The economics of animal communication: theory and experiments integrating receiver choice and strategic signal reliability

A DISSERTATION
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

Timothy J. Polnaszek

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

David W. Stephens

December 2015

Acknowledgements

This dissertation would not be possible without the help of many people, and here I would like to offer you all a sincere, hearty ‘thank you’. Though I do not mention everyone by name, know that I truly appreciated your support, friendship, and love.

To the many amazing undergraduates who kept the Blue Jay Lab enterprise running; without them, none of these research projects would have been completed.

To my funding sources, including ScifFund donors, the University of Minnesota, the Bell Museum, the International Society for Behavioral Ecology and the Animal Behavior Society.

To my committee Mark Bee, Mark Borrello, and Keith Barker, for all their support, letter writing, research and career advice. Also to the entire greater-EEB department, for creating such a wonderful community, and providing examples of great teachers, researchers and mentors.

To my advisor Dave Stephens, for all his advice and guidance (on research, academia, teaching, etc.); for helping me think big in my research questions; and always urging me forward towards success and achievement.

To my friends who helped me keep my sanity; to those in EEB who made this stressful journey through graduate school an enjoyable one; to the many who have shared laughter and misery with me over a pint; to the folks who have shared my pursuit of chasing a disc across an open field.

To my family, for all their love; for supporting me at every step along the way (starting many years before I even contemplated graduate school); for all our shared laughter and memories.

To my children, for being my constant source of joy and happiness.

To Bonnie.

Dedication

Dedykuję tę pracę do moja najdroższa ukochana.

Ona zawsze upewniła się, że wiedziałem, gdzie mój ręcznik był.

Table of Contents

List of Tables

List of Figures

Introduction

Animal communication has a long history of study; partly because communication is ubiquitous in biology, but also because of the implications it can have in topics such as sociality or the origination and development of human language. Animal communication also involves many diverse and fascinating behaviors, including some of the most remarkable displays within the natural world. For example, the superb bird of paradise has a vibrant blue patch of feathers, which it displays while dancing and clicking to court females. The whole of this dissertation could be filled describing and discussing similarly incredible signaling behavior. Animals also signal in many contexts (foraging for food, selecting a mate, deterring potential predators, etc.) and the individuals involved do not always agree on the best outcome in these contexts. For example, prey should decrease the reliability of pursuit-deterrent signals and thereby overstate their ability to escape from predators. This creates a paradox because here, and in other contexts with conflicting interests, signalers should decrease reliability, but then receivers should stop using signals and communication would no longer occur. Yet we observe that communication exists in its many fascinating forms, so what maintains this diversity of signaling behavior if signalers and receivers have conflicting interests? The answer to this question has many potential answers, such as signal costs (i.e., handicaps), constraints on signal production (i.e, index signals), etc. (see Hurd & Enquist, 2005; Maynard Smith & Harper, 1995; Searcy & Nowicki, 2005), but no clear consensus has emerged for the extent to which various mechanisms are important, and in what circumstances.

In Chapter 1, I contribute a new perspective to these discussions by integrating a model of receiver choice and game theoretical approaches. From the model, an important theme emerges: receiver tolerance of imperfect reliability (abbreviated as receiver tolerance). Receiver tolerance, or the tendency to follow partially reliable signals, is an important topic in animal signaling, complementary to the typically emphasized topic of signal reliability. Understanding why signals are reliable and why receivers follow imperfect reliability are equally important; I expect the combination of reliability and receiver tolerance to ultimately determine the form and stability of signaler-receiver interactions. To explore these themes experimentally, I developed a signaling game that allows control over theoretically important variables (such as the cost of signals). The game places blue jay subjects (*Cyanocitta cristata*) in a signal-response game played for food rewards, and under various experimental conditions. Chapters 2 and 3 present a series of these signaling-game experiments that demonstrate the effects of signal cost on signal reliability (or honesty) and show the extent to which receivers are sensitive to uncertainty in the environment. Chapter 2 demonstrates that receiver tolerance increases when environments are uncertain (to the point that receivers are gullible), and that signalers are sensitive to the level of receiver tolerance – exploiting tolerance when signaler and receiver interests conflict. In Chapter 3, I show that high signal cost does increase honesty under conditions of conflict, but also that cost is unnecessary in mutualistic conditions. This research is significant because signal reliability enforced by signal cost (i.e., handicap signals) is an important topic in signaling theory, but lacks direct empirical support. Chapter 4 further analyzes current disagreement and controversy in ‘costly-signaling’ literature. Taken together, these results establish the value of considering both signal reliability and receiver tolerance.

Chapter 1: Flag-model receivers and the ‘problem of reliability’.

Introduction

A focus on signal reliability tends to dominate literature on animal communication, to the extent that answering the question ‘why are signals reliable?’ has been referred to as the most important pursuit in animal communication research (Maynard Smith & Harper, 2003). Discussions of signal reliability center around a paradox called the ‘problem of reliability’. The standard explanation of this phenomenon goes like this: signalers may benefit from signaling unreliably, but then receivers should simply stop using signals to make decisions, and this de-stabilizes communication because signaling is pointless if the receiver ignores signals. Importantly, however, this simplified ‘boy-who-cried-wolf’ story makes several simplifying assumptions regarding signaler-receiver interactions, which ultimately constrain our insight into this important topic. Here we integrate an economic model of receiver behavior into the more standard game theoretical approach to studying signal reliability to provide new perspectives on the problem of reliability.

The typical ‘problem of reliability’ explanation assumes the reliability of signals is dichotomous, either signals are reliable (often meaning perfectly reliable) or unreliable. Instead, signals can exist anywhere in a continuous range, from those that always indicate the correct action for receivers to take to those uncorrelated with the correct action. Students of animal signaling are likely aware that reliability can be graded, and we have many examples of reliability estimates in natural signaling systems – often measured as a correlation between states (say male quality or fighting ability) and signals (e.g., Fischer, Kitchen, Seyfarth, & Cheney, 2004; Hill, 1991; Møller, 1994; Tibbetts & Dale, 2004). This awareness of graded reliability is difficult to apply to signaling theory, however, because it is not always clear how reliable an imperfect signal must be to maintain receivers' use of signals when making their decisions. This relates to a second problematic simplification: the strategies available to the receiver are not often fully described. The standard description holds that receivers use 'reliable' signals to make decisions (termed 'signal following') and not 'unreliable' ones, but what are the alternative strategies for receivers? Clearly we cannot fully describe the 'problem of reliability' if we focus too narrowly on signalers because the receiver's alternative to signal following ultimately determines the consequences for both individuals if communication breaks down (Bradbury & Vehrencamp, 2000).

Other simplifications aside, it is crucial to acknowledge that knowing the level of reliability is not sufficient to determine whether following signals benefits receivers (e.g., McLinn & Stephens, 2010). Instead, signal following behavior depends on an interaction between reliability and the base rate of the events important to the receiver (such as the relative abundance of high quality males to low quality males in problems of mate choice). Yet some foundational models addressing the problem of signal reliability seem to conclude that the underlying distribution of states is unimportant in determining signaling solutions (e.g., Maynard Smith, 1991). This result runs contrary to intuition; information is more valuable when outcomes are uncertain and therefore receivers should follow signals with reduced reliability in these situations. Alternatively, if a particular state is highly likely, the receiver does not need signals to have a high likelihood of making the correct choice. Thus the same level of partial reliability may promote receiver signal use in some conditions but inhibit signal use in others.

Given that communication hinges on receivers heeding signals in some way, it is critical to understand how receivers deal with issues such as partial reliability and the base rate of events when making decisions. The flag-model of receiver behavior (McLinn & Stephens, 2006, 2010) focuses on the economics of receiver strategies to predict receivers' responses to signals and cues and, importantly, it provides clear definitions of receiver strategies, incorporates the base rate of events and also allows for the partial reliability of cues. The flag-model predicts the value of following signals from the perspective of the receiver, and thus provides a solid framework for demonstrating the conditions where communication could benefit both individuals, despite conflicts of interest.

The 'problem of reliability' implies signalers and receivers could benefit from communication, but incentives for the signaler to decrease reliability prevent this equilibrium from being realized. As such, our model first identifies the possible levels of signal reliability where the signaler benefits from signaling (as opposed to not signaling) and the receiver benefits from following the signals (compared to ignoring them). We then demonstrate whether these levels of reliability are stable against alternative reliability strategies, or if the reward for decreasing reliability is too high and the 'problem of reliability' manifests itself instead. Finally, we extend the basic signaling model to explore the effects of costly signals on the stability of signaling. This is a natural first step to adding complexity to our model because signal costs, or handicaps, are offered as the solution to the ‘problem of reliability’, but substantial disagreement exists over the role of costs in enforcing honest signaling (Grose, 2011; Számadó, 2012).

The flag-model of receiver behavior

Flag-model predictions for receiver behavior

Here I briefly review the flag-model of receiver behavior as developed by McLinn and Stephens (2006, 2010). Consider an individual that must choose between multiple actions in a varying environment. The term ‘environment’ is used to describe any feature external to the receiver (e.g., food item quality or predator presence). The environment can exist in either of two environmental states. For convenience, and to retain generality, we label the two states as ‘E1’ and ‘E2’. E1 occurs with the probability p and the E2 state with probability (1-p). The variable p describes the environmental certainty, where p=0.0 or p=1.0 indicate certain environments because in these extreme cases the state of the environment is always the same. The receiver chooses between two actions in this environment, where each action is best in only one of the two states of the environment. These actions could represent, for example, attacking a food item or ignoring it, or accepting or rejecting a potential mate. We label the receiver actions generically as A1 and A2. The receiver’s payoff is set such that it is rewarded for matching its action to the current state of the environment; the A1 action is rewarded in state E1 and the A2 action in state E2 (see Table 1). We imagine there is also a cue available to the receiver that indicates the current environmental state with a level of reliability described by the variable q, where q=1.0 is a perfectly reliable cue and q=0.5 is a random cue with no correlation to the state of the environment. So the receiver must decide between two actions, but neither action is correct all of the time. What decision-making strategy should the individual adopt under this uncertainty? Specifically, when does it pay to use the information provided by the cue?

The flag-model compares two general receiver strategies: use the cue to guide actions (cue-following) or ignore the cue and simply choose the single action that is best on average. The general result of the flag-model is that receivers should evaluate both p and q when choosing whether to attend to the cued information. To show this, we need to compare receiver cue-following strategies and ignoring strategies, where the receiver chooses the single action that is best on average. A cue-following strategy yields a payoff of R = ; the receiver is rewarded for each match of action to state, and by definition the signal matches the state a proportion q of the time. The payoff for an ignoring strategy depends on the base rate of the environmental states. Always choosing A2 yields R = , since the receiver is correct only when the state is E2 (occurs 1-p of the time). Alternatively, always choosing A1 pays R = . Thus we expect receivers that ignore cues will always choose A1 when p>0.5, and A2 when p<0.5. Optimal receiver behavior is to follow cues when $q > p$ and q > 1-p, but otherwise ignore the cues, Figure 1 shows this logic graphically.

Signaling to flag-model receivers: the basic game

Signal-response game

Adding a signaler to the flag-model creates a simple form of communication, the signal-response game. The basic components of communication are an environmental state, a signaler who provides signals that correspond to the state, and a receiver whose actions determine the payoffs for both individuals (Bradbury & Vehrencamp, 2011). Here we have two states (E1 or E2), a signal with two signal states (M1 or M2), and receiver actions (A1 or A2), and each individuals' payoff is set by the combination of receiver action and state (see Table 2A for definitions and 2B for payoff combinations). For simplicity, we restrict our attention to when $p \geq 0.5$. The commonness or relative frequency of each state of the environment is an important piece of signaler-receiver dynamics, as we will show, thus we will sometimes refer to E1 as the 'common state' (occurs with frequency p) and E2 the 'uncommon state' (occurs with frequency $1-p$).

A play of the game begins when the current state of the environment is set by some random process, using the complementary event probabilities from the flag-model (E1 with probability p, E2 with probability $1-p$). We assume the signaler has perfect information about the current environmental state and the receiver does not. The signaler can then use one of two signal states to indicate the current state to the receiver. We refer to these possible signal states as M1 and M2. The signaler controls the reliability of the signal ( ) by the extent to which its choice of signal state correlates to the state of the environment over time. We further divide signal reliability into two component reliabilities: q_1 for reliability in the common state (E1) and q_2 for reliability in the uncommon state (E2). For example, when the state is E1, the signaler emits the M1 signal a proportion q_1 of the time and emits the M2 signal $(1-q_1)$ of the time (see Table 2A).

In the flag-model, the reliability of the cue (q) is equivalent in the common state and the uncommon state. That is, regardless of the current state, the receiver observes the signal which indicates the correct state a proportion q of the time. Here the average reliability, , that determines whether the receiver should follow signals depends on the two component reliabilities, q_1 and q_2, but also on the frequency of each state (where =). We refer to the signaler's ability to set each component of reliability independently as ‘strategic reliability’. We restrict these component *q* values, such that ≥ 0.5. If, instead, < 0.5, then a receiver following signals should switch the sense of the signal, reversing the signal’s meaning (i.e., choose A2 in response to M1 and A1 for M2). Thus, by restricting ≥ 0.5, we assume a receiver playing our ‘Follow’ strategy uses the information in the signal and chooses the best signal convention, reversing signal meaning when necessary.

After the signaler chooses a signal state, according to , the receiver can then view or otherwise perceive the signal state before choosing an action. Again, the receiver’s choice of action is important to the signaler because the combination of the current environmental state and the receiver action determines the payoff for both individuals. As in the flag-model, the receiver is rewarded for matching its actions to the current state of the environment (Table 2B). The receiver action the signaler prefers in each state is determined by the variables *x* and *y*, respectively (Table 2B). The signaler has an incentive to decrease reliability if it prefers the opposite action of the receiver. For example, if $x>0$, the signaler obtains a higher benefit when the receiver chooses A2, rather than A1, in the environmental state E1. When the individuals’ interests conflict in this way, decreases in reliability lead to the action the signaler prefers, at the expense of the receiver. Thus the signaler should decrease q_1 if $x > 0$ and decrease q_2 if $y > 0$.

Signaler and receiver strategies

Table 3 shows the game table and payoffs for the signaler and receiver; with payoffs based on two receiver strategies (Follow signals and Ignore signals) and two forms of signaler strategy (Signal and No signal). In the Signal strategy, the signaler chooses a level of reliability for each state (q_1 and q_2) which results in an overall reliability ≥ 0.5. Based on the game structure outlined above, if the receiver follows the signals given, the signaler's payoff function depends on each component reliability: $S_{S,F} = p(1-q_1)x + (1-p)(1-q_2)y$. Whenever the signaler honestly signals the current state to a signal-following receiver ($q_1 = q_2 = 1$), its payoff is $S_{S,F} = 0$. The signaler earns x when the receiver makes a mistake in the common state (occurs $1-q_1$ of the time, by definition) and earns y when the receiver makes a mistake in the uncommon state (occurs $1-q_2$ of the time). The receiver's payoff for the follow strategy is $R_{F,S} = pq_1 + (1-p)q_2$ and its payoff is $R_{I,S} = p$ if it ignores signals (instead choosing the action that is best, on average). In the No Signal strategy, the signaler simply chooses not to signal. The receiver must choose an action without the signal in this case, and so always chooses action A1 (which is the correct action in E1, the common state). Thus $S_{N,F} = S_{N,I} = (1-p)y$ and $R_{F,N} = R_{I,N} = p$ when the signaler uses the No Signal strategy.

Basic signaling game: stable equilibria

In the following paragraphs we evaluate the stability of the Signal/Follow strategies. Signal/Follow is a stable equilibrium for the signaler strategy set of q_1 and q_2 when the following conditions hold: [1]

For the receiver:

Equation 1) $R_{F,S} > R_{I,S}$

And, for the signaler:

[1] Note, the following equations use strict inequalities. Whereas weak Nash Equilibria exist when two expected values are equivalent, we assume the payoff for the Signal strategy and the Follow strategy must be strictly greater than the No Signal and Ignore strategies, respectively. We make this assumption based on the observation that signaling and signal following likely incur a small cost.

Equation 2) $S_{S,F} > S_{N,F}$

)

These two conditions require that neither the signaler nor the receiver can benefit by unilaterally switching strategies. We initially solve for the when Eq. 1 is true, showing the range of q_1 and q_2 conditions where signal following benefits the receiver when compared to ignoring the signal (choosing the action that is best on average). From the flag-model, we know $S_{S,F} > S_{N,F}$ whenever $> p$, where our average reliability depends on the component reliabilities q_1 and q_2. We then evaluate the maximum of $S_{S,F}$ within a restricted range ($1 \geq \quad \geq p$) determined by Eq. 1 to demonstrate whether there exists a q_1,q_2 strategy set that fulfills the conditions for Eq. 1 and Eq. 2; such a q_1, q_2 set would result in a stable Signal/Follow equilibrium with respect to No Signal (on the part of the signaler) and Ignore (on the part of the receiver).

Notice, however, that it is also possible the signaler could increase its overall payoff with an alternative Signal strategy; i.e., a different q_1, q_2 pair outside the range where receivers follow signals. The initial analysis above does not consider the range between $0.5 \leq q \leq p$. Assuming the signaler is free to explore all q_1 and q_2 combinations (i.e., considering the entire range $0.5 \leq \quad \leq 1$), the stability of the Signal/Follow strategies then requires an additional third condition for the signaler:

Equation 3) $S_{S,F}\ (q_1,q_2) = \qquad [S_{S,F}\ (q_1, q_2)]$

Equation 3 holds when the signaler cannot obtain a higher payoff for alternative values of q (the strategy set q_1,q_2 is the maximum of the signaler's payoff function, given that the receiver uses the Follow strategy). Because $S_{S,F}$ (q_1,q_2) is linear with respect to both arguments, we know $\qquad [S_{S,F}\ (q_1,q_2)]$ occurs at the boundaries of the conditions for q_1

and q_2, where $0.5 \leq$ ≤ 1; this is a problem solved via linear programming. Figure 2 shows an example of the full set of q_1, q_2 conditions where ≥ 0.5. We know the maximum payoff, for the signaler, will occur at one of the four vertices (1,1), (1, 0) , (—, 1) or (—, 0) (where these are q-value strategy sets in the form (q_1, q_2)). If all three equations are true, we can say Signal(q_1,q_2)/Follow is a Nash Equilibrium (NE) with respect to the both the No Signal strategy and all alternative Signal strategies. From the signaler payoff function, the sign of x determines whether $S_{S,F}$ is an increasing or decreasing function with respect to q_1, and y determines whether $S_{S,F}$ is an increasing or decreasing function with respect to q_2. As such, we analyze stability for separate cases:1) x and y < 0; 2) x > 0 and y < 0; 3) x < 0 and y > 0; and 4) x and y > 0.

