Chapter 5
Why Complex Signals Matter, Sometimes

Tricia L. Rubi and David W. Stephens

Abstract Animal signals commonly consist of multiple components—say a sound and a display—and students of signaling have offered many perceptual and cognitive explanations for why compound signals should be more effective. Yet, the economic benefits that receivers obtain by following multiple signal components remain unclear. Superficially, it would seem that a single discriminable difference should be sufficient to discriminate between underlying states, such as high-quality versus low-quality mates. This chapter asks when receivers can benefit by responding to combinations of signals. While there are many situations in which it is best to follow the single most reliable signal and ignore others, our model suggests that it can pay to follow signal combinations when these combinations indicate the occurrence of a rare event. This chapter develops the logic of this *confirmation of rare events* hypothesis of multiple signal use and discusses the implications of this idea for future studies of signaling.

5.1 Introduction

Drosophila males woo prospective mates with an elaborate mating display that includes singing, dancing, and tapping and licking the female. Eland bulls broadcast their fighting ability via a prominent dewlap, a tuft of dark facial hair, and a loud clicking produced by a tendon in the knee joint. Barn swallow nestlings beg for food by thrusting their bodies upward, vocalizing, and displaying a colorful gape that reflects both visible and ultraviolet wavelengths. Investigators have observed

T.L. Rubi (✉)
Department of Psychology, University of Michigan, Ann Arbor, MI, USA
e-mail: tricia.rubi@gmail.com

D.W. Stephens
Department of Ecology, Evolution, and Behavior, University of Minnesota, Twin Cities, St. Paul, MN, USA
e-mail: dws@umn.edu

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multicomponent signals, also known as complex signals, across a wide range of taxa and in every major type of signaling interaction, including courtship (reviewed in Candolin 2003), aposematism (reviewed in Pearson 1989; Rowe and Halpin 2013), agonism (e.g., Deag and Scott 1999; Chap. 4), begging displays (e.g., Leonard et al. 2003; Kim et al. 2011), sex identification (Page and Jaeger 2004), conspecific identification (de Caprona and Ryan 1990), and eavesdropping (Chap. 11). Signal components may be discrete qualities, such as the song and plumage of a courting bird or the color and odor of a baboon sexual swelling. Alternatively, components may be more tightly integrated, such as the structural and pigmentary properties of a single color patch (Grether et al. 2004) or lip movements and speech sounds in human verbal communication (Massaro and Cohen 1990). As our ability to observe and quantify traits improves, an increasing number of communication researchers argue that most signals consist of multiple components (e.g., Partan and Marler 1999; Rowe and Skelhorn 2004; Hebets and Papaj 2005; Wilson et al. 2013).

A large body of work indicates that additional signal components can increase the effectiveness of signals via a range of perceptual and cognitive mechanisms. Evidence shows, for example, that additional components can improve both the probability and speed of detection (reviewed in Rowe 1999; Hebets and Papaj 2005). Moreover, noisy environments can amplify these effects, especially if different sources of environmental noise have different effects on signal components (Candolin 2003; Hebets and Papaj 2005; Wilson et al. 2013). Some investigators have suggested that additional signal components may improve receiver performance through attentional effects. In the phenomenon of alerting, for example, a conspicuous component draws a receiver's attention to an informative component (Hebets and Papaj 2005). Multicomponent signals may also be learned faster and remembered longer (reviewed in Rowe 1999; Hebets and Papaj 2005).

The focus on perceptual and cognitive effects in the complex signaling literature is due, in part, to the fact that economic models of communication rarely find that following multiple components can be a viable receiver strategy. From a purely informational perspective, a single discriminable difference is sufficient to distinguish between two underlying states or conditions. While some authors have outlined specialized conditions that can favor complex signaling (e.g., specific cost structures or multiple receiver types), economic models have repeatedly found that for a basic signal (i.e., a redundant, reliable, cost-free signal), multiple components are no better than one component (Schluter and Price 1993; Johnstone 1995; Bro-Jørgensen 2010; Wilson et al. 2013; Dunlap and Stephens 2014; Rubi and Stephens 2016). Complex signals are prevalent in nature, suggesting that they are broadly beneficial across diverse signaling systems. Therefore, this is a surprising result even given the perceptual and cognitive benefits described above. Economic benefits and perceptual and cognitive benefits are often presented as alternatives; however, they are not mutually exclusive. Indeed, one might expect these effects to be intimately related; natural and sexual selection arising from communication can shape perceptual and cognitive mechanisms, and perceptual and cognitive mechanisms can impose selection on signals. Identifying the economic benefits of complex signaling may help us better understand the perceptual and cognitive mechanisms used by receivers to process multiple components.

