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4 Signal detection and the evolution of communication

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2 Signal Detection and Decision Theories have had limited
3 application so far in studies of animal behavior. Yet, in addition to
4 their utility in particular cases, they provide a way to understand
5 the evolution of communication in general. The essential
6 contributions of these theories are (1) a distinction between the
7 detectability of a signal and the criteria for a receiver's response
8 and (2) a realization that any decision by a receiver to respond or
9 not has four possible outcomes, not all of which are independent.
10 As a consequence, all receivers must make compromises. They can
11 only optimize their errors, not eliminate them. This constraint on
12 receivers provides sufficient explanations for the evolution of
13 exaggerated signals and deception. Signal detection theory further
14 indicates that exaggeration of signals should occur in ways that
15 improve the detectability or discriminability of signals by intended
16 receivers. Furthermore, these theories suggest that the evolution of
17 exaggerated signals is subject to compromises, not only as a result of
18 increasing costs, but also as a result of diminishing returns. As a
19 result of the constraints on both receivers and signalers, we suggest
20 that the evolution of communication is the optimization of a signal-
21 detection balance, in which signals reach optimal but not complete
22 detectability and receivers reach optimal but not ideal performance.

1 For half a century, Signal Detection Theory has had wide
2 application in psychophysics and cognitive psychology, where it has
3 provided a way to separate the motivation of subjects from the
4 detectability of signals. Decision Theory, developed in economics to
5 characterize rational or optimal choices, is familiar to behavioral
6 ecologists, who routinely consider costs, benefits, and probabilities
7 of alternatives in order to predict optimal behavior. Although these
8 two bodies of theory have remained peripheral in studies of animal
9 communication, we propose that they explain some basic
10 adaptations for communication and reveal some unrecognized
11 problems.

12 Signal Detection Theory addresses the problem of signals in
13 the presence of noise. Whenever a receiver samples the input of its
14 receptors, in all but ideal conditions, and makes a decision to
15 respond or not, there are four possible mutually exclusive outcomes:
16 correct detection, correct rejection, false alarm, and missed
17 detection. In Signal Detection Theory the detectability of signals by
18 a receiver's receptors and the receiver's criterion for response
19 together determine the probabilities of the four possible outcomes.
20 When signals of interest to a receiver cannot be completely
21 separated from other incident energy, the receiver inevitably makes
22 errors in deciding whether or not a signal has occurred (Box 1).

1 Decision Theory provides a way to determine the optimal
2 performance of a receiver when there is more than one possible
3 outcome of a decision to response. It computes the expected utility
4 of a decision from the payoffs (positive or negative) and
5 probabilities of each of several independent outcomes. von
6 Neumann and Morgenstern ¹ introduced a measure of the expected
7 utility of a decision, $E(U) = \sum(i) U(i)p(i)$, the sum of the utility, $U(i)$,
8 times the probability, $p(i)$, of each of i mutually exclusive outcomes
9 of a particular course of action. If these alternative outcomes are
10 not independent, it is often not possible to obtain the maximal
11 benefits with the minimal costs. Instead the decision-maker must
12 optimize its performance by maximizing $E(U)$.

13 Although not necessarily identified with Signal Detection and
14 Decision Theories, similar ideas underlie much of optimal foraging
15 theory ² and have been applied to optimal mate choice ³⁻⁶. A case in
16 which all of the elements of these theories have been included is the
17 rejection of atypical eggs by the hosts of brood parasitic birds (Box
18 2). Predation on distasteful models and their mimics invites similar
19 analysis ⁷. Signal detection theory, however, is not yet recognized as
20 a general model for communication.

21

1 Signal Detection Theory as a General Model for Communication

2

3 To justify generalizing this situation, we must address what

4 constitutes a signal, what constitutes a receiver, and what

5 constitutes an error by a receiver. First, a signal must affect some

6 receiver's behavior. In other words, signals are associated with

7 responses^{8,9}, either actions or changes of state such as memory.

8 Beyond this basic definition, there have been proposals to separate

9 signals from signs (characterized by representation), cues

10 (characterized by a lack of intention or evolutionary specialization),

11 or indices (characterized by an invariant relation with some

12 property of interest to a receiver)^{10,11}. These distinctions have

13 proven difficult to characterize operationally.

14 The present perspective can ignore these distinctions. A signal

15 is any form of energy (or matter) that influences a receiver's

16 behavior, without providing all of the power for that behavior¹². At

17 least some (often most) of the energy for the receiver's response

18 must come from the receiver. According to this definition, moving

19 out of the way as a result of a push is not evidence of

20 communication, but jumping aside in response to a shout, or even

21 in response to the sound of approaching danger, is. The essential

22 feature of any signal is its limited power, insufficient to produce the

1 response. As a result, the receiver itself has a crucial role in
2 determining the response. The receiver is in a position to get what
3 it wants ¹³, although, as we show below, only within some
4 limitations.

