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Receiver tolerance for imperfect signal reliability: results from experimental signalling games

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This paper presents an alternative approach to studying signaller–receiver interactions. The conventional approach focuses on signal reliability; instead, we focus on receivers' willingness to tolerate imperfect reliability (receiver tolerance). Both approaches aim to explain what promotes and maintains communication. We define receiver tolerance as following a signal in the face of reduced reliability. We used experimental signalling games with blue jay, *Cyanocitta cristata*, subjects to demonstrate whether uncertain environments generate receiver tolerance for imperfect reliability. Many models of signalling games ignore environmental certainty or predictability, but this certainty is a key part of understanding receiver tolerance. For example, low environmental certainty should increase tolerance since receivers are more uncertain about which action to take. We also tested whether signallers exploit receiver tolerance by signalling dishonestly. The results show that receivers are more likely to heed signals when environments are uncertain. Moreover, signallers are sensitive to this receiver tolerance and, when signallers and receivers have opposing material interests, low environmental certainty promotes dishonest signalling and high certainty restricts it. Our results highlight the usefulness of an approach emphasizing receiver tolerance and demonstrate the critical importance of environmental certainty for signaller–receiver interactions.

The literature of animal communication emphasizes signal reliability. Reliability is thought to present a problem, since signallers can often gain from dishonesty, but reducing reliability should destabilize signaller–receiver interactions. Maynard Smith and Harper (2003, Preface) called this problem of reliability ‘the central problem for evolutionary biologists interested in signals’. A huge literature exists on this ‘problem of reliability’ and the mechanisms that potentially prevent dishonesty (e.g. Maynard Smith, 1991; McGraw, Hill, & Parker, 2005; Polnaszek & Stephens, 2014; Reby & McComb, 2003; Zahavi, 1975; and see Searcy & Nowicki, 2005). The problem of reliability arises because if a signaller reduces the reliability of its signal, the receiver may stop attending to the signal, so that the signal–response equilibrium becomes unstable. The problem of signal–response stability is, therefore, jointly a problem of signaller reliability and receiver tolerance for imperfect reliability (or simply ‘receiver tolerance’); even though the determinants of the receiver's willingness to follow imperfectly reliable signals are seldom addressed. Notice that we conceive of reliability as a continuous variable, so that a signal can be partially reliable. Receiver tolerance, then, measures the extent to which a receiver follows a signal in the face of reduced reliability. Receiver tolerance need not be an error; as we explain below, it can pay to follow a partially reliable signal.

Our paper offers two experiments focused on receiver tolerance. These experiments seek to understand the conditions under which receivers are tolerant of imperfect reliability (i.e. the causes of receiver tolerance) and demonstrate the effects of receiver tolerance on signaller–receiver interactions (i.e. the consequences). To frame these experiments, we develop a simple model that asks when a receiver should follow a partially reliable signal.

Imagine that a receiver faces a binary choice (say accept or reject, for concreteness) and it observes a partially reliable signal that indicates the correct action (meaning the one with the highest payoff) with probability q. An unreliable signal has a $q = 0.5$ (it is just random noise), and a perfectly reliable signal has a $q = 1$ (it correlates with the correct action perfectly). Suppose, next that reject is the correct response with probability p (here termed environmental certainty). If $p = 1$, then the environment is certain and reject is always the correct action; if $p = 0.5$, then the environment is uncertain and the correct action is a 50/50 gamble. Thus, as the parameter p varies from 0.5 to 1 it measures the receiver's certainty about the environment. When $p = 0.5$, the receiver is

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completely uncertain about how to act, and when $p = 1$, receivers can be certain that the correct action is to reject.

Clearly, the signal is most valuable to the receiver when it is most uncertain about the appropriate action. It follows that receivers can benefit even from an unreliable signal when environmental certainty is low. The higher the certainty, the more reliable a signal must be to merit the receiver's attention. Figure 1 shows this logic graphically: more ‘signal-following’ space when environments are unpredictable, less when predictable (adapted from the flag-model of receiver behaviour: McLinn & Stephens, 2006). For example, when $p = 0.5$, following a perfectly reliable signal ($q = 1$) or a mediocre signal (say $q = 0.6$), both lead to the correct action more often than acting without the signal (because $q > p$). Alternatively, when environmental certainty is high, receivers should only follow extremely reliable signals. Therefore, the certainty of the environment should constrain the set of strategies available to signallers, and whether they can use complete honesty (i.e. perfect reliability), dishonesty, or something in between (we develop a model to explore this idea at length in the Supplementary material).

In natural signalling problems, certainty refers to a receiver's prior information about behaviourally relevant states. If, for example, 90% of males are high quality, then female receivers can be relatively confident about the quality of a particular signalling male; at the other extreme, if only 50% of males are high quality, then female receivers will be relatively uncertain about the quality of a signalling male. More generally, certainty, and its polar opposite uncertainty, reflects the variability in the prior distribution of the states that animals ‘signal about’, whether these states are differences in patch richness, male quality, motivation to fight, or hunger. If there are only two possible states, as in our experiment, the base rate p is sufficient to describe this uncertainty. In more complicated situations, with many possible states, one could use variance or the Shannon index (e.g. Shannon, 1948) to measure uncertainty.