Case 1 – complete shared interest (x<0; y<0)

As in the flag-model, $R_{F,S} > R_{I,S}$ whenever $\geq p$; following signals is best when the average reliability level ( ) exceeds the uncertainty in the environment (p). To find if there exists q_1, q_2 conditions where Signal is also better than No Signal for the signaler, we can then solve for [$S_{S,F}$ (q_1,q_2)] within the restricted range where $\geq p$ (the region where $R_{F,S} > R_{I,S}$). To begin, we note the signaler's payoff ($S_{S,F}$) increases with respect to q_1 and q_2 because both x and y are negative values. Thus the overall maximum of $S_{F,S}$ occurs at (1,1), including when we consider the full range of q-values where $\geq$ 0.5. Thus Signal(1,1)/Follow is a Nash Equilibrium, with respect to No Signal and all other signal reliability sets q_1,q_2; an intuitive result because both individuals benefit from correct receiver decisions, and increasing q-values increases these correct decisions. The only minor exception to this equilibrium is that in completely certain environments (p=1.0) all signal reliability strategies would be weak NE ($S_{S,F} = S_{N,F} = 1$), because the receiver can choose correctly regardless of signal reliability and so all reliability strategies are equivalent. Given signaling and signal following come with some costs, however, we expect Not Signal and Ignore to yield higher payoffs when p=1.0.

Case 2 – shared interest in the uncommon state, conflict common (x>0; y<0)

$R_{F,S} > R_{I,S}$ again whenever $\geq p$, and we again solve for the maximum payoff for the signaler within this restricted range to show whether it is possible that $S_{S,F} > S_{N,F}$. When there is shared interest in the uncommon state, we begin by setting $q_2 = 1$ because $S_{S,F} =$ is an increasing function with respect to q_2. The signalers payoff is then $S_{S,F} =$, which we can easily compare to $S_{N,I} =$. We find $S_{S,F} > S_{N,I}$ for all values of q_1 because $S_{S,F} \geq 0$ (since $x>0$) and $S_{N,I} < 0$ ($y<0$). Here, maintaining signal following by the receiver always yields a higher payoff for the signaler and so signaling always benefits the signaler; there clearly exist q_1, q_2 conditions where Signal/Follow benefits both individuals. We also check the critical level q_1 that ensures receivers profit from a signal following strategy, which occurs when $\geq p$, setting $q_2 = 1$ (where, again, =). We find signalers need to maintain a level of reliability such that ——; only then should receivers continue to follow the signal. Since $S_{S,F}$ decreases with respect to q_1, we know $S_{S,F}$ is maximized at (—— , given the restriction $\geq p$.

We next determine if the possible Signal/Follow equilibrium above is stable over the entire range of q-values available to the signaler ($1 \geq$ ≥ 0.5). Again x > 0, and so the signaler maximizes its payoff by decreasing q_1, here to q_1= —. We then compare to the No Signal payoff and find $S_{S,F} = - > S_{N,F} =$ because $x > 0$ and $y < 0$.

However, we also find = $0.5 \leq p$ and so $R_{F,S} \leq R_{I,S}$ for the set of reliability levels

(—, 1). Therefore, the Signal/Follow equilibrium is not stable in this case; signalers benefit from decreasing reliability past the critical level necessary to maintain the incentive for receivers to follow signals.

Case 3 – shared interest in the common state, conflict rare (x<0; y>0)

In this case of conflict in the uncommon state, $S_{S,F}$ increases with respect to q_1 and decreases with respect to q_2. Thus setting $q_1 = 1$ and decreasing q_2 increases the expected value of the Signal strategy when the receiver follows signals. When $q_1 = 1$, the minimum of the second reliability component is $q_2 = 0$, such that $S_{S,F} = (1-p)y$. The average reliability for this strategy set is = p, so this is the maximum of $S_{S,F}$ whether we consider the range $1 \geq$ ≥ 0.5 or $1 \geq$ $\geq p$. The default action of a receiver that acts without signals is A1 (because A1 is the correct action for the receiver in the common state, E1). Here the signaler is always rewarded when the receiver chooses action A1. A signaler's payoff from this receiver strategy is $S_{N,F} = S_{N,I} = (1-p)y$, which is equivalent to the maximum payoff for $S_{S,F}$ in this case. Thus $S_{N,F} \geq S_{S,F}$, and the Signal/Follow equilibrium is not stable for any reliability strategy set.

Case 4 – No shared interest between signaler and receiver (x>0; y>0)

Next we examine whether circumstances exist where the signaler and receiver both benefit from signaling, despite completely conflicting interests. This is more complicated than previous cases because signalers could reduce q_1 or q_2, and either reduction would benefit the signaler. To begin, we assume the signaler initially partitions all decreased reliability into the condition where it pays the most, similar to *Case 2*, because these reductions in reliability are limited.

When $y > x$, we initially hold q_1=1 and solve for when ≥ p; that is, when is $p + q_1$ (1-p) > p. We find the signaler can reduce q_2 to 0, but even then the expected value of $S_{S,F} = S_{N,F}$. Decreasing q_1 would only further decrease to the point where < p, meaning receivers would not benefit from following signals. Thus no q_1, q_2 conditions exist where the signaler and receiver both benefit at the Signal/Follow equilibrium.

Alternatively, when $y < x$, we let q_2=1. Similar to case of partial interest (*Case 2*), ≥ p if $q_1 \geq$ —— and so $S_{S,F}$ = (1-p)x which is always greater than $S_{N,F}$ = (1-p)y (because here $y < x$). Overall, signalers and receivers can simultaneously benefit from communication under complete conflicts of interest, but only when $y < x$ (when the outcome in the more common state is more economically important to the signaler).

We next consider for the overall maximum of $S_{S,F}$ where 1 ≥ ≥ 0.5. Again, $S_{S,F}$ is decreasing with respect to q_1 and q_2 (x and y > 0), so [$S_{S,F}$ (q_1 q_2)] occurs at one of the two strategy sets (— , 1) and (—, 0). Both of these strategies sets yield an average reliability of = 0.5. Thus, regardless of which strategy set is best for the signaler, the receiver does not follow signals because = 0.5 ≤ p, and so $R_{I,S} \leq R_{F,S}$ and signal following is not stable (again, assuming some small cost to the Follow strategy). In complete conflicts of interest, no Signal/Follow strategy that is stable against all possible q_1, q_2 values (for the signaler) and the Ignore strategy (for the receiver) when both x and y > 0.

Basic signaling game: results summary and discussion

We focus on the solutions where the Signal/Follow equilibrium is stable because this equilibrium fits within the commonly accepted definitions of communication (e.g., Bradbury & Vehrencamp, 2011; Hauser, 1996; Searcy & Nowicki, 2005). Figure 3 summarizes the conditions where q_1, q_2 strategy sets exist that could stabilize Signal/Follow with respect to the No Signal strategy (specifically in range $1 \geq \quad \geq p$). Figure 4 illustrates whether these possible q_1, q_2 solutions are also stable against all possible q_1, q_2 strategies from $1 \geq \quad \geq 0.5$ (where 0.5 is the minimum average reliability). Common interest and the base rate of events together determine whether q_1, q_2 conditions exist where both individuals benefit from a Signal/Follow equilibrium (Figure 3). Partial common interest is not always sufficient to create conditions where both individuals can benefit from signaling (quadrant [i]) and under other conditions partial common interest is not necessary (quadrant [ii] and when $x > y$). These results generally agree with other 'economics of signaling' approaches that explore the value of communication (Bradbury & Vehrencamp, 2000), but they do not fully characterize the stability of communication in a game theoretic context (see Godfrey-Smith & Martínez, 2013) if signalers are completely free to vary q_1 and q_2. It is also important to determine whether the Signal/Follow equilibrium is stable when compared with all other signal reliability strategy sets. Evaluating the additional third stability condition, where the signaler is free to choose any reliability level where $\quad \geq 0.5$, we find that a Signal/Follow strategy pair is only stable when the signaler and receiver always agree on the best receiver action (Figure 4).

Comparing the two analyses recaptures the classic conundrum in signaling theory, the 'problem of reliability', but the problem is only present in certain conditions (the cross-hatched region in Figure 3). In each case of conflict (whether partial or complete), the signaler payoff function $S_{S,F}$ increases with decreasing q-values in at least one of the environmental states; i.e., decreasing reliability pays. In a subset of these conditions of conflict, intermediate q-values (1 ≥ ≥ p) would maintain signal following and yield a higher payoff for both individuals when compared to the No Signal and Ignore strategies, but the incentive to decrease q pushes the signaler strategy past the breaking point = p. Thus we see conflicts of interest cause signalers to reduce reliability (decrease), receivers stop paying attention (use the Ignore strategy) and communication breaks down (Signal/Follow equilibrium is no longer stable). The model re-characterizes this 'problem of reliability' in a signaling game with a more realistic, flexible receiver strategist by utilizing the flag-model of receiver behavior. This approach allows us to address several key issues related to the problem of reliability: it eliminates the false dichotomy between reliable and unreliable signals; it specifies the receiver's alternative to following signals; and it highlights the important themes of the base rate of events and uncertainty in the environment.

Partial reliability and strategic signal reliability

Framing our signaling game around the flag-model sets a clear minimum level of reliability (≥ p) necessary to maintain receiver signal-following behavior. Descriptions of communication stability frequently oversimplify the issue of signal reliability, characterizing receiver behavior as following reliable signals and ignoring unreliable ones. Yet the breaking point between reliability and unreliability is left undefined, leaving no information regarding the level of partial reliability necessary to maintain receiver signal-following behavior. Economic models of communication, in particular Bradbury and Vehrencamp (2000), help us recognize the importance of graded reliability and discuss the minimum level of reliability which maintains receiver signal use. Our model adds a significant element to this body of literature by considering strategic reliability (i.e., state dependent reliability levels). This is important because when incentives align in a particular environmental state, there is no reason for signalers to signal deceptively in that state.

To meet the critical reliability level, $\geq p$ in our model, signalers must manage the frequency of mismatches between signal state and environmental state. In the context of signaling, it is possible for reliability to benefit the signaler in one state while deception pays in the other state (our independently varying x and y capture this possibility). From the signaler's perspective, it is inefficient to use up any mismatches between signal and environmental state (a reduction in observed reliability) when incentives align. Thus, it is critical to allow signalers to set reliability independently in each state – to signal reliably when both individuals agree on the best receiver action and unreliably when the signaler is rewarded for receiver mistakes. Despite the importance of this strategic reliability, theoretical treatments of animal communication often use a simpler universal level of reliability (e.g., Bradbury & Vehrencamp, 2000; Hackett, Schaefer, & Ruxton, 2014) or only consider perfectly reliable (q=1) versus perfectly unreliable signals ($q=0$), as in the Sir Philip Sidney (SPS) game (Maynard Smith, 1991). Adding strategic reliability leads to different conclusions for some 'problem of reliability' models, such as the SPS game. For example, including partial reliability in the SPS model changes whether the base rate of events and uncertainty in the environment (p) are important in the game solutions (see discussion on these topics to follow). The concept of strategic reliability may also help researchers identify cases of true deception in animal signaling, rejecting alternatives such as simple signaler error, because we expect certain patterns in the state dependent reliability – greater reductions in reliability in the environmental states where individuals disagree on the best action (Searcy & Nowicki, 2005; Zollman, Bergstrom, & Huttegger, 2013).

Base rate and receiver averaging

Similar to the value of signals or cues from a receiver's perspective (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; McLinn & Stephens, 2006), the value of providing signals, for the signaler, is set by whether the decisions of an informed receiver yield a higher payoff than the decisions of a receiver that is forced to choose the one action that is best on average (in agreement with Bradbury & Vehrencamp, 2000). The key difference is that the signaler is unable to select what action an uninformed receiver chooses. Instead, the commonness of events determines the receiver's default strategy, which is then critical in defining whether communication can benefit the signaler. The base rate of the two states of the environment shifts the signalers incentive to provide information via signals – especially when there is conflict between the signaler and receiver.

The clearest example of this phenomenon is the comparison of conditions of partially opposed incentives. The signaler can benefit from signaling only when the condition of conflict is common. Otherwise, when conflict is rare, the receiver's default action agrees with the signaler's preferences in both conditions. Here the standard 'problem of reliability' remains unchanged when conflict is common: the signaler always benefits from communication in this case, but incentives to decrease reliability destabilize the Signal/Follow equilibrium. On the other hand, signalers should be uninterested in maintaining communication when the condition of conflict is rare, and this presents an entirely different challenge to the stability of communication. Our extension of the basic model explores this concept further (see *Signaling game extension: costly signals*).

The commonness of environmental conditions and their relative payoffs also regulates whether there is an economic imperative for the signaler to provide signals in the incentives completely opposed case. When the more common environmental condition has higher stakes for the signaler there is more to gain from signaling (a higher expected value from maintaining the Signal/Follow equilibrium). This is because when signaling fails the receiver's default action prevents the signaler from obtaining the higher payoff, and does so quite frequently. If the signaler and receiver always disagree on the best option, but one state provides a larger reward, the signaler can essentially 'buy credibility' by signaling reliably in the environmental state where it has comparatively little to gain.

Uncertainty and receiver tolerance for imperfect reliability

Research shows that environmental uncertainty (p near 0.5 in our model) creates receiver tolerance for imperfectly reliable signals; that is, uncertainty predisposes receivers to follow signals (e.g., Dunlap & Stephens, 2009; McLinn & Stephens, 2006; Polnaszek & Stephens, 2014a). The model we outline here is based on the flag-model of receiver behavior, and so our receiver's decision to follow signals also depends on the interaction between uncertainty and the average reliability of the signal (follow signals when $\geq p$). The significance of the relative frequency of each environmental condition and its relationship with signal reliability extends to the signaler, because uncertainty sets the limit for strategic reductions in reliability. For example, when signaler and receiver disagree in the common state (*Case 2* in the model), we find signalers need to maintain a level of reliability in the state of conflict such that ; only then should receivers continue to follow the signal. This inequality can be rearranged to , where is a measure of dishonesty (a decrease in reliability) and is the relative likelihood of the uncommon state. Therefore, dishonesty is limited by the relative likelihood of the state the signaler is dishonestly indicating; receivers should tolerate lower levels of dishonesty as this likelihood decreases.

Thus uncertainty in the environment determines the extent to which signalers can reduce reliability and yet still maintain receiver signal following. When p=0.5, the environment is uncertain and receivers should tolerate of imperfect reliability (referred to as receiver tolerance). Alternatively, if p = 0.99, signals become useless if they are anything less than perfectly reliable (=1). Of course, the effects of receiver tolerance on the stability of signaling depend on how free the signaler is to reduce reliability. We end up with the ‘problem of reliability’ if signalers can completely reduce reliability in cases of conflict. However, dishonesty may be limited for various reasons (see Enquist, Hurd, & Ghirlanda, 2010; Maynard Smith, 1982; Searcy & Nowicki, 2005), and then the stability of communication would depend on the interaction between these limitations on signal reliability and receiver tolerance for imperfect reliability.

Overall, uncertainty in the environment should be important in all communication contexts (e.g., each of our cases of shared and conflicting interests) because receivers’ decisions always depend on the interaction between p and . Yet this issue is often finessed (e.g., models assume $p=0.5$) or simply ignored in discussions of animal communication (discussed in McLinn & Stephens, 2010; Polnaszek & Stephens, 2014a; Searcy & Nowicki, 2005). Uncertainty should create opportunity for signalers to reduce reliability in conditions of conflict (as discussed above), but also minimize receiver demands on signal reliability in mutualistic cases. We know that the perceived reliability of a signal is reduced by noise and other factors (Bradbury & Vehrencamp, 2011; Wiley, 1994), and signal design must overcome these reductions in perceived reliability. Communication should be more easily maintained despite partial reliability when the environment is uncertain (p near 0.5) because small reductions in reliability will not prompt receivers to ignore signals; this is true whether the realized imperfect reliability is determined by strategic deception, signaler errors, or errors in receiver perception.

Signaling game extension: costly signals

In this section we develop an extension to our basic model of signaler-receiver interactions. The extended model focuses on signal cost, which is an important reliability enforcement mechanism and the most discussed solution to the important 'problem of reliability'.

Signal costs, or handicaps, are considered by many to be critical to the maintenance of communication (see Grafen, 1990; A. Zahavi, 1975; Amotz Zahavi, Zahavi, Balaban, & Ely, 1999, etc.). Here we explore the effects of signal costs by building on the flag-model signaling game developed above. When implementing signal costs into the signaling game, various cost structures are possible. For example, costs may depend on the type of signal, the state of the environment, or an interaction between the two and these differences cost structure can have important implications in the outcome of signaling interactions (Polnaszek & Stephens, 2015; Számadó & Penn, 2015). Here we create a generalized cost structure, with the variables c_1 through c_4 controlling the costs of signaling (see Table 4). We continue to use the generalized signaler payoff structure (see Table 2B) from the basic model above. We analyze two cases from our general model, both where incentives partially oppose: 1) when the signaler's and receiver's interests conflict in the common state (*Case 2* above, when when $x>0; y<0$) and 2) when interests conflict in the uncommon state (*Case 3* above, when $x<0; y>0$). From the general signaler payoff structure, when we add signal costs:

$S_{S,F} =$

Signal costs when there is conflict in the common state, $x>0, y<0$

Using the results from the general signaling game without signal costs, we know

$[S_{S,F}\ (q_1,q_2)]$ occurs when the signaler chooses the reliabilities (—,1). We will refer to this reliability set as the Dishonesty strategy (S_D). We also consider the perfect reliability signaler strategy (1,1), referred to as the Honesty strategy (S_H). Table 5A compares the payoffs for these signaler strategies, as well as the No Signal strategy, when played against the receiver strategies Follow and Ignore. To determine when signal costs enforce honesty and stabilize the Honest/Follow equilibrium, we simply need to compare the values in the top row (under the Honesty strategy, Follow is the best receiver strategy, $R_{F,H}$=1). Honesty is better than Dishonesty when:

— — < .

Solving the inequality, signal cost maintains Honesty, with respect to the Dishonesty strategy, whenever . The variable x is the change in payoff, for the signaler, when the receiver's action changes from 'A1' to 'A2' in the common state (this is a change from the correct response to the incorrect one, from the receiver's perspective). We also evaluate the conditions where Honesty exceeds the benefits a No Signal strategy.

As in the general model, the No Signal payoff is $S_{N,F}$= $S_{N,I}$=(1-p)y. Thus Honesty yields higher benefits whenever:

< , or we can rearrange to —

Here the variable *y* represents a loss to the signaler ($y < 0$), and this loss must be greater than the right hand side, which depends on *p* and the two costs of honestly signaling the true environmental states (c_1 and c_4).

Signal costs when there is conflict in the uncommon state, x<0, y>0

In this case, [$S_{S,F}$ (q_1,q_2)] occurs when the signaler signals with the reliability set (1,0). We redefine the Dishonesty strategy set for this case as q_1=1, q_2=0, but keep the same Honesty definition (q_1=1, q_2=1). Table 5B outlines the game table comparing these updated strategy definitions. Honesty ($S_{H,F}$) exceeds Dishonesty ($S_{D,F}$) whenever:

<

Rearranging the terms above, we see that $S_{H,F} > S_{D,F}$ if . Similar to *Case 2* in the cost model, Honesty is better than Dishonesty when the costs of changing the receiver's response in the environmental state of conflict exceeds the benefit (*y*). However, when we compare Honesty and the No Signal strategy ($S_{N,F}$):

<

Assuming positive costs of signaling, the right hand side above is negative. Therefore the No Signal strategy payoff (which is positive, y>0) always exceeds the Honesty payoff. From the basic signaling game, we also know No Signal exceeds Dishonesty, too (see *Case 3* in the basic signaling game).