5 Second, as a result of the insufficient power of signals, any
6 receiver includes three essential components: a transducer, a switch
7 or gate, and an amplified output. If the receiver is an animal, the
8 basic components are often sensory receptors, a set of associative
9 neurons, and effectors (motor neurons and a musculo-skeletal
10 system). The effectors need not produce an overt response. It
11 could instead be an altered state of a nervous system (memory).
12 This conception of a receiver is general enough to include any form
13 of communication whatsoever.

14 Third, what constitutes an error by a receiver? If our goal is to
15 understand the evolution of communication, then our concern is the
16 relative rates of spread of alleles associated with receivers that differ
17 in their criteria for response. Whenever a receiver samples its
18 receptors and makes a decision to respond or not, its criterion
19 determines the probabilities of the four possible outcomes and thus
20 the expected utility of its behavior ^{12, 14}. The expected utility is a
21 measure of natural selection on any alleles associated with the

1 receiver's criterion. Any of the possible outcomes that tends to
2 reduce a receiver's chances of survival or reproduction is an error.

3 We can imagine an ideal situation in which a signal contrasts
4 so extremely with its background that overlap with other sources of
5 energy approaches zero. Yet in actual situations, irrelevant sources
6 of energy are more or less always present. In a number of
7 important cases, such as communication at long range or in dense
8 aggregations of individuals, noise almost overwhelms receivers.
9 Below we show that evolution is not likely to result in absolutely
10 detectable signals, so receivers in natural situations must usually
11 deal with noise (Box 3).

12

13 Applications of Signal Detection Theory to Animal Communication

14

15 The application of Signal Detection Theory to human
16 psychophysics has provided quantitative confirmation of many of
17 its predictions. Controversies in this field have focused on the
18 validity of assumptions for mathematical convenience, rather than
19 on the underlying trade-off any receiver must face ¹⁴.

20 Experiments in psychophysics have repeatedly demonstrated
21 that a receiver's performance increases with higher signal-to-noise
22 ratios. Furthermore, performance improves under any conditions

1 that allow a receiver to predict the timing and features of a signal.
2 Identifying intervals when a signal might occur, providing signals
3 with features known in advance, and redundancy (predictable
4 temporal or spatial structure) all increase performance ¹⁴. Other
5 aspects of receiver psychology ^{15, 16}, including the widespread "peak
6 shift" in discrimination learning ^{17, 18}, also follow from Signal
7 Detection Theory.

8 Receivers' criteria for response can vary in complexity. A
9 simple case is a threshold on a single dimension of a signal, such as
10 frequency or intensity. Other cases can include multidimensional
11 criteria for responses to complex patterns of stimulation.
12 Experimental demonstrations that a species' own vocalizations are
13 easier to detect in background noise, for instance, indicate that
14 channels for filtering and decision-making have evolved complex
15 filters for detection of these signals ¹⁹⁻²¹.

16 These results from experimental psychophysics have recently
17 found applications in natural circumstances ²². Birds, for instance,
18 increase the intensity of their vocalizations in the presence of high
19 levels of background sound ²³⁻²⁵, presumably to increase their
20 detectability. In another case, two closely related populations of
21 birds differ in the dominant frequencies in their songs, so that each
22 minimizes overlap of its songs with background noise ²⁶. Receivers

1 evolve adaptations to background noise as well. The frequency for
2 greatest detectability of sound by great tits *Parus major* is higher in
3 the presence of natural noise such as wind in a forest than it is in
4 quiet conditions such as in a sound-attenuating chamber, and the
5 higher frequency in natural conditions is the better match for the
6 dominant frequencies in the species' vocalizations ²⁷.

7 Background sound also limits the active space of a signal ²⁸. A
8 striking example of this limitation occurs in choruses of frogs. The
9 phonotactic responses of female green treefrogs *Hyla cinerea* to calls
10 of individual males differ in the presence and absence of sound
11 from a chorus of these frogs ²⁹. Females preferentially approach a
12 male's calls only when the calls exceed the sound of the chorus by 3
13 dB. A male's call attenuates by spherical spreading alone to this
14 level in a distance of about 1 meter. Female frogs in such a chorus
15 would thus respond to individual males only within this short
16 distance. As a result of the spacing of calling males, even in the
17 densest part of a chorus, a female is within this distance of only 2-3
18 males at a time. To sample more males, she would have to move
19 around and risk exposure to predators such as snakes. A similar
20 conclusion was reached by Wollerman ³⁰ for female *Hyla ebraccata*
21 at a large chorus with eight species of frogs in a Costa Rican

1 rainforest. Because of background noise, a female's choice of males
2 is much more limited in a large aggregation than we might imagine.

3

4 Detection Versus Discrimination

5

6 The problem for a receiver becomes more complicated when
7 the task is to classify two or more relevant signals as well as to
8 detect the presence or absence of any one signal ^{31, 32}. This problem
9 arises whenever a receiver must make appropriate but different
10 responses to more than one signal. A predator that must respond in
11 different ways to different types of prey might face this situation.
12 Social situations that require recognition of several different
13 individuals also fit this situation. Another case involves
14 appropriate responses to signals associated with the presence of
15 distinct kinds of predators ³³⁻³⁶.

