



## Cheap talk when interests conflict

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Most evolutionary analyses of animal communication suggest that low-cost signals can evolve only when both the signaller and the recipient rank outcomes in the same order. When there is a conflict of interest between sender and receiver, honest signals must be costly. However, recent work suggests that low-cost signals can be evolutionarily stable, even when the sender and the receiver rank outcomes in different orders, as long as the interest in achieving coordination is sufficiently great. In this paper, we extend this body of work by analysing a game theory model that shows that low-cost signals can evolve when there are conflicts of interest and no interest in coordination, as long as individuals interact repeatedly. We also present an empirical example indicating that female rhesus macaques, *Macaca mulatta*, use honest, low-cost, vocal signals to facilitate interactions when conflicts of interest exist.

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The dynamics of signalling in contests has received considerable attention in the last two decades. In contests, communication is complicated by the fact that animals may often benefit from deceiving their opponents about their fighting ability or motivation to escalate. If deception is beneficial, then signallers will often lie. If signallers frequently convey unreliable information, then recipients will stop attending to their signals, and communication will become meaningless (Dawkins & Krebs 1978; Maynard Smith 1982). Zahavi (1975) was the first to resolve this paradox by suggesting that the reliability of signals will be maintained by their cost. Signals given during contests will be evolutionarily stable only if the costs or negative consequences associated with lying are greater than the benefits that would be obtained from giving false signals. Signals that are costly to produce or risky to give are incorruptible because it would not be possible or profitable for low-quality or poorly motivated individuals to produce them (Zahavi 1977, 1993; Enquist 1985; Grafen 1990; Adams & Mesterton-Gibbons 1995). The roars of red deer, *Cervus elaphus* (Clutton-Brock & Albon 1979), stotting by Thompson's gazelles, *Gazella thomsonii* (Fitzgibbon & Fanshawe 1988), and musth in male African elephants, *Loxodonta africana* (Poole 1987, 1989), provide examples of costly signals. A similar logic applies to communication in some other situations such as courtship and resource transfers between parents and offspring.

However, not all honest signals need be costly (Krebs & Dawkins 1984; Maynard Smith 1991, 1994). When

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signallers gain nothing by deceiving their partners, low-cost signals ('cheap talk') can evolve. Maynard Smith (1991, 1994) explored the dynamics of low-cost signalling when there is no conflict of interest between participants. He devised the Philip Sidney game, in which a potential donor (Sir Philip Sydney) is paired with a potential beneficiary (a soldier) on a battlefield. The donor has a resource (water bottle) which can be given to the beneficiary. The donor suffers some decrement to his own fitness if he gives up the water bottle, and the beneficiary benefits from receiving the water bottle, particularly if he is thirsty. Maynard Smith demonstrated that if the donor and beneficiary have some stake in each other's survival, because they are kin or share a common interest in the outcome of the battle, then cost-free signals of the beneficiary's need for the resource can evolve (Maynard Smith 1991). Moreover, evolution may also favour the evolution of cost-free signals of the donor's willingness to give the resource under certain conditions (Maynard Smith 1994).

Although Maynard Smith's results demonstrated that low-cost signals can evolve if there is no conflict of interest between participants, Zahavi (1993) has argued that 'It is difficult to imagine any social interaction in which there is no potential for conflict at some time or another'. If Zahavi's intuition is correct, then Maynard Smith's results are largely irrelevant to the evolution of animal signals. However, in Maynard Smith's model, low-cost signals can evolve when both players rank outcomes in the same order, even though they may differ in the extent to which they value these outcomes.

The circling displays of male blue-headed wrasses, *Thalassoma bifasciatum*, seem to fit the parameters of

**Table 1.** The structure of payoffs obtained by each player in the Battle of the Sexes game

		Chris	
		Zoo	Rock Gym
Pat	Zoo	1,2	0,0
	Rock Gym	0,0	2,1

Each player's preferred destination is indicated with bold type. Both players obtain higher payoffs when they are together than when they are alone, but they do not benefit to the same extent because their preferred destinations differ.

Maynard Smith's models. Some males in this species defend individual territories and spawn singly with females that choose males on the basis of the qualities of their territories (Dawkins & Guilford 1994). Males spend a considerable amount of time defending their territories against intruders, and during these periods they are not available to mate with females. To indicate their readiness to spawn, males perform a stereotyped display. The male's body colour changes from green during aggressive chases to opalescent grey during courtship. Dark spots appear on the end of the pectoral fins. The male swims in tight circles around and above the female moving his spotted pectoral fins rapidly back and forth. The female responds by swimming upward with her head up. This behaviour initiates the spawning dash to the surface. Because the male and the female benefit from the simultaneous release of gametes, there is no conflict of interest between them. As Dawkins & Guilford (1984) point out, 'neither sex gains from deceiving the other about when they are ready to mate', so these signals need not be costly.

