Evolutionarily stable communication between kin: a general model

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SUMMARY

At present, the most general evolutionary theory of honest communication is Grafen's model of Zahavi's 'handicap' signalling system, in which honesty of signals about the signaller's quality (e.g. mate suitability or fighting ability) is maintained by the differentially high cost of signals to signallers having lower quality. The latter model is here further generalized to include any communication between signallers and receivers that are genetically related (e.g. parents and begging offspring, cooperative or competing siblings). Signalling systems involving relatives are shown to be evolutionarily stable, despite a potential pay-off for false signalling, if the Zahavian assumption of differential signal costs holds and there are diminishing reproductive returns to the signaller as the receiver's assessed value of its attribute increases, or if, regardless of whether the Zahavian assumption holds, signallers with high values of the attribute benefit more from a given receiver assessment than signallers with low values (e.g. begging chicks that are hungrier benefit more from being fed). In stable systems of signalling among kin, it is also shown to be generally true that (i) levels of signalling and thus observed signal costs will decline as relatedness increases or as the receiver's reproductive penalty for erroneous assessment increases, and (ii) receivers will consistently, altruistically overestimate the true value of the signalled attribute.

1. INTRODUCTION

Recently, the evolution of honest communication has received intense theoretical attention (Zahavi 1977; Krebs & Dawkins 1984; Grafen 1990; Godfray 1991, 1995; Maynard Smith 1991, 1994; Johnstone & Grafen 1992; Johnstone 1998). Currently, the most general evolutionary theory of honest communication is Grafen's (1990) model of Zahavi's 'handicap' signalling system, in which honesty of signals about the signaller's quality is maintained by the differentially high cost of signals to signallers having lower quality. Grafen's (1990) model involves communication between non-relatives, but there has been increasing recent interest in the influence of kinship on the evolution of honest signalling, primarily in the context of the communication of resource need between relatives (Godfray 1991, 1995; Maynard Smith 1991, 1994; Johnstone & Grafen 1992).

Below, I generalize Grafen's (1990) signalling model to encompass all communication between relatives, including both signalling of resource need (as in much parent-offspring communication) and aggressive signalling (as in territorial or dominance interactions between relatives living together in social groups). The expanded model: (i) yields general sufficient conditions for the evolutionary stability of reliable signalling among kin; (ii) generalizes theoretical results from the more specific need-communication models about the effect of relatedness on evolution-

arily stable levels of signalling; and (iii) reveals the striking general result that receivers genetically related to signallers should consistently overestimate the value of the signalled attribute as a kind of reproductive altruism.

2. THE GENERAL MODEL

What action is favoured for a signaller or a receiver will be governed by Hamilton's rule (Hamilton 1964), i.e. action i will be favoured over action j if

$$(P_i - P_j) + r(K_i - K_j) > 0, \quad (1)$$

where r is the coefficient of relatedness between the interactants, P_i (or P_j) is the personal reproduction (offspring number) associated with action i (or j) and K_i (or K_j) is the other party's reproduction if action i (or j) is performed. The discrete form of Hamilton's rule (1) implies that selection will favour the value of a continuous behavioural variable, z , that maximizes the inclusive fitness quantity

$$I(z) = P(z) + rK(z), \quad (2)$$

where $P(z)$ is the reproduction of the actor and $K(z)$ is that of the recipient. (The validity of use of expression (2) as the appropriate fitness measure rests upon the assumption of continuous behavioural strategies (Grafen 1979) or conditional expression of these strategies for individuals in signaller versus receiver roles (Parker 1989).) In the case of communica-

Figure 1. The receiver's fitness $k(p - q)$ is assumed to decline with increasing discrepancy $h = p - q$ between the assessed value of the signaller's attribute p and its actual value q . The evolutionarily stable value of h^* must be positive, since the tangent to $k(h)$ at that point must be negative (equation (7) and condition (ii)).

tive interactions in which a signaller's reproduction is s and a related receiver's reproduction is k , a signaller should choose a signal level a that maximizes

$$I_s = s(a) + rk(a), \quad (3)$$

where $s(a)$ and $k(a)$ are functions relating s and k to the signal level a .

On the other hand, the receiver should assess the signal as $p(a)$ so as to maximize

$$I_r = rs(p(a)) + k(p(a)), \quad (4)$$

where s and k are now seen as functions of the assessed value p of the signalled attribute, this assessed value itself being a function of the signal level a .