This chapter presents a model that identifies economic situations in which receivers benefit from attending to combinations of signal components. We first review a "single-signal component" model (i.e., the flag model, McLinn and Stephens 2006; Dunlap and Stephens 2009; McLinn and Stephens 2010). We then build on this model by adding a second independent signal component. A key step in this model is to rigorously specify what it means to follow a combination of signal components. In agreement with previous economic models, our results show that a single signal component is often sufficient. However, we also identify a specific situation in which a receiver can economically benefit from attending to signal combinations. We argue that situations of this type may be reasonably common in nature.

5.2 The Model

5.2.1 Alternative Actions, Uncertainty About Actions, Payoffs, and Signals

Consider an animal that must choose between two actions. We call these options accept and reject, although we could equally well call them actions a and b. We suppose that uncertainty exists about which action is best, and we represent this uncertainty via a simple Bernoulli probability. The accept action is best with probability p, and we say that the "good condition" holds; it follows that the reject action is best with probability $(1 - p)$, and we say that the "bad condition" holds. (Both of these probabilities provide a measure of the animal's uncertainty about the best action—hereafter, we use the terms p and "environmental uncertainty" interchangeably.) We consider a simple payoff structure in which the animal obtains one unit of benefit if it correctly matches its action to the environmental condition (i.e., if it accepts in the good condition or it rejects in the bad condition), and similarly it obtains zero units of benefit if it chooses the incorrect action (i.e., if it accepts in the bad condition or it rejects in the good condition). The animal can observe two forms of experience (or signals) that we call S and T. Each of the two signals can take one of two forms: S can take forms S+ or S−, and T can take forms T+ or T−. These are signals in the sense that the states of S and T are statistically related to the underlying condition (i.e., the good or accept-is-best condition and the bad or reject-is-best condition).

5.2.2 Reliabilities

We define the variable q such that $P(S+|\text{Good}) = P(S-|\text{Bad}) = q$. The variable q represents the reliability of S because if $q = 1.0$, then S is a perfect indicator of the underlying condition, but if $q = 0.5$ then S carries no information about the

Table 5.1 Variables and their definitions

Variable	Definition
p	Probability that the true condition is "Good"/ Environmental uncertainty
$1 - p$	Probability that the true condition is "Bad"
q	Reliability of signal S (more reliable signal)
r	Reliability of signal T (less reliable signal)
S+	Form of signal S indicating that the true condition is "Good"
S−	Form of signal S indicating that the true condition is "Bad"
T+	Form of signal T indicating that the true condition is "Good"
T−	Form of signal T indicating that the true condition is "Bad"

underlying condition. The model does not allow q values lower than 0.5, although they are perfectly reasonable biologically. We exclude them as a matter of definition because if q is less that 0.5 we simply can relabel the states of the signal so that S− becomes S+ and S+ becomes S−, which has the effect of keeping q in the range of 0.5–1.0. Now we define a similar variable r to represent the reliability of the second signal T so that P(T+| Good) = P(T−| Bad) = r. Again, we restrict r to the range 0.5–1.0. In addition, we assume that $q \geq r$, so that we can be sure that S is the more reliable of the two signals. All variables and their definitions are listed in Table 5.1.

5.2.3 *Preliminaries: When Should a Single Signal Be Followed?*

Under what conditions does it pay for a receiver to attend to both S and T? This is actually a somewhat more difficult and subtle question than it appears. To begin, it is important to understand the predicted use for a single signal, S. By signal use, we mean following a rule of the form accept when S+ is observed and reject when S− is observed. The alternative to signal use is, obviously enough, to choose the same action regardless of the observed state of the signal. So we must compare the value of signal use to the value of two alternative strategies: namely, always accept and always reject. Since the variable p gives us the relative likelihood of the good and bad conditions, we can easily calculate the payoffs associated with the three strategies of interest.

