HOW COSTLY IS THE HONEST SIGNALING OF NEED?[1]

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Summary

ESS models of biological signaling have shown that costly signals can provide honest information. In the context of parent-offspring conflict over the allocation of resources by parents to their young, the theory explains costly offspring solicitation behavior as an accurate signal of offspring need to parents who cannot assess offspring condition directly. In this paper, we provide a simple but general characterization of the honest signaling of need in models of parent-offspring conflict: the offspring's signaling cost is proportional to the parent's fitness loss from satisfying the offspring's resource requirement. The factor of proportionality is given by a measure of the extent of parent-offspring conflict that depends only on coefficients of relatedness. These results hold for interbrood conflict with uniparental investment even if the relationship between offspring condition and resource requirement is not monotonic, and extend to cases of biparental care, uncertainty concerning the parent's condition, and intra-brood conflict.

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HOW COSTLY IS THE HONEST SIGNALING OF NEED?

by Georg Nöldeke and Larry Samuelson

1 Introduction

Recent theoretical work has used game theoretic models of biological signaling to explain off-spring solicitation as a costly signal of need. In these models (Godfray, 1991; Godfray, 1995b), offspring vary in condition in a way that parents are unable to assess directly. The equilibrium level of offspring solicitation uniquely reflects offspring condition, thus communicating accurate information to the parent about the benefits of providing the offspring with resources. Parents respond to more intense begging by allocating more resources to the offspring. To ensure the evolutionary stability of the signaling system, begging must be costly. This costly-signaling requirement is obtained as a consequence of parent-offspring conflict over the optimal distribution of the resources (Trivers, 1974; Godfray, 1995a), which makes cost-free, perfectly informative communication between the parent and offspring impossible.

This paper sharpens these insights by providing a simple characterization of the honest signaling of need. Our approach is game-theoretic (Grafen, 1990a; Grafen, 1990b; Johnstone (1998)). We concentrate on the signaling of need (Maynard Smith (1991, 1994), Godfray (1991, 1995b) and Johnstone and Grafen (1992)) rather than quality (Grafen 1990a, Johnstone 1995b), meaning that the sender's condition does not affect the cost of signaling in our model, but does affect the benefits conferred by the receiver's actions. Finally, we concentrate on honest signaling, in the sense that we examine equilibria in which signals allow the receiver to infer the need of the sender. Rodríguez-Gironés *et al.* (1996), Bergstrom and Lachmann (1997), and Lachmann and Bergstrom (1998) discuss the existence of pooling equilibria, in which need is not revealed.

Our characterization focuses on the offspring's resource requirement (Godfray 1995b), which is the level of resource transfer to the offspring that maximizes the parent's inclusive fitness.

We show that the offspring's equilibrium costs of signaling are proportional to the parent's fitness loss from satisfying the offspring's resource requirement, with the proportionality factor determined by the coefficients of relatedness. Factors such as offspring condition and the benefit the offspring derives from parental resources, investigated as determinants of signaling costs by Godfray (1995b) and Johnstone and Grafen (1992), respectively, affect the offspring's signaling costs only to the extent that they affect the parent's fitness loss.

We first develop these points in the setting considered by Godfray (1991), in which there is only one offspring and one parent. The model is presented in Section 2. In Section 3 we state and explain our result on the evolutionary stability of costly signaling. Section 4 uses this result to extend an example of Godfray (1991), demonstrating that commonly-imposed monotonicity conditions on the relationship between offspring condition and offspring fitness benefits from parental resource transfers (Godfray 1991, 1995b; Grafen, 1990a; Johnstone and Grafen, 1992; Maynard Smith 1991) are unnecessary for the evolutionary stability of signaling equilibria. Section 5 extends the results to allow for biparental care (Parker, 1985), uncertainty about the parent's condition (yielding the Sir Philip Sidney game as studied by Johnstone and Grafen (1992) as a special case), and sibling rivalry (Godfray, 1995b).

2 The Signaling Model

Our basic model is adapted from Godfray (1991). It considers a parent and an offspring. The offspring is characterized by its condition c, where a larger value of c can be interpreted as denoting a healthier offspring. This condition cannot be assessed directly by the parent. The distribution of offspring condition is described by a density $\rho(c)$, assumed to be strictly positive on the interval $[\underline{c}, \overline{c}]$.[1]

The offspring can engage in the costly solicitation of a resource, such as the energy-

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[1] We follow the common practice of assuming that offspring condition varies continuously (Godfray 1991, 1995b; Grafen, 1990a, 1990b; Johnstone and Grafen, 1992). This assumption eliminates the indeterminacy in equilibrium signaling costs that appears in models with a finite set of conditions (Hurd, 1995).

consuming begging for food. The level of this signaling activity is denoted by $x \geq 0$. The parent observes the level of the signaling activity and responds by providing an amount of resource $y \geq 0$ to the offspring, while retaining $z \geq 0$, where $y + z = \overline{y}$. We can interpret $\overline{y} > 0$ as a given amount of food to be distributed between the parent and the offspring.

In order to study the signaling of need, we follow Godfray (1991, 1995b) and Johnstone and Grafen (1992) in taking the cost of soliciting at a given level to be independent of both offspring condition and the amount of food obtained from the parent. The fitness of an offspring in condition c who receives y units of the resource from the parent and signals at level x is given by $f(c, y) - x$, where f is assumed to be continuously differentiable and increasing in y. Given that the costs of solicitation are independent of condition, taking the cost of signal x to be simply x requires only that solicitation levels are measured in the same units as offspring fitness and is not a substantive assumption.

Transferring resources to the offspring reduces the parent's fitness by decreasing her future reproductive success. We let $g(z) = g(\overline{y} - y)$ denote the fitness of the parent when transferring quantity y of the resource to the offspring, where g is continuously differentiable and strictly increasing in the amount z of resource retained.

The inclusive fitness of the offspring is given by

$$u(c, x, y) = f(c, y) - x + \psi g(\overline{y} - y),$$

where $0 < \psi \leq 1$ is the coefficient of relatedness between the offspring and future siblings. The inclusive fitness of the parent is

$$v(c, x, y) = g(\overline{y} - y) + \gamma[f(c, y) - x],$$

with $0 < \gamma \leq 1$. We assume that ψ and γ are not both equal to one, ensuring that there is some conflict of interest between the parent and offspring (see Section 3).