Signallers should use receiver tolerance as an opportunity to influence receivers to make decisions that benefit themselves; this means signalling reliably when signallers and receivers agree on the best outcome, but decreasing reliability when conflict exists. The ability of signallers to capitalize flexibly on receiver tolerance depends on the assumption that signallers are sensitive to their influence over receivers. Our first experiment tests this assumption by showing the extent to which signallers exploit a unilaterally tolerant receiver (i.e. one that always follows signals). We expect signallers to change their signalling strategy in response to this receiver tolerance and opportunistically reduce reliability when conflict exists. Second, we test the hypothesis that unpredictable environments cause receivers to tolerate imperfectly reliable signals, which in turn allows signallers to signal dishonestly and exploit this tolerance. We expect the level of environmental certainty to modify receiver tolerance, and thus change whether signallers can signal dishonestly without causing the receiver to ignore signals.

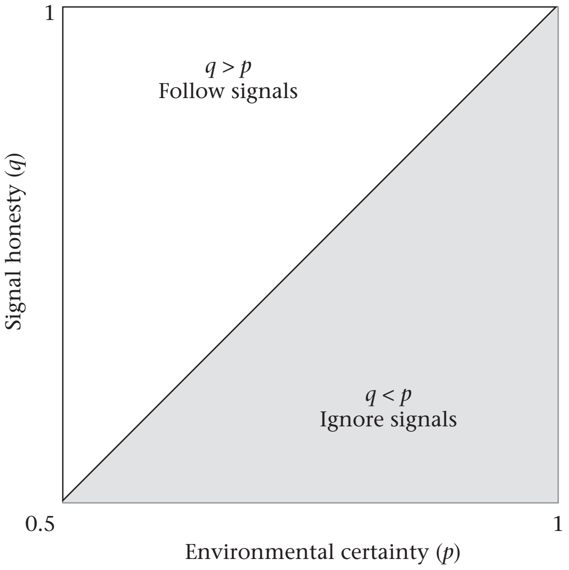

Figure 1. Relation between signal reliability (q) and environmental certainty (p). Receivers should only follow signals when $q > p$. There is more signal-following space (indicated by the white area) in uncertain environments (when p is near 0.5). Almost no signal-following space exists in certain environments (when p is near 1).

This set of two experiments placed pairs of captive blue jays, *Cyanocitta cristata*, in adjacent operant chambers (Fig. 2), where they played a signal—response game. The signaller used positional signals to indicate to the receiver which of two perches was rewarded with food. Using this design, we explored signalling equilibria achieved by learning in a novel laboratory situation. This is an atypical approach because most studies have focused on signals in natural contexts, where equilibria are maintained across generations and the interaction between genes and experience is typically undefined. Importantly, though, our methodology allows precise control over theoretically important variables. For example, we can precisely control environmental certainty by manipulating the probability that each of two perches is rewarded with food. We can also manage the incentives of signallers and receivers by regulating food rewards; creating conditions of mutual benefit or conflict.

GENERAL METHODS

Definitions: Honesty and Reliability

It is rather straightforward to measure the reliability of signallers' actions (e.g. signal A is consistently given in state A). It is less clear whether reliability is the equivalent of honesty, or if a lapse in reliability is dishonest (rather than an ‘honest mistake’) (Bradbury & Vehrencamp, 2000; Wiley, 1994). As such, we use the following definitions to identify signaller actions as honest or dishonest (although other definitions exist, we follow Polnaszek & Stephens, 2014; Searcy & Nowicki, 2005). First, the receiver must have a history of responding to signal S with action A. The action of a signaller is then ‘honest’ if it gives signal S when action A is in the best interest of the receiver. The same signal, S, is ‘dishonest’ when action A is in the best interest of the signaller but not in the best interest of the receiver. In the context of our game, an honest signal, when considered together with historical receiver responses, allows receivers to reliably identify the true state. In our experimental signalling games we know the economic payoffs to both players and thus can determine when these definitions are fulfilled.

Subjects, Housing, Experimental Apparatus

We randomly selected adult blue jays from our larger colony of jays. The group of subjects was of mixed sex, age and experimental histories. We kept subjects in individual operant boxes for 23 h/day throughout the duration of training and the experiments. The intervening 1 h provided time for daily health and weight checks, as well as the opportunity to clean and sanitize the operant boxes. We maintained the subjects on a 12:12 h light:dark cycle and provided water ad libitum. We tested the subjects in a closed economy, meaning all food was earned during the experiment.