16 These situations require classification (often called
17 discrimination) of signals, in other words, different responses to
18 each of several signals. In contrast, detection requires the same
19 response to one or more signals. A test for discrimination thus
20 requires a comparison of appropriate responses to two different sets
21 of signals. For a realistic test, both signals would be mixed with
22 background sound. Studies of detection, as described above,

1 present a signal mixed with noise from one speaker and nothing but
2 noise from the other. A complete analysis would require three
3 situations, noise with each of two signals and alone.

4 In a complete analysis of discrimination between two signals,
5 there are nine possible outcomes as viewed by a privileged observer,
6 instead of the four possibilities for detection. There are three states
7 of the world (noise with signal 1, noise with signal 2, or noise alone),
8 and there are three possible responses of the subject (appropriate
9 for signal 1, for signal 2, or none). The analysis of this situation is
10 correspondingly complex, with more than twice the number of
11 relevant probabilities and utilities.

12 Despite this complexity, applying Signal Detection Theory to
13 discrimination leads to an important prediction^{32, 37}: a reduction in
14 performance of receivers in tasks that require discrimination in
15 comparison to detection only. Consequently, we expect to find
16 signal-to-noise ratios (S/N) in which individuals detect signals but
17 do not discriminate between them, although in conditions with
18 higher S/N they do discriminate between them.

19 This possibility arises for female frogs mating in a dense
20 chorus. For several species, we know that females prefer
21 conspecific male advertisement calls with lower dominant
22 frequencies. This preference has, for instance, been confirmed for

1 *Hyla ebraccata* in Costa Rica ³⁸. As already discussed, we know that
2 female frogs, including *H. ebraccata*, have difficulty detecting
3 individual male's calls in large choruses. Do they have even greater
4 difficulty discriminating males' dominant frequencies?

5 In a test of discrimination in natural levels of noise,
6 Wollerman and Wiley ³⁹ presented gravid female *H. ebraccata* with
7 males' calls mixed with the background sound of a chorus. One
8 speaker presented calls with a dominant frequency at the
9 population mean, while a second speaker presented calls with a
10 dominant frequency two SD below the mean. With no added chorus
11 noise (S/N > 25 dB), females reliably preferred the lower frequency.
12 With added chorus noise (S/N = 6 and 9 dB), they no longer
13 preferred the lower frequency, although they still detected
14 (responded preferentially to) a single male's calls in chorus sounds.
15 The discrimination made in relatively quiet conditions thus
16 disappeared in conditions that still allowed detection of the signals.
17 This result is thus in agreement with the prediction of Signal
18 Detection Theory: discrimination is a more difficult task than
19 detection and, for the same level of performance, requires signals
20 with higher detectability.

21

22 Evolution of Receivers

1

2 Signal Detection and Decision Theories provide a way to think
3 in general about the evolution of communication. In particular, this
4 section suggests that the constraints on any receiver provide a
5 sufficient explanation for such problematic features of
6 communication as the persistence of deception and the exaggeration
7 of signals. In addition, these theories suggest that the co-evolution
8 of receiving and signaling lead to a signal-detection balance.

9 Because receivers provide the power necessary for a response,
10 they evolve to optimize performance in the conditions they
11 experience. The first step in understanding the evolution of
12 communication is thus an explanation for a receiver's decisions to
13 respond or not. This explanation in turn requires optimization of
14 the expected utility, $E(U)$, of the receiver's criterion for response.
15 Procedures for calculating optimal thresholds for response have
16 been presented elsewhere ¹². Here we use some limiting cases to
17 illustrate the main conclusions. Compare, for instance, situations in
18 which missed detections have relatively high costs with those in
19 which false alarms have relatively high costs.

20 Missed detections might be especially costly when an
21 individual is listening for alarm calls. A missed detection (failing to
22 respond to an alarm call) is likely to mean increased exposure to a

1 predator. A false alarm (briefly fleeing when there is no alarm call)
2 would often require only a little time lost from other activities. If
3 predators are a relatively frequent danger, the cost of a missed
4 detection times its probability might dominate the expected utility
5 for thresholds of response. In this case, a low threshold is optimal.
6 The result would be a receiver with "adaptive gullability" ¹², one
7 prone to false alarms but subject to few missed detections. Such an
8 individual would be susceptible to deception, for instance, when
9 occasional calls that mimic alarms allow a subordinate individual to
10 take advantage of a dominant rival.

11 Examples of adaptive gullability include birds that respond to
12 false alarms by subordinates that usurp food or by rivals that
13 interrupt sexual activity ⁴⁰⁻⁴². Monkeys are also manipulated by
14 subordinates in this way ³⁴. Another example comes from species in
15 which satellite males encroach upon matings by dominant males.
16 In many cases, the subordinate males look like females. Dominants
17 trying to detect cheating males thus run the risk of false alarms,
18 with the consequence that they chase away some females. When
19 missed detections are expensive, adaptive gullability should evolve
20 and dominant males would fail to exclude all satellites from
21 matings.

