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1 On the evolutionary stability of zero-cost 2 pooled-equilibrium signals

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4
5 M. Broom¹ and G.D. Ruxton^{2,3}

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7 1. Department of Mathematical Science, City University London, Northampton
8 Square, London EC1V 0HB, UK

9 2. School of Biology, University of St Andrews KY16 7TH, UK

10 3. Corresponding author: gr41@st-andrews.ac.uk; tel. +44 781 331 2841

11 12 13 **Abstract**

14 A key question in the development of understanding of animal communication has
15 been what maintains the honesty of signals, stopping dishonesty (cheating) from
16 spreading. The dominant theory used to address this question is a refinement of
17 Zahavi's Handicap Principle. The vital thing about handicap signals is that their
18 honesty requires that those signals are costly to the sender over and above the
19 minimum costs associated with transmission; these costs are generally called strategic
20 costs. An alternative "pooled equilibria" has been proposed. If signalling is
21 constrained to two levels, then it can be demonstrated that even if there is no cost
22 associated with giving a signal, there can be a signalling evolutionarily stable strategy
23 (ESS) where signallers are arranged into pools according to their state: those below a
24 threshold give one signal, those above this threshold always give the other. Further,
25 this can be generalized to any finite number of discrete signals. Here we explore the
26 consequence of generalizing to a continuously varying signal form. We show that
27 unless there is some physical impediment to the diversity of signals possible, then
28 pooled-equilibrium signalling strategies are not stable. Such a strategy would be
29 invaded by a more complex signal, where some individuals within a "pool" benefit

30 from signalling their difference from other individuals within the pool. We suggest
31 that such impediments to variation in signal form will be uncommon in nature, and
32 thus so will pooled equilibria.

33

34

35 **Introduction**

36 A key question in the development of understanding of animal communication has
37 been the evolutionary stability of signalling [1,2]. Signals must be honest (that is,
38 conveying useful information to the receiver) most of the time, or else receivers
39 would be selected to ignore the signal, and the signalling system would break down.
40 Thus the key question is what maintains the honesty of signals, stopping dishonesty
41 (cheating) from spreading. The dominant theory used to address this question is a
42 refinement of Zahavi's Handicap Principle [3]. In its more generalised form the key
43 assumption of this theory is that the effective cost of a signal is lower for individuals
44 giving stronger signals; either because higher quality individuals (that are more able
45 to bear the higher costs of stronger signals) give such stronger signals or because
46 individuals in greater need (who would benefit most from a specific action by the
47 receiver) signal strongest [1]. The vital thing about handicap signals is that their
48 honesty requires that those signals are costly to the sender over and above the
49 minimum costs associated with transmission; these costs are generally called strategic
50 costs [4].

51 However, there are a number of alternative situations that can also allow
52 evolutionary stability of signalling without reliance on strategic costs. One of these is
53 that the form of the signal is causally linked to the quality of interest to receivers, such
54 that dishonest signals are physically not possible. Such an "unfakable" signal is

55 generally called an index [1]. Consider an example where a female tiger moves
56 through the territories of several males, she is the receiver and what she is interested
57 in is the size of the territory-holding male (preferring larger males). Imagine that
58 males signal their size by stretching up a tree trunk with their forelegs to leave scratch
59 marks as high up as they can. This may be an example of an index. Smaller males are
60 simply unable to make marks as high as larger males can. Males have no incentive to
61 scratch less high than as physically possible for them and so scratch marks are a
62 reliable signal of male size.

63 Another situation that ensures honest signalling is complete congruence of
64 interests, where signaller and receiver always place the possible outcomes of an
65 interaction between them in the same rank order. A simple example of this could be a
66 situation involving anti-predatory alarm calling when signaller and receiver are
67 related. There are two situations, either a predator is present or not; and two possible
68 outcomes of one individual detecting a predator, emission of an alarm call or not. If a
69 predator is present then both receiver and signaller benefit if an alarm call is given:
70 presuming that the receiver can act on the alarm call to reduce its risk of predation and
71 that the signal is not overly costly to the signaller. If a predator is not present, then
72 both signaller and receiver benefit from no call being given, if the receiver's response
73 to a call adversely affects non-predation aspects of fitness (say by expending energy
74 or reducing opportunity to feed). In such an example there is no incentive to be
75 dishonest, because both parties' interests always align.

76 It may also be possible to have honest signalling in a situation where the
77 individuals have different preferred outcomes of an interaction but share an
78 overwhelming interest in common. An example of this might be an aggressive
79 competitive interaction over a low-value resource (such as a small food item); each

80 individual would rather that their opponent retreated yielding the resource to them, but
81 both are anxious to avoid an escalated contest that could be very damaging to the
82 loser.