Costly signals results summary and discussion

The results demonstrate that signal costs can enforce the Honesty, but only in certain circumstances. Signal costs stabilize Honesty when there is a conflict of interest in the common state (*Case 2*, where $x > 0$ and $y < 0$). In this situation, though, only two of the four signal costs are important in preventing the Dishonest strategy; $S_{H,F} \geq S_{D,F}$ when $> x$. In contrast, signal costs cannot change the stability of signaling (whether Honesty or Dishonesty) if the signaler and receiver only disagree on the best action in the uncommon state (*Case 3,* when $x<0$ and $y>0$) and the No Signal strategy is best.

Signal costs and the 'problem of reliability'

Literature on animal communication presents signal costs as a solution to the 'problem of reliability'. Our results support this assertion in some conditions, but not all (c.f. Zahavi, 1977). Evaluating whether there exists a strategy set q_1,q_2 where both signaler and receiver could benefit from signaling in the basic model provided insight into the conditions (e.g., x and y values) where the stability of communication may be salvaged by reliability enforcement mechanisms (signal costs, in this model). The No Signal strategy is already better than the Signal strategy when conflicts of interest are uncommon, and the cascade of events leading to the 'problem of reliability' never occurs when the signaler is uninterested in signaling at any reliability level. Adding signal costs only serves to further decrease the value of signaling ($S_{H,F}$ or $S_{D,F}$) when compared to the payoff from simply not signaling ($S_{N,F}$). When considering further extensions to the basic model, this may serve as an example of how to predict which mechanism(s) could stabilize communication in different circumstances. For example, perhaps manipulation, receiver biases or sensory exploitation (see Endler & Basolo, 1998; Ryan, Fox, Wilczynski, & Rand, 1990; Trivers, 1974) are more important for maintaining communication in cases where signal reliability enforcement mechanisms are unlikely to have any effects.

Which costs enforce honesty?

When signalers and receivers disagree in the common state, costs stabilize Honesty with respect to Dishonesty whenever the marginal cost of indicating the uncommon state when the common state is true exceeds the benefit gained by this dishonest signal (x). Though there are four possible signal-state costs (c_1 through c_4) only two (c_1 and c_3) have any effect on the 'problem of reliability' (i.e., the stability of Honesty compared to Dishonesty). This is a critically important point because it shows how measuring a signal cost in nature is far from sufficient to demonstrate whether signal costs enforce honesty (see Lachmann, Szamado, & Bergstrom, 2001; Searcy & Nowicki, 2005; Számadó, 2011); especially because some costs of honest signals (i.e., c_4), which are completely unimportant when comparing Honesty and Dishonesty, may be the easiest to measure in signaling systems (Grose, 2011; Kotiaho, 2001). Moreover, measured signal costs in nature are often considered too small to be consistent with the 'cost enforced honesty' idea (reviewed in Bergstrom & Lachmann, 1998). But the costs of honest signaling (i.e., c_1 and c_4) are necessarily small; otherwise the expected value of the No Signal strategy would exceed that of the Honesty strategy.

Resolving disagreements between theoretical and empirical 'signal costs' research

The results of our 'signal cost' model reinforce the growing disparity between theoretical predictions in the costly signaling literature and empirical studies of signal costs. These differences exist primarily because it is difficult to separate and manipulate the necessary costs (c_3 and c_1) to test whether costs enforce honesty (which is the central claim of the handicap principle and costly signaling literature). In addition to the issues raised above, cost is predicted to be unimportant in stabilizing Honesty if interests are completely aligned (when x and $y < 0$, model above, Bergstrom & Lachmann, 1998; Maynard Smith, 1991), in this case there is no incentive to signal dishonestly. These disparities call for novel approaches to studying costly signaling, approaches that recognize and address this disconnect between the existing costly signaling literature and the question of why signals are reliable (Kotiaho, 2001; Polnaszek & Stephens, 2014b; Számadó, 2011). Both separating and manipulating the four distinct signal costs are critical challenges for future costly signaling research, because each cost influences signaling stability in different ways.

Further questions and model extensions

Here we use the receiver economic approach (when does it pay to follow signals) as the foundation of our model, incorporating signaler behavior into the flag-model of receiver behavior. Readers may note that while we address a few important assumptions regarding the problem of reliability, communication can be more complex than the simple signal-response game presented here (e.g., more than two environmental states or graded signal states). In the next paragraphs we discuss two potentially important extensions to our model, but recognize this does not represent an exhaustive list.

A hallmark of the flag-model is its simplicity and extensibility, so a natural next step is to build on the flag-model and change our assumptions of receiver behavior. Here we consider the strategies of individuals in a game theory context, and an excellent way to add further complexity to our game is to consider themes from receiver psychology

(Guilford & Dawkins, 1991), such how receivers respond to imperfectly discriminable signals. The current model assumes the signaler fully controls the average reliability of signals, but this reliability is decreased if the receiver sometimes makes mistakes in identifying signals. For example, if an honest M1 signal is perceived as M2, this leads to the incorrect action A2. The perceived signal was unreliable in this instance, from the perspective of the receiver. Borrowing from signal detection theory (Green & Swets, 1966; Wiley, 1994), we could vary the discriminability of the two signal states and evaluate 1) the stability of communication and 2) the conditions where signalers should invest in making the signal states more easily discriminable. For example, when individuals disagree on the best action, mistakes in signal assignment could actually benefit the signaler. Exploring signaler investment in the distinctiveness of signal states would also connect the model results with ideas of signal exaggeration and conspicuousness (Dawkins & Guilford, 1997; Enquist & Arak, 1998). This and other extensions to this basic game that build from receiver perception and processing of signals should help bridge the gap between game theoretical and receiver psychology approaches, which are sometimes cast as polemical opposites.

Another extension would be considering the strategic use of combinations of multiple signals. Until this point, we have considered a signaling system where the signaler uses one simple signal that can take on only two signal states. Yet some argue that such a simplified signaling system is rare in nature, and instead many systems involve signals with multiple components or multiple signals (Hebets & Papaj, 2004; Partan & Marler, 1999); we will refer to these as ‘complex signals’. For example, male wolf spiders of the genus *Habronattus* use complex signals with a combination of sound, color and movement when courting females (Elias, Maddison, Peckmezian, Girard, & Mason, 2012). Each of these components could be assessed by the female when making her mate choice decisions, but in theory she could consider them independently or in some combination. In the context of our game, we expect the use of complex signals could function as 'backup messages' (Rufus A. Johnstone, 1996) when the payoff outcome of a signaling interaction is especially high (x and y take on extreme values in our model). In cases of conflict, signalers benefit from receiver mistakes, so we could also ask whether combinations of signals exist that enable signalers to more easily elicit their preferred receiver responses at the expense of the receivers. In general, complex signals are thought to benefit receivers for various psychological and signal processing reasons (e.g., learned faster or remember longer, Rowe, 1999). Recent research shows that certain environmental uncertainty conditions also favor the use of complex signals from an economic perspective (Rubi & Stephens, in press). Given the relative abundance of complex signals and their emphasis in animal signaling literature (see Hebets & Papaj, 2004; Higham & Hebets, 2013; S. R. Partan, 2013; Rowe, 1999, etc.), it is important to ask what conditions create an advantage for signalers sending these complex signals that would also fit the expectations for receiver complex signal use.

Final Summary

The simple structure of the flag-model has proven rather powerful in predicting receivers' use of cues on multiple timescales. The key prediction, that receivers are sensitive to the interaction of environmental certainty (related to the base rate of events) and signal reliability has been repeatedly tested empirically; both through studies on learned cue use (McLinn & Stephens, 2006, 2010) and evolved cue use (Dunlap &

Stephens, 2009, 2014). The simplicity of the flag-model has also enabled researchers to build upon it and explore additional phenomena, such as multicomponent signal use (Rubi & Stephens, in press) or social information use (Heinen & Stephens, in press). Because the flag-model identifies situations where receivers are most likely to follow partially reliable signals or cues in its external environment, it also provides an excellent way to generate predictions of signalers strategic use of signals on a continuum from perfectly reliable to completely unreliable.

Here we extend the flag-model by considering signal reliability that is set by a signaler whose payoff is contingent on the receiver's choice of action, rather than a cue set exogenously by the environment. Our model adds to current theoretical literature by reframing the classic 'problem of reliability' and highlighting the comparison between conditions where communication is mutually beneficial to both parties and the overall stability of communication, which are sometimes taken as equivalent (Godfrey-Smith & Martínez, 2013). We discuss how identifying conditions where signaling is valuable to both players, but communication may not be stable, should prove useful when considering the interplay between reliability enforcement mechanisms and receiver biases. Moreover, signaling systems may never evolve to their equilibrium points (Enquist, Arak, Ghirlanda, & Wachtmeister, 2002; Enquist et al., 2010), so broadening our search for conditions that enable communication helps overcome this limitation of game theoretic approaches.

Our results suggest important roles for the base rate of events and uncertainty in the environment in signaling games. We find that conflict in the common state may result in the 'problem of reliability', but conflict only in the uncommon state does not – instead we have the problem of ‘no signaling’. Uncertainty changes the extent to which receivers will continue to follow signals despite reduced reliability. This is a concept we refer to as receiver tolerance, and it represents a significant yet under-studied complement to signal reliability (Polnaszek & Stephens, 2014a). The importance of environmental uncertainty emerges from our consideration of strategic (or partial) reliability; removing strategic reliability diminishes the role of uncertainty in signaling games.

Overall, we advocate an approach that combines economic models of communication with the more typical signal reliability models. Such an approach would focus on integrating two key questions underlying communication 1) ‘when should signalers communicate reliably?’ and 2) ‘to what extent should receivers tolerate imperfect reliability’? We argue that these two questions are at the heart of communication, yet the field of animal communication tends to either focus exclusively on signal reliability or consider mechanisms of receiver choice, but less frequently integrate the two halves. We hope this research provides a framework for future theoretical and empirical research to further connect ideas and themes from the literatures on signal honesty and receiver choice.

Table 1.1

Receiver payoffs, as determined by receiver action and environmental state

Receiver Payoffs

	State E1	State E2
Action A1	1	0
Action A2	0	1

Table 1.2A

Definitions of terms and variables	
p	*Probability of E1(the common state)*
$1-p$	*Probability of E2 (the uncommon state)*
q_1	*Probability of M1|E1* *Reliability of the signal in the common state*
q_2	*Probability of M2|E2* *Reliability of the signal in the uncommon state*
	$= pq_1 + (1-p)q_2$ *Average signal reliability, as observed by the receiver. Equivalent to the single q value in the flag-model.*
S_S	*Payoff function for the signaler for a Signal strategy*
S_N	*Payoff function for the signaler for a No Signal strategy*
R_F	*Payoff function for the receiver for a Follow strategy*
R_I	*Payoff function for the receiver for an Ignore strategy*

Table 1.2B

Signaling game payoffs for Receiver (upper) and Signaler (lower) given each combination of state and receiver action.

	State E1 (Common State)	State E2 (Uncommon State)
Receiver Payoff		
Action A1	*1*	*0*
Action A2	*0*	*1*
Signaler Payoff		
Action A1	*0*	*y*
Action A2	*x*	*0*

Table 1.3

Payoff table for signalers for each strategy (Signal or No Signal) against receiver strategies (Follow or Ignore).

		Signaler Strategy	
		Signal with reliability (S)	No Signal (N)
Receiver Strategy	Follow (F)	$S_{S,F}$ =] $R_{F,S} = pq_1 + (1\text{-}p)q_2$	$S_{N,F}$ = $R_{F,N} = p$
	Ignore (I)	$S_{S,I}$ = $R_{I,S} = p$	$S_{N,I}$ = $R_{I,N} = p$

Table 1.4
Signal costs for each signal type in each state of the environment.

Signal Costs		
	State E1 (Common State)	State E2 (Uncommon State)
M1 (indicates common state)	c_1	c_2
M2 (indicates uncommon state)	c_3	c_4

Table 1.5A

Signaler payoffs for each strategy, Honesty, Dishonesty and No Signal when played against the receiver strategies (Follow or Ignore).

		Signaler Strategy		
		Honest ($q_1 = q_2 = 1$) (H)	Dishonesty (q_1 = (—), q_2 = 1) (D)	No Signal (N)
Receiver Strategy	Follow (F)	$S_{H,F} = p$ $R_{F,H} = 1$	$S_{D,F}$ = — — $R_{F,D}$ = — -	$S_{N,F} = (1-p)y$ $R_{F,N} = p$
	Ignore (I)	$S_{H,I}$ = $R_{I,H} = p$	$S_{D,I}$ = — — $R_{I,D} = p$	$S_{N,I} = (1-p)y$ $R_{I,N} = p$

Table 1.5B

Signaler payoffs for each strategy, Honesty, Dishonesty and No Signal when played against the receiver strategies (Follow or Ignore).

		Signaler Strategy		
		Honest ($q_1 = q_2 = 1$) (H)	Dishonesty ($q_1 = 1$, $q_2 = 0$) (D)	No Signal (N)
Receiver Strategy	Follow (F)	$S_{H,F} = p$ $R_{F,H} = 1$	$S_{D,F}$ = $R_{F,D} = p$	$S_{N,F} = (1-p)y$ $R_{F,N} = p$
	Ignore (I)	$S_{H,I}$ = $R_{I,H} = p$	$S_{D,I}$ = $R_{I,D} = p$	$S_{N,I} = (1-p)y$ $R_{I,N} = p$

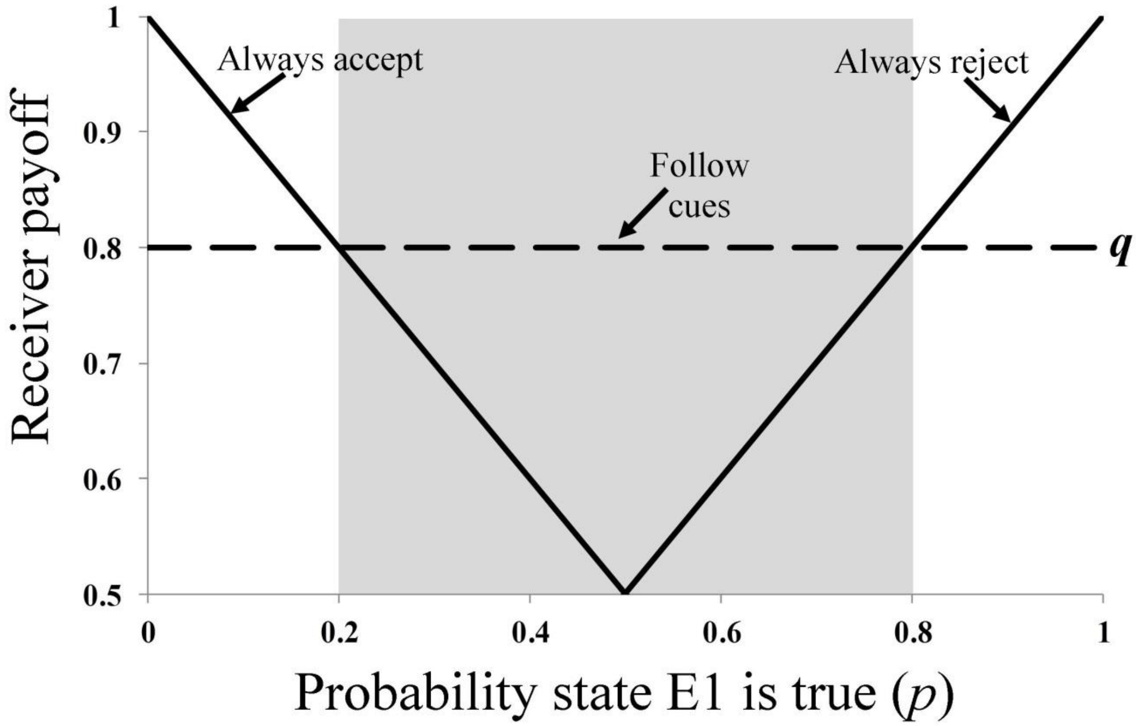

Figure 1.1: Payoffs for the receiver for choosing the single best action (solid lines) versus payoffs for following cues (dashed line). Following cues is best in the shaded region, when (1-p) < q < p. Adapted from McLinn and Stephens (2006).

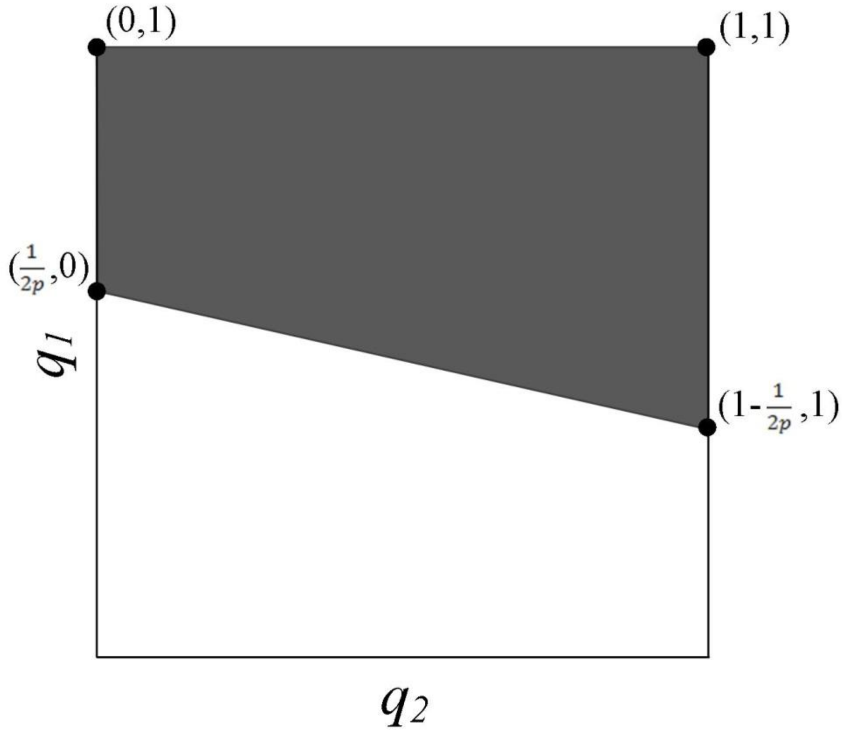

Figure 1.2: An example of the constraints on q_1 and q_2. The shaded region shows the allowable strategy sets (q_1, q_2) where ≥ 0.5. From linear programming (or linear optimization), we know the highest signaler payoff will occur at one of the four vertices of the shaded region.

