The limits to cost-free signalling of need between relatives

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Theoretical models have demonstrated the possibility of stable cost-free signalling of need between relatives. The stability of these cost-free equilibria depends on the indirect fitness cost of cheating and deceiving a donor into giving away resources. We show that this stability is highly sensitive to the distribution of need among signallers and receivers. In particular, cost-free signalling is likely to prove stable only if there is very large variation in need (such that the least-needy individuals stand to gain much less than the most-needy individuals from additional resources). We discuss whether these conditions are likely to be found in altricial avian breeding systems—the most intensively studied instance of signalling of need between relatives. We suggest that cost-free signalling is more likely to prove stable and will provide parents with more information during the earlier phases of chick growth, when parents can more easily meet the demands of a brood (and chicks are more likely to reach satiation). Later, informative yet cost-free signalling is unlikely to persist.

Keywords: cost-free signalling; pooling equilibria; signalling of need; information

1. INTRODUCTION

In a series of thought-provoking and insightful papers, Bergstrom & Lachmann (1997, 1998; Lachmann & Bergstrom 1998) have questioned the emphasis on costly signals in many analyses of communication of need between relatives (e.g. by offspring to their parents). They demonstrate that there are signalling equilibria, formerly neglected, that feature stable cost-free communication of need, even in the face of a conflict of interest between signallers and receivers. Drawing on the economics literature (e.g. Gibbons 1992), they term these new equilibria ‘pooling’ or ‘partially pooling’ equilibria—indicating that signallers of different need or quality are pooled together and employ the same signal. For the purposes of their analyses, they used the Sir Philip Sidney game (Maynard Smith 1991), a simple model of communication of need between relatives, which has been expanded upon and explored in various studies (e.g. Johnstone & Grafen 1992; Maynard Smith 1994; Johnstone 1998).

The basic Sir Philip Sidney game involves two related individuals—a donor who possesses a resource and a beneficiary who possesses none. The donor cannot perceive the need of the beneficiary but instead bases its choice of whether to donate the resource on its perception of a signal from the beneficiary. At a pooling equilibrium, the donor can attribute a level of need to a beneficiary corresponding only to the average for all beneficiaries that use the same signal. This is essential for the stability of cost-free signalling. It means that signallers cannot slightly exaggerate their perceived level of need—adopting the signal characteristic of a more needy pool will lead to substantial overestimation of their need by the receiver. As a result, deception entails the cost of fooling some donors of high need into giving away the resource inappropriately. In the words of Bergstrom and Lachmann, ‘signalling can

be cost-free when there is a gain to misrepresenting one’s condition to some, as long as there is on average no gain in misrepresenting one’s condition to everyone’ (Bergstrom & Lachmann 1998, p. 5101).

The costs and benefits of deception, however, depend upon the distribution of need among signallers and receivers. Most analyses based on the Sir Philip Sidney game have assumed, for convenience, that the benefit of obtaining (or retaining) the resource is uniformly distributed between zero and one for both donor and beneficiary (Johnstone & Grafen 1992; Bergstrom & Lachmann 1997, 1998; Johnstone 1998; Lachmann & Bergstrom 1998). Although apparently innocuous, this assumption has major consequences—in particular, it implies that an individual with the lowest possible level of need (zero, i.e. fully satiated) can never gain from the resource and will always favour its consumption by the other player. Consequently, our aim is to examine the effects on the stability of cost-free signalling when we alter the bounds of donor and beneficiary need (and, in particular, when we raise the lowest possible level of need above zero).

2. MATERIAL AND METHODS

The model involves two participants, a donor and a beneficiary, who are symmetrically related by coefficient r (where $0 \leq r \leq 1$). The donor possesses an indivisible resource, which it may donate to the beneficiary if it so chooses. Neither individual can directly perceive the need of the other (we define need as the additive fitness benefit an individual stands to gain by obtaining or retaining the resource, i.e. the needier the individual the higher the fitness gain should it consume the resource). Each individual, however, knows that the levels of need of both players are independently drawn from the same distribution, which ranges from lower bound l to upper bound u (previous analyses have focused on the special case of an even distribution with $l = 0$ and $u = 1$). We attempted to extend the model to cases where the distributions of need of donor and receiver differ, but

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unfortunately, it is not possible to provide a rigorous analysis of this more general scenario.