In the Philip Sidney game, both participants rank outcomes in the same order. This is not, however, a necessary condition for the evolution of low-cost signals. Farrell & Rabin (1996) have shown that low-cost signals can evolve when preferences are not ranked in the same order, as long as both parties benefit sufficiently from coordinating their interactions. This conclusion emerges from analysis of signalling in the Battle of the Sexes game. Imagine a situation in which two people are trying to arrange an outing: Pat wants to go rock climbing, but Chris wants to go to the zoo. Both would rather spend the day together than apart, but Pat would rather be together at the rock gym and Chris would rather be together at the zoo. The payoff structure for this game is shown in Table 1.

In the traditional version of the Battle of the Sexes game, both parties must choose their destination at the same time without communication. In this situation, the only evolutionarily stable strategy (ESS) is a mixed strategy in which each player chooses their own preferred destination with the same probability. At this ESS, Pat and Chris will often end up at different places, an outcome that neither party prefers. For example, Pat could end up alone at the zoo and Chris could end up alone at the rock gym. But as Farrell & Rabin note, this is not the

way that most people actually solve these kinds of problems. They discuss their preferences and reach a decision about where to go. Because neither party benefits from deceiving the other about their intentions, nothing is gained by lying and there is therefore no need for signals to be costly. Cheap talk is favoured in this situation even though individual preferences are not ranked in the same order because both parties would rather avoid a coordination failure than achieve their own most-preferred option. Cheap talk may help individuals to avoid coordination failures, but it does not necessarily ensure that they will obtain their most-preferred outcome. When preferred outcomes differ, the parties may have to negotiate, sometimes at length, or rely on a conventional asymmetry (e.g. take turns, flip a coin) to resolve the impasse.

Although this result is well known within economics, it is not widely recognized in the biological signalling literature. However, we believe that Farrell & Rabin's results are relevant to understanding some kinds of signals in animal groups. Ethological analyses of communication emphasize the importance of signals in coordinating activity in social groups (e.g. Markl 1985), and many of the signals used in these contexts are not costly. For example, wild dogs, *Lycaon pictus*, which hunt cooperatively, perform an intense series of greetings when they are ready to begin hunting (Creel & Creel 1995). Elephants give soft rumbles (Poole et al. 1988) and mountain gorillas, *Gorilla gorilla gorilla*, and savanna baboons, *Papio cynocephalus*, give soft grunts (Stewart & Harcourt 1994; Rendall et al. 1999) when they are ready to move from one place to another. Stewart & Harcourt (1994) suggest that 'gorillas use these signals to indicate their readiness to depart and to assess that readiness in others'. Hamadryas baboons, *Papio cynocephalus hamadryas*, use an elaborate series of signals to coordinate group movement and reunions (Sigg & Stolba 1981; Kummer 1995).

In the Battle of the Sexes game there is a conflict of interest, but also a strong interest in coordination. Here we explore the possibility that low-cost signals can evolve even when there is a genuine conflict of interest between signallers and recipients and no interest in coordination. Although Maynard Smith (1994) concluded that low-cost signals cannot evolve when there is a conflict of interest, his conclusion is derived from models in which individuals meet only once. If individuals meet repeatedly and use past experiences to evaluate the reliability of signals, then reputation may become an important factor in the assessment of signals (van Rhijn 1980; van Rhijn & Vodegel 1980; Maynard Smith 1982). We present a model that shows that cheap signals can evolve even when there is a conflict of interest, as long as individuals meet repeatedly, remember their interactions and modify their responses on the basis of past experience.

We also provide evidence that female rhesus macaques, *Macaca mulatta*, use quiet calls to signal their benign disposition to other females and these calls are effective in situations in which there is a conflict of interest between signallers and recipients. This analysis builds on previous work on savanna baboons which suggests that

monkeys may use quiet vocalizations to provide information about their disposition and motivation to behave affiliatively (Cheney et al. 1995; Silk et al. 1996; Cheney & Seyfarth 1997). Females often grunt as they approach other females (Cheney et al. 1995; Silk et al., in press). These grunts carry acoustic information about individual identity (Owren et al. 1997) and rudimentary referential information (Rendall et al. 1999). Grunts directed to lower-ranking females are effective in facilitating subsequent affiliation and inhibiting supplants (Cheney et al. 1995). Female baboons also grunt to former opponents in the minutes after conflicts have ended. Postconflict grunts are associated with a reduced likelihood that conflicts will be resumed and an increased likelihood that former opponents will interact peacefully (Silk et al. 1996). Playback experiments demonstrate that the grunts of former aggressors reduce the former victim's concern about becoming the target of redirected aggression by the aggressor (Cheney et al. 1995) and encourage former females to approach their former aggressors after conflicts have ended (Cheney & Seyfarth 1997). These results suggest that grunts are signals of the sender's benign disposition and provide reliable predictive information about their subsequent behaviour.

It is not clear whether there is any conflict of interest between females in the situations described above, but similar signals are used in situations where conflicts of interest between signallers and recipients do exist. Female monkeys are strongly attracted to other females' infants and often attempt to handle them (reviewed by Maestriperieri 1994). Although infant handling is tolerated and even encouraged by mothers in some primate species, macaque and baboon mothers never initiate infant handling interactions (Maestriperieri 1994). Among macaques and baboons, maternal responses to infant handling range from passive to hostile (e.g. Altmann 1980; Bauers 1993; Paul & Kuester 1998; Silk 1999). It is not entirely clear why primate females are so strongly attracted to infants or why macaque and baboon mothers are so reluctant to accommodate other females' interest in their infants. None the less, infant handling interactions involve an apparent conflict of interest between mothers and prospective handlers.