83 Finally, honesty may be maintained if instances of cheating can be detected as
84 such and punished: either directly (by inciting an aggressive response from the
85 receiver) or indirectly through a loss of reputation (which affects the receiver's
86 treatment of the cheating signaller in subsequent interactions in a way that
87 disadvantages the signaller).

88 In addition to these uncontroversial mechanisms, Bergstrom & Lachmann [5]
89 proposed an alternative model of cost-free signalling: "pooled equilibria". Imagine
90 this in the context of interactions between a parent and a single offspring. Across
91 interactions the offspring varies continuously in the benefit it would gain from being
92 fed during an interaction, and the parent varies continuously in the cost to them of
93 feeding the offspring in a given interaction. The parent has a binary choice to make in
94 each interaction: whether to feed or not. It is clear that it is not possible for both the
95 donor to benefit by giving and the receiver to benefit by not receiving in the same
96 interaction. Thus, ignoring this unbiological situation, there are three further
97 possibilities for a given outcome (from an inclusive fitness perspective):

98

- 99 (i) both parties benefit if the parent feeds the offspring;
- 100 (ii) both parties benefit if the parent does not feed its offspring;
- 101 (iii) the offspring would benefit from the parent feeding it, but the parent would
102 not.

103

104 If signalling of need by the offspring is constrained to only two levels (e.g. either a
105 signal of fixed intensity is given or it is not), then Bergstrom & Lachmann [5], in an
106 elaboration of the Sir Philip Sidney game [6], demonstrate that even if there is no cost
107 associated with giving a signal, there can be a signalling evolutionarily stable strategy
108 (ESS) where offspring are arranged into pools according to their state: those below a
109 threshold value of need do not signal, those above this threshold always signal. At this
110 ESS, signalling increases the willingness of parents to feed. Since it is an ESS, the
111 particular threshold value is such that no individual benefits from adopting an
112 alternative threshold value. These authors further demonstrate that the theory can
113 generalize to a greater number of pools each corresponding to a fixed signalling level.

114 This pooled-equilibrium model relies on relatedness between signaller and
115 receiver for stability of the signal. Brilot & Johnstone [7] show that cost-free
116 signalling is stable in the two-pool system only if the ratio of maximum to minimum
117 need of the signaller exceeds a critical value that increases as the relatedness of
118 signaller and receiver decreases.

119 As well as relatedness between signaller and receiver, an important
120 assumption of the model of Bergstrom & Lachmann [5] (as opposed to the extension
121 considered in this paper) is that signalling can take only a finite number of values, as
122 can the number of responses. In the simple case here, all offspring in a signalling pool
123 will signal with exactly the same intensity, despite the fact that individuals in the same
124 pool vary continuously in need. This seems biologically restrictive, since one might
125 naturally expect those individuals in the signalling pool with greatest need to signal
126 more vigorously than the others (perhaps only a little and perhaps only sometimes), or
127 those parents whose costs just tip them into the position of being willing to feed might
128 sometimes be slightly more reluctant to do so than individuals for whom the costs are

129 lower. Maynard Smith & Harper [1] argue verbally that the no-cost signalling ESS
130 will not be robust to such a violation of model assumptions. Here we will investigate
131 this more fully with a formal model. Before relaxing the restriction of the fixed
132 number of signalling levels – we quickly review the key features of the original
133 model.

134

135 **The Original Model**

136 Suppose that we have a population which contains both signallers and receivers. It
137 might be the case that members of the population are always in one of the roles (e.g.
138 males signalling to females) or that every individual can be in either role at some
139 point in their lives (e.g. chicks signalling to parents). We note that for the type of
140 solutions that we describe below to occur, there needs to be a degree of relatedness
141 between signaller and receiver, so that the second of these scenarios is the more
142 natural to consider. A strategy in this context involves both how to behave as a
143 signaller and how to behave as a receiver.

144

145 The two-pool case can be represented as follows.

146

147 The states of individual signallers of interest to the receiver is their health (x), which
148 is continuously distributed within the range $[0,1]$. Signallers with low health are in
149 most need of donation of resources from the signal receiver (hereafter called the
150 donor). At the ESS, the signaller signals “high-need” if it is in health range $0 \leq x < a$
151 and “low-need” if it is in health range $a < x \leq 1$.

152 The health of donors are also continuously distributed across $[0,1]$. A donor can
153 respond in an interaction with a signaller by either donating resources or not.

