

Signalling among Relatives

II. Beyond the Tower of Babel

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Models of costly signalling are commonly employed in evolutionary biology in order to explain how honest communication between individuals with conflicting interests can be stable. These models have focused primarily on a single type of honest signalling equilibrium, the *separating* equilibrium in which any two different signallers send distinct signals, thereby providing signal receivers with complete information. In this paper, we demonstrate that in signalling among relatives (modelled using the Sir Philip Sidney game), there is not one but a large number of possible signalling equilibria, most of which are *pooling* equilibria in which different types of signallers may share a common signal. We prove that in a general Sir Philip Sidney game, any partition of signallers into equi-signalling classes can have a stable signalling equilibrium if and only if it is a contiguous partition, and provide examples of such partitions. A similar (but slightly stricter) condition is shown to hold when signals are transmitted through a medium with signalling error. These results suggest a solution to a problem faced by previous signalling theory models: when we consider the separating equilibrium, signal cost is independent of the frequency of individuals sending that signal and, consequently, even very rare signaller types can drastically affect signal cost. Here, we show that by allowing these rare signallers to pool with more common signallers, signal cost can be greatly reduced. © 1998

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Now the whole world had one language and a common speech.

—Genesis 11:1

1. INTRODUCTION

Honest communication among individuals with conflicting interests can be stable. In some models of signalling, this stability is achieved by imposing a cost on the signals, so that deception is not worthwhile. Such models were proposed by Zahavi (1975, 1977), solidified with mathematical analysis by Grafen (1990a, 1990b), and expanded upon by many authors. In general, this costly signalling framework has been developed with implicit assumptions that make all signalling equilibria *separating*: Signals provide complete information in the sense that different signallers always send distinct signals (see e.g., Fudenberg and Tirole 1991). However, if signalling has to be completely separating, then there can be only one possible signalling equilibrium. In the signalling

system, there can then be only one possible relation between signal and meaning, one possible “language.”

If signals are not completely separating, there might exist signalling equilibria in which some signallers of different qualities send identical signals. Can a signalling equilibrium of this kind, termed a *pooling* equilibrium, exist in systems of signalling among relatives?

Here, we use the Sir Philip Sidney (SPS) game (Maynard Smith 1991) to investigate this and related questions. We demonstrate that in the SPS game, pooling equilibria can indeed be stable. This result uncovers an additional complexity in the theory of animal signalling. It reveals a world in which there exist multiple stable signalling equilibria, multiple possible relations between signal and meaning, multiple possible “languages.”

The basic models of costly signalling (e.g., Grafen 1990a, Maynard Smith 1991) did not take into account perceptual error on the part of the signal receiver. Johnstone and Grafen investigate the effects of perceptual error on signalling equilibria, and demonstrate that costly signalling can be stable even with perceptual error (Johnstone and Grafen 1992b; Grafen and Johnstone 1993; Johnstone 1994). In this paper we prove that in systems with perceptual error, as in systems without, there are multiple possible signalling equilibria.

We will show that for a given *setting* there exist multiple signalling equilibria. A *setting* will be defined by the conditions of the participants, the fitnesses, and the signalling medium. These participant *conditions* are the possible initial states for the signaller and the associated probabilities of these states, the possible initial states of the donor and the associated probabilities, and the available donor responses. The *fitnesses* are the possible fitness values (after all interactions have occurred) of donor and signaller for all combinations of conditions. The signalling *medium* defines a probability distribution of perceived signals for every signal sent. In Sections 2, 3, 5, and 6, we assume that the medium is error-free, which means that the signal received is always identical to the signal sent. In Section 4 other media will be taken into account.

A *signalling equilibrium* is a tripartite entity: a set of possible signals with their costs, a signaller strategy specifying which of these signals to send for each of her conditions, and a donor strategy specifying the donor's response to each of the signals received, depending on her own condition. This equilibrium is required to be a Nash equilibrium with respect to a unilateral change of the signaller's or the donor's strategy: No signaller will gain by sending different signals, and no donor will gain by responding differently to signals. Notice that this definition is broader than that given in the first paper of the series (Bergstrom and Lachmann 1997, referred to from here on as Signalling I) as it now encompasses even the completely pooling equilibrium, the "no-signalling equilibrium," as a signalling equilibrium. In this paper we ignore a class of degenerate mixed-strategy equilibria known as hybrid equilibria (Fudenberg and Tirole 1991) which exist for some settings. As in the previous paper, we assume that the cost of the signal is incurred by the signaller regardless of the donor response. The final fitness of the signaller in a particular setting will be a function of her own initial condition, the donor's initial condition, the signal which she sends, and the response of the donor to this signal.

In Section 2, we consider a discrete SPS game and demonstrate that for the same signallers and donors, different sets of signals and costs lead to different stable

equilibria. At one particular equilibrium, each different type of signaller distinguishes herself from every other type. At other equilibria, two or more types send the same signal. In Section 3, we prove that any partition of signallers into contiguous classes (by quality) can be a stable pooling equilibrium. In Section 4, we investigate the effect of perceptual error on signalling equilibria. Here we extend the methods of the previous section to prove that multiple signalling equilibria also exist in systems with perceptual error. In Section 5, we consider a question raised at the end of Signalling I. Since, as demonstrated in that paper, signal cost is independent of signaller frequency, a single signaller can have disproportionately large effects on signal cost structure. Under such circumstances, other signallers might benefit from allowing such an individual to "cheat," to send a signal which is interpreted by signal receivers as indicating a state other than the true state. We demonstrate that this is indeed the case, and that such reorganizations of the signalling system serve to create pooling equilibria out of what were previously separating equilibria. In Section 6 we consider the question of when signallers in a completely pooling equilibrium benefit from adding a new signal, to form two equi-signalling sets of individuals. In that section we also show that the cost of the signal does not have to stem from a conflict of interest between signaller and signal receiver. Indeed, there can be costly signalling equilibria even when signaller and receiver have identical interests. In the discussion, we explain the relationship of this paper to previous models, and address the question of donor response to novel signals. In the appendix, signal costs for stable signalling systems are computed using the methods developed in Section 3.

In this paper we rely on game-theoretic analysis of individuals attempting to maximize their inclusive fitnesses. We consider equilibria in the Nash sense, such that neither player benefits from unilateral alteration of her strategy. While this approach simplifies the analysis considerably, the limitations discussed in Signalling I remain.

2. MULTIPLE SIGNAL EQUILIBRIA IN THE DISCRETE SIR PHILIP SIDNEY GAME

Consider a discrete SPS game, similar to that described in the first paper of the series. Two players, a signaller and a donor, are kin, with a coefficient of relatedness k (Hamilton 1964; Cavalli-Sforza and Feldman 1978). The donor is in possession of a single indivisible resource which will guarantee fitness 1 (or 1 minus signal cost for

the signaller) to whomever consumes it; she must decide whether to consume it herself or to transfer it to her relative. The signaller, in turn, may choose to send a costly signal of need in an effort to influence the behavior of the donor. The cost of the signal is incurred whether or not the donor responds.

This section is intended to provide an introductory illustration of the major results proven later in this paper: that a single signalling setting can have several different signalling equilibria, and that stable signalling equilibria can exist in which different signallers send the same signal. For this purpose, we will examine a simple setting, namely the following discrete SPS game. The signaller is in one of three equally probable states: “desperate,” “needy,” or “healthy.” The donor is initially equally likely to be in either of two possible states: “needy” or “healthy.” Table 1 shows, for the particular example treated here, the probabilities and fitnesses in the absence of the resource for each state. The responses available to the donor are to transfer the resource, or to retain it.

This setting, given the definition of a signalling equilibrium provided in the introduction, has four signalling equilibria—one in which all signallers send the same signal, two equilibria in which two distinct signals are sent, and one equilibrium with three distinct signals. The equilibria are illustrated in Figs. 1a–1d.