There is some evidence that monkeys use quiet calls to facilitate infant handling interactions. Female baboons that grunt to former opponents after conflicts have ended are more likely to handle their former opponents' infants than females that remain silent after conflicts (Silk et al. 1996). Vocalizations also play an important role in infant handling interactions in stump-tailed macaques, *Macaca artoidea*. Mothers are less likely to respond aggressively to females that give quiet staccato grunts before they attempt to handle their infants than to females that remain silent (Bauers 1993).

Here we show that female rhesus macaques use two types of quiet calls (grunts and girneys) to signal their benign disposition to other females. Like the grunts of female baboons, these calls appear to be honest predictive signals that convey information about the signaller's disposition, and they are effective in facilitating grooming and in reducing aggression. These signals also play an

important role in infant handling interactions. Rhesus females typically call before attempting to handle other females' infants, and these calls provide reliable predictive information about the nature of the females' subsequent behaviour towards infants.

## MODEL OF THE EVOLUTION OF LOW-COST SIGNALS

### When Individuals Interact Only Once

We begin by considering the dynamics of honest, low-cost, predictive signals among pairs of individuals that interact only once. One individual, the actor, approaches a second individual, the recipient. For a fraction of the time ( $p$ ), the actor's disposition is peaceful, while for a fraction of the time ( $1 - p$ ), the actor's disposition is hostile. The actor's disposition is not known to the recipient initially. When the actor approaches the recipient, the actor can produce a signal that conveys information about its disposition. If the individual has a peaceful disposition, the cost of the signal is  $t$ ; if the individual is hostile, the cost is  $k$ . Thus,  $t$  is the cost of an honest signal and  $k$  is the cost of a dishonest one. After the actor approaches the recipient and has an opportunity to signal, the recipient may decide to stay and interact, or flee. If the actor's intentions are benign, the two interact affiliatively, and the actor receives a payoff,  $I$ , and the recipient gets  $i$ . If the actor is hostile, players interact aggressively and the actor receives  $E$  and the recipient receives  $-e$ . Finally, if the recipient chooses to flee, the actor and recipient receive  $D$  and  $-d$ , respectively. The sequence of behaviours and their payoffs are summarized in the form of the game tree shown in Fig. 1.

Actors can follow three different strategies: truthful (TF), always signal (AS), or never signal (NS). TF individuals signal when they intend to behave peacefully, and do not signal when they intend to behave aggressively.

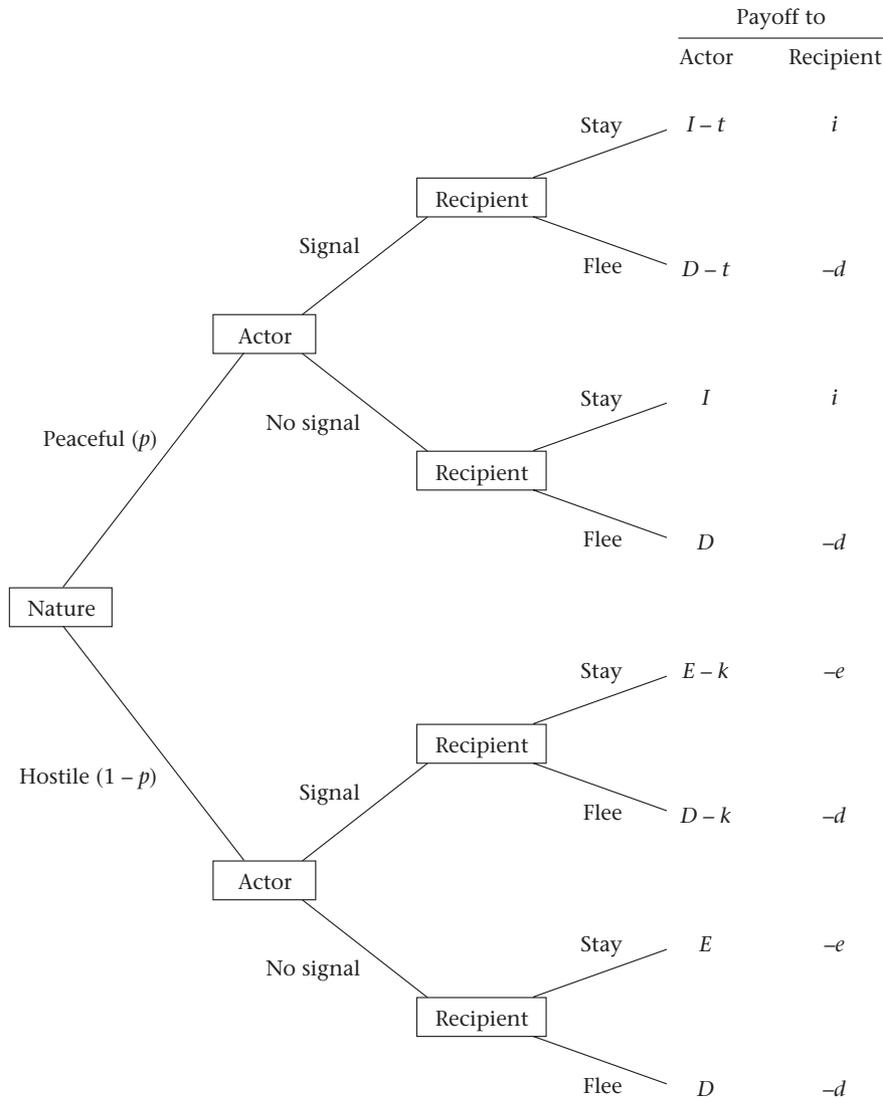
AS individuals always signal, regardless of their internal state, and NS individuals never signal. Recipients have three strategies as well: they may always interact (AI), always flee (AF), or adopt a third strategy, which we label 'Believers' (BV). Believers expect signallers to behave peacefully and those that do not signal to behave aggressively. Therefore, Believers stay and interact when they receive signals, but flee when they do not receive signals.

