Original Article

Should receivers follow multiple signal components? An economic perspective

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Animal signals commonly consist of many components. Students of signaling have suggested that these complex, multicomponent signals are beneficial because they are more effective at influencing receiver behavior. This "more is better" view, however, is at odds with economic models, which predict that a single signal component is often sufficient to guide receiver behavior. This study develops a model that asks how receivers should respond to a simple 2-component signal. Our model predicts that receivers will follow the single most reliable component and ignore the second component. We tested this model experimentally using captive blue jays (Cyanocitta cristata) as experimental receivers. We presented receivers with artificial signals composed of 2 components and assessed their responses to determine which component(s) they followed. Signals were composed of 2 visual components: a color and a pattern. We tested 3 levels of color reliability and 3 levels of pattern reliability in a factorial combination, resulting in 9 total treatments. We found that subjects followed a single signal component at a high level in every treatment, whereas the second component had a nearly negligible effect. Subjects generally followed the more reliable component, though they showed a bias in favor of color when the reliabilities of color and pattern were similar. We argue that alternative receiver benefits need to be considered to explain the prevalence of complex signals in nature.

Key words: animal communication, complex signals, multicomponent signals, signaling.

Complex signals, defined as signals consisting of multiple components, are prevalent in animal communication. Indeed, many researchers have suggested that most signals incorporate multiple components (Rowe and Skelhorn 2004; Hebets and Papaj 2005; Harper 2006; Hebets et al. 2013). The near ubiquity of complex signals likely indicates that they are beneficial for signalers, and a commonly proposed benefit is that complex signals are more effective at influencing receiver behavior. A number of empirical studies have supported this claim by showing that multiple components elicit enhanced or improved receiver responses (Rowe 2002; Kelly and Marples 2004; VanderSall and Hebets 2007; Kulahci et al. 2008; Siddall and Marples 2008; Uetz et al. 2009; Akre and Ryan 2010; Leonard et al. 2011), though it is not uncommon to find that receivers respond equivalently to isolated components (Costanzo and Monteiro 2007; Smith and Evans 2008) or prioritize certain components (Marples et al. 1994; Aronsson and Gamberale-Stille 2008; Uetz et al. 2009; Aronsson and Gamberale-Stille 2012; Amorim et al. 2013; Hebets et al. 2013; Zorzsinski et al. 2013).

Most of the studies listed above focus on the noneconomic benefits of complex signal following (such as improved learning rates or memorability). This is unsurprising given that economic models of receiver behavior predict that receivers should not follow multiple redundant components under basic conditions (e.g., Pomiankowski and Iwasa 1993; Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1995; Bro-Jørgensen 2010; Wilson et al. 2013). Instead, economic models of stable signal following behavior typically predict that receivers will follow the single most reliable component. It is widely accepted that signal reliability impacts receiver behavior (e.g., Zahavi 1993); however, no empirical studies (to our knowledge) have directly tested the role of component reliability in complex signal following by receivers. This seems like a critical first step; to truly understand when and how complex signals benefit receivers, we must first determine whether economic benefits alone are sufficient to explain preferences for multiple components. In this study, we develop a simple economic model examining receiver behavior when stably following a signal with 2 reliable components, then test it experimentally with live receivers (captive blue jays, Cyanocitta cristata). Our aim is to determine whether receivers will incorporate multiple signal components into decision making under a basic economic framework.

Our development follows the basic structure of the flag model (see McLinn and Stephens 2006; Stephens and Dunlap 2009). Imagine that a signaler produces a signal about some true state,
which may be “good” or “bad” (e.g., high-quality mate or low-quality mate, palatable prey or poisonous prey, etc.). The receiver must choose between 2 actions, which we call “accept” and “reject.” The receiver should accept when the true state is good and reject when the true state is bad. We assume that the true state is good half the time and bad half the time, so that a receiver who acts without a signal (e.g., one who guesses) will choose correctly 50% of the time. First, consider a single-component signal (S), for example, a color. The signal can take 2 forms, S+ (e.g., red) or S− (e.g., green). The signal is useful to the receiver because the 2 forms are statistically associated with the true state; S+ is associated with the good state, and S− is associated with the bad state. We measure the reliability of this association using the conditional probability \( q = P(\text{Good} | S+) = P(\text{Bad} | S-) \), which ranges between 0.5 and 1. If \( q = 1.0 \), the signal form is perfectly correlated with the true state, but if \( q = 0.5 \), the signal’s information is no better than chance. When \( q = 0.5 \), the receiver will perform better if it follows the signal (i.e., if it accepts when it observes S+ and rejects when it observes S−).