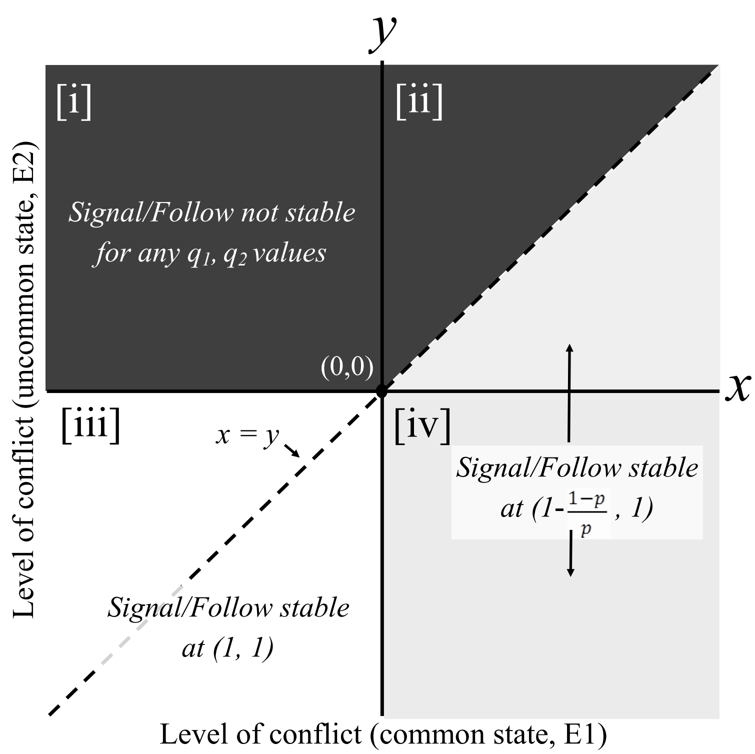

Figure 1.3: The values x and y measure the conflict of interest between signaler and receiver, both individuals agree on the best receiver action when these variables take values less than zero (agree in the common state if $x < 0$, agree in the uncommon state if $y < 0$). We subdivided the graph into four quadrants. [i] Signaler and receiver disagree only in the uncommon state, [ii] signaler and receiver interests always conflict; [iii] signaler and receiver interests never in conflict; and [iv] signaler and receiver disagree only in the common state. Shading indicates whether q_1,q_2 conditions exist where $S_{S,F} > S_{S,F}$ and $R_{F,S} > S_{I,S}$; where dark gray indicates no such conditions exist. Text labels and cross-hatching indicate the signaler strategy set, in the form (q_1,q_2), where Signal/Follow is stable and signalers earn the highest payoff within the range 1 ≥ ≥ p. The reliability set – is best in the cross-hatched region, and no cross-hatching

indicates (1,1) is best (not necessarily stable equilibria with respect to all other q_1,q_2 strategy sets).

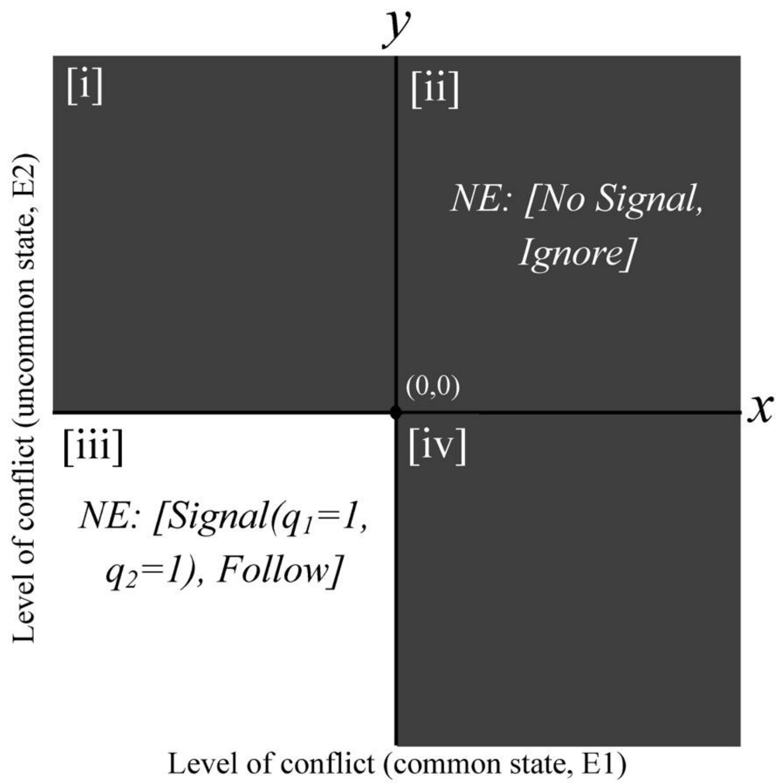

Figure 1.4: The values x and y measure the conflict of interest between signaler and receiver, both individuals agree on the best receiver action when these variables take values less than zero (agree in the common state if $x < 0$, agree in the uncommon state if $y < 0$). The Signal/Follow equilibrium is only stable in region [iii], where individuals agree on the best receiver action in both environmental states. In regions [ii] and [iv], Signal/Follow is not a stable equilibrium even though some Signal strategy sets (q_1,q_2) benefit both individuals compared to equilibria with the No Signal and/or Ignore strategy (see Figure 3).

Chapter 2: Receiver tolerance for imperfect signal reliability: results from experimental signaling games[2]

Abstract

This paper presents an alternative approach to studying signaler-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 signaling games with blue jay subjects (*Cyanocitta cristata*) to demonstrate whether uncertain environments generate receiver tolerance for imperfect reliability. Many models of signaling 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 signalers exploit receiver tolerance by signaling dishonestly. The results show that receivers are more likely to heed signals when environments are uncertain. Moreover, signalers are sensitive to this receiver tolerance and, when signalers and receivers have opposing material interests, low environmental certainty promoted dishonest signaling and high certainty restricted it. Our results highlight the usefulness of an approach emphasizing receiver tolerance and demonstrate the critical importance of environmental certainty for signaler-receiver interactions.

---

[2] This chapter is published as: Polnaszek, T. J. & Stephens, D.W. (2014) Receiver tolerance for imperfect signal reliability: results from experimental signaling games. Animal Behaviour, 98 (1-8).

Introduction

The literature of animal communication emphasizes signal reliability. Reliability is thought to present a problem, since signalers can often gain from dishonesty, but reducing reliability should destabilize signaler-receiver interactions. Maynard Smith and Harper (2003) 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, 2014b; Reby & McComb, 2003; Searcy & Nowicki, 2005; A. Zahavi, 1975). The "problem of reliability" arises because if a signaler 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 signaler 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 signaler-receiver interactions (i.e., the consequences). To frame these experiments, we develop 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 perfectly reliable signal has a q=1.0 (it correlates with the correct action perfectly). Suppose, next that reject is the correct response with probability p (here termed environmental certainty). If p=1.0, the environment is certain and reject is always the correct action; if p=0.5 the environment is uncertain and the correct action is a 50/50 gamble. Thus as the parameter p varies from 0.5 to 1.0 it measures the receiver's certainty about the environment. When p=0.5, the receiver is completely uncertain about how to act and when p=1.0 receivers can be certain 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 from even 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 behavior, McLinn & Stephens 2006). For example, when p=0.5, following a perfectly reliable signal (q=1.0) 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, receivers should only follow extremely reliable signals when environmental certainty is high. Therefore, the certainty of the environment should constrain the set of strategies available to signalers, 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 appendix).

In natural signaling problems, certainty refers to receiver's prior information about behaviorally relevant states. If, for example, 90% of males are high quality, then female receivers can be relatively confident about the quality of a particular signaling 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 signaling 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 (Shannon, 1948) to measure uncertainty.

Signalers should use receiver tolerance as an opportunity to influence receivers to make decisions that benefit themselves; this means signaling reliably when signaler and receiver agree on the best outcome, but decreasing reliability when conflict exists. The ability of signalers to flexibly capitalize on receiver tolerance depends on the assumption that signalers are sensitive to their influence over receivers. Our first experiment tests this assumption by showing the extent to which signalers exploit a unilaterally tolerant receiver (i.e., one that always follows signals). We expect signalers to change their signaling 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 signalers to signal dishonestly and exploit this tolerance. We expect the level of environmental certainty to modify receiver tolerance, and thus change whether signalers can signal dishonestly without causing the receiver to ignore signals.

This set of two experiments placed pairs of captive blue jays in adjacent operant chambers (Fig. 2), where they played a signal-response game. The signaler used positional signals to indicate to the receiver which of two perches was rewarded with food. Using this design, we explored signaling 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 signalers 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 signalers' 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, 2011; Wiley, 1994). As such, we use the following definitions to identify signaler actions as honest or dishonest (though other definitions exist, we follow Searcy & Nowicki 2005; Polnaszek & Stephens 2014). First, the receiver must have a history of responding to signal S with action A. The action of a signaler 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 signaler, 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 signaling 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 h light / 12 h dark light-cycle and provided water *ad libitum*. We tested the subjects in a closed economy, meaning all food was earned during the experiment. However, we provided supplemental food to any subjects that earned less than 7 grams 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 signaling arena (Fig 2). The subjects in adjacent boxes formed a signaler/receiver dyad. During the experiment, two transparent partitions between the boxes allowed the signaler 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 signaler had a private light cue that indicated which side the receiver should hop to for a reward.

Experiment 1: The consequences – Do signalers exploit receiver tolerance?

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

Experiment 1: Methods

The design of the experiment was a 2 x 2 factorial, where we tested two levels of shared incentives between individuals (*Aligned* or *Opposed*) and two types of receiver strategy (*Follow* or *Ignore* signaled information). We controlled the incentives of the signaler by creating situations where the signaler 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 signaler'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 behavior, we trained receivers to exclusively follow experimenter provided cues (i.e., lights only visible to the receiver). In the *Receiver Follow* treatment, we directed the receiver to always choose the signaled side. We directed the receiver to choose the left or right side randomly (i.e., no correlation to the signaled side) in the *Receiver Ignore* treatment. In this situation we predict that signaler behavior will be determined by an interaction between receiver behavior (follow vs. ignore) and the underlying economic incentives. Incentives should not affect signaler behavior when the receiver ignores the signaler, but when the receiver blindly follows signaler actions we expect that signalers will exploit this by matching the true state when incentives are aligned and by choosing the opposite of the true state (non-matching) 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 signaler, 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 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 signaler and receiver actions (signaler forced to left, right, or center perch; receiver left or right) paired with each state (left or right 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 inter-trial interval (ITI) of 120 seconds, 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 signaler's box, indicating whether left or right was the 'true' side on a given trial. The signaler 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 signaler 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 receiver appeared to ignore the signaler's actions. In the 'follow' treatment, the computer switched on the light adjacent to the signaler's choice so the receiver appeared to be following the signaler's actions. We only activated the perch that the computer indicated the receiver to use, such that receivers could only progress through the trial if they followed their private light cue. Neither the signaler nor receiver were allowed to change their perches after they made their initial choices. To achieve this, the computer was programmed to 'abort a trial' (meaning no food is 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 very rare.

When the signaler chose a signaling perch in front of the transparent partitions, its payoff depended on which perch the computer program chose for the receiver to use; the signaler either received three 20 mg food pellets or zero pellets (Table 1). If the signaler chose the center, non-signal 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 minutes.

Forced trials

During forced trials, the signaler was forced in its choice of perch by deactivating all other perches. For example, on a forced signaler-left trial only the left perch allowed the signaler to proceed through the trial. The pair of birds completed every combination of perch choices (signaler – left, right or center; 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 signaler accurately matched the true state. A value of 1.0 means that a signaler always matched the true state, and a value of 0.0 that a signaler consistently indicated the opposite of the true state. To exploit receivers that follow signals, we expect signalers to match the true state when incentives align and mismatch the true state when incentives oppose.

Experiment 1: Results

Repeated measures ANOVA showed a significant Receiver Strategy x Incentives interaction effect on the proportion of state matching by signalers ($F_{1,3}=35.049$, $p=.0096$). When receivers ignored signals (choosing perches randomly), the signalers signaled randomly (Fig 3). In this case, there was no difference in signaler behavior regardless of whether incentives were opposed or aligned (Tukey HSD, p = 0.8876). In the ‘follow’ treatment, signalers 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.

Discussion in Brief

The results demonstrate that signalers adjusted reliability based on the economic payoffs and these two extreme cases of receiver behavior. Specifically, signalers 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 expect that the degree of signal following exhibited by freely acting receivers will likely fall between these two extremes of programmed behavior in Experiment 1. Experiment 2 tests freely acting signalers and receivers in a similar signaling game, demonstrating whether signaling 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 signalers exploit low certainty in the environment by decreasing reliability as certainty decreases. Our model (see appendix) 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 signalers should capitalize on greater receiver uncertainty through dishonest signaling, 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 signaler should always signal honestly – provided the receiver is following signaled information.

Experiment 2: Methods

The second experiment used the basic two box signaler-receiver design outlined in Experiment 1. During a trial, the signaler viewed a private light cue indicating the current state. The signaler 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 signaling game there are two possible states of the environment, labeled as 'true' or 'false'. The receiver also has two possible actions, labeled 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 different treatment variables: environmental certainty and shared incentives between signaler and receiver. We used food rewards to create treatment conditions of mutual benefit (signaler-receiver incentives 'aligned') or conditions of conflict (incentives 'partially opposed'). The signaler 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 1.0, 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.

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 3 probe trials. We randomly interspersed probe trials between the free trials. During free trials, signaler and receiver acted freely, but probe trials consisted of a forced signaler action (signal p state, 1-p state, or no signal) paired with a free receiver choice. We forced the required signaler action by inactivating all other perches during a probe trial. We used probe trials to measure the contingency between signaler action and receiver action – in other words, the degree to which receivers followed signals. If signalers 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 signaler and receiver actions (signaler forced to left, right, or center perch; receiver left or right) in each of two states (state ‘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. All birds 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 3 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* section from Experiment 1). For a brief summary: after an 120 s inter-trial interval, a state light indicates the current state of the environment to the signaler, the signaler chooses an action and the receiver responds. As with Experiment 1, after the signaler 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

In order to measure honesty, we first calculated the consistency with which the signaler's perch choice matched the true state, *p(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(match state)* – 0.5)| + 0.5). An absolute value is necessary because, unlike Experiment 1, there were two possible signaling conventions that depend on the historical responses of receivers. If the receiver typically matched the signaler'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 signaler could send an honest 'do not visit this side' signal. In this second case, honest signaler behavior results in a proportion match of 0.0. Our methods did not allow us to exclude either of these signaling conventions and subjects used both (that is, some receivers consistently matched the signaler's position and others consistently avoided it). The measure we used allowed for either convention subject pairs used, essentially measuring the distance from random (*p(match state)* = 0.5). Adding 0.5 simply changes the range of possible *q* values; from $0.0 \leq q \leq 0.5$ to a more intuitive $0.5 \leq q \leq 1.0$, where 0.5 is random and 1.0 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 can 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(signal follow)* = |*p(match signal)* – 0.5)| + 0.5). As with the honesty measure, this allowed for either signaling convention; the receiver could 'follow' the signal by consistently matching or avoiding the position of the signaler. The signal following measure ranges from 0.5 to 1.0, where values of 1.0 indicate the receiver either consistently matched or consistently avoided the signaler's position. There were no qualitative differences in examining receiver following behavior with data from probe or free trials. Further, 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.

Experiment 2: Results

Signaler Strategy - Results

Repeated Measures ANOVA reveals three significant effects on signaler honesty (q). First, there is a significant incentives x certainty interaction ($F_{2,14}=3.756$, $p=.049$). There are also significant main effects of incentives ($F_{1,7}=17.162$, $p=.004$) and certainty ($F_{2,14}=11.265$, $p=.001$) on signaler strategy. Overall, signalers signaled less honestly when incentives were opposed. The largest difference in signaler honesty between the two incentives treatments occurred when the environment was unpredictable (i.e., p = 0.5, Fig. 4). When p = 1.0 the environment was completely predictable and there was no qualitative difference in signaler honesty.

Signaler Strategy – Discussion in brief

First, higher certainty in the environment influenced signalers to be more honest. In other words, the data show that when receivers are more certain of the best action it helps prevent dishonesty even when there is an economic imperative for the signaler to cheat. Second, signalers showed high levels of fixity in perch choice (e.g. always choose left) in the completely predictable environment. However, based on probe and free trial data, receivers chose independently of signaler action in these treatments – even though signalers 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. Signalers exploit this by dramatically decreasing honesty when incentives oppose. To demonstrate receiver tolerance, and that this dishonesty is successful (that is, receivers still follow signals), we next examine receiver behavior.

Receiver Strategy - Results

Repeated Measures ANOVA showed a significant effect of environmental certainty (*p*) on signal following ($F_{2,14}=10.140$, $p=.0019$). Signal following decreased as certainty in the environment increased (Figure 5). We found no significant direct effect of incentives, or interaction effect between certainty and incentives.

Receiver strategy – Discussion in Brief

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 but 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 signalers signaled 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 percent more food per day in this condition than a ‘signal-ignoring’ receiver.

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 signaler-receiver interactions. We tested how signalers respond to receiver tolerance and what role environmental certainty plays in shaping signaler and receiver strategy. The results show that signalers capitalize on receiver tolerance by signaling honestly when their incentives align with receivers, and dishonestly when incentives do not align. We know signalers change signaling behavior 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, signalers exploited the receiver tolerance caused by an unpredictable environment.

Results in context

Environmental certainty and receiver uncertainty in context

A key result here is that environmental certainty determines how reliable signalers must be to influence receiver behavior. This is a significant claim since models of honest signaling 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 be more likely to accept the lie "I am a high quality male" then if high and low quality males are equally 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 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 signaling 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 signalers (as in Johnstone & Grafen 1993) or individual signalers playing a mixed strategy (see Huttegger & Zollman, 2010; Zollman et al., 2013 for more on the importance of mixed strategies). In the experiment described here, the $q > p$ condition applies over the short time scales 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 time scales (Dunlap & Stephens 2009).

Receiver tolerance in context

Focusing on receiver tolerance for imperfect reliability complements research on signal reliability. The basic question of a receiver tolerance-centered research program is why receivers follow signals despite imperfect reliability. Two different 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 et al., 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 et al., 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 signalers 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 signaler-receiver interactions seem far removed from natural signaling systems. The signaler and receiver behaviors involved here are artificial, but we remark that the experimental signaling game does capture the essential pieces of signaling (a state of interest, a signaling action and a response action – see Bradbury & Vehrencamp 2011). Moreover, this experimental signaling game allows direct control over critical variables which 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 signaling is a diverse topic, such that no approach is sufficient by itself.

A critic may also point out that animal signaling research often focuses on traits or strategies that are subject to selection on an evolutionary timescale, yet here we study signaler and receiver strategies based on learned behavior. Differences between these two cases may offer an interesting contrast to study, but there is no reason to exclude learned behavior from discussions on animal signaling. In general, we know learning and experience play large roles in signaler-receiver interactions (sexual imprinting, mate-choice copying, song development, etc.). Moreover, behavioral 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 signaling is but one example. Our signaling games, especially in concert with more traditional approaches, should lead to new insights on the important themes of environment certainty, receiver tolerance for imperfect reliability, and signaler exploitation of this receiver tolerance.

Conclusions

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

	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

Table 2.1: Payoff for the signaler for the two incentives treatments (α = aligned, ω = opposed). In the aligned treatment, signalers are rewarded when receivers match their action to the current state (accepting when true, rejecting when false). Signalers are rewarded when receivers mismatch action and state in the incentives opposed treatment.

	Receiver Follows	Receiver Ignores
Incentives Aligned	Always match state (*q*=1.0)	Random signaling (*q*=0.5)
Incentives Opposed	Always mismatch state (*q*=0.0)	Random signaling (*q*=0.5)

Table 2.2: Predicted signaler behavior for each level of ‘Incentives’ and ‘Receiver strategy’. When receivers ignore, signalers cannot influence receiver behavior, and should signal randomly. If receivers follow, reliability should depend on the incentives – either extreme state matching or state mismatching.