We are already familiar with the form of the first equilibrium, in which all signallers send the same signal, with cost 0. We describe this equilibrium in the previous paper (there calling it the “no-signalling” equilibrium) and demonstrate how, at this equilibrium, donors decide whether to transfer or retain the resource, based on their own condition alone. For the probability distribution and fitnesses given in Table 1, a healthy donor will have higher expected inclusive fitness when she transfers the resource than when she retains it. By contrast, a needy donor will have a higher expected inclusive fitness when she retains the resource than when she transfers it. Consequently, at this equilibrium, the donor strategy is to

transfer if and only if she is healthy. This equilibrium is depicted in Fig. 1a.

A second equilibrium takes another familiar form. This is the purely separating equilibrium, in which different signallers send distinct signals. With the signallers behaving in this fashion, the donor has complete information about the signaller’s condition. A comparison of expected inclusive fitnesses reveals that a needy donor will do best if she transfers only to desperate signallers, whereas a healthy donor will do best if she transfers to both desperate and needy signallers, but not to healthy signallers. We suppose that three possible signals are available, with costs (here chosen arbitrarily for the purpose of providing an example) of $c_1 = 0$, $c_2 = 0.1$ and $c_3 = 0.2$. Healthy signallers will send signal 1, and never receive the resource from the donor. Needy signallers will send signal 2, and receive the resource from healthy donors but not from needy donors. Desperate signallers will send signal 3, and receive the resource from both types of donors. A comparison of expected inclusive fitnesses reveals that no signaller will benefit from altering her signal, given that the donor strategy is held constant. This equilibrium is depicted in Fig. 1b.

The third and fourth equilibria are of a type we have not seen before; they are partially pooling equilibria in which some types of signallers share the same signal. In the third, there are two available signals, with costs $c_1 = 0$ and $c_2 = 0.1$ again chosen arbitrarily for this example. Desperate and needy signallers are pooled together, each sending signal 2, while healthy signallers send signal 1. Needy donors do not benefit, on average, by transferring in response to either signal, whereas healthy donors benefit from transferring only in response to signal 2. The possibility of transfer from healthy donors is sufficient to maintain the more costly signal in desperate and needy signallers; the healthy signaller, by contrast, has a higher expected inclusive fitness by simply sending signal 1 and receiving no transfer. This equilibrium is depicted in Fig. 1c.

The fourth equilibrium is another pooling equilibrium, again with two available signals, $c_1 = 0$ and $c_2 = 0.2$. Here, the increased cost of signal 2 leads to a rearrangement of which signallers send which signal. Needy and healthy signallers are now pooled together, sending signal 1, while desperate signallers send the high-cost signal 2. Healthy donors maximize their expected inclusive fitness by transferring in response to either signal, whereas needy donors do best by transferring only in response to signal 2. No signaller type can gain by sending a different signal. The equilibrium is depicted in Fig. 1d.

At this point, we have described equilibria composed of every possible partition of the three signaller qualities

TABLE 1

Initial Conditions of Signallers and Donors in the Discrete SPS Game of this Section, with Associated Fitnesses and Probabilities.

Signaller	Desperate	Needy	Healthy
Fitness	0.3	0.6	0.9
Probability	1/3	1/3	1/3
Donor	Needy	Healthy	
Fitness	0.7	0.9	
Probability	1/2	1/2	

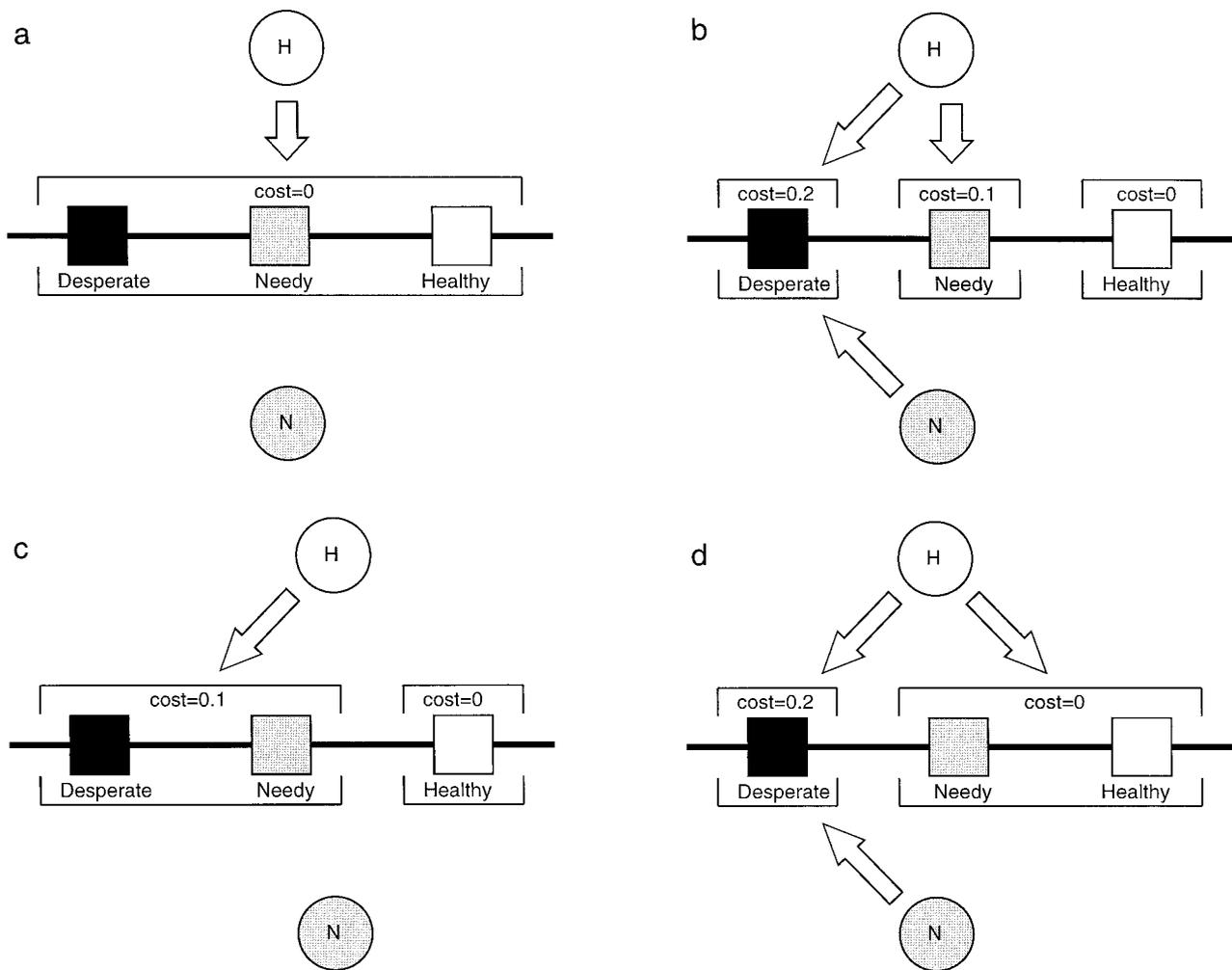


FIG. 1. Signalling equilibria in the discrete SPS game, for the setting described by Table 1. Squares represent desperate, needy, and healthy signallers. Circles represent needy (N) and healthy (H) donors. Square brackets enclose equi-signalling classes. Arrows indicate resource transfer from a donor type to a signaller class.

into signalling groups—with one exception. We have not provided an example of one in which desperate and healthy signallers send the same signal, while needy signallers, with intermediate fitness, send some other signal. In the next section, we prove that no such equilibrium can exist.