154 Donation costs the donor (and this cost is easiest to bear for those in best health), and
155 benefits the signaller (and is most valuable to low-health signallers). The fitness
156 benefit from an interaction to a donor is 1 if it keeps the reward, but a lower level y if
157 it donates it; the fitness benefit of an interaction for the signaller is x if there is no
158 donation and 1 if it receives a donation.

159 Given this, at the ESS, the donor will donate to the signaller if its own health y is
160 greater than y_1 when it receives the high-need signal, and if its own health y is greater
161 than y_0 when it receives the low-need signal. Clearly y_0 should be greater than y_1 in
162 any stable signalling system.

163 The donor and signaller have relatedness coefficient k ($k \leq 1$) such that the inclusive
164 fitnesses (payoffs) are as follows.

165 For the donor, the payoff is $1 + kx$ if there is no donation and $y + k$ if there is. For the
166 signaller the payoff is $x + k$ if there is no donation and $1 + ky$ if there is.

167

168 Thus, if complete information on the health state of both parties were available, then
169 the donor would prefer to donate provided that

170

$$171 \quad y > 1 + k(x - 1).$$

172

173 This is the area above line D in Figure 1a.

174

175 The signaller would prefer donation provided that

176

$$177 \quad y > 1 + \frac{x - 1}{k}.$$

178

179 This is the area above line S in Figure 1a.

180

181 Thus there is an area below line S where both parties agree that no donation is best, an
182 area above line D where both parties agree that donation is best, and the wedge-
183 shaped area between the two lines where the signaller would prefer that donation
184 occur but the donor would prefer that it did not.

185

186 We assume that the health of both receivers and donors are uniformly spread over
187 $[0,1]$. However, we believe that our key results would be qualitatively unchanged for
188 any alternative distribution which allowed all health values to occur at least
189 sometimes. We seek expressions for the ESS strategy of the signaller (the value of a)
190 and that of the donor (the values of y_0 and y_1).

191

192 For a given value of the signalling threshold (a), receiving the high-need signal means
193 that the signaller is equally likely to have a value anywhere in the range $[0,a]$ and so
194 on average the donor fitness from choosing not to donate is

195

196
$$\int_0^a \frac{1+kx}{a} dx = 1 + \frac{ka}{2}.$$

197

198 Alternatively, if the donor chooses to donate, its fitness is $y+k$. Thus the donor
199 should donate on encountering a high-need signaller if its fitness is greater by taking
200 that option: i.e. if

201

202
$$y+k > 1 + \frac{ka}{2} \Rightarrow y > 1 - k \left(1 - \frac{a}{2}\right).$$

203

204 This allows us to define y_l introduced above:

205

$$206 \quad y_l = 1 - k \left(1 - \frac{a}{2} \right). \quad (1)$$

207 It is clear that any other choice yields a strictly smaller payoff against the high need
208 signal. When receiving the low-need signal, the donor fitness when it does not donate
209 is

210

$$211 \quad \int \frac{1+kx}{1-a} dx = 1 + \left(\frac{k}{2} \right) (1+a).$$

212

213 Thus, in this case, it should donate when

214

$$215 \quad y + k > 1 + \left(\frac{k}{2} \right) (1+a) \Rightarrow y > 1 - \left(\frac{k}{2} \right) (1-a).$$

216

217 This allows us to define the second threshold value y_o :

218

$$219 \quad y_o = 1 - \left(\frac{k}{2} \right) (1-a). \quad (2)$$

220 It is clear again that any other choice yields a strictly smaller payoff against the low
221 need signal.

222 Thus, for a given signaller strategy (choice of a) we can find the best donor strategy
223 (choice of y_0 and y_l). Note that from (1) and (2) it follows that $y_0 - y_l = k/2$.

224

225 The strategy pair is unstable against a change in the value of a unless a signaller of
226 health a does equally well by signalling high- or low-need.

227

228 If it signals high need it gains:

229

$$230 \int_0^{y_1} (x+k)dy + \int_{y_1}^1 (1+ky)dy . \quad (3)$$

231

232 If it signals low need then it gains

233

$$234 \int_0^{y_0} (x+k)dy + \int_{y_0}^1 (1+ky)dy . \quad (4)$$

235

236 Equating (3) and (4), and substituting $x = a$, and y_0 and y_1 as defined in (1) and (2)
237 gives (after some simple calculations) a unique value of a :

238

$$239 a = \frac{4-3k^2}{4-2k^2} .$$

240 For an individual of health slightly higher (lower) than a , the payoff in (4) is higher
241 (lower) than the payoff in (3), so that any other choice of strategy yields a strictly
242 smaller payoff. Thus any change in strategy by either player yields a strictly smaller
243 payoff, and so the strategies of the signaller (a) and the donor (y_0 and y_1) are in a
244 strict Nash equilibrium pair, and so form an ESS pair.

