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

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Abstract

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

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

Introduction

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

However, there are a number of alternative situations that can also allow evolutionary stability of signalling without reliance on strategic costs. One of these is that the form of the signal is causally linked to the quality of interest to receivers, such that dishonest signals are physically not possible. Such an "unfakable" signal is generally called an index [1]. Consider an example where a female tiger moves through the territories of several males, she is the receiver and what she is interested in is the size of the territory-holding male (preferring larger males). Imagine that males signal their size by stretching up a tree trunk with their forelegs to leave scratch marks as high up as they can. This may be an example of an index. Smaller males are simply unable to make marks as high as larger males can. Males have no incentive to scratch less high than as physically possible for them and so scratch marks are a reliable signal of male size.

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

It may also be possible to have honest signalling in a situation where the individuals have different preferred outcomes of an interaction but share an overwhelming interest in common. An example of this might be an aggressive competitive interaction over a low-value resource (such as a small food item); each individual would rather that their opponent retreated yielding the resource to them, but both are anxious to avoid an escalated contest that could be very damaging to the loser.

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

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

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

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

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

As well as relatedness between signaller and receiver, an important assumption of the model of Bergstrom & Lachmann [5] (as opposed to the extension considered in this paper) is that signalling can take only a finite number of values, as can the number of responses. In the simple case here, all offspring in a signalling pool will signal with exactly the same intensity, despite the fact that individuals in the same pool vary continuously in need. This seems biologically restrictive, since one might naturally expect those individuals in the signalling pool with greatest need to signal more vigorously than the others (perhaps only a little and perhaps only sometimes), or those parents whose costs just tip them into the position of being willing to feed might sometimes be slightly more reluctant to do so than individuals for whom the costs are lower. Maynard Smith & Harper [1] argue verbally that the no-cost signalling ESS will not be robust to such a violation of model assumptions. Here we will investigate this more fully with a formal model. Before relaxing the restriction of the fixed number of signalling levels – we quickly review the key features of the original model.

The Original Model

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

The two-pool case can be represented as follows.

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

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

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

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

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

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

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

$$y > 1 + k(x - 1).$$

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

The signaller would prefer donation provided that

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

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

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

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

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

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

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

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

This allows us to define y_1 introduced above:

$$y_1 = 1 - k\left(1 - \frac{a}{2}\right). \qquad (1)$$

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

$$\int_a^1 \frac{1+kx}{1-a}dx = 1 + \left(\frac{k}{2}\right)(1+a).$$

Thus, in this case, it should donate when

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

This allows us to define the second threshold value y_o:

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

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

Thus, for a given signaller strategy (choice of a) we can find the best donor strategy (choice of y_0 and y_1). Note that from (1) and (2) it follows that $y_0 - y_1 = k/2$.

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

If it signals high need it gains:

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

If it signals low need then it gains

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

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

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

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

This equilibrium is illustrated in Figure 1a. Notice that the range of signaller health states corresponding to high-need only includes cases where the signaller would prefer that donation occurs; whereas low-need signalling involves all three situations, including situations where both parties would benefit from donation.

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

Consequences of allowing another signal

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

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

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

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

As mentioned above, we will focus on situation (2), as the most biologically interesting. We will consider a population comprising of both new and old type signallers, and new and old type donors. Firstly, suppose that a new type signaller and a new type donor meet. There is no reason why the response to the low-need signal will change because of the introduction of the ultra-high need signal. Thus y_0 is unchanged from old type signallers. The response of new type donors to these new type signallers will then be given by the critical values (y_0, y_1*, y_2): as shown in Figure 1.

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

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

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

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

Thus the signal will be responded to when $y > y_1*$, where

$$y_1* = 1 - k\left(1 - \frac{a}{2} - \frac{b}{2}\right). \tag{6}$$

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

$$0 < x < b \tag{7a}$$

and

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

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

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

$$b < x < a \tag{8a}$$

and

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

This is marked as region 2 of Figure 1b.

