PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1993 **340**, 245-250
doi: 10.1098/rstb.1993.0064

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SUMMARY

Evolutionarily stable strategy (ESS) models of biological signalling are important because the intimate coevolution of signalling and receiving strategies is complicated. Tentative results from a numerical study of error-prone signalling show the value of formal modelling. Error in perception can create discreteness in the distribution of signals produced, and so observed discreteness in nature may call for no more complicated explanation. Further developments in the theory of signalling may include a link with theories of aggression such as the sequential assessment game. The technical device of a 'scratch space' may allow a natural development of 'two-way' information games in which each contestant plays the roles of signaller and receiver simultaneously. This device may also incidentally derive mental states from purely strategic considerations.

1. INTRODUCTION

The applications of evolutionarily stable strategy (ESS) techniques (Maynard Smith 1982) to problems of biological signalling include those of Enquist (1985), Maynard Smith & Harper (1988), Grafen (1990*a*,*b*), Greenough (1991), Maynard Smith (1991), Godfray (1991), Johnstone & Grafen (1991, 1992, 1993), Johnstone & Norris (1993) and Hutchinson *et al.* (1993).

There are other types of mathematical theory about biological signals, for example the recent work of Enquist & Arak (this symposium) involving neural nets. Their model aims to explain the existence and form of latent preferences, that is, those for values of a trait that are not observed in nature, but which may nevertheless come into play as the system evolves. The quantitative genetics model of Iwasa *et al.* (1991) is related to signalling and has scope for development in that direction. The present paper, however, focuses on ESS signalling models, those that deal with the strategic choices of signalling and reception rules and with consequences of the assumption of evolutionary stability.

The virtues of ESS signalling models are those of ESS models in general. By making arguments explicit we can be sure what we are saying, we can detect mistakes more easily, and we can delve much deeper into the ramified logical consequences of the simple assumption of evolutionary stability.

Particular examples of useful ESS signalling models are not hard to find. Enquist (1985) constructed the first such model to scrutinize an alleged prediction from game theory that animals should never divulge their intentions (see, for example, Maynard Smith (1974, 1982); Caryl (1979, 1981)). He studied the very simplest model competent to tackle the question, and found circumstances in which it was evolutionarily stable to reveal intentions. This result is important, although it has been much neglected by those who like theories to make predictions, and the techniques and principles Enquist established are the foundations of ESS signalling theory.

Zahavi's (1975, 1977, 1987) handicap principle was refuted suspiciously many times before Grafen's (1990*a*,*b*) models made explicit the arguments that underlay it. Pomiankowski (1987*a*,*b*, 1988) had earlier suggested that it might be of importance as a modifier of the Fisher process, but from an ESS signalling perspective the handicap principle is a major and robust conclusion for a wide class of models, and an independent evolutionary force. See Greenough & Grafen (1993) for a fuller discussion of the literature on the handicap principle from this point of view.

The next part of this paper is a discussion of the consequences of uncertainty of perception in an ESS model of signalling during mate choice. Greenough (1991; see also Greenough & Grafen (1993) presents a model of sexual selection for good genes in which females pay immediate costs for genetic benefits. It was necessary for technical reasons to employ error-prone perception in this model, as it will be in a wide class of computer models of signalling. Johnstone & Grafen (1992) take a first step towards an analytical treatment of a simple signalling game with error-prone perception.

The topic is important because signal perception is in fact error-prone. It is also important as a preliminary to studying further questions. Multiple signalling, such as using a tail and a crest, of a single quality makes little sense unless perception is error-prone (Johnstone & Grafen 1992, 1993). Combining 'direct perception' of quality and signals of quality is unnecessary if either channel of communication is completely informative. One reason for extended signalling interactions may be that any given signal's information content is limited by the error-proneness of perception.

Phil. Trans. R. Soc. Lond. B (1993) **340,** 245–250
Printed in Great Britain

These further questions are becoming increasingly urgent as field studies of signalling become more frequent and more sophisticated. For example, multiple signals have been studied by Andersson (1991, 1992) and Evans & Hatchwell (1992*a*,*b*).

We are currently attempting a general analytical treatment of error-prone signalling. For the moment, we must confine ourselves to discussion of a small set of numerical results. First we describe the model, and discuss what might be expected on general grounds to be the effect of making perception error-prone. Then we present one figure to represent the results.

