

## Signalling of information that is neither cryptic nor private

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### Abstract

It is commonly assumed that in order for animal signals to be advantageous, the information being signalled could not have been obtained otherwise, and is therefore ‘cryptic’ or ‘private’. Here, we suggest a scenario in which individuals can gain an advantage by signalling ‘public’ information that is neither cryptic nor private. In that scenario, signalling increases the efficiency with which that ‘public’ information is transmitted. We formalize our idea with a game in which offspring can signal their condition to their parents. Specifically, we consider a resource-strapped parent who can only invest in one of its two offspring, and we allow offspring the chance to influence parental investment through a signal. A parent in the game seeks to invest in the higher-quality offspring, which it could identify either through a publicly available cue, such as body size, or by relying on a signal provided by the offspring. We find that if the signal can convey information about offspring quality more efficiently than cues, then signalling of condition between offspring and parents can be favoured by selection, even though parents could potentially have acquired the same information from the cue. Our results suggest that the biological function of signals may be broader than currently considered, and provide a scenario where low cost signalling can be favoured. More generally, efficiency benefits could explain signalling across a range of biological and economic scenarios.

### Introduction

Animals use signals to communicate information, ranging from their quality as a potential mate to their need for food (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). Signalling systems are vulnerable to collapse because individuals could potentially signal dishonestly to coerce others in ways that benefit the signaller (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). Evolutionary theory has provided solutions to this problem by showing that individuals can be selected to signal honestly for a number of reasons, such as if the signaller and receiver share a common interest, or if dishonest signals are too costly to produce (Zahavi,

1975; Grafen, 1990; Godfray, 1991; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). In these cases, signalling can be an evolutionary stable outcome when any potential benefits of signalling dishonestly are outweighed by the costs.

A prevailing explicit assumption in the signalling literature is that in order for signalling to be favoured, the information being signalled could not be obtained otherwise, and is therefore ‘cryptic’ or ‘private’ (e.g. Grafen, 1990; Godfray, 1991; Kilner & Johnstone, 1997; Bergstrom *et al.*, 2002; Johnstone 2004). We challenge this assumption here. Our hypothesis is that individuals can be favoured to signal information that is not cryptic or private, if signalling increases the efficiency with which that information can be transmitted. In order for this hypothesis to hold, it would require that the increase in efficiency outweighs the cost of signalling and that honest (or at least meaningful) signalling is favoured. Our aim was to investigate the theoretical plausibility of this hypothesis.

It is useful to consider our hypothesis in a specific scenario, and so we examine the case of offspring

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signalling their condition to their parents. We pick this scenario because it has been explicitly stated, on numerous occasions, that offspring must be signalling cryptic information (e.g. Godfray, 1991; Kilner & Johnstone, 1997; Johnstone 2004, Royle *et al.*, 2002). We focus on a scenario in which a parent has only enough food to feed one of its two offspring. Parents in this scenario will be favoured to invest in the higher-quality offspring, which they could identify via publicly available cues, such as body size (Lack, 1954; Mock & Parker, 1997; Davis *et al.*, 1999). This kind of scenario is reflected in the biology of bird species like the hoopoe (*Upupa epops*) and blue-footed booby (*Sula nebouxii*), as parents in those species tend to experience brood reduction, and preferentially feed larger, higher-quality, offspring (Drummond & Garcia Chavelas, 1989; Martin-Vivaldi *et al.*, 1999; Caro *et al.*, 2016). If parents in species like the hoopoe or the blue-footed booby could obtain information about offspring quality more quickly via offspring signals, then they would have more time to acquire food for the offspring. This efficiency benefit could potentially outweigh the costs of signalling, and make signalling evolutionarily stable (Fig. 1). We examine the theoretical plausibility of this scenario by proposing and solving a simple game theory model. We specifically want to determine the conditions under which production of the offspring signal will provide the parent with a means for distinguishing offspring on the basis of quality, at evolutionary equilibrium. In this sense, we are looking for an 'honest' signalling solution to the game. We then address the biological plausibility and empirical applications of the model in our discussion.