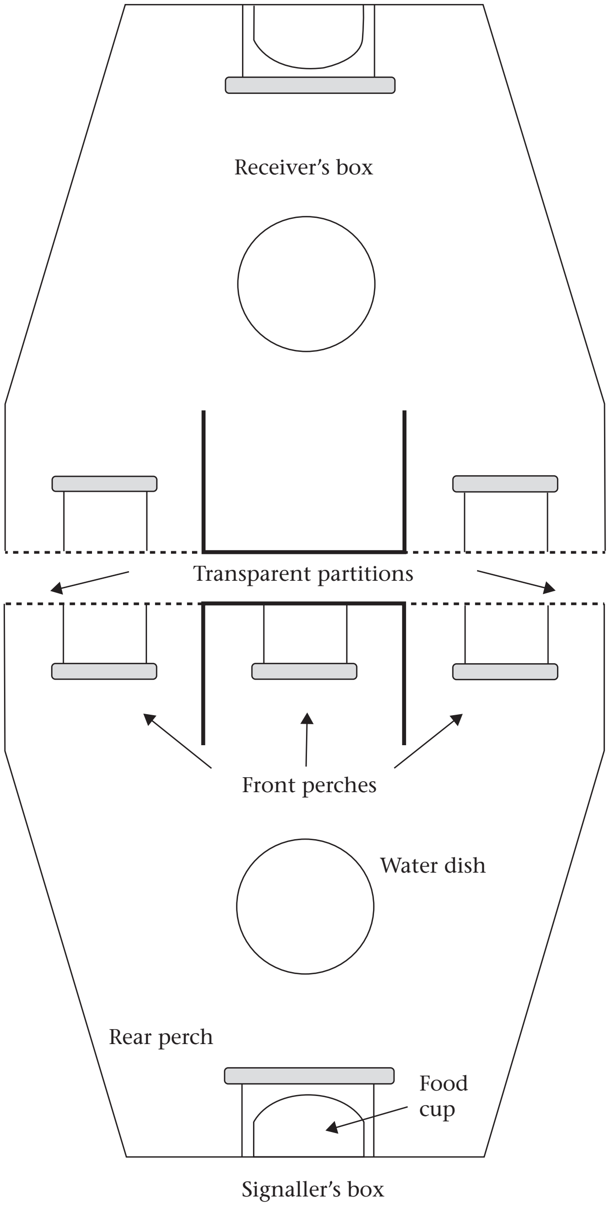

Figure 2. Overhead view of apparatus. Signaller provides positional cues by visiting the perches in front of transparent partitions (left and right), or can 'opt out' of signalling by visiting its middle front perch. After signaller action, receivers hop from their rear perch to one of two front perches.

However, we provided supplemental food to any subjects that earned less than 7 g per day. Some treatments involved interactions where one subject was rewarded at the expense of the other, so we set reward amounts that ensured no subject experienced periods of food deprivation. We positioned pairs of operant boxes adjacent to one another to create a signalling arena (Fig. 2). The subjects in adjacent boxes formed a signaller/receiver dyad. During the experiment, two transparent partitions between the boxes allowed the signaller to indicate to the receiver the perch location that offered a food reward by hopping to the corresponding side (either on the right or the left side of the box). Perches at the back of each box and on the shared wall at the front recorded the presence of the subjects. Each box was equipped with lights to indicate the timing of events within the experiment (e.g. when a trial started, when a choice was offered) and the signaller had a private light cue that indicated which side the receiver should hop to for a reward.

EXPERIMENT 1: THE CONSEQUENCES: DO SIGNALLERS EXPLOIT RECEIVER TOLERANCE?

Experiment 1 assessed the signaller's response to experimental manipulations of receiver behaviour; receivers followed signals in some treatments and ignored signals in others. The experiment tested the hypothesis that signallers strategically adjust signalling behaviour in response to receiver behaviour. This is an important claim, since it allows a feedback loop for signaller–receiver interactions. For example, signallers can exploit an uncertain environment, and any receiver tolerance it causes, only if they adjust signalling in response to changes in receiver behaviour.

Methods

The design of the experiment was a 2 × 2 factorial, where we tested two levels of shared incentives between individuals (aligned or opposed) and two types of receiver strategy (follow or ignore signalled information). We controlled the incentives of the signaller by creating situations where the signaller is rewarded when the receiver correctly matches the true state (termed 'incentives aligned') or when the receiver chooses the opposite of the true state ('incentives opposed'; Table 1). Notice that the signaller's reward solely depended on the action of the receiver in both of these treatments. We controlled receiver tolerance by experimentally manipulating receiver responsiveness to signals. To control receiver behaviour, we trained receivers to follow experimenter provided cues exclusively (i.e. lights only visible to the receiver). In the 'receiver follow' treatment, we directed the receiver always to choose the signalled side. In the 'receiver ignore' treatment, we directed the receiver to choose the left or right side randomly (i.e. no correlation to the signalled side). In this situation, we predict that signaller behaviour will be determined by an interaction between receiver behaviour (follow versus ignore) and the underlying economic incentives. Incentives should not affect signaller behaviour when the receiver ignores the signaller, but when the receiver blindly follows signaller actions we expect that signallers will exploit this by matching the true state when incentives are aligned and by choosing the opposite of the true state (nonmatching) when incentives are opposed (Table 2).

Subjects and overview

Eight blue jays of mixed experimental histories served as research subjects. We randomly grouped individuals into pairs, and each pair remained together for the duration of the experiment. Within each pair, one individual was randomly designated as the signaller and the other as the receiver; they remained in these roles throughout the experiment.

Trials, blocks and termination criteria

We organized trials into blocks of 72 trials. We did not vary the certainty of the environment in this experiment, and left and right

Table 1
Payoff for the signaller for the two incentives treatments (α = aligned, ω = opposed)

	Receiver chooses 'accept' perch	Receiver chooses 'reject' perch
State=True	α: 3 pellets ω: 0 pellets	α: 0 pellets ω: 3 pellets
State=False	α: 0 pellets ω: 3 pellets	α: 3 pellets ω: 0 pellets

In the aligned treatment, signallers are rewarded when receivers match their action to the current state (accepting when true, rejecting when false). Signallers are rewarded when receivers mismatch action and state in the incentives-opposed treatment.