We can readily calculate the expected value of "always accept" using the following logic. The good condition occurs with probability p, and in the good condition accepting yields one unit; the bad condition occurs with probability $(1 - p)$, and in the bad condition accepting yields zero. So we have:

$$p \times 1 + (1 - p) \times 0 = p$$

To calculate the expected value of "always reject," we follow the same type of reasoning, and we find:

$$p \times 0 + (1 - p) \times 1 = 1 - p$$

Next, we want to calculate the expected value of following the signal. Recall that the signal S matches the environmental condition with reliability q, and the "follow signal" strategy is defined to be "accept if S+ and reject if S−." When the condition is good, the signal shows S+ with probability q and S− with probability $(1 - q)$. So the signal follower will accept with probability q, gaining one unit, and reject with probability $(1 - q)$, gaining zero. Hence, a signal follower expects to gain $q \times 1 + (1 - q) \times 0$ in the good condition. Similarly, in the bad condition the signal shows state S+ with probability $(1 - q)$ and accepting yields zero; the signal shows state S− with probability q and rejecting yields 1 unit of benefit. Therefore, our signal follower expects to gain $(1 - q) \times 0 + q \times 1$ in the bad condition. Since the good condition occurs with probability p and the bad condition occurs with probability $(1 - p)$, the signal follower's overall expected gains are:

$$p \times [q \times 1 + (1 - q) \times 0] + (1 - p) \times [(1 - q) \times 0 + q \times 1] = q$$

Now we want to know which of these three strategies yields the highest expected benefit, and perhaps the easiest way to see this is to plot the three expected payoffs as functions of p (Fig. 5.1).

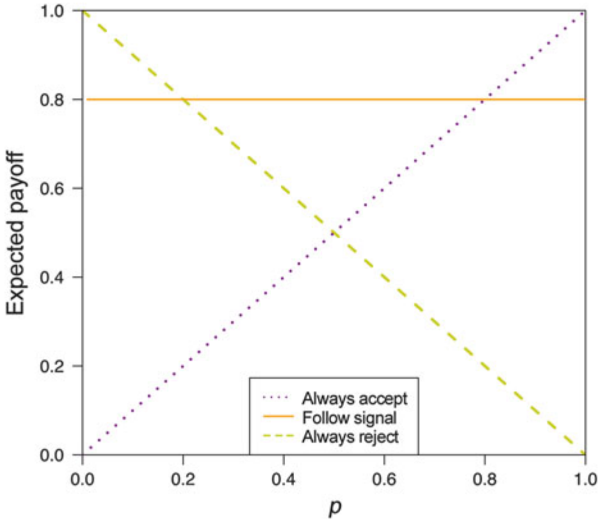
One can see that at the extreme values of p, it is better to ignore the signal. Specifically, if p is small it is better to ignore the signal and always reject because the fact that p is small means the bad condition is quite common and rejecting is the best single action. On the other hand, if p is large it is better to ignore the signal and always accept because the fact that p is large means that the good condition is quite common and accepting is the best single action. However, at intermediate values of p, when conditions are neither predominantly good nor bad, it is better to use the signal.

To summarize, for the single source of information case, we divide the p-axis into three regions: (1) for small p ($p < 1 - q$), it is best to ignore the signal and always reject; (2) for intermediate p ($1 - q < p < q$), it is best to follow the signals; and (3) for large p ($p > q$), it is best to ignore the signal and always accept. Some readers may recognize this as the so-called flag model (Dunlap and Stephens 2009; McLinn and Stephens 2010). This simple model is actually very rich and useful in its own right, but the goal of this paper is to consider economic benefits of using two signals in combination.

5.3 Following Two Signals

It may seem that the next step should be obvious. We already know the expected payoffs associated with using a single signal, so we simply want to compare this to the expected payoff associated with using two. However, it is not immediately obvious what it means to use two signals. Does it mean to accept if and only if S+

Fig. 5.1 When should a receiver follow a single signal? This plot shows expected values for three simple strategies as a function of p (on the x-axis): the increasing line shows the value of always accepting (p); the decreasing line shows the value of always rejecting ($1-p$); and the horizontal line of height q gives the value of changing behavior in response to the signal S



and T+ are observed, or does it mean to always accept when S+ is observed and accept at some reduced probability when T+ is observed? In fact, a two-signal rule could, in principle, take many possible forms. Consider Table 5.2, where a, b, c, and d represent different probabilities of "accepting" for the four possible combinations of signal states. Using this table, it is very clear what it means to follow only one signal. For a decision maker who follows only S (the most reliable of the two signals by assumption), we would set $a = c = 1$ and $b = d = 0$. However, it is much less clear what it means to follow two signals. We could infer that following two simply means not following one, so any values of a, b, c, and d other than $a = c = 1$, $b = d = 0$, could reasonably be called following two signals.