1 False alarms, on the other hand, might have especially
2 negative consequences when individuals make infrequent but
3 crucial choices. Mate choice might often fit this situation. In most
4 species a female chooses a mate infrequently and yet mismating
5 with a low-quality male, a male with inadequate resources, or even
6 another species could have large consequences for the spread of her
7 genes. In this case, a high threshold is optimal. The result would be
8 a receiver with "adaptive fastidiousness" ¹², one liable to miss
9 detections of suitable signals but subject to few false alarms. From a
10 privileged observer's perspective, such a receiver would appear to
11 be "choosy" or "coy", because they would often fail to respond to
12 suitable signals.

13 This situation would apply whenever reproductive success of a
14 female is limited by the number of eggs she matures, while
15 reproductive success of a male is limited by the number of matings
16 he gets. A mismating in this case has greater consequences for a
17 female than for a male. Females in many species have thus evolved
18 choosiness in mating and males have not because the consequences
19 of errors in mating differ for the two sexes ⁴³.

20 Adding Signal Detection Theory and Decision Theory to an
21 investigation of mating preferences and signals has advantages over
22 the usual approach based exclusively on sexual selection. First, it

1 emphasizes that the evolution of receivers is likely to depend on the
2 probabilities and consequences of all four outcomes of an
3 interaction. Second, it emphasizes the detectability of a signal,
4 which in relation to the receiver's criterion for response, determines
5 the probabilities of the possible outcomes. In general, it stresses an
6 understanding of communication under realistic conditions in
7 nature.

8

9 Evolution of Signals

10

11 Once the performance of receivers begins to evolve toward its
12 optimum, the evolution of signaling should adapt to the changing
13 behavior of receivers. On one hand, the presence of receivers with
14 "adaptive gullability" opens opportunities for signalers that can
15 manipulate receivers with misleading signals, like the deceptive
16 alarm calls mentioned above. The evolution of deceptive signals is
17 limited by the payoffs and probabilities of the four outcomes for
18 receivers and by the probabilities of honest and deceptive signals.

19 On the other hand, the presence of receivers with "adaptive
20 fastidiousness" favors signalers that produce exaggerated signals
21 that exceed the high thresholds or other stringent criteria set by
22 fastidious receivers. Furthermore, Signal Detection Theory predicts

1 that the evolution of exaggerated signals in response to fastidious
2 receivers should result in increased detectability or discriminability
3 of signals by intended receivers.

4 An indication of the importance of detectability for the
5 evolution of signals comes from recent studies of nestling birds
6 begging for food from their parents. When begging, nestlings often
7 reveal bright colors in their mouths, particularly red gapes and
8 yellow flanges. Heeb et al. ⁴⁴ showed that nestling great tits with
9 gapes and flanges that were more detectable under natural light
10 conditions (the dim light available in nest cavities) gained more
11 weight than did other nestlings. The detectability of signals was a
12 better predictor of parental response than was complexity or
13 redness (which might indicate the nestling's nutritional state).

14 Recent studies of fish have revealed a connection between
15 discriminability and the evolution of colorful signals for mate
16 choice. In Lake Victoria, female preferences for the colors of males
17 contribute to reproductive isolation between many overlapping
18 species of cichlids. Sedimentation in areas with high agricultural
19 runoff, however, has obscured colors and resulted in loss of
20 reproductive isolation ⁴⁵. Another case involves sticklebacks in lakes
21 of coastal British Columbia. In some populations males have bright
22 red on their underparts and in others they lack red, differences that

1 contribute to reproductive isolation between sympatric populations.
2 In lakes with high concentrations of tannin, the tea-colored water
3 masks red signals. In these lakes males have lost their red markings,
4 and females have lost not only their preferences for red males but
5 also their sensitivity to red light ⁴⁶. Colorful signals and receivers'
6 responses to them thus persist only where the background does not
7 mask them. Between populations, lower thresholds for responses to
8 red by females correlate with redder males. Within a population, on
9 the other hand, females with higher thresholds for red should tend
10 to mate with redder males.

11

12 Signal Detection in Relation to Previous Theories

13

14 Signal Detection Theory complements previous theories for
15 the evolution of signals based on sexual selection or costs. For
16 instance, the distinctive feature of sexual selection is the genetic
17 correlation that inevitably results from nonrandom mating between
18 individuals with a preference and those with the corresponding
19 trait. Consequently, it clearly applies whenever females with high
20 thresholds mate disproportionately with males with exaggerated
21 signals. Although a sufficiently strong genetic correlation can result
22 in the evolution of a costly trait, it puts no other constraints on the

1 nature of the cost, the preference, or the resulting trait. Signal
2 Detection Theory, on the other hand, narrows the predictions for
3 the evolution of preferences for costly traits. High thresholds for
4 responses by females should evolve when the benefits of optimal
5 matings for females or their offspring (correct detections) greatly
6 exceed those of suboptimal matings (false alarms). The costs,
7 benefits, and probabilities of the four possible outcomes of mating
8 preferences are all essential components in a complete analysis of
9 the evolution of preferences (Box 4).