In the context of an offspring signaling to a parent, $\psi < 1$ and $\gamma = 1$ is the most plausible case, implying that an offspring values his own fitness more than that of future siblings, while the parent weights the fitness of current and future offspring equally. We do not restrict our

attention to these values in order to allow for alternative interpretations of our analysis. In order to apply our results to the case of signaling between siblings, for example, assume $\psi = \gamma$. More generally, if the sender and receiver of a signal each have an interest in the survival of the other, as might be the case with a pair of mates, then both ψ and γ will be positive (Maynard Smith, 1991), but will typically be less than one.

For a given offspring condition c, the parent's inclusive fitness is a continuous function of y on the interval $[0, \overline{y}]$, and hence has a maximizer, which we assume to be unique for all c. The transfer $\tilde{y}(c)$ that maximizes the parent's inclusive fitness depends upon the offspring's condition c but is independent of the level of solicitation, and is the solution to

$$\max_{y} g(\overline{y} - y) + \gamma f(c, y). \tag{1}$$

We assume that $\tilde{y}(c)$ is piecewise continuously differentiable.[2] Following Godfray (1995b), we refer to $\tilde{y}(c)$ as the offspring's *resource requirement*.

A strategy for the offspring is a measurable function $x(c)$, specifying the level of solicitation for each possible offspring condition c. Because the parent cannot observe the condition of the offspring, her transfer cannot depend directly on the offspring's condition. A strategy for the parent is thus given by a measurable function $y(x)$, specifying the amount of the resource provided to an offspring soliciting at level x.

We now turn to the criteria for a pair of strategies $x^*(c)$, $y^*(x)$ to be evolutionary stable. First, these strategies must be a Nash equilibrium, meaning that $x^*(c)$, $y^*(x)$ must satisfy:

$$u(c, x^*(c), y^*(x^*(c))) \geq u(c, x, y^*(x)), \quad \text{for all } c, x, \tag{2}$$

$$\int_{\underline{c}}^{\overline{c}} v(c, x^*(c), y^*(x^*(c)))\rho(c)dc \geq \int_{\underline{c}}^{\overline{c}} v(c, x^*(c), y(x^*(c)))\rho(c)dc, \quad \text{for all strategies } y(x). \tag{3}$$

These match the equilibrium conditions formulated by Grafen (Grafen 1990a) for a signaling

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[2]A function is piecewise continuously differentiable if it is continuously differentiable except at a finite number of points and has left and right derivatives everywhere. Section 4 presents an example in which $\tilde{y}(c)$ fails to be differentiable at that value of c for which $\tilde{y}(c) = 0$, and it is this possibility that prevents us from making the more convenient assumption that $\tilde{y}$ is continuously differentiable everywhere.

model (see also Johnstone 1995a). Condition (2) requires that the offspring's strategy $x^*(c)$ maximizes the offspring's inclusive fitness given the parent's response. Condition (3) requires that the parent's response $y^*(x)$ maximize the parent's inclusive fitness given the signaling strategy of the offspring.

In addition, offspring whose condition causes them to receive the least desirable transfer should not engage in costly solicitation (Grafen 1990a; Godfray 1991; Johnstone and Grafen 1992). Hence, we require that there exist an offspring condition c^0 for which

$$x^*(c^0) = 0. \tag{4}$$

Because we are interested in honest signaling, we examine equilibria in which the offspring's signals provide the parent with sufficient information to infer the offspring's resource requirement, in which case (3) implies that the parent's transfer must satisfy:

$$y^*(x^*(c)) = \tilde{y}(c), \quad \text{for all } c. \tag{5}$$

We refer to such an equilibrium as a *signaling equilibrium.*

Other equilibria exist that satisfy (2)–(4) but not (5). For example, there is always a pooling equilibrium in which the offspring does not signal and the parent does not react to solicitation (Grafen, 1990b; Rodríguez-Gironés *et al.*, 1996; Bergstrom and Lachmann, 1997). As indicated by Lachmann and Bergstrom (1998) and discussed in the economics literature (Kreps and Sobel, 1994), there may be many other equilibria, including partially informative equilibria supported by costless signals (Maynard Smith, 1994) in which both the parent and all offspring attain higher fitnesses than they do in a signaling equilibrium (Bergstrom and Lachmann, 1997). Additional stability arguments are then required to justify the focus on signaling equilibrium (Grafen 1990a, 1990b).

3   Honest Signaling of Need: A Characterization

Parent-offspring conflict arises in our context because the parent's inclusive fitness places a larger relative weight on the parent's (rather than the offspring's) fitness than does the offspring's

inclusive fitness. In particular, if the offspring could induce the parent to transfer an arbitrary amount of resource y simply be engaging in *cost-free* solicitation behavior, then an offspring in condition c would be selected to obtain the transfer $y^\ddagger(c)$ which solves

$$\max_y [f(c,y) + \psi g(\overline{y} - y)]. \tag{6}$$

Letting a subscript denote a derivative with respect to the relevant variable, the first-order condition for this problem is (recall $z = \overline{y} - y$)

$$f_y(c,y) = \psi g_z(\overline{y} - y), \tag{7}$$

equating the offspring's marginal benefit from obtaining parental resources with the product of the coefficient of relatedness ψ and the parent's marginal cost of providing the resource. Taking a derivative and multiplying by the constant $1/\gamma$, the corresponding first-order condition for the parent's problem (1) can be written as

$$f_y(c,y) = \frac{1}{\gamma} g_z(\overline{y} - y). \tag{8}$$

For a given value of c, the solutions to these first order conditions are illustrated in Figure 1. Because γ and ψ are not both equal to one, we have $1/\gamma > \psi$, and hence $y^\ddagger(c) > \tilde{y}(c)$. The offspring prefers a larger transfer than does the parent.

The difficulty in ensuring the honest signaling of need is then that the offspring has an incentive to exaggerate its need, in quest of a larger transfer than is preferred by the parent. To counteract this incentive, signaling must be costly. In particular, suppose that in order to obtain a transfer y, the offspring must not only bear the marginal cost $\psi g_z(\overline{y} - y)$, but also an additional marginal cost arising from the necessity to engage in costly signaling. Honesty will be ensured if this additional cost causes the offspring to face precisely the same trade-off between the relative benefits and costs of resource transfer as does the parent. An offspring in condition c will then be selected to elicit the parent's preferred transfer $\tilde{y}(c)$.

