Discrete conventional signalling of a continuous variable*

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Abstract

In aggressive interactions, animals often use a discrete set of signals, while the properties being signalled are likely to be continuous, for example fighting ability or value of victory. Here we investigate a particular model of fighting which allows for conventional signalling of subjective resource value to occur. The result shows that neither perfect nor no signalling are evolutionarily stable strategies (ESSs) in the model. Instead, we find ESSs in which partial information is communicated, with discrete displays signalling a range of values rather than a precise one. The result also indicates that communication should be more precise in conflicts over small resources. Signalling strategies can exist in fighting because of the common interest in avoiding injuries, but communication is likely to be limited because of the fundamental conflict over the resource. Our results reflect a compromise between these two factors. Data allowing for a thorough test of the model are lacking; however, existing data seem consistent with the obtained theoretical results.

1 Introduction

Animals signalling in aggressive interactions use displays that are predominantly discrete (Cullen 1966; P. L. Hurd & M. Enquist, unpublished data), while the underlying properties being signalled are almost certainly continuous (e.g. relative fighting ability or estimated value of victory). It seems somewhat paradoxical that

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discrete displays should be used to signal continuous properties. One explanation is that the reduction in probability of errors in transmission favours discrete signals (Morris, 1957). Johnstone (1994) has modelled the evolution of this effect in the Sir Philip Sydney game.

An alternative explanation is that there is some strategic value in employing an ambiguous signal. Enquist (1985, model II) demonstrated this effect in a two-signal model. Here we present a generalized version of the model, analysing it further with respect to the tendency towards the use of discrete conventional displays.

2 Model and Results

Enquist (1985, model II) examined a situation in which two contestants meet over a non-divisible resource of some given size. The value, v, of this resource varies among contestants, so that different individuals are said to have different subjective resource values. When the contest starts each player knows his own subjective resource value but not that of the opponent.

The contest proceeds in one or two steps. In the first step each player shows a signal, or decides to give up, based on its own subjective resource value. Players act simultaneously. If both decide to give up the resource is randomly awarded to one of them. If one player gives up the resource is awarded to the other. No costs are paid in these cases. If both players give a signal the contest proceeds to the second step in which the contestants simultaneously decide whether to give up, or attack (and fight) based on the opponent's signal and their own subjective resource value. The minimum expected cost of a physical fight is c and additional costs of fighting depend on how willing the two players are to persist in an escalated contest. We will refer to c as the 'initial cost' of fighting. As we will see, the cost c is crucial for the stability of a signalling strategy, since it is the only factor that prevents bluffing. In reality, such a cost may arise from attacks by the opponent that cannot be avoided, even if the animal tries to flee.

Enquist (1985) considered the following communication strategy S: if v is above a threshold v_1 signal 1 is used; if $v_{i-1} \geq v > v_i$ then signal i is used and so on, and if $v \leq v_{n-1}$ then the decision is to give up (we can say that signal n is giving up). The contest proceeds to the second step if both players signal. If they use different signals, the individual that used the signal indicating the lowest subjective resource value decides to give up (i.e the signal with the higher index). If both players use the same signal they fight. This strategy reveals only some information about the state of the signaller, as each signal indicates a range of subjective resource values.

The strategy S was shown to be an ESS, given a set of assumptions: (a) two signals are used, in addition to the option of giving up; (b) subjective resource value is uniformly distributed in the population in the interval $[0, v_M]$; and (c) the cost of fighting, successive to the initial cost c, is modelled by the war of attrition with random rewards (Bishop et al., 1978).

Relaxing the first assumption, we find (see Appendix 1) that for a repertoire of n signals the thresholds are given by:

$$v_i = c\left(\sqrt{1+\frac{2v_{i-1}}{c}}-1\right) \qquad i = 1,\ldots,n-1 \tag{1}$$

where $v_0 = v_M$. We note that each threshold is defined by the higher ones (i.e. with lower indices), so that when passing from n signals to $n+1$ the thresholds that determine the use of the first n signals retain the same values, and the new signal 'eats up' some of the space that competed to giving up in the n-signal situation. Thus, when adding signals, these divide up the lower end of the resource interval, leaving unaltered the use of the pre-existing ones. This property is particular to the choice of a uniform distribution for the resource value, and it does not strictly hold for a generic distribution function. Even in other cases, however, the thresholds regulating the use of signals change very little when changing the repertoire size (see below), so that we can take the simpler case equation (1) to be representative of a more general situation.

It is clear from equation (1) that the interplay between initial cost c and the maximum resource value v_M determines the values of the thresholds v_i. To take into account this fact we introduce the variable f, defined as the ratio between c and the average of v. In the present case we have $f = 2c/v_M$, and in terms of f equation (1) becomes:

$$\frac{v_i}{v_M} = \frac{f}{2}\left(\sqrt{1+\frac{4}{f}\frac{v_{i-1}}{v_M}}-1\right) \tag{2}$$

so that the thresholds depend on v_M only as a scale factor (related to the units in which resource value is measured).

We see from equation (1) that it is the inescapability of the initial cost, c, that stabilizes communication; if in fact we consider the limit $c \to 0$, the result is $v_i = 0$ for all thresholds, i.e. no signalling, and no giving up either.