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

Table 2.3: Payoff for the signaler in the two incentives treatments (α = aligned, ω = opposed). Signalers always prefer receivers to choose the 'accept' perch in the opposed treatment. In the aligned treatment, signalers and receivers benefit when receiver actions correctly match the state (accept when true, reject when false).

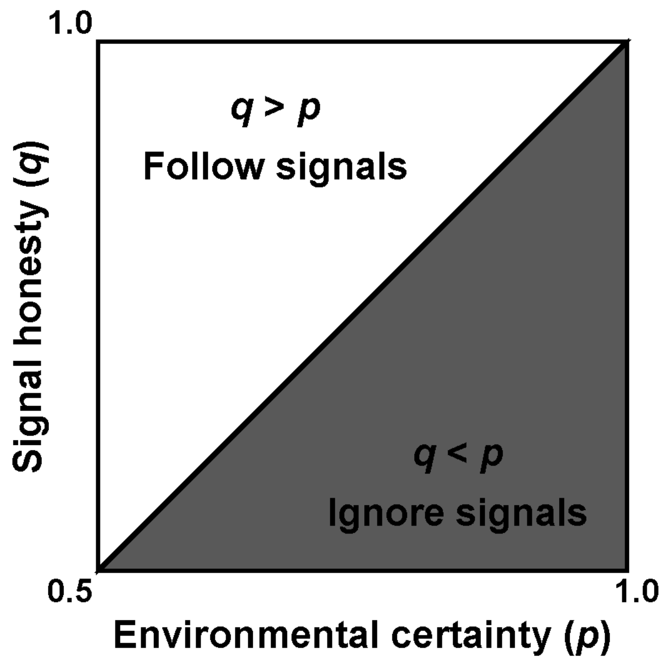

Figure 2.1: Environmental certainty is on the x-axis, signal reliability on the y-axis. Receivers should only follow signals when $q > p$. There is more signal-following space (indicated by the white area) in uncertain environments (when p is near 0.5). Almost no signal-following space exists in certain environments (when p is near 1.0).

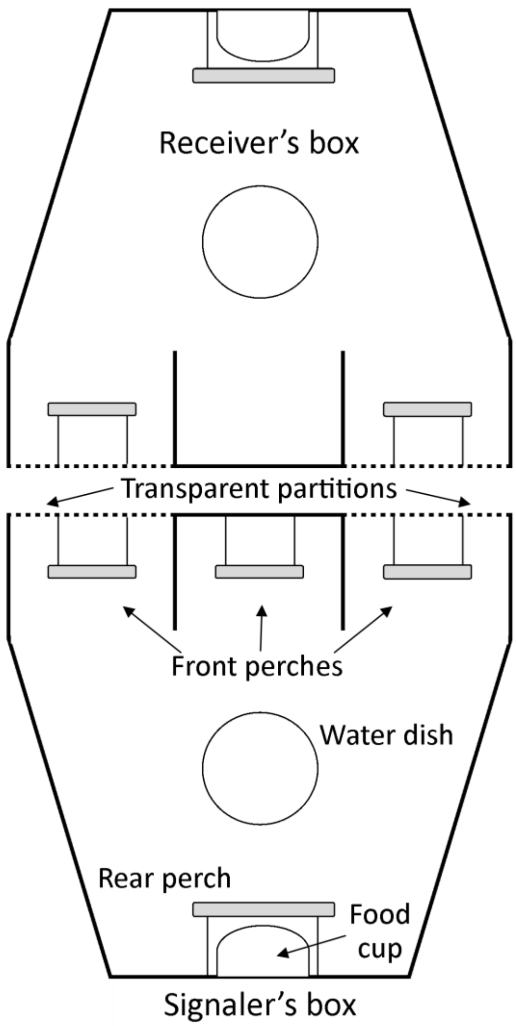

Figure 2.2: Overhead view of apparatus. Signaler provides positional cues by visiting the perches in front of transparent partitions (left and right), or can 'opt out' of signaling by visiting its middle front perch. After signaler action, receivers hop from their rear perch to one of two front perches.

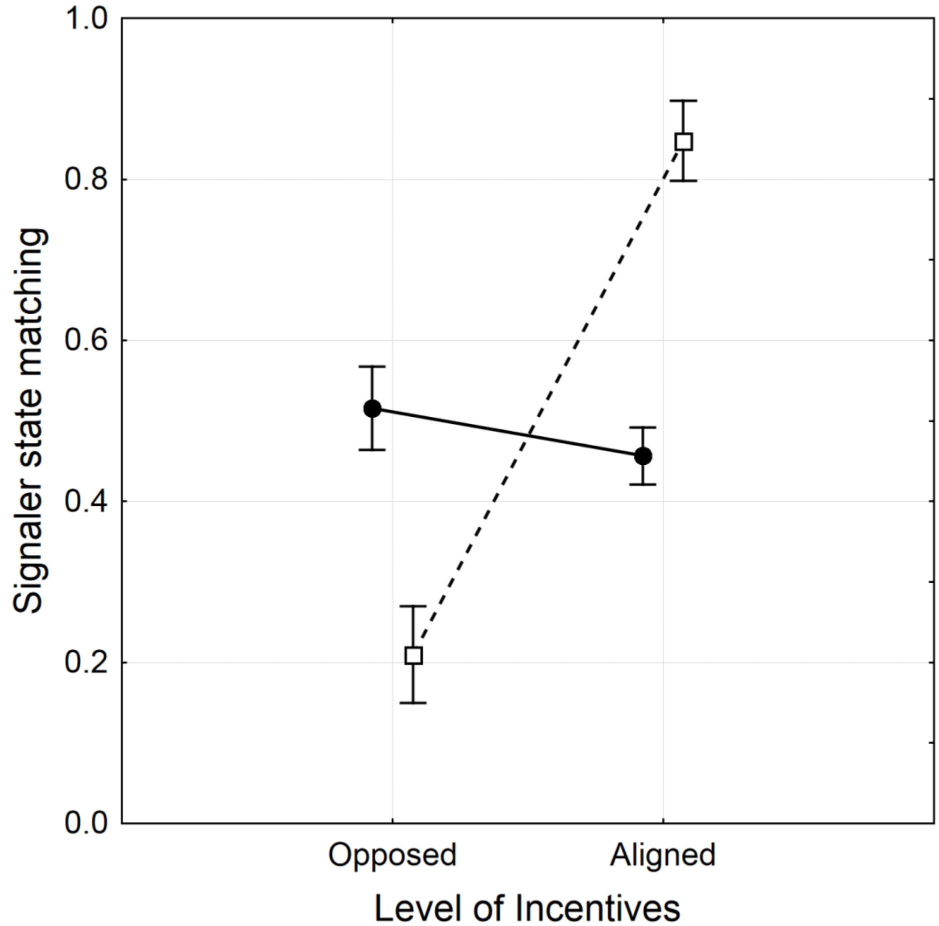

Figure 2.3: Relative frequency of state matching (Mean ± SE) for different levels of incentives (x-axis) and receiver strategy. Solid line shows signaling behavior when receivers ignored signals (choice determined randomly by computer), the dashed line represents when receivers followed signals –that is, they matched signaler position.

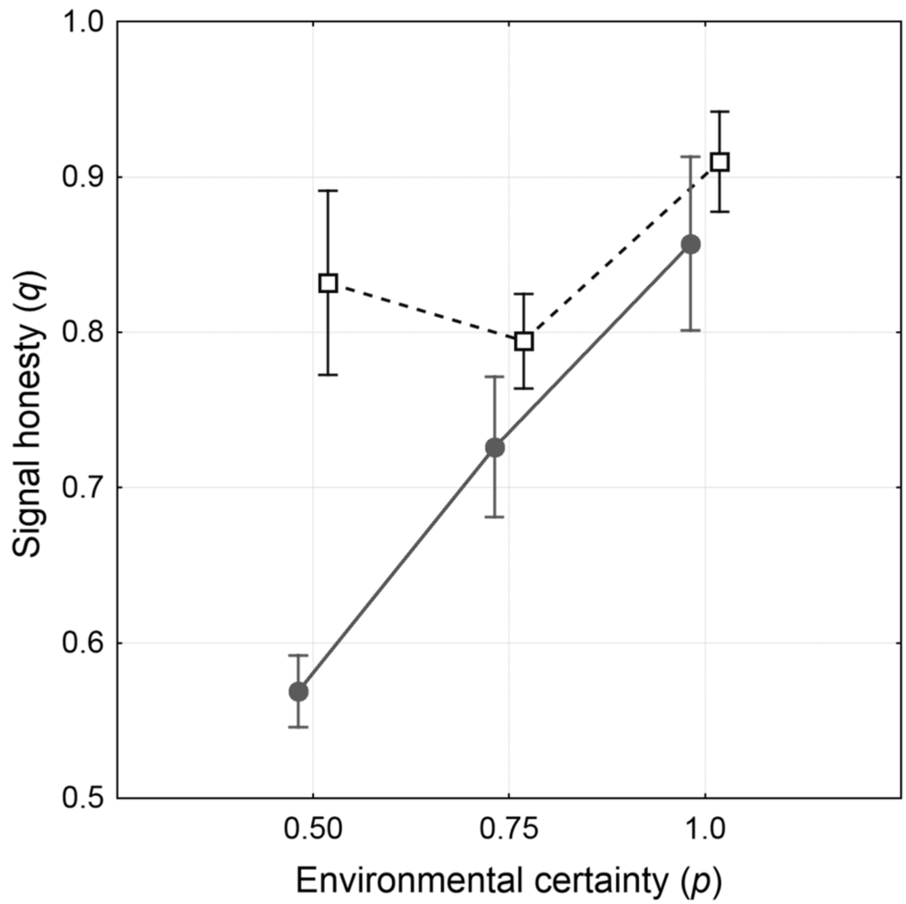

Figure 2.4: Observed signaler honesty for Experiment 2 (Mean ± SE). Level of environmental certainty is on the x-axis, and signal reliability on the y-axis. Solid line indicates reliability when incentives were opposed, and the dashed line when incentives aligned. Notice that the data points from the aligned and opposed treatments are slightly offset horizontally to facilitate visual comparisons.

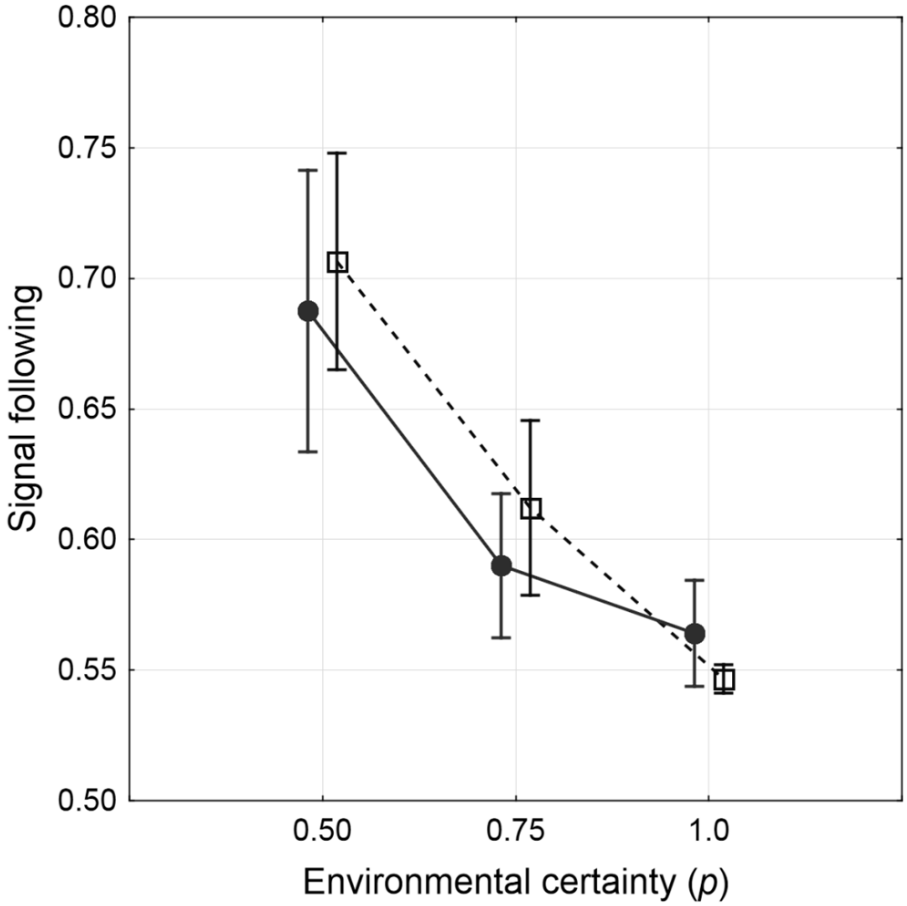

Figure 2.5: Frequency of receiver following (probe trials, Mean ± SE) for different levels of incentives (Aligned or Opposed) and levels of environmental certainty (p, on the x-axis). Solid line indicates signal following when incentives were opposed, and the dashed line when incentives aligned. Notice that the data points from the aligned and opposed treatments are slightly offset horizontally to facilitate visual comparisons.

Chapter 3: Why not lie? Costs enforce honesty in an experimental signaling game[3]

Abstract

Communication depends on reliability. Yet, the existence of stable honest signaling presents an evolutionary puzzle. Why should animals signal honestly in the face of a conflict of interest? While students of animal signaling have offered several theoretical answers to this puzzle, the mostly widely studied model, commonly called the 'handicap principle', postulates that the costs of signals stabilize honesty. This model is the motivating force behind an enormous research enterprise that explores signal costs – whether they are physiological, immunological, neural, developmental or caloric. While there can be no question that many signals are costly, we lack definitive experimental evidence demonstrating that costs stabilize honesty. This study presents a laboratory signaling game using blue jays (*Cyanocitta cristata*) that provides the first experimental evidence showing honesty persists when costs are high, and disappears when costs are low.

[3] This chapter is published as: Polnaszek, T. J. & Stephens, D.W. (2014) Why not lie? Costs enforce honesty in an experimental signaling game. Proceedings of the Royal Society B: Biological Sciences, 281(1774).

Introduction

Honesty and the Handicap principle

Why are signalers honest even though lying often produces higher benefits? The problem of honest (and dishonest) communication is important for many disciplines. In economics, for example, understanding the conditions in which we can expect agents to exchange honest information represents a fundamental problem in the analysis of markets (e.g., Spence, 1973). One could, moreover, make similar statements about nearly any field in the social and behavioral sciences including anthropology, behavioral ecology, cognitive science, linguistics, political science, psychology, sociology, and others. Although other models of honest signaling exist (reviewed in Számadó, 2011), Zahavi's handicap principle (A. Zahavi, 1975; A Zahavi, 1977) holds a central position in explaining the evolution of honest signaling. Handicap signals are generally defined as signals whose reliability "is maintained by signal production costs" (Bradbury & Vehrencamp, 2011). The handicap principle's focus on signal costs has produced a diverse and energetic research program that explores the mechanisms and nature of signal costs. This research program has considered many forms of signaling (e.g., mate choice (Rufus A. Johnstone, 1995), predator deterrence (Vega-Redondo & Hasson, 1993), and even the practice of religion (Bird & Smith, 2005), and many ways in which signals can be costly including the developmental costs of pigments (Huggins, Navara, Mendonça, & Hill, 2010), oxidative stress (Noguera, Morales, Pérez, & Velando, 2010), reduced immunocompetence (Moreno-Rueda, 2010), and heightened risk of predation (Ibáñez-Álamo, Arco, & Soler, 2012).

History & Criticisms

Notwithstanding the enormous efforts devoted to the study of signal costs, the absence of definitive experimental evidence of the role of costs in stabilizing honesty has made this an increasingly contentious research program (see Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005 for detailed historical overviews). Critics of the handicap principle have questioned the basic approach, often emphasizing the value of alternative ways to maintain honesty (summarized in (Számadó, 2011)). Some authors advance the claim that studies of costly signaling have simply measured the wrong costs (Getty, 2006; Grose, 2011; Lachmann et al., 2001). Other critics even question the value of demonstrating that signals have costs (see (Grose, 2011; Számadó, 2011)), since the mere existence of signal costs is necessary but far from sufficient to substantiate their role in the maintenance of honesty (Lachmann et al., 2001). Overall, critics offer a varied list of complaints about the literature on signal cost and cumulatively they underscore the urgency of the need for innovative and rigorous new approaches to test the claims of handicap models (Kotiaho, 2001; Moreno-Rueda, 2007; Roberts, Buchanan, & Evans, 2004) – models whose current influence clearly outweighs their own empirical support (Enquist et al., 2010; Grose, 2011; Rufus A. Johnstone, 1997).

In the face of these critiques, direct experimental evidence on the role of costs in maintaining honesty seems critically important. Evidence demonstrating the link between cost and honesty would narrow the gap between theory and empirical research. Yet, this represents a challenging experimental problem for at least two reasons. First, it is difficult to meaningfully manipulate the costs of natural signals like colorful tails or stridulation. Second, it can be difficult to characterize natural signals as honest or dishonest because we are seldom certain of the underlying states that animals signal about (Kokko, Brooks, Jennions, & Morley, 2003; Lotem, 1993).

This paper presents a direct experimental test of the role of costs in stabilizing honesty using a laboratory simulation of signaling that solves these problems. As a first step, we develop a simple model of ‘handicap signaling.’ Here we consider ‘handicaps’ in the general sense, where a handicap is any signal whose reliability is ensured by costs that exceed the minimal costs necessary to make the signal (Maynard Smith & Harper, 2003). Our model is a variant of Maynard Smith’s Sir Philip Sidney game (Maynard Smith, 1991), modified to suit our experimental situation.

Model and predictions

We imagine that some aspect of the environment exists in two possible *states* that we call “true” and “false.” We assume that the state is true with probability p, and we restrict our attention to the case where $0.5 \leq p < 1$. For any given play of this game, the signaler knows the state but the receiver does not. The receiver must choose between two alternative *actions* that we call “accept” and “reject.” The receiver does best by matching its action to the state of the environment; specifically, ‘accepting’ is best when the state is true and ‘rejecting’ is best when the state is false (Table 1A). Table 1B shows how the receiver’s actions interact with the state to determine the signaler’s benefits: when the state is true, the accept action is in the best interest of both players. There can be a conflict of interest, however, if the state is false. The receiver always benefits from rejecting a false state, but the signaler's best interests are determined by the parameters *a* and *b*. If $b > a$, we have a mutualism where the signaler's and receiver's incentives are aligned; if, however, $b < a$ we have a case where the incentives of the two individuals are opposed (such that the signaler benefits if the receiver 'accepts,' but rejecting is best for the receiver). Finally, we imagine that the signaler can choose between two actions that we call "signal"--meaning indicate the true state--and "no signal" (which indicates the false state). Note that while the terms used here are convenient, formally these are arbitrary labels for three general types of entities: states (here: true vs. false); receiver actions, (here: accept vs. reject); and possible signals, (here: signal vs. no). Table 1C shows the costs paid by the signaler to emit these two signal types. For simplicity, we assume cost is independent of environmental state. Table 2 shows a simple game matrix derived from these assumptions. We consider two signaler strategies. An honest strategist signals when the state is true and gives no signal when the state is false. A dishonest strategist signals in both true and false states. We also consider two receiver strategies. A follow strategist accepts when a signal is observed, and rejects when no signal is observed. An ignore strategist ignores the signal and adopts the strategy that is best on average, which is to always accept because $p \geq 0.5$. To determine stability of the Honest/Follow equilibrium, we compare the signaler's payoff in the Honest/Follow cell (upper left) to the signaler's payoff in the Dishonest/Follow cell (upper right), and we find that stability requires $c > a-b$. The handicap principle emerges here because honest signaling can only be stable when the cost of *dishonestly* signaling true (c) exceeds the difference $a-b$, which measures the conflict of interest between signaler and receiver. In this case, we can infer the effect of signal cost on honesty directly from the game matrix; we can also derive this condition by applying Grafen's authoritative cost condition (Grafen, 1990, p. 519-520). Following Grafen, our model assumes that costs and benefits accumulate additively; while multiplicative costs and benefits are important for some applications of the handicap principle (Getty, 2006), additive combinations are appropriate for our experimental situation. In general, we expect honesty whenever the costs exceed the benefits of dishonesty, and in our model these are parameterized by *c* and the difference *a-b* respectively.

