

The Continuous Sir Philip Sidney Game: A Simple Model of Biological Signalling

RUFUS A. JOHNSTONE AND ALAN GRAFEN

Department of Plant Sciences, South Parks Road, Oxford OX1 3RA, U.K.

*(Received on 14 May 1991, Accepted in the revised form on
9 September 1991)*

An analysis of Maynard Smith's two-player, ESS model of biological signalling, the "Sir Philip Sidney game", is presented. The stable strategies of the players in this game are shown to satisfy the conditions of Zahavi's handicap principle. At equilibrium, signals are honest, costly, and costly in a way that is related to the true quality revealed. Further analysis reveals that the level of cost required to maintain stability is inversely related to the degree of relatedness between the players. It therefore seems likely that stable biological signalling systems will feature lower signalling costs when communication occurs between relatives. A three-player, extended version of the model is investigated, in which signals are passed via an intermediate, or "messenger". It is shown that this destabilizes the signalling system, and leads to increased signalling costs. This result suggests that "kin conflict" theories of the evolution of the endosperm in flowering plants require further refinement. The introduction of a novel resource acquisition tissue, which mediates parent-offspring interaction during development, cannot be assumed to limit parent-offspring conflict simply because it carries an extra copy of the maternally inherited genes. The ability to add such complications to the Sir Philip Sidney game and still obtain solutions makes it a very useful modelling tool.

1. Introduction

The evolution of biological signals is a fascinating subject. The optimal "rule" of signalling behaviour for a signaller depends on the receiver's "rule" of interpretation. At the same time, the optimal interpretation rule depends on the signalling rule that is used. Signal and response behaviour therefore co-evolve, and the outcome of this co-evolution is difficult to predict. The confusing nature of signal evolution is illustrated by the long-running debate over deceit and honesty in animal communication—it is not immediately obvious whether or not animal signals should convey honest information, and different authors have held conflicting views on the subject (Zahavi, 1975, 1977, 1987; Dawkins & Krebs, 1978; Krebs & Dawkins, 1984).

Mathematical models provide an excellent tool for resolving conceptual problems of this kind. They are less prone to logical inconsistencies than are verbal arguments, and make their assumptions explicit. Grafen's (1990) "strategic handicap" model demonstrates how useful a rigorous, mathematical approach can be. His formal exposition of Zahavi's "handicap principle" revealed that, under fairly general conditions, stable signals are honest, costly, and costly in a way that depends on the true

quality revealed. However, there have been very few other attempts to model signal evolution (see Enquist, 1985; Godfray, 1991; Maynard Smith, 1991, for exceptions).

We present a two-player ESS model of signal evolution, the "Sir Philip Sidney game". The simple format of this model makes it easy to understand and manipulate, but at the same time it captures enough of the essential features of signal evolution to provide biologically meaningful results. This allows us to demonstrate the validity of the handicap principle in a way that is relatively easy to follow, and also to investigate some new questions relating to the "cost" of signals.

In section 2 we describe the basic model: the strategy sets of both players (i.e. the range of possible signalling and interpretation rules), the "payoff" to both players of the various possible outcomes, and so on. We then derive the evolutionarily stable pair of strategies, and demonstrate that they satisfy the conditions of the handicap principle. Section 3 looks at the effects of relatedness on the cost of the stable signals. Finally, in section 4 we investigate the way in which signal costs change when signals are relayed via an intermediate, or "messenger", rather than passed directly from signaller to receiver. This extension of the basic model sheds some light on "kin conflict" theories of the role of the endosperm in angiosperm seed development.

2. The Basic Model

Sir Philip Sidney, the famous soldier, statesman and poet, was mortally wounded in battle under the walls of the stronghold of Zutphen, in the year 1586. Despite his injury, he managed to escape from the conflict, and reached the English camp, which was a mile or two distant. There, parched for thirst, he called for a drink. A bottle of water was brought, but as Sidney was placing it to his lips, a grievously wounded soldier was borne past him. Rather than taking a drink himself, Sidney at once handed the bottle to the soldier, with the famous words: "Thy necessity is yet greater than mine". This incident inspired Maynard Smith to formulate the "Sir Philip Sidney game", an ESS model of biological communication of need (see Maynard Smith, 1991).

The Sir Philip Sidney game features two players; we will call them X and Y . Both are at risk of dying, their survival chances being x and y respectively ($0 \leq x \leq 1$ and $0 \leq y \leq 1$). X controls some resource, which he may choose to keep for himself or give to Y . If X keeps the resource, he ensures his own survival; if he gives it to Y , then Y 's survival is ensured. The coefficient of relatedness between the two players is r .

Clearly, X 's decision as to whether or not he keeps the resource will depend on how closely related he is to Y , and on their relative risks of dying. However, we assume that each player cannot directly perceive the other's survival chance (as far as X is concerned, y has a uniform probability distribution between 0 and 1, and as far as Y is concerned, x has a similar distribution). Y signals to X with a signal of variable magnitude ("magnitude" is defined in terms of the extent to which the signal reduces Y 's survival chance) and X must decide whether or not to relinquish the resource on the basis of this signal (Maynard Smith, 1991, analyses the situation in which Y 's signal, if given, is of a fixed magnitude).

For those who prefer a more concrete model, X and Y may be thought of as vampire bats in a day-time roost. X managed to obtain a blood meal during the previous night while Y did not. Y must therefore resort to begging for blood, and X must decide whether or not to feed it. Wilkinson's (1984) classic study of food sharing in wild vampire bats is often cited in discussions of behavioural reciprocity. However, the study showed that blood sharing depended equally and independently on degree of relatedness and an index of opportunity for reciprocation. The Sir Philip Sidney game, which models signals of need between relatives, can therefore be applied to this case. If X keeps the blood meal, then X is bound to survive until the next night, although Y may starve. Conversely, if X regurgitates the blood for Y , then Y is bound to survive, but X may itself starve. The optimal decision depends on the degree of relatedness of the two bats, and on their chances of starvation if left unfed. Neither bat can perceive directly the other's chance of starvation, so X must respond instead to the intensity of Y 's begging.