Table 2
Predicted signaller behaviour for each level of ‘incentives’ and ‘receiver strategy’

	Receiver follows	Receiver ignores
Incentives aligned	Always match state (q=1)	Random signalling (q=0.5)
Incentives opposed	Always mismatch state (q=0)	Random signalling (q=0.5)

When receivers ignore, signallers cannot influence receiver behaviour and should signal randomly. If receivers follow, reliability should depend on the incentives, either extreme state matching or state mismatching.

were the ‘true’ side for half of the trials within a block (in the terminology of our model, we set $p = 0.5$ for the duration of experiment 1). We further subdivided each block into groups of 36 trials. Each sub-block started with six forced trials followed by 30 free trials. There were 12 forced trial types, with every combination of possible signaller and receiver actions (signaller forced to left, right or centre perch; receiver left or right) paired with each state (left or right was the current true state). We randomly assigned the 12 forced trial types to the first or second sub-block for each block of trials. We also randomly assigned an order for the forced trials within each sub-block. All birds experienced each treatment until they completed 800 free trials, and we used the last 200 free trials to calculate relevant dependent measures.

Within-trial procedures

Free trials. After an intertrial interval (ITI) of 120 s, white lights at the back of each bird's box indicated the start of a new trial. We required each bird to move to the back perch (away from the shared partition) to begin the trial. A state light illuminated in the signaller's box, indicating whether left or right was the ‘true’ side on a given trial. The signaller then could choose to signal (either to the ‘true’ side or not), or choose not to signal (using the middle perch, in front of the opaque partition). After the signaller made its choice, the computer determined the receiver's action. The receiver had been previously trained to a light-following task, so that in ‘ignore’ treatments, the computer choose randomly and the receiver appeared to ignore the signaller's actions. In the ‘follow’ treatment, the computer switched on the light adjacent to the signaller's choice so the receiver appeared to be following the signaller's actions. We only activated the perch that the computer had indicated that the receiver should use, such that receivers could only progress through the trial if they followed their private light cue. Neither the signaller nor the receiver was allowed to change perches after it had made its initial choice. To achieve this, the computer was programmed to ‘abort a trial’ (meaning no food was delivered) if either player changed perches before food was delivered. After a brief period of acquisition, the bird quickly learned this contingency and perch switching was rare.

When the signaller chose a signalling perch in front of the transparent partitions, its payoff depended on which perch the computer program chose for the receiver to use; the signaller either received three 20 mg food pellets or zero pellets (Table 1). If the signaller chose the centre, nonsignal perch, it always received one 20 mg food pellet. The receiver always obtained two 20 mg pellets for following its computer-directed light cue. The free trial aborted if the pair did not progress through a trial within 7 min.

Forced trials. During forced trials, the signaller was forced in its choice of perch by deactivating all other perches. For example, on a forced signaller-left trial, only the left perch allowed the signaller to proceed through the trial. The pair of birds completed every combination of perch choices (signaller: left, right or centre; receiver: left or right) in each state (left true, right true) per block of trials. If a forced trial was not successfully completed within 7 min, the trial aborted and the pair faced the same type of forced trial after the ITI. All event timing and payoff structures were identical to free trials.

Dependent measures

In this experiment we measured the extent to which the signaller accurately matched the true state. A value of 1 meant that a signaller always matched the true state, and a value of 0 meant that a signaller consistently indicated the opposite of the true state. To exploit receivers that follow signals, we expected signallers to match the true state when incentives were aligned and to mismatch the true state when incentives were opposed.

Results and Discussion

Repeated measures ANOVA showed a significant receiver strategy∗incentives interaction effect on the proportion of state matching by signallers ($F_{1,3} = 35.049$, $P = 0.0096$). When receivers ignored signals (choosing perches randomly), the signallers signalled randomly (Fig. 3). In this case, there was no difference in signaller behaviour regardless of whether incentives were opposed or aligned (Tukey HSD: $P = 0.8876$). In the ‘follow’ treatment, signallers matched the ‘true’ side significantly more often when incentives were aligned (Tukey HSD: $P = 0.0141$). When incentives were opposed in this treatment, signals almost always indicated the opposite of the true state.