Experimental approach

We developed a laboratory signaling game that gave us direct control over the theoretically significant variables of our model. Using this approach, we tested our model in a factorial experiment which used four levels of signal cost and two distinct payoff structures: *incentives aligned*, in which signaler and receiver share a common payoff structure, and *incentives opposed*, in which the signaler sometimes benefits when the receiver acts against its own best interests (Table 1). Our model predicts that signalers will signal honestly in the incentives aligned condition regardless of cost, but that signalers will only signal honestly when costs are high in the incentives opposed condition.

Our approach is unconventional in at least two respects. While our discussion will address these issues in detail, they merit some mention here because they represent a fairly drastic departure from typical studies of handicap signaling. First, we have studied the role of costs in the maintenance of honesty in a game involving food reward rather than mate selection. While the handicap principle is most widely applied to sexual signaling, the effects of cost are clearly applicable to honesty in a much broader sense as both Grafen (1990) and Zahavi (1977) pointed out. Second, the game theoretical equilibria studied here are established and maintained by learning rather than fixed genetics. While we cannot know the extent to which our findings apply to other situations, our approach, with its dependence on learning, gives us access to variables that are very difficult to manipulate and even measure in other situations.

Methods

Procedural overview. We tested our model using a procedure in which pairs of blue jays (*Cyanocitta cristata*) assumed the roles of signaler and receiver in an experimental game played for food rewards (see Figure 1 for apparatus and within-trial details). The basic components of our signaling game, as in the model above, are: (i) two possible states of the 'environment' (designated "true" and "false"), (ii) two signal states ("signal" or "no signal"), and (iii) two possible receiver responses ("accept" or "reject"). To create the experimental incentive structures (*aligned* or *opposed*), we manipulated the payoffs (in food pellets) associated with each outcome of the game. We also directly controlled the level of cost, paid in 'shuttle flights' before the signaler can access the signaling option. Finally, we note that the game allows a clear operational definition of honesty (see below), because we can observe situations in which the signaler indicates an action that is not in the receiver's best interest.

Subjects, housing and experimental apparatus

We randomly selected 14 adult blue jays from our colony of individuals. All subjects had previous experience in other experimental signaling games. To minimize effects from previous experience, we grouped subjects into random pairs and randomly assigned roles (as signaler or receiver). During the experiment, we kept each member of the pair in separate but adjacent Skinner boxes. A transparent partition allowed signalers and receivers to interact, such that the signaler could provide a positional signal by hopping in front of the partition (Figure 1). We kept subjects in their Skinner boxes for 23 h / day. The one hour provided time for daily sanitation of boxes, as well as health and weight checks. We kept subjects on a 12 h light / 12 h dark light cycle and provided water *ad libitum*. The experiment maintained signalers and receivers on a closed economy, where each individual earned all its food from playing the signaling game, with a few exceptions. If an individual earned less than 6 g per day, we provided food up to this minimum amount. In addition, we closely monitored the overall health of the subjects, providing appropriate veterinary care as required.

Treatments, trials, and blocks

Table 1 shows the economic consequences associated with all possible combinations of signaler and receiver behavior. Our experimental conditions were factorial combinations of the four levels of signal cost (c in Table 1C; *0, 1, 4,* or *7* shuttle flights required to 'signal'), and two arrangements of incentives (incentives aligned and incentives opposed). These arrangements correspond to values of the variables a and b in Table 1B. In our *incentives aligned* condition $a=0.33$ (1 food pellet) and $b=1.0$ (3 food pellets), while in our *incentives opposed* $a=1.0$ and $b=0.33$.Whereas we cannot quantitatively predict the value of shuttle flights in terms of food pellets, these experimental conditions allowed us to qualitatively test our model and document the effects of increasing signal costs.

We presented forced (i.e., no-choice) and free trials in blocks of 36 trials. Each block started with 4 forced trials, followed by 32 free trials. We scheduled 8 types of forced trials, accounting for each permutation of state, signaler action and receiver response. Since only 4 types of forced trials were sampled per block, we restricted randomization of the appearance of forced trials such that each type occurred once within a set of two blocks of trials. We completely randomized the order of each set of 8 forced trials. We also randomized the current state for each free trial, but restricted such that 16 true and 16 false trials occurred per block.

Within-trial procedures

Free trials

An inter-trial interval (ITI) of 120 s preceded every free trial. After the ITI expired, a light illuminated at the rear of the signaler's box. The signaler moved to the rear perch, away from the shared partition, in order to begin a new trial. One of two red state lights illuminated, indicating the state for the given trial as either true or false. The signaler then could choose to either hop to the 'no signal' perch (on one side, in front of an opaque partition) or pay the cost of signaling. Note, when the cost of signaling was zero, the signaler could immediately choose between the 'no signal' perch and the 'signal' perch (in front of the transparent window into the receiver's box). If signaling was costly, the signaler indicated its choice to pay the cost of signaling by hopping to the cost perch. The trial aborted if the signaler used the signaling perch before paying signal costs. Therefore, to activate the signaling perch, the signaler needed to complete c shuttle flights between the cost perch and the rear perch, (where c = 0, 1, 4 or 7, depending on the current treatment). Each shuttle flight consisted of one circuit between the cost perch and the rear perch. After completing the shuttle flights, an orange LED indicated the signaler could access the signaling perch. Once the signaler either 1) completed paying the signal cost or 2) chose the 'no signal' perch, a light illuminated at the rear of the receiver's box. The receiver then proceeded to the back of the box (away from the signaler and its box) if not already at its rear perch station. Once at the rear perch, orange LEDs above each response perch illuminated and the receiver was free to choose either the 'accept' perch (in front of the window) or the 'reject' perch (in front of the opaque partition). After signaler action and receiver response, both individuals received food pellet rewards, the amount determined by the current treatment, the 'state of the environment' on given trial (true or false), and the receiver response. We manipulated the shared incentives between subjects by changing the pellet payoff for combinations of state and receiver response as shown in Table 1. The free trial aborted if the pair did not complete it within 7 minutes, and the pair repeated the same type of free trial after an ITI of 120 s.

Forced trials

Forced trials proceeded similar to free trials, except signalers and receivers were forced into particular actions and responses. Two possible states (true or false), two signaler actions (signal or no), and two receiver responses (accept or reject) create 8 possible combinations. In order to force a particular action or response, only the required perch was activated (e.g., on a forced accept trial, only hopping onto the accept perch allowed the receiver to progress through the trial). If a forced trial was not completed within 7 minutes, the trial aborted and the subject pair restarted the same type of forced trial. This ensured all subjects experienced each combination of events at least once every 72 trials. Otherwise, the payoffs and timing of events within forced trials were identical to free trials.

Termination criteria

Our experiment tested the stability of honest signals. The rationale for this is that game theoretical models predict the stability, but not necessarily the development of equilibrium states. To achieve these stability tests, we preceded each test condition (that is, each cost by incentive structure combination) with a mutualism treatment (similar to our *incentives aligned* treatment, such that signaler and receiver both obtained food only for correct receiver responses). All birds experienced this pre-treatment condition until subjects completed at least 300 trials and reached a signaling / signal-following equilibrium. We used a signaling criterion of >0.80 reliability of signaler action (i.e., 'signal' when state is true and 'no signal' when false). For signal following, the receiver response needed to match signaler action at a frequency of >0.80. We assessed these criteria at the end of each experiment day, requiring both values for either 1) the entire day or 2) the last 3 blocks of trials (96 free trials total) to exceed the critical value of 0.80. After signalers were consistently honest (matching signal state to environmental state) and receivers were consistently following the signaler's action in this mutualism pre-treatment, we changed the parameters of the signaling game to test the stability of communication in one of the treatment conditions specified in our factorial design. All subject pairs experienced the full set of treatments in a randomized order. Each pair of subjects experienced experimental treatment parameters for 900 free trials, and we used the final 300 in each treatment condition for our statistical analysis. In the results to follow, we first consider the observed behavior of signalers, and then the behavior of receivers.

While we have already defined the honest and dishonest strategists within the context our model and experimental game, we need to recognize specific actions as either honest or dishonest to analyze our data. We adopt, therefore, the following operational definition of honest and dishonest signals. Our definition has two components. First, the receiver must have a history of responding to signal S with action A. If this condition is satisfied, we say that the signaler is acting *dishonestly* if it emits S when action A is in the best interests of the signaler but not in the best interests of the receiver. Similarly, we say that the signaler is acting *honestly* if it emits S when action A is the best interests of the receiver but not in the best interests of the signaler. Notice that this definition can be applied directly and objectively within our experiment. Our mutualism pre-treatment establishes the history of receiver responses, and we recognize economic conflicts of interest because we have control of the payoff structure of the game.

Results

Signaler behavior

Figure 2a illustrates the significant interaction of cost and incentive structure on signaler honesty (Repeated measures ANOVA, $F_{3,18}=14.022, p=.00006$). We observe close to zero dishonesty in the *incentives aligned* treatment. Moreover, changing the cost of signals has virtually no effect of the frequency of dishonest signals when incentives are aligned. The data tell a different story, however, when incentives are opposed. When the costs of signaling are low, signalers are commonly dishonest in the sense that they signal an action that is not in the receiver's best interest. When the costs of signaling increase, we observe a dramatic decrease in the frequency of these dishonest signals.

Receiver behavior

Of course, we also predict that the receiver's behavior should be sensitive to the reliability of the signaler's signals. Receivers respond to the behavior of signalers as we expect, that is they follow signals more closely when they are reliable (Figure 2b; Repeated measures ANOVA, $F_{3,18}=4.9113, p=.0115$). Specifically, receivers dramatically decreased their signal-following behavior in our 'no cost' treatment where signalers often signaled unreliably.

Discussion

Significance of results

Models of handicap signaling (Grafen, 1990; A. Zahavi, 1975) hypothesize that signal costs stabilize honesty. Following accepted standards of scientific inference, experimental manipulation of costs should provide the strongest possible evidence that costs do, indeed, stabilize honest signaling. Our results provide the first experimental evidence of this type. Specifically, our experiment shows that in the presence of an incentive to cheat, subjects signaled honestly when costs were high but signaled dishonestly when costs were low; providing direct experimental support for the handicap principle's most basic causal hypothesis. Yet, our result also illustrates a simple but important limitation of the typical approach to studying handicaps, because costs did not affect signal honesty when signaler and receiver incentives were mutualistically aligned. Models of signaling have been clear about the unimportance of signal cost in mutualisms (e.g., Maynard Smith, 1991), but empirical studies of signal costs often proceed without first confirming that a conflict of interest exists.

In the shorthand of the signaling literature, investigators commonly emphasize the importance of differential costs or state dependent costs in the control of honesty. A reader with this terminology in mind may feel that the cost structure shown in Table 1C does not satisfy the requirements for handicap signaling, because the costs are the same in both the true and false states. It is more accurate to say, however, that handicap signaling requires 'differential marginal' costs, because this phrase captures the comparison of differences implicit in Grafen's cost condition. In our situation, this comparison of differences requires that the difference in payoff between the honest and dishonest strategists in the bad state (the cost of the dishonest strategy in the bad state) must be greater than the same difference in the good state (the cost of the dishonesty strategy in the good state). Recall, however, that a dishonest strategist signals correctly in the good state (because to do otherwise would be against the dishonest individual's best interests). This means that the dishonest and honest strategists behave the same way in the good state, so the difference in their expected payoffs (and hence the state-dependent cost of the dishonest strategy) is zero. The difference in marginal costs required by the handicap principle, therefore, depends on whether the 'cost of dishonesty in the bad state' is greater than zero, which is true when $c > a-b$ (which we can also directly observe from the game matrix, Table 2).

The approach adopted here is different, even radically different, from the traditions of 'costly signaling' research. While we will discuss the possible weaknesses of our approach in the following paragraphs, we remark that our approach also has many advantages. It allows the manipulation of many theoretically important variables and it lends itself to straightforward operational definitions of honesty and dishonesty. Overall, we argue that it offers a valuable new tool in the study of signaling games.

Results in context

Models of handicap signaling have motivated the publication of many studies of signal cost. These papers are diverse and ingenious. They include, for example, efforts to characterize the energetic and predation costs of begging (reviewed in Moreno-Rueda, 2007); and sophisticated studies emphasizing the developmental costs and signal value of carotenoid pigments (Fitze, Tschirren, Gasparini, & Richner, 2007; Hill, 1991; McGraw et al., 2005). There can be no doubt that signals have costs that take many forms (e.g. production costs, developmental costs, receiver-imposed costs) and arise via a wide range of mechanisms (increased predation risk, energetic, immunological, genetic etc.). Yet, we have a growing list of reviews that express their dissatisfaction with the signal cost literature (Grose, 2011; Kilner & Johnstone, 1997; Kotiaho, 2001; Moreno-Rueda, 2007;

Roberts et al., 2004; Searcy & Nowicki, 2005; Számadó, 2011). The litany of complaints includes: (i) the simple existence of signal costs tells us little about signal honesty; (ii) absolute costs of signaling are often small; and (iii) very few papers have measured the difference in marginal costs that is central to all handicap models. These critics unanimously stress the need for new approaches that rigorously make the connection between costs and honesty.

Most reviewers agree, though, that there are several examples that come close to demonstrating the hypothesized effects of cost – such as that of barn swallow tail length (discussed in Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005). Research shows that experimental tail elongations alter survival rates differently for individuals of different quality (inferred from original tail length) (Møller & de Lope, 1994) – which is consistent with the differential marginal costs that handicap models require. Additional evidence demonstrates that elongated tails are costly and that male tail length is related to aspects of male quality (e.g., Møller, 1989, 1994; Møller, de Lope, & Caballero, 1995; Saino & Møller, 1996). Overall, this system provides a substantial body of evidence showing the ways in which this signaling system is consistent with honesty stabilized by cost. However, not all are convinced (e.g., Saunders, 2009), and the evidence falls short of an experimental demonstration that increased costs promote honesty. Our study stands out because we directly control the level of signal cost in our experimental system and it allows clear operational definitions of what constitutes honest and dishonest signals. The approach allows us to address the concerns of some critics and measure honesty at different levels of signal cost.

Limitations and further questions

Does the handicap model apply outside of mate choice? The handicap principle leads two lives. For some investigators, it is 'the handicap model of sexual selection' (Hedrick, 2005; Matyjasiak et al., 1999; e.g., McGraw et al., 2005). This seems natural to some because Zahavi (A. Zahavi, 1975) originally proposed it in this context, because within the field of animal behavior it is most commonly discussed in this context, and most models of handicap signaling (such as Grafen 1990 and Getty 2006) develop this example. For others, it is a more general claim about the forces that stabilize honesty. For example, both Grafen (1990) and Zahavi (1977) took pains to point out the applicability of their ideas to problems beyond mate selection. Clearly, neither Grafen nor Zahavi felt that handicap signaling was limited to sexual advertisement. Similarly, students of handicap signaling have focused on signals that reveal information about the signaler—male quality, ability to escape, or hunger (Caro, 1995; Kilner & Johnstone, 1997; Rivero, Alatalo, Kotiaho, Mappes, & Parri, 2000). Again this is more important historically than conceptually. The claim that a low-quality signaler pays a larger 'marginal cost' to signal helps make the idea of marginal cost more intuitive. As we remarked in the introduction, it is straightforward to show that the conditions required for honesty in our simple experimental game are algebraically identical to a discrete version of Grafen's cost condition, which is widely regarded as the authoritative mathematical statement of the handicap principle. The algebra of the handicap principle does not depend on the example of mate choice signaling or the idea that signals necessarily indicate signaler quality. In general, the hypothesis holds that a dishonest strategist must pay larger marginal costs, but the dishonest individual does not have to be lying about its own abilities, reproductive or otherwise. Moreover, the idea that models and tests of handicap signaling ought to be restricted to special situations seems counter-productive. Surely, behavioral ecologists want to study broadly applicable models, such as the general determinants of honesty, that have relevance to questions in the behavioral sciences that go far beyond mate choice.

Learning? Traditional studies of signaling often emphasize genetically determined traits—like tail length—in natural or semi-natural situations. Readers from this tradition may be uncomfortable with studies of signaling equilibria that depend on relatively arbitrary learned behavior. While this sentiment is understandable, there are several reasons to think that this novel approach can provide useful insights. First, the game theoretical equilibria predicted by models of handicap signaling do not depend on the mechanism underlying their stability: Thorndike's law of effect or natural selection against a 'cheater gene' are equally admissible theoretically. Moreover, learning is a well-documented and well-understood biological mechanism (Domjan, 1998; Kandel, 2000; Thorndike, 1911), and this is surely why Maynard Smith devoted considerable theoretical attention to the role of learning in behavioral equilibrium (1982, chapter 5); reminding us that both 'learning and genetic change may in involved' (p. 77) in the establishment of behavioral equilibria (and see Fawcett, Hamblin, & Giraldeau, 2013; Giraldeau & Dubois, 2008; Morand-Ferron & Giraldeau, 2010). Second, as the quotation of Maynard Smith suggests, it is simply incorrect to think of learning and natural selection as incompatible opponents. Learning, like hormones and sensory receptors, is an evolved feature of animals (see Dunlap & Stephens, 2009). Moreover learning is clearly an important mechanism in animal social interactions including signaling. Finally, several recent reviews (Kilner & Johnstone, 1997; Kotiaho, 2001; Searcy & Nowicki, 2005; Számadó, 2011) have emphasized the difficulties faced by traditional approaches and called for fresh approaches to the study of signals and signal costs. Our studies will provide one new line of evidence that represents such a fresh approach. Our ultimate contribution will depend on how this new line of evidence interacts with and informs more traditional studies.