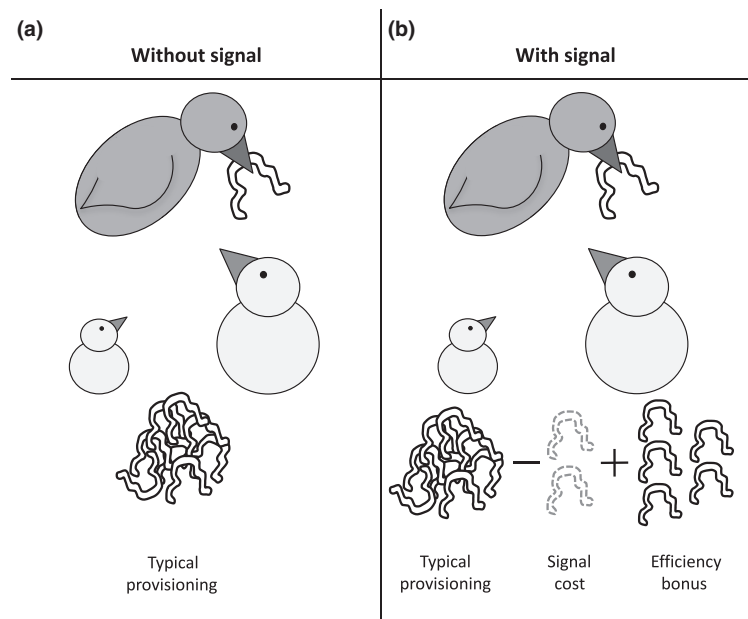
## The model

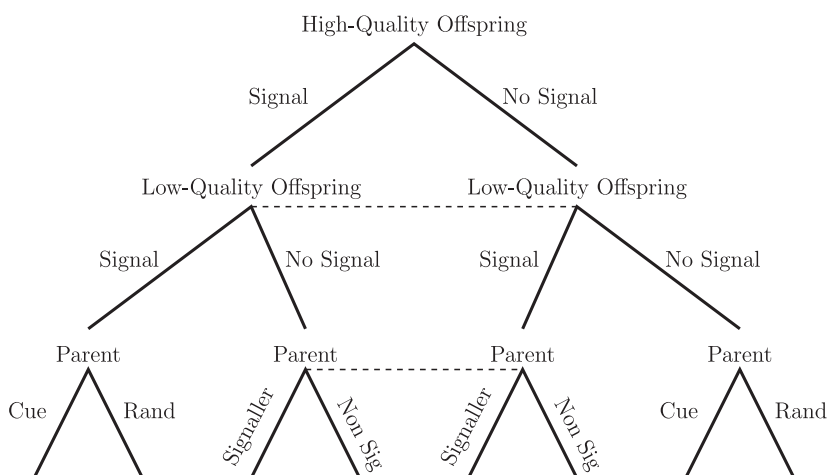
We consider a parent that has one low-quality offspring and one high-quality offspring. Offspring quality is not cryptic, and the parent can distinguish the low-quality offspring from the high-quality one by investigating some cue (e.g. body size). Our starting point could mirror some natural cases, such as blue-footed boobies, where two eggs hatch asynchronously, leading to a large size disparity (Drummond & Garcia Chavelas, 1989).

We assume, first, that a parent can also distinguish offspring from one another through means other than the cue. Specifically, the parent can respond to a signal (possibly) produced by the offspring. We assume further that assessing the signal is more efficient than assessing the cue, saving the parent time that can be spent acquiring more food. Signalling can, however, be costly to the offspring.

We then assume that the parent, after producing two offspring, is experiencing relatively poor environmental conditions. Conditions are so poor, in fact, that the parent can successfully rear only one of its two offspring. Therefore, the parent must decide which offspring it will invest in, and which offspring it will allow to die. Offspring, in turn, must decide on what information (if any) to attempt to convey to the parent via the signal. We assume that a high-quality offspring who receives parental investment has fitness equal to 1 and that a low-quality offspring who receives parental investment has a fitness equal to  $0 < v < 1$ . An offspring who does not receive investment has fitness equal to zero. We assume parents have complete

**Fig. 1** Costly signals of noncryptic condition are biologically feasible. (a) Parents can distribute food amongst their offspring by relying on a cue of condition, such as body size. (b) Alternatively, parents could distribute food amongst their offspring by relying on a signal of noncryptic condition, such as mouth gape area, begging calls or begging height. If it is much faster for parents to use the signal, they could spend more time foraging for additional caterpillars to feed their brood. As long as the efficiency benefit of using the signal outweighs the cost of producing the signal, this communication system can be advantageous, even if the information encoded in the signal is noncryptic.





control over the distribution of resources like food (e.g. Godfray, 1991).