Following Grafen (1990), I decompose the reproduction of the signaller into three components, i.e. $s = s[a, p, q]$, where a is the advertisement or signal level and p is the receiver's assessed value of the signaller's attribute q . The direct reproduction of the receiver depends only on the difference $h = p - q$, with the highest reproductive output accruing to the receiver who responds as if $p = q$ exactly, i.e. $k(h)$ is a maximum at $h = 0$ (e.g. figure 1). After Grafen (1990), I adopt the simplified notation

$$\begin{aligned} \frac{\partial s}{\partial a} &= s_1, & \frac{\partial s}{\partial p} &= s_2, & \frac{\partial^2 s}{\partial p^2} &= s_{22}, \\ \frac{\partial^2 s}{\partial p \partial q} &= s_{23}, & \frac{\partial^2 s}{\partial a \partial q} &= s_{13}. \end{aligned}$$

In all cases, $s_{xy}[a_0, p_0, q_0]$ means s_{xy} evaluated at $a = a_0$, $p = p_0$ and $q = q_0$.

I assume the following conditions: (i) $s_1 < 0$ (i.e. signalling is costly); (ii) $s_2 > 0$ (i.e. signaller reproduction increases with increases in the receiver's assessed value p of the signalled trait q); (iii) $s_{13} \geq 0$, (signallers with higher values of q do not suffer an increased cost of signalling at a given level a); and either (iv) $s_{23} > 0$ (i.e. signallers with higher q benefit more from higher receiver assessment of q , e.g. needier, begging relatives benefit more from receiving a given amount of resource), or (v) $s_{23} = 0$ and

$s_{22} < 0$ (i.e. there are diminishing reproductive returns to the signaller as the receiver's assessed value of its attribute increases, e.g. begging relatives experience diminishing survivorship benefits with increasing amount of resource received).

Given the above conditions, the evolutionarily stable signalling system is described by the following relations, where $A^*(q)$ is the signaller's evolutionarily stable level of signalling, given that its attribute is q , and $P^*(a)$ is the receiver's evolutionarily stable assessment of q , given that it perceives a level of signalling a by the signaller:

$$P^{*'}(a) = \frac{-s_1[a, P^*(a), P^*(a) - h^*]}{s_2[a, P^*(a), P^*(a) - h^*](1 - r^2)}, \quad (5)$$

$$P^*[A^*[q]] = q + h^*, \quad (6)$$

$$k'[h^*] = -rs_2[a, P^*[a], P^*(a) - h^*]. \quad (7)$$

The formal proof of stability, which extends the logic of Grafen (1990), proceeds as follows.

Proof of stability of signaller's general signalling rule. From equation (2), and the definitions in text, the signaller's inclusive fitness, given that the receiver is optimally assessing the signal, is $I_s = s[a, P^*(a), q] + rk(P^*[a] - q)$. Thus,

$$\begin{aligned} \frac{\partial I_s}{\partial a} &= s_1[a, P^*[a], q] \\ &+ P^{*'}(a)s_2 + rP^{*'}(a)k'[P^*(a) - q]. \end{aligned} \quad (8)$$

Now $\partial I_r / \partial p$ must equal zero (if the receiver is at an inclusive fitness maximum), so $P^*(a)$ must satisfy $k'[P^*(a) - q] = -rs_2[a, P^*(a), q]$ (see below). The right-hand side of (8) becomes, after the latter substitution,

$$\begin{aligned} \frac{\partial I_s}{\partial a} &= s_1[a, P^*[a], q] \\ &+ P^{*'}(a)s_2[a, P^*(a), q](1 - r^2). \end{aligned} \quad (9)$$

Next we substitute (5) in for $P^{*'}(a)$ in the right-hand side of (9), then divide by the positive quantity $s_2[a, P^*[a], q]$ to obtain the expression

$$\frac{s_1[a, P^*(a), q]}{s_2[a, P^*(a), q]} - \frac{s_1[a, P^*(a), P^*(a) - h^*]}{s_2[a, P^*(a), P^*(a) - h^*]}. \quad (10)$$

The sign of (10) is the same as the sign of $\partial I_s / \partial a$. Now conditions (i), (ii), (iii) and (iv) or (v) are sufficient to ensure that the left-hand side of (10) increases with q (with inequality (iii) becoming strict if (v) holds), because the derivative of this expression with respect to q has the same sign as $s_2s_{13} - s_{23}s_1$. Thus, if $q = P^*(a) - h^*$, expression (10) is zero, corresponding to an inclusive fitness extremum. If $q < P^*(a) - h^*$, which, by equations (6) and (5) and conditions (i) and (ii), corresponds to $a > A^*(q)$, then (10) will be negative and selection will decrease the level of signalling. If $q > P^*(a) - h^*$, which corresponds to $a < A^*(q)$, then (10) will be positive and selection will increase the level of signalling. This establishes that $A^*(q)$ given by (5) and (6) is the evolutionarily stable signalling level for a signaller with attribute value q . ■