3. MULTIPLE SIGNALLING EQUILIBRIA WITH RELIABLE SIGNALLING

Consider the general SPS game treated in Section 4 of Signalling I. Two players, signaller and donor, with coefficient of relatedness k , have initial fitnesses (in the

absence of the resource) of x and y respectively. Signaller fitness is drawn from a distribution P on $[0, 1]$, with probability density $p(x)$. Donor fitness is drawn independently from another distribution Q also on $[0, 1]$, with probability density $q(y)$. Each signaller sends some signal s with a cost $c(s)$ on the interval $[0, 1]$, which is paid in full by the signaller, whether or not the donor transfers the resource. We define a *pool* of signallers to be the set of all signallers sending a particular signal. We then ask how the signallers can be partitioned into pools such that the resulting signalling system is stable.

As the only property distinguishing different signallers in this game is fitness, we can simply label the signallers by their fitnesses. A signaller who has fitness x without the resource will be called signaller x . Then the set of all signallers is the interval $[0, 1]$, and we can partition this

interval into pools. As we will prove later, a partition of the fitness interval into pools can be a signalling equilibrium if and only if the split is *contiguous*, as defined below.

Let us define a partial ordering on the pools of signallers: if X_1 and X_2 are two distinct pools, we will say that $X_1 < X_2$ if all signallers in X_1 have a lower fitness than the signallers in X_2 , i.e., for all x_1 in X_1 and x_2 in X_2 we have $x_1 < x_2$. Notice that there can be pools X_1 and X_2 of signallers such that neither $X_1 < X_2$ nor $X_2 < X_1$. A partition of the signallers into pools is *contiguous* if for every two distinct pools X_i and X_j in the partition, either $X_i < X_j$ or $X_j < X_i$.

THEOREM 1. *In an SPS game with a donor distribution $q(y)$ which is positive everywhere on $[0, 1]$, a partition of the signaller fitness interval into pools can have a signalling equilibrium if and only if the partition is contiguous.*

First we will show that the donors treat a member of a pool as if her fitness is the average fitness of the individuals in that pool.

LEMMA 1. *Let X_s be the pool of signallers sending signal s . Then at a signalling equilibrium a donor with fitness y will donate in response to this signal if and only if $y > 1 + kw^*(s) - k$, where $w^*(s)$ is the average fitness of the signallers in X_s .*

As in Signalling I, at a signalling equilibrium a donor will donate if and only if her expected inclusive fitness from doing so exceeds her expected inclusive fitness from retaining the resource. This must hold for each signal received. For a given signal s sent by the pool of signallers X_s , this condition is

$$\int_{X_s} [y + k] p(x) dx > \int_{X_s} [1 + kx] p(x) dx \quad (1)$$

or, equivalently,

$$k + y > k \frac{\int_{X_s} xp(x) dx}{\int_{X_s} p(x) dx} + 1. \quad (2)$$

Define the average fitness of the signallers in X_s as $w^*(s) \equiv \int_{X_s} xp(x) dx / \int_{X_s} p(x) dx$. Then a donor with fitness y will donate under guesswork if and only if $y > 1 + kw^*(s) - k$. A similar result is obtained by Maynard Smith (1994). Additionally, this result recalls the analysis in Section 4 of Signalling I, in which we proved that in the completely pooling equilibrium (referred to there as the “no-signalling” equilibrium), the

donor uses a criterion based on average signaller fitness to determine whether to transfer or retain the resource.

Now we return to the proof of the theorem. Let X_1, X_2 be two pools of signallers. The signallers in X_1 send signal 1, and those in X_2 send signal 2. Let $w^*(1)$ and $w^*(2)$ be the average fitnesses, and assume without loss of generality that $w^*(1) \leq w^*(2)$. Let the cost of signal 1 be $c(1)$, and that of signal 2 be $c(2)$. The system is at a signalling equilibrium with respect to the signallers if and only if the following two conditions hold. First, every signaller $x_2 \in X_2$ must be better off sending signal 2 than sending signal 1.

$$\begin{aligned} & \int_0^{1+kw^*(1)-k} (x_2 + k) q(y) dy \\ & + \int_{1+kw^*(1)-k}^1 (1 + ky) q(y) dy - c(1) \\ & \leq \int_0^{1+kw^*(2)-k} (x_2 + k) q(y) dy \\ & + \int_{1+kw^*(2)-k}^1 (1 + ky) q(y) dy - c(2) \quad (3) \end{aligned}$$

i.e.,

$$\int_{1+kw^*(1)-k}^{1+kw^*(2)-k} (1 + ky - x_2 - k) q(y) dy \leq c(1) - c(2) \quad (4)$$

for all $x_2 \in X_2$. Second, every signaller $x_1 \in X_1$ must be better off sending signal 1 than sending signal 2:

$$\int_{1+kw^*(2)-k}^{1+kw^*(1)-k} (1 + ky - x_1 - k) q(y) dy \leq c(2) - c(1) \quad (5)$$

or

$$\int_{1+kw^*(1)-k}^{1+kw^*(2)-k} (1 + ky - x_1 - k) q(y) dy \geq c(1) - c(2). \quad (6)$$

Therefore for all $x_1 \in X_1, x_2 \in X_2$

$$\begin{aligned} & \int_{1+kw^*(1)-k}^{1+kw^*(2)-k} (1 + ky - x_1 - k) q(y) dy \\ & \geq \int_{1+kw^*(1)-k}^{1+kw^*(2)-k} (1 + ky - x_2 - k) q(y) dy. \quad (7) \end{aligned}$$

From this it follows that $x_2 \geq x_1$, given that integral of $q(y)$ is positive over the interval $[1 + kw^*(1) - k, 1 + kw^*(2) - k]$. Since x_1 can be anything in X_1 and x_2 can be anything in x_2 , by definition, $X_1 < X_2$. As this holds for every pair of pools in the partition, the partition must be contiguous. When $\inf(X_2) = \sup(X_1)$ (the smallest number bigger than all X_1 is equal to the biggest number smaller than all X_2) we have, by the sandwich principle

$$\begin{aligned} & \int_{1 + kw^*(1) - k}^{1 + kw^*(2) - k} (1 + ky - \sup(X_1) - k) q(y) dy \\ & = c(1) - c(2). \end{aligned} \quad (8)$$

Now we prove the converse: if a partition is contiguous then there exists a signalling equilibrium over this partition. Let \hat{c} be a cost function defined such that, for every X_1 and X_2 for which $X_2 > X_1$, the following two relations hold:

$$\int_{1 + kw^*(1) - k}^{1 + kw^*(2) - k} (1 + ky - \sup(X_1) - k) q(y) dy \geq \hat{c}(1) - \hat{c}(2) \quad (9)$$

and

$$\int_{1 + kw^*(1) - k}^{1 + kw^*(2) - k} (1 + ky - \inf(X_1) - k) q(y) dy \leq \hat{c}(1) - \hat{c}(2). \quad (10)$$

Using this cost function \hat{c} , Eqs. (4) and (6) will hold, and consequently the system will be at a signalling equilibrium. To find cost function such that this relation holds, we use Eq. (8). In the appendix, we provide two examples of pooling equilibria for the SPS game, constructed using the results from this section.

4. ERROR-PRONE SIGNALLING

4.1. The Existence of Multiple Signalling Equilibria

In this subsection we will analyse the general SPS game (described in Section 3) where there is imperfect information transfer between the signaller and the donor. In this case, the signal that is received is not necessarily identical to the signal that was sent. Rather, the signal is conveyed through a medium which determines probabilistically which signal will be received.

To simplify the analysis, we introduce new notation. Let S be the set of all signals sent and R be the set of all signals received. $M(s, r)$ is the probability of receiving signal r when signal s was sent. The pool of signallers who send signal s will be marked by X_s . Again, $p(x)$ is the probability density of signallers, and $q(y)$ the probability density of donors, where x and y index signaller and donor by fitness, as before.

We will prove a theorem very similar to the theorem in Section 3. As before, we begin with a lemma.