Comparing the first-order conditions in (7) and (8), signaling costs will compensate for the parent-offspring conflict, eliminating the offspring's incentive to exaggerate its need, when
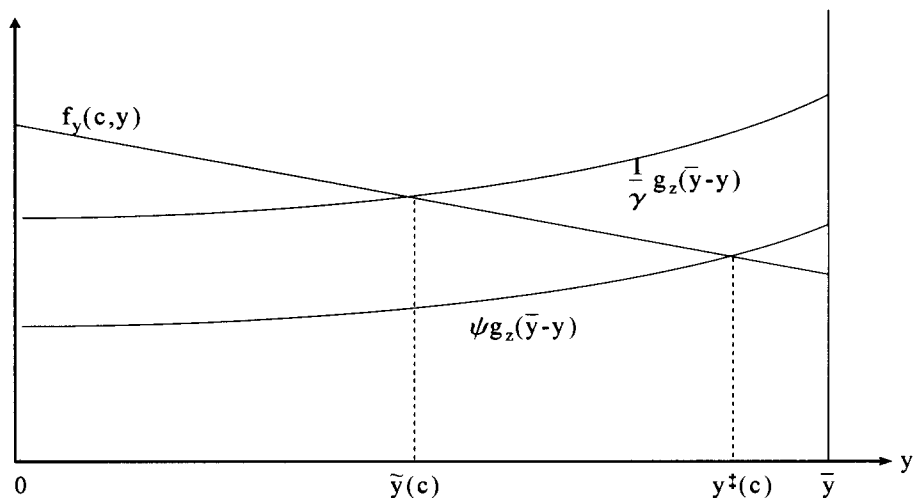
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Figure 1: Solutions to the offspring and parent optimization problems. The offspring's marginal benefit ($f_y(c, y)$) and marginal cost ($\psi g_z(\overline{y} - y)$) of obtaining transfer y are shown as a function of y. The functions $f_c(c, y)$ and $(1/\gamma)g_z(\overline{y} - y)$ have analogous interpretations for the parent. Optimal transfers balance these marginal costs and benefits, with the parent's optimal transfer given by $\tilde{y}(c)$ and the offspring's optimal transfer given by $y^{\ddagger}(c)$.

marginal signaling costs are given by $mg_z(\bar{y} - y)$, where

$$m = \frac{1}{\gamma} - \psi.$$

We can interpret m as a measure of parent-offspring conflict. This measure depends only upon the coefficients of relatedness ψ and γ, with ψ being the relative weight put on the parent's fitness in the offspring's inclusive fitness function and $1/\gamma$ being the relative weight put on the parent's fitness in the parent's inclusive fitness function. Parent-offspring conflict exists when $m > 0$.

These observations suggest that in a signaling equilibrium, the slope of the offspring's signaling cost function should be given by $x_c^*(c) = mg_z(\bar{y} - \tilde{y}(c))\tilde{y}_c(c)$. Integrating this equation

leads to

$$x^*(c) = k - mg(\bar{y} - \tilde{y}(c)), \tag{9}$$

where the constant k must chosen to ensure that the offspring whose condition elicits the smallest equilibrium transfer from the parent incurs no signaling cost. This will be the case if we set $k = mg(\bar{y} - y^0)$, where $y^0 = \min_c \tilde{y}(c)$ is the resource requirement of the offspring in the least needy condition, to whom the parent would make the smallest resource transfer. Defining

$$L(y) = g(\bar{y} - y^0) - g(\bar{y} - y),$$

we may then rewrite (9) as

$$x^*(c) = mL(\tilde{y}(c)). \tag{10}$$

The function $L(y)$ is the fitness loss incurred by the parent in making transfer y rather than y^0. Hence, $L(\tilde{y}(c))$ is the parent's fitness loss from satisfying the resource requirement of an offspring in condition c, rather than satisfying the requirement y^0 of the least needy type of offspring.

The following proposition, proven in the Appendix, builds upon this intuition to establish that a signaling equilibrium exists and that (10) characterizes every signaling equilibrium.

Proposition. A signaling equilibrium exists. In every signaling equilibrium, the cost of the signal sent by an offspring in condition c is given by $x^*(c) = mL(\tilde{y}(c))$.

This proposition is a precise statement of the implications of honest signaling theory for the advertisement of need. The equilibrium signaling cost of an offspring in condition c is proportional to the fitness loss the parent must incur to provide the offspring's resource requirement (rather than the smallest possible resource requirement). The factor of proportionality is the measure m of relatedness. Because the parent's fitness loss is bounded, costless signals (Maynard Smith, 1991) suffice for a signaling equilibrium in the limit as m approaches zero and hence the conflict of interest disappears. Costly signals are required when interests conflict.

4 Example

We can illustrate our analysis by extending an example taken from Godfray (1991). Let offspring fitness be given by

$$f(c, y) - x = U \cdot (1 - e^{-c\theta y}) - x,$$

where U is a strictly positive constant and $\theta > 0$ is a parameter measuring how effective parental transfers are at increasing offspring fitness, with larger value of θ indicating more effective transfers. Let the fitness of the parent be given by

$$g(\overline{y} - y) = G \cdot (\overline{y} - y),$$

where G is a strictly positive constants.

To find the offspring's resource requirement, we can differentiate the parent's inclusive fitness function to obtain the first-order condition $-G + \gamma U c\theta e^{-c\theta y} = 0$. (The second derivative, given by $-\gamma U(c\theta)^2 e^{-c\theta y}$, is strictly negative for $c > 0$, ensuring that the second-order conditions for a maximum are satisfied.) If this first-order condition has an interior solution, then the resource requirement is positive. Otherwise, we have a boundary solution with $\tilde{y}(c) = 0$. Hence, we obtain:[3]

$$\tilde{y}(c) = \max \left\{ 0, \frac{1}{c\theta} \ln \frac{\gamma U c\theta}{G} \right\}. \tag{11}$$

This function is illustrated in Fig. 2.

The equilibrium signaling function is, from (10):

$$x^*(c) = \max \left\{ 0, \left(\frac{1}{\gamma} - \psi \right) G \left(\frac{1}{c\theta} \ln \frac{\gamma U c\theta}{G} - y^0 \right) \right\}. \tag{12}$$

Godfray assumes that the offspring's resource requirement $\tilde{y}(c)$ is monotonically decreasing in c by assuming the parameter values used in our Fig. 2 and assuming $c \in [0.5, 2.5]$. An offspring in condition $\overline{c} = 2.5$ then receives the smallest equilibrium transfer and sends no signal, so that

