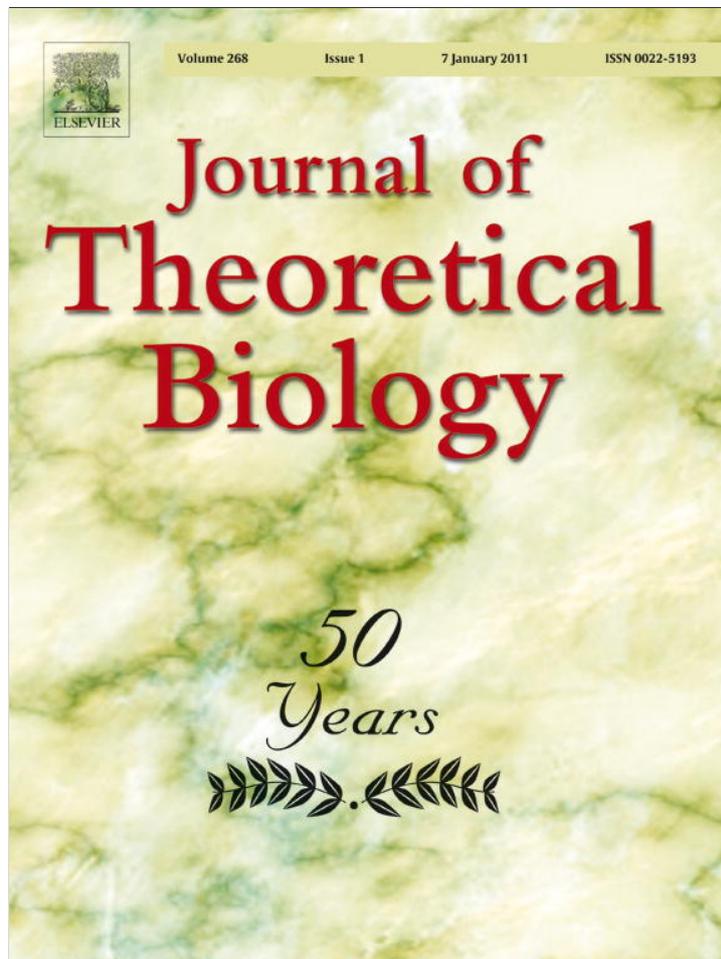


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Incentives in the family II: Behavioral dynamics and the evolution of non-costly signaling

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ABSTRACT

In many biological and social interactions, individuals with private information have incentives to misrepresent their information. A prominent example is when offspring know their need or condition but the parents do not. Theory showed that signal costs can ensure truthful communication in such situations, but further studies have cast in doubt whether empirically measured costs are high enough to sustain honesty, and whether the costly signaling equilibrium represents a fitness advantage over non-signaling. Here, I tackle these issues with a model of signaling that takes place at the behavioral time-scale through dynamic responses of individuals to each other. I then embed this behavioral model in an evolutionary one that asks how the decision rules of the parent and offspring evolve in response to the trade-off between signal costs and the costs of provisioning. I find that a non-costly honest signaling equilibrium can evolve when relatedness between siblings is above a certain threshold. This threshold is lower when (i) offspring get satiated more quickly, (ii) the cost of provisioning to the parent escalates less rapidly, or (iii) the variation in offspring need is higher. These results provide a potential resolution to the apparent paradox of costly begging. I also discuss the relation between costly signaling and mechanism design theories.

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1. Introduction

An important problem for evolutionary theory has been to elucidate why natural selection would favor behaviors or traits that benefit other individuals. Theory developed in the past five decades (reviewed in Sachs et al., 2004; Lehmann and Keller, 2006; Nowak, 2006) showed that cooperative behaviors can evolve through a variety of mechanisms, which can be classified in two overall categories: direct fitness mechanisms, where cooperative behavior ultimately increases the lifetime fitness of the actor, and indirect fitness (or kin-selection) mechanisms, where the cooperative behavior ultimately decreases the personal lifetime fitness of the actor, but increases the lifetime inclusive fitness (Hamilton, 1964, 1975). The most prominent of the direct fitness mechanisms is termed reciprocal altruism, or reciprocity (Trivers, 1971; Axelrod and Hamilton, 1981), where cooperative individuals are more likely to receive help later, yielding net benefits to cooperation over their lifetime.

The general problem of supplying direct benefits can be framed in terms of supplying individuals the incentives to cooperate with each

other. When both parties are perfectly informed about each other's payoff functions, or preferences, it is relatively easy to construct incentives that ensure a mutually beneficial outcome (Worden and Levin, 2007; Akçay et al., 2009; Akçay and Roughgarden, 2011). However, the problem gets confounded when one or more parties have private information, i.e., information that cannot be directly verified by others. In these cases, even if the social partner of a focal individual is able to perfectly commit to any payments or punishments necessary to incentivize cooperation, it can be the case that the focal individual will be able to subvert the incentives by misrepresenting their own preferences. Hence, in games with private information, special incentive structures have to be used to induce agents to reveal their private information truthfully.

This basic problem appears in all disciplines studying social interactions. In economics, an instance of this problem is found in auctions and negotiations (Vickrey, 1961; Myerson, 1979, 1981), where individuals might benefit from behaving as if they are willing to pay less than their true valuation for an item in order to negotiate a better price. In public policy, the provision of public goods presents a similar problem: residents of a city might have different valuations for a park, and would benefit from misrepresenting their information, so that someone else pays for the value of the park. Economists have developed a body of theory, called mechanism design, that studies how incentives can be setup to achieve well-defined objectives when agents possess private

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information. On the other hand, biological theory has concentrated on private information problems in the context of mate-choice (Grafen, 1990), animal contests (Maynard Smith and Parker, 1976), and parent–offspring interactions (Godfray, 1991). Here, I present a model of incentive structures between parents and offspring, and establish the connection between mechanism design theory and biological signaling.

An evolutionary conflict of interest between parents and offspring arises because while the parent is equally related to all its offspring, an offspring is more related to self than its sibs. Therefore, each offspring has an incentive to obtain more resources from the parent than it is optimal for the parent to supply (Trivers, 1974). At least for young offspring, the parent can be assumed to be in control of the resources (Alexander, 1974), and hence it might at first blush appear that the offspring's incentives are moot. However, in many cases the offspring might be better informed about its own need and condition than the parent. This information asymmetry gives the offspring some power to subvert parental control by exaggerating its need, and a private information problem ensues. Godfray (1991) showed that when begging is costly, there is an evolutionarily stable strategy (ESS) where offspring in different condition beg at different intensities, and begging intensity is a strictly decreasing function of the condition (condition being negatively related to need). This allows the parent to deduce the need from the begging intensity, leading to a “honest signaling” equilibrium (also termed a separating equilibrium). One interpretation of this equilibrium is that it represents a “payment scheme” set up by the parent that aligns the offspring's fitness interest with that of the parent (Nöldeke and Samuelson, 1999). Subsequent work has modeled related situations such as assigning a single, non-divisible resource among relatives (Maynard Smith, 1991; Johnstone and Grafen, 1992; Johnstone, 2000), or communication between a single parent and multiple offspring (Godfray, 1995; Johnstone, 1999).