245

246 This equilibrium is illustrated in Figure 1a. Notice that the range of signaller health
247 states corresponding to high-need only includes cases where the signaller would

248 prefer that donation occurs; whereas low-need signalling involves all three situations,
249 including situations where both parties would benefit from donation.

250

251 Donation occurs in the two rectangular boxes whose upper side is the horizontal line
252 where $y = 1$. Thus instances of donation span all three possible outcomes, including
253 situations where neither party benefits from donation. Instances of no-donation also
254 cover cases of all three possible combinations of outcomes.

255

256 **Consequences of allowing another signal**

257

258 Suppose we allow a new type of signaller into the population described above that can
259 use another signal that is indicative of ultra-high need for very low health individuals,
260 so the signaller strategy for this new type of signaller is a pair of values a and b such
261 that those with health ranges $(0, b)$ use this new signal of ultra-high need, those with
262 health in the range (b, a) use the same signal of high-need as used by the old signallers
263 across the wider range $(0, a)$, and those with health $(a, 1)$ give the same low-need
264 signal that old signallers gave in this range. We assume the value of a is the same for
265 the new signaller type as for the old type described in the last section. Suppose that a
266 new type of donor also appears in the population, either because a single mutation
267 alters the behaviour in both roles of individuals who sometimes play as signaller and
268 sometimes as donor; or because genetic drift first introduces new behaviour on the
269 part of individuals who act only as donors, and then a mutation introduces new
270 behaviour on the part of individuals who act only as signallers. We consider two
271 possibilities for this new donor behaviour

272

273 One can potentially imagine two types of donor responses, that is two different types
274 of new donor responses to this new signaller type.

275

276

277 1) The donor recognizes the new ultra-need signal and responds by increasing the
278 range of its own health status over which it will donate in response to this
279 ultra-high need signal; however it treats the other two signals exactly as
280 donors treated those signals when given by the old type signallers. In this
281 situation, the new strategy offers a selective advantage to the signaller and
282 should spread. Thus in our analysis we shall concentrate on mutants of the
283 second type.

284

285 2) The donor can differentiate between old and new type signallers, and behave
286 towards their signals accordingly. We note that it is by no means clear that
287 mutants will be able to make such a distinction, but that if they cannot,
288 mutants will be of the first type, and so invasion will clearly be possible. If
289 distinction can be made by donors, they realise that an old type signal that
290 signals high-need will indicate health somewhere between 0 and a , whereas a
291 similarly signalling new type individual will have health between b and a , and
292 thus will on average be healthier. Thus, although the donor will be more
293 prepared to donate to ultra-high signalling by the new type signaller (shown as
294 the region (1) in figure 1b) it will also become less willing to donate to new
295 signallers that use the high-need signal (shown as the region (2) of Figure 1b).

296

297 As mentioned above, we will focus on situation (2), as the most biologically
 298 interesting. We will consider a population comprising of both new and old type
 299 signallers, and new and old type donors. Firstly, suppose that a new type signaller
 300 and a new type donor meet. There is no reason why the response to the low-need
 301 signal will change because of the introduction of the ultra-high need signal. Thus y_0 is
 302 unchanged from old type signallers. The response of new type donors to these new
 303 type signallers will then be given by the critical values (y_0, y_I^*, y_2) : as shown in
 304 Figure 1.

305

306 By analogy with equation (1), the donor will donate if it obtains the ultra-high-need
 307 signal and its own health is greater than y_2 , where

308

$$309 \quad y_2 = 1 - k \left(1 - \frac{b}{2} \right). \quad (5)$$

310

311 If it receives the intermediate (high-need) signal, it donates if

312

$$313 \quad y + k > \frac{1}{a-b} \int_b^a (1+kx) dx \Rightarrow y > 1 - k \left(1 - \frac{a}{2} - \frac{b}{2} \right).$$

314

315 Thus the signal will be responded to when $y > y_I^*$, where

316

$$317 \quad y_I^* = 1 - k \left(1 - \frac{a}{2} - \frac{b}{2} \right). \quad (6)$$