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[3]For sake of convenience we assume that the constraint $\tilde{y}(c) \leq \overline{y}$ is not binding, so that the parent never transfers all the resource.
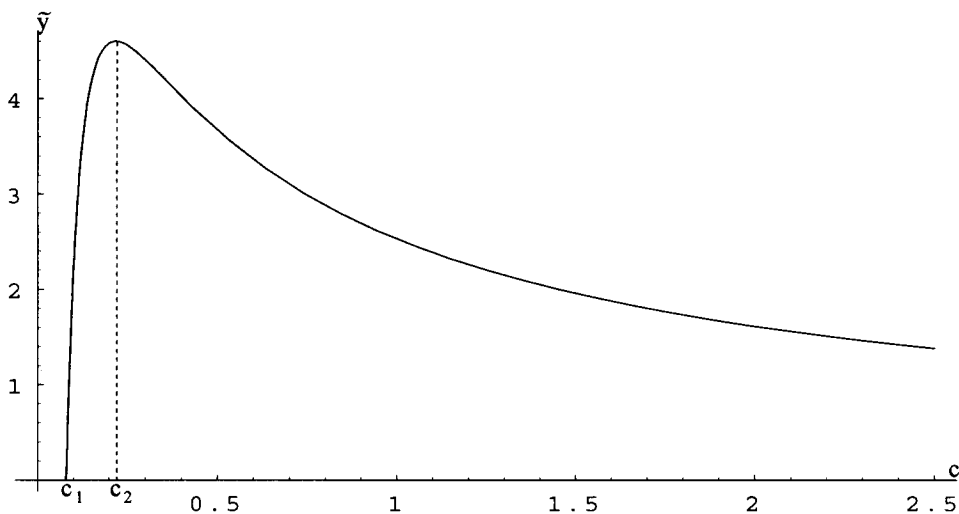
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Figure 2: Offspring resource requirement $\tilde{y}$, given by (11), as a function of offspring condition c, where $G = 0.08$, and $U = \gamma = \theta = 1$. These parameter values are chosen so that the offspring resource requirement function (11) duplicates the "Resources obtained" function in Godfray (1991, Fig. 1) when $\underline{c} = 0.5$ and $\bar{c} = 2.5$. $c_1 = 0.08$ and $c_2 \approx 0.22$.

$c^0 = \bar{c}$, while offspring in poorer condition send more costly signals and receive larger transfers. Because signals are monotonically decreasing in offspring condition, equilibrium signals allow the parent to infer the offspring's condition.

Starting with Godfray's parameter values, consider an increase in θ, so that parental transfers become more effective in enhancing offspring fitness. Doing so illustrates the link between signaling costs and parental fitness losses (rather than offspring benefits): From (11)–(12), it is straightforward to calculate that the offspring equilibrium fitness benefits from the parent's transfer, given by $\theta \tilde{y}(c)$, increase in θ. However, the parent's fitness loss from providing these transfers, and hence the offspring's equilibrium signaling costs, *decrease*.

In Godfray's example, the parent makes larger transfers to offspring in poorer condition. In some circumstances, however, the parent may prefer to transfer more food to offspring in

better rather than worse condition. Grafen (1990a, p. 527) notes that the parent may prefer to give more food to offspring in better condition "so as not to waste any food on the sick" while Godfray (1991, p. 328) notes that the parent may "be selected to cease feeding completely if the young is in very poor condition."

Figure 2 shows that this possibility is easily captured in the present model by allowing for sufficiently low offspring conditions. For offspring conditions somewhat less than $c_2 = eG/(\gamma U \theta)$, poorer conditions elicit smaller transfers. Furthermore, there is a critical condition below which the parent stops feeding the offspring, given by $c_1 = G/(\gamma U \theta) > 0$.

Assuming $\underline{c} = 0$ and $\bar{c} > c_2$ produces a signaling equilibrium in which offspring in sufficiently low condition do not signal and receive no resources. We then have $y^0 = 0$ in (12), giving $x^*(c) = mG\tilde{y}(c))$. For offspring in better condition, signaling costs are increasing up to condition c_2 and decreasing thereafter. Signaling costs are strictly positive for offspring in the best possible condition because these offspring receive a strictly positive transfer rather than the minimum transfer of zero. A signaling equilibrium thus does not require that offspring in poorer condition send more costly signals.

If the minimum offspring condition $\underline{c}$ is lower than c_2, while $\bar{c} > c_2$, then the relationship between offspring condition and the resource requirement is not monotonic. Because equilibrium signaling costs are a function of resource requirements (see (10)), there is then no signaling equilibrium in which offspring signals reveal their conditions. However, it suffices for a signaling equilibrium that the offspring's resource requirement is revealed, or $\tilde{y}(c) \neq \tilde{y}(c') \Rightarrow x^*(c) \neq x^*(c')$, which is ensured by the proportionality of signaling costs and parent fitness losses.

Because the need for costly signals arises out of the parent's inability to directly assess the offspring's condition, one might expect signaling costs to decline as the variation in possible offspring conditions declines. If the optimal transfer function $\tilde{y}(c)$ is not monotonic, however, this need not be the case. Figure 3 shows the relationship between expected signaling costs and the degree of uncertainty concerning offspring condition. The mean offspring condition is kept fixed at $c = 1.25$ throughout, while the support of a uniform distribution over offspring conditions
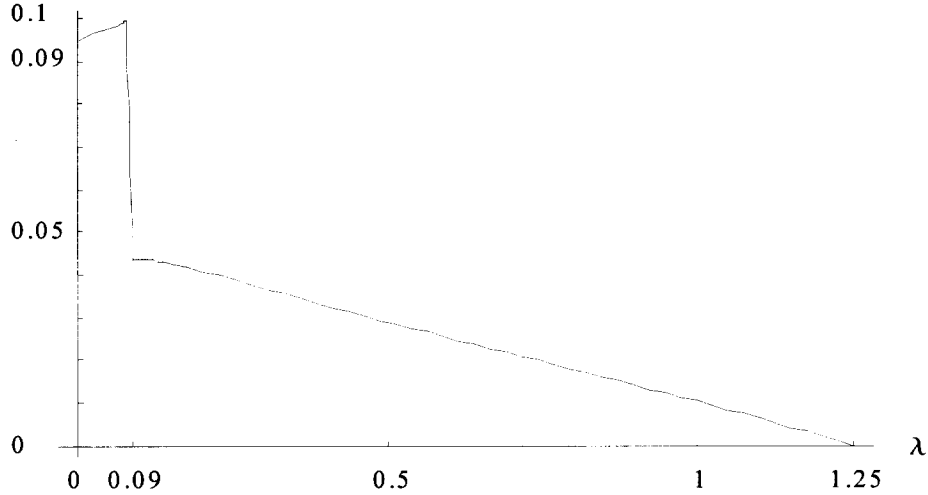
Figure 3: Expected signaling costs as a function of λ, where larger values of λ correspond to *decreased* uncertainty concerning offspring condition. Offspring condition is uniformly distributed on the interval $[\lambda, 2.5 - \lambda]$, so that the support of the distribution over offspring conditions shrinks from $[0, 2.5]$ to a degenerate distribution at $c = 1.25$ as λ increases from zero to 1.25. Signaling costs are given by (12), where $G = 0.08$ and $U = \gamma = \theta = 1$ and $\psi = \frac{1}{2}$. As λ increases from $\lambda = 0$ to $\lambda = .08$, y^0 remains fixed at zero and expected signaling costs increase, as the distribution of offspring conditions becomes more concentrated on offspring that receive positive transfers and incur positive signaling costs. As λ increases above .08, y^0 begins to rise and expected signaling costs decrease continuously but sharply. The kink at $\lambda \approx 0.09$ marks the point at which the offspring in largest (rather than smallest) condition begins to receive the smallest transfer, after which y^0 increases (and expected signaling costs decrease) less rapidly in λ.