While this initial set of models established the possibility of truthful communication between parents and offspring through costly begging, later work has questioned whether such an outcome is theoretically expected or empirically valid. On the theoretical side, models suggested that the signal costs might frequently be higher than the efficiency gain they enable, so that both parties prefer no-signaling to signaling (Rodríguez-Gironés et al., 1996) (although the scope for signaling equilibria being better was higher when multiple offspring were considered (Johnstone, 1999)). At the same time, some partially informative signaling equilibria (termed pooling equilibria) were shown to exist that can be maintained without any costs (Bergstrom and Lachmann, 1998). However, these costless pooling equilibria transmit relatively little information (Brilot and Johnstone, 2002) and tend to be stable only when there is a wide range of variability of need (Brilot and Johnstone, 2003). Honest signaling might therefore be too costly to be adaptive relative to no signaling, and therefore the initial evolution of begging behaviors might have been driven by non-communicative functions (Rodríguez-Gironés et al., 1996). On the empirical side, some studies did find appreciable energetic (McCarty, 1996; Bachman and Chappell, 1998; Kilner, 2001; Rodríguez-Gironés et al., 2001), predation (Haskell, 1994; Leech and Leonard, 1997), and immunological costs to begging (Moreno-Rueda, 2010). However, the energetic costs that have been reported appeared to be low (McCarty, 1996; Bachman and Chappell, 1998) and subsequent studies found that predation costs might have been partly due to the mismatch between the nesting habits of the species and the experimental setup (Haskell, 2002; Moreno-Rueda, 2007). Overall, it appears that while begging can be costly in some species and ecological contexts, it is relatively cheap in other species and contexts (Kilner and Johnstone, 1997; Moreno-Rueda, 2007).

At the same time, a significant gap in the theoretical literature on parent–offspring signaling is the lack of models that incorporate the effects of behavioral interactions between parents and offspring, even though there is ample empirical evidence that both parties adjust their behavior dynamically in response to each other (Rodríguez-Gironés et al., 2002; Grodzinski et al., 2007). The related literature on parent–offspring coadaptation (Wolf et al., 1999; Kölliker et al., 2005) does model reactions of the parents and offspring to each other, but as they stand, these models do not incorporate the private information problem.

Against this background, Roughgarden (2009) and Roughgarden and Akçay (2010) have recently proposed that interactions within the family can be viewed from the perspective of organizational economics that study how incentives within firms can be setup to ensure proper functioning. These incentives act in the behavioral time-scale, while the evolution of the traits that provide them takes place over evolutionary time (Akçay et al., 2009; Akçay and Roughgarden, 2011). Roughgarden and Song (2011) have recently used a model of a conglomerate's resource allocation to its subsidiaries through an internal market clearing mechanism (Groves, 1973) to model parent–offspring interactions. Their model considered the growth of the offspring as a result of the provisioning and the eventual weaning of offspring. However, they did not model variation in offspring need, or the evolution of parental and offspring decision rules.

Here, I develop a model that is similar in spirit, but explicitly geared towards integrating the behavioral dynamics of the signaling interaction with the evolutionary change in parent and offspring decision rules. My behavioral model relies on aligning the behavioral interests (as represented by behavioral objective functions) of the parent and offspring, and is closely related to the canonical model of mechanism design theory, the Vickrey–Clarke–Groves (VCG) auction (Vickrey, 1961; Clarke, 1971; Groves, 1973). I then embed this behavioral model in an evolutionary-tier analysis to ask how the behavioral objectives of the parent and offspring evolve in the face of the trade-offs between the costs of provisioning and begging at the behavioral signaling equilibrium. I show that while signaling is predicted to be costly for some ecological settings, other settings produce evolutionary equilibria where the parent is expected to forsake the effort to lower offspring demand by making them pay. In both cases, offspring demand is perfectly informative about the offspring's need (i.e., the signaling equilibrium is separating). These results provide a possible explanation for the apparent lack of begging costs in some species and contexts, and generates new predictions that can be tested using comparative and empirical data. In the discussion, I point out the connection between the biological literature on costly signaling and the economic theory of mechanism design.

2. Parent–offspring signaling in the behavioral time-scale

In this section, I construct a signaling model that mathematically reproduces the results of Godfray (1991) and Nöldeke and Samuelson (1999). However, I take this equilibrium to be the result of behavioral dynamics driven by the decision rules of the parent and the offspring, which I will subsequently allow to evolve.

Suppose the offspring has a certain level of need, denoted by n . The growth of an offspring with need n that receives an amount p of food is given by the function $g(p, n)$. I take the growth of an offspring to be proportional to its survival probability, and assume $\partial g / \partial p > 0$, $\partial^2 g / \partial p^2 < 0$, and $\partial^2 g / \partial n \partial p > 0$. The last inequality reflects the assumption that as the offspring becomes more needy, it has more to gain by having more food. I assume that providing food is costly for the parent, and her expected

survival is given by a function $f(p)$ that is decreasing in p (and $\partial^2 f / \partial p^2 < 0$).¹

I assume that the provisioning level p , as well as the begging level and the attending cost are determined through a behavioral dynamic, which is defined through behavioral objectives of the parent and offspring. Biologically, the behavioral objective can be thought of as representing the reward sensation of the animal (Akçay et al., 2009), which the animal tries to maximize. As such, the behavioral objectives constitute the proximate causes of parent and offspring behavior, providing a sort of “myopic” decision rule. These decision rules are similar to models of bounded rationality in economic theory (see Discussion for more on the connections and differences between the current model and the economics literature).

Suppose for the moment that the parent aims to behaviorally maximize the sum of the offspring growth and her survival, i.e., her behavioral objective function is $x_p = g(p, n) + f(p)$. On the other hand, the offspring's behavioral objective function is $x_o = g(p, n) + r_s f(p) - c(p)$ where r_s is the offspring's relatedness to the parent's other offspring, and $c(p)$ is the amount of begging (as measured by its energetic cost), if any, the offspring has to do to obtain the provisioning level p . These behavioral objective functions, used here as examples, correspond to the fitness functions used in previous models (Godfray, 1991; Nöldeke and Samuelson, 1999). However, since the behavioral objectives correspond to the proximate mechanisms based on reward sensation, they need not be identical to the fitness interests of either the parent or the offspring (Akçay et al., 2009). The parent's problem is that she does not know n , and hence cannot compute her optimal provisioning level. However, she can get around this problem by making the offspring “pay” for more food so that the offspring will only demand more food when it is *also* in the parent's (behavioral) interest to do so. In economic theory, such a payment scheme is called “incentive compatible” (Myerson, 1979). Note that the terms “payment” and “payment scheme” here and throughout the paper refer not to any monetary exchange, but rather the amount of costly begging the offspring has to do in order to receive a given amount of food.