2. CONCEPTUAL DESCRIPTION OF THE MATE CHOICE MODEL

There are a fixed number of male qualities, coded as integers from $q_{\min}$ to $q_{\max}$. The probability distribution of male types is $g(q)$. A male strategy is a single non-negative real number for each quality, representing its advertising level. We represent such a strategy as a function $A(q)$, for integers q between $q_{\min}$ and $q_{\max}$. Each possible advertisement is perceived as falling into one of a range of advertising categories, coded as integers from $p_{\min}$ to $p_{\max}$. The family of probability distributions that define perceptual error is represented by $f(p;a)$. This is a probability distribution for p, integers between $p_{\min}$ and $p_{\max}$, with the advertising level a as a continuous parameter. For example $f(p;a)$ could be a binomial distribution, with a as the mean. Various choices have been made for f. The results we present are based on a 'discrete triangular' distribution of error.

The female strategy is a function $I(p)$ that represents an inference about the quality of the signalling male. Females are assumed to minimise the expected sum of squared discrepancies between actual and estimated quality. $I(p)$ in equilibrium will therefore be the mean quality of males perceived as signalling at level p. The males are assumed to maximise the expected value of a function $u(a,i,q)$, that depends on a, his advertising level, i the inference females make about his quality, and q, his quality. The function chosen has parameters a_0, q_0 and i_0 and is

$$u(a,i,q) = (a - a_0)\ln\left(\frac{q - q_0}{1.01(q_{\max} - q_0)}\right) + r\ln(i + i_0)$$

The constant 1.01 ensures that advertising is not cost-free for the highest quality males ($q = q_{\max}$). This function obeys all the requirements for the existence of an equilibrium in the case without error (Grafen 1990*a*), although these requirements have as yet no formal standing in a theory with error. There are many other such functions that are equally plausible.

An equilibrium of the model is a pair of strategies A^*, I^*, such that A^* maximizes the male maximand, and I^* gives the least square estimates of male quality for each advertising category.

The equilibria are found as follows. We begin with an initial pair of strategies A_0, I_0. The best reply A_{0r} to (A_0,I_0) is found, and a new strategy $A_1 = \lambda A_{0r} + (1 - \lambda)A_0$ is calculated. Then the best reply I_1 to A_1 is found, and the process can be repeated until convergence. The value of λ is adjusted according to the form of convergence. λ is increased if convergence is directional and slow, and decreased if convergence is oscillating. Local maxima appear in the male maximand, and this makes finding best replies more time-consuming. The whole procedure is carried out for a coarse grid of values of A, whose equilibrium is then used as the starting point for the whole procedure applied again for a finer grid of A, and so on until a desired level of precision is attained.

The probability distribution $f(p;a)$ is the focus of the study. The mean perceived signal should increase with a. To study the effect of variation in the magnitude of error, we need a distribution with an additional parameter v that changes the variance. The 'discrete triangular' distribution is defined by

$$f(p;a) \propto \max\{1 - \frac{|p - a|}{v}, 0\} \quad \text{and} \quad \sum_p f(p;a) = 1,$$

v is a half-width, so that any value outside the range $a \pm v$ has probability zero.

It is difficult if not impossible to find a discrete error function with continuous parameter a that satisfies three desirable properties: (i) the mean is a; (ii) the variance does not depend on a; and (iii) condition (3*b*) of Johnstone and Grafen (1992), which states that a higher level of advertising is more likely to be perceived as any higher level than any lower level, relative to a lower level of advertising. Formally this condition is

$$\frac{f(x_{\text{high}},a_{\text{high}})}{f(x_{\text{high}},a_{\text{low}})} > \frac{f(x_{\text{low}},a_{\text{high}})}{f(x_{\text{low}},a_{\text{low}})}$$

for any $x_{\text{low}} < x_{\text{high}}$ and $a_{\text{low}} < a_{\text{high}}$.

Other possible choices of error function include the negative binomial distribution, limiting to a Poisson at its minimum variance; and a translation of a hypergeometric distribution, limiting to a binomial at its maximum variance.

3. NAIVE EXPECTATIONS

The most basic question is whether the existence of uncertainty might destabilize the advertising equilibrium altogether. The importance of honesty of signals might suggest that if information is incomplete, then receivers will use it less, reducing the advantage to signalling and in turn the information provided by it. If the equilibrium still does exist, an important question is whether increased error in perception is associated with an increased or decreased amount of advertising. The reduced amount of information conveyed would suggest that increasing error should decrease the amount of advertising.

