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1 **Signal verification can promote reliable signalling**

2 Mark Broom<sup>1</sup>, Graeme D Ruxton<sup>2</sup> & H. Martin Schaefer<sup>3</sup>

3 1. Department of Mathematics, City University London, London EC1V 0HB, United  
4 Kingdom

5 2. School of Biology, University of St Andrews, St Andrews KY16 9TH, UK

6 3. Faculty of Biology, University of Freiburg, Department of Evolutionary Biology and  
7 Animal Ecology, Hauptstr. 1, 79104 Freiburg, Germany

8           **Summary**

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

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

26

27

28 **Introduction**

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

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

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

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

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

103 We assume that birds that ignore the signal and visit any detected plant (non-responding birds) visit  
 104 plants at a rate  $k$ . Notice that this value is the same no matter the signalling strategy of plants, so the  
 105 signal does not make plants more easily found by birds. That is, signalling plants do not receive an  
 106 additional benefit in being more conspicuous at a distance than non-signallers. This assumption was  
 107 adopted for simplicity and to isolate the informational consequences of signalling from any other  
 108 benefits. Essentially we assume that appearance and volatile emissions of the non-signalling plants  
 109 may be selected to enhance their conspicuousness to frugivores, but that they have not been  
 110 selected to communicate information about plant quality; if there is additional selection pressure on  
 111 these traits to link them to plant quality then this change does not impact on conspicuousness. This  
 112 assumption simplifies our model, but our qualitative results are not contingent on this assumption. If  
 113 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  
 114 fraction of plants (of either quality) that signal. This captures the idea that responding only to  
 115 signalling plants will increase the amount of time that must be invested to find each suitable plant (a  
 116 cost of choosiness). However, this discount factor need not simply be  $s$ , since not all the bird’s time  
 117 will be spent searching; some of the time will be spent in visiting a plant. Thus, for example, if the  
 118 overall density of flowers is high, the cost of responding only to signallers is reduced and  $\lambda$  takes a  
 119 higher value.

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

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

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

### 135 **The payoffs**

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

$$139 \quad E_{GS} = V_S N_G \alpha \left( 1 - r + \frac{r\lambda}{s} \right) - C.$$

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

$$141 \quad E_{PS} = V_S N_P \alpha \left( 1 - r + \frac{r\lambda}{s} \right) - C.$$

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

$$143 \quad E_{GN} = V_N N_G \alpha (1 - r);$$

144 and for a poor quality non-signaller,

$$145 \quad E_{PN} = V_N N_P \alpha (1 - r).$$

146 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.

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

$$171 \quad E_{BR} = 0 < E_{BN}.$$

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

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

$$174 \quad E_{GS} - E_{GN} > E_{PS} - E_{PN},$$

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

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

$$181 \quad \frac{N_G \alpha \lambda(G)}{G} > C > \frac{N_P \alpha \lambda(G)}{G}. \quad (1)$$

182

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

$$184 \quad \lambda(G)R_G > GR_G + (1 - G)R_P. \quad (2)$$

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

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

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

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

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

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

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

219 then (from eqn. 2) we would only expect the signalling equilibrium to exist when  $G > 0.25$ . If we

220 further assume that  $\alpha = 1$ ,  $N_P = 1$ ,  $N_G = 1.5$

221 then (1) simplifies to

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

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

## 225 Discussion

226 In our simple model we have demonstrated that there are parameter value combinations where the  
227 ability of the perceiver to verify the reliability of a signal and act on it can allow for signal reliability  
228 (where only good quality plants signal in our model and birds bias their visits to signalling plants).

229 Notice that such a bias is not a case of punishment of deceptive plants by birds. There is already an  
230 established theory on signal reliability driven by the risk of deception being discovered and punished  
231 (e.g. [7]). Punishment involves the perceiver realising that it has been deceived and paying the  
232 additional cost of punishment itself in order to inflict a cost on the signaller. In our case, crucially,  
233 although a bird leaves a poor quality plant earlier than it leaves a good quality plant, its decision to  
234 leave is unaffected by whether it decided to visit the plant on the basis of responding to a signal or  
235 not. Further, in doing this, the bird is not paying a cost in order to inflict a cost on the plant; rather  
236 the cost to the plant of earlier departure by the bird is driven entirely by the bird's self-interest and  
237 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 verification” 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.