The areas of both regions 1 and 2 are $0.5kb(a-b)$. The gain to the signaller in region (1) from the new signal is given by

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

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

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

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

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

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

$$-\frac{kb}{2}\int_{0}^{a}\left(1-k^{2}\left(1-\frac{a}{2}\right)-x\right)dx=-\left(\frac{kba}{2}\right)\left(1-k^{2}+\frac{k^{2}a}{2}-\frac{a}{2}\right). \qquad (10)$$

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

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

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

The donor gain in region (1) is given by

$$-\int_{0}^{b}\int_{1-k\left(1-\frac{b}{2}\right)}^{1-k\left(1-\frac{a}{2}\right)}(1+kx-y-k)dydx.$$

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

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

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

In region (2) the donor gain is given by

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

The same limiting case, allows us to simplify this to

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

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

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

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

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

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

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

Discussion

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

It should be noted that it was not necessary for our analysis to consider some of the important features of signalling systems, because we only needed to show that certain types of signalling strategies are not stable. In particular, a question we have not addressed is how can a population resist invasion by strategies which differ only in how a receiver responds to a signal not received in the equilibrium (perhaps genetic drift could lead to suboptimal receiver responses, which may then allow different signalling strategies to invade)? A reasonable assumption would be to use the trembling hand idea of [8], which effectively assumes that occasional "mistakes" occur (either individuals giving the wrong signal by mistake, or mutant individuals with poor strategies) which means that every strategy is met occasionally. Thus any stable strategy must respond optimally even against strategies that are not seen in the equilibrium, and such neutral invasion is often avoided. To demonstrate stability we would have to consider carefully how mutant strategies arise in such a population, and different assumptions in this regard could lead to different results.

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

Our work can be seen as extending the work of Brilot & Johnstone [7], who demonstrated that the stability of a pooled-equilibrium against mutants with different threshold levels (different values of a in our model) will be dependent on the distributions of need across the populations of signallers and donors. Specifically they show a requirement for this type of stability is that the ratio of maximum to minimum need of the signaller exceeds a critical value that increases as the relatedness of signaller and receiver decreases. From this they conclude that their results "suggest that the necessary conditions for cost-free communication of need are, in fact, quite restrictive". Our work amplifies this conclusion, emphasizing pooled-equilibrium theory's critical dependence on the restriction of the available signal levels to a finite number, in addition to the restriction that Brilot & Johnstone [7] demonstrate.

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

A related model of the type of signaling system we have described was considered in [10]. In this paper a signaller observes a piece of information which affects the potential reward to both itself and a receiver. The signaller then sends a signal to the receiver conveying some information about its observation, after which the receiver makes a choice which determines the result of the game. An interesting feature of this game is that it was proved that there is an upper bound on the number of distinct signals that can feature in an optimal signalling strategy (unless the interests of both signaller and receiver completely coincide), even when the number of available is unlimited, as opposed to our case. The main differences between this model and ours is that while there is effectively an infinite number of signalling types in each case, in [10] there is only one receiver type (which has an infinite number of potential choices), whereas we have an infinite number of receiver types (with two potential choices). In particular in our model no matter how many signals there are, there will likely be circumstances when the associated choices lead to both individuals making the wrong choice (see Figure 1), as opposed to the one if they knew both of the health values, and there is thus always scope for a new signal to improve the communication, whereas this does not occur in [10].

In many situations, signallers that vary continuously in quality and are capable of continuous variation in the level of signalling of that quality, in fact restrict their use of this flexibility, using only a limited number of different signal strength levels [11]. However, this observation does not provide support for the assumption of pooled-equilibrium theory of the restriction of signals to a finite number of levels. Firstly, the theory of such "all or nothing" signalling involves such limitations to the signal strengths used as emergent predictions of the theory; the signallers remain physically capable of using other levels of signal intensity, they simply play a strategy that does not use this ability [12]. This is quite different from the assumption of pooled-equilibrium theory that such flexibility is impossible. Secondly, current understanding of the evolution of all or nothing signalling is based on the theory of costly signalling [11], rather than the no-cost signalling that is the focus of pooled equilibrium theory. The type of pooled equilbiria described in this paper also occur for costly signals, and they are often (but not always) stable against invasion [13]. This is because at the boundary, the signal chosen is just costly enough so that signalling or not would be equally profitable. Given the signal level, any change in the boundary would give a worse payoff. Whether a change in signal level is stable depends upon how individuals respond to non-received signals, and this will in turn depend upon how such mutants occur.