318

319 Thus donation happens for the new signaller where it did not happen for old signallers
320 when

321

$$322 \quad 0 < x < b \quad (7a)$$

323

324 and

325

$$326 \quad 1 - k \left(1 - \frac{b}{2} \right) < y < 1 - k \left(1 - \frac{a}{2} \right). \quad (7b)$$

327

328 The region associated with (7a) and (7b) is marked as region 1 of Figure 1b.

329

330 However, donations now no longer happen for new signallers when they did happen
331 for old signallers, when

332

$$333 \quad b < x < a \quad (8a)$$

334

335 and

336

$$337 \quad 1 - k \left(1 - \frac{a}{2} \right) < y < 1 - k \left(1 - \frac{a}{2} - \frac{b}{2} \right). \quad (8b)$$

338

339 This is marked as region 2 of Figure 1b.

340

341 The areas of both regions 1 and 2 are $0.5kb(a-b)$. The gain to the signaller in region

342 (1) from the new signal is given by

343

344
$$\int_0^b \int_{1-k\left(\frac{1-\frac{a}{2}}{1-\frac{b}{2}}\right)}^{1-k\left(\frac{1-\frac{a}{2}}{2}\right)} (1+ky-x-k)dydx.$$

345

346 If we assume that b is very small (so the ultra-high-need signal is only given by
347 individuals of a very low health state), then this expression is well approximated by
348 the simpler form

349

350
$$b \int_{1-k}^{1-k+\frac{ka}{2}} (1-k+ky)dy = \left(\frac{kba}{2}\right) \left(1-k^2 + \frac{k^2a}{4}\right). \quad (9)$$

351

352 Similarly the signaller gain in region (2) from the new signal is given by

353

354
$$- \int_b^a \int_{1-k+\frac{ka}{2}}^{1-k\left(\frac{1-\frac{a+b}{2}}{2}\right)} (1+ky-x-k)dydx.$$

355

356 Assume again that b is very small, then this expression is well approximately by the
357 simpler form

358

359
$$-\frac{kb}{2} \int_0^a \left(1-k^2\left(1-\frac{a}{2}\right)-x\right)dx = -\left(\frac{kba}{2}\right) \left(1-k^2 + \frac{k^2a}{2} - \frac{a}{2}\right). \quad (10)$$

360

361 Combining (9) & (10) the overall gain from regions (1) and (2) for the new type
362 signaller is given by

363

364 $\frac{bka^2}{4} \left(1 - \frac{k^2}{2}\right).$

365

366 Thus, since $k < 1$, overall the signallers gain from using the new type signal.

367

368 The donor gain in region (1) is given by

369

370
$$- \int_0^b \int_{1-k\left(\frac{1-b}{2}\right)}^{1-k\left(\frac{1-a}{2}\right)} (1+kx-y-k) dy dx.$$

371

372 Using the same assumption as for the signaller, this is well approximated by

373

374
$$-b \int_{1-k}^{1-k+\frac{ka}{2}} (1-k-y) dy = \frac{bk^2a^2}{8}. \quad (11)$$

375

376 Thus donors gain from their responses to the new signal in region (1).

377

378 In region (2) the donor gain is given by

379

380
$$\int_b^a \int_{1-k\left(\frac{1-a}{2}\right)}^{1-k\left(\frac{a+b}{2}\right)} (1+kx-y-k) dy dx.$$

381 The same limiting case, allows us to simplify this to

382

383 $\frac{kb}{2} \int_0^a \left(kx - \frac{ka}{2} \right) dx = 0$. (12)

384

385 There is no gain or loss to donors in this region which sits close to the borderline
386 determining whether it is optimal for the donor to donate or not, and spans cases
387 above and below that borderline (line D in figure 1b).

388

389 Thus, overall both donors and signallers benefit from the new signalling strategy
390 when they meet.

391

392 Any interaction between a new type signaller and an old type donor which cannot
393 distinguish the new ultra-high need signal from the high-need signal will be exactly
394 the same as one involving an old type signaller and an old type donor.

395

396 Similarly when a new type donor meets an old type signaller, the donor recognizes
397 that it is an old type signaller and responds to signals optimally (i.e. identically to an
398 old type donor) and so the rewards will again be exactly the same as one involving an
399 old type signaller and an old type donor.

400

401 Thus, in a well-mixed population of old and new type signallers and old and new type
402 donors both of the new types will out-compete the old types until both of the new
403 types dominate the population. This means that the original pooled equilibrium is not
404 stable against invasion by at least this type of very-needy signaller.