It is obvious, we think, that to make progress, we must focus our attention on a reasonable subset of possible "two-signal" rules. To achieve this, we present the following argument. First, we consider only rules in which a, b, c, and d are set to either zero or one[1]. Second, we restrict our attention to rules in which $a = 1$ and $d = 0$. The argument here is that any rule that can reasonably be called a signal-following rule should accept when "plus–plus" combinations occur and reject when the "minus–minus" combination occurs. Recall that the "plus" states of the two signals are, by definition, statistically associated with the good condition; so, for example, a rule that set $a = 0$ and $d = 1$ would be a sort of anti-following rule, and would not make sense. Third, we can now restrict our attention to four possible "two-signal" rules that depend on the values of the anti-diagonal elements b and c. We consider them in turn: $b = 1$, $c = 0$, corresponds to follow only S rule discussed above, so we do not need to consider it as a "two-signal rule"; similarly, if $c = 1$ and

[1]There is no need to consider other values because the expected benefit of any rule specified by the acceptance probabilities a, b, c, and d will be a linear function of a, b, c, and d, and the maximal benefit will, therefore, occur at the extreme values of one or zero.

Table 5.2 Probabilities of accepting each of the four possible combinations of signal states for signal S and signal T. These probabilities (a, b, c, and d) are used to outline the signal-following rules

Signal T	Signal S	
	S+	S−
T+	a	b
T−	c	d

$b = 0$ then we have to follow only T rule which again is not a "two-signal rule." This leaves us with two plausible two-signal rules.

Two-signal rule #1. The *preponderance of positive evidence rule*: accept if and only if S+ and T+ are observed ($a = 1$, $b = c = d = 0$)

Two-signal rule #2. The *preponderance of negative evidence rule*: reject if and only if S− and T− are observed ($a = b = c$, $d = 0$).

Now we can make progress. We can calculate the expected payoff derived from following each of two "two-signal rules" and superimpose the results on our "single-signal" analysis. So, in this new, larger analysis, we will compare the expected payoffs of five strategies. These five strategies are: (1) ignore all signals and always reject; (2) the preponderance of positive evidence rule (accept only when both S+ and T+ are observed); (3) follow the single most reliable signal (accept if S+, reject if S−); (4) the preponderance of negative evidence rule (reject only when both S− and T− are observed); and (5) ignore all signals and always accept.

To make specific algebraic predictions about these five possibilities, we must first specify the expected benefits associated with the two "new" two-signal rules. To calculate these expected payoffs, we follow the same basic logic as in our calculation of the expected benefits from following a single signal. Specifically, we first calculate the expected payoffs to a "two-signal user" given that the condition is good, then calculate the expected payoffs given that the condition is bad, and finally we combine these using the fact that the parameter p specifies the relative frequency of the good and bad conditions. The expected payoff from the preponderance of positive evidence rule is:

$$pqr + (1 - p)[1 - (1 - q)(1 - r)]$$

and the expected payoff from the preponderance of negative evidence rules is:

$$p[1 - (1 - q)(1 - r)] + (1 - p)qr$$

Figure 5.2 plots these two terms as functions of p and superimposes the results on our single-signal plot (shown in Fig. 5.1) to find a plot that includes the two two-signal rules.

Figure 5.2 shows separate lines for each of the five possible strategies (always reject, preponderance of positive evidence, follow the single most reliable signal, preponderance of negative evidence, and always accept). As the figure shows, each

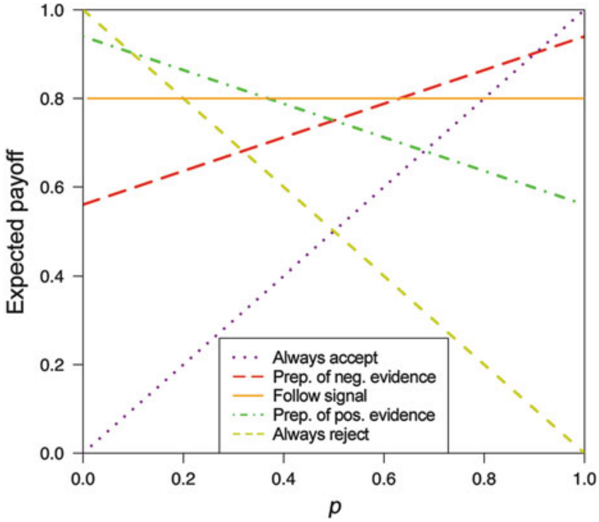


Fig. 5.2 When should a receiver follow two signals? This plot shows a modified version of Fig. 5.1, in which we have added expected payoff lines for the two "two-signal" rules. In general, the model predicts five different levels of p in which each of five possible strategies is best. The text gives the details.

