Signal verification can promote reliable signalling

Mark Broom[1], Graeme D Ruxton[2] & H. Martin Schaefer[3]

1. Department of Mathematics, City University London, London EC1V 0HB, United Kingdom
2. School of Biology, University of St Andrews, St Andrews KY16 9TH, UK
3. Faculty of Biology, University of Freiburg, Department of Evolutionary Biology and Animal Ecology, Hauptstr. 1, 79104 Freiburg, Germany

Summary

The central question in communication theory is whether communication is reliable, and if so, which mechanisms select for reliability. The primary approach in the past has been to attribute reliability to strategic costs associated with signalling as predicted by the handicap principle. Yet, reliability can arise through other mechanisms, such as signal verification; but the theoretical understanding of such mechanisms has received relatively little attention. Here, we model whether verification can lead to reliability in repeated interactions that typically characterise mutualisms. Specifically, we model whether fruit consumers that discriminate among poor and good quality fruits within a population can select for reliable fruit signals. In our model plants either signal or they do not; costs associated with signalling are fixed and independent of plant quality. We find parameter combinations where discriminating fruit consumers can select for signal reliability by abandoning unprofitable plants more quickly. This self-serving behaviour imposes costs upon plants as a by-product, rendering it unprofitable for unrewarding plants to signal. Thus, strategic costs to signalling are not a prerequisite for reliable communication. We expect verification to more generally explain signal reliability in repeated consumer-resource interactions that typify mutualisms but also in antagonistic interactions such as mimicry and aposematism.

Keywords: handicap principle, sanction, plant-animal communication, honest signalling, mimicry, aposematism

Introduction

The dominant issue in the study of animal communication in recent decades has been how (more or less) reliable communication can be maintained when signaller and perceiver differ in their selfish interests [1,2]. That is, the challenge is to explain how a correlation is maintained between variation in a signal and in an unobservable quantity that the perceiver is interested in, despite the potential for the signaller to gain by misinforming. The dominant theory used to explain honest communication in the face of conflicting interest between the signaller and perceiver has been the Handicap Principle [3,4]. This principle essentially assumes that there is a strategic cost to signalling over and above any costs associated with simply communicating efficiently, and this higher cost varies between signallers or brings varied benefits across signallers. Generally, this theory rests on the assumption that high-quality individuals are better able to bear the cost of a particular signal. This cost structure causes different types of signaller to invest differentially in signalling and thus allows the signal to be associated with information about the underlying variation among signallers. We refer to previous definitions of information as being a property of the perceiver and as being associated with a given sensory stimulation (see [5] for more details). In an important recent work, Számadó [6] argued that in fact the key to understanding signal reliability is that cheating will prosper unless it is more costly than reliability, and the signalling cost structure required by the Handicap Principle is only one way to achieve this situation; indeed Számadó lists ten different alternative mechanisms. However, here we suggest that the ability of the perceiver to verify the accuracy of the signal after it has responded to the signal is another, likely-widespread, but relatively neglected mechanism (but see [7]) that might be important in explaining some cases of reliable communication.

The likely reason that signal verification has been largely overlooked is that (for reasons of mathematical tractability rather than biological realism) the theory of animal communication rests

almost exclusively on situations where individuals interact with each other only once, or (equivalently) that individuals encounter each other randomly and hold no memory of previous interactions [1,2]. In such cases, there is no benefit to the perceiver verifying that the signal was reliable or not, since it cannot act on this information. This is realistic for some situations, such as mate choice by females in species where individuals reproduce only once in their lifetime. However, in some species individuals do have the chance to evaluate to consequences of acting on a signal and modify their subsequent behaviour accordingly. Consider a long-lived avian species where females often keep the same sexual partner for several breading seasons. She may initially select males on the basis of some signal (e.g. song structure or plumage coloration) that is expected to correlate well with the male's ability to provide food for chicks. After having selected a particular male to breed with in her first season, she is able to monitor the male's chick provisioning. That is, having initially acted on the signal in mate choice, she is subsequently able to verify the reliability of that individual's signal. She can then act on the information gained through signal verification, tending to stay with an honest signaller for the next breeding attempt or select a new male otherwise.