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collapses from $[0, 2.5]$ to a degenerate distribution at $c = 1.25$. Reducing the uncertainty over offspring types initially *increases* expected signaling costs, with costs subsequently falling to zero. The initial reduction in uncertainty eliminates the possibility of offspring who are in very poor or very good condition, both of whom pay relatively small signaling costs, while increasing the probability attached to offspring conditions that entail relatively high signaling costs (and leaving these signaling costs unchanged). Eventually, virtually all of the variation in offspring condition is eliminated, obviating the value of information about offspring condition and causing signaling costs to shrink to zero.

5   Extensions

This section illustrates applications of our characterization of signaling equilibria beyond the simple parent-offspring conflict of Section 2.

5.1   Biparental Care

Suppose that two parents share the responsibility of nurturing the offspring. Assume pairing occurs for each brood, consisting of one sibling, and that each parent has a fixed quantity of resource to divide with the offspring. Then the direct fitness of a parent may be taken to be independent of the investment of the other parent. In addition, let $\gamma = 1$. Then the inclusive fitnesses of the parents are given by

$$g_1(\overline{y}_1 - y_1) + f(c, y_1 + y_2) - x \tag{13}$$

$$g_2(\overline{y}_2 - y_2) + f(c, y_1 + y_2) - x, \tag{14}$$

where y_1 and y_2 are the transfers made to the offspring by parents 1 and 2. The offspring's inclusive fitness is given by

$$f(c, y_1 + y_2) - x + \psi(g_1(\overline{y}_1 - y_1) + g_2(\overline{y}_2 - y_2)).$$

After observing the offspring's signal, the parents simultaneously choose their transfers. For an offspring in condition c, the parents' fitnesses are maximized by a pair of transfers $\tilde{y}_1(c)$ and

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$\tilde{y}_2(c)$ with the property that $\tilde{y}_1(c)$ maximizes (13) given $\tilde{y}_2(c)$, while $\tilde{y}_2(c)$ maximizes (14) given $\tilde{y}_1(c)$. These transfers are the analog of $\tilde{y}(c)$ in the single-parent case, and we accordingly refer to $\tilde{y}_1(c)$ and $\tilde{y}_2(c)$ as the offspring's resource requirement.

The offspring's equilibrium signaling cost is now given by

$$x^*(c) = m\left[L_1(\tilde{y}_1(c)) + L_2(\tilde{y}_2(c))\right]. \tag{15}$$

Here, $L_i(y) = g_i(\bar{y}_i - y_i^0) - g_i(\bar{y}_i - y)$ and y_1^0 and y_2^0 are the resource requirement of the least needy offspring, i.e., the offspring whose condition solves $\max_c[g_1(\bar{y}_1 - y_1(c)) + g_2(\bar{y}_2 - y_2(c))]$. Signaling costs are thus proportional to the *sum* of the parents' fitnesses losses.

To derive (15), notice that the direct fitness of each parent depends only upon its own contribution to the offspring, while parents share identical interests in the survival of the offspring. As a result, the resource requirements $\tilde{y}_1(c)$ and $\tilde{y}_2(c)$ that separately maximize the parents' inclusive fitness functions also solve the following maximization problem:

$$\max_{y_1,y_2}[g_1(\bar{y}_1 - y_1) + g_2(\bar{y}_2 - y_2) + (f(c, y_1 + y_2) - x)].$$

We can then apply our previous results, proceeding as if there is a single parent whose fitness is $g_1(\bar{y}_1 - y_1) + g_2(\bar{y}_2 - y_2)$, yielding (15).

5.2 Uncertainty about the Parent's Type

The characterization of signaling costs given by (10) extends to cases in which the offspring does not know the parent's condition, with the parent's fitness loss in (10) now replaced by the parent's *expected* fitness loss.

Let the parent be characterized by a condition b whose distribution is described by the strictly positive density $\zeta(b)$ on the interval $[\underline{b}, \bar{b}]$. We assume that the offspring cannot observe the parent's condition when choosing which signal to send.

The parent's fitness now depends upon both the parent's condition and resource transfer, and is given by $g(b, \bar{y} - y)$. The parent's inclusive fitness is given by

$$g(b, \bar{y} - y) + \gamma[f(c, y) - x].$$

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We can maximize this inclusive fitness to obtain the offspring's resource requirement $\tilde{y}(b,c)$, giving the amount of resource a parent in condition b would prefer to transfer to an offspring in condition c. In a signaling equilibrium, a parent in condition b makes the transfer $\tilde{y}(b,c)$ to an offspring in condition c, and our attention turns to characterizing the costs incurred by the offspring.

If the condition of the parent were known to the offspring, an immediate application of our Proposition implies that offspring signaling costs are given by $x(b,c) = mL(b, \tilde{y}(b,c))$, where $L(b,y) = g(b, \bar{y} - y^0(b)) - g(b, \bar{y} - y)$ and $y^0(b) = \min_c \tilde{y}(b,c)$. Hence, conditioning on c, the expected signaling costs of the offspring are given by

$$x^*(c) = m \int_{\underline{b}}^{\bar{b}} L(b, \tilde{y}(b,c))\zeta(b)db. \tag{16}$$