4. RESULTS

The results are presented as those of work in progress. Numerical studies by their nature produce tentative results. We use them as helpful preliminaries to an analytical assault on the problem. The main points of this paper are to show what kinds of questions ESS

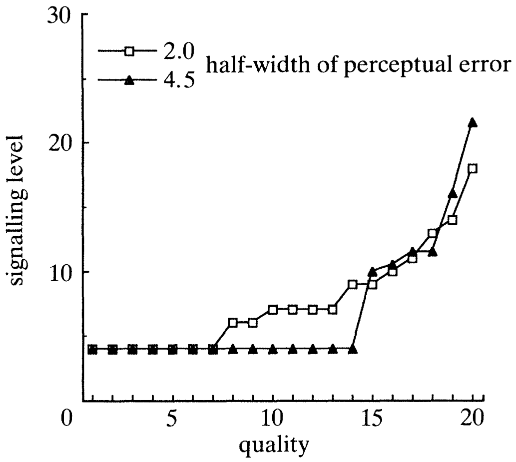

Figure 1. Evolutionarily stable signalling rule for the model described in the text with two different values of the half-width parameter determining the amount of error in perception. Increasing the error increases the range of qualities for which signalling is minimal, but does not affect the general level of signalling among those qualities of male that signal supra-minimally.

signalling theory can answer and what kind of phenomena it can discover. The smallness of the sample of results presented here is unlikely to be misleading on those counts.

Figure 1 shows the equilibrial signalling rules with two different half-widths of error in the discrete triangular error distribution. Further intermediate values would make the figure harder to read, and serve to confirm the following features of the curves:

1. There is an initial interval of quality for which males advertise at the lowest possible level. We shall refer to this as the 'initial flat'.
2. The initial flat is longer the greater the perceptual error.
3. There is a jump at the end of the initial flat that takes the signalling rule immediately up to the general level of the equilibrial signalling rules for lower degrees of perceptual error.
4. After the initial flats the curves move roughly together upwards.
5. There are secondary flats, at which several consecutive qualities share the same non-minimal signalling level, but these are not at the same places in the different curves.

Features 1–4 will be discussed first, as we believe feature 5 is of a different nature. Increasing perceptual error does turn out to decrease the level of advertising, but in a rather surprising way. Good males continue to signal at much the same level, but fewer and fewer males signal at all above the minimal level.

Increased perceptual error can therefore abolish signalling altogether, if the initial flat is so long that even the highest quality males are included in it. What determines that threshold level of perceptual error is one of the most important questions to be asked of an analytical theory. At the moment we lack not only this theoretical understanding but also any empirical work that measures the factors likely to be relevant. We are therefore doubly unable to say whether only unusually accurately perceived characters can possibly function as signals; or whether even unusually inaccurately perceived characters could do so.

We now turn to the secondary flats. These flats always occur as near as possible to integer values of advertising, and at first sight resemble modelling artefacts. They are almost certainly due to small non-linearities in the error function. Specifically, the mean of a discrete triangular distribution does not equal its central parameter (the x-value at the peak of the triangle). The secondary flats occur at the most advantageous advertising levels for gaining as high as possible a perceived average value for as low an expenditure as possible. In a continuous model with a smoothly translated error function, these secondary flats would not occur. In that sense they are an artefact of the computer model.

However, parallel to a point made about chaos by May (1976), there is a sense in which the discrete computer model is more realistic than the abstract continuous analytical model. In nature there will almost certainly be non-linearities of the same kind as introduced in the computer model, and probably greater in magnitude. For example, some magnitudes of signal may be more easily perceived than others, some may be more easily confused with stronger signals while others may more easily be confused with weaker signals. The implication of the secondary flats is that continuous variation in quality may well be reflected in a few discrete levels of signal.

The sharp division between minimal and non-minimal signallers, and the existence of secondary flats, may be related to phenomena such as the different breeding plumages of young males, or plumage dimorphisms among same aged males, or to the ritualisation of threat displays (Huntingford & Turner 1987; Archer 1988). Many other factors could be responsible for these observed discretenesses, but it is of considerable interest that they might be an evolutionary response to perceptual error alone. As perceptual error will always be present, we should demand positive evidence before we accept that any further factor is needed to explain discreteness of any set of signals. It is unlikely this consequence of perceptual error would have been discovered without formal modelling.