LEMMA 2. *At a signalling equilibrium a donor with fitness y will respond to signal r by donating her resource if and only if $y > 1 + kw^{**}(r) - k$, where $w^{**}(r)$ is the average fitness of the signaller conditional on the donor having received signal r .*

The probability that signal s will be sent is

$$P(s \text{ sent}) = \int_{X_s} p(x) dx. \quad (11)$$

The probability that the donor will receive signal r is

$$P(r \text{ received}) = \sum_{s \in S} P(s \text{ sent}) M(s, r). \quad (12)$$

Having received a signal r , the conditional probability that it was sent by a signaller in X_s is given by the expression below. Notice that since M can be viewed as a conditional probability matrix, this is simply Bayes' rule:

$$P(s \text{ sent} | r \text{ received}) = \frac{P(s \text{ sent}) M(s, r)}{P(r \text{ received})}. \quad (13)$$

If a donor of fitness y receives signal r , and transfers the resource, her average inclusive fitness will be

$$\begin{aligned} & \sum_{s \in S} P(s | r) \frac{\int_{X_s} (y + k) p(x) dx}{\int_{X_s} p(x) dx} \\ & = \sum_{s \in S} P(s | r)(y + k) = y + k. \end{aligned} \quad (14)$$

If she does not transfer the resource, her average inclusive fitness will be given by the following expression, where $w^*(s)$ is the average fitness of signallers sending signal s .

$$\sum_{s \in S} P(s | r) \frac{\int_{X_s} (1 + kx) p(x) dx}{P(s \text{ sent})} = \sum_{s \in S} P(s | r)(1 + kw^*(s)) \quad (15)$$

Therefore she will transfer the resource when the following condition holds:

$$y + k \geq 1 + \sum_{s \in S} P(s | r)(kw^*(s)). \quad (16)$$

We can define the $w^{**}(r)$ as the mean fitness of a sender whose signal is perceived as r :

$$w^{**}(r) \equiv \sum_{s \in S} P(s | r) w^*(s). \quad (17)$$

This provides the following condition for the donor to transfer the resource when she receives signal r :

$$y \geq 1 + kw^{**}(r) - k. \quad (18)$$

THEOREM 2. *In the general SPS game with signalling error, where the donor distribution $q(y)$ is positive everywhere on $[0, 1]$, a partition of the signaller fitness interval into pools can have a signalling equilibrium only if the partition is contiguous.*

A signaller who has fitness without the resource of x and sends signal s with cost $c(s)$, has expected inclusive fitness

$$\sum_{r \in R} M(s, r) \left(\int_0^{1+kw^{**}(r)-k} (x+k) q(y) dy + \int_{1+kw^{**}(r)-k}^1 (1+ky) q(y) dy \right) - c(s). \quad (19)$$

Now we introduce the following notation: the proportion of donors who will *not* transfer the resource when they receive signal r will be labelled $Q_n(r)$, and is

$$Q_n(r) = \int_0^{1+kw^{**}(r)-k} q(y) dy. \quad (20)$$

The proportion of donors who will *transfer* the resource when they receive signal r will be $Q_t(r)$. The average fitness of a donor who transfers the resource in response to signal r will be $v_t^*(r)$, and is

$$v_t^*(r) = \frac{\int_{1+kw^{**}(r)-k}^1 yq(y) dy}{Q_t(r)}. \quad (21)$$

Then we can rewrite Eq. (19) for expected signaller fitness as

$$\sum_{r \in R} M(s, r)((x+k) Q_n(r) + (1+kv_t^*(r)) Q_t(r)) - c(s). \quad (22)$$

Let X_1 and X_2 be two pools of signallers sending signals 1 and 2 respectively. For all signallers x_1 in X_1 it has to be true that

$$\begin{aligned} \sum_{r \in R} M(1, r)((x_1+k) Q_n(r) + (1+kv_t^*(r)) Q_t(r)) - c(1) \\ \geq \sum_{r \in R} M(2, r)((x_1+k) Q_n(r) + (1+kv_t^*(r)) Q_t(r)) - c(2) \end{aligned} \quad (23)$$

i.e.,

$$\begin{aligned} (x_1+k) \sum_{r \in R} (M(1, r) - M(2, r)) Q_n(r) \\ + \sum_{r \in R} (M(1, r) - M(2, r))(1+kv_t^*(r)) Q_t(r) \\ \geq c(1) - c(2). \end{aligned} \quad (24)$$

We have not assumed anything about X_1 and X_2 , therefore we can assume without loss of generality that

$$\sum_{r \in R} M(1, r) Q_n(r) \geq \sum_{r \in R} M(2, r) Q_n(r). \quad (25)$$

For expression (24) to hold for all $x_1 \in X_1$, we require that

$$\begin{aligned} (\inf(X_1) + k) \sum_{r \in R} (M(1, r) - M(2, r)) Q_n(r) \\ + \sum_{r \in R} (M(1, r) - M(2, r))(1+kv_t^*(r)) Q_t(r) \\ \geq c(1) - c(2). \end{aligned} \quad (26)$$

Similarly for all $x_2 \in X_2$ we require

$$\begin{aligned} (x_2+k) \sum_{r \in R} (M(2, r) - M(1, r)) Q_n(r) \\ + \sum_{r \in R} (M(2, r) - M(1, r))(1+kv_t^*(r)) Q_t(r) \\ \geq c(2) - c(1), \end{aligned} \quad (27)$$

and consequently

$$\begin{aligned}
 & (\sup(X_2) + k) \sum_{r \in R} (M(1, r) - M(2, r)) Q_n(r) \\
 & + \sum_{r \in R} (M(1, r) - M(2, r))(1 + kv_r^*(r)) Q_t(r) \\
 & \leq c(1) - c(2). \tag{28}
 \end{aligned}$$

Therefore $\inf(X_1) \geq \sup(X_2)$ and $X_1 > X_2$; this means that, as in Section 3, each pool will be contiguous in fitness. Here, however, we have the additional requirement that for every two (distinct and contiguous) pools of signallers, inequality (25) holds if and only if $X_1 > X_2$, i.e., when $X_1 > X_2$ then $\sum_{r \in R} M(1, r) Q_n(r) \geq \sum_{r \in R} M(2, r) Q_n(r)$, and when $X_2 > X_1$ then $\sum_{r \in R} M(2, r) Q_n(r) \geq \sum_{r \in R} M(1, r) Q_n(r)$.

We summarize these results in the following:

THEOREM 3. *In a general SPS game with signalling error, for a medium M and donor distribution $q(y)$ which is positive everywhere on $[0, 1]$, a given partition of the signallers into pools can have a signalling equilibrium if and only if (1) the partition is contiguous and (2) for any two distinct and contiguous pools X_1 and X_2 of signallers sending signals 1 and 2, when $X_1 > X_2$ then $\sum_{r \in R} M(1, r) Q_n(r) \geq \sum_{r \in R} M(2, r) Q_n(r)$, and when $X_2 > X_1$ then $\sum_{r \in R} M(1, r) Q_n(r) \leq \sum_{r \in R} M(2, r) Q_n(r)$, where $Q_n(r)$ is the probability that a donor will not respond to signal r at the equilibrium.*

This condition requires that the signalling medium M will be orderly in the following sense. Consider any two pools meeting the appropriate contiguity condition (i.e., with all signallers in one pool having lower fitness than any signaller in the other pool). Given these two pools, donors must be more likely to transfer in response to the signal sent by the signallers in the lower-quality pool. By contrast, it is trivial to construct a medium M for which contiguity does not imply the existence of a stable signalling equilibrium.

4.2. An Example of Error-Prone Signalling

The formulae developed in the previous subsection allow us to determine analytically the equilibrium signal costs and player strategies, for any particular setting of the SPS game with error in signal transmission. Below, we provide a simple example using Johnstone and Grafen's (1992) continuous SPS game. This version of the game is equivalent to the general SPS game of Section 3, for a specific pair of donor and signaller fitness distributions. The donor and signaller, related by k , have

fitnesses x and y in the absence of the resource, where x and y are drawn independently from a uniform distribution on $[0, 1]$. The signaller can choose a signal with cost c from the interval $[0, 1]$, and the donor decides whether to transfer or retain the resource based on the values of x and c .