10 Signal Detection Theory also puts the costs of signals in a new
11 perspective. Exaggeration of signals often incurs additional costs for
12 signalers. In some cases, these additional costs could alone increase
13 the discriminability of high-quality mates, those able to absorb the
14 additional costs. From the perspective of Signal Detection Theory,
15 however, the costs themselves are secondary. The primary
16 consideration is the discriminability of signals from the perspective
17 of receivers. If costly signaling does not increase the performance
18 of receivers, it should not evolve.

19 Exaggeration of signals in response to fastidious receivers
20 must inevitably increase the costs for signalers. These costs might
21 include any of those previously identified for signals: additional
22 time and energy, developmental compromises with other traits as a

1 result of physiological interactions or genetic epistasis, and risks of
2 interception by unwanted receivers, like predators, parasites, and
3 conspecific rivals^{47, 48}. Although an exaggerated signal might
4 increase the probability of response by the intended receiver, this
5 benefit is inevitably offset by some increase in costs. These costs, in
6 the context of Signal Detection Theory, lead to a new prediction that
7 the evolution of communication should end in an equilibrium: a
8 signal-detection balance.

9

10 Signal-Detection Balance

11

12 Signal Detection Theory identifies an additional consequence
13 of exaggeration: diminishing returns for a signaler. As a signal
14 becomes more detectable or discriminable, the probabilities of
15 errors by receivers decrease asymptotically toward zero. As a
16 consequence, exaggeration of signals has progressively less effect on
17 the optimal performance of intended receivers, and correspondingly
18 less advantage for signalers. Eventually an equilibrium between
19 diminishing benefits and augmenting costs of exaggeration would
20 put an end to further exaggeration of a signal. Furthermore, this
21 equilibrium would be reached at a point short of perfect
22 discriminability of signals by intended receivers.

1 At this equilibrium for signalers, receivers would make some
2 mistakes, and signals would fail to evoke the intended response
3 every time. Receivers would have evolved optimal, not ideal,
4 performance, and signalers would have evolved optimal, not
5 complete, efficiency. Both receivers and signalers would have
6 adapted to the external constraints on signal detection or
7 discrimination.

8 It seems likely that most communication is poised in such a signal-
9 detection balance. If so, the properties of communication would be
10 difficult to understand without an investigation of all the constraints on
11 optimal performance of receivers and on optimal detectability or
12 discriminability of signals.

13

1 BOX 1. A receiver's double bind

2 The receiver's dilemma results from the convergence of signal
3 and noise on a common channel. A simple example is a sensory
4 neuron tuned to a particular frequency of sound. If the signal is a
5 tone of this frequency with random variation around a mean
6 intensity, then both the mean and the variance of activity in the
7 receiver's channel is greater during the presence of a signal than
8 during its absence. If the probability density functions for activity
9 of a receptor in the presence and absence of a signal overlap at all,
10 then the receiver cannot absolutely avoid errors.

11 The possibility of error is the inevitable result of making a
12 decision based on the output of such a channel. A decision to
13 respond or not requires a criterion for response, the simplest of
14 which is a threshold. Of course, criteria for response based on any
15 one receptor can be more complex. Furthermore, a decision can be
16 based on the inputs from many receptors. The basic conundrum for
17 a receiver, however, is not affected by the complexity of criteria or
18 the number of inputs. Elsewhere we ¹² discuss other possible
19 criteria.

20 Any choice of a threshold for response fixes probabilities for
21 each of the four mutually exclusive and exhaustive outcomes.

22 Receivers thus face an inevitable trade-off between the

1 consequences of false alarms and missed detections (or between
2 correct detections and correct rejections). This trade-off is
3 equivalent to the well-known trade-off in electronic receivers
4 between sensitivity and selectivity. Only by accepting more false
5 alarms (less selectivity) can a receiver reduce missed detections
6 (more sensitivity). Evolution should result in receivers that
7 optimize the expected utility, $E(U)$, of their criteria for response ¹².

8 It is also important to realize that a receiver only “knows” two
9 states of the world prior to its decision to respond: input above
10 criterion or input below criterion. Only a privileged observer, one
11 with a special vantage or special equipment, can know whether or
12 not a signal has actually occurred.

1 BOX 2. Mimicry as an example of signal detection

2 A form of communication already framed in terms of Signal
3 Detection Theory is recognition of alien eggs by the hosts of brood
4 parasites. Brood parasites include birds such as some cowbirds and
5 cuckoos that lay their eggs in other species' nests. The hosts are left
6 to raise the parasite's young, often at a cost of raising fewer or none
7 of their own. The hosts of these brood parasites vary in their
8 responses to parasitic eggs deposited in their nests. In some of
9 these species individuals usually remove such eggs or abandon or
10 rebuild their nests. Even for these "rejector" species, not all
11 parasitic eggs elicit a response. To compensate for rejection by
12 hosts, some species of brood parasites (particularly those in which
13 individuals specialize on a single species of host) have evolved
14 mimetic eggs that can closely resemble the hosts' own eggs.