Honest signalling is an ESS if TF can resist invasion by other actor strategies when BV is common, and BV can resist invasion by other recipient strategies when TF is common. First, we determine whether actors should adopt the truthful strategy when they interact with believers, by comparing the relative fitnesses of each actor strategy (TF, AS and NS) when BV is common. The expected fitnesses of the three strategies are:

$$V(\text{TF}|\text{BV}) = p(I - t) + (1 - p)D$$

$$V(\text{AS}|\text{BV}) = p(I - t) + (1 - p)(E - k) \quad (1)$$

$$V(\text{NS}|\text{BV}) = pD + (1 - p)D$$



**Figure 1.** This decision tree summarizes the sequence of possible moves and associated payoffs for each player. Initially, the actor's disposition is either benign or hostile, and this internal state is known only to the actor. The actor may signal at some cost  $t$ , or not signal. The recipient may interact, or flee. The payoffs reflect the actor's internal disposition and the recipient's response.

Thus, TF can resist invasion by individuals that always signal (AS) when  $V(TF|BV) > V(AS|BV)$ , which requires that  $D > E - k$ . TF can also resist invasion by individuals that never signal (NS) when  $V(TF|BV) > V(NS|BV)$ , which requires that  $I - t > D$ . Thus, the strategy pair (TF, BV) is an ESS whenever

$$I - t > D > E - k \tag{2}$$

Truthful signalling is evolutionarily stable in a one-shot game only if the net benefit to a peaceful actor of interacting is greater than that of displacing the recipient, which in turn must be greater than that of engaging in an escalated contest when the actor is hostile. Put another way, if a hostile actor would rather fight the recipient than displace her ( $E > D$ ), and the benefits of the fight are greater than the cost of lying ( $E - D > k$ ), lying pays and therefore signalling is not evolutionarily stable.

We use the same logic to determine whether BV can resist invasion by the other strategies available to recipients (AF and AI), when TF is common. We compute the fitness of each strategy when TF is common.

$$\begin{aligned} V(BV|TF) &= pi - (1 - p)d \\ V(AF|TF) &= -d \\ V(AI|TF) &= -e \end{aligned} \tag{3}$$

Then, we compare the fitnesses of the two pairs of strategies,  $V(BV|TF)$  versus  $V(AF|TF)$  and  $V(BV|TF)$  versus  $V(AI|TF)$ . We find that when TF is common, BV can resist invasion by AI individuals if  $i + d > 0$ , which means that recipients would rather interact than be displaced; and by AF individuals if  $-d > -e$ , which means that recipients would rather be displaced than attacked. We will assume from now on that both of these inequalities are true. BV can resist invasion from AI and AF when TF is common.

Now, assume that these signals are cheap, so that  $t \approx k = 0$ . From equation (3) we know that signalling is an ESS only if  $I > D > E$  which means that actors and recipients rank outcomes in the same order. Thus, in this one-shot game, low-cost signals of intent are evolutionarily stable when there is no conflict of interest between the actor and the recipient. This replicates the result obtained in the Phillip Sydney game by Maynard Smith (1991, 1994).

### When Interactions are Repeated

One-shot games ignore an important feature of social life: pairs of individuals meet and interact repeatedly. Repeat interactions may alter the effectiveness of bluffing if individuals can recognize their partners and remember past interactions (van Rhijn 1980; van Rhijn & Vodegel 1980). Intuition suggests that actors that give false signals may benefit initially from deceiving their partners, but the benefits of deception will not be sustained over time if recipients cease to believe actors that have previously deceived them.

To test this intuition, we constructed a model in which individuals meet and interact repeatedly. We assume that the cost of signalling is negligible,  $t \approx k = 0$ . As before, actors may adopt one of three strategies: truthful (TF), always signal (AS), or never signal (NS). Recipients also have three possible strategies: they may always interact (AI), always flee (AF), or they may condition their responses on the actor's previous behaviour, as 'conditional believers' (CB), which believe the actor until they are deceived, and thereafter always flee.

