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An overly simplistic view of evolution would say that it consists only of competition between individuals to survive. However, in actuality ecosystems are often characterized by partial common interest, that is at least some of the time it is in individuals' best interest to cooperate. Most obviously this occurs in the case of close kin, who share a large portion of common genes and thus will be at least partially successful at passing on their genes to the next generation should their actions ensure the survival of their kin at their own expense. Less obvious but still worth mentioning is that partial common interest can arise between species, even ones with an antagonistic relationship. Consider a predator species A and its prey species B. Members of A can only catch the weaker members of B, if they attempt to catch a strong member of B both will expend resources in the chase and A will get no dinner from it. This is an outcome that neither the strong member of B nor the member of A would like, and so it is in their best interest to develop some way in which the members of B can indicate if they are strong. However, weak members of B who will be eaten if they are chased, have it in their best interest to mimic the "strong signal." Thus there is only partial common interest, for some individuals it is best to cooperate with the enemy and for others it is best to deceive them.

It should be noted in the above example that if both the strong members and the weak members of the prey group send the "strong signal" then the signal will be meaningless. This is a general problem with situations of partial common interest. The solution due to Amotz Zahavi (1975) is to add a cost to signaling. If it is assumed that honest signalers get more utility out of

the preferred outcome, then by adding a high enough cost to signaling one finds that it is no longer worth it for the dishonest signalers to lie (because they lose more from signaling than they gain from the preferred outcome). Thus all members of the signaling group will signal honestly and the group that receives the signals will be able to act on them appropriately. Huttegger and Zollman (2010) found that there can actually be two types of signaling in situations like this. One type allows for perfectly honest signaling to occur but requires an extremely expensive signal. The other relies on a much cheaper signal, but at the cost of some dishonesty remaining in the system. Because nature contains both high and low cost signals these findings raise the question of whether high or low cost signaling is more likely to evolve. To answer this question I have created a new version of the Sir Phillip Sidney game, a traditional model of partial common interest, that features three signals, one with a cost in the range where perfectly honest signaling can be found, one in the range discussed by Huttegger and Zollman which can lead to partial honesty and the standard costless signal of not sending a signal. The important question is if all of these were possible signals, which would be the most likely to see use.

In the traditional set up of the Sir Phillip Sidney game, originally developed by John Maynard Smith, there are two players, a donor and a receiver. There are further two states of the world; the receiver is either needy or healthy. While the receiver can directly observe these states the donor cannot, they must rely on the receiver to communicate whether they are in fact needy or healthy. In the traditional version of the game the receiver can either send a signal and pay some associated cost or remain silent which is costless. The donor can then choose whether or not to transfer a resource to the receiver, if the donor does they hurt themselves as they no longer have access to that resource. In the context we are dealing with the donor is the parent, the receiver is the child and the resource is food, though the mathematical structure of the game

can be used to represent other situations. At the end of each round of interaction the players receive payoffs depending both on their own actions and the actions of the other player.

To be more specific each round of the Sir Phillip Sidney game can be thought of as containing three parts. First nature flips a coin to decide if the receiver is healthy or needy with probability p of being needy and probability $1-p$ of being healthy. Then the receiver sends the costly signal or does not signal. Finally the donor chooses to either donate the resource or not. Should the receiver get the resource they have a payoff of 1 regardless of whether they were needy or healthy. However, if they are needy and they do not get the resource then they receive a payoff of $1-a$ (where a is a positive number less than one) whereas a healthy receiver who does not get the resource gets a payoff of $1-b$ (where b is some positive number less than a). Because of the difference in payoffs for receivers who do not get the resource both needy and healthy receivers will want the resource, but needy ones will want it more. In addition the receiver loses the cost of any signals that they sent, represented by c . This means that a needy receiver who sent the expensive signal and received the resource would have a payoff of $1-c$. For the donor the payoffs are much simpler. If the donor keeps the resource they receive a payoff of 1, while if they send the resource they receive a payoff of $1-d$ (where d is a positive number less than 1). Finally, because we assume that the donor and receiver are related to some degree, there is a relatedness parameter k such that each player receives k times the other's payoffs. Thus in the above example the actual payoff for the receiver would be $1-c+k(1-d)$. For the purposes of this paper the only value of k that will receive attention is $k=.5$, because a parent and child share half of their genes and so ought to value the other's success half as much as their own.