We model the decisions made by the parent and offspring as moves in a three-player evolutionary game (Fig. 2). In this game, the high-quality offspring moves either by producing a signal (strategy  $H_1$ ), or by not signalling at all (strategy  $H_2$ ). At exactly the same time, the low-quality offspring also moves either by producing a signal (strategy  $L_1$ ), or by not signalling at all (strategy  $L_2$ ). Any offspring that signals reduces its fitness by a fraction  $c$ , which reflects the cost of signal production.

The parent's move in the game follows those made by the offspring, and its available moves vary depending on the situation. If both offspring signal, or if neither offspring signals, then the parent cannot use the signal to distinguish one offspring from the other. In these two cases, the parent moves either by using the cue to direct investment to the high-quality offspring, or by investing in a randomly chosen offspring. Assessing the cue is assumed to incur some time cost, such that investing at random confers an efficiency benefit, which means that the parent is able to improve the fitness of the offspring who receives investment. Here, the improvement is modelled by a multiplying fitness by  $(1 + b)$ . If only one offspring signals, then we assume the parent moves either by investing in the signaller, or by investing in the nonsignaller. In this case, the parent also avoids the cost of assessing the cue, and so gains the multiplicative efficiency benefit  $b$ . Because the parent can choose between two moves in each of three different situations, there are eight parental strategies in this game ( $P_1$  to  $P_8$  in Table 1).

## Method of analysis

We solve the game proposed in the previous section by identifying strategies that are likely to remain fixed in a

**Fig. 2** Tree depiction of the game proposed in the main text. Individual decision-makers appear at nodes, and solid branches indicate different actions available to individual decision-makers. Nodes linked by dashed lines indicate that the corresponding decisions are made by individuals who have been given the same information. In particular, the fact that offspring decide upon their respective strategies simultaneously means that the nodes depicting the low-quality offspring's decision must be connected by a dashed line.

**Table 1** Description of the eight possible parental strategies,  $P_1$  to  $P_8$ , in the game. Each strategy specifies a course of action given the presence or absence of offspring signals.

Strategy	Both offspring signal	Only one offspring signals	Neither offspring signals
$P_1$	Feed according to cue	Feed signaller	Feed according to cue
$P_2$	Feed according to cue	Feed signaller	Feed at random
$P_3$	Feed according to cue	Feed nonsignaller	Feed according to cue
$P_4$	Feed according to cue	Feed nonsignaller	Feed at random
$P_5$	Feed at random	Feed signaller	Feed according to cue
$P_6$	Feed at random	Feed signaller	Feed at random
$P_7$	Feed at random	Feed nonsignaller	Feed according to cue
$P_8$	Feed at random	Feed nonsignaller	Feed at random

population. The solution concept we turn to is the Nash equilibrium. Here, the Nash equilibrium is a strategy profile  $(H_i, L_j, P_k)$  that produces a pay-off to each player that cannot be improved upon by a unilateral change in strategy. The Nash equilibrium is a necessary condition of Maynard Smith's (1982) evolutionarily stable strategy (ESS). The Nash equilibrium has also been the solution concept used in other theoretical treatments of signals between offspring and parents (e.g. Rodriguez-Girones, 1999). We are particularly interested in those equilibria in which one, and only one, offspring signals. The signal would then provide a parent with a clear means of distinguishing offspring based on quality. In those cases, the signal conveys meaningful (or, in some sense, 'honest') information to the parent.

To find the Nash equilibrium, we translate the consequences of the various strategies into inclusive fitness pay-offs (Hamilton, 1964). The inclusive fitness pay-off

awarded to an offspring depends upon the relatedness between it and its sibling,  $0 < r < 1$ . In contrast, relatedness factors out of any inclusive fitness pay off the parent receives, because the parent is equally related to both offspring.

**Results**

The Nash equilibria we obtain vary according to whether investment using the public cue of quality is more or less profitable than investment at random. If the efficiency benefit  $b$  (or potential efficiency benefit) lies below a threshold value of  $(1 - v)/(1 + v)$ , then using the cue is more profitable and we obtain one set of Nash equilibria. If  $b$  exceeds the threshold value of  $(1 - v)/(1 + v)$ , then investing at random is more profitable and we obtain a different set of Nash equilibria. The details surrounding the equilibria are given below.