405

406 In addition, by analogous reasoning to that presented above, it is likely that the
407 population of new type signallers and donors will similarly not be stable and will be
408 vulnerable to subsequent invasion by another even more complex signaller. A pooled
409 equilibrium system with an infinite number of strategies, whilst mathematically
410 possible, is not biologically realistic; eventually, we might expect the pooled
411 equilibrium to break down and be replaced by a cost-based continuous signalling
412 system. Consequently the only situation where we expect pooled equilibria to be
413 stable is where there is some physical constraint on signal production or signal
414 reception that leads to only a finite number of discrete signal types being possible,
415 each signal being given by signallers or received by donors in exactly the same way
416 despite the fact that they are generated and received by individuals from across a
417 range of different inherent qualities.

418

419 **Discussion**

420 In this paper we have considered a population where individuals can be in one of two
421 main roles, signaller and receiver. The signaller sends a signal to the receiver, and the
422 receiver must decide how to act based upon the signal received. We considered an
423 important model of this type of system due to Bergstrom and Lachmann [5], and have
424 demonstrated that under reasonable assumptions such a system will not be stable.

425

426 It should be noted that it was not necessary for our analysis to consider some of the
427 important features of signalling systems, because we only needed to show that certain
428 types of signalling strategies are not stable. In particular, a question we have not
429 addressed is how can a population resist invasion by strategies which differ only in
430 how a receiver responds to a signal not received in the equilibrium (perhaps genetic

431 drift could lead to suboptimal receiver responses, which may then allow different
432 signalling strategies to invade)? A reasonable assumption would be to use the
433 trembling hand idea of [8], which effectively assumes that occasional "mistakes"
434 occur (either individuals giving the wrong signal by mistake, or mutant individuals
435 with poor strategies) which means that every strategy is met occasionally. Thus any
436 stable strategy must respond optimally even against strategies that are not seen in the
437 equilibrium, and such neutral invasion is often avoided. To demonstrate stability we
438 would have to consider carefully how mutant strategies arise in such a population, and
439 different assumptions in this regard could lead to different results.

440

441 Our result shows that unless there is some physical impediment to the diversity of
442 signals possible, then pooled-equilibrium signalling strategies do not seem stable.
443 Such a strategy would be invaded by a more complex signal, where some individuals
444 within a "pool" benefit from signalling their difference from other individuals within
445 the pool. It is difficult to think of biological situations where such restrictions will
446 apply to either the mechanisms of signal transmission or reception that would
447 constrain signals to a small number of discrete levels. Hence, we suggest that the
448 assumption of pooled equilibrium theory that such restriction occurs considerably
449 decreases the biological relevance of this theory.

450

451 Our work can be seen as extending the work of Brilot & Johnstone [7], who
452 demonstrated that the stability of a pooled-equilibrium against mutants with different
453 threshold levels (different values of a in our model) will be dependent on the
454 distributions of need across the populations of signallers and donors. Specifically
455 they show a requirement for this type of stability is that the ratio of maximum to

456 minimum need of the signaller exceeds a critical value that increases as the
457 relatedness of signaller and receiver decreases. From this they conclude that their
458 results “suggest that the necessary conditions for cost-free communication of need
459 are, in fact, quite restrictive”. Our work amplifies this conclusion, emphasizing
460 pooled-equilibrium theory’s critical dependence on the restriction of the available
461 signal levels to a finite number, in addition to the restriction that Brilot & Johnstone
462 [7] demonstrate.

463

464 A rather different scenario involving discrete signals to communicate a continuous
465 hidden need state when competing for a resource in a zero-cost signalling game was
466 investigated in [9]. In this game both players signalled (or declined to signal and
467 immediately conceded) and the one with the lower signal conceded the resource, with
468 identical signals leading to a fight. When an additional signal was made available,
469 optimal play involved the lowest signal being used for a range of need values which
470 led to no signal in the original game. Thus individuals did not change the size of the
471 pool used by signals other than that for no signal. In that case, a different type of
472 model, with a different biological interpretation than nestling begging, does not result
473 in a decay of discrete signal use.

474

475 A related model of the type of signaling system we have described was considered in
476 [10]. In this paper a signaller observes a piece of information which affects the
477 potential reward to both itself and a receiver. The signaller then sends a signal to the
478 receiver conveying some information about its observation, after which the receiver
479 makes a choice which determines the result of the game. An interesting feature of this
480 game is that it was proved that there is an upper bound on the number of distinct

481 signals that can feature in an optimal signalling strategy (unless the interests of both
482 signaller and receiver completely coincide), even when the number of available is
483 unlimited, as opposed to our case. The main differences between this model and ours
484 is that while there is effectively an infinite number of signalling types in each case, in
485 [10] there is only one receiver type (which has an infinite number of potential
486 choices), whereas we have an infinite number of receiver types (with two potential
487 choices). In particular in our model no matter how many signals there are, there will
488 likely be circumstances when the associated choices lead to both individuals making
489 the wrong choice (see Figure 1), as opposed to the one if they knew both of the health
490 values, and there is thus always scope for a new signal to improve the communication,
491 whereas this does not occur in [10].