When studying the traditional game (with only one costly signal) there are a total of four strategies for either player. The receiver can signal when needy, signal when healthy, always

signal, or never signal. The donor on the other hand can donate only when they receive a signal, donate only when they do not receive a signal, always donate or never donate. Arising from these four strategies in the traditional game are four Nash equilibria (stable systems where each party repeatedly plays the same strategies or set of strategies) of interest to us. Nash equilibria arise because neither player can do better by changing their strategy or set of strategy without the other player also changing their strategy. The first two called pooling equilibria feature no actual communication because the two states of the world are pooled into one signal which means the donor cannot differentiate between healthy and needy receivers. The first of these can occur when

$$d > k(pa + (1 - p)b)$$

in other words when the cost to the donor of donating is greater than the expected value of donating (that is the expected benefit to the receiver multiplied by the relatedness parameter) the donor may choose the strategy never donate. If they do the receiver will in turn choose the strategy never signal because there is no point to signaling if the donor never responds. On the other hand if the inequality is reversed and the expected benefit of donating is greater than the cost then the other pooling equilibria, where the donor always donates and the receiver still never signals, becomes possible. It should be point out that for any values of the parameters some pooling equilibria can occur, what we will turn our attention to in the simulation section of the paper is under what conditions they are least likely to occur.

Of more interest to us are the two signaling equilibria, equilibria where the signals carry meaning and affect the actions of the donor. In order for either of these equilibria to be Nash equilibria the following must hold

$$a \geq \frac{d}{k} \geq b$$

this inequality implies that the donor would prefer to give the resource only to needy receivers and not give it to healthy ones. Further in order for the strategy pair signal only if needy donate only if signal to be a Nash equilibrium it must be the case that

$$a \geq c + kd \geq b$$

meaning that the receiver prefers paying the cost to signaling and the loss of the donor to not getting the resource when needy but does not when healthy. The other signaling equilibrium, signal only if healthy donate only if no signal occurs when

$$a \geq kd - c \geq b$$

however, this equilibrium is not particularly relevant to this paper as it requires values of k that are rather large, indicating a greater investment in the well-being of the other player than is realistic.

The equilibria that we have discussed so far are all what is called pure strategy equilibria, because in them each player plays one and only one strategy. Also of interest are what Hutteger and Zollman (2010) call hybrid equilibria. In these equilibria at least one player randomizes over two or more strategies. Hybrid equilibria occur when a player is indifferent between two or more strategies (and they have no better strategies) and neither player can do better by unilaterally deviating from the current strategy setup. The first hybrid equilibrium of interest is the one discussed by Hutteger and Zollman where the receiver plays some mixture of signal only if needy and always signal and the donor plays some mixture of donate only if signal and never donate. This equilibrium can occur only when

$$a \geq \frac{d}{k} \geq b$$

as in the signaling equilibrium and

$$b > c + kd$$

unlike the signaling equilibrium. It is particularly important to note that it is impossible for both the hybrid and signaling equilibria to exist simultaneously if there is only one signal because they require signal costs that are mutually exclusive.

The preceding represents the traditional understanding of the Sir Phillip Sidney game. To answer the question of whether the high cost signaling equilibrium or the low cost Huttegger and Zollman hybrid equilibrium is more likely to evolve I developed a new version of the game featuring two costly signals, c_1 and c_2 , with the former being in the range in which honest signaling can occur and the latter being in the range in which the hybrid equilibrium is possible. The addition of this signal increases the strategy space from four strategies for donors and four for receiver to eight strategies for donors and nine for receivers. It should be noted however, that this new version of the game contains all of the equilibria that the old version contains, though the strategies are slightly different. For example the signaling equilibrium is now composed of the strategy send c_1 when needy, do not signal when healthy, never send c_2 and either the strategy donate when c_1 , do not donate when no signal or c_2 or the strategy donate when c_1 or c_2 , do not donate when no signal.