Verification can play an important role in many other communication systems, particularly in mutualisms that typically involve repeated consumer-resource interactions where a consumer is likely to evaluate the quality of the resource [8]. A good example is plant-animal communication. Consider a pollinating insect that will often visit a number of flowers from the same plant in quick succession, but is more likely to leave the plant and travel a considerable distance before visiting the next flower if it encounters rewardless flowers [9]. Likewise, experiments have shown that hawkmoths reduce their effort invested in exploring a flower if this is relatively unrewarding compared to other flowers of the same species [10]. This behaviour can be characterised as self-serving behaviour based on the verification of signalling and is expected to contribute to limiting cheating in plant-animal communication. As yet, a formal model to evaluate this conjecture is missing.

77 In seed dispersal mutualisms, consumers such as birds will often consume a number of fruits during
78 a visit to a single plant, but can be sensitive to small variation in the nutritional contents of fruit [11].
79 Such fruit consumers are likely to leave a plant more quickly (consuming fewer fruits from it, and so
80 potentially being less useful to the plant as a seed disperser) if the nutritional results from the first
81 fruits it samples do not match its expectation from the signals (e.g. fruit coloration and odour) that
82 first attracted it to the plant. We will focus on this last situation, and explore whether the ability to
83 verify the signal (by evaluating the contents of consumed fruit) and act accordingly (abandoning
84 plants that provide lower-value fruits after consuming fewer fruits) can drive reliable signalling. We
85 consider a very simple system, since our aim is to evaluate the plausibility of this mechanism in
86 general terms, rather than model any one particular system.

87 **The model**

88 We assume that there are *N* fruiting plants in a population, of which a fraction *G* are good quality
89 and a fraction *P* (= 1-*G*) are poor quality; and there are *n* frugivorous birds, assuming that *N* and *n*
90 are large. The type of a given plant (good or poor) is exogenously determined, and not a matter of
91 active choice or strategy by the plant. A plant's strategy is either to signal or not (denoted by the
92 subscripts *S* or *N*); a bird's strategy is whether to be responsive to the signal or not. Specifically V_S is
93 the probability that a detected signalling plant is then visited by the bird. Since we assume that the
94 seed disperser cannot evaluate the quality of the fruits prior to visiting the plant, it seems rational
95 for V_S to be either 0 or 1. The probability of visiting a detected non-signalling plant is V_N, and similarly
96 this is assumed to be either 0 or 1. It is not logical for a plant to invest some resources into a signal
97 that reduces its attractiveness to birds; hence we can assume that birds are not less likely to respond
98 to a signalling plant than to a non-signalling plant ($V_S \geq V_N$), since such a situation would be
99 evolutionarily unstable. Similarly, it seems illogical for the birds to ignore all plants, and thus $V_S > 0$,
100 so that we assume that $V_S = 1$ and thus consider only two rational bird strategies: visit all plants ($V_S =$

$V_N = 1$) or visit only signallers ($V_s = 1$, $V_N = 0$). We call the second strategy "responder", since it is signal sensitive, versus the other "non-responder" strategy of visiting all plants encountered.

We assume that birds that ignore the signal and visit any detected plant (non-responding birds) visit plants at a rate k. Notice that this value is the same no matter the signalling strategy of plants, so the signal does not make plants more easily found by birds. That is, signalling plants do not receive an additional benefit in being more conspicuous at a distance than non-signallers. This assumption was adopted for simplicity and to isolate the informational consequences of signalling from any other benefits. Essentially we assume that appearance and volatile emissions of the non-signalling plants may be selected to enhance their conspicuousness to frugivores, but that they have not been selected to communicate information about plant quality; if there is additional selection pressure on these traits to link them to plant quality then this change does not impact on conspicuousness. This assumption simplifies our model, but our qualitative results are not contingent on this assumption. If a bird visits only signalling plants then it visits plants at a rate $k\lambda(s)$, where $s \leq \lambda(s) \leq 1$ and s is the fraction of plants (of either quality) that signal. This captures the idea that responding only to signalling plants will increase the amount of time that must be invested to find each suitable plant (a cost of choosiness). However, this discount factor need not simply be s, since not all the bird's time will be spent searching; some of the time will be spent in visiting a plant. Thus, for example, if the overall density of flowers is high, the cost of responding only to signallers is reduced and λ takes a higher value.