The original motivation for the development of pooled-equilibrium theory was that it has proven challenging to demonstrate empirically in many signalling systems the strategic costs required to maintain signalling honesty through handicap theory [5]. This remains an important issue in our understanding of animal communication [5], and we feel that it is important that other potential honesty-ensuring mechanisms are given consideration alongside the highly-influential handicap theory (see [14] for a thorough discussion of these). In particular, we feel that the potential for verification and thus identification and punishment of lying, may warrant closer consideration. For example, like much theory in animal-communication, pooled-equilibrium theory was developed with begging signals of avian chicks in mind. An important issue here is that many theories, including pooled equilibrium theory, have assumed that each interaction between signaller and receiver occurs independently, with the interactants having no memory of any the previous interactions with their current signalling partner. This may be quite a poor representation of the relationship between chick and feeding parent. In small passerine birds it may not be uncommon for a parent to visit the nest with food over a hundred times in a single day [15]. Birds have been shown to demonstrate considerable feats of memory [16]. It seems not impossible that a parent bird could recall a chick's recent history (over a number of nest visits) of call intensity along with the recent history of its own reactions to such calls, and compare these with visible changes in the chick (say in terms of appetite or size). This comparison might allow the parent to make inferences about the honesty of the chick's recent signalling. That is, the parent might not be able to detect that any one particular signal was dishonest, but could measure the long-term average honesty of signals received from a particular chick. If such signalling was (on average) sufficiently dishonest, this adult should certainly be capable of responding to this, by reducing the influence of that chick's future signalling in making its feeding decisions. As such, honesty might be maintained by the costs that are imposed on cheating signallers by the loss of trust given to them by receivers.