The conditional believer strategy is one simple way to capture the idea that recipient behaviour is contingent on the previous behaviour of the actor; recipients believe actors that have been truthful in the past and do not believe actors that have been deceitful. A wide variety of such contingent strategies is possible, and experience in modelling the structurally similar repeated Prisoner's Dilemma indicates that the exact nature of the strategy favoured by selection depends on the details of the situation. The conditional believer strategy is a strategy that is provoked by a single lie. Analysis of the repeated Prisoner's Dilemma suggests that such highly provokable strategies do well in noise-free environments like the one that we assume here. If there are errors or misperceptions, less provokable strategies tend to do better (Boerlijst et al. 1997).

We first consider the conditions in which CB can resist invasion by other recipient strategies (AI, AF) when TF is common. Because pairs meet repeatedly, the fitness of each of the three strategies reflects the payoff associated with the present interaction plus the payoffs derived from future interactions. Future payoffs are equal to the product of the probability that interactions will continue,  $w$ , and the expected payoff of subsequent interactions. The fitness of each strategy when TF is common can be expressed as:

$$\begin{aligned} V(\text{CB}|\text{TF}) &= pi - (1 - p)d + w V(\text{CB}|\text{TF}) \\ V(\text{AI}|\text{TF}) &= pi - (1 - p)e + w V(\text{AI}|\text{TF}) \\ V(\text{AF}|\text{TF}) &= -d + w V(\text{AF}|\text{TF}) \end{aligned} \quad (4)$$

When TF is common, CB can resist invasion whenever  $i + d > 0$  and  $-d > -e$ . These are the same conditions that govern the stability of CB in the one-shot game. This makes sense because in a world where TF is common CB individuals experience deception only when interacting with rare mutant AS individuals.

To determine whether TF can resist invasion by AS and NS when CB is common, we compare the payoffs associated with three actor strategies. Again, the fitnesses of each of the three strategies reflect the payoffs associated with the present interaction plus the payoffs derived from future interactions. The payoffs can be expressed as:

$$\begin{aligned} V(\text{TF}|\text{CB}) &= pI + (1 - p)D + w V(\text{TF}|\text{CB}) \\ V(\text{AS}|\text{CB}) &= pI + (1 - p)E + w\{p V(\text{AS}|\text{CB}) + (1 - p)V(\text{AS}|\text{AF})\} \\ V(\text{NS}|\text{CB}) &= D + w V(\text{NS}|\text{CB}) \end{aligned} \quad (5)$$

Note that when AS is paired with CB, AS behaves deceptively with probability  $1 - p$ . However, individuals with AS that behave aggressively will only benefit from deceiving CB once because CB individuals always flee after they have been deceived.

When CB is common, TF can resist rare NS whenever  $V(\text{TF}|\text{CB}) > V(\text{NS}|\text{CB})$ . Using the expressions in equation (5), it can be shown that this outcome occurs whenever there is some positive probability that the actor has peaceful intentions. TF can resist invasion by the deceitful strategy, AS, if  $V(\text{TF}|\text{CB}) > V(\text{AS}|\text{CB})$ , which is equivalent to:

$$\frac{w}{1 - w} p(I - D) > (E - D) \quad (6)$$

This inequality says that TF is an ESS if the future benefit to the actor of being believed exceeds the short-term benefit the actor can achieve by lying. The expression  $w/(1 - w)$  is the number of future interactions,  $p$  is the probability of having peaceful intentions, and  $I - D$  is the incremental benefit to the actor of being believed when the actor's intentions are peaceful. Thus, the left side of equation (6) gives the future benefit to the actor of telling the truth. The right side gives the benefit to the actor of lying when the actor's intentions are hostile.

For animals that live in social groups, equation (6) indicates that quiet, honest signals will be favoured under very plausible conditions. To see why, it is useful to rewrite equation (6) as follows:

$$\frac{w}{1 - w} p > \frac{(E - D)}{(I - D)} \quad (7)$$

The left side of equation (7) is the average number of future interactions in which the actor will have benign intentions, and  $I - D$  is the benefit to the actor of being able to interact with the recipient in such situations.  $E - D$  is the benefit to the actor of being able to attack the recipient when she is hostile. Long-lived members of group-living species may interact many times. If a pair of individuals interacts 100 times, then equation (7) says

that quiet, truthful signalling will be evolutionarily stable as long as the benefit of each lie is less than 100 times the benefit of being believed when the actor wants to interact peacefully.

The ESS in the repeat game differs from the ESS in the one-shot game in an important way. When individuals interact repeatedly, truthful low-cost signals can evolve even if actors and recipients do not rank outcomes in the same order. Thus, if there are repeated interactions, low-cost, honest signals of intent can evolve, even if there is a conflict of interest between actors and recipients.

Below, we present an empirical example of low-cost, truthful signals among rhesus macaques. We show that quiet vocalizations provide reliable predictive information about the actor's subsequent behaviour and facilitate peaceful interactions among adult females. These vocal signals are effective even when there is a conflict of interest between actors and recipients.