For convenience we define the parameter α by $\alpha = nk/N$. This represents the rate at which each plant is visited in a population of non-responding birds. We also define r as the proportion of birds that are responsive to the signal. Then non-signalling plants get visited by birds at a rate $\alpha(1-r)$, whereas signalling plants get visited at a rate $\alpha(1-r+(r\lambda/s))$.

Signalling costs the plant a fixed cost C per unit time, which is independent of plant quality. Importantly, unlike the assumptions of the Handicap Principle, the cost of signalling is the same for

both plant types. There is a benefit to the plant in being visited by a bird, this benefit is considered to increase linearly with the number of berries consumed by the bird during its visit. We assume this number is independent of whether the plant signals or not, but is dependent on plant (and thus berry) quality. A bird visiting a good plant consumes N_G berries, a bird visiting a poor quality plant consumes N_P berries; with $N_P < N_G$. The total benefit that the bird gains from visiting a good plant (R_G) is higher than the benefit from visiting a poor plant (R_P); because more berries are consumed and these berries are of higher quality. We emphasize our assumption that the behaviour of the bird after reaching the plant is unaffected by whether its arrival at that particular plant was influenced by signalling or not.

The payoffs

Based on the assumptions above, we can define payoffs for plants as a function of quality and strategy, and for birds as a function of strategy. We define the payoff to a good-quality plant that signals, E_{GS}, as

$$E_{GS} = V_S N_G \alpha \left(1 - r + \frac{r\lambda}{s}\right) - C.$$

Similarly, the payoff for a poor-quality plant that signals is

$$E_{PS} = V_S N_P \alpha \left(1 - r + \frac{r\lambda}{s}\right) - C.$$

For a good quality plant that does not signal, the payoff becomes

$$E_{GN} = V_N N_G \alpha (1 - r);$$

and for a poor quality non-signaller,

$$E_{PN} = V_N N_P \alpha (1 - r).$$

For a bird that ignores the signal the payoff is

147 $E_{BN} = k(GR_G + PR_P)$.

148 For birds that visit only signalling plants (i.e. that are responsive to signals), the payoff will depend
149 on which plants are signalling. The particular expression can be constructed easily for any particular
150 case. As an example, where good quality plants signal and poor quality plants do not, this payoff is
151 simply

152 $E_{BR} = k\lambda(G)R_G$.

153 **Identification of evolutionarily stable strategies**

154 Using the payoff structure defined above, we can find evolutionarily stable strategies where it pays
155 no individual to deviate. We will consider only pure strategies (where plants of a given quality always
156 or never signal, and birds always or never respond to signals), since there is not an obvious selecting
157 force for intermediate (mixed) strategies. There are three types of individuals (good plants, poor
158 plants & birds) each of which has two pure strategy options. This gives eight possible behavioural
159 combinations across the ecosystem. However, of these eight possibilities some can quickly be
160 discarded as evolutionarily unstable. Firstly, if birds do not respond to the signal, then no plant
161 should invest in costly signals. Thus, if birds do not respond to the signal, the only stable option for
162 plants is for both poor and good quality individuals not to signal. Thus we turn our attention to the
163 situation where birds respond to the signal: thus $r = 1$, $V_S = 1$ and $V_N = 0$. In this situation, there is
164 considerable simplification of the payoffs to plants:

165 $E_{GS} = N_G\alpha\left(\frac{\lambda(s)}{s}\right) - C$,

166 $E_{PS} = N_P\alpha\left(\frac{\lambda(s)}{s}\right) - C$,

167 $E_{GN} = E_{PN} = 0$.

168 We need to consider four cases.

Case (i): Neither type of plant signals. In this case a bird that only visits signalling plants does poorly compared to one that visits all plants it discovers.

$$E_{BR} = 0 < E_{BN}.$$

Thus, it is not stable to have no signalling plants but a signal-responsive bird.

Case (ii): Poor plants signal; good plants do not. For all parameter values it is easy to show that

$$E_{GS} - E_{GN} > E_{PS} - E_{PN},$$

which means that if it is advantageous for poor plants to signal, then it will always also be advantageous for good plants to signal. Thus, there is no stable situation where only poor plants signal. This makes sense since the costs of signalling are the same for both plant types, but the benefits can never be less for the good plant type compared to the poor plants.