It is sensible to end with a caution. Numerical studies are rarely to be trusted, and some particular points may disappear on further work, or on completion of the analytical attack on the problem. One specific point is that the discontinuity at the end of the initial flat may well depend on concavity of the male maximand in perceived quality. Such concavity could result from a winner-take-all system, and so is not at all implausible in sexual selection. The general lesson that uncertainty in perception can be responsible for discrete levels of signalling is unlikely to be reversed even if it is qualified.

5. FUTURE DIRECTIONS

An analytical treatment of error-prone signalling is required. With a fuller understanding, we can proceed more confidently to study multiple signalling systems and combinations of signalling and 'direct perception' of quality. One pertinent question is whether multiple signals are likely to arise when a single quality is being advertised (Johnstone & Grafen 1992; and see Hasson (1989, 1991) for discussion of 'amplifying' displays); or if multiple signals should suggest the existence of multiple qualities, of different interest to different classes of receiver (Wedekind 1992).

These questions are all within our grasp at the moment. We now turn to a more complex problem, and make a methodological suggestion whose implementation will probably have to wait while more experience is gained with the technically simpler problems mentioned in the previous paragraph.

Error-proneness of perception limits the rate of information transfer, and so is one possible cause of extended signalling interactions. All the models we have discussed so far are 'one-way' signalling systems. There has been one signaller and one receiver. Many though not all signalling systems in nature are likely to be 'two-way' systems, in which two interactants play both roles simultaneously. One of the outstanding achievements of ESS theory has been Leimar and Enquist's 'sequential assessment game' (Leimar 1988; Enquist & Leimar 1990; Enquist *et al.* 1990, Leimar *et al.* 1991), directed to almost exactly this problem. It combines great technical difficulty with robust results predicting the existence of, and some details of, the frequently observed bout structure of animal contests.

In one important respect, however, the sequential assessment game is unsatisfactory. The combatants are constrained in the way they may use the information provided by their opponent. They maintain a rationally updated estimate of their opponent's strength, and must base their decisions just on the current value of that estimate. This leaves no scope for drawing inferences about an opponent's strength from his choice of behaviour. Thus combatants attend to the direct information supplied in the contest, but not to any signalling information. It is an interesting question in what circumstances only direct information should be used, but this question cannot be answered in the framework of a model in which this limitation is imposed.

The sequential assessment game is a good example of a 'two-way' information game. The central problem is that in the simple full game theoretic approach the strategy set is immensely unwieldy. Every possible history of an interactant must have its own specification of action. This is not only difficult to handle, but causes technical problems. Most possible histories will not arise in equilibrium, including some that are essential in supporting the equilibrium. (A very minor form of this problem is evaded by Grafen (1990*a*,*b*) using local flat extrapolation.)

The natural modelling response is to constrain the way information is used. The sequential assessment game allows combatants to use only the rationally updated estimate of opponent's quality. But any particular choice of what information to use imposes a character on the outcome of the game, in this case abolishing signalling.

We would like to suggest a possible line of attack on 'two-way' information games that restricts the amount of information a contestant can use but does not specify in advance what that information is to be. The idea is that a contestant has a fixed number of registers each of which contains a real number. His memory consists only of the contents of those registers, and so the number of registers measures how much information a contestant can retain. This is one formal way of representing the obvious fact that there is a limit to what an animal can remember.

The use to which those registers is to be put is part of the strategy. In an extension of the sequential assessment game, a possible strategy is to reserve one register for a rationally updated estimate of the opponent's strength, and to employ another to maintain an estimate of the opponent's apparent willingness to escalate. One register might contain an estimate of strength based on very recent evidence, in case injuries or fatigue have altered it. Another register might contain as assessment of the opponent's likely response to a rapid escalation.

With n registers, the animal essentially has an internal n-dimensional 'scratch space' that must serve as the animal's memory. The current position in the scratch space has no consequences other than its use as a memory. In this way it differs from the state space of Macfarland & Houston (1981), which represents physiological states such as hunger and thirst. Another difference is frequency dependence: the best use of the scratch space for one individual depends strongly on how other individuals are using theirs.

Suppose the approach proves feasible and we obtain an equilibrium rule. The uses to which the space is put can be thought of as defining concepts. The totality of information available momentarily to the animal at every instant has to be condensed into a few pieces of information which alone are able to influence future behaviour. We expect that discernible in the information stored would be: (i) 'facts' such as a rationally updated summary of the direct information on the opponent's strength; (ii) 'guesses', such as a guess about the opponent's strength based on all information; and (iii) 'intentions' such as the immediate response the animal would make if the opponent attacked now.