**Case 1: Following the cue is better than investing at random**

We first consider the scenario where the efficiency benefits gained from not investigating the cue are low,  $b < (1 - v)/(1 + v)$ . In this scenario, following the cue is better than investing at random. Consequently, we are able to examine a reduced game that excludes the parental strategies that rely on random investment (Table 2). In that reduced game, there may be two Nash equilibria at which one, and only one, offspring signals.

The first candidate Nash equilibrium is the triplet  $(H_1, L_2, P_1)$ . This triplet corresponds to the situation in which only the high-quality offspring signals, and the parent directs its investment towards that signal in an efficient manner. In keeping with definition of the

**Table 2** Reduced pay-off matrix for the case when investing in offspring based on the cue is more profitable than investing at random ( $b < (1 - v)/(1 + v)$ ). Each cell presents the pay-off to the parent (row player), the low-quality offspring (column player) and the high-quality offspring (super-column player), in that order.  $H_1$  and  $L_1$  indicate that high- and low-quality offspring produce the signal, whereas  $H_2$  and  $L_2$  indicate that offspring do not signal.  $P_1$  and  $P_3$  correspond to parental strategies in Table 1.

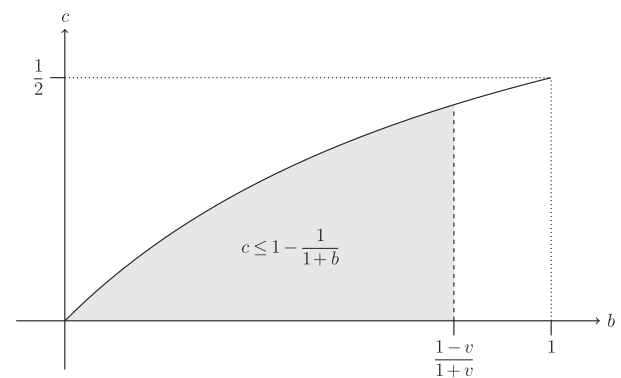
	$H_1$		$H_2$	
	$L_1$	$L_2$	$L_1$	$L_2$
$P_1$	$(1 - c)$ $r(1 - c)$ $(1 - c)$	$(1 - c)(1 + b)$ $r(1 - c)(1 + b)$ $(1 - c)(1 + b)$	$v(1 - c)(1 + b)$ $v(1 - c)(1 + b)$ $rv(1 - c)(1 + b)$	1 $r$ 1
$P_3$	$(1 - c)$ $r(1 - c)$ $(1 - c)$	$v(1 + b)$ $v(1 + b)$ $rv(1 + b)$	$(1 + b)$ $r(1 + b)$ $(1 + b)$	1 $r$ 1

Shaded cells indicate Nash equilibria where signalling can be stable.

Nash equilibrium, a unilateral switch from  $L_2$  to  $L_1$  will not increase the low-quality offspring’s inclusive fitness pay-off. However, unilateral switches from  $H_1$  to  $H_2$ , or from  $P_1$  to  $P_3$  may be rewarded, and so there is a chance the definition of a Nash equilibrium will not be met. To ensure strategy switches made by the high-quality offspring and the parent, respectively, are not rewarded, we must have  $(1 + b)(1 - c) \geq \max\{1, v(1 + b)\}$ , or equivalently  $c \leq 1 - \max\{1/(1 + b), v\}$ . Because we have assumed  $b < (1 - v)/(1 + v)$ , we can be sure that  $v < (1 - b)/(1 + b)$ , which implies that  $\max\{1/(1 + b), v\} = 1/(1 + b)$ . The condition for  $(H_1, L_2, P_1)$  to be a NE, therefore, can be stated simply as  $c \leq 1 - 1/(1 + b)$ . In other words, the cost of signalling cannot be too high. This Nash equilibrium condition is illustrated in Fig. 3 alongside the constraints imposed by other model assumptions. As the figure shows, the largest permissible cost increases as the efficiency benefit rises, and is independent of the relatedness between siblings.