Y 's strategy in the game is a signalling rule that determines how strongly he should signal on the basis of any particular survival chance—if we refer to the strength of the signal as q , then this becomes some function $Q(y)$ that determines q given y . X will give up the resource if this signal exceeds a certain threshold, which we shall refer to as p . Since the threshold that X sets depends on his own survival chance, his strategy becomes some function $P(x)$ that determines p given x .

What is the equilibrium pair of strategies? Zahavi's handicap principle suggests that, at equilibrium, Y will signal honestly. X will then be able to extract accurate information about y from q . It might be the case, however, that Y will "cheat" by signalling strongly even when he has a high survival chance. If this is so, then X would probably evolve to ignore the signal altogether. As the next subsection will show, the equilibrium strategies of X and Y do, in fact, satisfy the conditions of the handicap principle.

2.1. THE SIGNALLING EQUILIBRIUM

The utility functions of the two players may be written as follows:

$$U(x, p) = \int_{p > Q(y)} (1 + ry) dy + \int_{p < Q(y)} (x + r) dy - rq \quad (\text{for } X \text{ at } x, \text{ with threshold } p)$$

$$V(y, q) = \int_{P(x) > q} (r + y) dx + \int_{P(x) < q} (rx + 1) dx - q \quad (\text{for } Y \text{ at } y, \text{ signalling } q).$$

In both formulae, the first integral covers those cases where the magnitude of Y 's signal falls below X 's threshold, and X consequently keeps the resource. The second integral covers the remaining cases, where Y 's signal is strong enough to persuade X to give him the resource.

At equilibrium,

$$U(x, P(x)) \geq U(x, p) \quad \forall p \quad (1a)$$

$$V(y, Q(y)) \geq V(y, q) \quad \forall q. \quad (1b)$$

That is, $Q(y)$ is the optimal signalling strategy for Y [given that X is playing the strategy defined by $P(x)$], and $P(x)$ is the optimal interpretation strategy for X [given that Y is playing the strategy defined by $Q(y)$].

Given that U and V can be differentiated, this implies that

$$\left. \frac{\partial U(x, p)}{\partial p} \right|_{p=P(x)} = 0 \quad \forall x$$

$$\left. \frac{\partial V(y, q)}{\partial q} \right|_{q=Q(y)} = 0 \quad \forall y.$$

So we can determine the equilibrium strategies of the two players by differentiating their utility functions (see Appendix A).

The equilibrium strategies are

$$P(x) = \frac{1}{2} \cdot \left(\frac{1}{r} - r \right) \cdot (1-x)^2 \quad (2a)$$

$$Q(y) = \frac{1}{2} \cdot r \cdot (1-r^2) \cdot (1-y)^2. \quad (2b)$$

Figures 1 and 2 show graphs of these two functions. The combined result of the two strategies is that X transfers the resource whenever

$$1 + ry < x + r$$

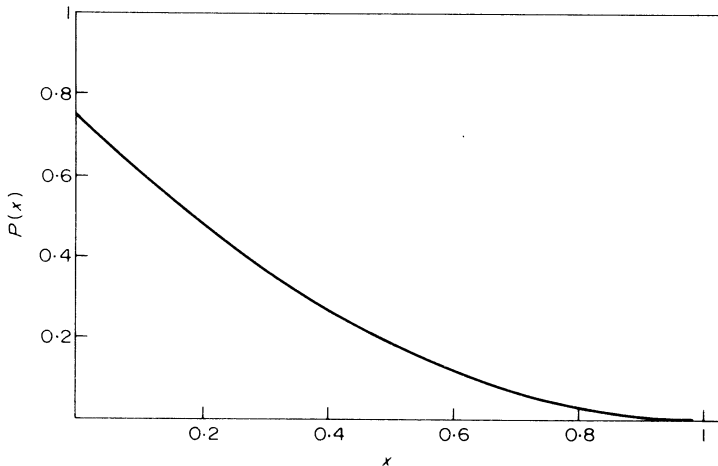


FIG. 1. The ESS response threshold for player X , $P(x)$, as a function of his survival chance, x , when $r=0.5$. Other values of r yield qualitatively similar functions.

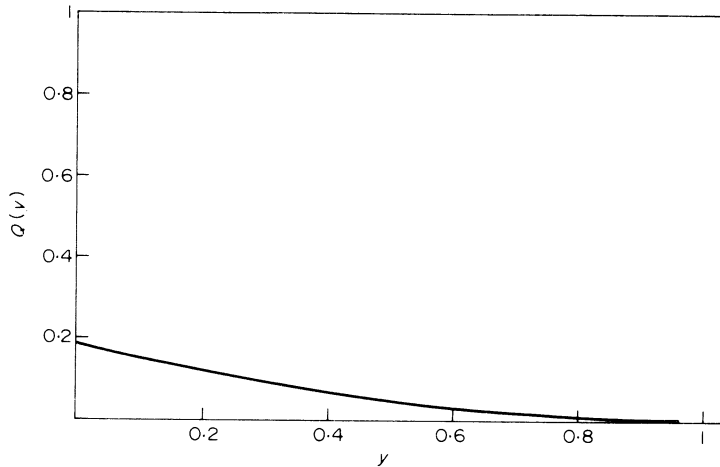


FIG. 2. The ESS signalling rule for player Y , $Q(y)$, as a function of his survival chance, y , when $r = 0.5$. Other values of r yield qualitatively similar functions.

which is the optimal decision and satisfies Hamilton's rule. The fact that X follows the optimal decision rule shows that, at equilibrium, he is perfectly informed. In other words, the equilibrium strategies of the two players satisfy the conditions of Zahavi's handicap principle: Y signals honestly, and as a result, X can extract the information he needs from the signal.

The honesty of the system is maintained by the cost of signalling, in particular by the fact that a signal of a given magnitude effectively costs more when y is higher. If Y has a high survival chance, then he has little to gain from acquiring the resource, and so will only signal weakly. If, on the other hand, Y is very likely to die without the resource, then the potential gain from acquiring it is high and justifies a strong signal. In the next section we will consider just how costly signals are at equilibrium.