Case (iii): Good plants signal and poor plants do not. For this to occur, we need the following conditions to hold for the plant strategies to be stable:

$$\frac{N_G \alpha \lambda(G)}{G} > C > \frac{N_P \alpha \lambda(G)}{G}. \quad (1)$$

To make it profitable for the birds to respond to the signal, we require that

$$\lambda(G)R_G > GR_G + (1-G)R_P. \quad (2)$$

A necessary (but not sufficient) requirement for satisfying this condition is that that $\lambda(G) > G$, which we expect to be generally satisfied in any situation where a non-trivial amount of time is required to interact with any plant visited.

Case (iv): In a situation where all plants are signalling (so that $s=\lambda(s)=1$), stability against either plant type switching to not signalling requires that $N_P\alpha > C$, otherwise poor plants at least would switch.

When all plants signal, $E_{BR} = E_{BN}$, and so stability against a change of bird strategy is not immediately clear. However, such a situation is only potentially stable in our model because (for simplicity) we have assumed that there is no cost to the bird in recognising a signal. In reality, it is likely that when all flowers are signalling, birds that are unresponsive to the signal are likely to have higher fitness than those that must decide whether a fruit is signalling before deciding whether to land or not. This cost might be in investment in the cognitive processing associated with deciding whether a signal is present or not, or in occasionally making a mistake and rejecting a fruit because the signal was present but not properly detected. Thus, we would not expect to find the equilibrium where both plant types signal in the real world.

In summary, the situation where no plant ever signals and birds are unresponsive to signals is always stable. However, another situation where poor plants do not signal and good plants do signal, with birds being responsive to the signal and only being interested in signalling (good quality) plants can also be stable, but only if the conditions described in (1) & (2) are met. Equation 1 suggests that the signalling equilibrium is stable only for a range of intermediate costs to signalling. If signalling costs are too low, then even poor-quality plants will benefit from signalling; if the costs are too high then even good quality plants do not benefit from signalling. The range of suitable cost values increases the more that good plants benefit from a bird's visit relative to the benefit of a visit to a poor plant. Both the upper and lower boundaries for suitable costs increase with α (the rate at which birds visit plants in the absence of any signalling) and with $\lambda(G)$: the modulation in rate of fruit visits that a bird experiences if it is responsive to the signal (which will increase as plants become abundant and/or conspicuous in the environment). Both limits vary inversely with the fraction of good quality plants in the population. Equation (2) suggests that the signalling equilibrium will be more likely to be stable the more common good-quality plants are within the population. Satisfying this condition also places a lower limit on the ratio of the benefits to the bird of visiting a good quality plant relative to a poor quality one. The higher this ratio, the easier this condition will be to satisfy. It makes intuitive

sense that birds would benefit from attending to the signal when good plants are relatively valuable and are not too rare.

Let us consider an illustrative example. If $R_G = 3$ and $R_P = 1$ and

$$\lambda(G) = \sqrt{G},$$

then (from eqn. 2) we would only expect the signalling equilibrium to exist when $G > 0.25$. If we further assume that $\alpha = 1$, $N_P = 1$, $N_G = 1.5$

then (1) simplifies to

$$\frac{1.5}{\sqrt{G}} > C > \frac{1}{\sqrt{G}}.$$

Figure 1 shows the range of *G* and *C* values for which the signalling equilibrium exists in this example.

Discussion

In our simple model we have demonstrated that there are parameter value combinations where the ability of the perceiver to verify the reliability of a signal and act on it can allow for signal reliability (where only good quality plants signal in our model and birds bias their visits to signalling plants). Notice that such a bias is not a case of punishment of deceptive plants by birds. There is already an established theory on signal reliability driven by the risk of deception being discovered and punished (e.g. [7]). Punishment involves the perceiver realising that it has been deceived and paying the additional cost of punishment itself in order to inflict a cost on the signaller. In our case, crucially, although a bird leaves a poor quality plant earlier than it leaves a good quality plant, its decision to leave is unaffected by whether it decided to visit the plant on the basis of responding to a signal or not. Further, in doing this, the bird is not paying a cost in order to inflict a cost on the plant; rather the cost to the plant of earlier departure by the bird is driven entirely by the bird's self-interest and maximising its long-term reward rate. Our model thus assumes that birds sanction less-rewarding

238 partners by performing a self-serving behaviour that imposes costs on these partners as a by-
239 product (see [12] for discussion on punishment and sanctions). Sanctions in general, and our model
240 in particular, give a biological interpretation to the concept of an *optimization cost* introduced by
241 Számadó [6] as a cost "that is independent of the signalling game and that results from making a
242 bad decision in the underlying optimization problem." Sanctions and optimization costs rely on
243 signal verification, which is an important parameter in all repeated interactions between signaller
244 and perceiver.