Figure 2. Major predictions of the generalized model of signalling between relatives. (a) Evolutionarily stable signalling level a as a function of signalled attribute q , for three values of genetic relatedness; and (b) the evolutionarily stable bias h^* in receiver's assessment of the attribute as a function of its true value q . For these graphs, $k(p - q) = \exp[-10(p - q)^2]$ and $s = \exp[p - q(1 - a)]$, $0 \leq a, q \leq 1$.

Proof of stability of receiver's general assessment rule. Condition (iv): the receiver's inclusive fitness $I_r = rs[a, p, q] + k[p - q]$ is at an extremum in p when $\partial I_r / \partial p$ is equal to zero, i.e. when $P^*(a)$ satisfies $rs_2[a, P^*(a), q] + k'[P^*(a) - q] = 0$. Substituting (7) into the left-hand expression yields

$$r\{s_2[a, P^*(a), q] - s_2[a, P^*(a), P^*(a) - h^*]\}. \quad (11)$$

Thus, if $q = P^*(a) - h^*$, expression (11) is zero, corresponding to an inclusive fitness extremum. If $q < P^*(a) - h^*$ (which is the same as $P^*(a) > q + h^*$), then, by condition (iv), (11) will be negative and selection will decrease the assessment p . If $q > P^*(a) - h^*$, (which is the same as $P^*(a) < q + h^*$), then, by condition (iv), (11) will be positive and selection will increase the assessment p . This establishes that $P^*(a)$ given by equations (5) and (7) is the evolutionarily stable assessed value of the attribute given a signal level a .

Condition (v): since $\partial^2 I_r / \partial p^2 = rs_{22}[a, p, q] + k''[p - q] < 0$, because of condition (v) and the assumed form of $k[h]$, the solution $p = P^*(a)$ to equations (5)–(7) will correspond to a local maximum in I_r . ■

The quantity h^* represents the amount by which the receiver overestimates the attribute q of the signaller. By equation (7) and condition (ii), this quantity must be such that the slope of the tangent line to $k[p - q]$ is negative and this only occurs for $p > q$, i.e. for positive h (figure 1). The assessment bias h^* itself can be a function of q and, in particular, will increase as q increases (figure 2) if signallers with a higher q benefit more from a given increase in p (equation (7) and condition (iv)).

A central prediction of the above signalling model is that higher relatedness should reduce the signaller's signal level, and thus the observed costli-

Figure 3. Relationship between relatedness r and evolutionarily stable signalling level.

ness of signalling (figures 2, 3), and provides a firm theoretical foundation for the idea that substantial overlap in genetic interests between signallers and receivers should lead to low cost 'conspiratorial whispers' (e.g. Krebs & Dawkins 1984). Thus, the model greatly generalizes similar arguments made from more specific models of communication between relatives (Godfray 1991, 1995; Maynard Smith 1991, 1994; Johnstone & Grafen 1992), showing that they apply to a wide variety of signalling contexts, e.g. even territorial-agonistic interactions among kin. For example, the model may explain the puzzling lack of overt dominance displays between closely related, competing male breeders in colonies of the eusocial naked mole-rat (Lacey & Sherman 1991). The prediction also explains why so many cooperative communication systems in groups of relatives (such as many eusocial insect societies) involve signals that are so subtle that they are often difficult to decode (Seeley 1996). In addition, the general model predicts that evolutionarily stable signals may not be very costly even if relatedness is not high, provided that the receiver's fitness function (figure 1) is sufficiently sharply peaked, i.e. there is a rapidly increasing receiver penalty for overestimating q . In the latter case, by equation (7), h^* will be smaller for a steeper $k[h]$ curve, leading to a lower evolutionarily stable level a of signalling (see figure 3 for a geometrical representation of this and the other model predictions).