3. Signalling Costs

Zahavi's handicap principle states that stable signalling systems will be honest if, and only if, there is a cost to signalling (and this cost is dependent on the true quality revealed). In the previous section, it was shown that the model's predictions do match those of the handicap principle. But now that we know Y 's equilibrium signalling rule in the game, we can do more than simply state that signals are costly; we can calculate precisely the mean signalling cost at equilibrium [assuming that y has an even probability distribution between 0 and 1, we can simply integrate $Q(y)$ between those limits]. The mean cost is

$$\frac{1}{6} \cdot r \cdot (1 - r^2).$$

The fact that signal cost depends on the degree of relatedness between the two players is not surprising. We would, however, expect high relatedness to yield low

cost signals, and low relatedness to yield high cost signals. The function shown above, in contrast, sometimes increases with relatedness (see Fig. 3). This reflects the fact that as r increases, X becomes more likely to transfer the resource, and consequently Y has more to gain from signalling. By contrast, where $r=0$, X will never transfer the resource, so Y has nothing to gain. This means that Y will not bother to signal, and the mean signal cost is zero.

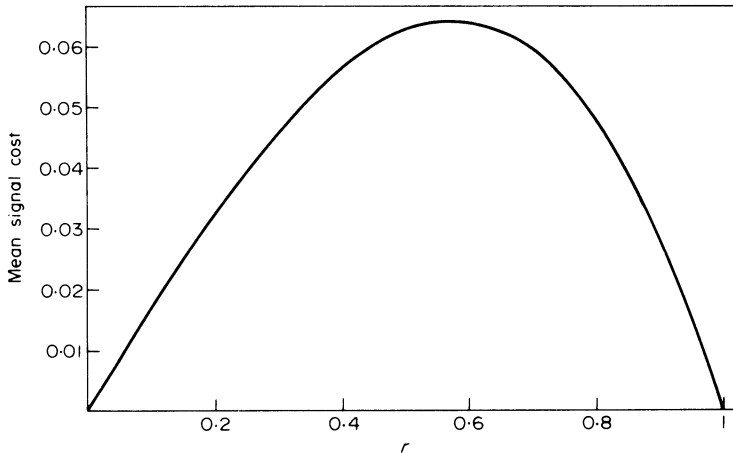


FIG. 3. This shows mean signalling cost as a function of r , the coefficient of relatedness between the two players.

In order to rule out the effect of relatedness on X 's probability of response, we can divide the mean signal cost by the probability of his giving up the resource. This will give us the cost per benefit transferred. Given that X transfers the resource whenever

$$1 + ry < x + r$$

and both x and y have uniform probability distributions between 0 and 1, the probability of the transfer must be $r/2$. Cost per benefit is therefore

$$\frac{1}{3} \cdot (1 - r^2)$$

which is strictly decreasing in r (see Fig. 4).

The model therefore suggests that stable biological signalling systems will feature lower signal costs when communication occurs between relatives, but that care should be taken in evaluating signal cost relative to the benefits obtained.

4. An Extended Model Involving a "Messenger"

The basic model involves only two players, X (the signaller) and Y (the receiver). In this section, we consider an extended version of the Sir Philip Sidney game that features a third player, Z (referred to as a "messenger"). X cannot perceive Y 's

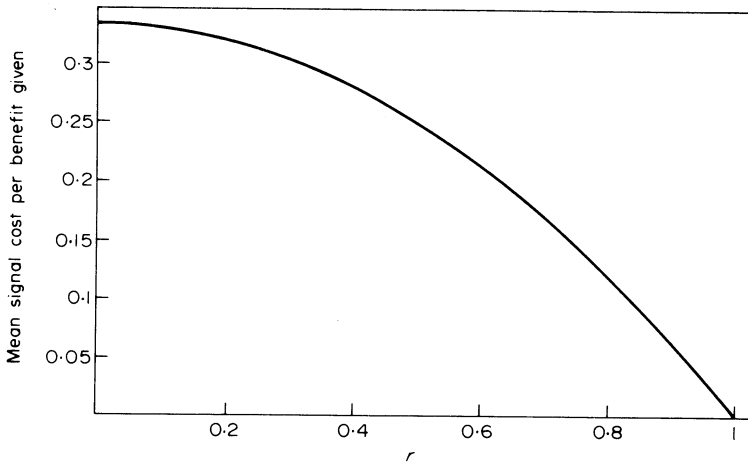


FIG. 4. Mean signalling cost per benefit transferred, as a function of r , the coefficient of relatedness between the players.

signal directly. Instead Y must signal to Z , and Z must in turn signal to X . We assume that the outcome of the signalling game does not influence Z directly, so that his utility function will reflect only the survival chances of the other two players, weighted according to the extent of their relatedness to him (the “cost” of Z ’s signal is the extent by which it reduces Y ’s survival chance). The coefficients of relatedness between the players are r_{xy} , r_{yz} and r_{xz} . Z ’s strategy in the game is defined by some function $T(q)$, which specifies t , the strength of the signal he will give, on the basis of q , the strength of the signal that Y gives.

This extended model captures something of the complexity of the potential conflict during seed development in angiosperms. During the development of a plant seed, resources are transferred from the maternal sporophyte to the growing embryo (the young sporophyte). As in animals, there is the potential for conflict between these two diploid generations. The mother should not favour any of her offspring on the basis of relatedness, because maternal alleles have the same 50% chance of having been transmitted to each offspring. In contrast, an offspring allele is sure to benefit from maternal investment in that particular offspring, while investment in its siblings will benefit identical copies of the allele only some of the time. Offspring will therefore be selected to try to acquire more resources than the mother is selected to give (Trivers, 1974; Cook, 1981; Westoby & Rice, 1982; Queller, 1983; Haig, 1987).

At first glance, it seems likely that the maternal plant can enforce its own interests. However, if offspring are able to assess their own quality better than the mother can, it may pay her to be responsive to offspring signals. This sets the stage for a signalling “game” in which offspring may try to deceive the mother as to their quality, in order to obtain a greater share of maternal resources (see Godfray, 1991). But a two-player ESS model such as the basic Sir Philip Sidney game fails to capture the essentials of the situation, because the parental and offspring sporophyte do not directly interact.

In most angiosperm plants, resource acquisition is carried out by a third tissue, the endosperm (Johri, 1984). Offspring signals must be “relayed” to the mother via the endosperm, which acts as a “messenger”. Hence, we require an extended, three-player version of the Sir Philip Sidney game in order to determine the kinds of behaviour that the three tissues might exhibit.