15 Mimicry by parasites presents a problem for hosts that remove
16 strange eggs from a nest. From the host's perspective, there is
17 always the possibility of removing one of its own eggs by mistake.
18 There is also the possibility of damaging an egg during removal, an
19 egg that by chance would most often be one of the host's own.
20 Several hypotheses for the evolution of European Cuckoos *Cuculus*
21 *canorus* and their hosts incorporate signal detection as the
22 limitation on further evolution of mimicry and rejection. For a host,

1 increasing the ejection of parasitic eggs (by lowering the threshold
2 for ejecting an egg and thus reducing missed detections) necessarily
3 results in increasing the ejection of its own eggs (false alarms). In
4 this situation it is unlikely that perfect discrimination would evolve
5 ⁴⁹⁻⁵¹.

6 This approach suggests that the optimal threshold for ejection
7 of eggs should be low when the cost of missed detections is high (for
8 instance, when a host loses all of its own young if it fails to reject a
9 cuckoo's egg) but should be high when this cost is low. Black-billed
10 Magpies *Pica pica* parasitized by Great Spotted Cuckoos *Clamator*
11 *glandarius* in Spain fit the latter prediction. Pairs often raise their
12 own young with a cuckoo's, so the cost of a missed detection is
13 lower than otherwise, and they rarely eject eggs. Furthermore, the
14 magpies receive retaliatory attacks on their nests by cuckoos that
15 have had eggs rejected. This retaliation reduces the payoff from
16 correct rejection ^{52, 53}.

17

18

1 BOX 3. The nature of errors in communication

2 Errors can occur for several reasons. First, signals arrive at the
3 receiver's receptors attenuated, degraded in structure, and mixed
4 with background energy. Probably all signals dissipate in some way
5 during propagation or persistence in the environment, so that
6 signals are less intense as received than as sent. In the case of
7 acoustic signals, degradation also includes a number of other
8 complex changes, such as excess attenuation, reverberation, random
9 amplitude fluctuations, and boundary-layer effects ⁵⁴⁻⁵⁸. In addition,
10 sounds from other sources mix with signals. Other members of the
11 same species or similar species often produce patterns of sound
12 similar to the signal of interest to a particular receiver.

13 Examples of particularly noisy environments for acoustic
14 communication include the complex soundscape of a forest with
15 diverse birds and insects ⁵⁹, the din produced by a large chorus of
16 many species of frogs ³⁰, and the cacaphony of a colony of seabirds
17 where every bird must locate its own mate, parent, or offspring ⁶⁰.
18 In addition, inanimate objects such as wind, moving vegetation, and
19 running water include energy in frequencies and sometimes even
20 temporal patterns used by animals for communication. As a result
21 of the degradation of signals or the mixing with extraneous sources,
22 two situations for communication seem particularly prone to the

1 problems of external noise: communication over long distances or
2 communication in dense aggregations^{12, 57, 58}.

3 Second, errors occur because of random perturbations in
4 receptors, associative mechanisms, and effectors. In electronic
5 apparatus, this noise is the inevitable thermal noise from filters,
6 relays, and amplifiers. The more sensitive a receiver is to impinging
7 signals (the more you turn up the gain), the more internal noise it
8 produces. Because receivers provide most of the power for a
9 response, ultimately the dissipation of heat from this amplification
10 must introduce random perturbation in the output. A female frog is
11 bound to be less predictable than a billiard ball. Although both
12 react to input, only the frog responds to signals.

13

1 BOX 4. Signal Detection Theory and the direction of evolution for
2 signals

3 Although sexual selection can explain the rate of evolution of
4 preferences and traits, it does not explain the direction of evolution.
5 Genetic correlation and drift during sexual selection could in
6 principle either augment or diminish a signal. To fill this gap, it has
7 been argued that high costs of display are necessary to insure
8 honesty in signaling ^{11, 13, 61, 62}. However, this argument is equivocal
9 because (1) all signals presumably have some costs (even when they
10 might also have some benefits in contexts other than signaling), (2)
11 some costs do not insure honesty ^{9, 63}, and (3) preferences for any
12 level of display can differentiate individuals that differ in capacity
13 to bear those costs ^{64, 65}.

14 Signal detection, in contrast, provides an unequivocal
15 prediction that signals intended for fastidious receivers should
16 evolve exaggeration. Furthermore, they should evolve to increase
17 the discriminability of correct signals in the local environment from
18 the receivers's point of view. In other words, signals should evolve
19 to reduce the possibility of confusion with the background including
20 alternative sources ^{12, 32, 66}.