Now, we extend this scenario to a 2-component signal. Consider a signal that consists of a color (C) and a pattern (P). The components independently indicate the true state with reliabilities \( q_{\text{color}} \) and \( q_{\text{pattern}} \), respectively. Both components are always visible in a signal, resulting in 4 possible signals: C+P+, C+P−, C−P+, and C−P−. Subjects follow color by accepting a C+ or rejecting a C− and follow pattern by accepting a P+ or rejecting a P−. When the components agree it does not matter which component the subject follows, but when the components disagree receivers should always follow the more reliable component. A receiver that only follows the more reliable component will always do as well or better than a receiver that incorporates both. When the signals are exactly equally reliable a receiver can follow either component, but there is no advantage to following both. We predict therefore that an optimal signal follower will follow color if the reliability of color exceeds the reliability of pattern and vice versa. Figure 1 shows this prediction graphically. We predict color following in the triangular region above the diagonal and pattern following below the diagonal. Notice that the model makes no explicit predictions about what should happen along the diagonal (\( q_{\text{color}} = q_{\text{pattern}} \)); following color and following pattern are equivalent strategies. In a pilot study, we observed that when reliabilities are equal some subjects prefer to follow color and some prefer to follow pattern, so in these treatments we expect to see a mix of strategies across subjects.

When reliabilities are unequal the more reliable component will always do as well or better than pattern (\( q_{\text{color}} > q_{\text{pattern}} \)), 3 treatments in which pattern was more reliable than color (\( q_{\text{color}} < q_{\text{pattern}} \)), and 3 treatments in which color and pattern were equally reliable (\( q_{\text{color}} = q_{\text{pattern}} \)). At the end of each treatment, we quantified the degree to which subjects were responding to color, pattern, and combinations of color and pattern. All subjects completed all treatments in a different, randomly chosen order, and comparisons across treatments were made using repeated measures analyses.

### Subjects

Eight adult blue jays of unknown sex, randomly selected from a captive colony, served as the test subjects (band numbers 10, 11, 24, 86, 206, 207, 208, and 330). During the experiment subjects were housed individually in the testing chambers for 23 h/day (they were removed for an hour for cleaning and maintenance). Subjects ran trials from 7 AM to 3 PM daily for the duration of the experiment, typically around 12 weeks. They received water ad libitum and were maintained on a 12 h light:dark cycle. The experiment operated in a closed economy, that is, subjects received all of their food from the experiment. To ensure our subjects’ well being, we provided additional food in cases where a bird’s body weight dropped below 85% of its measured ad libitum weight.

### Testing apparatus

Figure 2a depicts an overhead view of the testing apparatus. A perch lever was located at the rear of the box directly below a standard pigeon key (MED Associates ENV-123AM). At the front of the box (Figure 2b), stimuli were presented on an LCD screen (Accelevision LCDP7W) located behind a transparent responding apparatus, a pane of Plexiglass wired to a response mechanism. When the apparatus presented an image on the screen, subjects could either accept it by pecking the stimulus itself or reject it by pecking a pigeon key located to the right of the stimulus screen.
Trials were separated by an intertrial interval (ITI) of 90 s. At the start of each free trial, the computer determined whether the true state would be “good” or “bad.” The probability that the true state was good was 0.5, so half of the time the rewarded action was accept and half of the time the rewarded action was reject. The computer then independently assigned the forms of the color and pattern components based on the component reliabilities. To begin the trial, a flashing light at the rear of the box indicated that the trial was ready to begin. Once the subject hopped to the rear perch, the flashing light extinguished and the stimulus and reject key illuminated at the front of the box. Subjects responded by either accepting or rejecting the stimulus as described in the Testing apparatus section. Once the subject responded, the computer extinguished the stimulus and the reject key and delivered the programmed food reward, accompanied by a flashing magazine light. The apparatus rewarded correct responses with 3 food pellets (approximately 0.06 g) and delivered no food for incorrect responses. If a subject did not respond to a stimulus in 15 minutes, the trial aborted, the ITI restarted, and the trial was repeated.

