution of communication *ab initio* must cross a hurdle.

NEW SIGNALS AND RESPONSES CAN EVOLVE BY EXPLOITATION

There are two ways that might lower or eliminate this hurdle. Appropriate terms for these two options are *sensory exploitation* by receivers and incipient signallers and *motor exploitation* by signallers and incipient receivers. ‘Exploitation’ here is meant to suggest that both signallers and receivers can jointly take advantage of their particular features, not that one party takes advantage of the other (Ryan, 1990, suggests instead that signallers exploit receivers). Sensory exploitation would occur when some individuals, as a result of adaptations having nothing to do with communication or at least with the newly evolving form of communication, already have responses to particular sensory input. As a result, an incipient (mutant) signal that also evoked that response might encounter initial conditions for evolution outside the problematic quadrant of adaptive fields for joint evolution of signaller and receiver in noise.

The exact initial conditions would depend on the payoffs for the receivers and the costs and benefits of exaggeration for the signallers and the relative frequency of the new signal. If the initial conditions avoided the collapse of communication in the problematic quadrant, then joint evolution of signals and responses would proceed towards the appropriate joint optimum. Both parties would evolve in this process, so there would be no implication that one party was taking advantage of the other. Both might however benefit from the circumstances that allowed a new system of signalling and responding to jump the hurdle for their evolution *ab initio*. Sensory exploitation in this sense is related to previous proposals, but without the implication that one party takes advantage of the other.

The alternative way to jump the hurdle *ab initio* is motor exploitation. In this case an action (a movement or a synthesis of a structure or molecule) might already exist as an adaptation unrelated to communication (or the novel form of communication). For instance, consider the suggestion by early ethologists that comfort movements or 'displacement activities' often provide the initial condition for the evolution of new displays (Tinbergen, 1940, 1959). Such actions might also indicate something about the performer that could make it advantageous for another individual to respond. Just as with sensory exploitation, this situation could provide initial conditions for the evolution of a new system of signal and response that lay outside the problematic corner of the adaptive landscape for evolution in noise. As before, the initial conditions would then result in joint evolution of signalling and responding towards a joint optimum for signallers and receivers. It would not be a case of one party exploiting the other. Instead both parties would exploit their complementary features that permit the evolution of a mutually beneficial signal and response. Sensory and motor exploitation are examples of cooptation in evolution.

JOINT EVOLUTION OF SIGNALLERS AND RECEIVERS HAS A PREDICTABLE DIRECTION

The evolution of communication in noise evolves towards a joint optimum of thresholds for response and exaggeration of signals. Exaggeration in this context consists of adaptations that increase the detectability of the signals. Detectability (or discriminability) of signals depends partly on the properties of the receiver's sensors including their thresholds or filtering of input and their levels of intrinsic noise. Detectability is also influenced by the properties of signals. The relevant properties are often summarized as the signal/noise ratio.

Contrast between signal and noise is directly related to this ratio. Contrast results from the intensity of a signal, especially in those features with low intensity in external noise. Saturation (concentration of energy or matter in particular features of the signal) also contributes to contrast provided the appropriate receivers' sensors can differentiate these features. Examples include a concentration of acoustic energy in a particular frequency of sound at any instant, as do many birds' songs, or concentration of optic energy in a particular wavelength at any point (~1/frequency), as do iridescent colours. The evolution of communication in noise predicts that signals evolve optimal levels of exaggeration in the specific sense of contrast with environmental noise (whether from nonbiological, heterospecific or conspecific sources).

Predictability also contributes to the detectability of signals. Almost any prior knowledge about (or prior experience with) parameters of a signal (including its timing and location) makes it more detectable. For instance, an alerting signal, easily detectable but information-sparse, is one way to increase the predictability of a contiguous signal that is information-dense (Wiley & Richards, 1982). *Redundancy*, as well known, also enhances the detectability of signals. Contrast, predictability and redundancy are the features of 'ritualized' signals, which early ethologists proposed had evolved to facilitate communication. They had, however, not emphasized the particular advantage of these features of signals for communication in noise.

Notice that sexual selection also predicts progressive evolution of signals in accordance with one sex's preferences. It provides quantitative predictions for the dynamics of this joint evolution. On the other hand, it does not provide predictions about the direction of evolution. The theory of communication in noise, summarized here, has complementary advantages and disadvantages. It predicts the direction (and ultimate equilibrial optimum) but not the dynamics of the joint evolution of signals and responses.

CONCLUSION

These dozen points about the evolution of communication in noise suggest that the evolutionarily optimal properties of communication should be understandable in detail in any particular situation. Noise is critical for this understanding, because the most basic prediction from analysing the evolution of communication in noise is that communication does not evolve to eliminate noise. Noise is thus expected to be a persistent feature of all communication. These dozen points are conclusions and extrapolations from a full mathematical analysis presented elsewhere (Wiley, 2013a, 2015). Perhaps the biggest lesson from this analysis is the number of parameters that must be understood to explain the evolution of communication in noise. There are 10 of these parameters (Wiley, 2015, p. 185). Most have received little attention by students of animal (or any other form of) communication. Those most neglected do not seem inherently more difficult to measure than those that have already received some study. Until all of these parameters get some attention, the predictions from the mathematical analysis will remain untested. Only by accounting for noise will it be possible to understand the evolution of communication.