Under these circumstances, can it be evolutionarily stable for beneficiaries to advertise their need to the donor using a cost-free signal? Suppose (focusing on the possibility of a two-pool signalling equilibrium) that recipients above some critical level of need v employ the signal, while those whose need falls below this threshold refrain from doing so (where $l < v < u$). Under these circumstances, a donor should transfer the resource to a recipient who refrains from signalling if and only if its own need falls below a threshold value t_1 given by

$$t_1 = r \frac{\int_l^v b f(b) db}{\int_l^v f(b) db}, \quad (2.1)$$

where $f(b)$ denotes the probability density function for the distribution of beneficiary need (which we assume is continuous). In words, t_1 is equal to r times the expected need of a recipient who refrains from signalling.

Similarly, a donor should transfer the resource to a recipient who gives the signal if and only if its own need falls below a threshold value t_2 ($> t_1$) given by

$$t_2 = r \frac{\int_v^u b f(b) db}{\int_v^u f(b) db} \quad (2.2)$$

(in words, t_2 is equal to r times the expected need of a recipient who gives the signal).

Now, suppose that donors adopt the strategy described above, i.e. that they transfer the resource to a recipient who refrains from signalling if and only if their own need falls below a threshold value t_1 , and to a recipient who gives the signal if and only if their own need falls below a threshold value t_2 ($> t_1$). Under these circumstances, a recipient should signal if and only if its own need exceeds a threshold value v given by

$$v = r \frac{\int_y^x df(d) dd}{\int_y^x f(d) dd}, \quad (2.3)$$

where $x = \min(t_2, u)$ and $y = \max(t_1, l)$ and $f(d)$ denotes the probability density function for the distribution of donor need. This threshold level of need is equal to r times the expected need of that class of donors whose decision is influenced by the signal, i.e. those whose need lies between t_1 and t_2 (those donors whose need is less than t_1 always donate the resource regardless of whether a signal is given, while those whose need is greater than t_2 always keep the resource). The upper limit of integration (x) is the lesser of t_2 and u , while the lower limit of integration (y) is the greater of t_1 and l , because the lower and upper bounds on need may be such that no donor falls below the threshold t_1 (in which case the class of donors whose decision is influenced by the signal will include only those whose need lies above l rather than t_1) or above the threshold t_2 (in which case the class of donors whose decision is influenced by the signal will include only those whose need lies below u rather than t_2).

For given values of the parameters r , l and u , the model yields a unique set of values v , t_1 and t_2 that jointly satisfy equations (2.1)–(2.3). These values describe a unique cost-free signalling

equilibrium, provided that $l < v < u$ (as stated above). Such an equilibrium is possible if and only if

$$l < \frac{r \int_l^{\bar{b}} df(d) dd}{\int_l^{\bar{b}} f(d) dd}, \quad (2.4)$$

i.e. if and only if l (the minimum beneficiary need) is less than r times the mean need of those donors whose need falls between l and $\bar{b}$ (which represent the class of donors who will be influenced by a signal that is withheld only by beneficiaries of minimum need); here, $\bar{b}$ denotes the overall mean need of beneficiaries. If, however, this condition is not met, then cost-free signalling cannot be stable (given the assumptions of our model), since no equilibrium is possible at which some recipients should give the signal and some should withhold it.

To derive explicit solutions from the model we must specify the distribution of need. For illustrative purposes, we will focus here on a uniform distribution ranging from l to u , which yields a simple analytical solution. For non-uniform distributions of need, the model is less tractable, although it yields qualitatively similar results. In § 3, we illustrate graphically (in addition to the results for a uniform distribution) numerical results for a range of symmetrical beta distributions of differing variance.