The most straightforward way that the parent can implement an incentive compatibility is to make the offspring pay a cost corresponding to the difference between its own objective and that of the parent. Throughout, we will assume both begging and provisioning vary continuously, and work with infinitesimal variations in these quantities. Suppose the offspring receives an amount p , and considers whether to beg for an additional – infinitesimal – food item of size dp . The parent determines how much additional begging the offspring must do (i.e., what cost it must pay) before she will yield the additional food item. Label this additional infinitesimal cost by dc . Then, the total differentials of the parent's and offspring's objective functions are given by

$$dx_p = \left(\frac{\partial g}{\partial p} + \frac{\partial f}{\partial p} \right) dp, \quad (1)$$

$$dx_o = \left(\frac{\partial g}{\partial p} + r_s \frac{\partial f}{\partial p} \right) dp - dc. \quad (2)$$

Incentive compatibility is satisfied when $dx_o = dx_p$, which happens when

$$dc = \left(\frac{\partial g}{\partial p} + r_s \frac{\partial f}{\partial p} - \frac{\partial g}{\partial p} - \frac{\partial f}{\partial p} \right) dp = (r_s - 1) \frac{\partial f}{\partial p} dp. \quad (3)$$

In other words, the parent should “charge” the offspring the decrease in her future reproductive success, multiplied by $r_s - 1$.

The marginal cost dc given in (3) therefore aligns the behavioral objectives of the parent and offspring.

To implement this incentive compatible payment scheme in a dynamic setting, suppose the offspring continuously adjusts its begging level, as measured by the cost c , in behavioral time and suppose the rate of change of c with time is given by the derivative of its objective function with respect to p at that point, which is

$$\frac{\partial x_o}{\partial p} = \frac{\partial g}{\partial p} + r_s \frac{\partial f}{\partial p} - \frac{dc}{dp}. \quad (4)$$

When the right-hand side of (4) vanishes, the offspring will stop adjusting its begging level; the begging level will have reached the behavioral equilibrium. I assume that the behavioral dynamics leading up to the equilibrium take place quickly, and the parent–offspring pair spend most of the interaction at this behavioral equilibrium. Thus, for most of the remaining, I focus on the equilibrium of these behavioral dynamics. This simplifying assumption will allow me to equate the behavioral equilibrium payoffs of the parent and the offspring with their evolutionary fitness (McNamara et al., 1999; Akçay et al., 2009).

The position of the behavioral equilibrium then determines the parent's and offspring's final payoffs. Since f and g are fixed given the offspring need n , the only variation of the behavioral equilibrium is caused by the last term in (4), dc/dp , which in turn reflects how the parent's rate of provisioning changes in response to changing offspring. The incentive compatible payment scheme ensures that the offspring's begging level will only increase if the resulting increase in provisioning also increases the parent's objective function. This happens when the parent increases provisioning p with increasing c at a marginal rate that satisfies

$$\frac{dp}{dc} = \left[(r_s - 1) \frac{\partial f}{\partial p} \right]^{-1}. \quad (5)$$

Note that (4) and (5) completely define the dynamics of both c and p . The equilibrium of these dynamics is found by substituting the inverse of (5) into the right-hand side of (4) and setting it equal to zero²:

$$\frac{\partial g}{\partial p} + \frac{\partial f}{\partial p} = 0. \quad (6)$$

Thus, the behavioral equilibrium provisioning level is guaranteed to maximize the parent's behavioral objective.³ I denote the provisioning level satisfying the equilibrium by p^* . The cost the offspring pays at this equilibrium, denoted by c^* , is found by integrating (3). The lower limit for the integration, p_0 , is the provisioning that the parent is willing to undertake for the lowest need offspring, which in turn has nothing to gain by begging (Godfray, 1991). Thus, we have

$$c^* = (r_s - 1) \int_{p_0}^{p^*} \frac{\partial f}{\partial p} dp = (r_s - 1)(f(p^*(n)) - f(p_0)), \quad (7)$$

where p^* is a function of the offspring's need, n . Given the assumptions on g and f , it can be easily verified that $p^*(n)$ is strictly increasing in n ; hence this equilibrium is separating. In the next section, I turn to the objective functions x_p and x_o that induce the behavioral dynamics and the resulting signaling equilibrium.

Before moving on, I note that this derivation of the marginal cost dc essentially follows in the same way as the payment in the

¹ See Electronic Supplementary Material (ESM) for a more formal definition of the player and strategy sets.

² This assumes that both c and p are continuously differentiable functions, which is satisfied for fully separating signaling equilibria that we focus on here.

³ Because the behavioral dynamic for c , given Eq. (5), is one-dimensional, the second order condition $\partial^2 g / \partial p^2 + \partial^2 f / \partial p^2 < 0$ (satisfied by assumption) is sufficient to guarantee the stability of the behavioral equilibrium.

canonical mechanism of mechanism design theory, the Vickrey–Clarke–Groves auction (Vickrey, 1961; Clarke, 1971; Groves, 1973). I return to the connection between this model and the Vickrey–Clarke–Groves auction in the discussion.

3. The evolution of behavioral objectives

To model the evolution of the parent's behavioral objective, I introduce a heritable trait that modifies the parent's objective function and determines the evolutionarily stable (ES) value of this trait. This modeling approach was recently developed by Akçay et al. (2009) to study the evolution of behavioral objectives in animal social interactions, and is similar to the "indirect evolution" approach in economics where the preference function of agents evolve (e.g., Güth, 1995; Heifetz et al., 2007; see Akçay et al., 2009 for more on the connection between my approach and the indirect evolution literature). One slight difference in the current model is that because the parent over evolutionary time scale will face a distribution of offspring need, we need to consider the expected values of the behavioral outcomes. I also assume that the parent imposes an incentive compatible payment scheme on the offspring that aligns the offspring's behavioral interests with her own.

While in principle the parental trait can modify the parent's objective function in infinitely many different ways, some are more theoretically salient and biologically relevant. In the present case, the need for costly signaling is caused by the difference between how the parent's and offspring's objectives weigh the parent's survival, f . This suggests that parents that "discount" (or overvalue) their own survival would require lower (higher) payments from the offspring, which would increase (decrease) the provisioning levels and lower (increase) the cost for a given p .

To make this argument precise, I assume that the parent has a trait, denoted by δ (> 0) that determines how she weighs her own survival:

$$x_p = g(p, n) + \delta f(p). \quad (8)$$

Here, δ is a heritable trait through which natural selection acts on the parent's objective function. If $\delta < 1$, the parent discounts her future offspring. It should be emphasized that only the motivational value of future broods is changing with δ , not the actual survival probability or future fecundity as a function of provisioning effort. However, because δ affects the demand by the offspring and the cost offspring pays, it will have an effect on the overall fitness of the parent. Fig. 1 represents graphically the effect of δ on the parent's objective function. As can be seen in the figure, as the parent's δ comes closer to r_s , the provisioning amount maximizing the parent's objective approaches the value that maximizes the offspring's objective. Hence, the behavioral conflict of interests between the parent and the offspring due to divergence of objective functions is reduced with lower δ .