**Trial overview**

The first 400 trials of each treatment constituted the learning phase, which allowed time for subjects to learn the treatment parameters. We did not use these trials in the analysis. During the learning phase, subjects experienced 2 types of trials, forced and free. Forced trials (also known as “no choice” trials) are similar to free trials, except that they require subjects to respond in a predetermined way and experience the associated reward; this ensures that subjects experience all possible choices and outcomes in a treatment. For example, in a forced correct accept trial, the computer assigned the stimulus and the apparatus illuminated the stimulus and rejecting key, exactly as in free trials. However, the trial only ended when the subject pecked the stimulus (i.e., the reject key was not responsive). The subject received a reward in forced correct trials, but not forced incorrect trials. Trials were grouped into blocks of 40, and the first 8 trials of every block were forced trials: 2 correct accepts, 2 incorrect accepts, 2 correct rejects, and 2 incorrect rejects, presented in random order. The remaining 32 trials in a block were free trials, in which subjects responded freely and were rewarded according to

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**Stimuli**

We created 9 sets of stimuli, one for each treatment, using Adobe Illustrator (Adobe Systems, San Jose, CA). Each set had a different hue (e.g., red or green) spaced at equal intervals around the Adobe Illustrator color wheel and a unique line pattern. Within a stimulus set, color had 2 possible values, light or dark, corresponding to differences in brightness (e.g., bright red or dark red). Pattern had 2 possible values, thick lines or thin lines. These stimuli were chosen to standardize differences across treatments; differences between light/dark and thick/thin were the same in each treatment (brightness was standardized using the Adobe Illustrator Live Color tool). Each stimulus had both a color and a pattern, resulting in 4 possible stimuli: light/thin, light/thick, dark/thin, and dark/thick. Figure 3 shows all 9 stimulus sets. (For simplicity, throughout this paper we refer to brightness and thickness cues as “color” and “pattern,” respectively.)

Each subject completed all 9 treatments in a different order, and we analyzed the results using repeated measures ANOVA. In a given treatment, each subject experienced a different stimulus set, and subjects experienced each stimulus set once during the course of the experiment. For each subject in each treatment, we randomly assigned light and dark as the positive or negative color state (hereafter C+/C−), and thick and thin as the positive or negative pattern state (hereafter P+/P−). We constrained this randomization such that each subject experienced each possible C+P+ combination (e.g., light/thick) at least twice.

**Free trial walkthrough**

Trials were separated by an intertrial interval (ITI) of 90 s. At the start of each free trial, the computer determined whether the true stimulus and the apparatus illuminated the stimulus and reject key , for example, in a forced correct accept trial, the computer assigned the stimulus and the apparatus illuminated the stimulus and reject key , exactly as in free trials. However, the trial only ended when the subject pecked the stimulus (i.e., the reject key was not responsive). The subject received a reward in forced correct trials, but not forced incorrect trials. Trials were grouped into blocks of 40, and the first 8 trials of every block were forced trials: 2 correct accepts, 2 incorrect accepts, 2 correct rejects, and 2 incorrect rejects, presented in random order. The remaining 32 trials in a block were free trials, in which subjects responded freely and were rewarded according to the programmed food reward, accompanied by a flashing magazine light. The apparatus rewarded correct responses with 3 food pellets (approximately 0.06 g) and delivered no food for incorrect responses. If a subject did not respond to a stimulus in 15 minutes, the trial aborted, the ITI restarted, and the trial was repeated.

**Figure 2**

Diagrams of the testing apparatus. (a) Overhead view. (b) Front panel.
responses. The total number of trials completed in the treatment was calculated at the end of each day. When this number exceeded 400, the learning phase ended and the subject advanced to the data collection phase of the treatment.

In order to maintain the proper conditional reliabilities of the components, some compound stimuli (namely, C+P+ and C−P−) occurred more frequently in free trials. The most extreme case was the treatment in which both color and pattern were 100% reliable; in this treatment, free trials could only be C+P+ or C−P− because both components indicated the correct response with perfect reliability. This extreme treatment necessitated the use of probe trials, defined as unrewarded trials presented at a low frequency (in this experiment, 7.5% of all trials). These trials consisted of all 4 compound stimuli (C+P+, C+P−, C−P+, and C−P−) during a period of stable responding. Once all 56 probe trials were observed (typically over 4–5 experimental days), we assessed the free trials from that period to determine if behavior was stable. Specifically, we calculated the mean accept rates to each of the 4 stimulus types over all days, and determined if the daily accept rates differed from the overall accept rates by less than 25%. This indicated that accept rates had reached an asymptote for all 4 stimulus types. If so, we considered responses stable and ended the treatment. If not, we allowed subjects to continue in the treatment until all probes were collected from a period of stable responding.