In this example, we postulate a particular pair of signaller and donor strategies and they solve for the signal cost which, together with these strategies, constitutes a signalling equilibrium for the setting described above.

Consider an equilibrium in which there are only two distinct signals, labelled 1 and 2. We postulate a signaller strategy as follows: signallers in the region $(1/2, 1]$ send signal 1, with cost 0, while signallers in the region $[0, 1/2]$ send signal 2 with some cost c . Since there are two signals, the medium M can be represented by a two-by-two matrix. Here, we will consider a medium that transmits the signals faithfully with probability 0.9.

$$M = \begin{pmatrix} 0.9 & 0.1 \\ 0.1 & 0.9 \end{pmatrix} \tag{29}$$

Since signallers are uniformly distributed on $[0, 1]$ and the partitions are of equal size, each signal will be sent with probability $1/2$. Moreover, transmission error as represented by M occurs symmetrically, so the probability of receiving signal 1 is $1/2$, as is the probability of receiving signal 2. The conditional probability that signal i was sent given that signal j was received is then 0.9 when $i = j$, and 0.1 otherwise.

As a consequence of the uniform signaller distribution, the average fitness of signallers sending signal 1, $w^*(1)$, will be 0.75, while the average fitness of signallers sending signal 2, $w^*(2)$, will be 0.25. Using Eq. (17), the average fitness of signallers who send signals perceived as signals 1 and 2 and will be $w^{**}(1) = 0.7$ and $w^{**}(2) = 0.3$ respectively. Consequently, Eq. (18) reveals that at equilibrium, a donor will transfer in response to signal 1 if her fitness exceeds 0.85 and will transfer in response to signal 2 if her fitness exceeds 0.65. From Eq. (21), the mean fitnesses of donors transferring in response to signals 1 and 2 are then 0.93 and 0.83 respectively.

Using Eq. (22), we compute the expected inclusive fitness of a signaller with initial fitness x to be $0.66 + 0.83x$ if she sends signal 1, and to $0.80 + 0.67x - c$ if she sends signal 2. Equation (24) then returns our desired result: this particular combination of strategies and costs will be a stable signalling equilibrium when $c = 0.06$.

In general, as the fidelity of the medium decreases, the minimum cost of the stable equilibrium signals also decrease. In the example above, the signal cost necessary for this partition to be an equilibrium would be $c = 0.09$

in the case of an error-free medium. In Signalling I, we demonstrate that some stable signalling equilibria are too costly to be worthwhile for signaller or donor; note that it is thus possible to have a system in which, with the signaller strategy held constant, the donor always prefers higher fidelity of the medium, and yet both signaller and donor would benefit from moving to a new equilibrium in a medium with lower fidelity.

5. THE EFFECT OF RARE SIGNALLER TYPES ON SIGNAL COST

At the conclusion of Signalling I, we asked a question which seemed quite disturbing when one considered only *separating* equilibria. At a separating equilibrium the signal costs depend only on the signaller types present, and not on the frequencies of these types (see Signalling I). Consequently, the addition of even a single signaller of a novel type can dramatically increase the signal cost for all other signallers, because they all need to distinguish themselves from the new signaller. Could an equilibrium not be reached, we asked, in which the newcomer “poses” as one of the other types, thereby avoiding the increase in signal cost?

In Section 3, we develop the framework necessary to answer this question, proving that signalling equilibria can take the pooling form. Therefore, it is entirely possible that the scenario described above could result in a pooling equilibrium instead of a fully separating equilibrium. In this pooling equilibrium, the newcomer would be posing as one of the more common signallers. Moreover, the signal costs at the separating equilibrium could easily be so high that all signallers would be better off in the pooling equilibrium than in the separating equilibrium.

This can be illustrated using the discrete SPS game described in Section 2. Before doing so, it is useful to reintroduce the concept of the *least costly believable signal*, used extensively in Signalling I in treating separating equilibria. The least costly believable signal, \hat{c} , of a particular state is defined as the least costly signal which is too costly to be sent by a signaller in a healthier state.

Consider the discrete setting described in Section 2, with one modification. Only desperate signallers with initial fitness of 0.3 and needy signallers with initial fitness of 0.6 are present, each in the same frequency. There are no healthy signallers. The donors, as before, are either needy, with initial fitness of 0.7, or healthy with initial fitness of 0.9, in equal frequencies. Since the needy signallers are currently the best-off, we assume that

they can signal their state with cost 0. Moreover, notice that the healthy donors will benefit (on average) from transferring to both desperate *and* needy signallers. Consequently the signal serves only to influence the behavior of the needy donors, who should ideally transfer only to desperate signallers. Adapting slightly the formula for \hat{c} from Signalling I, the least costly believable signal for the desperate signallers is given by the following expression, where k is the coefficient of relatedness between signaller and donor:

$$\hat{c} = (1 - 0.6)/2 - 0.3k/2 = 0.2 - 0.15k. \quad (30)$$

When desperate signallers send this signal, and needy signallers send the other, zero-cost signal, the signalling equilibrium is completely separating, as depicted in Fig. 2a.

Suppose now that a single individual of a new type, a “healthy” signaller with initial fitness 0.9, is introduced. If the new signalling equilibrium is to remain purely separating, by the definition of least costly believable signal, the needy signallers must now send a signal of at least $\hat{c}_1 = 0.05 - 0.05k$. Similarly, the desperate signallers must send a signal of at least $\hat{c}_2 = \hat{c} + \hat{c}_1 = 0.25 - 0.2k$ to distinguish themselves from the needy signallers. The resulting equilibrium is depicted in Fig. 2b.

Thus, in order to distinguish the needy signallers from this single healthy arrival, all signallers other than the healthy individual must pay an additional amount $0.05(1 - k)$. Since donors are related to these individuals by k , this change costs them an additional amount $0.05k(1 - k)$ whenever they are paired with a desperate or needy signaller.

What is gained by distinguishing needy from healthy signallers? Absolutely nothing, from the standpoint of the signallers. Suppose that instead of distinguishing themselves, the needy and healthy signallers both send the same zero-cost signal. Desperate signallers can send the same signal as before the arrival of the healthy individual and thus distinguish themselves from the others. This is the pooling equilibrium depicted in Fig. 2c. Notice that at this equilibrium, both the needy and the desperate signallers fare exactly as before the arrival of the healthy individual; needy signallers enjoy transfer from the healthy donors, and desperate signallers enjoy transfer from both needy and healthy donors.

