Anim. Behav., 1991, **42**, 1034–1035

Honest signalling: the Philip Sidney game

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(Received 4 April 1991; initial acceptance 10 May 1991; final acceptance 20 May 1991; MS. number: sc-649)

Zahavi (1977, 1981) has argued that if a signal is to be 'honest', in the sense that it represents accurately the state of the sender, it must be costly. More recently, Enquist (1985) showed that a signal made in the course of a fight between two animals can accurately represent the state of the signaller, but only if it is risky to make. Grafen (1990) has given a more general proof of Zahavi's argument, in the context of sexual selection. His paper is important because of its generality, but the mathematics will not be easily followed by many biologists. The present note presents a very simple model that illustrates the argument: its aim is simplicity, not generality or realism.

It is reported that Sir Philip Sidney, lying wounded on the battlefield at Zutphen, handed his water bottle to a dying soldier with the words 'Thy necessity is yet greater than mine'. This unusual example of altruism by a member of the English upper classes was the inspiration for the following game.

The two players are a potential donor, D, and a beneficiary, B. The donor has an indivisible resource, the water bottle, that he can give to the beneficiary. If he keeps the water he is certain to survive, but if he donates it his chance of survival, S, is less than 1. The beneficiary may be in one of two states, thirsty or not thirsty: his state cannot be directly perceived by the donor. The beneficiary's chance of survival depends both on his state, and on whether he receives the water, as follows: thirsty/gets water, 1; thirsty/does not get water, 0; not thirsty/gets water, 1; not thirsty/does not get water, V, where $0 < V < 1$. Thus it pays the beneficiary to get the water, and the gain is greater if he is thirsty.

Suppose that the behaviour of donor and beneficiary is determined by natural selection maximizing their chances of survival. Clearly, the donor will not hand over the water. But suppose that they are related, with a coefficient of relatedness r. Then selection will maximize inclusive fitness, and it may pay the donor to give the water. In particular, it might pay him to do so if the beneficiary is thirsty, but not otherwise. Therefore, it might pay the beneficiary to send a signal if he is thirsty. But can it be evolutionarily stable for the beneficiary to signal only if he is thirsty? That is, can the following pair of strategies be stable.

Beneficiary signals only if thirsty.

Donor hands over resource only if beneficiary signals?

To investigate Zahavi's argument, we must allow for the possibility that signalling is costly. Therefore, the survival probability of a beneficiary who signals is reduced by a factor $(1-t)$, where t is the cost of the signal.

It is convenient to assume that the probability that a beneficiary is thirsty is p, although the value of p does not affect the outcome. Consider first the stability of the donor strategy, D0 (give only if beneficiary signals), against invasion by the two possible mutants, Dm1 (always give) and Dm2 (never give). If beneficiaries signal only when thirsty, the inclusive fitnesses are

$$W(\mathrm{D0}) = (1-p)(1+rV) + p[S + r(1-t)]$$
$$W(\mathrm{Dm1}) = (1-p)(S+r) + p[S + r(1-t)]$$
$$W(\mathrm{Dm2}) = (1-p)(1+rV) + p$$

and hence the strategy D0 is stable if

$$1 + rV > S + r \qquad (1a)$$

and

$$S + r(1-t) > 1 \qquad (1b)$$

If (1a) does not hold, a donor mutant that always gives can invade, and if (1b) does not hold, a mutant that never gives can invade.

Now consider the stability of the beneficiary strategy B0 (signal only if thirsty), against the possible mutants Bm1 (always signal) and Bm2 (never signal). Given that donors give only if the beneficiary signals, the inclusive fitnesses W, of these strategies are

$$W(\mathrm{B0}) = (1-p)(V+r) + p(1-t+rS)$$
$$W(\mathrm{Bm1}) = (1-p)(1-t+rS) + p(1-t+rS)$$
$$W(\mathrm{Bm2}) = (1-p)(V+r) + pr$$

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and hence B0 is stable if

$$1 - t + rS > r \tag{2a}$$

and

$$V + r > 1 - t + rS \tag{2b}$$

If (2a) does not hold, a mutant that never signals can invade, and if (2b) does not hold a mutant that always signals can invade.

The next step is to show that, if there is a conflict of interest between donor and beneficiary, condition (2b) can be satisfied only if $t > 0$ (signalling is costly). In an evolutionary context, a 'conflict of interest' can be defined as follows (Trivers 1974; Parker & MacNair 1978). If natural selection would produce a different outcome of the interaction (e.g. giving the water, as opposed to not giving), depending on whether the outcome is determined by genes in the donor or in the beneficiary, then a conflict of interest exists. Suppose that the beneficiary is not thirsty. The beneficiary will favour the giving of the water if the effect is to increase its inclusive fitness: that is, if

$$1 - V > r(1 - S) \tag{3a}$$

and the donor will oppose the transfer if

$$1 - S > r(1 - V) \tag{3b}$$

Note that these conditions connot be simultaneously true if $r = 1$: there can be no conflict of interest between genetically identical individuals. (Formally, there would be a conflict if both inequalities were reversed, but this is impossible unless $r > 1$.) Condition (2b) can be rewritten

$$1 - V - t < r(1 - S)$$

This can be compatible with (3a) only if $t > 0$. In other words, if there is a conflict of interest, honest signalling can be evolutionarily stable only if the signal is costly. If signalling was cost-free, and if there was a conflict of interest, a mutant causing the beneficiary to signal even when not thirsty would invade. Note, however, that conditions (1) and (2) can be satisfied if $t > 0$. For example, if $r = 0{\cdot}5$, the values $S = V = 0{\cdot}8$, $t = 0{\cdot}4$ satisfy the conditions. Costly signals can be honest.

Note also that conditions (1) and (2) can be satisfied when $t = 0$, provided that there is no conflict of interest. Suppose, for example, $r = 0{\cdot}5$, $S = 0{\cdot}8$, $V = 0{\cdot}95$, $t = 0$. Then conditions (1) and (2) are satisfied. There is, however, no conflict of interest: condition (3a) is not satisfied. Hence cost-free signals can be honest if there is no conflict of interest between signaller and receiver.

Thus it has been shown, for a simple model, that honest signals must be costly if there is a conflict of interest between signaller and receiver, but that cost-free signals can be honest if there is no such conflict. The model assumes that the interacting individuals are relatives, but this is not an essential feature. What is essential is that the fitness of each participant is influenced by the survival of the other. A similar model could be constructed assuming, for example, that the participants were members of a mated pair in a species in which both parents care for the young.

The simplicity of the model depends critically on the assumption that both the cost of a signal, and the value of the resource, are constant, and hence that t, S and V are constant. It would be more realistic to assume that t, S and V are variables. Grafen (1990) has analysed such a model. His paper shows that the conclusions reached here for a simple model hold also for a more realistic one.

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