By using the same methodology as in Section 2, we can show that the incentive compatible cost function is

$$c^*(\delta) = (r_s - \delta)(f(p^*(\delta, n)) - f(p_0(\delta))), \quad (9)$$

where p_0 is also a function of δ , since the provisioning that the parent undertakes for the lowest need (non-begging) offspring will vary with δ . Note that this cost function implies that δ cannot be less than r_s ; otherwise, the cost of begging would be negative, i.e., the parent would have to pay the offspring to get it to demand food. Since the parent has no instruments (such as money) to make such a payment, her discounting is bounded below by r_s . By the same token, when $\delta = r_s$, the parent charges no signal costs to the offspring, and simply delivers as much food as the offspring

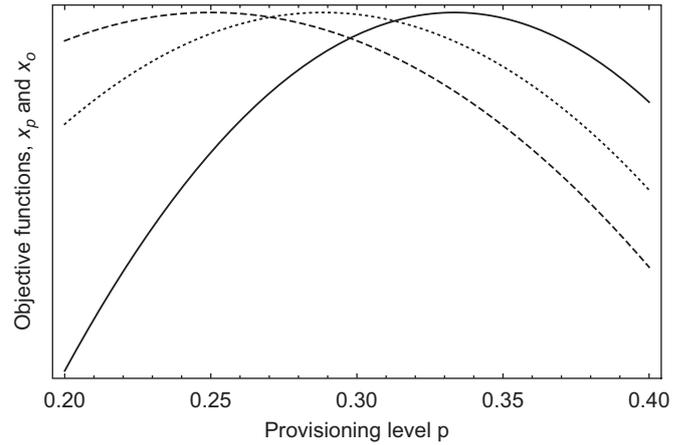


Fig. 1. A graphical representation of the effect of the parental discounting trait δ . The solid curve represents the offspring objective function $x_o = g(n, p) + r_s f(p)$, where the relatedness to future sibs $r_s = 0.25$. The dashed and dotted curves correspond to the parental objective $x_p = g(n, p) + \delta f(p)$, which are two different values of the parental discounting trait δ : for the dashed curve $\delta = 1$; for the dotted curve $\delta = 0.6$. All three functions are scaled so that their maximum value is one, to emphasize the importance of the location of the maximum, rather than the absolute value of the objective. One can see that the location of the maximum of x_p moves closer to the maximum of x_o , as δ gets closer to r_s . For these curves, the growth and future reproduction functions $g(n, p) = (n + 1)p - 2p^2$ and $f(p) = 1 - p^2$, respectively, with the offspring need $n = 0.5$.

demands. The offspring in turn demands so as to maximize its own objective function x_o .⁴

Given the cost function (9), the provisioning level at the behavioral equilibrium for a given parental δ and need n , $p^*(\delta, n)$, satisfies

$$\left[\frac{\partial g}{\partial p} + \delta \frac{\partial f}{\partial p} \right]_{p=p^*(\delta, n)} = 0. \quad (10)$$

The parent is equally related to all her offspring, so her fitness W_p is proportional to the sum of the offspring growth and parent survival, minus the cost the offspring pays

$$W_p(\delta, n) \propto g(p^*(\delta, n), n) + f(p^*(\delta, n)) - (r_s - \delta)(f(p^*(\delta, n)) - f(p_0(\delta))). \quad (11)$$

Since the parent faces a distribution of offspring needs, we need to take the expected value of $W_p(\delta, n)$ over n . The first order condition for the ES δ then becomes

$$\frac{d}{d\delta} E[W_p] = 0, \quad (12)$$

where $E[\cdot]$ denotes the expectation over the distribution of offspring need n . Taking the derivative inside the expectation, applying the chain rule and rearranging, we obtain for the first order condition:

$$E \left[(1 - r_s) \frac{df}{dp} \Big|_{p=p^*} \frac{\partial p^*}{\partial \delta} \right] + (r_s - \delta) \frac{df}{dp} \Big|_{p=p_0} \frac{dp_0}{d\delta} = f(p_0) - E[f(p^*)]. \quad (13)$$

The interpretation of this equation is that the indirect effect of changing δ through changing the demand by the offspring (given by the left-hand side of (13)) has to be equal to the direct effect, i.e., the reduction on the payment schedule (given by the right-hand side). Note that the function g does not factor directly in this first order condition. This is because the growth of the offspring is a common interest to both the parent and the offspring, and hence does not directly affect the tradeoff the parent faces. (However, g does affect the location of the behavioral equilibrium

⁴ Note that the demand by the offspring will be finite in this case when $r_s > 0$.

and how p^* and p_0 change with δ .) If the first order condition (13) is not satisfied for a $\delta \geq r_s$, then the ES δ will be equal to the lower bound, r_s . In particular, this happens when

$$E\left[\left(\frac{\partial g}{\partial p} - \frac{df}{dp}\right) \frac{\partial p^*}{\partial \delta}\right] \leq f(p_0) - E[f(p^*)], \quad (14)$$

with p_0 and p^* calculated from Eq. (10) with $\delta = r_s$. This inequality means that the expected benefit from any reduction in the demand from the offspring's optimum is less than the signaling costs it would entail, and hence, the parent is better off not imposing any costs.

To evaluate Eq. (13), we need to calculate the changes in the equilibrium demand by the offspring, which we can do by implicitly differentiating the behavioral equilibrium condition (10):

$$\frac{\partial p^*}{\partial \delta} = -\frac{df}{dp} / \left(\frac{\partial^2 g}{\partial p^2} + \delta \frac{d^2 f}{dp^2} \right), \quad (15)$$

where the derivatives are evaluated at $p = p^*(\delta, n)$. Our assumptions on the derivatives of f and g imply that $dp^*/d\delta < 0$, meaning that as the parent places higher value on her own survival, the offspring's provisioning demand for the same level of need goes down. Using Eqs. (13) and (15), we can determine the candidate ESS values of δ (see ESM for the second order ESS conditions; Maynard Smith and Price, 1973).

3.1. Example: quadratic growth and survival functions

To illustrate the results of the model, I use particular functional forms for f and g that are similar to previous literature (e.g., Hinde et al., 2010):

$$g(p, n) = (n + n_0)p - ap^2,$$

$$f(p) = 1 - bp^2,$$

where a and b are positive parameters modulating the change in the marginal benefits and costs of provisioning, and $n_0 > 0$ is the minimum need an offspring can have. These parameters depend on the physiology of offspring growth and the ecology of provisioning by the parent. Higher a means that the offspring becomes satiated faster with increased provisioning; whereas higher b means that the cost (e.g., predation risk) to the parent from increased provisioning effort escalates faster. In general, we would expect the effect of the marginal food item to be larger for the offspring (especially for young offspring) than for the parent, and hence we might expect $a > b$. Note that the function g will have a maximum in p after which it will decline. While this is unrealistic, our model will never predict p to exceed the maximum of g , and hence we can restrict our attention to the region where g is monotonically non-decreasing. Under these assumptions, we can solve for the equilibrium provisioning levels p^* given n , and obtain

$$p_i^* = \frac{n_0 + n}{2(a + b\delta)}. \quad (16)$$

To integrate W_p over the distribution of offspring need, we assume that n is distributed according to a beta distribution with support $[n_0, n_0 + \Delta n]$ and shape parameters $\alpha = \beta = 2$. Evaluating the expected value and solving for the value of parental discounting satisfying the first order ES condition (13), δ^* , we find

$$\delta^* = \frac{b((1-r_s)(20n_0\Delta n + 6\Delta n^2) + 20n_0^2) - a\Delta n(3\Delta n + 10n_0)}{b(10n_0\Delta n + 3\Delta n^2 + 20n_0^2)}. \quad (17)$$