Donors, likewise, gain little from being able to distinguish needy signallers from the lone healthy signaller. The only advantage from their perspective is that healthy donors can avoid transfer to the lone healthy signaller. This benefit is vanishingly small in large populations and

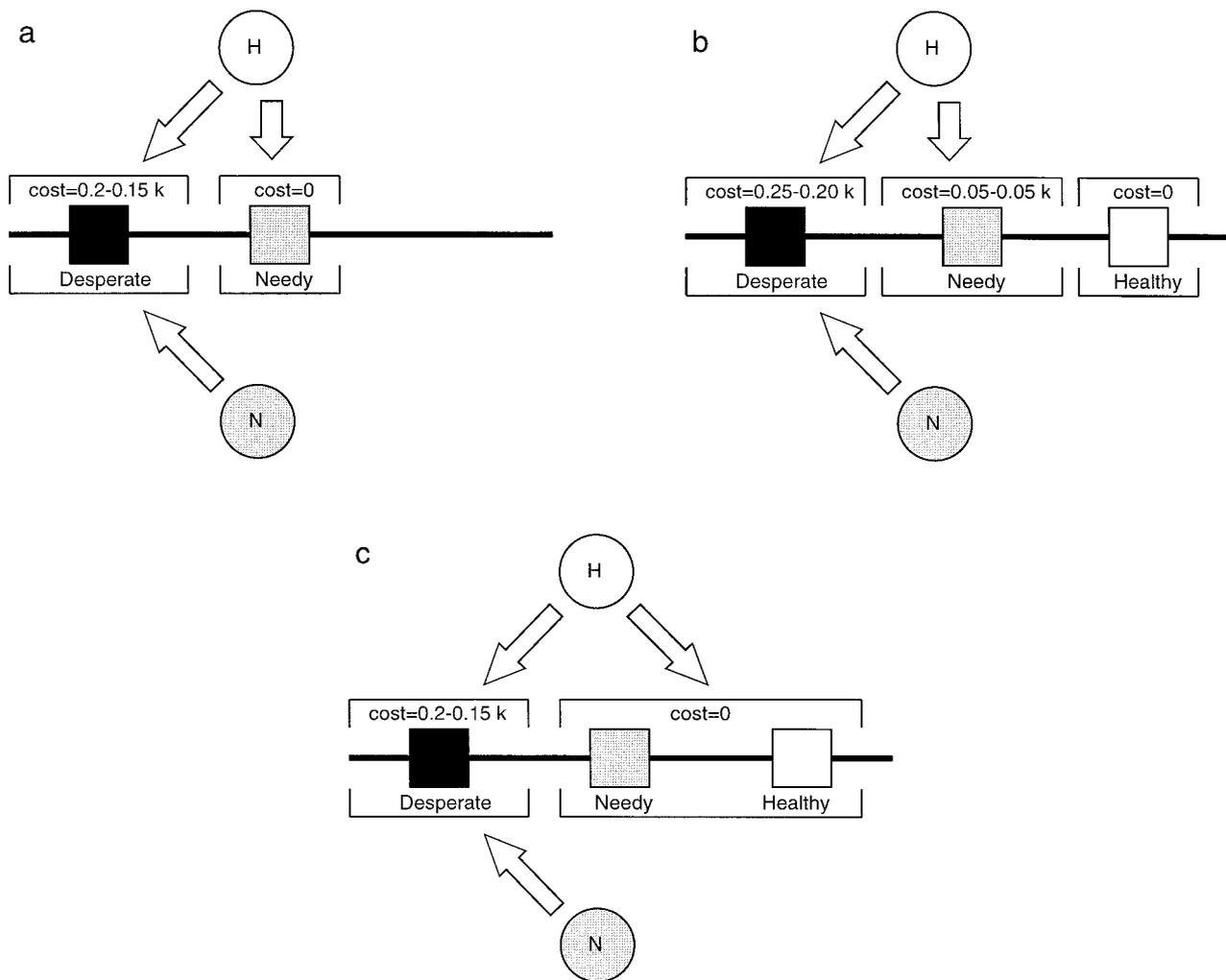


FIG. 2. Signalling equilibria in the discrete SPS game, for the setting described in Section 5. Squares represent desperate, needy, and healthy signallers. Circles represent needy (N) and healthy (H) donors. Square brackets enclose signalling pools. Arrows indicate resource transfer from a donor type to a given pool.

does not compensate for the inclusive-fitness cost of the increased signal expenses.

Clearly, both signallers and donors will do better if they behave as suggested at the end of Signalling I: a signalling equilibrium should be achieved in which healthy individual “poses” as a needy individual. All signallers and all donors benefit from this response to the healthy individual’s arrival.

Here, we have an example in which a pooling equilibrium is preferable from the standpoint of all signallers to the separating equilibrium. One can ask when, in general, the signallers in one pool do better at an equilibrium in which they distinguish themselves by sending two different signals. We provide an answer to this question in the following section.

6. WHEN SHOULD ONE POOL SPLIT TO FORM TWO?

In this paper, we show that a single signalling setting allows multiple signalling equilibria. In Signalling I we demonstrated that in some cases the no-signalling equilibrium, in which all signallers send the same signal, gives a higher average payoff for both signaller and donor than the fully separating equilibrium in which different signallers send different signals. It is therefore natural to ask the following question: Which of the different possible signalling equilibria is optimal? Which partitioning of the signallers will yield the highest average payoff?

A full analysis of this problem is beyond the scope of the current paper; the problem is treated further in

Bergstrom and Lachmann (1998). Here, we restrict our analysis to the question of whether moving from an equilibrium with a single pool of signallers to a different equilibrium with this pool split into two, will give an advantage. This question is addressed without regard to the dynamics by which the system moves toward a particular equilibrium.

Consider the generalized SPS game treated in Section 3, with signaller quality drawn with a probability density function $p(x)$ and donor quality drawn with probability density $q(y)$. Starting with the completely pooling equilibrium, we ask which division of the signallers into two distinct pools will give the biggest benefit. As we show in Section 3, the cost paid for the signal when the boundary dividing the two pools is located at \tilde{x} is

$$\int_{1+kw(1)^*-k}^{1+kw(2)^*-k} (1+ky-\tilde{x}-k) q(y) dy = c(1) - c(2). \quad (31)$$

Here $w(1)^*$ is the average fitness of the signallers in the pool with fitnesses in $[0, \tilde{x}]$, sending the first signal with cost $c(1)$, and $w(2)^*$ is the average fitness of the signallers in the pool $(\tilde{x}, 1]$, sending the second signal with cost $c(2)$. This cost is paid by all signallers sending the first signal, so the average cost paid by each signaller is

$$\int_0^{\tilde{x}} p(x) \int_{1+kw(1)^*-k}^{1+kw(2)^*-k} (1+ky-\tilde{x}-k) q(y) dy dx + c(2). \quad (32)$$

The difference in average fitness of the signallers before and after dividing into two pools is

$$\begin{aligned} & \int_0^{w^*} p(x) \int_{1+kw(1)^*-k}^{1+kw^*-k} (k+x-ky-1) q(y) dy dx \\ & + \int_{w^*}^1 p(x) \int_{1+kw^*-k}^{1+kw(2)^*-k} (ky+1-k-x) q(y) dy dx. \end{aligned} \quad (33)$$

Here w^* is the average fitness of all signallers (prior to the division). Adding these two terms and simplifying, we get

$$\begin{aligned} & \int_0^{w^*} (x-\tilde{x}) p(x) dx \int_{1+kw(1)^*-k}^{1+kw^*-k} q(y) dy \\ & + \int_{w^*}^1 (x-\tilde{x}) p(x) dx \int_{1+kw^*-k}^{1+kw(2)^*-k} q(y) dy \\ & + \int_{1+kw^*-k}^{1+kw(2)^*-k} (1+ky-\tilde{x}-k) q(y) dy. \end{aligned} \quad (34)$$

By way of an example, we use these equations to examine the continuous SPS game as described by Johnstone and Grafen (1992) and detailed here in Section 4. In Fig. 3 we see both the fitness advantage gained by signalling, and the cost of signalling for this setting. One can see that the maximum advantage will occur when the signal has cost 0.

In this setting, the value of the cost function described by Eq. (32) drops below 0 for some parts of its domain. How are we to interpret negative signal cost? Recall that the cost function (31) describes not the absolute cost but the difference between two signal costs. Consequently, the average signal cost graphed in Fig. 3 is actually based on the *difference* between the cost of signal 1 and signal 2. When this average is positive, signal 1 costs more than signal 2; we assume that signal 2 has zero cost. When it is negative, signal 2 costs more than signal 1; we assume that signal 1 has zero cost. This is interesting, for at these equilibria the high-quality signallers send a costly signal indicating that they do not want the resource. The low quality signallers send a free signal indicating that they do want the resource.