Assuming that need is evenly distributed between l and u , equations (2.1)–(2.3) may be written as

$$t_1 = \frac{r(l + v)}{2}, \quad (2.5)$$

$$t_2 = \frac{r(u + v)}{2}, \quad (2.6)$$

$$v = \frac{r(\max(t_1, l) + \min(t_2, u))}{2}. \quad (2.7)$$

Given equations (2.5)–(2.7), we find that cost-free signalling proves stable if and only if

$$\frac{u}{l} > \frac{4 - 2r - r^2}{r^2} \quad (2.8)$$

and, if this condition is met, v , t_1 and t_2 are given by

$$v = \frac{r^2(l + u)}{4 - 2r^2}, \quad (2.9)$$

$$t_1 = \frac{4rl + r^3(u - l)}{8 - 4r^2}, \quad (2.10)$$

$$t_2 = \frac{4ru - r^3(u - l)}{8 - 4r^2}, \quad (2.11)$$

for

$$\frac{u}{l} > 1 + \frac{8 - 4r(1 + r)}{r^3} \quad (2.12)$$

(under which circumstances $t_1 > l$, implying that some donors will hand over the resource even if the beneficiary does not signal), and by

$$v = \frac{r(ru + 2l)}{4 - r^2}, \quad (2.13)$$

Figure 1. The ratio of maximum to minimum need above which cost-free signalling is stable, as a function of relatedness. As relatedness falls the minimum ratio required for stable signalling increases ever more rapidly. The uppermost line shows the results for a uniform distribution of need—successively lower curves show results for symmetrical beta distributions with variances of 0.6 and 0.2, respectively, times that of a uniform distribution of equal range. Note that the minimum ratio of upper bound to lower bound is plotted on a log-scale.

$$t_2 = \frac{r(2u + rl)}{4 - r^2}, \quad (2.14)$$

for

$$\frac{4 - 2r - r^2}{r^2} < \frac{u}{l} < 1 + \frac{8 - 4r(1 + r)}{r^3} \quad (2.15)$$

(under which circumstances $t_1 < l$, implying that no donor will ever hand over the resource if the beneficiary does not signal; hence no condition is given for t_1). Note that, whenever a signalling equilibrium exists, $t_2 < u$, implying that there are always some donors whose need is great enough that they will keep the resource regardless of whether the beneficiary signals.

3. RESULTS

Equation (2.8) revealed that, given a uniform distribution of need, cost-free signalling will prove stable only if the ratio of maximum to minimum need (u/l) exceeds some critical value, which depends on the relatedness between signaller and receiver. Other distributions yield similar results. Figure 1 shows that as relatedness between the participants falls so the critical ratio of maximum to minimum need increases, tending to infinity as r tends to zero. This implies that maximum need must be infinitely greater than minimum need. There is only one circumstance in which this condition can be met, and that is when the minimum need is zero. As mentioned in § 1, this is precisely the assumption made in previous models. The possibility of a cost-free signalling equilibrium (even at low levels of relatedness) was thus guaranteed by the choice of the upper and lower bounds on need.

Changing the shape of the distribution of need does not qualitatively alter the above pattern, although it has some influence on the critical ratio of maximum to minimum need above which cost-free signalling is stable. Figure 1 also shows the critical ratios for symmetrical beta distributions of lower variance than a uniform distribution of

Figure 2. Information content of the signal (i.e. an observer's uncertainty as to whether a signal will be given or not), measured in binary bits, assuming the distribution of need is a symmetrical beta distribution. Information is plotted as a function of the variance of the distribution of need relative to that of a uniform distribution of equal range (a value of 1 thus indicating that need is uniformly distributed), and of the ratio of maximum to minimum need. Minimum need is held constant at 1. Relatedness between donor and receiver is 0.5.

equal range. As can be seen, the lower the variance, the lower the critical ratio of maximum to minimum need. The reason is that, given a beta distribution of lower variance, donors who are influenced by a signal given only by beneficiaries of low need have, on average, higher need themselves. This means that signallers are less willing to signal and hence cost-free signalling is more likely to prove stable.

In addition to our observations on the stability of the cost-free signalling equilibrium, we would also like to draw attention to another drawback of these signals. This involves measuring the amount of information that is actually broadcast, formally known as the entropy index. It gives a measure of how much the receiver's uncertainty of the signaller's state decreases after a signal is given (Applebaum 1996). (For a more detailed discussion on the application of this information index to signalling models, see Brilot & Johnstone (2002)).

Figure 2 shows the amount of information in a cost-free signal, again assuming that need follows a symmetrical beta distribution, as a function of the variance in need (relative to that of a uniform distribution of equivalent range) and the ratio of maximum to minimum need. This confirms that there is no stable signalling equilibrium when the ratio is small, and hence no broadcast information. However, even when the ratio of maximum to minimum need is large and stable cost-free signalling is possible, little information may be broadcast if the variance in need is low. This is because few beneficiaries will then refrain from signalling. Hence, a donor will receive a signal on most encounters—and the display thus conveys little information.