245 The cost of cheating to a poor-quality plant that signals is that it does not get sufficient return from
246 the birds it attracts to justify the cost invested in the signal. This is typical for mutualism with
247 repeated interactions among the same partners. Note that the return obtained from seed dispersers
248 in response to signalling are expected to depend on whether interactions are repeated or not. If
249 plant species are primarily bird-dispersed and produce fruit during avian migration, as many
250 temperate species do in late summer, it may pay even for poor-quality plants to signal and attract
251 migrants even if these leave the plants after consuming only a few fruits. Unlike the repeated
252 interactions modelled above, this would be an advertising strategy suited for one-shot interactions
253 with many different consumers. This strategy is equivalent to a "tourist trap" with more investment
254 in attracting consumers rather than retaining a relationship with them after their first visit.

255 The hawkmoth pollination study of [10] provides a clear empirical example of the general
256 mechanism modelled in our paper. These authors exposed hawkmoth pollinators to either wild-type
257 *Petunia integrifolia* or individuals genetically modified to reduce the volume of nectar offered by the
258 flowers. The hawkmoths did not discriminate between the two types of plant in terms of
259 preferentially visiting more rewarding individuals. However, hawkmoths spent less time probing
260 genetically modified plants, and this led to reduced seed production in this type compared to the
261 more rewarding wild type. Hand pollination experiments demonstrated that the GM plants actually
262 had greater reproductive potential than the wild-type and their reduced seed set was thus caused by

263 the behaviour of the hawkmoth pollinators. The authors conclude that “a simple self-serving
264 pollinator behaviour –the adjustment of probing time in response to nectar volume – may select
265 against reducing nectar and protect plant-pollinator mutualisms against drift towards parasitism.” In
266 terms of the framework introduced in our paper, the floral displays remains a reliable signal of
267 nectar reward because pollinating insects can verify the reliability of the signal and take action that
268 harms the plant but benefits the pollinator by quitting unrewarding plants earlier. Given the
269 simplicity of the model introduced here, we think there is reason to expect that many other natural
270 examples of signal reliability maintained by signal verification await discovery.

271 Readers should be aware that by “signal vertification” we mean that a signal perceiver is able to
272 evaluate the consequences for it of reacting to a signal and modify its subsequent behaviour in the
273 light of that information. In our model, the signal influences whether a bird visits a particular plant or
274 not, but the factors influencing the decision to visit the plant (including the signal) do not influence
275 the evaluation of the value of the plant or the response of the bird to that evaluation. Some authors
276 might use a narrower definition of verification, where the signal has a greater influence: not just on
277 the decision to visit a plant, but on the bird’s reaction to evaluation of plant quality. For example, a
278 bird’s reaction to sampling poor quality fruit on a plant might be influenced by whether they were
279 induced to visit the plant by apparent signalling of higher quality (i.e. by whether they had an
280 expectation that this plant would offer high quality fruit). Such “expectation effects” are very
281 plausible and well documented in other contexts. However, our aim here was to explore whether
282 reliable signalling could be maintained by even simpler behaviour by signal perceivers. The signalling
283 discussed in this paper might also serve as an important stepping stone in the evolution of any more
284 complex perceiver behaviours.

285

286 There are parallels between our model of signalling, and an existing model of cleaner fish
287 mutualisms [13]. In such interactions there is a temptation for the cleaner to cheat and try and eat

288 the flesh of the client fish as well as any parasites. However, their model predicted that this
289 tendency for mutualism to slide into parasitism can be resisted providing the client has sufficient
290 control over the duration of interactions, tending to terminate increasingly parasitic interactions
291 increasingly quickly. This is very similar to our hypothetical model system where the reliability of
292 signalling by plants is maintained by the tendency of the birds to quit plants that offer lower returns
293 more quickly. Both their model and ours should have wide applicability. Reliability in the cleaner fish
294 mutualism is further enforced by an audience effect, where cleaner fish are more cooperative in the
295 presence of potential clients that witness their cleaner behaviour [14]. This additional mechanism
296 that could enforce reliability is not expected to occur in plant-animal communication. However, if
297 fruit consumers spend longer in more rewarding plants, this self-serving behaviour may alert other
298 fruit consumers and attract them as a by-product to the food sources which are often (but not
299 always) bonanza resources that are difficult to defend. This could be a mechanism through which
300 rewarding plants obtain more dispersal services.