Final summary

Our results represent the first experimental test of the causal relationship between signal costs and honesty. While recent criticisms have characterized the efforts to connect cost and honesty as misguided or incomplete, our results suggest a position that lies somewhere between the critics and the supporters of the 'signals as costly handicaps' research program. The experimental signaling game defines signal costs and other game parameters, and allows this research to begin addressing the concerns raised by 'signal cost' detractors. Our results support the role of costs in some situations, but they also place the onus on students of signal costs to clearly demonstrate that signaler's and receiver's incentives are indeed opposed. That is, the costliness of signals itself does not imply the role of signal cost in honesty; mutualisms or other mechanisms can also drive honesty. However, as we demonstrate, costs do enforce honesty in some cases. While studies of animal signals probe ever deeper into the physiological and genetic mechanisms that make signals costly or condition dependent, these studies seem increasingly distant from the problem of honesty. Our approach represents an effort to re-connect these studies with the question that motivated them: how and when do costs affect signal reliability?

		state	
		true	false
(A) receiver's pay-offs			
receiver action	accept	1	0
	reject	0	1
(B) signaller's pay-offs			
receiver action	accept	1	*a*
	reject	0	*b*
(C) signalling costs			
signal emitted	signal	*c*	*c*
	no signal	0	0

Table 3.1: Payoff matrices for our experimental game[4].

A. Receiver's payoffs: the receiver always does best by matching its behavior to the state of the environment. The receiver obtains 1 unit of food (3 pellets in the experiment) if it chooses the accept action in the true state, or choosing the reject action in the false state; otherwise it obtains nothing. **B.** Signaler's payoffs: if the state is true, the signaler obtains 1 unit of food (3 pellets) when the *receiver* chooses accept. If the state is false however, the variables a and b determine whether the signaler's incentives are aligned with the receiver's. When $a > b$, the signaler does best when the receiver 'accepts' regardless of which state applies. When $a > b$, therefore, the signaler and receiver incentives are opposed when the state is false. In the reverse situation, when $b > a$, the signaler and receiver incentives are always aligned. In our *incentives aligned* condition $a=0.33$ and $b=1.0$, while in our *incentives opposed* $a=1.0$ and $b=0.33$. **C.** Signaling costs: If the signaler chooses to signal, it must pay a cost (c) determined by the current treatment (where $c = 0, 1, 4$, or 7 perch hops). Models predict stable honest signaling when $(a-b) < c$. In order to make correct comparisons, we assume that the parameters a, b, and c are normalized to the value of a single unit of food.

[4] Chapter 3 tables and figures from Polnaszek & Stephens (2014), reproduced with permission.

Receiver	Signaler: *Honest*	Signaler: *Dishonest*
Follow	1 | $A+b(1-p)$	p | $A+(1-p)(a-c)$
Ignore	p | $A+a(1-p)$	p | $A+(1-p)(a-c)$

Table 3.2: Game matrix based on the model we outlined. Here we assume ($p>0.5$), and set $A=p(1-c)$. The strategies Honest/Follow are stable under two conditions. 1) When $b>a$, this is when signaler and receiver incentives are aligned. 2) When $c > (a-b)$, which means the cost of signaling is greater than the benefit gained from deceiving the receiver.

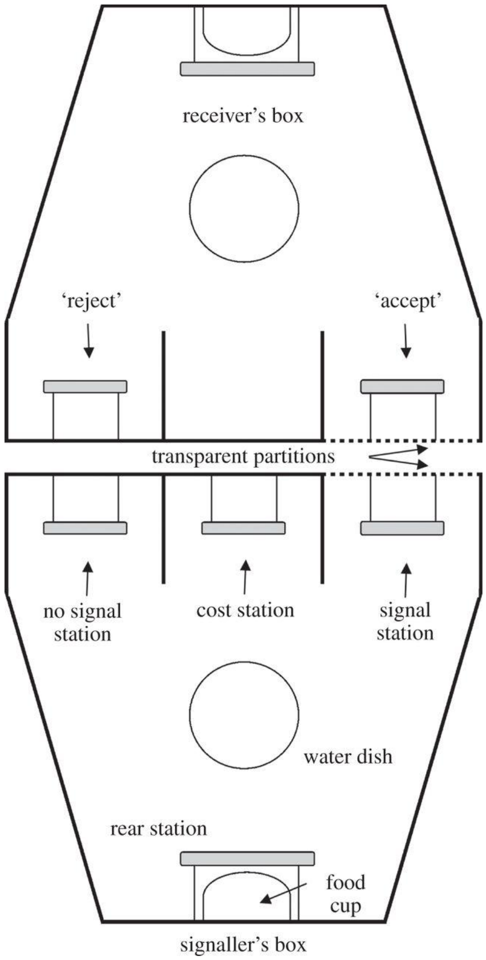

Figure 3.1: Apparatus. Blue jays occupied side-by-side skinner boxes with one jay assigned to the role of signaler and another assigned to the role of receiver. Each box was fitted with two perch stations, which could record subject's presence or absence. The signaler and receiver used these perches to play a signaling game in a sequence of trials during the course of the day. At the beginning of each trial, a computer determined the 'state of environment' to be true or false (see Table 1). The state in a given trial was unknown to the receiver but revealed privately to the signaler via a system of cue lights. Signalers provided positional signals to the receiver by choosing either the 'signal' or 'no signal' perch station. In response, the receiver must choose between one of two stations at the front of its chamber. If the state was true, the receiver could only obtain food by hopping onto the 'accept' perch; and if the state was false the receiver could only obtain food by hopping onto the 'reject' perch (Table 1A). Table 1B shows how the receiver's action determined the payoffs received by the signaler. To implement signal costs, the signaler was required to hop back and forth between the cost and rear stations *c* times (Table 1C). The signaler was always free to choose the 'no signal' station without cost.

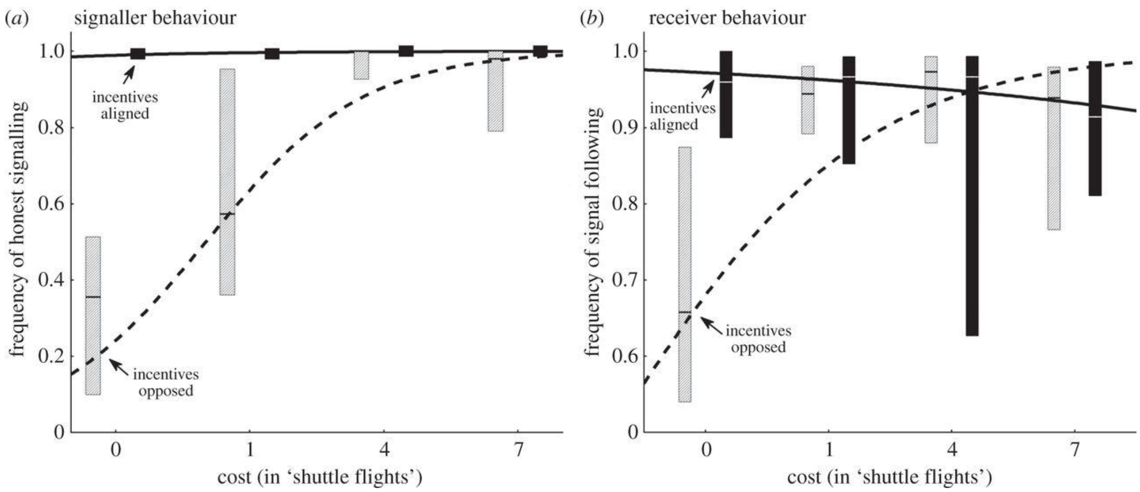

Figure 3.2: The observed level of honest signaling **(A)** and signal following **(B)** for each of 8 different treatments. Box plots summarize the results for each treatment (medians plus or minus upper and lower quartiles), and accompanying curves show the best fitting logistic regressions. **A.** The y-axis shows the relative frequency with which the signaler honestly chose the "no signal" action when "reject" was the receiver's best option. **B.** Identical to panel A except that the y-axis shows the relative frequency with which the receiver followed the signaler's action (e.g., "accept" if "signal"; note, the y-axis scale differs from A). For both panels the x-axis shows the four levels of signal cost (*c= 0, 1, 4 or 7*), measured in 'shuttle flights'. The light-gray boxes and accompanying dashed curve show our *incentives opposed* treatments. The black boxes and accompanying solid curve show our *incentives aligned* treatments.

Chapter 4: Why are signals reliable? Costs enforce honesty, sometimes.[5]

Introduction

The cost-enforced signaling experiment described in Chapter 3 (Polnaszek & Stephens, 2014) is the target of recent criticism (Számadó & Penn, 2015). Szamado and Penn's article raises several important conceptual misconceptions within the literature regarding handicaps and costly signaling, and here we address the issues raised in the critique. Our experiments provide direct experimental evidence that signal costs can stabilize honest signaling, a central claim of handicap literature. Szamado and Penn agree that we have demonstrated the effect of signal cost on honesty, but dispute the relevance of this result to handicap signaling. The handicap signaling literature is a veritable sea of claims and counter-claims. Some of these claims are plausible and well supported while others are simply wild assertions. Our experiment does not test all of these claims, and it was not intended to do so. Yet at several points Szamado and Penn's critique seems to focus on the more extreme assertions of the handicap literature, even though our study does not address or claim to address them. Therefore, this chapter aims to both reinforce our views on several key themes in costly signaling literature, as well as help resolve confusion over important topics and terminology.

[5] This chapter is adapted from: Polnaszek, T. J. & Stephens, D.W. (2015) Why are signals reliable? Costs enforce honesty, sometimes. Animal Behaviour, *in press*.

Costs are not always necessary for honesty

We agree with the emerging consensus in the literature that costs are not universally necessary to stabilize signaling. Our manuscript does not support the idea that all honest communication involves costly signals nor do we imply complete confirmation of the handicap principle as proposed by Zahavi and Zahavi (1999). Many models of signaling, like our template model (the Sir Philip Sidney game – Maynard Smith, 1991) conflict with the idea that honesty can only exist in the presence of handicapping signal costs. The clearest example is mutualism: if there is no incentive to cheat, costs are unnecessary. Our results support this limitation because we found that signal costs did not affect honesty in the mutualism treatments.

The cost of cheating enforces honesty

From a game theoretical perspective, it is the cost of dishonesty, not the signal costs paid by honest 'high quality' individuals, that enforces honesty (here 'high quality' relates to the 'true' condition in our experiment). That is, honest 'high quality' individuals could pay low or no costs, the crucial questions are what does it cost to signal dishonestly and what can dishonest individuals can gain? Theoretical models, in particular those framed as action-response games (e.g., Hurd, 1995), highlight this important distinction. We agree that it is the cost of dishonesty that stabilizes honest signaling, as demonstrated by our 'signal costs' model in Chapter 1. Although we recognize the important distinction between the types of costs and their predicted effects on honesty, our experiment did not test this hypothesis. As a first experiment using our experimental signaling games we chose to test a simpler situation in which the costs paid by honest and dishonest signalers were systematically related. Testing this subtler hypothesis would be a natural next step in this experimental program. Which is to say, we agree with Szamado and Penn that different assumptions regarding the cost structure could, in theory, stabilize honest signaling without a high cost for honest signalers.

While theory continues to reiterate the point that signal costs do not imply cost enforced honesty (or handicaps), this idea is difficult to navigate in practice. As our model in Chapter 1 points out, the observed costs of honesty at equilibrium do not matter (and see Számadó, 1999). Thus, demonstrating the costs of signaling mate quality (e.g., Møller & de Lope, 1994), hunger levels (e.g., Moreno-Rueda, Redondo, Trenzado, Sanz, & Zúñiga, 2012), etc. does not necessarily help us resolve the question 'what makes signals reliable?'. All readers may not agree with our experimental approach in Chapter 3 (e.g., Számadó & Penn, 2015), but most agree that new perspectives and novel approaches are necessary to move forward in the study of 'costly signaling' (Kotiaho, 2001; Moreno-Rueda, 2007).

Continuous vs. discrete signaling games

We realize that the terminology appropriate for discrete models (like our experimental game) differs somewhat from the terminology of continuous models that represent the traditional approach to handicap signaling. These terminological differences are clearly a source of some confusion and disagreement in costly signaling literature (e.g., between Polnaszek & Stephens, 2015; Számadó & Penn, 2015). We remark, however, that while mathematicians recognize some important differences between continuous and a discrete systems (e.g. discrete can become chaotic at lower dimensions than continuous systems) none of these issues are relevant here. The translation from the continuous to discrete case here is straightforward and even pedestrian.

State-dependent differences in marginal costs

A key claim of many handicap models is that the marginal costs of dishonesty must vary between states (e.g., between the True and False states in our game, see Table 1). This is often given in the form: 'low quality signalers must pay greater marginal costs for dishonesty'. Szamado & Penn deliver what is apparently a crushing critique of our experiment on this score when they say: "The costs imposed on the signallers were the same in the two different conditions, and thus, by definition there cannot be any difference in the marginal costs." The reader can easily see Szamado and Penn's point by considering the 'cost table' from our paper (Table 1). The cost structure in the True and False states is the same, and so it would seem that the marginal costs (c-0) are the same. This analysis is subtly, but importantly incorrect, because we are interested in the marginal costs of dishonesty, not the marginal costs of two arbitrary signalling actions. An honest signaller, of course, indicates True when the state is True, and False when the state is False. However, a dishonest signaller always indicates True regardless of state (as clearly stated in our paper); notice that the dishonest signaller does not just signal the opposite of the actual state, because this would mean that it acts against its own best interests in the True state. With this in mind, it's easy to re-write the Table 1 in terms of honesty and dishonesty (Table 2). Clearly, the marginal cost of dishonesty in the True state is zero—because honest and dishonest strategists behave in the same self-interested way in the True state, while the marginal cost of dishonesty in the False state is c, which is clearly greater than zero. It is, therefore, somewhat simplistic to assert that there cannot be a state-dependent difference in marginal costs in our experiment. In connection with this point, Szamado & Penn rely heavily on Hurd's analysis of a two-by-two signalling game (1995) that is somewhat more general than the two-by-two signalling game that we studied experimentally. They claim that these so-called action-response games imply a marginal cost condition that is qualitatively different from the condition proposed by Grafen (1990). This appears to be at variance with Hurd's own analysis of the action-response game. Hurd concludes that support for Grafen's differential marginal cost claim 'follows directly' from his analysis (p. 219).

The (non)-importance of efficacy costs and strategic costs

The intended utility of these two terms is to isolate situations where reliability depends on cost (strategic costs) from those where costs are important in transmitting signals but unrelated to honesty (efficacy costs) (Maynard Smith and Harper, 1995). Thus it seems our costs may fit the spirit of the 'strategic' definition because reliability depended on cost in some experimental treatments. Yet we feel this label is ultimately unimportant, especially because it tends to conflate the important issues at hand. Our experimental signaling system allows us to directly test whether costs are necessary for honesty, negating the utility of separating types of cost.

After chastising us for failing to distinguish between efficacy and strategic costs, Szamado & Penn conclude with the observation that the distinction is misleading and impossible to study in practice. We agree that, in practice, separating efficacy and strategic costs is a futile exercise; especially because observed costs in signaling systems may simultaneously fulfill both definitions from above! So while we understand that this distinction is important to some students of costly signaling (e.g. Maynard Smith & Harper 1995), our paper makes no claim to have demonstrated any such distinction. Moreover, the model that motivated our experiment does not depend on this distinction. Investigators who wish to pursue the distinction more directly will have to design a different experiment, yet the central result of our paper – that experimentally manipulated signal costs stabilize honesty – seems like a good starting point to us.

Signal costs, handicaps and indices

Szamado and Penn assert that the effect of costs on honesty shown in our study cannot be an instance of handicap signaling because our experiment created an instance of 'index signaling.' The idea is that some signals are so tightly correlated with the states they indicate that they are uncheatable, and therefore no further reliability-maintaining mechanisms are required. We cannot agree that our experimental signals served as indices. We can be sure, however, that they were not 'uncheatable,' because our subjects did, in fact, cheat. Subjects sometimes signaled dishonestly in all our treatment conditions, although the relative frequency of this cheating depended on signal cost. Surely, a defining property of index signaling is that it should not depend on signal cost. The central idea of indices is an inescapable correlation between state ('True' or 'False' in our experiment) and signal. The key factor that invalidates the premise of our experimental signals being indices is that in our experiment the correlation between state and signal was entirely under the signaller's control. The jays could freely choose whether to signal or not, and indeed our signallers varied the properties of the state-signal correlation in an orderly and systematic way with experimentally manipulated cost and payoff parameters. The correlation that Szamado and Penn seem to be complaining about is the correlation between cost and emitted signal, which we did control experimentally. It may be more costly to produce a larger tail (a cost-to-signal correlation), but this is only an index if, for example, you are advertising tail length (causing a strict state-to-signal correlation). This does not correspond to the situation modeled in our experiment.

Unobservable costs

Szamado and Penn point out that some versions of the handicap hypothesis require that the receiver perceive the costliness of signals. Our experiment did not explore this claim because the cost-imposing ‘shuttle flights’ took place out of the receiver’s sight. We suspect that making the costs visible to receivers would not change our result, although they only way to know for sure is to conduct the experiment. One could easily design an experiment where signal costs are visible to the receiver, but even then we cannot know what the receiver or the signaler ‘know’ about the signal costs. Thus, centering a model on the idea that receivers must have some direct knowledge or perception of the costs paid seems untenable. We remark however that a program of research that focuses on the perceptions and cognitive representations of signalers and receivers-while potentially fascinating—is fraught with all the practical and philosophical difficulties that characterize the study of non-human cognition. We certainly do not claim to have solved the significant problems such a research program presents.

Moreover, if a signal is kept honest by costs, then it must be ‘perceptibly costly’ in some sense. Let us imagine a system where tail color is a signal of male quality, where high quality males have long tails and low quality males have short tails. Additionally, tail length is costly, such that it does not pay to use the signal dishonestly. If females choose based on tail length they must differentiate between tail lengths. Thus producing a long tail (or any signal linked to cost) is 'perceptibly costly' by definition because it has higher costs and is perceptibly different from a short tail. Females do not need to perceive or assess costs, but rather the fruits of those costs (the signals), which in turn may or may not be linked to cost

Conclusion – What's in a name?

Clearly, conflict over terms and historical baggage related to the handicap principle contributed to the disagreement outlined in these two papers. There are many conflicting definitions of handicap signaling (e.g., Bradbury & Vehrencamp, 2011; Emlen, Warren, Johns, Dworkin, & Lavine, 2012; Hurd & Enquist, 2005; Husak, Henningsen, Vanhooydonck, & Irschick, 2015; Mautz, Møller, & Jennions, 2013; Maynard Smith & Harper, 2003; Ougham, Thomas, & Archetti, 2008; Roulin, 2015; Ruxton & Schaefer, 2011; Ryan & Wilczynski, 2011; Számadó, 2011), and even recommendations to completely retire the term (Getty, 2006). Nevertheless, the term remains firmly entrenched in the literature and we attempted to frame our experiments using this common language from animal signaling.

In the end, exploring the conditions where costs stabilize honesty is more important than the naming of these costs. Our primary goal was to reconnect the costly signaling literature with the questions that motivated the field – why are signals reliable? A clear starting point is to establish a direct causal relationship between signal costs and honesty;

a claim central to costly signaling theory (including the handicap hypothesis). Szamado and Penn agree that our experiment demonstrates that costs stabilize honesty, specifically in conditions of conflict. “If agreement exists on the mechanisms that underlie the enforcement of signal reliability, not too much importance should be given to how the signal is labeled” (Searcy & Nowicki, 2005 pg. 217).

		State	
		True	False
Signal emitted	Signal (Indicate True)	c	c
	No-Signal (Indicate False)	0	0

Table 4.1: The costs of the signaling actions 'signal' vs. 'No-signal' did not differ between the True and False state in our experiment (from Polnaszek & Stephens, 2014).