Figure 4 shows an example of this progression (a bird showing pattern following; behavior changes dramatically during the learning phase (days 1–3), and then begins stabilizing during days 4–5. Days 6–10 fulfilled the stability criterion, and responses from those days were used in the analysis. If behavior was still unstable after 1000 free trials had been completed, we ended the treatment anyway (this only occurred in 5 out of 72 possible cases).

Data analysis
To analyze the data, we calculated the acceptance rates for each of the 4 possible component combinations (C+P+, C+P−, C−P+, and C−P−) using 14 probe trial responses each (56 responses in total). In some cases, there were more than 14 probe trials for a given subject in a given treatment. In these cases, we randomly selected 14 probe trial responses to each of the 4 stimulus combinations (56 responses in total) in order to ensure that our data provided a balanced representation of the behavior of each subject in each treatment. We used these responses to calculate acceptance rates, which we then placed in a 2 × 2 table (see Table 1). Using these acceptance rates, we defined 3 dependent measures: the color effect, the pattern effect, and the interaction effect.

We calculated the color effect as the average row effect in the 2 × 2 table, that is, \( \frac{(a−c)+b−d}{2} \), following the notation shown in Table 1. This measures the average effect of a change in the state of the color stimulus (C+ to C−) at each of the 2 possible states of the pattern stimulus. We calculated the pattern effect in the same way, but using the average difference between entries in the 2 columns, that is, \( \frac{(a−b)+(c−d)}{2} \). Both the color and pattern effect ranged from 0, indicating no effect, to 1, indicating a strong effect. We also calculated an interaction effect, which addressed whether the state of color affected the subject’s behavior differently at different levels of pattern. Using the notation described in Table 1, the term \( a−b \) represents the effect of pattern when color is in the C+ state, whereas \( c−d \) represents the effect of pattern when color is in the C− state. We therefore used the difference \( a−b−(c−d) \) to assess the interaction effect. In the absence of an interaction, this difference should be 0. Strong interaction is indicated by values of −1 or 1, depending on the nature of the interaction.

All housing and experimental procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (protocol #1109A04421).

RESULTS
There were 8 subjects and 9 treatments, resulting in 72 subject/treatment cases. In 5 of these cases, behavior had not stabilized
The central goal of our experiment was to test the hypothesis that receivers follow the most reliable signal component. Figure 5 gives an overview of the observed effects of color and pattern as a function of the experimentally manipulated differences in color reliability (q_color) and pattern reliability (q_pattern). We performed repeated measures ANOVA for each of these dependent measures (color effect and pattern effect), and these analyses detected no interaction between color and pattern reliability for either dependent measure (color: $F_{4,28} = 1.248$, $P = 0.314$; pattern: $F_{4,28} = 2.187$, $P = 0.096$). The same analyses revealed significant main effects of color and pattern reliability on both dependent measures (main effect of color reliability: color: $F_{2,11} = 15.435$, $P < 0.001$; pattern: $F_{2,11} = 6.728$, $P = 0.009$; and main effect of pattern reliability: color: $F_{2,11} = 8.711$, $P = 0.003$; pattern: $F_{2,11} = 14.330$, $P < 0.001$).

A secondary goal of our experiment was to ask whether the combinations of signal components were more effective than single components. As explained in the methods, we constructed an interaction score to test this possibility. Figure 6 illustrates the observed interaction effect for each of the 9 treatments. The mean interaction effect was near zero in every treatment (mean = $-0.063 \pm 0.025$) and did not differ between treatments (repeated measures ANOVA: $F_{8,56} = 0.205$, $P = 0.989$).

Finally, we sought to explore the claim that receivers should only follow 1 stimulus component rather than some combination of both. In order to do this, we classified component types (i.e., color and pattern) as either the “component of larger effect” or “the component of smaller effect.” The rationale for this approach is that in certain treatments, we expected some birds to follow color and some to follow pattern; this approach allowed us to assess whether all subjects, as a whole, were following 1 or 2 components. Figure 7 shows the larger and smaller effects (white and gray bars, respectively) across all treatments. The figure shows a clear and striking difference in the sizes of the 2 effects; the larger effect (mean = $0.675 \pm 0.319$) was roughly 11 times greater on average than the smaller effect (mean = $0.062 \pm 0.133$). The mean smaller effect did not differ from zero in any treatment and did not differ significantly between treatments (repeated measures ANOVA: $F_{8,56} = 0.560$, $P = 0.777$). This result highlights an important point about the color/pattern follow rates shown in Figure 5. The intermediate values seen in 2 treatments ($q_{\text{color}} = 0.6/q_{\text{pattern}} = 0.8$ and $q_{\text{color}} = 0.8/q_{\text{pattern}} = 1.0$) do not indicate intermediate follow rates for both components. Rather, they are the result of pooling data across color and pattern followers.