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APPENDIX

(1) Optimal Levels of Exaggeration for Advertisement

In this case the costs of signalling are lower survival and the benefits are higher reproduction. Such a situation might apply to males advertising for mates. Suppose that (1) signals have costs and benefits that increase with exaggeration, (2) costs can be expressed as decreased survival, (3) benefits can be expressed as increased reproduction, and (4) the influence of natural selection on the spread of genes can be approximated by survival × reproduction of phenotypes associated with those genes. If the cost increases (survival decreases) linearly with exaggeration and the benefit (reproduction) increases linearly with exaggeration, then taking the derivative of the product of these two functions with respect to exaggeration and setting the derivative to 0 shows that maximal survival × benefit occurs when

$$e^* = -i/2m - o/2g$$

In this expression, e^* is the optimal level of exaggeration, i is intrinsic survival (in the absence of any signalling), m is the marginal cost of exaggeration (the negative slope of survival as a function of exaggeration), o is the offset for reproduction ($o > 0$ indicates a residual level of reproduction without signalling and $o < 0$ indicates that exaggeration must reach some level before any reproduction occurs), and g is the marginal gain in reproduction (the positive slope of reproduction as a function of exaggeration). The second derivative of survival × reproduction with respect to exaggeration confirms that this optimal level of exaggeration is indeed a maximum, provided $m < 0$ and $g > 0$. The above expression shows that signallers with higher intrinsic survival or lower marginal cost of exaggeration have higher optimal levels of exaggeration. Signallers with higher quality by either of these two measures should thus have more exaggerated signals, provided all signallers produce optimal levels of exaggeration. It would not pay for low-quality signallers to produce as much signal as high-quality signallers, even though their overall survival × reproduction is less.

(2) Optimal Levels of Exaggeration for Solicitation

In this case signallers balance one source of mortality against another. Young begging for food from parents might fit this situation, when begging decreases the risk of starvation but increases the risk of predation (for instance, if begging attracts predators or parasites). If the first risk exceeds the second, then begging pays and natural selection would favour signals that minimize the overall risk of death. A complexity arises because the probability of starvation $P(\mathrm{s})$ is not independent of the probability of predation $P(\mathrm{p})$, so the overall mortality equals $P(\mathrm{s}) + P(\mathrm{p}) - P(\mathrm{s})\,P(\mathrm{p})$.

Assume that the probability of starvation $P(\mathrm{s}) = S + e\,s'$, where e is the exaggeration of signals, S is the intrinsic risk of starvation without any signalling, and s' is the negative marginal risk of starvation with increasing exaggeration (negative to indicate that the chance of starvation decreases with increased begging). Analogously, assume that the probability of predation $P(\mathrm{p}) = P + e\ p'$, where P is the intrinsic risk of predation without any signalling and p' is the positive marginal risk of predation with increasing exaggeration of signal (positive to indicate that the chance of predation increases with increased exaggeration).

Expanding the equation above for overall mortality, then taking the derivative of the result with respect to e and zeroing the derivative, reveals a unique level of exaggeration that minimizes overall mortality:

$$e^* = \frac{1}{2}\left(\frac{1-P}{p'} + \frac{1-S}{s'}\right)$$

provided that P and $S > 0$, $p' > 0$ and $s' < 0$. The optimal exaggeration of soliciting signals thus increases as each of the four parameters, P, S, p' or s', increases. Because s' is negative by definition, an increase in s' is equivalent to a decrease in the absolute value of s'. In the case of young sharing a nest, if one is in better condition (better fed, for instance) than another, it might thereby have lower S and lower s'. In other words, it might be intrinsically less likely to starve and also its chance of starvation might decrease proportionately less for each unit of exaggeration. On the other hand, P and p' might not differ among nestlings regardless of their condition, if predators are likely to take all young once a nest is discovered. If so, the preceding equation predicts that well-fed nestlings maximize survival by begging less than other nestlings.

These calculations have not included any indirect effects of an individual's behaviour on survival of relatives, such as siblings and parents. Incorporating these effects would require rephrasing the argument in terms of a change in the expected number of copies of a gene in the next generation, by adding any effects of an individual's signals on the expected survival of relatives, depreciated by their genealogical relatedness, to the individual's own expected survival. Because an individual's signals would usually decrease the expected number of relatives in the next generation (particularly when begging decreases a parent's condition or increases predation on nests), these effects would tend to reduce the optimal exaggeration of individuals' signals for begging (see Godfray, 1995).

These calculations also do not take into account the coevolution of joint optima by signaller and receiver, as summarized above.