## EMPIRICAL METHODS

### Study Site and Research Subjects

This study was conducted on Cayo Santiago, part of the Caribbean Primate Research Center. Cayo Santiago is a 15.2-ha island situated approximately 1 km off the south-eastern coast of Puerto Rico. Rhesus macaques range freely on the island and live in naturally formed social groups, but they are provisioned with food and water. During the study period, there were seven groups on the island, ranging in size from 50 to nearly 400 individuals. These groups are composed of matrilineal kin and unrelated males. Males transfer from their natal groups at approximately 4–5 years of age, while females are philopatric. Research was conducted on group F, which was composed of 364 individuals when the study began. Life history archives provide information about age and maternal kin for all individuals.

### Data Collection

Twenty-one of the 104 adult females (>5 years old) from group F were selected as subjects for focal sampling (Altmann 1974). All behavioural observations were conducted by E.K. To obtain a representative sample of females of different dominance ranks and lineage membership, subjects were drawn at random from each of the four matrilineal groups in the group. The number of subjects from each matriline was proportional to the size of the matriline. Thus, eight focal females were randomly chosen from the largest matriline, which contained 40 adult females, six from the second-largest matriline ( $N=30$ ), five from the third-largest matriline ( $N=20$ ), and two from the smallest matriline ( $N=11$ ).

Each focal female was the subject of one 60-min sample per week over a period of 10 weeks. All vocalizations, approaches to within arm's reach, and social interactions between the focal animal and adult females were recorded. Additionally, all behavioural interactions and vocalizations between the focal female and all infants,

excluding her own, were recorded. For the purposes of this analysis, affiliative interactions included grooming and 'sitting in contact'. Aggressive interactions included bite, chase, fight, lunge, grab, hit, threaten and supplant. Submissive gestures included cower, flee, grimace and scream. Infant handling was recorded when one female touched, sniffed, inspected or held another female's infant. Rough infant handling was scored if the handler bit, grabbed or hit the infant, or if the infant screamed while in contact with the handler.

Rhesus macaques produce three types of vocalizations in friendly contexts: grunts, girneys and coos (Rowell & Hinde 1962; Erwin 1975; Hauser et al. 1993). Each of these calls is distinct and recognizable to the human ear. Although all grunts, girneys and coos were scored during data collection, analysis focused on grunts and girneys because adult females produced these calls most frequently in social contexts. Grunts are short, harsh sounds produced through open lips with a slightly dropped jaw (Hauser et al. 1993). Girneys are soft, low-frequency, chewing noises accompanied by rapid lip movement (Green 1975). For further acoustic treatment of these calls see Hauser et al. (1993).

Outcomes of all aggressive/submissive interactions between group members were recorded ad libitum. All females could be ranked in a linear dominance hierarchy.

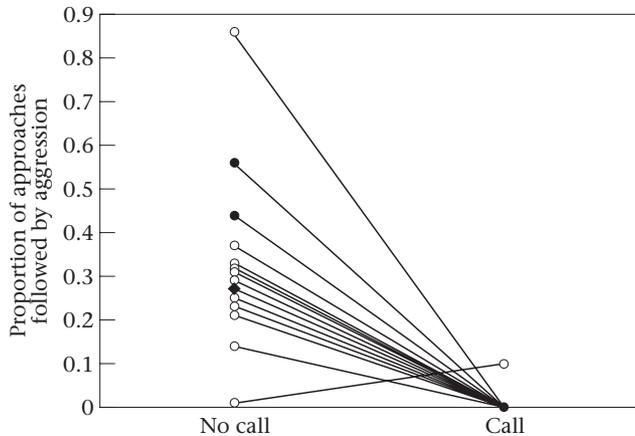
### Analysis

The analysis is based on the sequence of events that followed 'approaches'. In some cases the approach was accompanied by a grunt or girney. We tabulated and compared the proportion of approaches with and without calls that were followed by specific types of behaviour. Initially, we analysed approaches to higher- and lower-ranking females separately. In many cases the relative ranks of the actor and recipient did not influence the subsequent sequence of events. In these cases, we combined the data and present them jointly below.

Both grunts and girneys often preceded interactions between females and interactions between females and infants. Preliminary analyses revealed no significant differences in the usage of grunts and girneys or in the behavioural outcomes associated with these calls. Females were as likely to grunt as they were to girney when they approached females with infants (Wilcoxon signed-ranks test:  $Z = -0.98$ ,  $N=18$ ,  $P=0.33$ ) and grunts and girneys were equally likely to lead to affiliation ( $Z = -0.88$ ,  $N=16$ ,  $P=0.38$ ). Thus, grunts and girneys were combined in our analyses.

For each female, we compared the sequence of behavioural events following approaches with and without calls, that is, each female served as her own control. We used Wilcoxon signed-ranks tests to evaluate the effects of calls on subsequent events. All statistical tests were two tailed.