These results demonstrate that signallers adjusted reliability based on the economic payoffs in these two extreme cases of receiver behaviour. Specifically, signallers decreased state matching when incentives opposed, but they reliably matched the true state when incentives aligned. Here, we controlled the level of receiver tolerance by using experimentally controlled receivers; receivers either followed all signals (regardless of reliability) or acted randomly. We expected that the degree of signal following by freely acting receivers would fall between these two extremes of programmed behaviour in experiment 1. In experiment 2, we tested freely acting signallers and receivers in a similar signalling game,

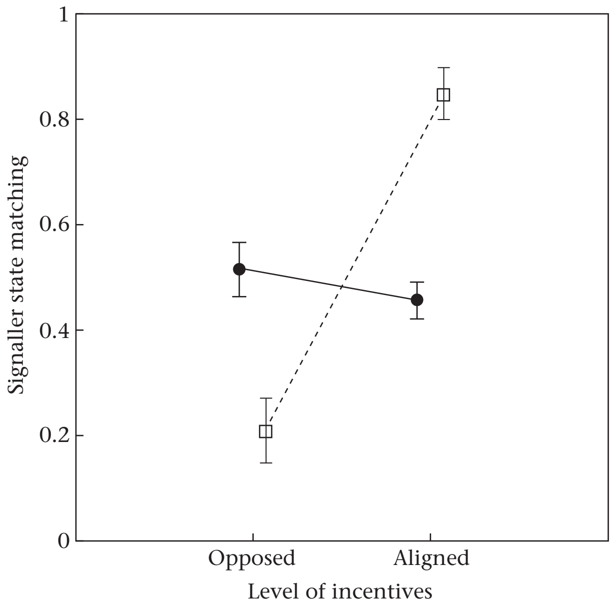

Figure 3. Relative frequency of state matching (mean ± SE) for different levels of incentives (opposed versus aligned) and receiver strategy (followed versus ignored). Solid line shows signalling behaviour when receivers ignored signals (choice determined randomly by computer); the dashed line represents when receivers followed signals; that is, they matched signaller position.

demonstrating whether signalling strategy changes based on receiver tolerance induced by changes in environmental certainty.

EXPERIMENT 2: THE CAUSES: DOES UNCERTAINTY INCREASE RECEIVER TOLERANCE FOR REDUCED RELIABILITY?

This experiment tested whether signallers exploit low certainty in the environment by decreasing reliability as certainty decreases. Our model (see Supplementary material) predicts that low environmental certainty creates 'exploitable space' by increasing receiver uncertainty. That is, when environments are unpredictable, receivers are uncertain which action is best. The model predicts that signallers should capitalize on greater receiver uncertainty through dishonest signalling, but only when incentives oppose. When the receiver faces a fairly predictable environment, however, there is little opportunity for dishonesty. Even when incentives are opposed, environmental certainty helps enforce signal honesty. When incentives align, the signaller should always signal honestly, provided the receiver is following signalled information.

Methods

The second experiment used the basic two-box signaller–receiver design outlined in experiment 1. During a trial, the signaller viewed a private light cue indicating the current state. The signaller then provided a positional signal to the receiver. Instead of manipulating receiver responses (as in experiment 1), the receiver subject responded freely to the signal. A freely acting receiver could choose to attend to the positional signal or track its environment (i.e. choose the perch which is best on average, a choice independent of the signal). We designed experiment 2 following the general structure of the Sir Philip Sidney game (Maynard Smith, 1991). In our experimental version of this signalling game there are two possible states of the environment, labelled as 'true' or 'false'. The receiver also has two possible actions, labelled as the 'accept' or 'reject' perch. For each treatment, we randomly designated the perch on either the left or right side as the 'accept' perch.

Using a within-subjects factorial design, we manipulated two treatment variables: environmental certainty and shared incentives between signaller and receiver. We used food rewards to create treatment conditions of mutual benefit (signaller–receiver incentives 'aligned') or conditions of conflict (incentives 'partially opposed'). The signaller and receiver always agree on the best receiver action in the aligned treatment, but sometimes disagree in the partially opposed treatment. Table 3 describes the payoff structures, in food pellets, for each incentives treatment, and combinations of state and receiver response. We manipulated environmental certainty by controlling the probability that the current state was 'true' or 'false'. We tested three levels of environmental certainty: $p = 0.5$, 0.75 and 1, where p is the probability that the state was 'false'. The probability of the 'true' state was complementary to the probability of the 'false' state, such that the probability 'true' $= 1 - p$. Overall, the design involved six treatment combinations, which we assigned in a random order to each subject pair.

Table 3
Payoff for the signaller in the two incentives treatments (α = aligned, ω = opposed)

	Receiver chooses 'accept' perch	Receiver chooses 'reject' perch
State=True	α: 4 pellets	α: 0 pellets
	ω: 4 pellets	ω: 0 pellets
State=False	α: 1 pellet	α: 4 pellets
	ω: 4 pellets	ω: 1 pellet

Signallers always prefer receivers to choose the 'accept' perch in the opposed treatment. In the aligned treatment, signallers and receivers benefit when receiver actions correctly match the state (accept when true, reject when false).

Trials, blocks and termination criteria

We divided trials into blocks of 90 trials. We further split each block into sub-blocks of 45 trials. Each sub-block started with six forced trials followed by 36 free trials and three probe trials. We randomly interspersed probe trials between the free trials. During free trials, signaller and receiver acted freely, but probe trials consisted of a forced signaller action (signal p state, $1 - p$ state, or no signal) paired with a free receiver choice. We forced the required signaller action by inactivating all other perches during a probe trial. We used probe trials to measure the contingency between signaller action and receiver action; in other words, the degree to which receivers followed signals. If signallers and receivers both consistently choose only one action during free trials, there is no method to determine whether the receiver is using the signal to inform its action. In this case, probe trials provide a way to show whether the receiver is actually matching the signal or not.