It can be seen from (17) that the ES δ^* is linearly decreasing in relatedness r_s . In other words, the more related current offspring are to future offspring, the more the parent should discount

future offspring. The reason behind this result is that as r_s goes up, the conflict of interest between the parent and the offspring is reduced and the optimal provisioning levels from the parent's and offspring's perspectives move closer to each other. Hence, the relative benefit to the parent of ensuring truthful revelation through costly signals goes down. While signal costs also go down (since they are scaled by the factor $(r_s - \delta) < 0$), this reduction in cost is not enough to compensate for the loss in benefit and hence the parent's optimal discount rate goes down with r_s . This pattern is depicted in Fig. 2, which plots δ^* as a function of the relatedness of the offspring to its sibs, r_s for a particular parameter set. The ES discounting δ^* decreases with r_s until it hits the lower bound r_s , which in this example occurs at $r_s \approx 0.54$; δ^* tracks r_s for higher values of relatedness. When δ^* is against the lower bound, signaling is costless, but still perfectly informative, as discussed above.

We can do a similar analysis for how the optimal discounting changes with the variation in offspring need. Fig. 3 shows that as Δn , the difference between the highest and lowest need offspring, increases, the ES discounting δ^* decreases. The reason for this pattern is that with low variation in need, the costs that are required to ensure truthful communication are small, and therefore, the parent does not lose much by aligning the offspring's interests to be closer to her own. As the variation in need grows, however, the average costs of ensuring honesty increases, and therefore avoiding these costs starts to take precedence over aligning the offspring's interests with the parents'.

Another comparative statics of interest is how the minimum relatedness required to sustain cost-free communication between the offspring and the parent changes as a function of the ecological parameters. In the ESM, I show that the critical value of r_s that sustains cost-free signaling is decreasing in a , but increasing in b . Hence, costless signaling is more likely when the offspring satiates faster with increased provisioning, and less likely when parent's cost accelerates faster. The reason for this pattern is that while the costs are determined by the survival function f , the benefit from signaling to the offspring depends on g . Hence, when the offspring get satiated faster, the incentive for offspring to misrepresent their need is lower, which diminishes

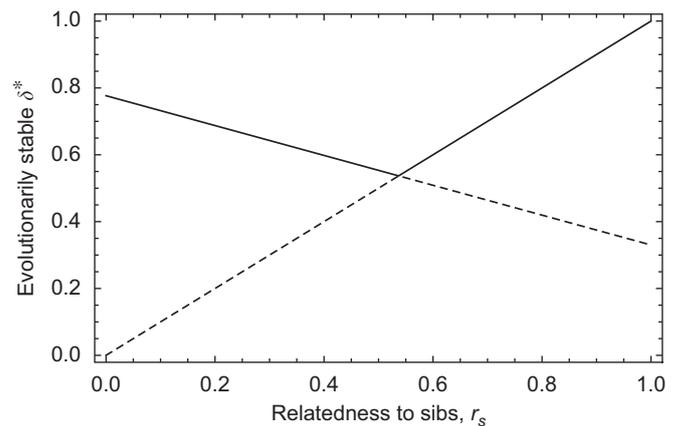


Fig. 2. The evolutionarily stable discounting δ^* , as a function of r_s . The solid line in both graphs depicts the evolutionarily stable δ^* , taking into account the constraint that the discounting δ has to be greater than the relatedness of the offspring to the future offspring, r_s . The dashed line shows r_s when $\delta^* > r_s$, i.e., below the intersection of the two curves; afterwards, the dashed line depicts the optimal δ that would have solved the first order ES condition (13), but cannot be implemented because of the constraint that the parent cannot make transfers to the offspring other than food. Parameters used in this figure are: minimum offspring need $n_0 = 1$, difference between minimum and maximum offspring need $\Delta n = 1$, offspring's marginal benefit parameter $a = 2$, and parent's marginal cost parameter $b = 1$.

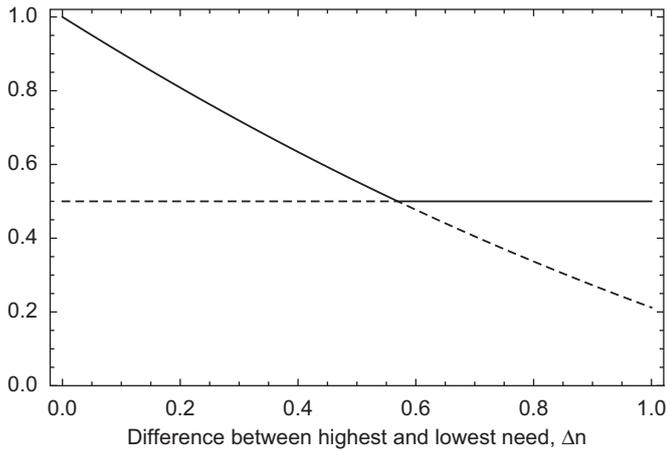


Fig. 3. The evolutionarily stable discounting δ^* as a function of the difference between the highest and lowest possible offspring need (Δn). As in Fig. 2, the solid line depicts the ES δ^* subject to the constraint that δ has to be greater than the relatedness of the offspring to the future offspring, r_s . The dashed line is either r_s , or the value of δ that would solve the first-order ES condition (13). Parameters are the same as in Fig. 2, except $r_s=0.5$.

the benefit to the parent from imposing costs. On the other hand, as b increases, provisioning at higher levels becomes more costly to the parent, and hence the benefit from tamping down offspring demand increases. Fig. 4 depicts the critical value of relatedness r_s required to sustain cost-free signaling as a function of a and b , and for different levels of variation in offspring need, Δn .

3.2. The evolution of the offspring's objective

The analysis above assumes that the offspring's behavioral objective coincides with its inclusive fitness. In the ESM, I analyze a life-history model where the offspring's valuation of parental survival can also vary, and show that a "selfish" objective is indeed the only ES objective for the offspring. The reason is that the parent cannot distinguish between offspring with different objective functions, because she cannot tell whether a change in behavior by the offspring is due to the change of the objective function, or need. Hence, the offspring has no way of influencing the parent's decision rule (i.e., the payment schedule). Given that, the best the offspring can do is to try to maximize its inclusive fitness given the payment scheme imposed by the parent.