The second Nash equilibrium is the triplet  $(H_2, L_1, P_3)$ . It corresponds to the situation in which the low-quality offspring signals in order to efficiently guide the parent’s investment towards the nonsignalling, high-quality offspring. The triplet follows the definition of a Nash equilibrium, because:

- 1 a unilateral switch from  $H_2$  to  $H_1$  penalizes the high-quality offspring by an amount  $(1 + b) - (1 - c) = (b + c)$ ;
- 2 a unilateral switch from  $L_1$  to  $L_2$  penalizes the low-quality offspring by an amount  $r(1 + b) - r = rb$ ;
- 3 a unilateral switch from  $P_3$  to  $P_1$  penalizes the parent by an amount  $(1 + b) - (1 + b)(1 - c)v = (1 + b)(1 - (1 - c)v)$ .



**Fig. 3** If the efficiency benefit is small, meaning  $b < (1 - v)/(1 + v)$  then the strategy profile  $(H_1, L_2, P_1)$  is a Nash equilibrium provided  $b, c$  parameters remain in the shaded region. The shaded region is bounded by a curve describing maximum permissible cost,  $c = 1 - 1/(1 + b)$ , and the maximum  $b$  in this case. One can see that the conditions under which  $(H_1, L_2, P_1)$  is a Nash equilibrium become more restrictive either as  $b$  decreases or as  $v$  increases.

The fact that  $(H_2, L_1, P_3)$  is a Nash equilibrium is quite intuitive. Indeed, the effective cost of signalling, here, is actually zero, because the offspring who signals ultimately dies.

**Case 2: Investing at random is better than following the cue**

We now consider the scenario where the efficiency benefits gained from not assessing the cue are high,  $b > (1 - v)/(1 + v)$ . Under this condition, investing at random is better than following the cue, and so we consider a reduced game that excludes the parental strategies that rely on the cue (Table 3). As in the previous case, we identify two Nash equilibria, at which only one offspring signals.

We first consider the triplet  $(H_1, L_2, P_6)$ , where only the high-quality offspring signals, and only the high-quality offspring receives parental investment. In this case,  $(H_1, L_2, P_6)$  fails to be a Nash equilibrium when either:

- 1 the signal is so costly that it is better, from the parent’s perspective, to invest in the offspring whose quality is not diminished by the signal,
- 2 it is in the high-quality offspring’s best interest, in an inclusive fitness sense, to stop signalling and suffer the possible consequences of its parent’s random investment, or
- 3 it is in the low-quality offspring’s best interests, in an inclusive fitness sense, to start signalling in order to receive a chance parental investment.

From Table 3, we see that (i) and (ii) can be ruled out when  $(1 - c) \geq \max\{v, (1 + rv)/2\}$ , whereas (iii)

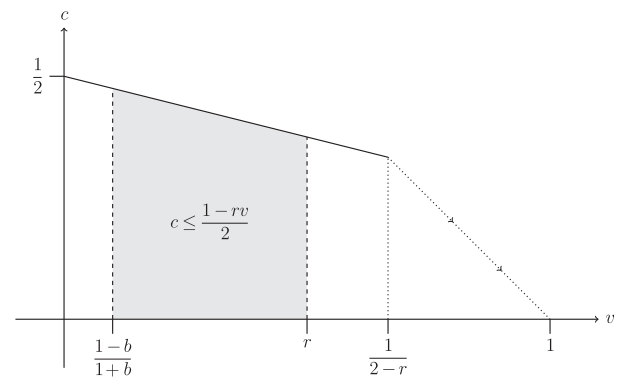
**Table 3** Reduced pay-off matrix for the case when investing in offspring randomly is more profitable than investing based on the cue ( $b > (1 - v)/(1 + v)$ ). Each cell presents the pay-off to the parent (row player), the low-quality offspring (column player) and the high-quality offspring (super-column player), in that order.  $H_1$  and  $L_1$  indicate that high- and low-quality offspring produce the signal, whereas  $H_2$  and  $L_2$  indicate that offspring do not signal.  $P_1$  and  $P_3$  correspond to parental strategies in Table 1.