The endosperm is unique to angiosperms (in gymnosperms, for instance, it is usually the female gametophyte which acts as the resource acquisition and storage tissue—Singh, 1978), and its adaptive significance (if any) is something of a puzzle. Recent theories have concentrated on its role in kin conflict (Westoby & Rice, 1982; Queller, 1983, 1989; Willson & Burley, 1983). The endosperm genotype is identical to that of the embryo, but it possesses one extra copy of all maternally inherited genes. This difference means that endosperms will not be selected to acquire extra resources at the expense of other embryos as strongly as the embryos themselves would be. Consequently, interposing the endosperm between mother and embryo may reduce the degree of kin conflict. In terms of the signalling “game” between parent and offspring, this implies that the introduction of a “messenger” (who is more closely related to the receiver than is the original signaller) will reduce overall signalling costs.

In the next subsection, we show that the introduction of a messenger in fact destabilizes the signalling system, and is unlikely to reduce signal costs.

4.1. THE THREE-PLAYER EQUILIBRIUM

The utility functions of the players may be written as follows:

$$\begin{aligned}
 U(x, p) &= \int_{p > T(Q(y))} (1 + r_{xy}y) \, dy \\
 &\quad + \int_{p < T(Q(y))} (x + r_{xy}) \, dy - r_{xy} \cdot (q + t) \quad (\text{for } X \text{ at } x, \text{ with threshold } p) \\
 V(y, q) &= \int_{P(x) > T(q)} (r_{xy} + y) \, dx \\
 &\quad + \int_{P(x) < T(q)} (1 + r_{xy}x) \, dx - q - T(q) \quad (\text{for } Y \text{ at } y, \text{ signalling } q) \\
 W(q, t) &= \int_{P(x) > t} (r_{xz} + r_{yz}y) \, dx \\
 &\quad + \int_{P(x) < t} (r_{xz}x + r_{yz}) \, dx - r_{yz}(q + t) \quad (\text{for } Z \text{ receiving } q, \text{ signalling } t).
 \end{aligned}$$

An attempt to calculate the stable strategies of the players by differentiation of these functions reveals that there is no stable solution (see Appendix B). When

$$\frac{r_{xz}}{r_{yz}} > r_{xy}$$

then the messenger, *Z*, is less prone to “exaggeration” than is the signaller, *Y*. The messenger’s signal, $T(q)$, thus tends to decrease, but as a consequence the signaller tends to signal more strongly, leading $T(q)$ to decrease even further etc. When

$$\frac{r_{xz}}{r_{yz}} < r_{xy}$$

then the messenger, *Z*, is more prone to “exaggeration” than is the signaller, *Y*. The messenger’s signal, $T(q)$, tends to increase, so that the signaller tends to signal less strongly, so that $T(q)$ increases even further etc.

Stability can be imposed on either of these cases by specifying a minimum signalling level. In the first case, if the messenger’s signal, $T(q)$, cannot drop below εq (where $\varepsilon > 0$ but is very small) then there is a stable state, in which the signaller signals strongly and the messenger “whispers” (see Appendix C). In the second case, if the initial signal, $Q(y)$, cannot drop below $\varepsilon(1-y)$ then there is a stable state in which the signaller “whispers” and the messenger “exaggerates” this by signalling strongly to the receiver (see Appendix D). In either situation, the overall level of signalling cost is set by the individual (signaller or messenger) who is more prone to exaggeration. The introduction of a “messenger” may therefore increase signalling costs, if he is more prone to exaggeration than the original signaller, but cannot reduce them, even if he is less prone to exaggeration.

4.2. IMPLICATIONS FOR THE ROLE OF THE ENDOSPERM

These results seem to suggest that interposing the endosperm between the maternal sporophyte and the developing embryo cannot reduce kin conflict. We do not wish to claim, however, that “kin conflict” theories of the role of the endosperm are invalid, merely that they require further refinement. One cannot assume that the introduction of a novel resource acquisition tissue will limit conflict simply because it carries an extra copy of the maternally inherited genes. We suggest that kin conflict theories need to place greater emphasis on the information available to each component involved in seed development. Given that the endosperm has qualitatively the same genome as the embryo, it may be able to assess offspring quality better than the parent can. If so, this would limit the possibilities for “cheating” on the part of the embryo. Refined kin conflict theories could, then, explain the triploid genome of the endosperm: the resource acquisition tissue must contain a copy of the paternal genome in order to restrict deceit of the mother by the developing embryo, because this allows it to assess offspring quality better than the mother can. At the same time, it must be sufficiently closely related to other offspring, otherwise its interests will

coincide with those of the embryo. This means that a single copy of the paternal genome must be combined with two or more copies of the maternal genome.

REFERENCES

- COOK, R. E. (1981). Plant parenthood. *Nat. Hist.* **90**, 30–35.
- DAWKINS, R. & KREBS, J. R. (1978). Animal signals: information or manipulation. In: *Behavioural Ecology: An Evolutionary Approach* (Krebs, J. R. & Davies, N. B., eds) pp. 282–309. Oxford: Blackwell.
- ENQUIST, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Anim. Behav.* **33**, 1152–1161.
- GODFRAY, H. C. J. (1991). Signalling of need by offspring to their parents. *Nature, Lond.* **352**, 328–330.
- GRAFEN, A. (1990). Biological signals as handicaps. *J. theor. Biol.* **144**, 517–546.
- HAIG, D. (1987). Kin conflict in seed plants. *Trends Ecol. Evol.* **2**, 337–340.
- JOHRI, B. M. (ed.) (1984). *Embryology of Angiosperms*. Berlin: Springer-Verlag.
- KREBS, J. R. & DAWKINS, R. (1984). Animal signals: mind-reading and manipulation. In: *Behavioural Ecology: An Evolutionary Approach* 2nd edn (Krebs, J. R. & Davies, N. B., eds) pp. 380–402. Oxford: Blackwell.
- MAYNARD SMITH, J. (1991). Honest signalling—the Philip Sidney game. *Anim. Behav.* **42**, 1034–1035.
- QUELLER, D. D. (1983). Kin selection and conflict in seed maturation. *J. theor. Biol.* **100**, 153–172.
- QUELLER, D. D. (1989). Inclusive fitness in a nutshell. In: *Oxford Surveys in Evolutionary Biology* Vol. 6 (Harvey, P. H. & Partridge, L., eds) pp. 73–109. Oxford University Press.
- SINGH, H. (1978). *Embryology of Gymnosperms*. Gebruder Borntraeger.
- TRIVERS, R. L. (1974). Parent–offspring conflict. *Am. Zool.* **14**, 249–264.
- WESTOBY, M. & RICE, B. (1982). Evolution of seed plants and inclusive fitness of plant tissues. *Evolution* **36**, 713–724.
- WILKINSON, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature, Lond.* **308**, 181–184.
- WILLSON, M. F. & BURLEY, N. (1983). *Mate Choice in Plants: Mechanisms and Consequences*. Princeton, NJ: Princeton University Press.
- ZAHAVI, A. (1975). Mate selection—a selection for a handicap. *J. theor. Biol.* **53**, 205–214.
- ZAHAVI, A. (1977). The cost of honesty (Further remarks on the handicap principle). *J. theor. Biol.* **67**, 603–605.
- ZAHAVI, A. (1987). The theory of signal selection and some of its implications. In: *International Symposium of Biological Evolution* (Delfino, V. P., ed.). Bari: Adriatica Editrice.