This illustrates the fact that stable costly signalling does not require a conflict of interest between signaller and signal receiver. Above, we noticed that for certain partitions of the signallers into two pools, the high quality signallers have to send the more costly signal, to indicate that they do not want to get the resource. Here, it is the cost of the signal that makes the system stable. Signallers who are just under the division point would also enjoy higher inclusive fitness were the donor to simply retain the resource. However, because of the cost of signalling high-quality, they do better by signalling with the low-quality pool and consequently will not switch to signal that they are of the high-quality type.

It is illuminating to consider the case of $k = 1$. Here, there is no conflict of interest, and in the separating equilibrium signal cost is 0. For a pooling equilibrium, however, there can still be a signal cost. In a pooling equilibrium signallers do not signal their exact quality, but only partial information about it, namely, to which pool they belong. This admits the possibility that signaller and donor might both benefit from a “white lie.” A signaller might be in one pool, but deceiving and sending the signal of another pool might actually provide the donor with a “better” estimate of her quality. In this case there would be an incentive for the signaller to deceive, and a signal cost would be required to maintain honesty.

For example, suppose that there are two pools, with a split at 0.9. Donors then treat signaller as either having fitness 0.45, or 0.95. A signaller in the first pool, with fitness 0.8, is treated as having fitness 0.45 but would rather

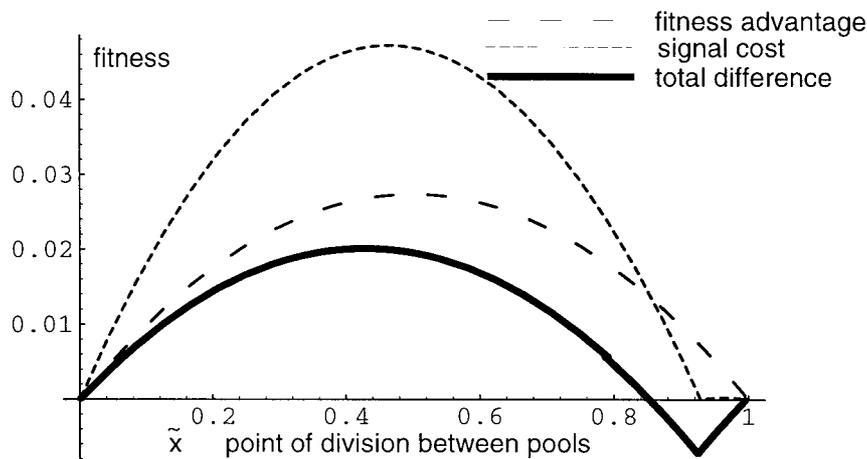


FIG. 3. The advantage of splitting the signallers at fitness \tilde{x} , the total cost of the signal incurred by this partition, and the total difference between the average fitness of the signallers without a partition and with a partition. It is clear that the biggest fitness gain from the split arises when the partition is set such that the signal has cost 0. The curves were plotted for $k = 0.5$.

be treated as having fitness 0.95. Consequently this signaller would benefit from “deceiving” and sending the signal of the healthier pool. For this to be an equilibrium, this “healthy” signal has to be costly.

In general, it might seem unlikely that a system with $k = 1$ would actually settle on a costly pooling equilibrium such as this, for reasons of efficiency. However, consider the case of signalling inside a multicellular body, with only two distinct signals available. These two signals will necessarily have associated physiological costs, and thus we would expect the system to settle on the appropriate costly pooling equilibrium for these particular costs and $k = 1$. This point generalizes to an arbitrary number of signals.

7. DISCUSSION

In this paper, we have examined the nature of signalling equilibria in communication among relatives. Using the SPS game as a model, we have shown that when signalling is error-free, any contiguous partition of signaller qualities into pools has a stable signalling equilibrium. When signals are transferred through an error-prone medium, again signal partitions must be contiguous in order to form stable equilibria. In addition, a second condition requiring a kind of “regularity” of the signal medium must also be met; this condition is given in Theorem 3.

In deriving these results, as in the associated numerical illustrations, we postulate a particular partition of signaller qualities into pools and then compute the signal costs required to enforce a stable signalling equilibrium

with signallers distributed into precisely these pools. There is no mathematical reason why the reverse approach could not be used; one could begin with a set of known signal costs and compute the equilibrium partition of signallers into signalling classes given this particular set of signal costs. Such an approach might prove useful in evaluating a system with measurable signal costs.

Qualitative Conclusions

We have at least four conclusions of general interest. First, *pooling equilibria*, in which signallers of different qualities send identical signals, are possible in costly signalling games. This is true for both discrete and continuous games, and whether or not there is error in signal transmission. Consequently, it is possible for signallers to provide only partial information to the donors at a signalling equilibrium.

Second, since pooling equilibria are possible, we find that signalling equilibria are far more numerous than previously thought. A setting is not limited to a single equilibrium, but rather allows many signalling equilibria. As we have demonstrated, this holds whether the game is discrete or continuous, and whether or not there is error in signal transmission.

Third, even when looking beyond separating equilibria, the general conclusions of Grafen (1990a) appear to hold: though there are multiple signalling equilibria, and different signallers may send the same signals, the partition of signallers into equi-signalling classes must always be contiguous. There can never be a case in which a high quality signaller gives the same signal as a low

quality signaller, while a different signal is sent by an intermediate signaller. Consequently, it is reasonable to conclude that while the signals may convey less than complete information about signaller quality, they remain essentially honest.

Fourth, for pooling equilibria in the SPS game, the signal cost may be paid by the signallers who do *not* wish to receive the resource. This highlights the fact that with pooling equilibria, signal cost serves to maintain pool boundaries. Consequently, conflict of interest between signaller and receiver is not required for stable costly signalling.

Relation to Previous Models

Given the abundance of pooling equilibria in continuous signalling models, why have the previous models of biological signalling treated only the single separating equilibrium allowed by each setting? The answer is, in part, methodological. In the analysis of continuous signalling games, one can proceed by solving differential equations to determine optimal signaller and donor strategies, or, as we do in this paper, one can solve for the signal costs required to make an equilibrium stable. For the former approach, one must assume that the signaller's strategy is a differentiable function; this excludes all non-continuous strategies. All equilibria other than the simplest single-signal equilibrium and fully separating equilibrium feature non-continuous signalling strategies and consequently will be overlooked by this approach.

Previous models of signalling among relatives (Godfray 1991; Johnstone and Grafen 1992a) take the differential equation approach, and therefore cannot consider pooling equilibria within their respective frameworks. In his original formulation of signalling equilibria, Grafen (1990a) takes a similar approach to provide what he considers to be necessary conditions for the existence of a stable signalling equilibrium. However, he assumes that the optimal advertising level is strictly increasing in signaller quality. This assumption is not necessary for a signalling equilibrium to exist. Under our assumptions about the allowable form of the advertising strategy, the necessary conditions for existence of signalling equilibrium are more general, and thus we are able to reveal a set of additional signalling equilibria.

Response to Novel Signals

One possible criticism of the model presented in the body of this paper is that in each equilibrium we allow

signallers to send only signals chosen from a defined set, and the donors to respond only to these signals. What happens when other, out-of-equilibrium signals are sent? What happens when for each pair of signals with different costs, the signallers can also send another signal, with an intermediate cost? Can pooling still be stable in such a case?

This depends on how the donors respond to signals which are not sent at the pooling "equilibrium." Certain donor strategies (which specify the behavior of the donor, given the donor's condition and the signal sent) will allow a given pooling equilibrium to remain stable, while others will destabilize the pooling equilibrium. Thus if we allow intermediate signals, we may have a more restrictive set of necessary conditions for stable equilibrium, but this will not rule out the possibility of stable pooling equilibria. While of considerable interest, characterization of these conditions is beyond the scope of this paper.