The importance of 'facts' is obvious. The importance of 'guesses' is that the relative advantage to different courses of action depends on the truth, not on how much of it has been discovered. Wearing a leotard and sporting a crooked nose near a wrestling ring are not hard evidence of fighting ability. Nevertheless one might be well advised to assume that a man who exhibits these traits is a wrestler, and make an educated guess about his likely fighting ability, preferably quickly enough to avoid gaining any hard evidence!

The importance of 'intentions' is that the information in the scratch space is wanted to influence future action. Information is processed in between being perceived and affecting actions. It may be more economical of storage to keep different pieces of information in different stages of processing. The more processed it is, the more it resembles mental states and the less it resembles perceptions.

The beauty of the scratch space approach, if it can be made to work, is that the way information is processed and stored will emerge from the equilibrium to the game. The mental-state-like information will be derived from considerations based only on strategy and economy of information storage.

With continuous scratch spaces, the topology of the real numbers must be respected. One way to ensure this would be to add an inescapable element of Brownian motion to the deterministic equations chosen as the strategy. Error-proneness of memory might therefore be a technically important part of scratch space models, though the same role could be played by error-proneness of perception if continuity of the effect of perception on scratch state can conveniently be enforced.

How would the scratch space idea be implemented formally? n registers specify an n-dimensional scratch space. The idea is that a strategy specifies how the scratch state should vary as a function of the current scratch state and the opponent's action; and also how the individual's own action should depend on the scratch state. These elements of strategy are functions from $\boldsymbol{R}^a$ to $\boldsymbol{R}^b$ for some a and b. This is not very far removed from the strategy sets used in Grafen (1990*a*,*b*) and Johnstone & Grafen (1991), which are functions form $\boldsymbol{R}$ to $\boldsymbol{R}$. Abstract strategy spaces allow more natural and general conclusions to be drawn in ESS signalling theory. The scratch space approach is admittedly sophisticated technically, but its advantages make it well worth a serious attempt.

A simpler form of scratch model would allow an animal a finite number of scratch states. For each scratch state, it would have as part of its strategy a rule about how to act and also a rule about which state to move to next depending on the opponent's action. This effectively models animals as game-playing Turing machines.

6. DISCUSSION

ESS signalling models have an important part to play in discovering the logic of animal signalling. There are other aspects to communication too. The physical and mechanical properties of signals, and the physiological properties of perceptual systems are important (Guilford & Dawkins 1992; Endler 1992). Information gleaned from non-signal characters will also be relevant (what we have called 'direct perception' of quality above). In sexual selection models, it is possible that linkage disequilibrium between preference and trait loci has a role to play (Kirkpatrick & Ryan 1991), and that sensory biasses are important (Ryan 1990; Ryan & Rand, 1990; Ryan & Keddy-Hector, 1992). Where strategic signalling is involved, however, ESS signalling models are essential as a conceptual aid.

The situation we would like to see in signalling is the one that now obtains in ESS models of aggression. There is a large body of theory to inform biologists about the logical structure they should expect to find in aggressive contests (see Huntingford & Turner (1987) and Archer (1988) for reviews). Basic ideas of asymmetries, continuous and discrete strategies, degree of information, and competing asymmetries, have all been worked out. Empirical biologists work against a logical and useful conceptual background when they study aggression.

Cynics may feel that theory has outstripped fact in aggression and strategic signalling models, but this is wrong. The technical difficulties of the models certainly make them inaccessible to those without mathematical skills. However, the biological content of the models is very limited. No existing model copes with two-way information flow in a signalling game, or with many receivers of one signal, although there has been verbal discussion of these possibilities (see McGregor, this symposium). The existing body of theory is probably too simple to be applied convincingly to any empirical example. An essential challenge for theoreticians is to draw biological conclusions for their models in a way that empiricists find useful.

The high point of ESS models of aggression is the sequential assessment game (Leimar 1988; Enquist & Leimar 1990; Enquist *et al.* 1991; Leimar *et al.* 1991). To take this line further and develop yet more realistic models of contests, it is essential to model how animals use information. The experience gained from the development of ESS signalling theory may therefore stimulate a new phase in our understanding of animal contests.

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