492

493 In many situations, signallers that vary continuously in quality and are capable of
494 continuous variation in the level of signalling of that quality, in fact restrict their use
495 of this flexibility, using only a limited number of different signal strength levels [11].
496 However, this observation does not provide support for the assumption of pooled-
497 equilibrium theory of the restriction of signals to a finite number of levels. Firstly, the
498 theory of such “all or nothing” signalling involves such limitations to the signal
499 strengths used as emergent predictions of the theory; the signallers remain physically
500 capable of using other levels of signal intensity, they simply play a strategy that does
501 not use this ability [12]. This is quite different from the assumption of pooled-
502 equilibrium theory that such flexibility is impossible. Secondly, current understanding
503 of the evolution of all or nothing signalling is based on the theory of costly signalling
504 [11], rather than the no-cost signalling that is the focus of pooled equilibrium theory.
505 The type of pooled equilibria described in this paper also occur for costly signals, and

506 they are often (but not always) stable against invasion [13]. This is because at the
507 boundary, the signal chosen is just costly enough so that signalling or not would be
508 equally profitable. Given the signal level, any change in the boundary would give a
509 worse payoff. Whether a change in signal level is stable depends upon how
510 individuals respond to non-received signals, and this will in turn depend upon how
511 such mutants occur.

512

513 The original motivation for the development of pooled-equilibrium theory was that it
514 has proven challenging to demonstrate empirically in many signalling systems the
515 strategic costs required to maintain signalling honesty through handicap theory [5].
516 This remains an important issue in our understanding of animal communication [5],
517 and we feel that it is important that other potential honesty-ensuring mechanisms are
518 given consideration alongside the highly-influential handicap theory (see [14] for a
519 thorough discussion of these). In particular, we feel that the potential for verification
520 and thus identification and punishment of lying, may warrant closer consideration. For
521 example, like much theory in animal-communication, pooled-equilibrium theory was
522 developed with begging signals of avian chicks in mind. An important issue here is
523 that many theories, including pooled equilibrium theory, have assumed that each
524 interaction between signaller and receiver occurs independently, with the interactants
525 having no memory of any the previous interactions with their current signalling
526 partner. This may be quite a poor representation of the relationship between chick and
527 feeding parent. In small passerine birds it may not be uncommon for a parent to visit
528 the nest with food over a hundred times in a single day [15]. Birds have been shown
529 to demonstrate considerable feats of memory [16]. It seems not impossible that a
530 parent bird could recall a chick's recent history (over a number of nest visits) of call

531 intensity along with the recent history of its own reactions to such calls, and compare
532 these with visible changes in the chick (say in terms of appetite or size). This
533 comparison might allow the parent to make inferences about the honesty of the
534 chick's recent signalling. That is, the parent might not be able to detect that any one
535 particular signal was dishonest, but could measure the long-term average honesty of
536 signals received from a particular chick. If such signalling was (on average)
537 sufficiently dishonest, this adult should certainly be capable of responding to this, by
538 reducing the influence of that chick's future signalling in making its feeding
539 decisions. As such, honesty might be maintained by the costs that are imposed on
540 cheating signallers by the loss of trust given to them by receivers.

541

542 In conclusion, we suggest that pooled-equilibrium theory does not offer a likely
543 alternative to handicap theory for situations where the strategic costs of signal
544 production required for handicap theory appear to be absent. However, there may be
545 uncontroversial but under-considered alternative explanations for minimal cost
546 signalling; and we recommend that signal verification and the discovery of cheating
547 may be an important mechanism.