of the five possible strategies gives the highest payoff in a different region of the p-axis. As p—the relative frequency of the good condition—increases from zero to one, we see an orderly progression in which each of the five possible rules is best in a different interval of p value (we call these intervals "layers" below). We can see that there exist four values of p, $p_1 < p_2 < p_3 < p_4$, such that the following is true:

Layer 1: $0 \leq p < p_1$: Always reject
Layer 2: $p_1 < p < p_2$: Use the preponderance of positive evidence rule
Layer 3: $p_2 < p < p_3$: Follow the single most reliable signal
Layer 4: $p_3 < p < p_4$: Use the preponderance of negative evidence rule
Layer 5: $p_4 < p \leq 1$: Always accept.

Notice that the preponderance of positive evidence rule can only pay off when $p < 1/2$. This occurs because when $p < 1/2$, it is, on average, best to reject. This makes sense because the preponderance of positive evidence rule is biased in favor of rejection. We can interpret the preponderance of positive of evidence rule as "normally reject, but accept if and only if two '+' signals are observed." Similarly, the preponderance of negative evidence rule can only pay off when $p > 1/2$ (when it is best, on average, to accept), and we can interpret the preponderance of negative evidence rule as: "normally accept, but reject if and only if two '−' signals are observed." Finally, notice that when $p = 1/2$, it can never pay to use a combination of signals. We predict instead that when the good and bad conditions are equally likely, the animal should always follow the single most reliable signal.

It may be surprising to some that the base rate p, the probability of the good condition, or environmental uncertainty more broadly, is *the* critical element in making signal combinations important. In our model, combinations can become important because they can tell you when to depart from the default (best on average) behavior. This is quite different from the folk wisdom about the statistical value of multiple signals. People tend to think that multiple sources of information will necessarily lead to better decisions, but this is not generally true. The value of signal combinations here derives from their power to indicate when you should deviate from your default action. In the absence of a default action (i.e., when $p = 1/2$) you should never use multiple signals but instead follow the single most reliable source of information. Moreover, there is a sense in which the two "two-signal rules" (preponderance of positive and negative evidence) represent a relatively weak form of signal use. In these rules, the animal only changes its behavior for certain specific and special signal combinations, otherwise it proceeds merrily along following its default "averaging" behavior. In contrast, an animal following the single most reliable signal matches its behavior to the signal every time the signal is observed.

5.4 Effects of Environmental Uncertainty and Signal Reliability

While the results above give us the general qualitative form of the solution—that is, the five layers—we would like to know how our focal variables [environmental uncertainty (p) and signal reliability (q and r)] influence these layers. To answer this question, we seek algebraic expressions for the four break points (p_1, p_2, p_3, p_4). This is not difficult mathematically, because each break point is defined by the intersection of two well-specified straight lines. Figure 5.3 uses these calculations to show the optimal strategies across a range of values for our three key variables: the reliability of the most reliable component S (given by q), the reliability of the less reliable component T, (given by r, $q > r$), and the relative frequency of the good condition (p). The three panels of Figure 5.3 show the plots of r versus p at each of three separate values of q (Fig. 5.3a, low $q = 0.65$; Fig. 5.3b, intermediate $q = 0.795$; and Fig. 5.3c, high $q = 0.99$). Notice that the scale of the r-axis varies between the plots even though each plot occupies the same visual space; r ranges from 0.5 to q, because the reliability of the second most reliable component is necessarily less than or equal to the reliability of the most reliable component. The plots show that our five regions are each roughly triangular and that they nest together in a tooth-like way (though these trends become somewhat distorted at high values of q). We make three observations about this figure. First, notice that when $r = 1/2$, so that the second signal is completely unreliable, our model is identical to the single-signal model. The animal should always accept if $p > q$, use the signal if $(1 - q) < p < q$, and always reject if $p < (1 - q)$ (just as in Fig. 5.1). Second, as the reliability of the second signal (r) increases, the layers in which signal combinations matter (layers 2 and 4) also increase in size, as we would expect. When the two components are equally reliable ($r = q$), it no longer makes sense to follow the most reliable component. As one might expect, the mathematics