APPENDIX A

Determining the Equilibrium Strategies in the Basic Model

We wish to prove that there is a solution to the ESS conditions given in eqn 1(a) and (b), and to show that it is of the form given in eqn 2(a) and (b).

The utility functions of the two players in the game may be written as follows:

$$U(x, p) = \int_{p > Q(y)} (1 + ry) dy + \int_{p < Q(y)} (x + r) dy - rq$$

(for X at x , with threshold p) (A.1a)

$$V(y, q) = \int_{P(x) > q} (r + y) dx + \int_{P(x) < q} (rx + 1) dx - q$$

(for Y at y , signalling q). (A.1b)

Suppose that there exist equilibrium strategies $P_{eq}(x)$ and $Q_{eq}(y)$, with both functions decreasing smoothly over the ranges $0 \leq x \leq 1$ and $0 \leq y \leq 1$, such that they can be differentiated. Then at equilibrium we must have

$$\left. \frac{\partial U(x, p)}{\partial p} \right|_{p=P_{eq}(x)} = 0 \quad \forall x.$$

From eqn 3(a) we can see that

$$\frac{\partial U}{\partial p} = -Q^{-1}(p) \cdot (1 + rQ^{-1}(p) - x - r)$$

(the initial minus sign is there because Q is assumed to be a decreasing function)

$$\Rightarrow 1 + rQ_{eq}^{-1}(P_{eq}(x)) - x - r = 0 \quad \forall x$$

$$\Rightarrow P_{eq}(x) = Q_{eq}\left(\frac{x+r-1}{r}\right). \tag{A.2}$$

Similarly, equilibrium implies that

$$\left. \frac{\partial V(y, q)}{\partial q} \right|_{q=Q_{eq}(y)} = 0 \quad \forall y$$

From eqn (A.1b) we can see that

$$\frac{\partial V}{\partial q} = -P^{-1}(q) \cdot (-r - y + sP^{-1}(q) + 1) - 1$$

(the initial minus sign is there because P is assumed to be a decreasing function)

$$\Rightarrow -P_{eq}^{-1}(Q_{eq}(y)) \cdot (-r - y + rP_{eq}^{-1}(Q_{eq}(y)) + 1) - 1 = 0 \quad \forall y.$$

If we now let

$$y = \frac{x+r-1}{r}$$

then using eqn (A.2) yields

$$\begin{aligned} & -P_{eq}^{-1}(P_{eq}(x)) \cdot \left(-r - \frac{x}{r} + \frac{1}{r} + rP_{eq}^{-1}(P_{eq}(x))\right) - 1 = 0 \\ \Rightarrow P_{eq}^{-1}(P_{eq}(x)) &= \frac{-1}{\left(-r + rx - \frac{x}{r} + \frac{1}{r}\right)} \\ \Rightarrow P_{eq}^{-1}(P_{eq}(x)) &= \frac{-1}{\left(\frac{1}{r} - r\right) \cdot (1-x)}. \end{aligned}$$

Now

$$P_{eq}^{-1'}(P_{eq}(x)) = \left[\frac{dP_{eq}(x)}{dx} \right]^{-1}$$

$$\Rightarrow \frac{dP_{eq}(x)}{dx} = -\left(\frac{1}{r} - r \right) \cdot (1-x).$$

This is an ordinary, linear differential equation, so we can integrate to obtain

$$P_{eq}(x) = \frac{1}{2} \cdot \left(\frac{1}{r} - r \right) \cdot (1-x)^2 + C$$

where C is the constant of integration. We know that if player X is bound to survive, then his optimal strategy is to give away the resource whatever the strength of Y 's signal. This means that we must have $P_{eq}(1) = 0$. Consequently, the constant of integration must be zero in this case, which leaves us with

$$P_{eq}(x) = \frac{1}{2} \cdot \left(\frac{1}{r} - r \right) \cdot (1-x)^2.$$

Substitution of this expression for $P_{eq}(x)$ into eqn (A.2) now allows us to calculate that

$$Q_{eq}(y) = \frac{1}{2} \cdot r \cdot (1-r^2) \cdot (1-y)^2.$$

These two formulae, which match eqn (2a) and (b), satisfy the ESS conditions given in eqn 1(a) and (b), and therefore represent the equilibrium strategies of the two players.