We now argue that if offspring resource requirements are strictly decreasing in offspring condition, then (16) also describes the signaling costs of an offspring in condition c when the parent's condition is unknown to the offspring. The assumption that resource requirements are decreasing in offspring condition implies that $x^*(c)$, as defined in (16), satisfies the initial condition $x^*(\bar{c}) = 0$ and is strictly decreasing, ensuring that the parent can infer offspring condition by monitoring the offspring's solicitation level. Hence, when offspring behavior is given by (16), the equilibrium strategy of the parent will satisfy the signaling requirement

$$y^*(b, x^*(c)) = \tilde{y}(b,c), \ \forall(b,c).$$

Using this relationship, we may verify that the expected inclusive fitness of a mutant offspring in condition c who signals at $x = x^*(c') \neq x^*(c)$ is given by

$$\int_{\underline{b}}^{\bar{b}} \left[f(c, \tilde{y}(b,c')) + \psi g(b, \bar{y} - \tilde{y}(b,c')) - mL(b, \tilde{y}(b,c')) \right] \zeta(b)db =$$
$$\frac{1}{\gamma} \left(\int_{\underline{b}}^{\bar{b}} \left[g(b, \bar{y} - \tilde{y}(b,c')) + \gamma f(c, \tilde{y}(b,c')) - \gamma mg(b, \bar{y} - y^0(b)) \right] \zeta(b)db \right). \tag{17}$$

Apart from the addition of a constant, the integrand in (17) coincides with the parent's inclusive fitness of providing transfer $\tilde{y}(b,c')$ when the parent's condition is b and the offspring's condition

is c. But for these conditions, $\tilde{y}(b, c)$ maximizes the parent's inclusive fitness. It thus follows that the inclusive fitness of the mutant offspring is reduced by signaling at $x^*(c')$ rather than $x^*(c)$. Using this result, a straightforward modification of the proof of our Proposition allows us to conclude that if the integral appearing in (17) is a piecewise continuously differentiable function of c', then a signaling equilibrium exists and, in every signaling equilibrium, an offspring in condition c sends the signal in (16).

The signaling function (16) again indicates that offspring signaling costs are proportional to the parent's fitness loss from satisfying the offspring's resource requirement. Because of the uncertainty regarding the parent's condition, it is now the expected fitness loss of the parent that is relevant, where expectations are taken over the parent's (but not the offspring's) condition.

Example: Sir Philip Sidney. To illustrate this approach to uncertainty concerning the receiver, we provide a simple derivation of the signaling equilibrium in the Sir Philip Sidney game (Maynard Smith, 1991; Johnstone and Grafen, 1992).

There are two related animals in the Sir Philip Sidney game, called the donor and the beneficiary. The donor controls a resource and corresponds to the parent in our model. The beneficiary may engage in costly signaling and corresponds to the offspring in our model. The donor may either keep all of the resource or give all of it to the beneficiary.

In the formulation of the Sir Philip Sidney game considered by Johnstone and Grafen (1992), the condition of the beneficiary, c, is taken to be distributed uniformly on $[0, 1]$ and is interpreted as the probability of surviving. The beneficiary's fitness if he does not receive the resource is simply c. If he receives the resource, his fitness is 1. The donor's condition b is also assumed to be distributed uniformly on $[0, 1]$ and is again interpreted as a survival probability. When in condition b, the fitness of the donor is given by 1 if he keeps the resource and by b if he gives it to the beneficiary.

As in Johnstone and Grafen (1992), we take the degree of relatedness between the two animals to be symmetric, so that $0 < \gamma = \psi < 1$ and $m = 1/\gamma - \gamma$. The donor's inclusive fitness

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from keeping the resource is $1 + \gamma(c - x)$, while giving the resource to the beneficiary yields an inclusive fitness of $b + \gamma(1 - x)$. Hence, the donor will find it optimal to give the resource to the beneficiary only if the donor is in relatively high condition. Solving, the offspring's resource requirement $\tilde{y}(b, c)$ is given by

$$\tilde{y}(b, c) = \begin{cases} 0 & \text{if } b < 1 - \gamma(1 - c) \\ 1 & \text{if } b > 1 - \gamma(1 - c). \end{cases}$$

The resource requirement is zero for a beneficiary in condition 1, no matter what the condition of the donor, so that $y^0(b) = 0$ for all b. Hence, the donor's fitness loss is given by

$$L(b, \tilde{y}(b, c)) = \begin{cases} 0 & \text{if } b < 1 - \gamma(1 - c) \\ 1 - b & \text{if } b > 1 - \gamma(1 - c), \end{cases}$$

and the equilibrium strategy for the beneficiary is then given by

$$x^*(c) = m \int_0^1 L(b, \tilde{y}(b, c)) db = m \int_{1-\gamma(1-c)}^1 (1-b) db = \left(\frac{1}{\gamma} - \gamma\right) \left[\frac{1}{2}\gamma^2(1 - c)^2\right] = \frac{1}{2}\gamma(1-\gamma^2)(1-c)^2,$$

coinciding with and providing a simple alternative derivation of the result obtained by Johnstone and Grafen (1992, p. 218).

Our result on the costs of honesty in the Sir Philip Sidney game, again summarized by the statement that offspring signaling costs are proportional to the parent's expected fitness loss from satisfying the offspring's resource requirement, differs from the one presented in Johnstone and Grafen (1992, Section 3) in two respects. First, their result is concerned with the *expected* signaling costs of the beneficiary, while ours holds for every realization of beneficiary condition. Second, Johnstone and Grafen consider the cost per probability of transfer (i.e., the fitness loss to the beneficiary due to signaling divided by the probability that the resource is transferred) as a function of relatedness.

5.3 Sibling Rivalry

The analysis of the previous subsection can be applied to the study of interbrood conflict. The model we consider is based on Godfray (1995b). Suppose that a parent has a fixed amount $\bar{y}$

of food to allocate between two offspring. The conditions c_1 and c_2 of offspring 1 and 2 vary independently with densities $\rho_1(c_1)$ and $\rho_2(c_2)$ defined on the intervals $[\underline{c}_1, \bar{c}_1]$ and $[\underline{c}_2, \bar{c}_2]$. The fitness of offspring i is given by $f_i(c_i, y_i)$, where y_i is the transfer made to offspring i. The inclusive fitness functions are given by

$$f_1(c_1, y_1) + f_2(c_2, y_2) \qquad \text{for the parent,}$$

$$f_1(c_1, y_1) + \psi f_2(c_2, y_2) \qquad \text{for offspring 1,}$$

$$f_2(c_2, y_2) + \psi f_1(c_1, y_1) \qquad \text{for offspring 2.}$$

In a signaling equilibrium, the parent satisfies the resource requirements $\tilde{y}_1(c_1, c_2)$ and $\tilde{y}_2(c_1, c_2)$ of her offspring, where $\tilde{y}_1(c_1, c_2)$ and $\tilde{y}_2(c_1, c_2)$ maximize the parent's inclusive fitness function subject to the constraint $y_1 + y_2 = \bar{y}$. Assume that the offspring send their signals simultaneously, and that an offspring's signal cannot be conditioned on the signal sent by the offspring's sibling. Then offspring 1 faces uncertainty about the condition of offspring 2 when choosing its signal. Furthermore, the fitness loss to offspring 2 caused by an increased resource transfer to offspring 1 plays the same role as parental fitness loss in our previous analysis. We can then apply the arguments from our study of uncertain parental condition to obtain