	$H_1$		$H_2$	
	$L_1$	$L_2$	$L_1$	$L_2$
$P_6$	$(1 - c)(1 + b)(1 + v)/2$	$(1 - c)(1 + b)$	$v(1 - c)$	$(1 + b)(1 + v)/2$
	$(1 - c)(1 + b)(r + v)/2$	$r(1 - c)(1 + b)$	$v(1 - c)$	$(1 + b)(r + v)/2$
	$(1 - c)(1 + b)(1 + rv)/2$	$(1 - c)(1 + b)$	$rv(1 - c)$	$(1 + b)(1 + rv)/2$
$P_8$	$(1 - c)(1 + b)(1 + v)/2$	$v(1 + b)$	$(1 + b)$	$(1 + b)(1 + v)/2$
	$(1 - c)(1 + b)(r + v)/2$	$v(1 + b)$	$r(1 + b)$	$(1 + b)(r + v)/2$
	$(1 - c)(1 + b)(1 + rv)/2$	$rv(1 + b)$	$(1 + b)$	$(1 + b)(1 + rv)/2$

Shaded cells indicate Nash equilibria where signalling can be stable.

can be ruled out when  $r \geq v$ . Furthermore, if we do have  $r \geq v$ , then we can be sure that  $v < 1/(2 - r)$  so that  $\max\{v, (1 + rv)/2\} = (1 + rv)/2$ . It follows that  $(H_1, L_2, P_6)$  is a Nash equilibrium if and only if  $r \geq v$  and  $c \leq (1 - rv)/2$ . The latter condition sets the largest permissible signalling cost, and it depends on the relatedness between siblings (Fig. 4). In addition, the largest permissible cost does not depend on the efficiency benefit  $b$  beyond the mathematical requirement that defines this case. Of course that mathematical requirement, namely  $b > (1 - v)/(1 + v)$ , can be rearranged as  $v > (1 - b)/(1 + b)$ , which puts a lower bound on  $v$  (Fig. 4).

The second candidate Nash equilibrium we consider is  $(H_2, L_1, P_8)$ , which corresponds to yet another situation in which only the offspring destined to die provides the signal. However, in contrast to the analogous situation described for the previous case, this triplet is not guaranteed to be an equilibrium. Efficiency gains are now large enough to provide a parent with an incentive to invest at random when there is no signal to guide its behaviour. This means that a low-quality offspring may be able to increase its pay-off by switching from  $L_1$  to  $L_2$ , that is by turning off its signal. To ensure this kind of gain cannot be made, we must have  $r \geq v$ , so that the low-quality offspring values its high-quality sibling more than it values itself. In contrast to the previous case, examination of the consequences of other unilateral deviations from  $(H_2, L_1, P_8)$  shows that  $r \geq v$  is the only condition that needs to be satisfied if the triplet is to be a Nash equilibrium (Table 3).



**Fig 4** If the efficiency benefit is large, meaning  $b > (1 - v)/(1 + v)$  then the strategy profile  $(H_1, L_2, P_6)$  is a Nash equilibrium provided  $v, c$  parameters remain in the shaded region. The shaded region is bounded by a curve describing maximum permissible cost,  $c = (1 - rv)/2$ , and the minimum and maximum, respectively, in this case. One can see that the conditions under which  $(H_1, L_2, P_6)$  a Nash equilibrium become more restrictive as  $v$  increases. By contrast, an increase in  $r$  has mixed effects, broadening the range of possible  $v$  values on the one hand, but reducing the maximum permissible cost on the other hand (as indicated by the dotted arrows).

## Discussion

Broadly speaking, our game-theoretical model results show that natural selection can lead offspring to signal their quality, even if that quality is not cryptic. This agrees with the hypothesis presented in the introduction, but contradicts the common assumption in the field of parent–offspring communication that offspring signals of need or quality must transmit information that cannot be obtained by parents in any other way (e.g. Grafen, 1990; Godfray, 1991; Kilner & Johnstone, 1997; Bergstrom *et al.*, 2002; Johnstone 2004). One implication of our results is that empirical researchers attempting to identify precisely what is encoded in offspring signals should consider the possibility that the biologically relevant aspects of condition may be public. Furthermore, we have focused on the extreme case where cues and signals carry the same information. In reality, signals could have multiple functions, conveying both public information more efficiently, and cryptic information, which could make them even more likely to be favoured. More generally, although we have modelled signals of noncryptic quality in the context of parent–offspring communication, similar outcomes could be expected in other honest signalling scenarios in the fields of biology and economics, such as sexual selection (Grafen, 1990), or even competition in the labour market.