As with experiment 1, there were 12 forced trial types, with every combination of possible signaller and receiver actions (signaller forced to left, right or centre perch; receiver left or right) in each of two states ('true' or 'false'). We randomly assigned the 12 forced trial types to the first or second sub-block per each full block of trials. The forced trials assigned to a sub-block were completed in a random order. Each bird experienced each treatment until it completed 1200 free trials, and we used the last 200 free trials to calculate relevant dependent measures. We also used the data from probe trials that fell within the last 200 free trials (delivered at a rate of three probe trials per 36 free trials).

Within-trial procedures

The within-trial procedures closely matched those of experiment 1, for both forced and free trials (see Within-trial procedures from experiment 1). Briefly, after an 120 s intertrial interval, a state light indicates the current state of the environment to the signaller, the signaller chooses an action, and the receiver responds. As with experiment 1, after the signaller chose a position, it could not change its choice or the trial aborted. The economic payoff, in pellets, for each player depends on the current state, receiver action and the level of shared incentives (aligned or partially opposed). Table 3 shows the food pellet payoffs for each combination of these variables. One key difference from the experiment 1, as indicated above, is that we allowed the receiver freedom to choose a response to the signal.

Dependent measures

To measure honesty, we first calculated the consistency with which the signaller's perch choice matched the true state, $p(\text{match state})$. Then we converted this to an overall honesty measure by subtracting 0.5, taking the absolute value, and adding 0.5 to the result (honesty $(q) = |p(\text{match state}) - 0.5)| + 0.5$). An absolute value is necessary because, unlike experiment 1, there were two possible signalling conventions that depend on the historical responses of receivers. If the receiver typically matched the signaller's position, an honest signal would be hopping to the rewarded side (receiver matches, earns a reward). If the receiver typically chose the opposite perch, the signaller could send an honest 'do not visit this side' signal. In this second case, honest signaller behaviour results in a proportion match of 0. Our methods did not allow us to exclude either of these signalling conventions, and subjects used both (i.e. some receivers consistently matched the signaller's position and others consistently avoided it). The measure we used allowed for either convention that subject pairs used, essentially measuring the distance from random $(p(\text{match state}) = 0.5)$.

Adding 0.5 simply changes the range of possible q values; from $0 \leq q \leq 0.5$ to a more intuitive $0.5 \leq q \leq 1$, where 0.5 is random and 1 is perfectly honest.

We also documented whether or not the receiver followed the signals given. We assessed signal following using probe trial data because we could measure receiver response to all possible signals. Specifically, we calculated the consistency with which the receiver's choice matched the positional signal (designated as p(match signal)). We converted this to an overall signal-following measure using the same method as signal reliability ($p(\text{signal follow}) = |p(\text{match signal}) - 0.5)| + 0.5$). As with the honesty measure, this allowed for either signalling convention: the receiver could ‘follow’ the signal by consistently matching or avoiding the position of the signaller. The signal-following measure ranges from 0.5 to 1, where a value of 1 indicates that the receiver either consistently matched or consistently avoided the signaller's position. There were no qualitative differences in examining receiver following behaviour with data from probe or free trials. Furthermore, the receiver-following measures from free trials and probe trials were significantly correlated ($r^2 = 0.407$, $F_{1,46} = 31.524$, $P < 0.005$), so herein we present the data from probe trials only.

Results and Discussion

Signaller strategy

Repeated measures ANOVA revealed three significant effects on signaller honesty (q). First, there was a significant incentives∗certainty interaction ($F_{2,14} = 3.756$, $P = 0.049$). There were also significant main effects of incentives ($F_{1,7} = 17.162$, $P = 0.004$) and certainty ($F_{2,14} = 11.265$, $P = 0.001$) on signaller strategy. Overall, signallers signalled less honestly when incentives were opposed. The largest difference in signaller honesty between the two incentives treatments occurred when the environment was unpredictable (i.e. $P = 0.5$; Fig. 4). When $p = 1$, the environment was completely predictable and there was no qualitative difference in signaller honesty.

Higher certainty in the environment influenced signallers to be more honest. In other words, when receivers are more certain of the best action, it helps prevent dishonesty even when there is an economic imperative for the signaller to cheat. Signallers also showed high levels of fixity in perch choice (e.g. always chose left) in the completely predictable environment. However, based on probe and free trial data, receivers chose independently of signaller action in these treatments, even though signallers were, by definition, reliably honest. Here, receivers are sure of the best action without using the signal. Finally, low levels of environmental certainty cause receivers to tolerate imperfectly reliable signals. Signallers exploit this by dramatically decreasing honesty when incentives oppose. To demonstrate receiver tolerance, and that this dishonesty is successful (i.e. receivers still follow signals), we next examine receiver behaviour.

Receiver strategy

Repeated measures ANOVA showed a significant effect of environmental certainty (p) on signal following ($F_{2,14} = 10.140$, $P = 0.0019$). Signal following decreased as certainty in the environment increased (Fig. 5). We found no significant direct effect of incentives and no interaction effect between certainty and incentives.