APPENDIX B

The Three-player Game Lacks an Equilibrium

We wish to demonstrate that there is no solution to the ESS conditions given below:

$$U(x, P(x)) \geq U(x, p) \quad \forall p \tag{B.1a}$$

$$V(y, Q(y)) \geq V(y, q) \quad \forall q \tag{B.1b}$$

$$W(q, T(q)) \geq W(q, t) \quad \forall t \tag{B.1c}$$

where the utility functions of the players (X , Y and Z) may be written as follows:

$$U(x, p) = \int_{p > \pi(Q(y))} (1 + r_{xy}y) dy + \int_{p < \pi(Q(y))} (x + r_{xy}) dy - r_{xy}(q + t)$$

(for X at x , with threshold p) (B.2a)

$$V(y, q) = \int_{P(x) > T(q)} (r_{xy} + y) dx + \int_{P(x) < T(q)} (1 + r_{xy}x) dx - q - T(q)$$

(for Y at y , signalling q) (B.2b)

$$W(q, t) = \int_{P(x) > t} (r_{xz} + r_{yz}y) dx + \int_{P(x) < t} (r_{xz}x + r_{yz}) dx - r_{yz}(q + t).$$

(for Z receiving q , signalling t .) (B.2c)

Suppose that there exist equilibrium strategies $P_{\text{eq}}(x)$, $Q_{\text{eq}}(y)$ and $T_{\text{eq}}(q)$ which satisfy the ESS conditions given in eqn (B.1a-c). If these functions are smoothly decreasing, such that they can be differentiated, then at equilibrium we must have

$$\left. \frac{\partial U(x, p)}{\partial p} \right|_{p=P_{\text{eq}}(x)} = 0 \quad \forall x.$$

From eqn (B.2a) we can see that

$$\frac{\partial U}{\partial p} = -Q^{-1}(T^{-1}(p)) \cdot T^{-1}(p) \cdot (1 + r_{xy}Q^{-1}(T^{-1}(p)) - x - r_{xy})$$

(the initial minus sign is there because Q is assumed to be a decreasing function)

$$\Rightarrow 1 + r_{xy}Q_{\text{eq}}^{-1}(T_{\text{eq}}^{-1}(P_{\text{eq}}(x))) - x - r_{xy} = 0 \quad \forall x$$

$$\Rightarrow P_{\text{eq}}(x) = T_{\text{eq}}\left(Q_{\text{eq}}\left(\frac{x + r_{xy} - 1}{r_{xy}}\right)\right). \quad (\text{B.3})$$

Similarly, at equilibrium

$$\left. \frac{\partial V(y, q)}{\partial q} \right|_{q=Q_{\text{eq}}(y)} = 0 \quad \forall y.$$

From eqn (B.2b) we can see that

$$\frac{\partial V}{\partial q} = -P^{-1}(T(q)) \cdot T'(q) \cdot (-r_{xy} - y + 1 + r_{xy}P^{-1}(T(q))) - 1 - T'(q)$$

(the initial minus sign is there because P is assumed to be a decreasing function)

$$\begin{aligned} \Rightarrow -P_{\text{eq}}^{-1}(T_{\text{eq}}(Q_{\text{eq}}(y))) \cdot T'_{\text{eq}}[Q_{\text{eq}}(y)] \cdot (-r_{xy} - y + 1 + r_{xy}P_{\text{eq}}^{-1}(T_{\text{eq}}(Q_{\text{eq}}(y)))) \\ - 1 - T'_{\text{eq}}(Q_{\text{eq}}(y)) \\ = 0 \quad \forall y. \end{aligned}$$

If we now let

$$y = \frac{x + r_{xy} - 1}{r_{xy}}$$

then using eqn (B.3) yields

$$-P_{\text{eq}}^{-1}(P_{\text{eq}}(x)) \cdot P'_{\text{eq}}(x) \cdot \left(-r_{xy} - \left[\frac{x+r_{xy}-1}{r_{xy}}\right] + 1 + r_{xy}x\right) - 1 - P'_{\text{eq}}(x) = 0.$$

Now

$$\begin{aligned} P_{\text{eq}}^{-1}(P_{\text{eq}}(x)) &= \left(\frac{dP_{\text{eq}}(x)}{dx}\right)^{-1} \\ \Rightarrow P'_{\text{eq}}(x) &= -\left(-r_{xy} - \left[\frac{x+r_{xy}-1}{r_{xy}}\right] + 1 + r_{xy}x\right) - 1 \\ \Rightarrow P'_{\text{eq}}(x) &= \left(r_{xy} - \frac{1}{r_{xy}}\right) \cdot (1-x) - 1. \end{aligned}$$

This is an ordinary, linear differential equation, so we can integrate to obtain

$$P_{\text{eq}}(x) = \frac{1}{2} \cdot \left(\frac{1}{r_{xy}} - r_{xy}\right) \cdot (1-x)^2 - x + C$$

where C is the constant of integration. As in the two player game, we know that when X has no chance of dying, his optimal strategy is to transfer the resource to Y , whatever the strength of the signal that he receives from Z . This means that we must have $P_{\text{eq}}(1) = 0$. Consequently, the constant of integration must be 1 in this case, and we are left with

$$P_{\text{eq}}(x) = \frac{1}{2} \cdot \left(\frac{1}{r_{xy}} - r_{xy}\right) \cdot (1-x)^2 - x + 1. \quad (\text{B.4})$$

This is apparently the first part of the solution to the problem.

Equilibrium, however, also implies that

$$\left.\frac{\partial W(q, t)}{\partial t}\right|_{t=\tau_{\text{eq}}(q)} = 0 \quad \forall q$$

From eqn (B.2c), we can see that

$$\frac{\partial W}{\partial t} = -P^{-1}(t) \cdot (-r_{xz} - r_{yz}Q^{-1}(q) + r_{xz}P^{-1}(t) + r_{yz}) - r_{yz}$$

(the initial minus sign is there because P is assumed to be a decreasing function)

$$\Rightarrow -P_{\text{eq}}^{-1}(T_{\text{eq}}(q)) \cdot (-r_{xz} - r_{yz}Q_{\text{eq}}^{-1}(q) + r_{xz}P_{\text{eq}}^{-1}(T_{\text{eq}}(q)) + r_{yz}) - r_{yz} = 0 \quad \forall q.$$

If we let

$$q = Q_{\text{eq}}\left(\frac{x+r_{xy}-1}{r_{xy}}\right)$$

then using eqn (B.3) yields

$$\begin{aligned}
 & -P_{\text{eq}}^{-1}(P_{\text{eq}}(x)) \cdot \left(-r_{xz} - r_{yz} \left[\frac{x + r_{xy} - 1}{r_{xy}} \right] + r_{xz}x + r_{yz} \right) - r_{yz} = 0 \\
 \Rightarrow & (P'_{\text{eq}}(x))^{-1} = \frac{-r_{yz}}{-r_{xz} - r_{yz} \left(\frac{x + r_{xy} - 1}{r_{xy}} \right) + r_{xz}x + r_{yz}} \\
 \Rightarrow & P'_{\text{eq}}(x) = \left(\frac{r_{xz}}{r_{yz}} - \frac{1}{r_{xy}} \right) \cdot (1-x).
 \end{aligned}$$