In figure 3, as r increases, by equation (5), $P^*(a)$ increases both because of the direct contribution by r and because of the effect of r on h^* ; by equation (7), h^* increases as r increases, and increased h^* increases the right-hand side of equation (5) (recall that, by assumption, s_1/s_2 decreases with decreased value of the third argument, so $-s_1/s_2$ must increase with decreased value of the third argument). This means that the curve $P^*(a)$ rises more steeply with signalling level a as r increases. At a stable signalling equilibrium, $P^*(a) = P^*(A^*(q)) = q + h^*$ (by equation (6)). Thus, the same graph can be used to relate the signaller's level of signalling $A^*(q)$ to its attribute value q . A more sharply rising $P(A^*(q))$ curve for kin than for non-kin interactions means that the evolutionarily stable signalling level $A^*(q)$ when relatedness is positive must be lower than that when relatedness is zero (a_1 and a_2 , respectively).

Proof. By differentiating both sides of equation (7), i.e. $P^*[A^*(r), h^*(r), r] = q + h^*(r)$ with respect to relatedness r , we obtain, from the multivariable chain rule,

$$\frac{\partial P^*}{\partial A^*} \frac{\partial A^*}{\partial r} + \frac{\partial P^*}{\partial h^*} \frac{\partial h^*}{\partial r} + \frac{\partial P^*}{\partial r} = \frac{\partial h^*}{\partial r},$$

which simplifies to

$$\frac{\partial P^*}{\partial A^*} \frac{\partial A^*}{\partial r} + \frac{\partial P^*}{\partial r} = \frac{\partial h^*}{\partial r} \left(1 - \frac{\partial P^*}{\partial h^*} \right).$$

Since $P^* = q + h^*$, it must be that $\partial P^*/\partial h^* = 1$, so the previous equation becomes

$$\frac{\partial P^*}{\partial A^*} \frac{\partial A^*}{\partial r} + \frac{\partial P^*}{\partial r} = 0.$$

Since $\partial P^*/\partial A^*$ and $\partial P^*/\partial r$ are both positive (from assumed conditions and above arguments), it must be that $\partial A^*/\partial r < 0$, i.e. the stable signalling level will decrease with increasing relatedness. The generalized model of signalling between kin reduces to the Grafen (1990) handicap model when $r = 0$ (h^* becomes 0 (by (7)) and $P^*(A^*(q)) = q$). ■

Signals in stable honest signalling systems involving kin need not be very costly in an absolute sense and, in addition, they need not be differentially costly to signallers having lower values of the signalled attribute (e.g. fighting ability, quality). Such differential signal costliness (i.e. condition (iii) as a strict inequality) is central to Zahavi's verbal model of honest communication (Zahavi 1977; Grafen 1990) but is not required for honest signalling to be stable among relatives, even when there is potential pay-off for providing false signals. The stability of honest signalling when $s_{13} = 0$ but $s_{23} > 0$, i.e. when signallers with high values of the attribute benefit more from a given receiver assessment than signallers with low values, supports and generalizes results from recent models of honest communication of need between relatives (Godfray 1991, 1995; Maynard Smith 1991, 1994; Johnstone & Grafen 1992).

Interestingly, the general model predicts that receivers should consistently overestimate the attributes q of kin. This effect represents a kind of altruism on the part of the receiver: receivers pay a personal cost for overestimating the attribute of the signaller, but gain an indirect fitness benefit by increasing the reproductive output of the genetically related signaller. Thus, although signalling among kin can be honest under the given conditions, in the sense that there will be a predictably positive relationship between attribute value and signalling level, it is not generally the case that the receiver will appear to accurately infer the value of the signalled attribute.

The general signalling model can be applied to communication even between effectively sterile relatives (e.g. workers in a eusocial group) if s and k in the inclusive fitness expressions (3) and (4) refer to the production of collateral relatives that are respectively more and less closely related to the signaller (and, symmetrically, less and more closely related to

the receiver). In such a case, r represents the signaller's or receiver's relatedness to the less-closely related kin class (e.g. half-siblings), divided by the signaller's or receiver's relatedness to the more-closely related kin class (e.g. full siblings).

Finally, the general model may have unusual consequences for the communication of kinship itself, i.e. where q is the coefficient of relatedness (known to signaller but incompletely or not at all by the receiver) and p represents the assessed relatedness, which dictates the amount of altruism to be directed by the receiver to the signaller. If the above conditions are met (now with $k'[p - q] < 0$ for all p), it is possible that more-closely related kin will signal kinship in a costlier manner, provided receivers cannot directly assess kinship. Thus, the model raises the intriguing theoretical possibility that kinship can be honestly signalled even when kin do not directly exhibit kin-correlated labels such as odours or morphological features.

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