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

Figure Caption

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

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

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Figure 1a

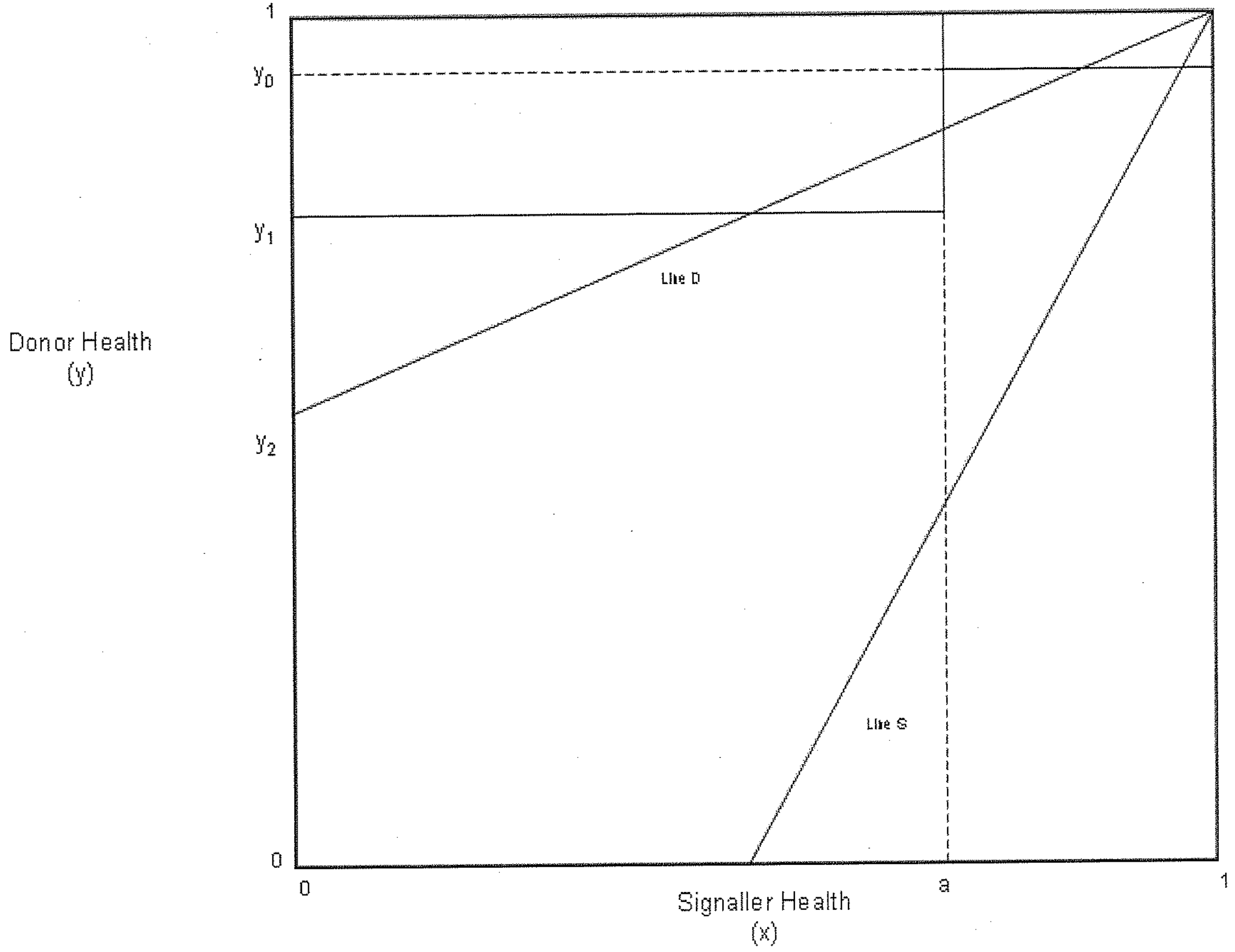
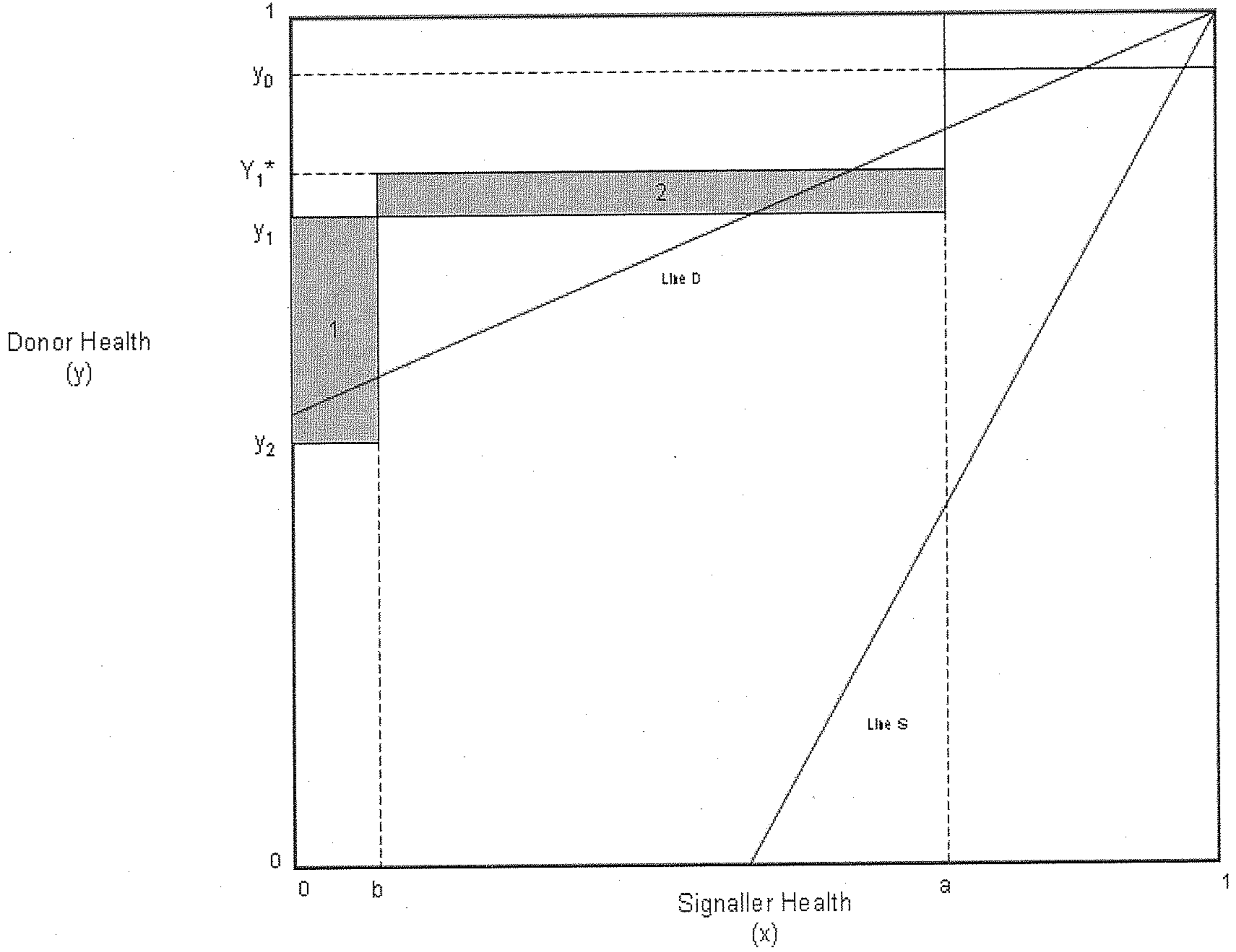


Figure 1b



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