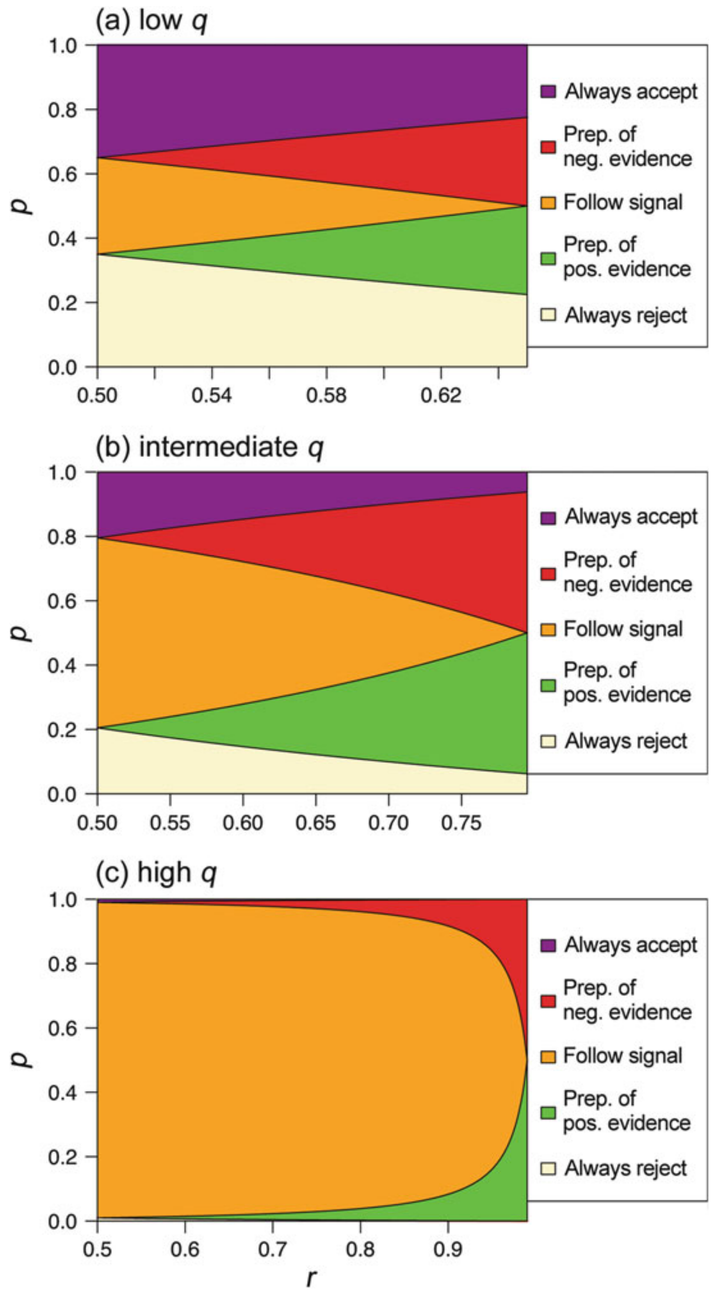


Fig. 5.3 The joint effects of environmental uncertainty and signal reliability on following two signals. Optimal strategies as a function of p and r, at three different levels of q: (**a**) $q = 0.65$, (**b**) $q = 0.795$, and (**c**) $q = 0.99$. Note that the scale of the x-axis changes between plots; since the reliability of the less reliable component (r) is lower than the reliability of the more reliable component (q), the x-axis ranges from $0.5 \leq r \leq$ q

reveals a limiting case in which the "follow the most reliable" region disappears. In this case, when signal following pays, it always pays to attend to both signal components. Specifically, whenever $p > 1/2$, the animal should either follow the preponderance of negative evidence rule or always accept, depending on the precise level of p; whenever $p < 1/2$, the animal should either follow the preponderance of positive evidence rule or always reject, again depending on the precise level of p. Finally, notice that as q approaches 1, the conditions that favor multiple signal use become increasingly narrow.

5.5 Environmental Uncertainty and Complex Signaling

With this model, we have illustrated that receivers can benefit economically from following two signals at certain combinations of environmental uncertainty (p) and signal reliability (q and r). Generally speaking, two-signal strategies are favored at intermediate levels of environmental uncertainty, that is, when the environment is neither highly certain ($p = 0$ or $p = 1$) nor highly uncertain ($p = 0.5$). This raises many questions about whether specific examples of complex signals are indeed correlated with intermediate levels of uncertainty as we hypothesize. While we suspect that new empirical studies will be needed to adequately test our hypothesis, we argue that there is broad qualitative support for our central predictions in the signaling literature.