		State	
		True	False
Strategy	Honest	c	0
	Dishonest	c	c

Table 4.2: This table also shows the cost structure from Polnaszek and Stephens (2014), but illustrates the costs for each strategy (Honest vs. Dishonest). The new visualization of the costs of signaling makes the difference in cost more readily apparent; a dishonest strategist pays a higher cost in the False state.

References

Basolo, A. L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science (New York, N.Y.)*, *250*(4982), 808–810. http://doi.org/10.1126/science.250.4982.808

Bergstrom, C. T., & Lachmann, M. (1998). Signaling among relatives. III. Talk is cheap. *Proceedings of the National Academy of Sciences*, *95*(9), 5100–5105.

Bird, R. B., & Smith, E. A. (2005). Signaling Theory, Strategic Interaction, and Symbolic Capital. *Current Anthropology*, *46*(2), 221–248. http://doi.org/10.1086/427115

Bradbury, J., & Vehrencamp, S. (2000). Economic models of animal communication. *Animal Behaviour*, *59*(2), 259–268. http://doi.org/10.1006/anbe.1999.1330

Bradbury, J., & Vehrencamp, S. L. (2011). *Principles of Animal Communication, Second Edition* (2nd ed.). Sunderland, MA: Sinauer Associates, Inc.

Caro, T. M. (1995). Pursuit-deterrence revisited. *Trends in Ecology & Evolution*, *10*(12), 500–503. http://doi.org/10.1016/S0169-5347(00)89207-1

Dall, S. R. X. (2010). Managing risk: the perils of uncertainty. In D. Westneat & C. Fox (Eds.), *Evolutionary Behavioral Ecology* (pp. 194–206). New York: Oxford University Press.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*(4), 187–193. http://doi.org/10.1016/j.tree.2005.01.010

Dawkins, M. S., & Guilford, T. (1997). Conspicuousness and Diversity in Animal Signals. In D. H. Owings, M. D. Beecher, & N. S. Thompson (Eds.), *Communication* (pp. 55–75). Springer US. Retrieved from http://link.springer.com/chapter/10.1007/978-1-4899-1745-4_3

Domjan, M. (1998). *The Principles of Learning and Behavior* (4th ed.). Belmont, CA: Wadsworth.

Dunlap, A. S., & Stephens, D. W. (2009). Components of change in the evolution of learning and unlearned preference. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3201 –3208. http://doi.org/10.1098/rspb.2009.0602

Dunlap, A. S., & Stephens, D. W. (2014). Experimental evolution of prepared learning. *Proceedings of the National Academy of Sciences*, *111*(32), 11750–11755. http://doi.org/10.1073/pnas.1404176111

Elias, D. O., Maddison, W. P., Peckmezian, C., Girard, M. B., & Mason, A. C. (2012). Orchestrating the score: complex multimodal courtship in the Habronattus coecatus group of Habronattus jumping spiders (Araneae: Salticidae). *Biological Journal of the Linnean Society*, *105*(3), 522–547. http://doi.org/10.1111/j.1095-8312.2011.01817.x

Endler, J. A., & Basolo, A. L. (1998). Sensory ecology, receiver biases and sexual selection. *Trends in Ecology & Evolution*, *13*(10), 415–420. http://doi.org/16/S0169-5347(98)01471-2

Enquist, M., & Arak, A. (1998). Neural representation and the evolution of signal form. In R. Dukas (Ed.), *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making*. University of Chicago Press.

Enquist, M., Arak, A., Ghirlanda, S., & Wachtmeister, C.-A. (2002). Spectacular phenomena and limits to rationality in genetic and cultural evolution. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *357*(1427), 1585–1594. http://doi.org/10.1098/rstb.2002.1067

Enquist, M., Hurd, P. L., & Ghirlanda, S. (2010). Signaling. In D. F. Westneat & C. W. Fox (Eds.), *Evolutionary Behavioral Ecology* (pp. 266–284). New York: Oxford University Press.

Fawcett, T. W., Hamblin, S., & Giraldeau, L.-A. (2013). Exposing the behavioral gambit: the evolution of learning and decision rules. *Behavioral Ecology*, *24*(1), 2–11. http://doi.org/10.1093/beheco/ars085

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*(2), 140–148. http://doi.org/10.1007/s00265-003-0739-4

Fitze, P. S., Tschirren, B., Gasparini, J., & Richner, H. (2007). Carotenoid-Based Plumage Colors and Immune Function: Is There a Trade-Off for Rare Carotenoids? *The American Naturalist*, *169*(S1), S137–S144. http://doi.org/10.1086/510094

Getty, T. (2006). Sexually selected signals are not similar to sports handicaps. *Trends in Ecology & Evolution*, *21*(2), 83–88. http://doi.org/10.1016/j.tree.2005.10.016

Giraldeau, L.-A., & Dubois, F. (2008). Social foraging and the study of exploitative behavior. In *Advances in the Study of Behavior* (Vol. Volume 38, pp. 59–104). Academic Press. Retrieved from http://www.sciencedirect.com/science/article/pii/S0065345408000028

Godfrey-Smith, P., & Martínez, M. (2013). Communication and Common Interest. *PLoS Comput Biol*, *9*(11), e1003282. http://doi.org/10.1371/journal.pcbi.1003282

Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*(4), 517–546. http://doi.org/10.1016/S0022-5193(05)80088-8

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics* (Vol. xiii). New York: Wiley.

Grose, J. (2011). Modelling and the fall and rise of the handicap principle. *Biology and Philosophy*, *26*(5), 677–696. http://doi.org/10.1007/s10539-011-9275-1

Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, *42*(1), 1–14. http://doi.org/10.1016/S0003-3472(05)80600-1

Hackett, S., Schaefer, H. M., & Ruxton, G. D. (2014). Linking signal fidelity and the efficiency costs of communication. *Journal of Evolutionary Biology*, *27*(9), 1797–1810. http://doi.org/10.1111/jeb.12427

Hauser, M. D. (1996). *The Evolution of Communication*. MIT Press.

Hebets, E. A., & Papaj, D. R. (2004). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, *57*(3), 197–214. http://doi.org/10.1007/s00265-004-0865-7

Hedrick, A. (2005). Environmental condition-dependent effects on a heritable, preferred male trait. *Animal Behaviour*, *70*(5), 1121–1124. http://doi.org/10.1016/j.anbehav.2005.02.011

Heinen, V. K., & Stephens, D. W. (in press). Blue jays (Cyanocitta cristata) devalue social information in uncertain environments. *Animal Behaviour*.

Higham, J. P., & Hebets, E. A. (2013). An introduction to multimodal communication. *Behavioral Ecology and Sociobiology*, *67*(9), 1381–1388. http://doi.org/10.1007/s00265-013-1590-x

Hill, G. E. (1991). Plumage coloration is a sexually selected indicator of male quality. *Nature*, *350*(6316), 337–339. http://doi.org/10.1038/350337a0

Huggins, K. A., Navara, K. J., Mendonça, M. T., & Hill, G. E. (2010). Detrimental effects of carotenoid pigments: the dark side of bright coloration. *Naturwissenschaften*, *97*(7), 637–644. http://doi.org/10.1007/s00114-010-0679-6

Hurd, P. L., & Enquist, M. (2005). A strategic taxonomy of biological communication. *Animal Behaviour*, *70*(5), 1155–1170. http://doi.org/16/j.anbehav.2005.02.014

Huttegger, S. M., & Zollman, K. J. S. (2010). Dynamic stability and basins of attraction in the Sir Philip Sidney game. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1689), 1915 –1922. http://doi.org/10.1098/rspb.2009.2105

Ibáñez-Álamo, J., Arco, L., & Soler, M. (2012). Experimental evidence for a predation cost of begging using active nests and real chicks. *Journal of Ornithology*, *153*(3), 801–807. http://doi.org/10.1007/s10336-011-0797-8

Johnstone, R. A. (1995). Sexual Selection, Honest Advertisement and the Handicap Principle: Reviewing the Evidence. *Biological Reviews*, *70*(1), 1–65. http://doi.org/10.1111/j.1469-185X.1995.tb01439.x

Johnstone, R. A. (1996). Multiple Displays in Animal Communication:`Backup Signals' and `Multiple Messages'. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *351*(1337), 329–338. http://doi.org/10.1098/rstb.1996.0026

Johnstone, R. A. (1997). The evolution of animal signals. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural Ecology: An Evolutionary Approach* (4th ed., pp. 155–178). Blackwell, Oxford.

Johnstone, R. A., & Grafen, A. (1993). Dishonesty and the handicap principle. *Animal Behaviour*, *46*, 759–764.

Kandel, E. R. (2000). Cellular mechanisms of learning and the biological basis of individuality. In E. R. Kandel, J. H. Schwartz, & T. M. Jessell (Eds.), *Principles of neural science* (4th ed., pp. 1247–1279). New York: McGraw-Hill.

Kilner, R., & Johnstone, R. A. (1997). Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology & Evolution*, *12*(1), 11–15. http://doi.org/10.1016/S0169-5347(96)10061-6

Kokko, H., Brooks, R., Jennions, M. D., & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1515), 653–664. http://doi.org/10.1098/rspb.2002.2235

Kotiaho, J. S. (2001). Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews*, *76*(3), 365–376. http://doi.org/10.1017/S1464793101005711

Lachmann, M., Szamado, S., & Bergstrom, C. T. (2001). Cost and conflict in animal signals and human language. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(23), 13189–13194. http://doi.org/10.1073/pnas.231216498

Lotem, A. (1993). Secondary sexual ornaments as signals: the handicap approach and three potential problems. *Etologia*, *3*, 209–218.

Matyjasiak, P., Jaboń, P. G., Ski, Olejniczak, I., Boniecki, P. I., & Lee, S.-D. (1999). Foraging Cost of a Long Tail Ornament: An Experiment with Sand Martin Females. *Ethology*, *105*(6), 521–530. http://doi.org/10.1046/j.1439-0310.1999.00422.x

Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press.

Maynard Smith, J. (1991). Honest signalling: the Philip Sidney game. *Animal Behaviour*, *42*(6), 1034–1035. http://doi.org/16/S0003-3472(05)80161-7

Maynard Smith, J., & Harper, D. (2003). *Animal signals*. Oxford University Press.

Maynard Smith, J., & Harper, D. G. C. (1995). Animal Signals: Models and Terminology. *Journal of Theoretical Biology*, *177*(3), 305–311. http://doi.org/10.1006/jtbi.1995.0248

McGraw, K. J., Hill, G. E., & Parker, R. S. (2005). The physiological costs of being colourful: nutritional control of carotenoid utilization in the American goldfinch, Carduelis tristis. *Animal Behaviour*, *69*(3), 653–660. http://doi.org/10.1016/j.anbehav.2004.05.018

McLinn, C. M., & Stephens, D. W. (2006). What makes information valuable: signal reliability and environmental uncertainty. *Animal Behaviour*, *71*(5), 1119–1129. http://doi.org/10.1016/j.anbehav.2005.09.006

McLinn, C. M., & Stephens, D. W. (2010). An experimental analysis of receiver economics: cost, reliability and uncertainty interact to determine a signal's value. *Oikos*, *119*(2), 254–263. http://doi.org/10.1111/j.1600-0706.2009.17756.x

Møller, A. P. (1989). Viability costs of male tail ornaments in a swallow. *Nature*, *339*(6220), 132–135. http://doi.org/10.1038/339132a0

Møller, A. P. (1994). Male ornament size as a reliable cue to enhanced offspring viability in the barn swallow. *Proceedings of the National Academy of Sciences*, *91*(15), 6929–6932.

Møller, A. P., & de Lope, F. (1994). Differential Costs of a Secondary Sexual Character: An Experimental Test of the Handicap Principle. *Evolution*, *48*(5), 1676–1683. http://doi.org/10.2307/2410256

Møller, A. P., de Lope, F., & Caballero, J. M. L. (1995). Foraging costs of a tail ornament: Experimental evidence from two populations of barn swallows Hirundo rustica with different degrees of sexual size dimorphism. *Behavioral Ecology and Sociobiology*, *37*(5), 289–295. http://doi.org/10.1007/BF00174132

Morand-Ferron, J., & Giraldeau, L.-A. (2010). Learning behaviorally stable solutions to producer–scrounger games. *Behavioral Ecology*, *21*(2), 343–348. http://doi.org/10.1093/beheco/arp195

Moreno-Rueda, G. (2007). Is there empirical evidence for the cost of begging? *Journal of Ethology*, *25*(3), 215–222. http://doi.org/10.1007/s10164-006-0020-1

Moreno-Rueda, G. (2010). An immunological cost of begging in house sparrow nestlings. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1690), 2083–2088. http://doi.org/10.1098/rspb.2010.0109

Moreno-Rueda, G., Redondo, T., Trenzado, C. E., Sanz, A., & Zúñiga, J. M. (2012). Oxidative Stress Mediates Physiological Costs of Begging in Magpie (Pica pica) Nestlings. *PLOS ONE*, *7*(7), e40367. http://doi.org/10.1371/journal.pone.0040367

Noguera, J. C., Morales, J., Pérez, C., & Velando, A. (2010). On the oxidative cost of begging: antioxidants enhance vocalizations in gull chicks. *Behavioral Ecology*, *21*(3), 479–484. http://doi.org/10.1093/beheco/arq005

Partan, S., & Marler, P. (1999). Communication Goes Multimodal. *Science*, *283*(5406), 1272–1273. http://doi.org/10.2307/2896573

Partan, S. R. (2013). Ten unanswered questions in multimodal communication. *Behavioral Ecology and Sociobiology*, *67*(9), 1523–1539. http://doi.org/10.1007/s00265-013-1565-y

Patricelli, G. L., Uy, J. A. C., Walsh, G., & Borgia, G. (2002). Sexual selection: Male displays adjusted to female's response. *Nature*, *415*(6869), 279–280. http://doi.org/10.1038/415279a

Polnaszek, T. J., & Stephens, D. W. (2014a). Receiver tolerance of imperfect reliability: results from experimental signaling games. *Animal Behaviour*, *Provisionally accepted.*

Polnaszek, T. J., & Stephens, D. W. (2014b). Why not lie? Costs enforce honesty in an experimental signalling game. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1774). http://doi.org/10.1098/rspb.2013.2457

Polnaszek, T. J., & Stephens, D. W. (2015). Why are signals reliable? Honesty depends on costs, sometimes. *Animal Behaviour*. http://doi.org/10.1016/j.anbehav.2015.09.011

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, *65*(3), 519–530. http://doi.org/10.1006/anbe.2003.2078

Rivero, A., Alatalo, R. V., Kotiaho, J. S., Mappes, J., & Parri, S. (2000). Acoustic signalling in a wolf spider: can signal characteristics predict male quality? *Animal Behaviour*, *60*(2), 187–194. http://doi.org/10.1006/anbe.2000.1452

Roberts, M. L., Buchanan, K. L., & Evans, M. R. (2004). Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour*, *68*(2), 227–239. http://doi.org/10.1016/j.anbehav.2004.05.001

Rodríguez, R. L., Haen, C., Cocroft, R. B., & Fowler-Finn, K. D. (2012). Males adjust signaling effort based on female mate-preference cues. *Behavioral Ecology*, *23*(6), 1218–1225. http://doi.org/10.1093/beheco/ars105

Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, *58*(5), 921–931. http://doi.org/10.1006/anbe.1999.1242

Rowe, C. (2013). Receiver psychology: a receiver's perspective. *Animal Behaviour*, *85*(3), 517–523. http://doi.org/10.1016/j.anbehav.2013.01.004

Rubi, T. L., & Stephens, D. W. (in press). Should receivers follow multiple signal components? An economic perspective. *Behavioral Ecology*. http://doi.org/10.1093/beheco/arv121

Ryan, M. J., Fox, J. H., Wilczynski, W., & Rand, A. S. (1990). Sexual selection for sensory exploitation in the frog Physalaemus pustulosus. *Nature*, *343*(6253), 66–67. http://doi.org/10.1038/343066a0

Saino, N., & Møller, A. P. (1996). Sexual ornamentation and immunocompetence in the barn swallow. *Behavioral Ecology*, *7*(2), 227–232. http://doi.org/10.1093/beheco/7.2.227

Saunders, S. (2009). Costly signalling: a work in progress. *Biology & Philosophy*, *24*(3), 405–416. http://doi.org/10.1007/s10539-007-9100-z

Searcy, W. A., & Nowicki, S. (2005). *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press.

Shannon, C. E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, *27*(3), 379–423. http://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Spence, M. (1973). Job market signaling. *The Quarterly Journal of Economics*, *87*(3), 355–374. http://doi.org/10.2307/1882010

Stephens, D. W. (1989). Variance and the Value of Information. *The American Naturalist*, *134*(1), 128–140.

Sullivan-Beckers, L., & Hebets, E. A. (2011). Modality-specific experience with female feedback increases the efficacy of courtship signalling in male wolf spiders. *Animal Behaviour*, *82*(5), 1051–1057. http://doi.org/10.1016/j.anbehav.2011.07.040

Számadó, S. (1999). The validity of the Handicap Principle in discrete action–response games. *Journal of Theoretical Biology*, *198*(4), 593–602. http://doi.org/10.1006/jtbi.1999.0935

Számadó, S. (2011). The cost of honesty and the fallacy of the handicap principle. *Animal Behaviour*, *81*(1), 3–10. http://doi.org/10.1016/j.anbehav.2010.08.022

Számadó, S. (2012). The rise and fall of handicap principle: a commentary on the "Modelling and the fall and rise of the handicap principle." *Biology and Philosophy*, *27*(2), 279–286. http://doi.org/10.1007/s10539-011-9299-6

Számadó, S., & Penn, D. J. (2015). Why does costly signalling evolve? Challenges with testing the handicap hypothesis. *Animal Behaviour*. http://doi.org/10.1016/j.anbehav.2015.06.005

Thorndike, E. L. (1911). *Animal intelligence: Experimental studies*. New Brunswick, NJ: Transaction Publishers.

Tibbetts, E. A., & Dale, J. (2004). A socially enforced signal of quality in a paper wasp. *Nature*, *432*(7014), 218–222. http://doi.org/10.1038/nature02949

Trivers, R. L. (1974). Parent-Offspring Conflict. *American Zoologist*, *14*(1), 249–264.

Vega-Redondo, F., & Hasson, O. (1993). A game-theoretic model of predator-prey signaling. *Journal of Theoretical Biology*, *162*(3), 309–319. http://doi.org/10.1006/jtbi.1993.1089

Wiley, H. (1994). Errors, exaggeration, and deception in animal communication. In L. Real (Ed.), *Behavioral mechanisms in evolutionary ecology*. University of Chicago Press.

Zahavi, A. (1975). Mate selection--A selection for a handicap. *Journal of Theoretical Biology*, *53*(1), 205–214. http://doi.org/10.1016/0022-5193(75)90111-3

Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, *67*(3), 603–605.

Zahavi, A., Zahavi, A., Balaban, A., & Ely, M. P. (1999). *The handicap principle: a missing piece of Darwin's puzzle*. Oxford University Press US.

Zollman, K. J. S., Bergstrom, C. T., & Huttegger, S. M. (2013). Between cheap and costly signals: the evolution of partially honest communication. *Proceedings of the Royal Society B-Biological Sciences*, *280*(1750). http://doi.org/10.1098/rspb.2012.1878