$$x_1^*(c_1) = (1 - \psi) \int_{\underline{c}_2}^{\bar{c}_2} \left[f_2(c_2, \bar{y} - y_1^0(c_2)) - f_2(c_2, \bar{y} - \tilde{y}_1(c_1, c_2)) \right] \rho_2(c_2) dc_2 \qquad (18)$$

for the signaling costs of offspring 1. Here $y_1^0(c_2) = \min_{c_1} \tilde{y}_1(c_1, c_2)$. A symmetric argument yields the signaling costs of offspring 2, given by

$$x_2^*(c_2) = (1 - \psi) \int_{\underline{c}_1}^{\bar{c}_1} \left[f_1(c_1, \bar{y} - y_2^0(c_1)) - f_1(c_1, \bar{y} - \tilde{y}_2(c_1, c_2)) \right] \rho_1(c_1) dc_1. \qquad (19)$$

These results, showing that offspring signaling costs are proportional to the expected fitness loss of siblings, differ from the ones obtained in Godfray (1995b) because our model is static, excluding the possibility that each offspring is able to monitor and react to the level of solicitation displayed by its brood mate. This simpler model has the advantage of allowing us to characterize the signaling equilibrium for general fitness functions.

6 Discussion

We have derived a precise statement of the implications of honest signaling theory for the advertisement of need. The equilibrium signaling cost of an offspring is proportional to the fitness loss the parent must incur to provide the offspring's resource requirement (rather than the smallest possible resource requirement). The factor of proportionality m is a measure of the extent of parent-offspring conflict that depends only on coefficients of relatedness.

Kilner and Johnstone (1997) report that empirical studies of signaling have found signaling costs to be surprisingly small, posing a challenge to signaling theory because such small costs seem sufficient to attract potentially large fitness gains only if the conflict of interests is quite small. Our analysis of signaling costs shows that, for given coefficients of relatedness, equilibrium signaling costs are proportional to the fitness losses to the parent of satisfying offspring resource requirements rather than the fitness benefits to the offspring. Small signaling costs can attract large fitness benefits, despite sharply conflicting interests, as long as providing these benefits does not impose a large fitness cost on the parent.

More generally, we show that for given coefficients of relatedness, the theory yields a simple and general prediction concerning the relationship between offspring signaling cost and parent fitness loss: if we observe an offspring soliciting at a level which causes a fitness loss of x to the offspring, then we should observe the parent transferring an amount of resource which causes a fitness loss of l to the parent (compared to satisfying the minimal possible resource requirement of the offspring), where

$$x/l = m.$$

This relationship holds independently of the offspring's condition and any underlying factors such as the fitness benefits the offspring obtains from parental provisioning, the level of resources available to the parent, the range of possible offspring conditions, and the distribution of offspring condition.

The effect of variations in the coefficients of relatedness, which have been examined from

different perspectives by Godfray (1995b) and Johnstone and Grafen (1992), are also apparent from our characterization of equilibrium signaling costs. First, an increase in the coefficient of relatedness between the offspring and future siblings, ψ, decreases the conflict-of-interest measure m, but does not affect the parent's inclusive fitness function. Hence, both the offspring's resource requirement and the parent's fitness loss from satisfying this requirement remain unchanged. The theory then predicts that for all offspring conditions, signaling cost will be reduced by the same factor. Second, as noted by Johnstone and Grafen (1992), evaluating the effect of variations in γ, the coefficient of relatedness between the parent and offspring, is less straightforward. An increase in γ raises the parent's incentive to provide the offspring with the resource. Hence, the resource requirement of every offspring condition rises, including the minimum resource requirement. This has an ambiguous effect on the parent's fitness loss from satisfying the resource requirement of an offspring, and hence an ambiguous effect on the offspring's signaling costs. While these complications make it impossible to establish general predictions concerning the level of the offspring's signaling cost, the theory makes an unambiguous prediction concerning marginal costs. An increase in γ reduces the conflict-of-interest measure m, and the relationship $x = ml$ then implies that the offspring's marginal cost of obtaining an additional unit of parental investment, where the latter is measured in terms of the parent's fitness loss, also decreases.

Our characterization of signaling costs applies to situations in which the relationship between the offspring's condition and resource requirement is not monotonic. We show that offspring in poorer condition may send *less* costly signals in a signaling equilibrium, and that reducing the uncertainty concerning offspring condition may *increase* signaling costs.

The proportionality of offspring signaling costs and parent fitness losses provides a characterization of signaling equilibria in a variety of contexts, including cases in which both parents care for the offspring, in which there is interbrood conflict, and in which there is uncertainty about the parent's as well as offspring's condition.

7 Appendix

Proof of Proposition. [EXISTENCE] Let $x^* : [\underline{c}, \overline{c}] \to [0, \infty]$ be given by (10). Let c^0 be an offspring condition for which $\tilde{y}(c^0) = y^0$. Then $x^*(c^0) = mL(\tilde{y}(c^0)) = 0$, and hence condition (4) is satisfied. Let $x^1 = \max_{c \in [\underline{c}, \overline{c}]} x^*(c)$. Because $L(y)$ is strictly increasing on $[y^0, \overline{y}]$, it has an inverse which we denote by $L^{-1}(y)$. We can then define $y^*(x)$ by

$$y^*(x) = \begin{cases} L^{-1}(x/m) & \text{if } x \le x^1 \\ L^{-1}(x^1/m) & \text{if } x > x^1. \end{cases} \tag{20}$$

This associates a response with every possible signal, including those that will never be sent if the offspring's behavior is given by $x^*(c)$.

The parental response function $y^*(x)$ satisfies (5) by construction, since for all $c \in [\underline{c}, \overline{c}]$,

$$y^*(x^*(c)) = y^*(mL(\tilde{y}(c))) = L^{-1}(L(\tilde{y}(c))) = \tilde{y}(c).$$

Since $\tilde{y}(c)$ maximizes $v(c, x^*(c), y)$ for all c, (5) implies (3):

$$\int_{\underline{c}}^{\overline{c}} v(c, x^*(c), y^*(x^*(c))) \rho(c) dc = \int_{\underline{c}}^{\overline{c}} \max_{y \in [0, \overline{y}]} v(c, x^*(c), y) \rho(c) dc \ge \int_{\underline{c}}^{\overline{c}} v(c, x^*(c), y(x^*(c))) \rho(c) dc$$

for all strategies $y(x)$.