However, the edition of a second costly signal creates the possibility of another kind of hybrid equilibrium that to the best of my knowledge has not been discussed in the literature. In the context of the Sir Phillip Sidney game this equilibrium consists of the receiver randomizing

between the expensive and cheap signals when needy and randomizing between the cheap signal and no signal when healthy while the donor always donates when given the expensive signal, never donates when given the no signal and randomizes between donating and not donating when they receive the cheap signal. Due to the complexity of this equilibrium the conditions under which it can arise are also rather complicated.

The equilibrium is decidedly simpler on the donors side because the donor can be thought of as randomizing over two strategies (donate only if sent the expensive signal and donate if sent either the cheap or expensive signal). If we begin by assuming that the sender sends either signal c_1 or c_2 (on probabilities $1-m$ and m respectively) when needy and sends signal c_2 or no signal (on probabilities n and $1-n$ respectively). If the donor receives a signal of c_1 or no signal they have perfect information and act accordingly (by donating and not donating respectively). If the donor receives signal c_2 however the donor only has partial information about the state of the world. The probability, x , that the sender is needy given that signal c_2 was sent is given by:

$$x = \frac{mp}{mp + n(1 - p)}$$

In order for the new hybrid equilibrium to occur it must be the case that the donor is indifferent between donating and not donating when they receive signal c_2 (additionally it must be the case that the donor wants to donate given c_1 and does not given no signal in other words $a \geq \frac{d}{k} \geq b$).

Thus the following equality must hold:

$$k(1 - c_2) + 1 - d = x(k(1 - a - c_2) + 1) + (1 - x)(k(1 - b - c_2) + 1)$$

where the left side represents donating and the right side represents not donating. This equation can be simplified to:

$$x = \frac{d - kb}{k(a - b)}$$

Which must fall between zero and one since x is a probability.

The analysis of the sender's behavior in the new hybrid equilibrium is more complicated since we must determine their indifference not over two but four strategies, as there are multiple pairs of strategies that when randomized over can create the new hybrid equilibrium. To begin with we must assume that when the sender sends signal c_1 the donor will donate, when the sender sends no signal the donor will not donate, and when the sender sends signal c_2 the donor will donate some with probability q and not donate with probability $1-q$. There are then four strategies of interest:

1. Send signal c_1 if needy and c_2 if healthy.
2. Send signal c_2 if needy and no signal if healthy.
3. Send signal c_1 if needy and no signal if healthy
4. Always send signal c_2 .

In particular we will see that there are three possible combinations of these strategies that can lead to the new hybrid equilibrium, 1 and 2, 3 and 4, and finally all four together. Though being indifferent between any three of the strategies would also lead to the new hybrid equilibrium I will show that it is not possible to be indifferent between any three without also being indifferent towards the fourth. There are six total ways in which the sender can be pairwise indifferent and I will examine all of them starting with indifference between 1 and 2:

$$q(1 - p)(b - kd) - c_2 - pc_1 + pc_2 + pb - pkd = q(pa - pkd) + pb - pa - pc_2$$

$$q = \frac{c_2 + pc_1 - 2pc_2 - pa + pkd}{b - kd - pb - pa + 2pkd}$$

indifference between 1 and 3:

$$q(1 - p)(b - kd) - c_2 - pc_1 + pc_2 + pb - pkd = pb - pc_1 - pkd$$

$$q = \frac{c_2}{b - kd}$$

indifference between 1 and 4:

$$q(1 - p)(b - kd) - c_2 - pc_1 + pc_2 + pb - pkd = q(pa - pb + b - kd) + p(b - a) - c_2$$

$$q = 1 - \frac{c_1 - c_2}{a - kd}$$

indifference between 2 and 3:

$$q(pa - pkd) + pb - pa - pc_2 = pb - pc_1 - pkd$$

$$q = 1 - \frac{c_1 - c_2}{a - kd}$$

indifference between 2 and 4:

$$q(pa - pkd) + pb - pa - pc_2 = q(pa - pb + b - kd) + p(b - a) - c_2$$

$$q = \frac{c_2}{b - kd}$$

indifference between 3 and 4:

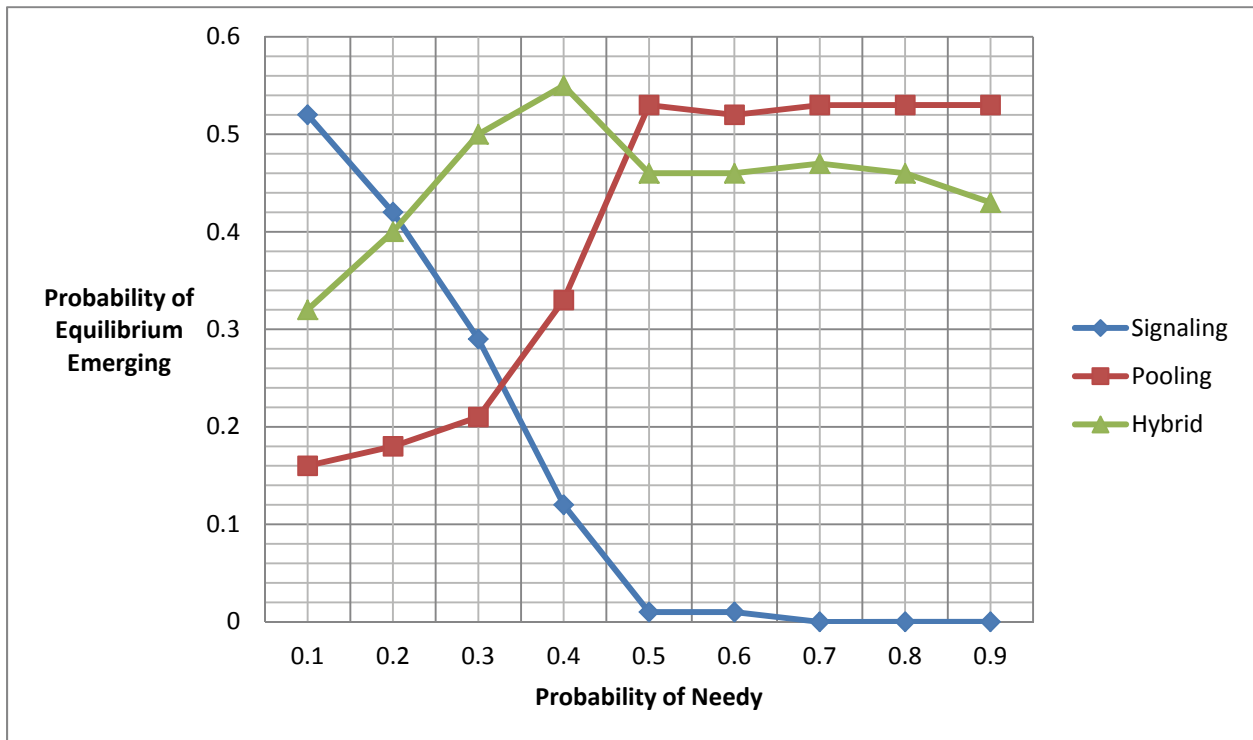
$$pb - pc_1 - pkd = q(pa - pb + b - kd) + p(b - a) - c_2$$

$$q = \frac{c_2 + pa - pc_1 - pkd}{pa - pb + b - kd}$$

Of particular importance to note is that the condition for being indifferent between 1 and 3 is the same as the condition for indifference 2 and 4, and likewise for indifference between 1 and 4 and between 2 and 3. This feature of the indifference requirements is what allows us to remove the four possible equilibria in which the sender is indifferent between three of the strategies from consideration, since by satisfying the indifference criteria for three of the strategies the sender must also be indifferent to the fourth.