Our analysis considered small and large efficiency benefits separately. In both cases, we identified two distinct instances in which a signal conveyed meaning at equilibrium (Table 4). In the first instance, only the low-quality offspring produced the signal, and the parent used that signal to direct investment towards the signaller's high-quality counterpart. In the second instance, only the high-quality offspring produced the signal that attracted parental investment away from the low-quality offspring. In both instances, the family group can be understood as using the signal for the purpose of making inclusive fitness gains. Aligned interests such as these can contribute to the stability of offspring–parent signals (Maynard Smith, 1991; Rodriguez-Girones, 1999), but it has not been previously shown that efficiency benefits

are able to bring interests into alignment. That said, our results do rely critically on the assumption that offspring differ in quality. As the variation in offspring quality is diminished (i.e. as  $v$  increases), the conditions for one and only one signal at equilibrium become more restrictive, and in the limit as  $v$  goes to 1, none of the conditions can be met (Table 4).

Signalling models often predict the existence of multiple equilibria (Bergstrom & Lachmann, 1997; Lachmann & Bergstrom, 1998), and ours is no exception. Indeed, the two distinct instances identified above could *simultaneously* be solutions to the game we proposed. It is important to recognize, though, that the mathematical requirements in the first instance (only the high-quality offspring signals) were more restrictive than those in the second (only the low-quality offspring signals). We found that if the high-quality offspring was predicted to signal at equilibrium, then the cost of signalling could not exceed some threshold value. By contrast, no such requirement on cost was made of a low-quality signaller at equilibrium, because, when it signalled at equilibrium, the low-quality offspring did not receive any parental investment, and will therefore die. The actual cost of the signal produced by the low-quality offspring at equilibrium, then, is extremely low. Had we relaxed the assumption that the offspring who does not receive parental investment dies, we would have expected the contrast between equilibrium signalling from the high- and low-quality offspring, respectively, to be weaker. However, it is likely that in order to be maintained at equilibrium, signals provided by the low-quality offspring would have continued to require the costs of signalling to be sufficiently low. Still, we expect that the threshold condition for the maintenance of the signal from the low-quality offspring only would have continued to be more restrictive.

There are some conceptual similarities between our model and a scenario discussed in Lachmann *et al.* (2001). Those authors suggest a verbal model for sparrows in which individuals can produce a relatively cheap signal that indicates aggressiveness, fighting ability or other correlates of their resource-holding potential. In their model, individuals who signal dishonestly are punished by conspecifics, which imposes a cost of dishonest signalling. Similarities between our model and that of Lachmann *et al.* (2001) include: (i) the potential for honest (or meaningful) signalling at equilibrium despite low realized costs of signalling, and (ii) the possibility for individuals to avoid other types of costs, for example agonistic interactions in the sparrow example, by signalling. In the case of (ii), the absence of other types of cost parallels the efficiency benefits introduced here, but the two are distinct – the absence of a cost of dishonesty, on the one hand, and the presence of an efficiency benefit, on the other hand. Differences between the two models

**Table 4** Summary of mathematical conditions associated with the two instances of Nash equilibrium solutions at which one, and only one, offspring signals. The marginal case  $b = (1 - v)/(1 - v)$  has been neglected.

Case	Only low-quality offspring signals, high-quality offspring receives parental investment	Only high-quality offspring signals, and high-quality offspring receives parental investment
$b < (1 - v)/(1 + v)$	Not applicable (always Nash equil)	$c \leq 1 - 1/(1 + b)$
$b > (1 - v)/(1 + v)$	$r \geq v$	$c \leq (1 - v)/2$ and $r \geq v$

include: (i) the consideration we give to interactions between relatives; (ii) an explicit efficiency benefit from following signals, relative to using cues (our *b* term); (iii) our presentation of explicit conditions for stability of honest signalling; and (iv) our examination of stability against invasion by non-signal-based means of achieving efficiency benefits (i.e. investing at random).

Our model also shares some similarities with models of amplifier signals (Hasson, 1989; Bogaardt & Johnstone, 2016). Amplifiers are traits that magnify differences in cues of quality, and are typically considered in terms of sexual signalling. In both cases, a receiver prefers higher-quality individuals and can use a cue to distinguish between individuals of differing quality, and those cues are linked to a separate trait, which may or may not evolve as a stable signal. The key difference between our models lays in the benefit of the signal: in our model, the benefit is increased efficiency, which increases the amount of parental investment possible, whereas in amplifier models, the benefit is to reduce perceptual errors in the assessment of male cues. Furthermore, amplifiers increase the total amount of information available to receivers, because signallers can vary their level of amplification. In our model, signalling is stable even though receivers never experience an increase in the amount of information they can gain, whether they respond to the cue, the signal, or both.