In baboons, behavioural evidence and playback experiments both indicate that grunts serve reconciliatory functions and convey information about the behavioural context (Cheney et al. 1995; Silk et al. 1996; Cheney & Seyfarth 1997; Rendall et al. 1999). Here we rely upon



**Figure 2.** The proportion of approaches with and without calls that were followed by aggression is compared here for each focal female. ○: Single female; ●: pairs of females that had identical values; ◆: three females that had identical values. Three females that never behaved aggressively after approaching other females are not plotted.

behavioural analyses alone, leaving open the possibility that other behaviours may contribute to the regulation of behavioural interactions following approaches among rhesus macaques.

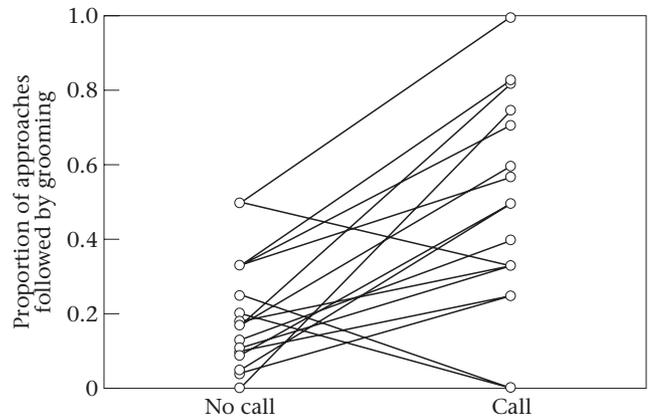
## EMPIRICAL RESULTS

### Grunts and Girneys of Female Rhesus Macaques are Honest Signals of Benign Intent

If grunts and girneys are reliable signals of a female rhesus macaque's benign disposition and if they predict that her subsequent behaviour will be peaceful, then she should not behave aggressively after she gives these calls. Moreover, grunts and girneys should allay anxieties of lower-ranking call recipients. Finally, these calls should increase the probability that callers will behave affiliatively towards recipients. The data support all three of these predictions.

Females were much less likely to initiate aggression if they called as they approached than if they remained silent ( $Z = -3.68$ ,  $N=21$ ,  $P < 0.001$ ; Fig. 2). The magnitude of this effect was substantial. On average,  $29 \pm 0.05\%$  ( $\bar{X} \pm SE$ ) of all approaches that were not accompanied by calls were followed by aggression. In contrast, less than  $1 \pm 0.01\%$  of all approaches that were accompanied by calls were followed by aggression.

Females that called as they approached other females were also less likely to elicit spontaneous submissive gestures or supplants than females that remained silent while approaching other females ( $Z = -2.71$ ,  $N=21$ ,  $P = 0.007$ ). When females approached and remained silent, their partners behaved submissively  $4 \pm 0.01\%$  of the time, and when females approached and called, their partners reacted submissively less than  $1 \pm 0.001\%$  of the time. Although the absolute difference in rates of submission was small, females were four times more likely to behave submissively if they were approached by a female



**Figure 3.** The proportion of approaches with and without calls that were followed by grooming is compared here for each focal female. ○: Individual females. Four females that never groomed after approaching other females are not plotted.

that remained silent than if they were approached by a female that grunted or girneyed.

Females that called were also more likely to groom their partners than females that remained silent when they approached ( $Z = -2.91$ ,  $N=21$ ,  $P = 0.004$ ; Fig. 3). Calling doubled the likelihood of grooming on average (approach, no call:  $0.17 \pm 0.03$ ; approach, call:  $0.39 \pm 0.07$ ).

### Grunts and Girneys Signal the Female's Benign Disposition towards Infants

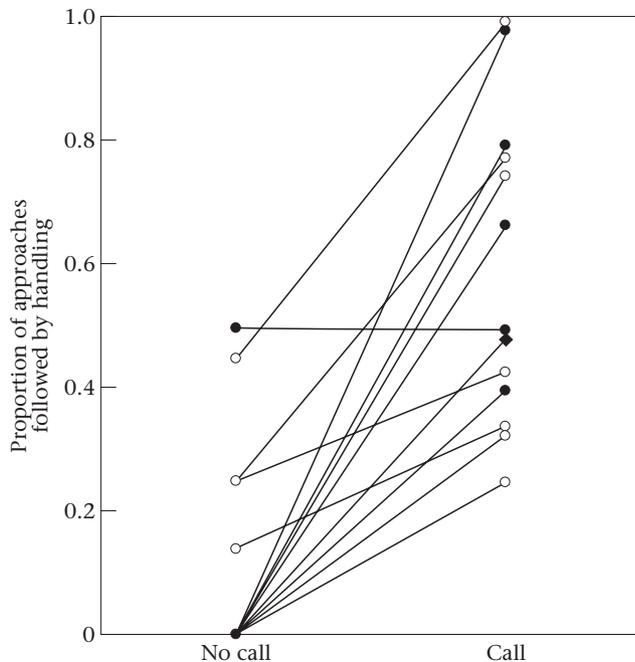
If grunts and girneys signal a female's benign disposition, then females that call as they approach the mother of a newborn should behave nonaggressively towards that mother's infant, calling should facilitate infant handling interactions, and females that call should be more likely to handle infants than females that remain silent. These predictions are also supported by the data.