The results show that uncertainty in the environment is a key factor in determining signal use. Unpredictable environments generated receiver tolerance and increased signal following. Literature on receiver signal use often focuses on signal reliability, not environmental uncertainty (McLinn & Stephens, 2010). Our results also demonstrate that the importance of reliability depends on the context of environmental uncertainty. In the most unpredictable environment (when $p = 0.5$), receivers followed signals equivalently in both incentives treatments. Even though signallers signalled less reliably in the incentives-opposed case, receivers still followed at relatively high rates. This is not unexpected because an average ‘signal-following’ receiver earned 13.3% more food per day than an average ‘signal-ignoring’ receiver in this condition.

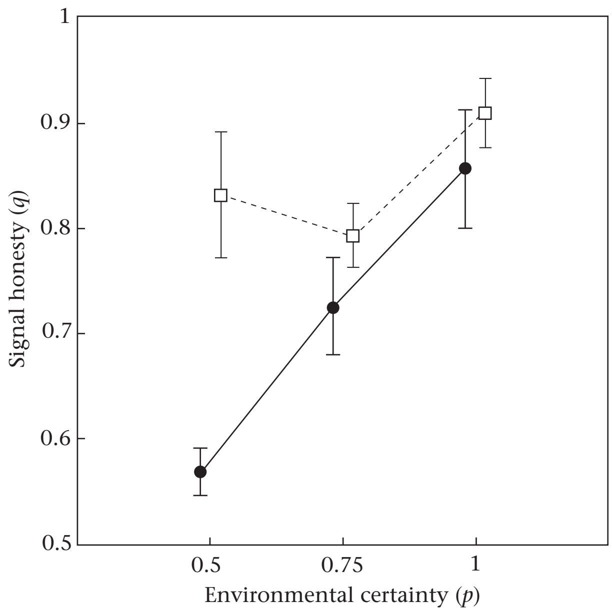

Figure 4. Relation between signaller honesty (q) and environmental certainty (p) in experiment 2 (mean ± SE). Solid line indicates reliability when incentives were opposed; the dashed line indicates reliability when incentives were aligned. Notice that the data points from the aligned and opposed treatments are slightly offset horizontally to facilitate visual comparisons.

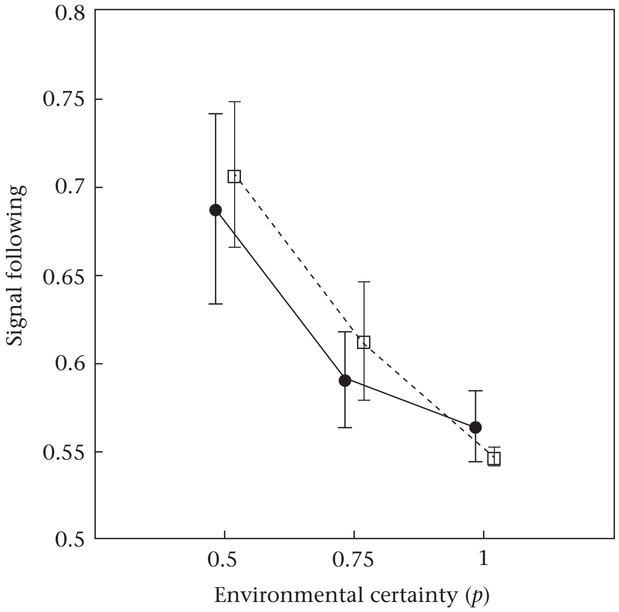

Figure 5. Frequency of receiver following (probe trials, mean ± SE) for different levels of incentives (aligned or opposed) and levels of environmental certainty (p). Solid line indicates signal following when incentives were opposed; dashed line indicates signal following when incentives were aligned. Notice that the data points from the aligned and opposed treatments are slightly offset horizontally to facilitate visual comparisons.

GENERAL DISCUSSION

The experiments here consider the determinants of receiver tolerance for imperfect reliability, and the results demonstrate the value of this alternative perspective to the study of signaller–receiver interactions. We tested how signallers respond to receiver tolerance and what role environmental certainty plays in shaping signaller and receiver strategies. The results show that signallers capitalize on receiver tolerance by signalling honestly when their incentives align with receivers and by signalling dishonestly when their incentives do not align. We know signallers change signalling behaviour in response to cues from receivers (e.g. Patricelli, Uy, Walsh, & Borgia, 2002; Rodríguez, Haen, Cocroft, & Fowler-Finn, 2012; Sullivan-Beckers & Hebets, 2011), so it is unsurprising that they are sensitive to their level of influence over receivers (i.e. the degree of receiver signal following). Our results in the second experiment show that unpredictable environments promote receiver tolerance for imperfect reliability. Receivers increased signal following and followed less honest signals in response to uncertainty about how to act. When the incentives between individuals conflicted, signallers exploited the receiver tolerance caused by an unpredictable environment.

Results in Context

Environmental certainty and receiver uncertainty

A key result here is that environmental certainty determines how reliable signallers must be to influence receiver behaviour. This is a significant claim since models of honest signalling often ignore environmental certainty; for example, in the original form of the Sir Philip Sidney game (Maynard Smith, 1991). The implied unimportance of certainty is surprising, because the idea that environmental certainty influences receiver tolerance for imperfect reliability is straightforward and intuitive. If high-quality males are common, receivers should more readily accept the lie 'I am a high-quality male' than if high-quality males are less common. Clearly, the theoretical importance of base rate to honesty is compelling and broadly applicable. This idea applies with equal force to dishonesty about food reward, mate quality, fighting motivation, or prey profitability.