This is an ordinary, linear differential equation, so we can integrate to get

$$P_{\text{eq}}(x) = \frac{1}{2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1-x)^2 + C$$

where C is the constant of integration. Once again, we must have $P_{\text{eq}}(1) = 0$, so the constant in this case must be zero. We are therefore left with

$$P_{\text{eq}}(x) = \frac{1}{2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1-x)^2. \quad (\text{B.5})$$

This formula for $P_{\text{eq}}(x)$ differs from eqn (B.4), the solution which we derived previously. The two equations are only equivalent when

$$x = \frac{\left(\frac{r_{xz}}{r_{yz}} - r_{xy} \right) + 2}{\left(\frac{r_{xz}}{r_{yz}} - r_{xy} \right)}.$$

As x , r_{xy} , r_{xz} and r_{yz} all have values between 0 and 1, this condition can never be satisfied. Equations (B.4) and (B.5) cannot both be true in any one case. We may therefore conclude that there is no solution to the ESS conditions given in eqn (B.1a-c), so the three-player game lacks an equilibrium.

APPENDIX C

Imposing Stability When Z is Less Prone to Exaggeration Than is Y

We wish to demonstrate that if

$$\frac{r_{xz}}{r_{yz}} > r_{xy}$$

then there exists an equilibrium solution to the ESS conditions

$$U(x, P(x)) \geq U(x, p) \quad \forall p \quad (\text{C.1a})$$

$$V(y, Q(y)) \geq V(y, q) \quad \forall q \quad (\text{C.1b})$$

$$W(q, T(q)) \geq W(q, t) \quad \text{for } t \geq \varepsilon q. \quad (\text{C.1c})$$

Inspection of these conditions suggests defining the equilibrium strategy $T_{\text{eq}}(q)$ by

$$T_{\text{eq}}(q) = \varepsilon q \quad (\text{C.2})$$

where $0 < \varepsilon \ll 1$. If (C.2) does represent an evolutionarily stable strategy, then at equilibrium, using (B.2c), we must have

$$\left. \frac{\partial W(q, t)}{\partial t} \right|_{t=\varepsilon q} = -P^{-1}(t) \cdot (-r_{xz} - r_{yz}Q^{-1}(q) + r_{xz}P^{-1}(t) + r_{yz}) - r_{yz} \leq 0. \quad (\text{C.3})$$

We now demonstrate that the condition specified in eqn (C.3) is satisfied.

Suppose that there exist equilibrium strategies $P_{\text{eq}}(x)$ and $Q_{\text{eq}}(y)$, which satisfy the conditions given in eqn (C.1a and b). If these functions are smoothly decreasing, such that they can be differentiated, then at equilibrium we must have

$$\left. \frac{\partial U(x, p)}{\partial p} \right|_{p=P_{\text{eq}}(x)} = 0 \quad \forall x.$$

From Appendix B we know that this condition yields the following formula:

$$P_{\text{eq}}(x) = T_{\text{eq}} \left(Q_{\text{eq}} \left[\frac{x + r_{xy} - 1}{r_{xy}} \right] \right). \quad (\text{C.4})$$

Similarly, equilibrium implies that

$$\left. \frac{\partial V(y, q)}{\partial q} \right|_{q=T_{\text{eq}}(q)} = 0 \quad \forall q.$$

From Appendix B we know that

$$\frac{\partial V}{\partial q} = -P^{-1}(T(q)) \cdot T'(q) \cdot (-r_{xy} - y + 1 + r_{xy}P^{-1}(T(q))) - 1 - T'(q)$$

(the initial minus sign is there because P is assumed to be a decreasing function)

$$\Rightarrow -P_{\text{eq}}^{-1}(\varepsilon Q_{\text{eq}}(y)) \cdot (-r_{xy} - y + 1 + r_{xy}P_{\text{eq}}^{-1}(\varepsilon Q_{\text{eq}}(y))) - (1 + \varepsilon) = 0 \quad \forall y.$$

If we now let

$$y = \frac{x + r_{xy} - 1}{r_{xy}}$$

then using eqn (C.4) yields

$$-P_{\text{eq}}^{-1'}(P_{\text{eq}}(x)) \cdot \left(-r_{xy} - \left[\frac{x + r_{xy} - 1}{r_{xy}} \right] + 1 + r_{xy}x \right) - (1 + \varepsilon) = 0.$$

Given that $0 < \varepsilon \ll 1$, this approximates to

$$-P_{\text{eq}}^{-1'}(P_{\text{eq}}(x)) \cdot \left(-r_{xy} - \left[\frac{x + r_{xy} - 1}{r_{xy}} \right] + 1 + r_{xy}x \right) - 1 = 0.$$

Now

$$\begin{aligned} P_{\text{eq}}^{-1'}(P_{\text{eq}}(x)) &= \left(\frac{dP_{\text{eq}}(x)}{dx} \right)^{-1} \\ \Rightarrow P'_{\text{eq}}(x) &= \left(r_{xy} - \frac{1}{r_{xy}} \right) \cdot (1 - x). \end{aligned}$$

This is an ordinary, linear differential equation, so we can integrate to obtain

$$P_{\text{eq}}(x) = \frac{1}{2} \cdot \left(\frac{1}{r_{xy}} - r_{xy} \right) \cdot (1 - x)^2 + C$$

where C is the constant of integration. We know that when X has no chance of dying, his optimal strategy is to transfer the resource to Y , whatever the strength of the signal that he receives from Z . This means that we must have $P_{\text{eq}}(1) = 0$. Consequently, the constant of integration must be 0 in this case, and we are left with

$$P_{\text{eq}}(x) = \frac{1}{2} \cdot \left(\frac{1}{r_{xy}} - r_{xy} \right) \cdot (1 - x)^2. \quad (\text{C.5})$$

Combining eqns (C.4) and (C.5) yields

$$T_{\text{eq}}(Q_{\text{eq}}(y)) = \frac{r_{xy}^2}{2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1 - y)^2 + r_{xy}(1 - y)$$