Our first prediction is that signals should not be used at all in highly certain conditions ($p = 0$ and $p = 1$). Instead, animals should adopt inflexible strategies. In general, this appears to be true; we do not expect to see communication when a receiver should always do the same thing. For example, female ornaments are uncommon in traditional mating systems; typically, males maximize their fitness by mating with all available females (that is, they should follow the rule "always mate"), so females need not invest in costly courtship displays. Signaling should arise in uncertain conditions, when receivers can use signals to inform a decision between multiple behavioral responses. Specifically, our model predicts that intermediate uncertainty ($p > 0.5$ or $p < 0.5$) will favor complex signals while maximal uncertainty ($p = 0.5$) will favor simple signals. Quantifying uncertainty in natural systems is a nontrivial task; researchers must define "good" and "bad" states and determine their relative abundances. Some signaling systems will be more amenable to this classification scheme than others; ideally, states should be binary, clearly delineated, and easily categorized by researchers.

As an illustrative example of intermediate uncertainty, consider identity signals. Identity signals function to facilitate individual recognition, and should arise when it is favorable for a signaler to be correctly identified by conspecifics (Johnstone 1997; Tibbetts and Dale 2007; Chaps. 7 and 8). Upon encountering a conspecific, a receiver must determine if that individual is, say, "Frank" or "not Frank" based on an identity signal. (Note that this signal fits our criteria nicely—it is binary, clearly delineated, and easily observed by researchers.) Uncertainty will always be skewed in such signals; there is only one Frank in a population of size n, so the value of p will be $1/n$. Our model predicts, then, that identity signals should have multiple components and that is indeed what we observe. The need for multiple characteristics is intuitive in individual recognition; at a minimum, individuals must vary in enough qualities that they can be identified as unique. Researchers have shown that increasing population size results in increased signal variation (Pollard and Blumstein 2011, 2012) and have further argued that the need for individual recognition should promote or maintain signal diversity (Beecher 1989; Dale et al. 2001; Tibbetts 2004; Tibbetts and Dale 2007). Individual recognition is seen across a range of taxa, and different species rely upon different signal types; however, multicomponency of identity signals is ubiquitous. Such signals can range from complex chemical profiles (e.g., Steiger et al. 2008; delBarco-Trillo et al. 2012), to visual characteristics (e.g., Dale et al. 2001; Tibbetts 2002), to vocalizations (e.g., Clark et al. 2006; Chaps. 7 and 8), and, of course, traits across multiple modalities (e.g., Proops et al. 2008; Kondo et al. 2012).

Our model predicts that maximum uncertainty ($p = 0.5$) should favor simple signals. Perfect uncertainty (like any precise value) is likely to be rare in natural systems; however, some signal types might be more likely to occur near $p = 0.5$. For example, sex recognition signals might meet this criterion since sex ratios are often more or less balanced. Somewhat surprisingly, it is difficult to find evidence for "simple signals" in the existing literature. Many traditional communication studies focus on a single attribute of a signal; indeed, this is a popular criticism among complex signaling researchers (e.g., Hebets and Papaj 2005). However, such studies rarely seek to verify that receivers respond to *only* one component. Though complex signaling studies often attempt to isolate the effects of individual components, researchers may choose to study likely complex signals or treat simple signal following behavior as a negative result; either of these could result in a publication bias against reporting the existence of simple signals. There is, however, some support for our general prediction in lab-based, learned signal-following studies that test responses in perfectly uncertain environments (i.e., $p = 0.5$). Perfect uncertainty is a common experimental condition in learning studies because it is a theoretically important case and because perfect uncertainty maximally favors learning. Rubi and Stephens (2016) examined the responses of blue jays (*Cyanocitta cristata*) to two reliable signal components (a color and a pattern) at various combinations of q and r and found that receivers followed only one component (typically the more reliable one). Kazemi et al. (2014) found that blue tits (*Cyanistes caeruleus*) could learn to avoid color, pattern, and shape, but that color overshadowed the effect of the other two components in compound learning. In experiments on domestic chicks (*Gallus gallus domesticus*), Aronsson and Gamberale-Stille (2008) found that color overshadowed pattern, and Siddall and Marples (2011) found that color overshadowed auditory cues; however, in both of these studies the less salient stimulus was followed weakly or not at all, indicating that this behavior may have resulted from sensory constraints rather than informational strategies. More naturalistic studies necessarily have less control over parameters such as uncertainty and reliability; however, improved technology has made it possible to more thoroughly characterize what aspects of a signal are important for receivers. For example, Yorzinski et al. (2013) used telemetric gaze trackers to determine that peahens (*Pavo cristatus*) prioritize certain components of a peacock's courtship display and ignore other, highly conspicuous components. This example illustrates the danger of assuming that receivers will utilize all seemingly important components of a signal.