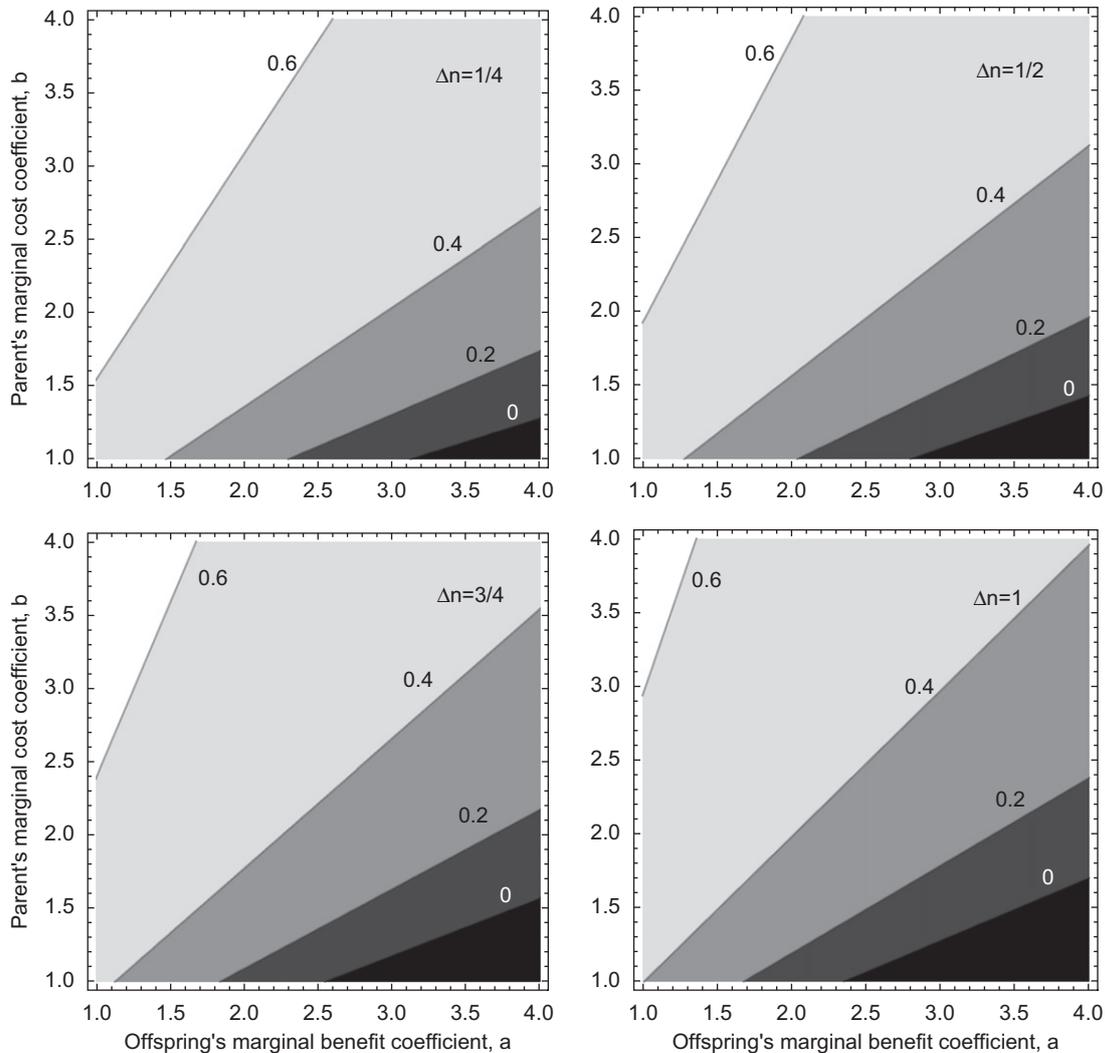


Fig. 4. Contour plots for the critical value of relatedness of the current offspring to future ones, r_s , where the ES discounting $\delta^* = r_s$, i.e., cost-free, separating signaling between parent and offspring is sustained. In all panels, the mean offspring need is equal to 1, while the spread between the minimum and maximum offspring needs (Δn) increases from left to right and top to bottom. The numbers on contour lines correspond to the value of critical r_s on that contour. For low b (parent's marginal cost parameters) and high a (offspring's marginal benefit parameter) values (lower right corner), this critical value is below 0, meaning that for all positive values of r_s , the parent's matches the offspring's.

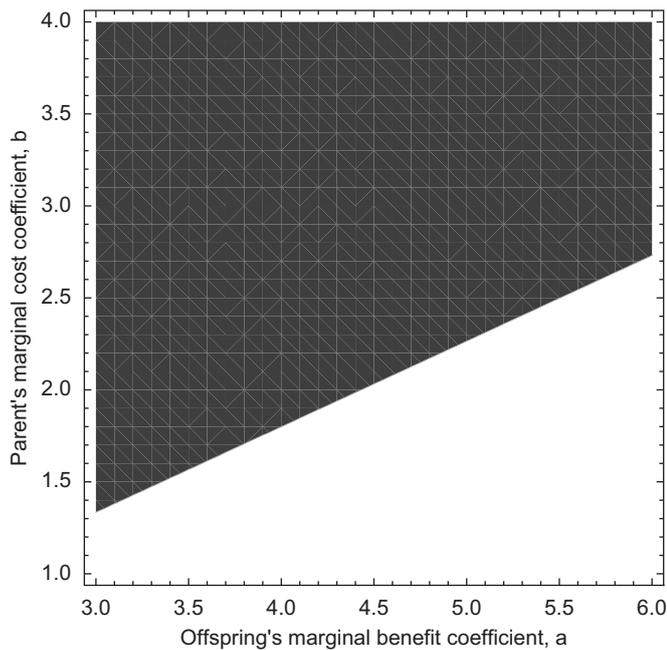


Fig. 5. The comparison of the expected fitness of the co-evolved signaling equilibrium with the no-signaling equilibrium. The black region denotes parameter values where no signaling has higher fitness (a greater rate-of-increase) than signaling; white regions vice versa. Parameter values are as follows: minimum offspring need $n_0 = 1/2$, difference between minimum and maximum offspring need $\Delta n = 1$, relatedness of the current offspring to future ones $r_s = 0.5$. Note that the plotted region encompasses a higher range in the offspring's marginal benefit parameter, a , than Fig. 4 to better illustrate the basic pattern.

3.3. Comparison with no signaling

We can also use the life-history model developed in the ESM to compare the fitness (defined as the leading eigenvalue of the Leslie matrix, Caswell, 2001) to an equilibrium where the offspring does not signal, and the parent delivers food at a level that maximizes the expected fitness. Fig. 5 shows that the signaling equilibrium can in fact have a higher fitness than no-signaling when a is high and b is low; i.e., when the offspring saturate faster and the cost of provisioning to the parent accelerates slower. Over the same parameter range, the signaling equilibrium without co-evolution of the objectives (i.e., when the objectives are fixed as $x_p = g(p, n) + f(p)$ and $x_0 = g(p, n) + r_s f(p)$) does strictly worse than the co-evolved equilibrium, and over the parameter range shown in Fig. 5 is never better than the no-signaling (not shown). Thus, the co-evolution of the behavioral objectives increases the scope for signaling being adaptive relative to non-signaling, but there is still a large range of ecological parameters where no-signaling fares better than even the co-evolved signaling equilibrium.

4. Discussion

The main contribution of this paper is to treat signaling as a result of behavioral dynamics produced by evolving decision rules. The most striking result from this two-tiered setup is that cost-free and perfectly informative signaling between parent and offspring can evolve through selection acting on the parent and offspring decision rules. This happens when the benefit from lowering the offspring demand through begging costs is outweighed by the costs themselves. This result presents a possible resolution to the apparent paradox in the field that signaling by

offspring does not often carry a high energetic cost while seemingly conveying reliable information about offspring need (Kilner and Johnstone, 1997; Moreno-Rueda, 2007).