While understanding the conditions under which equilibria can occur is quite useful, it does not help us to answer any of the three fundamental questions raised in this paper. Namely, how likely is it that any form of signaling will evolve relative to pooling, how likely is it that the honest signaling equilibrium will occur relative to the Huttegger and Zollman hybrid equilibrium, and is there any evolutionary significance to the new hybrid equilibrium? To answer these questions we must utilize a mathematical model known as the replicator dynamics, a model used to study how differential reproduction affects population composition. In the replicator dynamics we use the difference between an individual's payoff and the average payoff for individuals of that type (donor or receiver) as a stand in for biological fitness. In other words when individuals play do better than average playing a particular strategy they are more successful than average and produce more offspring than average who will play the same strategy in the next round. It should be noted that in the replicator dynamics players are paired at random and that the population must be effectively infinite. While these assumptions are a bit unrealistic I do not think they adversely affect the model's predictions.

In my simulations I was most interested in the size of the basins of attraction (areas in the strategy space that converge to an equilibrium) of the signaling equilibrium, the pooling equilibrium and the Huttegger and Zollman hybrid equilibrium as p varied. To study this I randomly selected an initial population, that is what portion of the population was playing each of the strategies (9 for receivers, 8 for donors) was random. As I previously mentioned because I was modeling a biological system I used the replicator dynamics which means that other than the first round (where I randomly decided the distribution) the portions of the population playing each strategy are determined by how well that strategy did in the preceding round. I let these simulations run for 1000 generations then looked to see which if any of the equilibria of interest the system was in. For each value of p I ran 1000 of these 1000 generation simulations and looked at the proportion which ended in each type of equilibria to determine its basin of attraction. The results can be seen in the following graph.



The graph shows probability of the receiver being needy (p) versus the probability of the equilibrium arising for the three equilibria of interest.

The values of the other parameters are as follows: $a=29/32$, $b=5/32$, $d=1/4$, $c_1=13/32$, $c_2=1/64$ and $k=1/2$.

As you can see at low values of p the signaling and hybrid equilibria have roughly equal basins of attraction (though the signaling equilibrium is larger) while the pooling equilibrium has a much smaller basin of attraction, and the new hybrid equilibrium never occurred. To put this in the context of the questions I wish to answer these results would seem to indicate that at low values of p signaling of any kind is much more likely than pooling, honest signaling is more likely than the Huttegger and Zollman hybrid and the new hybrid is not evolutionarily significant. However, as p rises the pooling equilibrium's basin of attraction grows while the signaling equilibrium's basin of attraction shrinks. While the hybrid equilibrium does undergo some changes in basin of attraction size it is the most consistent of the three. These results mean that as p increases it becomes less likely for any signaling to evolve, and that if signaling were to evolve at higher values of p it would most likely be of the Huttegger and Zollman hybrid variety.

As for the new hybrid equilibrium while it is theoretically very interesting it would appear to be unstable, as even in simulations in which I artificially placed the system into the equilibrium it rather quickly turned into honest signaling (recall that the third receiver strategy of comprising the hybrid is the honest signaling strategy). While this is somewhat disappointing I think that there is still more to learn from this hybrid equilibrium, as my study of it has not been exhaustive and a stable variation may in fact exist.

In conclusion it would seem that for almost all values of p the partially honest signaling discussed by Huttegger and Zollman is more likely to evolve. The exception is when the ailment is relatively rare. When this is the case honest signaling is more likely to evolve. This may indicate that the reason we rarely observe high cost purely honest signaling in nature is that we

are looking at relatively common behaviors (for example feeding). Were we instead to observe rather uncommon cases of need (such as sickness perhaps) we might observe high cost honest signaling.

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