### Empirical applications

Under what conditions would our hypothesis be most likely to apply in the real world? We showed that selection can favour signalling of information that is not cryptic or private, to increase the efficiency with which that 'public' information can be transmitted. Considering offspring soliciting their parents for food, this is more likely to be the case when: (i) it would be relatively difficult for parents to make use of public cues or signals of cryptic condition, due to acoustic interference from the environment, limited visibility or low variability in the public cue, such as in synchronously hatching broods where all nestlings are approximately the same size; (ii) when offspring condition hovers around the viability threshold, so that small increases in the total amount of provisioning could have large impacts on fitness; and/or (iii) when the cost of signalling is relatively low.

How plausible is this set of conditions, where the efficiency benefits from transmitting information with a signal can outweigh the cost of signalling? Consider a common bird species, the great tit (*Parus major*). The efficiency benefit (*b*) of responding to a low cost signal could be relatively high in birds such as the great tit, because: (i) they nest in dark tree holes, where it may be relatively hard to assess cues such as body size

(Wiebe & Slagsvold, 2012); (ii) they frequently experience brood reduction, so slight increases in provisioning rate could have especially large impacts on the fitness of marginal offspring (Bengtsson & Rydén, 1983); and (iii) their breeding period is constrained to the relatively short window when caterpillars are abundant, and so efficiency in distributing food could be important (Hinks *et al.*, 2015). Great tit parents can spend an average of 8 h per day foraging for their brood (Barba *et al.*, 2009; García-Navas *et al.*, 2013). Over a 15-day nestling period, these parents would have approximately 864 000 s of total foraging time. Great tit parents can make approximately 13 provisioning trips per hour, so a parent can return to the nest with prey, such as caterpillars, approximately every 138 s, on average (García-Navas *et al.*, 2013). If the smallest offspring are at a high risk of starvation, parents will be selected to feed the offspring in the best condition (Mock & Parker, 1997; Davis *et al.*, 1999; Caro *et al.*, 2016). Parents could determine condition either by directly assessing body size or by relying on a low cost signal that transmits the same information as body size, such as mouth gape area or begging call volume. For example, assume that parents could realize an efficiency benefit of 5 s per caterpillar by using the signal. In this scenario, parents relying on the signal would be able to bring back an additional 218 caterpillars over the 15-day nestling period. Even if producing the signal costs as much as one caterpillar per day per offspring, parents with a brood of seven offspring would experience a net increase of 113 caterpillars per brood. Those 113 extra caterpillars could be enough to tip the scales between the smallest nestling starving or surviving.

Ultimately, the plausibility of our hypothesis can only be determined with empirical work that explicitly measures the kinds of parameters used in our model. This would require measuring the efficiency of different parental allocation strategies, which could be done experimentally by varying the information available to parents and comparing the amount of time it takes a parent to feed its offspring. For instance, previous researchers have removed parents' ability to distribute food based on begging vocalizations by muting individual nestlings (Glassey & Forbes, 2002). Empirical work must also exclude the possibility that the biologically relevant aspect of condition being signalled is public and not cryptic, which would require measuring the association between signal intensity and various aspects of condition which are more or less public, such as plasma glucose levels as opposed to body mass (e.g. Quillfeldt *et al.*, 2009). Empirical confirmation of our hypothesis would also need to show that parents actively choose which offspring to feed rather than passively allocate food to the most conspicuous signaller (e.g. Heeb *et al.*, 2003; Dugas & Rosenthal, 2009; Wiebe & Slagsvold, 2012). Comparative studies could test whether signals of public information with efficiency benefits are more likely to

evolve when parents would have more difficulty utilizing cues of condition, such as in species that nest in dark cavities or have more synchronous hatching, or when the period of parental care is shorter. Finally, our model predicts that relatedness plays a key role in the establishment of meaningful signals at equilibrium only when efficiency benefits are large; empirical work could also attempt to verify this prediction.

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