Such costless signaling differs significantly from previous models of cost-free communication. Bergstrom and Lachmann (1998) show that non-costly pooling equilibria exist in the continuous Sir Philips Sidney game. However, these equilibria pool a lot of low need individuals with high need ones, which reduces the information content of such equilibria (Brilot and Johnstone, 2002). In contrast, the behavioral signaling equilibrium here remains separating for all δ under the assumptions made on the functions f and g . On the other hand, Lachmann et al. (2001) show that truthful signals with arbitrarily small costs can be maintained by off-equilibrium costs (i.e., cost that are only incurred while lying). However, such mechanisms require the costs for a given outcome to be dependent on the signaler's private information (e.g., the amount of begging required by the parent for a certain amount of food to be higher for a low-need individual). Since the parent cannot determine the private information independently from the signal, purely off-equilibrium costs cannot be implemented in the parent-offspring signaling.

Another closely related study is by Johnstone (1996), who considered the possibility that the parent might preemptively provide some amount of food before the offspring engages in costly begging. He found that in general, the parent will provide food in excess of the need of the lowest need individual, which means that some offspring (those with the lowest need) receive more food than they would receive in the signaling equilibrium without this initial transfer. The parent can gain by doing this, because these offspring do not signal in the second stage of the game, which causes all offsprings' signal costs to go down. While the intuition behind Johnstone's result is similar to the present one, the current model does not pool the low-need individuals together in order to achieve the reduction in costs.

I also showed that the co-evolution of the parental and offspring objectives makes it possible for the signaling equilibrium to outperform the no-signaling equilibrium under some parameter ranges, specifically when the benefits to the offspring saturate faster than the cost to the parent accelerate. However, there remains a large range where no-signaling is better, and the not co-evolving signaling equilibrium that is likely to be the ancestral signaling equilibrium always appears to be worse than the signaling. Hence, my results support the conjecture by Rodríguez-Gironés et al. (1996) that begging behaviors might have their origin in non-signaling functions, but once signaling is established, co-evolution of the parental and offspring objectives might lead to a better overall outcome than the no-signaling equilibrium.

4.1. Empirical tests

My model provides several comparative statics predictions that can be tested using comparative and experimental work. I show that the costless signaling is more likely (or equivalently, expected signal costs are lower) when the relatedness between siblings is high, when the benefits of provisioning to the offspring saturate faster or when the spread between the highest and lowest need offspring is greater. At the same time, costless signaling becomes less likely (expected signal costs are higher) when the cost of provisioning to the parent accelerates faster.

Empirically, the parent's δ trait can be measured as her willingness to take risks when provisioning the offspring, with experiments where the parent is exposed to playbacks or models of predators (e.g., as in Ghalambor and Martin, 2001). The prediction from the costly signaling literature in general (including earlier models, which effectively set $\delta = 1$) is for the parent to

increase the amount of begging necessary for a given amount of food when confronted with higher risk. The advantage of such an experiment over previous empirical studies of costly begging would be that it might avoid side effects of manipulating offspring directly by subjecting them to hunger experimentally (Mock et al., 2011). It is possible that offspring in high-risk treatments will experience lower provisioning levels and thus, will be more hungry, but this would be the result of the parent's behavioral response, and hence carry information about the equilibrium of the behavioral interaction. Furthermore, by measuring changes in costs with treatment, rather than absolute costs, such an experiment might provide a better test of costly signaling theory, especially when compared across different species with different breeding ecologies. Such an experimental design might also distinguish between the current model and earlier models by Godfray (1991) and Nöldeke and Samuelson (1999). In these previous models, the signaling cost for a given level of provisioning only depends on the parent's cost of provisioning f and not the shape of the growth function of the offspring (g). In contrast, my model predicts that parameters affecting the offspring's growth (e.g., offspring's rate of satiation as measured by the parameter a) affect the ES value of parental objective, and therefore influence the begging cost at a given level of provisioning. Hence, a correlation between signaling cost (controlling for the provisioning level) and physiological traits of the offspring would constitute evidence for my model.

Another comparative statics prediction that is shared by all models of parent–offspring signaling including the current one is that overall signal costs should decrease as the relatedness between offspring increases (Godfray, 1991; Nöldeke and Samuelson, 1999; Johnstone, 1999), because this reduces the evolutionary conflict of interest between parents and offspring. Although single offspring models such as the current one are not directly applicable to multiple-offspring situations, this effect is also expected in the latter case, and is in fact supported by some evidence: Briskie et al. (1994) has found that in a sample of 11 passerine birds, overall nestling loudness was higher in species with higher extra-pair paternity, which would act to decrease nestling relatedness to each other. More recently, Boncoraglio and Saino (2008) found that in barn swallows, offspring in nests with cross-fostered eggs begged louder than control nests under normal conditions, suggesting that offspring might facultatively adjust their begging to relatedness to their nestmates. In single-offspring broods, the relatedness to future offspring would be affected solely by the probability of mate switching between broods. To my knowledge, a correlation between mate-switching and begging intensity has not been investigated. More generally, despite the accumulation of large amounts of species-level data on offspring begging behavior, especially in birds, quantitative comparative studies remain few and far between. Such approaches represent one of the most promising avenues for empirical research on offspring begging.

4.2. Signaling in the behavioral tier as mechanism design

Viewed as a tool to align evolutionary or behavioral interests of individuals, costly signaling is closely related to a large body of theory in economics, called mechanism design, that studies how the payoffs from a game can be set up to induce agents to behave in particular ways. Examples of mechanism design problems are auctions (Vickrey, 1961; Myerson, 1981), or taxation of income and various economic activities by the government (Clarke, 1971). By analogy, the parent in models of costly signaling acts as a “mechanism designer”. Mechanism design theory deals with a vast array of strategic interactions and problems, and a full fledged review of this literature is beyond the scope of this

paper.⁵ My model is most closely related to one of the canonical models of mechanism design theory, the Vickrey–Clarke–Groves (VCG) auction (Vickrey, 1961; Clarke, 1971; Groves, 1973). The VCG auction deals with a situation where a set of items are to be auctioned off to a set of bidders, each bidder having their own independent, and private valuation of each item. The goal of the auction is to maximize the aggregate welfare (since this also maximizes the revenue of the auctioneer).

In the ESM, I outline a standard proof of the optimality of VCG auction, which I summarize here verbally. The auction, conducted by sealed envelopes, prescribes that bidders that win an auctioned item pay exactly the “harm” they cause to other bidders by participating in the auction and receiving the object (i.e., the difference between everybody else's actual payoff and their payoff had the focal bidder not a participant in the auction). The equilibrium of this game is then for everyone to reveal their valuations truthfully, and for the items to be allocated to maximize aggregate welfare. To see why truthful revelation is optimal, consider a focal bidder lying and receiving a different object than that they would receive at equilibrium. This deviation from the equilibrium would lower the aggregate welfare (since the object would have to be taken from someone who values it more). But the focal bidder now has to pay the entire decrease in aggregate welfare (in addition to what it paid before), which cannot compensate for the additional value the bidder gained by lying (otherwise, the aggregate welfare would not have gone down). In this way, it is optimal for everyone to tell the truth, and the VCG auction is guaranteed to maximize the aggregate welfare.