**DISCUSSION**

**Summary of results**

Our data clearly indicate that component reliability influenced how subjects followed our experimental signals. Receivers followed color in experimental treatments where color was more reliable than pattern and they followed pattern in experimental treatments where pattern was much more reliable than color. Another clear effect was the lack of interaction between signal components; subjects did not respond differently to different color/pattern combinations. Finally, in every case we observed a wide separation between
the rates at which the 2 components were followed. One component was followed at a high rate, whereas the other was followed at a very low rate or ignored completely.

Despite these strong trends, the results differed from our predictions in 2 notable ways. First, our data suggest that the secondary component may have a small main effect. Though our analysis did...
not find the “smaller effect” to be significant. Figure 7 illustrates that the values are generally positive, rather than equally distributed about zero as might be expected. We were not able to confirm this effect in this study, however, this could be an interesting phenomenon to explore; perhaps receivers utilize “extra” components in a manner distinct from how they use the primary component (e.g., following at a low background rate). Second, we observed a bias for following color. Although the predictions of Figure 1 held up nicely in the extreme treatments (the upper left and lower right corners), the region of color following was larger than expected (the midline was shifted down). That is, all subjects followed color when the 2 components were equally reliable, and we observed a mix of strategies (i.e., some subjects followed color and some followed pattern) when color was somewhat less reliable than pattern. This suggests that our subjects preferred to follow color, and occasionally did so to the detriment of their performance.

These results broadly support the predictions of several economic models of receiver behavior, which indicate that following the single most reliable signal component is typically the best strategy (e.g., Pomiankowski and Iwasa 1993; Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1995; Bro-Jørgensen 2010; Wilson et al. 2013). However, we also observed a notable bias for following color. The color bias in equal-reliability treatments was not inconsistent with our model; however, some subjects also followed color when pattern was somewhat more reliable, which is not an economically valid strategy. These results suggest that something other than component reliability made color a more salient stimulus in general. We discuss this idea further in the next section.

**Connections to salience**

This study is related to the psychological concept of stimulus salience in several ways. The term “salience” is used in many disciplines in the behavioral sciences to describe situations in which one type of experience is more prominent or influential than another. In this broadest sense, one can interpret our experiment as a study of the effects of component reliability on component salience. However, investigators also use the term salience in a narrower sense that stems from Rescorla and Wagner’s (1972) influential model of classical conditioning. Rescorla and Wagner conceived of salience as a fixed stimulus property determined by the physical attributes of the stimulus (brightness, contrast, etc.) and the animal’s sensory apparatus. This interpretation of salience is popular with behavioral biologists (e.g., Kazemi et al. 2014), presumably because it complements ideas from the biological signaling literature such as sensory drive, sensory exploitation, and pre-existing sensory biases (e.g., Endler and Basolo 1998; Ryan and Cummings 2013). In this narrower “fixed property” sense, our study could not be seen as a study of salience because the differences in component effects we report are learned differences and not fixed properties of the underlying stimuli. We point out, however, that psychologists began chipping away at the fixed property interpretation of stimulus salience almost immediately after the publication of the Rescorla–Wagner model (see Mackintosh 1973; Pearce and Hall 1980; Pearce and Bouton 2001). For example, in the conditioning phenomenon of latent inhibition, investigators find that prior exposure to a stimulus in the absence of reinforcement contingencies (say a green dot that is always in the background predicting...
nothing] inhibits later conditioning with this stimulus. Rescorla (1972) himself suggested that one could interpret this as learned change in stimulus salience (p. 30). Rescorla’s thinking here is very much in line with the hypothesis tested in this paper.

From the broadest biological perspective, it would seem reasonable to think of salience as an attribute of the behavioral phenotype that, like nearly every other aspect of behavior, is controlled by a complex interaction between genetically determined effects and environmentally controlled effects. If we accept this premise, then this experiment can be seen as a study of one environmentally controlled attribute of stimulus salience (component reliability). However, the study also shows the importance of pre-existing salience differences in the sense that it shows a bias favoring the color component of our experimental stimuli. Studies suggest that birds have innate color biases (e.g., Cook and Roper 1989; Schmidt and Schaefer 2004), as well as an innate tendency to weigh color differences more heavily than other types of cues (Aronsson and Gamberale-Stille 2008, 2012).