The decrease in information with decreasing range of need is because it becomes cheaper for an individual to misrepresent their condition to a donor. As the range decreases, so the average need of signallers decreases, and thus a cheating signaller will pay a reduced indirect cost of depriving a correspondingly less-needy donor. Hence, an individual is induced to signal on more occasions than it might otherwise have done and again the signal conveys little information.

4. DISCUSSION

Cost-free signalling equilibria are increasingly being considered as a viable stable alternative to costly signalling. However, our results suggest that the necessary conditions for cost-free communication of need are, in fact, quite restrictive. This fact has been obscured in previous analyses of the Philip Sidney game by the assumption that need ranges from 0 to 1 (which yields a ratio of maximum to minimum need that is infinitely large). This assumption implies that a minimum-need satiated individual can never gain from obtaining (or retaining) the resource. The stability of cost-free signalling is thus assured since at least some beneficiaries (no matter how rare the class) will refrain from signalling, and it will then pay at least some receivers to respond to the signal. When the assumption that need can drop to zero is relaxed, we see that cost-free signalling may easily become unsustainable, particularly if the relatedness between signaller and receiver is low.

How often are offspring sufficiently satiated that they stand to gain no benefit from food (i.e. how plausible is the assumption of a minimum need of zero)? Since the majority of begging work has been carried out on birds, and there is a correspondingly large amount of literature on avian digestion and physiology, we will confine our discussion to avian energetics. We do not intend this discussion to be an exhaustive review. Our aim is to highlight studies that go some way towards substantiating our claims and to suggest fruitful future directions for research.

To address the above question we need to examine two key issues. First, is there a physiological limit to the rate of digestion by an individual offspring (i.e. is the maximal rate of energy assimilation determined by the physiological limitations of the gut)? Second, will this maximal rate be attainable given the provisioning rate of the parents? The supply of food may fall short of an offspring's maximal-intake limit because of parental energy-budget limitations; in addition, even when they are capable of supplying more food, parents may refrain from doing so because of their own long-term needs and those of their future offspring.

The answer to the first question is most definitely yes. The existence of an upper limit on the rate of energy assimilation (termed $A_{\max}$) is a well-known phenomenon in birds (Karasov 1996). This limit, identified as that reached when birds are acclimated to temperatures at the lower limit of their tolerance (Karasov 1990; Weiner 1992), has been measured in adults in several studies but is less well quantified for nestlings of altricial species. It is thought, in general, that nestlings have a lower value of $A_{\max}$ than adults (Weathers 1992). Since the existence of an upper limit on assimilation is well established (Ricklefs 1983) it seems plausible that there are times when an offspring presented with a food resource would not benefit from accepting it.

Thus we come to the second question: given that there is an upper limit to assimilation by chicks, will enough food be provided by parents to allow their offspring to reach this limit? This is still a very open question: there are various competing theories to explain the observed patterns of avian growth (e.g. Schew & Ricklefs 1998; Karasov 1996), and the relative importance of the limitations imposed by the avian gut and by parental pro-

visioning rates have yet to be resolved (see Karasov & Wright (2002) for a review that includes implications for begging strategies).

A problem with any interpretation we choose here is that assimilation efficiency is not an inflexible physiological property—it is subject to change over both evolutionary and developmental time. Therefore, we must bear in mind the possibility that the assimilation efficiency of an offspring is adapted to match the level of food provisioning of the adult; there is, after all, no point in wasting energy on building a bigger or more efficient gut if parents are unable or unwilling to provide more food to fill it. This makes it very difficult if not impossible to prove that a parent is feeding its offspring to their maximal limit of food intake (though it has been shown that digestive capacity and not feeding rate limits the growth rate in house sparrows; Lepczyk *et al.* 1998; Caviedes-Vidal & Karasov 2001; and song thrushes; Konarzewski & Starck 2000). It is, however, possible to demonstrate that the parent is *not* feeding its offspring to their maximal assimilation ability. This can be done by demonstrating that an increase in the rate of food delivery to the offspring results in an increase in the rate of growth. This would conclusively show that the offspring is deriving benefit from the extra food it is receiving.