To see the connection of the VCG auction with my model, consider an “auction” with a single bidder, the offspring, for the infinitesimal food item dp . The auctioneer (the parent) prefers giving up the item if and only if this increases her own objective. Since this calculation depends on the offspring's private information, the best the parent can do is to ensure to impose costs on the offspring's objective to make it “bid” (by begging) if and only if this is in the parent's own interest, and award the food item in response to begging. The costs that ensure reaching the parent's optimum then reflect the harm caused to the parent's objective (rather than the aggregate objective).

Nonetheless, some important differences exist between conventional mechanism design theory and the current model. First, mechanism design theory usually assumes agents that – while imperfectly informed – are highly rational, meaning that when faced with a given mechanism, they are able to calculate the optimal strategy and play it. Furthermore, many mechanism design problems (such as auctions) operate in the context of an established economical institutions, where means of commitment such as contracts and means of exchange such as currency are available.⁶ These features enable a very wide range of possible strategies, and allow a designer to construct complicated incentives. Animals lack formal institutions that would enable contracts and cannot use money, which poses constraints on the allowable range of mechanisms. For example, payment schemes in an auction can depend on all players' bids, which the auctioneer can collect before deciding who is to pay what. Animals are unlikely to be able to implement such schemes. Nonetheless, some of the features of economic models of mechanism design can be recapitulated in biologically meaningful ways: the assumption that the objective

⁵ Akçay et al. (unpublished manuscript) provide a more in depth review of mechanism design theory and methods, and how they can be applied to different biological problems.

⁶ There are exceptions to this; mechanism design applied to international relations faces some of the same constraints as biological mechanism design, namely the lack of contract enforcing institutions above the state level (e.g., Meirowitz and Sartori, 2008).

function of the parent (determined by the trait δ and encoded in the brain circuitry) is a genetically fixed trait means that the parent cannot change it during the behavioral time-scale; she is committed to that objective function (Akçay and Roughgarden, 2011). At the same time, the behavioral dynamics allows the offspring to “learn” the optimal behavior in response to the parent’s cost function, instead of arriving at it through rational deliberation. These two features allow us to treat the interaction between one parent and one offspring in a broadly analogous way to economics models, apart from the constraint that the cost function $c(p)$ cannot be negative. However, in more complex models (e.g., with multiple offspring), the simple correspondence that we have here might break down. In general, while mechanism design holds promise for biological applications, care must be taken in evaluating the appropriateness of its assumptions in each specific contexts.

In addition to constructing some incentive compatible mechanisms, mechanism design also asks which mechanisms is optimal among a given set of mechanisms. In the current model, the parent’s objective function, parameterized by δ , and the attending cost function define a family of mechanisms with different equilibrium actions and costs. Finding the ES δ corresponds to finding the optimal mechanism out of this family, similar to designing an auction that maximizes the expected revenue to the auctioneer (Myerson, 1981). Such optimal mechanism design analyses have been missing from biological models of costly signaling, partly because biological models usually have dealt with genetically determined reaction norms (Godfray, 1991; Grafen, 1990) that do not allow agents to change their signals in response to new mechanisms. However, such an assumption means that a mutation resulting in a different provisioning rule by the parent cannot alter the offspring’s demand, which is clearly not a realistic result. Since many, if not all or most, instances of social communication in biology involve flexible behaviors and learning, a two-tiered analysis where agents can respond to new incentives appears more realistic, and opens the possibility for the evolution of incentives.

Finally, I also show that the offspring’s optimal objective is always identical to its fitness interests. The reason can be seen by considering the evolutionary game over the parental trait δ and the offspring trait (see the full model in the ESM). In this game, the parent moves first and commits to a mechanism (by having a genetically determined value δ which implies the payment scheme given by (9)), while the offspring moves second and responds to the mechanism. This means that the parent cannot respond to different offspring traits by changing her evolutionary strategy (i.e., δ), and hence the best the offspring can do is to maximize its own fitness given the parent’s δ . This is similar to models of the trust game without information about trustworthiness of the second mover (Güth and Kliemt, 2000). The implication is that the costless resolution of the conflict, if it happens, happens at the offspring’s optimum, because the offspring cannot move from that position. In contrast, Roughgarden and Song (2011) assume that the behavioral equilibrium between the parent and offspring involves repeated adjustments of both the demand function and the payment scheme. Even though they do not consider explicitly an evolutionary tier separate from the behavioral tier, their setup might yield a solution where the offspring might gain by evolving to value the parent’s survival higher, because the parent can react to the demand conveyed by the offspring. Therefore, different behavioral incentive structures might lead to different resolutions of the conflicts of interest between the parent and offspring.

4.3. Caveats and future work

Similar to many previous studies (Godfray, 1991; Nöldeke and Samuelson, 1999), my model is specifically designed for single

offspring broods, and care must be taken in generalizing the results to the general setting with multiple offspring. In particular, with multiple offspring, the behavioral dynamics between offspring including pre-begging interactions (e.g., Roulin et al., 2009) might become important. Although the main result of this paper (the possibility of costless signaling through the evolution of parental discounting) is likely to be robust to these considerations, other strategic issues need to be modeled explicitly. Moreover, in many species with parental care, there are more than one parent (or helper). Hence, the construction of incentives for honesty is likely to be more complicated. To my knowledge, only a few models (Godfray, 1995; Johnstone, 1999) deal with multiple offspring, and only one (Nöldeke and Samuelson, 1999) tackled the case with two parents. The approach developed here would allow addressing these more complicated cases in a systematic fashion.

Another caveat is about what aspect, if any, of the offspring condition the parents are uninformed about in reality. Even though my model deals with a generic variable n affecting the offspring’s growth function, the empirical consequences of the signaling equilibrium depends on the biological interpretation of the variable n . Specifically, I envisioned a scenario where all offspring are equivalent except for their need, with the more needy having more to gain from obtaining food. However, it might also be the case where some offspring might have intrinsically lower prospects for survival than others (e.g., some offspring might have better immunocompetence) (Mock et al., 2011). Many model results are unaffected if n is taken as indicating this intrinsic prospect of survival (subject to the constraint on the cross derivative of g). However, the biological interpretation and empirical prediction on who begs the most are reversed, with offspring that are in better condition begging more now as opposed to those who are in greater need (similar to costly signals in mate choice, Zahavi, 1975; Grafen, 1990). The difference between these two hypotheses (need vs. quality) would be crucial in a richer setting where offspring’s condition is affected by both its intrinsic quality and its short-term need is likely to yield new insights on the evolutionary and behavioral patterns of parent offspring conditions. Such a model, combined with a dynamic setting where offspring condition is affected by past provisioning (as in Roughgarden and Song, 2011) as well as environmental and genetic factors, presents a promising avenue for future research.

Finally, although I focused specifically on parent–offspring signaling, the potential application of mechanism design in biology is not restricted to signaling games between relatives. Biological interactions offer many examples of social interactions with asymmetric information (such as public goods games); mechanism design can be used to study the evolution of incentive structures in such situations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2011.10.031.

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