Handlers were usually unaggressive to infants, but these interactions sometimes caused infant distress. Females that grunted or girneyed as they approached infants were less likely to handle them roughly than females that did not call as they approached ( $Z = -2.71$ ,  $N=21$ ,  $P = 0.007$ ). There were only 10 cases in which females handled infants roughly, but in nine of these cases the handler did not call before initiating contact with the infant.

Females were more likely to handle infants nonaggressively if they called as they approached mothers and their infants than if they remained silent ( $Z = -3.73$ ,  $N=20$ ,  $P < 0.001$ ; Fig. 4). These data exclude one female that never approached and called to the mother of a young infant. Females that approached and remained silent handled infants  $10 \pm 0.04\%$  of the time, while females that approached and called handled infants  $61 \pm 0.05\%$  of the time.

## DISCUSSION

The game theory model developed in this paper demonstrates that honest, low-cost signals can evolve even when



**Figure 4.** The proportion of approaches with and without calls that were followed by infant handling is compared here for each focal female. When females called as they approached, they were more likely to handle infants. ○: Single female; ●: pairs of females that had identical values; ◆: three females that had identical values. One female that never approached and called to the mother of a young infant is omitted from this graph.

there is a conflict of interest between participants as long as partners interact repeatedly. These theoretical results extend the range of conditions under which honest, low-cost signals can evolve. Thus, honest, low-cost signals can evolve when the actor and recipient rank outcomes in the same order (Maynard Smith 1991, 1994; Johnstone & Grafen 1992), when outcomes are ranked differently but coordination is valued (Farrell & Rabin 1996), or when conflicts of interest exist but individuals interact repeatedly. This simple model is only meant to capture the basic logic of signalling when there are repeated interactions. It has a limited strategy set, and omits many possible complications, most notably errors and uncertainty. Almost 20 years of modelling the repeated Prisoner's Dilemma suggests that the basic qualitative result derived here will survive the addition of more complexity to the model. If interactions persist long enough, contingent strategies that lead to honest signalling will be favoured by selection. However, experience with the repeated Prisoner's Dilemma also suggests that detailed features of the strategy favoured by selection will depend on the details of the strategic setting.

Of course, just because low-cost, predictive signals could be maintained by selection does not mean that these kinds of signals will actually play an important role in nature. The empirical results presented here demonstrate that quiet signals do play an important role in regulating interactions that involve conflicts of interests among female rhesus macaques. Grunts and

girneys enable females to handle other females' infants, interactions which reflect a conflict of interest between prospective handlers and mothers. Grunts and girneys in rhesus macaques function much like grunts among female baboons (Cheney et al. 1995; Rendall et al. 1999).

In baboons and macaques, quiet, low-cost vocalizations provide reliable information about the caller's subsequent behaviour. Thus, these vocalizations are low-cost, 'predictive signals' (Hauser & Nelson 1991) or 'signals of intent', which provide information about the caller's disposition and subsequent behaviour. In the animal signalling literature, there is some disagreement about whether predictive signals can be maintained by selection (Hauser & Nelson 1991). Harper (1991, page 382) argued that 'Both games theory and gene selection approaches suggest that signals will rarely provide information about intentions' because signallers can lie and do not often benefit from revealing their subsequent actions. Harper's reasoning applies mainly to signals given in the context of conflict, and does not necessarily apply to other situations. Results from game theory models suggest that predictive signals can be evolutionarily stable under a fairly broad range of conditions. Low-cost, predictive signals may occur when signallers and recipients share a common objective and no advantage is gained through deception. Low-cost, predictive signals can also be evolutionarily stable when deception would be advantageous in the short run, but costly in the long run for individuals that interact repeatedly, remember their interactions, and modify their responses on the basis of previous experience.

The use of grunts and girneys to facilitate infant handling provides some insight about the function of infant handling in macaques and baboons. Female macaques and baboons are intensely interested in other females' infants, but the adaptive basis for females' attraction to infants is not well understood. Some researchers have interpreted females' persistent efforts to handle other females' infants as a form of reproductive competition (Silk 1980; Maestripiere 1994). It has been argued that females' interest in other females' infants may simply be a by-product of natural selection because females that are strongly motivated to interact with infants make good mothers (Paul & Kuester 1996; Silk 1999). The fact that female rhesus macaques invariably vocalize before they handle infants gently and do not vocalize on the rare occasions when they handle infants roughly, suggests that handlers' dispositions are typically benign and supports the by-product hypothesis.

Animals may use low-cost, honest signals to facilitate cooperation, enhance coordination and mediate interactions when there are conflicts of interest among individuals that interact repeatedly. While conflict generates conspicuous and costly signals that are designed to attract attention and command respect, communication in other contexts may be more like 'conspiratorial whispers' (Krebs & Dawkins 1984, page 391). Although these signals may be designed to be inconspicuous and private (Markl 1985, page 163), they may play an important role in the everyday lives of animals that live in social groups. Cheap talk may convey valuable messages.

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