21 This approach affects the possibilities for arbitrary mating
22 preferences and traits. A sufficiently strong genetic correlation

1 between any mating preference and its corresponding trait can in
2 theory overcome costs of the trait to produce runaway evolution of
3 both preference and trait ^{67, 68}. Nevertheless, the result of runaway
4 sexual selection depends on the costs, both of the preference and
5 the corresponding trait ⁶⁹⁻⁷¹. In this approach, arbitrary preferences
6 are thus those with exactly equal costs for receivers, and arbitrary
7 traits are those with exactly equal costs for signalers.

8 Signal Detection and Decision Theories indicate that
9 preferences could have equal costs only when receivers with
10 different criteria for response have equal expected utilities. This
11 condition requires that the four possible outcomes have equal
12 probabilities and equal consequences for receivers with different
13 criteria (or exactly compensating effects on the expected utility of
14 the receiver's criterion). In other words, alternative signals would
15 have equivalent consequences for a female only if they had exactly
16 the same correlation with male quality and exactly the same
17 detectability by females (or exactly compensating effects). Meeting
18 these conditions seems so unlikely that arbitrary signals and
19 preferences seem implausible. As a consequence, optimization of
20 females' performance would nearly always oppose runaway
21 evolution of arbitrary criteria and signals. A more likely result
22 would be coevolution of both receivers and signalers to a signal-

1 detection balance, in which *signals would reach optimal*
2 *detectability* from the perspective of signalers and *receivers would*
3 *reach optimal performance* in responding to those signals.

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7 1 Neumann, J.v. and Morgenstern, O. (1944) *Theory of*
8 *games and economic behavior*, Princeton University Press

9 2 Stephens, D.W. and Krebs, J. (1986) *Foraging theory*,
10 Princeton Univ. Press

11 3 Getty, T. (1995) *Am Nat* 145, 145-154

12 4 Reeve, H.K. (1989) *Am Nat* 133, 407-435

13 5 Pfennig, K.S. (1998) *Proc Roy Soc London B* 265, 1743-
14 1748

15 6 Pfennig, K.S. (2000) *Behav Ecol* 11, 220-227

16 7 Getty, T. (1985) *Am Nat* 125, 239-256

17 8 Enquist, M., Plane, E. and Roed, J. (1985) *Anim Behav* 33,
18 1007-1020

- 1 9 Hurd, P.L. (1995) *J Theor Biol* 174, 217-222
- 2 10 Markl, H. (1985) In *Manipulation, modulation,*
3 *information, cognition: some of the riddles of communication,*
4 (Holldobler, B. and Lindauer, M., eds.), pp. 163-194. Sinauer
- 5 11 Harper, D. and Maynard Smith, J. (2003) *Animal signals,*
6 Oxford University Press
- 7 12 Wiley, R.H. (1994) In *Errors, exaggeration, and deception*
8 *in animal communication,* (Real, L.R., ed.), pp. 157-189. University
9 of Chicago Press
- 10 13 Grafen, A. (1990) *J Theor Biol* 144, 517-546
- 11 14 Wiley, R.H. (2007) *Adv Study Behav* 37, xxx-xxx
- 12 15 Guilford, T. and Dawkins, M.S. (1993) *Trends Neurosci*
13 16, 430-436
- 14 16 Guilford, T. and Dawkins, M.S. (1991) *Anim Behav* 42, 1-
15 14
- 16 17 Enquist, M. and Arak, A. (1998) In *Neural representation*
17 *and the evolution of signal form,* (Dukas, R., ed.), pp. 21-87.
18 University of Chicago Press

- 1 18 Lynn, S.K., Cnaani, J. and Papaj, D.R. (2005) *Evolution* 59,
2 1300-1305
- 3 19 Okanoya, K. and Dooling, R.J. (1991) *J Comp Psych* 105,
4 60-72
- 5 20 Dooling, R.J., Brown, S.D., Klump, G.M. and Okanoya, K.
6 (1992) *J Comp Psych* 106, 20-28
- 7 21 Benney, K.S. and Braaten, R.F. (2000) *J Comp Psychol*
8 114, 174-182
- 9 22 Brumm, H. and Slabbekoorn, H. (2005) *Adv Study Behav*
10 35, 151-209
- 11 23 Brumm, H. and Todt, D. (2002) *Anim Behav* 63, 891-897
- 12 24 Pytte, C.L., Rusch, K.M. and Ficken, M.S. (2003) *Anim*
13 *Behav* 66, 703-710
- 14 25 Leonard, M.L. and Horn, A.G. (2005) *Proc Roy Soc London*
15 *B* 272, 651-656
- 16 26 Slabbekoorn, H. and Smith, T.B. (2002) *Evolution* 56,
17 1849-1858