Furthermore, it becomes crucial when examining these issues to distinguish the signal itself from the signal cost. Notice that the donor directly perceives the former, not the latter. Only when these are one-to-one is it even possible to infer the cost of the signal. Historically, Grafen (1990a) mentions this distinction briefly, but he then proceeds to examine the simplified case in which signals and their costs are indeed one-to-one. Most subsequent signalling analyses follow his model in this respect.

The simplification of identifying signal with signal cost has the undesirable side-effect that donors are not able to distinguish different signals which have the same cost, an artifact which certainly does not hold in nature. Maynard Smith (1994) provides an example which highlights this problem. He demonstrates that in the SPS game, there may exist signalling equilibria in which at least two distinct signals have the same cost. (This cost is zero, in his example.) Whenever this is the case, the signal clearly does not map one-to-one to signal cost and thus the two cannot be equated.

Consequently, the critique that equilibrium is defined only with respect to a certain set of "recognized" signals represent a valid criticism of the entire body of signalling theory literature following Grafen (1990a). This literature does not, at equilibrium, make predictions about how receivers will respond to novel signals and thus demonstrates stability only in a certain narrow sense. As can be seen from the discussion above, this problem is not a consequence of allowing pooling equilibria; the purely separating equilibrium traditionally characterized suffers equally from this weakness.

Other Remarks

The models in this paper deal strictly with the case of signalling among relatives as modelled by the SPS game. The general results, however, regarding the prevalence of multiple signalling equilibria are by no means restricted to this particular model of signalling. Similar results will hold for signalling among non-relatives as well, whether in the context of mate selection, predator-prey signalling, or other costly signalling scenarios.

Finally, what implications do the results of this paper have for empirical study of signalling systems? First of all, they suggest that we should not be at all surprised to discover “pooling” equilibria in nature. Moreover, while signaller error may also allow pooling instead of separating (Grafen and Johnstone 1993; Johnstone 1994), error is not necessary in order to explain the stability of a pooling equilibrium. Second, the potential for the same signalling system to evolve a range of distinct signalling equilibria suggests that it may be possible for signalling systems to be remarkably varied with regard to the partitions of signallers into pools. Two very similar signalling settings, or even two identical signalling settings, could end up with very different partition structures. Of course, which particular equilibrium will be reached is another question entirely, a question which cannot be addressed without also considering the *dynamics* of signal evolution.

APPENDIX: STABILITY OF MULTIPLE EQUILIBRIA IN THE CONTINUOUS SIR PHILIP SIDNEY GAME

The continuous SPS game, as described by Johnstone and Grafen (1992) (detailed here in Section 4) provides a useful illustration of the potential for multiple signalling equilibria.

We prove in Theorem 1 that any contiguous partition of signallers into pools can be a stable signalling equilibrium. There are an infinite number of such partitions, and consequently an infinite number of distinct signalling equilibria are possible in this game. Johnstone and Grafen describe one of these, the *completely separating* equilibrium in which the signaller of fitness y sends a signal with cost $1/2 k(1 - k^2)(1 - y)^2$, and the donor of fitness x transfers if this signal exceeds $1/2(1/k - k)(1 - x)^2$. Under this system, the donor is given complete information and consequently transfer occurs whenever $x > 1 - k + ky$. In Signalling I, we compared this equilibrium to the opposite end of the separating/pooling spectrum, the “no-signalling” or completely pooling

equilibrium. At this equilibrium, all signallers send a signal with cost 0 and donors transfer if $x > 1 - k/2$. Below, we detail two more elaborate pooling equilibria.

Example 1. A Partition with Two Equi-signalling Classes. First, consider a partition of the unit interval into two regions, $X_1 = (a, 1]$ and $X_2 = [0, a]$. Signallers in region X_1 send signal 1 with cost 0. Signallers in region X_2 send signal 2 with cost $c = k/2(1 - a + k^2(a/2 - 3/4))$. (In Section 6 we discuss the case in which this expression is negative.) Below, we demonstrate the manner in which c is derived to ensure that this is a stable signalling equilibrium.

Let the cost of sending signal 1 be 0. The cost c of sending signal 2 required to ensure honest signalling is the cost that makes it worthwhile for only the signallers of fitness less than a to send signal 2. Let \hat{p} be the probability of causing a donor to begin transferring by sending 2 instead of 1 and \hat{x} be the mean fitness of the donors who are thus induced to alter their behavior. We can compute values of \hat{p} and \hat{x} using the fact that at equilibrium, all donors respond to a given signal as if it were sent by an individual of the average fitness in that pool. At this equilibrium, there are two signals: signal 2 sent by individuals with mean fitness $a/2$, and signal 1 sent by individuals with mean fitness $(1 + a)/2$. Donors respond if $x > 1 - k + ky$, so a fraction $\hat{p} = k((1 + a)/2 - a/2) = k/2$ of the donors will transfer in response to 2 but not in response to 1. These switching donors will have mean fitness $\hat{x} = 1 - 3k/4 - ka/2$. Since c is equal to the probability of causing a donor to switch times the change in inclusive fitness resulting from such a switch, we can write

$$c = \hat{p}((1 - a) - k(1 - \hat{x})) \quad (35)$$

Since $\hat{p} = k/2$ and $\hat{x} = 1 - 3k/4 - ka/2$, we can write \hat{c} as

$$c = \frac{k}{2} \left(1 - a + k^2 \left(\frac{a}{2} - \frac{3}{4} \right) \right) \quad (36)$$

This signal cost has been defined precisely so that signallers with fitnesses in $[0, a]$ will send signal 2, and signallers with fitnesses in $(a, 1]$ will send signal 1. Donors will maximize fitness by treating each individual in a given pool as if she were the mean signaller in that pool. Consequently a donor will transfer in response to 2 only if her own fitness exceeds $1 + k - ka/2$, while she will transfer in response to 1 only if her own fitness exceeds $1 - k + k(1 + a)/2$. Neither donor nor signaller can benefit from altering this strategy, and thus we have a stable signalling equilibrium for the continuous SPS

game in which signallers partition themselves into two different pools

Example 2. Zeno's Partition. A pooling equilibrium does not need to be partitioned into a *finite* number of signal classes. Consider the following partition. Signallers with fitnesses in $X_1 = (1/2, 1]$ send signal 1, signallers in $X_2 = (1/4, 1/2]$ send signal 2, signallers in $X_3 = (1/8, 1/4]$ send 3, signallers in $X_i = ((1/2)^i, (1/2)^{i-1}]$ send signal i , and so on. We call this "Zeno's partition." Like the separating signalling equilibrium detailed by Johnstone and Grafen, Zeno's partition offers an infinite array of signals and can be a stable signalling equilibrium. In Zeno's partition, however, each signal is shared by signallers spanning a range of signaller fitnesses. As in the previous case, donors respond to each signal as if it were sent by the average signaller within the appropriate interval.

Using the logic similar to that of the previous example, we can compute the stable signal costs c_i of signalling S_i . Again we let the highest-fitness individuals signal for free, setting $c_1 = 0$, and notice that $\widehat{p}_i = 3k/2^{i+1}$ and $\widehat{x}_i = 1 - k + 9k/2^{i+2}$. To be stable, the cost of signalling i must be such that only those with fitness below $1/2^{i-1}$ benefit from sending a signal at least this high. Consequently, the cost of sending signal c_i is equal to c_{i-1} plus the gain, to an individual at the boundary between R_i and R_{i-1} , of sending i instead of $i-1$. Defining $c_1 = 0$, this can be written as

$$c_i = c_{i-1} + \widehat{p}_i k \left(1 - \frac{1}{2^{i-1}} \right) - k(1 - \widehat{x}_i) \quad (37)$$

Substituting for \widehat{p}_i and \widehat{x}_i , we arrive at the following recursive expression for signal cost:

$$c_1 = 0$$

$$c_i = c_{i-1} + \frac{3k}{2^{i+1}} \left(1 - \frac{1}{2^{i-1}} - k^2 + \frac{9k^2}{2^{i+2}} \right). \quad (38)$$

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