One such demonstration focused on pied kingfisher (*Ceryle rudis*) chicks (Reyer & Westerterp 1985). The study showed that parents from two different lake environments had differing food-provisioning capabilities. Parents exposed to the more favourable ecological conditions could supply their offspring with a greater food intake rate and their offspring had a correspondingly increased growth rate. Unfortunately, there is a potential confounding factor here, since parents on poor territories often take on helpers at the nest, and hence their offspring might benefit from having a greater intake capability (to take advantage of the extra provisioning by helpers). However, the study also examined chicks that were hand-reared and fed *ad libitum*. This experimental group showed even greater growth rates than those that were raised by parents in favourable ecological conditions. This suggests that even parents in favourable circumstances do not provision at a rate that exceeds the limit of assimilation of the chick (see Quinney *et al.* (1986) and McCarty (2001) for similar findings in tree swallows, *Tachycineta bicolor*).

Although there is no clear consensus as to whether offspring digestive capabilities or parental feeding strategies limit growth rate, a hint at the interplay between the two is given in a model by Winkler & Adler (1996). They modelled the growth rates of chicks, given certain physiological constants such as assimilation efficiency (though their analysis is currently incomplete in the sense that it does not include the provisioning decisions that a parent may make and how these, in turn, affect the evolution of physiological adaptations in the offspring). Their results suggest that it might be very easy for a parent to feed a chick to satiation in the early stages of its development but that older chicks 'are likely to be receiving substantially less than they are capable of ingesting' (Winkler & Adler 1996, p. 350).

In light of the above result, the present model predicts that we should observe changes in signal cost during the development of avian offspring. If young chicks are more

easily satiated (and therefore more likely to be fed to satiation by the parents) than are old chicks, then cost-free signalling is more likely to prove stable early on in the development of the brood. Later, when offspring are unlikely to achieve satiation, cheap signals are likely to become uninformative, owing to the disappearance (or decline in frequency) of the class of individuals who stand to gain no benefit from the resource (and hence will refrain from signalling). It has been noted that older chicks do beg more intensely and parents pay correspondingly less attention, though it was surmised that this is caused by the costs of begging (in terms of growth) being relatively cheaper for older chicks (Kilner 2001). Older chicks, as a result, should be forced to use a comparatively more expensive signal or the parents should be selected to ignore the signal.

Other predictions regarding the occurrence of cost-free signalling may be made in relation to ecological conditions. Consider the impact of food availability. In a year of plenty we should expect there to be at least some chicks whom their parents have succeeded in feeding to satiation at least some of the time. Hence, we have a class of individuals who could gain no benefit from the resource, supporting informative cost-free signalling. We do not especially expect the existence of this class of individuals in a year where food is not abundant and hence we might expect that in lean times a comparatively more expensive signal is required (though the effects of clutch-size flexibility and brood reduction might well be confounding). In the same vein, it is known that parents increase their overall provisioning rate with increasing brood size but with a decreasing rate per chick (e.g. in starlings; Wright & Cuthill 1990). This leads to increased (presumably more costly) begging levels per chick in the nest (Wright & Cuthill 1990). Finally, comparing different populations or species, we might expect that cost-free signalling is more prevalent in situations of resource abundance (where parents can more easily feed their chicks to satiation).

In conclusion, we have demonstrated that cost-free signalling equilibria (of the kind suggested by Bergstrom and Lachmann) are possible under a narrower range of conditions than previously suspected. In particular, we have shown that cost-free signal models have been supported by the inclusion of individuals of zero need. This leads, inevitably, to the stability of non-costly signalling since the class of zero-need individuals will never have cause to use the signal while they have an interest in the other party's survival. A number of studies suggest that parental provisioning rate is a major constraint on chick growth, which calls into question the occurrence of zero need, and hence the possibility of cost-free communication, in real signalling systems. However, we believe that this possibility should not simply be dismissed. Rather, the present model allows us to predict under what circumstances cost-free signalling is most likely to be stable—in particular, we suggest that cheap signals are more likely to be employed early on in the development of young and under conditions of high resource abundance (both factors that increase the possibility of satiation). In these cases cost-free signals will be informative. A switch to reliance on costly signalling may be caused by the decrease in information provided by the cost-free signal as conditions change, rather than a collapse in the stability of the signal.

We hope that these qualitative predictions will suggest some new and fruitful directions for empirical studies of begging.

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