It remains to verify the optimality condition (2) for the offspring's signals. For all offspring conditions c and signals x we have

$$f(c, y^*(x^*(c))) + \psi g(\overline{y} - y^*(x^*(c))) - x^*(c) =$$

$$f(c, \tilde{y}(c)) + \psi g(\overline{y} - \tilde{y}(c)) - mL(\tilde{y}(c)) =$$

$$\frac{1}{\gamma}[g(\overline{y} - \tilde{y}(c)) + \gamma f(c, \tilde{y}(c)] - mg(\overline{y} - y^0) \ge$$

$$\frac{1}{\gamma}[g(\overline{y} - y^*(x)) + \gamma f(c, y^*(x))] - mg(\overline{y} - y^0) =$$

$$f(c, y^*(x)) + \psi g(\overline{y} - y^*(x)) - mL(y^*(x)) \ge$$

$$f(c, y^*(x)) + \psi g(\overline{y} - y^*(x)) - x.$$

The first equality uses (5) and (10). The following equality uses $L(y) = g(\overline{y} - y^0) - g(\overline{y} - y)$ and then substitutes $m = 1/\gamma - \psi$ and rearranges terms. The next inequality follows from the fact

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that $\tilde{y}(c)$ is the solution to the parent's maximization problem (1) and thus maximizes the term in square brackets. The subsequent equality uses $m = 1/\gamma - \psi$ and $L(y) = g(\overline{y} - y^0) - g(\overline{y} - y)$ and rearranges terms. The final inequality follows from the definition of $y^*(x)$, given by (20), which ensures the cost required to obtain any given transfer y equals $mL(y)$ for $y < \overline{y}$ and otherwise is no greater than $mL(y)$. This sequence shows that an offspring in condition c receives a higher inclusive fitness from signal $x^*(c)$ than from any alternative signal x, establishing (2).

[CHARACTERIZATION] Let $(x^*(c), y^*(x))$ be a signaling equilibrium. We show that $x^*(c) = mL(\tilde{y}(c))$.

The offspring's optimality requirement (2) implies that, for all conditions c and $\hat{c}$,

$$u(c, x^*(c), y^*(x^*(c))) \geq u(c, x^*(\hat{c}), y^*(x^*(\hat{c}))).$$

Using the definition of the offspring's inclusive fitness $(u(c, x, y) = f(c, y) - x + \psi g(\overline{y} - y))$ and the signaling equilibrium condition (5), this is

$$f(c, \tilde{y}(c)) + \psi g(\overline{y} - \tilde{y}(c)) - x^*(c) \geq f(c, \tilde{y}(\hat{c})) + \psi g(\overline{y} - \tilde{y}(\hat{c})) - x^*(\hat{c}). \tag{21}$$

Because this inequality holds for all c and $\hat{c}$, it implies that for all c, $f(c, \tilde{y}(\hat{c})) + \psi g(\overline{y} - \tilde{y}(\hat{c})) - x^*(\hat{c})$ must be maximized by setting $\hat{c} = c$. For all c at which $\tilde{y}(c)$ and $x^*(c)$ are differentiable, the corresponding first-order condition is

$$[f_y(c, \tilde{y}(c)) - \psi g_z(\overline{y} - \tilde{y}(c))]\tilde{y}_c(c) = x_c^*(c). \tag{22}$$

Because $\tilde{y}(c)$ maximizes the parent's inclusive fitness (cf. (1)), we also have the first-order condition

$$\gamma f_y(c, \tilde{y}(c)) - g_z(\overline{y} - \tilde{y}(c)) = 0 \tag{23}$$

whenever $\tilde{y}_c(c)$ is nonzero. We can then combine (22)–(23) to give

$$x_c^*(c) = mg_z(\overline{y} - \tilde{y}(c))\tilde{y}_c(c). \tag{24}$$

In addition, if $\tilde{y}_c(c)$ is zero, then (24) is immediate from (22). Hence, (24) holds for all c at which $\tilde{y}(c)$ and $x^*(c)$ are differentiable.

Lemma 1 below shows that $x^*(c)$ is piecewise continuously differentiable. Hence, (24) holds almost everywhere, allowing us to integrate and obtain (Wheeden and Zygmund, 1977, Theorem 10.23):

$$\int x_c^*(c)dc = \int mg_z(\overline{y} - \tilde{y}(c))\tilde{y}_c(c)dc.$$

Because piecewise continuously differentiable functions are absolutely continuous (Royden, 1988, Chapter 5.4), we then have

$$x^*(c) = k - mg(\overline{y} - \tilde{y}(c)),$$

for some constant k. Condition (4) then gives $x^*(c) = mL(\tilde{y}(c))$. $\qquad \square$

Lemma 1 *Let $\tilde{y}$ be piecewise continuously differentiable and let x^* satisfy (21) for all c and $\hat{c}$ in $[\underline{c}, \overline{c}]$. Then x^* is piecewise continuously differentiable.*

Proof. Because (21) holds for all conditions c and $\hat{c}$, it must also hold when the roles of c and $\hat{c}$ are reversed, giving

$$f(\hat{c}, \tilde{y}(\hat{c})) + \psi g(\overline{y} - \tilde{y}(\hat{c})) - x^*(\hat{c}) \geq f(\hat{c}, \tilde{y}(c)) + \psi g(\overline{y} - \tilde{y}(c)) - x^*(c). \qquad (25)$$

Let $h(c, \hat{c}) = f(c, \tilde{y}(\hat{c})) + \psi g(\overline{y} - \tilde{y}(\hat{c})) - x^*(\hat{c})$. Then $h(c, \hat{c})$ is continuously differentiable in its first argument and piecewise continuously differentiable in its second argument.

Let $c > \hat{c}$. Then we can rearrange inequalities (21) and (25) to give

$$\frac{h(c, c) - h(c, \hat{c})}{c - \hat{c}} \geq \frac{x^*(c) - x^*(\hat{c})}{c - \hat{c}} \geq \frac{h(\hat{c}, c) - h(\hat{c}, \hat{c})}{c - \hat{c}}.$$

Let $\hat{c} \to c$. Then both the first and third terms converge to the left derivative of h with respect to its second argument, evaluated at (c, c). Repeating this argument with $c < \hat{c}$ yields an analogous result for the right derivative. The left and right derivatives of the strategy $x^*(c)$ thus exist and coincide with the left and right derivatives of h with respect to its second argument. Since h is piecewise continuously differentiable in its second argument, $x^*(c)$ is piecewise continuously differentiable. $\qquad \square$

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