If narrow-sense salience is an evolved feature of behavior, how would natural selection act on it? One reasonable hypothesis parallels the model developed here. Selection should act to increase the salience of stimuli that reliably predict biologically meaningful outcomes and decrease the salience of unreliable stimuli. This hypothesis is logically identical to our hypothesis, except that the reliability in question is reliability experienced over the selective history of the focal species. Dunlap and Stephens (2014) have recently tested exactly this hypothesis using the techniques of experimental evolution in replicate populations of Drosophila. Their results parallel the results presented here by showing that reliability experienced across selective history seems to shape biases, just as this study shows that reliability experienced within an animal’s lifetime influences the weight that signal component receives.

Alternative explanations for the prevalence of complex signals

In this study, receivers rarely, if ever, followed multiple components. However, we do not suggest that complex signals are never beneficial for the receiver; indeed, there is extensive experimental evidence that multiple signal components can be important (e.g., Kelly and Marples 2004; VanderSal and Hebets 2007; Siddall and Marples 2008; Uetz et al. 2009; Leonard et al. 2011). Researchers have proposed a variety of specific conditions that might favor complex signal following by receivers (see Wilson et al. 2013 for a recent overview). A particularly compelling argument is that complex signals (particularly multimodal signals) might be more detectable in environmental noise (Candolin 2003; Hebets and Papaj 2005), which is a ubiquitous problem in natural signaling systems. Another popular hypothesis, the multiple messages hypothesis, states that signal components might not be truly redundant, that is, different components may reflect different aspects of an underlying quality (Moller and Pomiankowski 1993; Johnstone 1995; Hebets and Papaj 2005). Several authors have argued that complex signal following is economically stable under a multiple messages framework (Moller and Pomiankowski 1993; Johnstone 1995; Wilson et al. 2013).

From the perspective of a purely strategic design, complex signals should be unstable; a single discriminable difference should be sufficient to signal an underlying state to a receiver e.g., (Wilson et al. 2013). This prediction makes 2 basic assumptions that are supported across a range of signaling systems, namely, that signals are reliable (e.g., Kilner 1997; Alonso-Alvarez et al. 2004; Ballentine et al. 2008; Blount et al. 2009) and that receivers are sensitive to signal reliability and alter their behavior accordingly (e.g., Blumstein et al. 2004; Gamberale-Stille and Guilford 2004; Skelhorn and Rowe 2006, 2007, 2010). However, unreliable cues can also influence receiver behavior in certain contexts (e.g., Moller and Pomiankowski 1993; Endler and Basolo 1998; Rendall et al. 2009). Multicomponent signals can pair reliable and unreliable cues, and researchers have proposed several ways in which following such signals might be a stable receiver strategy. Alerting and attention-altering hypotheses predict that a poorly reliable but conspicuous signal component might function to draw receiver attention to a second, reliable component (reviewed in Hebets and Papaj 2005). Rowe (1999) reviews several other ways in which a secondary signal component can improve the detectability, discriminability, and memorability of a primary component. Sexual signaling models have indicated that preferences for ornaments or Fisherian traits may be able to persist alongside preferences for reliable traits, provided that preference for the unreliable trait is weak (Iwasa and Pomiankowski 1994) and costs are low (Pomiankowski and Iwasa 1993). Moller and Pomiankowski (1993) hypothesized that this would be a dynamic process, that is, preferences for individual unreliable traits might not be stable, but over time the tendency to follow multiple components could be. The role of reliability in signaling is somewhat contentious, with several authors arguing that other considerations, such as transmission and receiver processing (Guilford and Dawkins 1991, 1993) or the ability to exploit receiver biases (Endler and Basolo 1998; Rendall et al. 2009; Owren et al. 2010) may play equal or greater roles in signal design. Complex signals could conceivably combine components optimized for different signaling roles, adding a new element to this debate.

CONCLUDING SUMMARY

Economic models of receiver behavior indicate that under basic conditions, following multiple redundant signal components is not a stable receiver strategy (e.g., Pomiankowski and Iwasa 1993; Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1995; Bro-Jørgensen 2010; Wilson et al. 2013). To our knowledge, this study has provided the first experimental test of this prediction. Our findings largely agree with these models; receivers followed a single component at a high rate and either ignored the second component or followed it at a very low rate. Component reliability had a clear and consistent effect on the extent to which receivers followed a signal component, though we also found that receivers tended to “over follow” the color component of our experimental signal.

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