301 Most models of the evolution of cooperation assume equality between partners in their ability to
302 respond to the behaviour of the other (often being based on the Iterated Prisoner's Dilemma game;
303 [15]), whereas many mutualisms (especially those between members of different species) involve
304 strong asymmetry between partners in their scope for direct exploitation of the other like that
305 considered by [13]. Similarly much signalling theory has been motivated by within-species
306 communication in mate choice, social signalling and begging by offspring; but many between-species
307 communication systems may offer the scope for the signal verification that is at the heart of our
308 model. Clear examples are aposematism and mimicry. In aposematism would-be predators are
309 educated to avoid potentially harmful prey. Studying signal design across populations varying in the
310 relative abundance of models and Batesian mimics is likewise telling for understanding the factors
311 influencing signal reliability [16].

312 The basic structure of our model has strong similarity to a “differential benefits” model of costly
313 signalling, such as that in the Sir Philip Sidney game. In our case, plants with good quality fruit
314 receive a larger benefit (namely, more seeds dispersed) than do plants with poor quality fruit. As a
315 result, these good quality plants are willing to pay more in the way of costs in order to reap their
316 respective benefits. This is the core principle driving our model, just as it is the core principle driving
317 the Sir Philip Sidney game. In this context, it is important to emphasize that the present analysis
318 considers only pure strategies. It is possible that there are also “hybrid equilibria” where high-quality
319 individuals always signal while low-quality individuals have a mixed strategy of sometimes signalling
320 and sometimes not signalling, and receivers always decline to act in the absence of a signal but
321 sometimes act and sometimes decline in the presence of a signal [17,18]. Such equilibria exist for the
322 Sir Philip Sidney game and may exist for the present game depending on the choice of parameters.
323 Exploration of this would be valuable.

324 We hope our work inspires others to explore the importance of signal verification to the
325 maintenance of signal reliability in real systems, and to expand on the generality of the proof-of-
326 concept theory presented here. We believe that verification plays an important role in many
327 communication systems given that signallers will naturally vary in quality owing to genetic and
328 environmental conditions. Thus, our concept can be expanded to analyze core issues in signalling
329 that still are controversial. First, what are the consequences of multivariate and continuous variation
330 in signaller quality? Second, how does variation in the ability of perceivers to discriminate among
331 different types of signals (or among signals that vary in their association to quality) influence the
332 evolutionary stability of signal reliability? Answering both questions will provide a more
333 encompassing functional understanding of the mechanisms promoting reliable communication in a
334 range of communication systems.

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375 19.

376 **Figure 1**: The range of *G* (fraction of plants in the population that are good quality) and *C* (the cost of
377 signalling) values that allow a signalling equilibrium as well as the non-signalling equilibrium that is
378 always stable. We assume that $R_G = 3$, $R_P = 1$ and $\lambda(G) = \sqrt{G}$, such that (from eqn. 2) the signalling
379 equilibrium exists when $G > 0.25$, which is to the left of the vertical broken line. We further assume
380 that $\alpha = 1$, $N_P = 1$, and $N_G = 1.5$, in which case eqn. (1) simplifies to

381 $\frac{1.5}{\sqrt{G}} > C > \frac{1}{\sqrt{G}}$, which gives the two solid lines in the figure. The Signalling equilibrium is stable only in
382 the region bounded by the three lines; the non-signalling equilibrium is always stable. R_G and R_P are
383 the benefits to the bird of visiting good and poor plants respectively; N_G and N_P are the benefits of a
384 bird's visit to good and poor plants respectively. The parameter α is the rate at which birds visit
385 flowers in the absence of any signalling, and $\lambda(G)$ is the modulating factor controlling how much a
386 bird's rate of visitation is reduced if it ignores non-signalling poor plants.