5.6 Economic Benefits Versus Psychological Benefits

In the complex signaling literature, sensory, perceptual, and cognitive benefits are often presented as alternatives to economic benefits. There is, however, no reason why these approaches should be considered mutually exclusive. It is perfectly plausible that complex signals confer both psychological and economic benefits to receivers simultaneously. While these may be truly independent effects, we argue that our approach may provide another explanation for why receiver brains seem to respond so strongly to complex signals. In psychology, multiple stimuli are traditionally discussed in the context of constraints. Classic learning theory predicts that multiple stimuli will interfere with each other by competing for associative strength (Rescorla and Wagner 1972) or receiver attention (Mackintosh 1975). Blocking and overshadowing are classic examples in which learning about one stimulus actively inhibits learning about a second, and studies focusing on divided attention often find deficits in performance when multiple components are present (Treisman and Gelade 1980; Dukas and Kamil 2000, 2001; Palmer et al. 2000; Clark and Dukas 2003). Thus, the classic view is that multicomponent stimuli present cognitive challenges, rather than cognitive advantages, to receiver processing. However, cognitive and perceptual processes are evolved traits like any other, and we expect natural and sexual selection to act on these processes when possible. When following multiple signal components is advantageous, selection should favor sensory systems and neural circuitry that minimize constraints or otherwise facilitate processing multiple stimuli. Researchers typically focus on the efficacy advantages of multicomponent signals such as improved signal reception; the economic advantages outlined here are another plausible driver of selection.

5.7 Limitations of this Approach

We acknowledge that our model makes some large simplifying assumptions that will need to be considered when applying it to specific natural systems. First, our model assumes dichotomous "good" and "bad" signaler states. This classification scheme will work for some signal types, such as identity signals (Sect. 5.5). Classification becomes trickier with qualities that vary more continuously, as is likely, for example, when signals are used to assess mate quality or fighting ability. Determining a threshold for a "good male" can be challenging. We have also assumed a highly simplified payoff structure in which any correct response is equally beneficial and any error is equally costly. The consequences of errors will vary greatly across systems; a missed mating opportunity is not the same as a missed foraging opportunity (Wiley 2015). Even within a system, the costs of different errors will likely differ; failing to consume a palatable prey item is likely less bad than consuming a poisonous one (see Chap. 11). Finally, this model assumes that receiver strategies are fixed across individuals and across time. There is good evidence, however, that receiver choosiness can vary with intrinsic factors, such as receiver need (Brower and Calvert 1985; Skelhorn and Rowe 2007).

5.8 Summary and Future Directions

While complex signals offer many perceptual and cognitive advantages over single component signals, economic models typically suggest that extra components provide no informational benefit to receivers. We offer a new model that contradicts this economic claim. We identify situations in which it pays to attend to signal combinations even when these combinations offer no psychological advantage. Our model suggests that it can pay to attend to signal combinations when each of two-signal components indicates that an animal should deviate from its normal or default behavior. This, in turn, depends on the underlying "base rate" of the conditions that animals signal about. For example, if males signal about their quality and poor quality males are more common, then receivers can benefit from responding to a combination of signals that jointly indicate the presence of a rare high-quality male. In contrast, if good and bad males were equally likely, we would expect receivers to follow the single most reliable signal component and ignore signal combinations. These predictions would be relatively straightforward to test in lab-based signaling games. In such systems, experimenters can manipulate the base rate of conditions. Once the receivers have adopted stable signal-following behavior, the experimenters can test responses to all combinations of components to characterize the strategy that the receivers adopt. Following the example we have laid out in this chapter, the base rate would be the proportion of the time the condition is "good." Quantifying the required response variables outlined in Table 5.2 (a, b, c, and d) would be a simple matter of testing responses to all four component combinations. These variables would then be used to characterize the adopted strategy.

We found that attending to combinations was beneficial when signaler states are asymmetrical, and we hypothesize that the required asymmetries exist in many natural signaling problems, such as mate quality signals, signals of fighting ability, and individual recognition signals. We do not offer this model as an alternative to the many documented perceptual and cognitive benefits of complex signals. Instead, we hypothesize that the economic advantages identified here will often work hand-in-hand with the well-documented psychological advantages of complex signals, giving us a new and more nuanced explanation of the prevalence of complex signals in nature.

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