So substitution of the formula for $T_{\text{eq}}(q)$ given in eqn (C.2) gives us

$$\begin{aligned} \varepsilon Q_{\text{eq}}(y) &= \frac{r_{xy}^2}{2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1 - y)^2 + r_{xy}(1 - y) \\ \Rightarrow Q_{\text{eq}}(y) &= \frac{r_{xy}^2}{2\varepsilon} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1 - y)^2 + \frac{r_{xy}}{\varepsilon} (1 - y). \end{aligned} \quad (\text{C.6})$$

We can now substitute the expressions for $P_{eq}(x)$ and $Q_{eq}(y)$ given in eqns (C.5) and (C.6) into eqn (C.3) to yield

$$\begin{aligned}
 & \sqrt{2 \cdot \left(\frac{1}{r_{xy}} - r_{xy}\right) \cdot t} \cdot \left(\frac{r_{yz}}{r_{xy}} \cdot \sqrt{\frac{2t}{\left(\frac{1}{r_{xy}} - r_{xy}\right)}} - r_{xz} \cdot \sqrt{\frac{2t}{\left(\frac{1}{r_{xy}} - r_{xy}\right)}}\right) - r_{yz} \leq 0 \\
 & \Leftrightarrow \frac{\left(\frac{r_{yz}}{r_{xy}} - r_{xz}\right)}{\left(\frac{1}{r_{xy}} - r_{xy}\right)} - r_{yz} \leq 0 \\
 & \Leftrightarrow \frac{r_{xy} r_{yz} - r_{xz}}{\left(\frac{1}{r_{xy}} - r_{xy}\right)} \leq 0. \tag{C.7}
 \end{aligned}$$

If, and only if, as specified earlier

$$\frac{r_{xz}}{r_{yz}} > r_{xy}$$

then condition (C.7) must be satisfied. We may therefore conclude that, in this case, the imposition of a minimum signalling level on player Z stabilizes the game.

APPENDIX D

Imposing Stability When Z is More Prone to Exaggeration Than is Y

We wish to demonstrate that if

$$\frac{r_{xz}}{r_{yz}} < r_{xy}$$

then there exists an equilibrium solution to the ESS conditions

$$U(x, P(x)) \geq U(x, p) \quad \forall p \tag{D.1a}$$

$$V(y, Q(y)) \geq V(y, q) \quad \text{for } q \geq \varepsilon(1-y) \tag{D.1b}$$

$$W(q, T(q)) \geq W(q, t) \quad \forall t. \tag{D.1c}$$

Inspection of these conditions suggests defining the equilibrium strategy $Q_{eq}(y)$ by

$$Q_{eq}(y) = \varepsilon(1-y) \tag{D.2}$$

where $0 \leq \varepsilon \ll 1$. If (D.2) does represent an evolutionarily stable strategy, then at equilibrium, using (B.2b) we must have

$$\left. \frac{\partial V(y, q)}{\partial q} \right|_{q = \varepsilon(1-y)} = -P^{-1}(T(q)) \cdot T'(q) \cdot (-r_{xy} - y + 1 + r_{xy}P^{-1}(T(q))) - 1 - T'(q) \leq 0. \quad (D.3)$$

We now demonstrate that the condition specified in eqn (D.3) is satisfied.

Suppose that there exist equilibrium strategies $P_{\text{eq}}(x)$ and $T_{\text{eq}}(q)$, which satisfy the conditions given in eqn (D.1a and c). If these functions are smoothly decreasing, such that they can be differentiated, then at equilibrium we must have

$$\left. \frac{\partial U(x, p)}{\partial p} \right|_{p = P_{\text{eq}}(x)} = 0 \quad \forall x$$

and

$$\left. \frac{\partial W(q, t)}{\partial t} \right|_{t = T_{\text{eq}}(q)} = 0 \quad \forall q.$$

From Appendix B we know that these conditions yield the following formulae:

$$P_{\text{eq}}(x) = T_{\text{eq}} \left(Q_{\text{eq}} \left[\frac{x + r_{xy} - 1}{r_{xy}} \right] \right)$$

and

$$\begin{aligned} P_{\text{eq}}(x) &= \frac{1}{2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1-x)^2 \\ \Rightarrow T_{\text{eq}}(Q_{\text{eq}}(y)) &= \frac{r_{xy}^2}{2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1-y)^2 \end{aligned} \quad (D.4)$$

Substitution of the formula given in eqn (D.2) for $Q_{\text{eq}}(y)$ thus yields

$$\begin{aligned} T_{\text{eq}}(\varepsilon(1-y)) &= \frac{r_{xy}^2}{2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot (1-y)^2 \\ \Rightarrow T_{\text{eq}}(q) &= \frac{r_{xy}^2}{2\varepsilon^2} \cdot \left(\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right) \cdot q^2. \end{aligned} \quad (D.5)$$

We can now substitute the expressions for $P_{\text{eq}}(x)$ and $T_{\text{eq}}(q)$ given in eqns (D.4) and (D.5) into eqn (D.3) to yield

$$\begin{aligned} & \left(\frac{r_{xy}^2}{\varepsilon^2} \cdot (1 - r_{xy}^2) \cdot q \right) - 1 - \left(\frac{r_{xy}^2}{\varepsilon^2} \cdot \left[\frac{1}{r_{xy}} - \frac{r_{xz}}{r_{yz}} \right] \cdot q \right) \leq 0 \\ & \Leftrightarrow \frac{r_{xy}^2}{\varepsilon^2} \cdot \left(\frac{r_{xz}}{r_{yz}} - r_{xy} \right) \cdot q - 1 \leq 0. \end{aligned}$$

Given that $0 < \varepsilon \ll 1$, this approximates to

$$\frac{r_{xy}^2}{\varepsilon^2} \cdot \left(\frac{r_{xz}}{r_{yz}} - r_{xy} \right) \cdot q \leq 0 \tag{D.6}$$

If, and only if, as specified earlier

$$\frac{r_{xz}}{r_{yz}} < r_{xy}$$

then condition (D.6) must be satisfied. We may therefore conclude that, in this case, the imposition of a minimum signalling level on player Y stabilizes the game.