- 1 27 Langemann, U. and Klump, G.M. (2001) *Eur J Neurosci*
2 13, 1025-1032
- 3 28 Brenowitz, E.A. (1982) *J Comp Physiol A* 147, 511-522
- 4 29 Gerhardt, H.C. and Klump, G.M. (1988) *Anim Behav* 36,
5 1247-1249
- 6 30 Wollerman, L. (1999) *Anim Behav* 57, 529-536
- 7 31 Green, D.M. and Birdsall, T.G. (1978) *Psychol Rev* 85,
8 192-206
- 9 32 Wiley, R.H. (2006) *Adv Study Behav* 36, 217-247
- 10 33 Owings, D.H. and Leger, D.W. (1980) *Z Tierpsychol* 54,
11 163-184
- 12 34 Cheney, D.L. and Seyfarth, R.M. (1990) *How monkeys see*
13 *the world*, University of Chicago Press
- 14 35 Blumstein, D.T. and Armitage, K.B. (1997) *Anim Behav*
15 53, 143-171
- 16 36 Burke da Silva, K., Kramer, D.L. and Weary, D.M. (1994)
17 *Can J Zool* 72, 1087-1092

- 1 37 Macmillan, N.A. (2002) In *Signal detection theory*,
2 (Pashler, H. and Wixted, J., eds.), pp. 43-90. John Wiley & Sons
- 3 38 Wollerman, L. (1998) *Anim Behav* 55, 1619-1630
- 4 39 Wollerman, L. and Wiley, R.H. (2002) *Anim Behav* 63, 15-
5 22
- 6 40 Munn, C.A. (1986) *Nature* 319, 1433-1435
- 7 41 Møller, A.P. (1988) *Ethology* 79, 25-30
- 8 42 Møller, A.P. (1990) *Behav Ecol* 1, 1-6
- 9 43 Wiley, R.H. and Poston, J. (1996) *Evolution* 50, 1371-
10 1381
- 11 44 Heeb, P., Schwander, T. and Faoro, S. (2003) *Anim Behav*
12 66, 637-642
- 13 45 Seehausen, O., Alphen, J. J. M. van and Witte, F. (1997)
14 *Science* 277, 1808-1811
- 15 46 Boughman, J.W. (2001) *Nature* 411, 944-948
- 16 47 McGregor, P.K. (1993) *Phil Trans Roy Soc London B* 340,
17 237-244

- 1 48 Zuk, M. and Kolluru, G.R. (1998) *Q Rev Biol* 73, 415-438
- 2 49 Davies, N.B., Brooke, M. de L. and Kacelnik, A. (1996)
- 3 *Proc Roy Soc London B* 263, 925-931
- 4 50 Servedio, M.R. and Lande, R. (2003) *Evolution* 57, 1164-
- 5 1175
- 6 51 Rodríguez-Gironés, M.A. and Lotem, A. (1999) *Am Nat*
- 7 153, 633-648
- 8 52 Soler, M. (1990) *Ornis Scand* 21, 212-223
- 9 53 Soler, M., Soler, J.J., Martinez, J.G. and Moeller, A.P.
- 10 (1995) *Evolution* 49, 770-775
- 11 54 Morton, E.S. (1975) *Am Nat* 109, 17-34
- 12 55 Marten, K. and Marler, P. (1977) *Behav Ecol Sociobiol* 2,
- 13 271-290
- 14 56 Marten, K., Quine, D. and P. Marler, P. (1977) *Behav Ecol*
- 15 *Sociobiol* 2, 291-302
- 16 57 Wiley, R.H. and Richards, D.G. (1982) In *Adaptations for*
- 17 *acoustic communication in birds: sound propagation and signal*

- 1 *detection*, (Kroodsma, D.E. and Miller, E.H., eds.), pp. 131-181.
2 Academic Press
- 3 58 Naguib, M. and Wiley, R.H. (2001) *Anim Behav* 62, 825-
4 837
- 5 59 Ryan, M.J. and Brenowitz, E.A. (1985) *Am Nat* 126, 87-
6 100
- 7 60 Aubin, T. and P. Jouventin, P. (1998) *Proc Roy Soc*
8 *London B* 265, 1665-1673
- 9 61 Johnstone, R.A. (1995) *Biol Rev* 70, 1-65
- 10 62 Zahavi, A. and Zahavi, A. (1997) *The Handicap Principle*,
11 Oxford University Press
- 12 63 Getty, T. (2006) *Trends Ecol Evol* 21, 83-88
- 13 64 Getty, T. (1998) *Anim Behav* 56, 253-255
- 14 65 Wiley, R.H. (2000) In *Sexual selection and mating*
15 *systems: trade-offs for males and females*, (Apollonio, M. et al.,
16 eds.), pp. 8-46. World Scientific Publishing
- 17 66 Endler, J.A. (1992) *Am Nat* 139 (Supplement), S125-S153
- 18 67 Lande, R. (1981) *Proc Nat Acad Sci USA* 78, 3721-3725

- 1 68 Kirkpatrick, M. (1982) *Evolution* 36, 1-12
- 2 69 Heisler, I.L. (1985) *Heredity* 55, 187-198
- 3 70 Pomiankowski, A.N. (1987) *J Theor Biol* 128, 195-218
- 4 71 Pomiankowski, A.N. (1988) *Oxford Surv Evol Biol* 5, 136-
- 5 184
- 6