335

336 **References**



- 337 1. Maynard-Smith, J. & Harper, D. G. C. 2003 *Animal Signals*. Oxford: Oxford University Press.
- 338 2. Searcy W. A., Nowicki S. 2005 *The evolution of animal communication*. Princeton: Princeton
- 339 University Press.
- 340 3. Zahavi A. 1975 Mate selection: a selection for handicap. *Journal of Theoretical Biology* 53,
- 341 205-214.
- 342 4. Grafen, A. 1990 Biological signals as handicaps. *Journal of Theoretical Biology* 144, 246-517
- 343 5. Ruxton G. D., Schaefer H. M. 2011 Resolving current disagreements and ambiguities in the
- 344 terminology of animal communication. *Journal of Evolutionary Biology* 24, 2574-2585.
- 345 6. Számadó S. 2011)The cost of honesty and the fallacy of the handicap principle. *Animal*
- 346 *Behaviour* 81, 3-10.
- 347 7. Lachmann, M., Számadó S. & Bergstrom, C. T. 2001 Cost and conflict in animal signals and
- 348 human language . *Proceedings of the National Academy of Sciences* 98, 13189-13194.
- 349 8. Schwartz M.W., Hoeksema J.D. 1998 Specialization and resource trade: biological markets as
- 350 a model of mutualisms. *Ecology* 79, 1029-1038.
- 351 9. Johnson S.D., Peter C.I., Agren J. 2004 The effects of nectar addition on pollen removal and
- 352 geitonogamy in the non-rewarding orchid *Anacamptis morio*. *Proceedings of the Royal*
- 353 *Society of London B* 271, 803-809.
- 354 10. Brandenburg, A., Kuhlemeier, C. & Bshary, R. (2012) Hawkmoth pollinators decrease seed
- 355 set of low nectar *Petunia axillaris* line through reduced probing time. *Current Biology* 22,
- 356 1635-1639
- 357 11. Schaefer H. M., Schmidt V., Bairlein F. 2003 Discrimination abilities for nutrients: which
- 358 difference matters for choosy birds and why? *Animal Behaviour* 65, 531-541.
- 359 12. Raihani N. J., Thornton A., Bshary R. 2012 Punishment and cooperation in nature. *Trends in*
- 360 *Ecology & Evolution* 27, 288-295.
- 361 13. Johnstone, R. A. & Bshary, R. 2002 From parasitism to mutualism: partner control in
- 362 asymmetric interactions. *Ecology Letters* 5, 634-639.

- 363 14. Pinto A., Oates J., Grutter A., Bshary R. 2011 Cleaner wrasses *Labriodes dimidiatus* are more  
364 cooperative in the presence of an audience. *Current Biology* 21, 1140-1144.
- 365 15. Alexrod, R., Hamilton, W.D. 1981 On the evolution of cooperation. *Science* 211, 1390-1396.
- 366 16. Harper G. R., Pfennig D. W. 2007 Mimicry on the edge: why do mimics vary in resemblance  
367 to their model in different parts of their geographical range? *Proceedings of the Royal*  
368 *Society of London B* 274(1621), 1955-1961.
- 369 17. Huttegger S.M., Zollman K.J.S. 2010 Dynamic Stability and Basins of Attraction in the Sir  
370 Philip Sidney game. *Proceedings of the Royal Society of London B* 277, 1915-1922.
- 371 18. Zollman K.J.S., Bergstrom, C.T., Huttegger, S.M. 2013. Between cheap and costly signals: the  
372 evolution of partially honest communication. *Proceedings of the Royal Society of London B*  
373 280, 20121878.
- 374

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  $\alpha$  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.