548

549

550 **Figure Caption**

551 **Figure 1:** Graphical summary of the different regions of interaction between potential
552 donor and signaller as a function of their health status (x and y respectively). **(a)** The
553 previously-studied system where only two signal types are possible; **(b)** The situation
554 introduced in this paper, where an additional signal is available to those signallers in

555 most need of donation. If complete information on the health state of both parties
556 where available, then the donor would prefer to donate in
557 the area above line D. The signaller would prefer donation in the area above line S.
558 Thus there is an area below line S where both parties agree that no donation is best, an
559 area above line D where both parties agree that donation is best, and the wedge-
560 shaped area between the two lines where the signaller would prefer than donation
561 occur but the donor would prefer that it did not. In the two-signal situation the
562 signaller signals "high-need" if it is in health range $0 \leq x < a$ and "low-need" if it is in
563 health range $a < x \leq 1$. The donor will donate to the signaller if its own health y is
564 greater than y_1 when it receives the high-need signal, and if its own health y is greater
565 than y_0 when it receives the low-need signal. In the three signal-system we add a
566 signal of very high need for $x < b$ and y_1 changes to y_1^* .

567

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Figure 1a

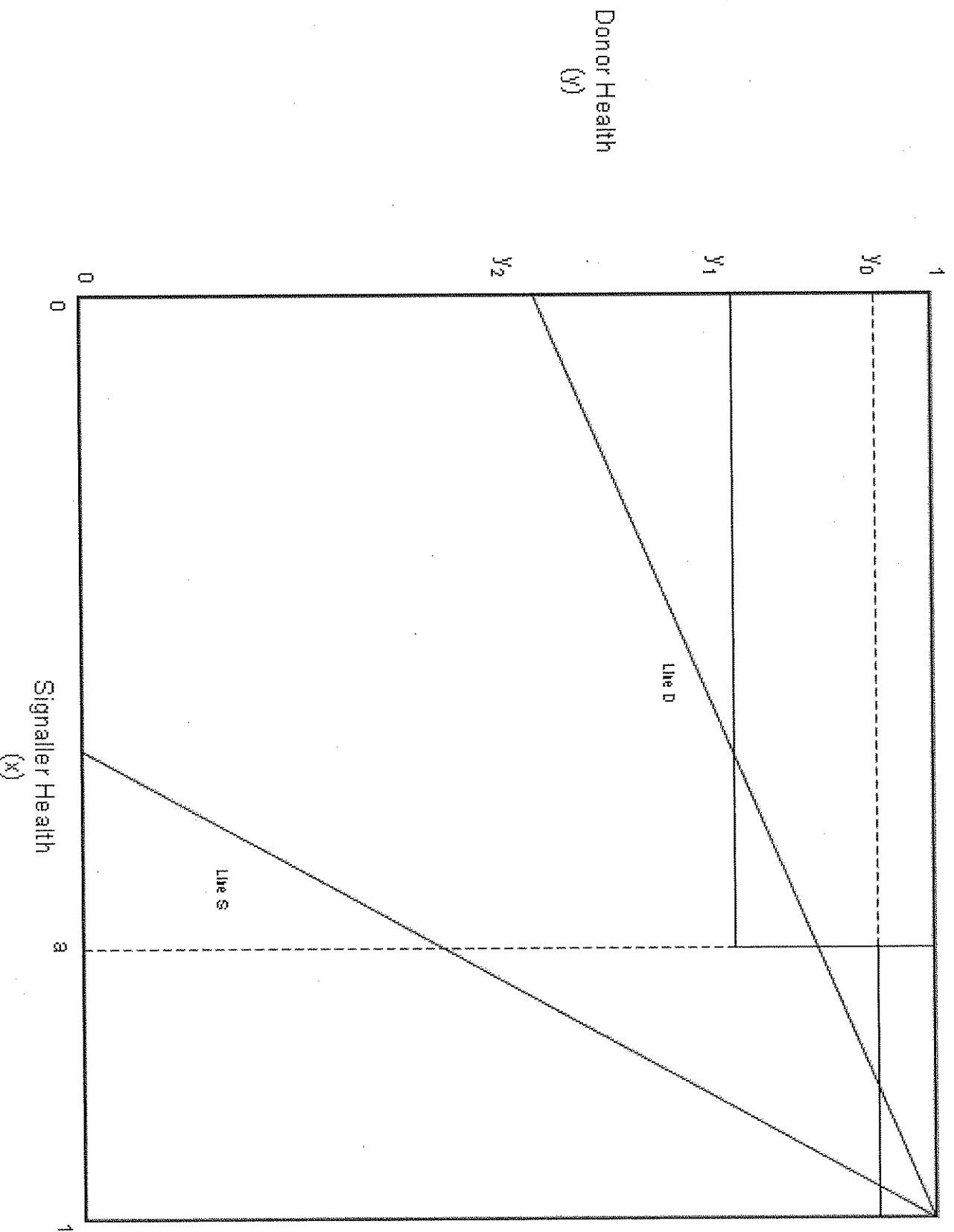


Figure 1b