Our results also illustrate that receiver tolerance induced by environmental uncertainty can potentially stabilize communication, even with frequently dishonest signals. When environments were unpredictable, receivers were more likely to continue paying attention to partially reliable or dishonest signals. This is an important point, since it highlights the interaction between signal reliability and receiver tolerance. Signals need not always be honest; sometimes it pays receivers to heed unreliable signals. Johnstone and Grafen (1993) also argued that signals do not need be perfectly honest, but rather 'honest on average' for communication to be stable. Our view is similar to this 'honest on average' argument, but here we reinterpret this statement as meaning that signals need to be 'sufficiently honest', such that $q > p$, for receivers to benefit from following signals. Rather than a fixed target, the 'sufficient' level of honesty changes with environmental certainty. The signalling system may ultimately fail if signals consistently fall short of this minimum level. The achieved level of honesty could result from different frequencies of certain types of signallers (as in Johnstone & Grafen, 1993) or individual signallers playing a mixed strategy (see Huttegger & Zollman, 2010; Zollman, Bergstrom, & Huttegger, 2013 for more on the importance of mixed strategies). In the experiment described here, the $q > p$ condition applies over the short timescales of learned responses (see McLinn & Stephens, 2006, 2010 for a related experimental result), interestingly we also have evidence from experimental evolution that this condition applies at evolutionary timescales (Dunlap & Stephens, 2009).

Receiver tolerance

Focusing on receiver tolerance for imperfect reliability complements research on signal reliability. The basic question of a receiver-tolerance-centred research program is why receivers follow signals despite imperfect reliability. Two approaches offer potential answers to this question. The first focuses on biases that may compel receiver tolerance. Literature on receiver psychology (see Guilford & Dawkins, 1991; Rowe, 2013 for an overview) emphasizes how the perceptual and cognitive attributes of receivers shape their responses to signals. These attributes can constrain or predispose receivers to following signals (sensory bias: Basolo, 1990; Ryan, Fox, Wilczynski, & Rand, 1990), potentially rendering them insensitive to changes in reliability. Experiment 1 provides a rough sketch of this phenomenon, since receivers were experimentally controlled to slavishly follow signals. A second approach is that of 'receiver economics' (McLinn & Stephens, 2010), which focuses on the economics of signal following to show when it pays to tolerate unreliable signals. The relationship between receiver tolerance and environmental certainty outlined here is closely aligned with approaches using statistical decision theory (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Stephens, 1989; Wiley, 1994), the economics of communication (Bradbury & Vehrencamp, 2000), and strategies for managing uncertainty and risk (Dall, 2010). We show that unpredictable environments create conditions where it benefits receivers to follow signals even though they make mistakes when the signal is dishonest. Our results demonstrate that signallers exploit receiver tolerance, whether it is generated by constraints on receiver responses (experiment 1) or by uncertainty in the environment (experiment 2). Thus, although these approaches initially focus on the decisions of the receiver, our results highlight the interplay between the problem of receiver tolerance and that of signal reliability.

Limitations and Further Questions

Our experimental approach may cause unease for some readers, as the laboratory-based signaller–receiver interactions seem far removed from natural signalling systems. The signaller and receiver behaviours involved here are artificial, but we remark that the experimental signalling game does capture the essential pieces of signalling (a state of interest, a signalling action and a response action; see Bradbury & Vehrencamp, 2011). Moreover, this experimental signalling game allows direct control over critical variables that are otherwise hard to manipulate (i.e. environmental certainty and the economic payoffs to each of the players). We do not offer this approach as a replacement to studying animal communication in other contexts, but rather as a tool to complement these studies. Animal signalling is a diverse topic, such that no approach is sufficient by itself.

A critic may also point out that animal signalling research often focuses on traits or strategies that are subject to selection on an evolutionary timescale, yet here we study signaller and receiver strategies based on learned behaviour. Differences between these two cases may offer an interesting contrast to study, but there is no reason to exclude learned behaviour from discussions on animal signalling. In general, we know learning and experience play large roles in signaller–receiver interactions (sexual imprinting, mate choice copying, song development, etc.). Moreover, behavioural equilibria determined by learning are as acceptable theoretically as those determined by genetics (see Maynard Smith, 1982). We expect that receiver tolerance can relax selection on honesty through various mechanisms and on different timescales; our study of learned signalling is but one example. Our signalling games, especially in concert with more traditional approaches, should lead to new insights on the important themes of environmental certainty, receiver tolerance for imperfect reliability, and signaller exploitation of this receiver tolerance.

Conclusions

Our approach, which emphasizes receiver tolerance for imperfect reliability, is an important counterpart to the more common perspective that emphasizes signal reliability. We suggest that signaller reliability and receiver tolerance are of equal importance to biologists interested in either signaller or receiver behaviour because the two topics are interrelated. For example, forces that promote either signaller reliability or receiver tolerance can stabilize signaller–receiver interactions, despite conflict of interest between individuals. Although we have focused on the behaviour of receivers, it is also clear that their sensitivity (or lack thereof) to reduced reliability has important implications for signaller strategy and the stability of signaller–receiver interactions.

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Supplementary Material

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