The general result is illustrated in Fig. 1, where we graph the partitioning of the resource interval for four values of f. When the initial cost of a fight is very low compared to the resource value, for example in fights over a valuable resource such as a mate or a territory, even animals with very low resource value use the most effective threat (leftmost bar in Fig. 1), and very few individuals choose to give up. In this case, as a consequence of a low value of f, very few signals are

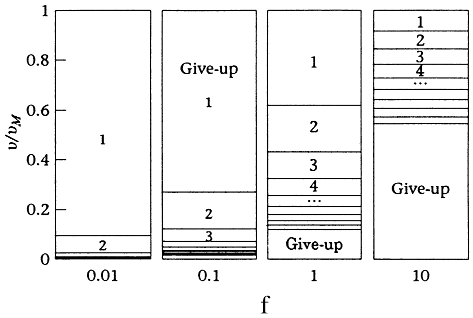

Figure 1: Use of signals as a function of subjective resource value for different values of f. Within each interval a given signal is used, as indicated. One interpretation of an increasing f is that the initial cost of fighting increases, while keeping the distribution constant. Another interpretation is that the initial cost is constant but the average subjective resource value decreases.

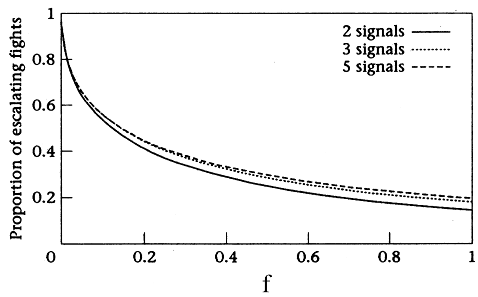

Figure 2: Proportion of interactions ending in a physical fight as a function of f when the repertoire size is two, three or five signals. Considering more than five signals gives results that are indistinguishable from the five-signal case in the graph. The formula for the proportion $p_n(f)$ of interactions resolved by a physical fight, is $p_n(f) = \sum_{i=1}^{n}(v_i - v_{i-1})^2$, with $v_n = 0$, and $v_0 = v_M$.

used with significant frequency even if a large number is available, and a great number of the interactions are settled by physical fighting (Fig. 2).

When f increases more and more signals are used in practice, the most effective one losing ground in favour of intermediate threats. This corresponds to situations in which the cost of being attacked is much more than the mean resource value, for example in the case of contests for a small amount of food or a resting site. In these cases (see e.g. the rightmost part of Fig. 1) the signals are more evenly spaced, meaning a more 'honest' communication of the individual's state: when fighting entails a high unavoidable cost, bluffing becomes less profitable. Note that in this situation each signal has the same likelihood of being followed by an escalated fight. This means that, for very high values of f, we should not necessarily expect a big difference among probabilities of escalation following different displays, suggesting that it might be difficult in practice to rank displays based on such data. Clear differences, however, are expected among displays with respect to probability of the winning.

The giving-up threshold, unlike the other thresholds, changes when varying the number of signals, making giving up progressively more rare as the repertoire size increases. The fact that individuals with low subjective resource value signal instead of giving up increases slighlty the number of contests escalating to physical fights (see Fig. 2), with respect to situations in which the repertoire is smaller. This result is counter-intuitive and potentially problematic. It seems to depend on the giving-up option having certain specific properties. If both players initially decide to give up, they are committed to sharing the resource (or to accept a random assignment). This assumption seems unrealistic. If both players observe the other giving up, an alternative strategy of trying to monopolize the resource is likely to do better than the strategy of sharing the resource (cf. the hawk-dove game, Maynard-Smith 1982). It is easy to remove the specific giving-up option from the model, by a straightforward modification of equation A1.1 (see Appendix 2). The model can be solved numerically and, as can be seen in Fig. 3, the structure of the solution is very much the same as in the previous case. The important difference in results is that when the repertoire size increases, the probability of escalation decreases rather than increases, as shown in Fig. 4. In addition, the thresholds became slighlty higher, meaning that individuals will be a little more cautious in using the more efficient threat signals.

As mentioned earlier, the above results do not qualitatively change when considering other probability distributions for the subjective resource value. In the general case we are not able to provide a simple formula as equation (1), but it is possible to solve the model numerically. As an example we provide Fig. 5, obtained with an exponential distribution, where we can see that the threshold for using the most effective threat moves slightly when adding four more signals to the repertoire, but qualitatively the results are the same as in the uniform-distribution

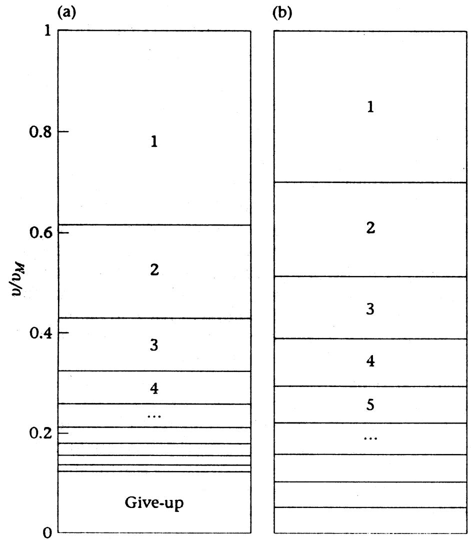

Figure 3: Effect of removing the giving-up option on the ESS. The thresholds values change from those in the left column to the values on the right, but the structure of the solution is the same. In the graph $f = 1$ is used.

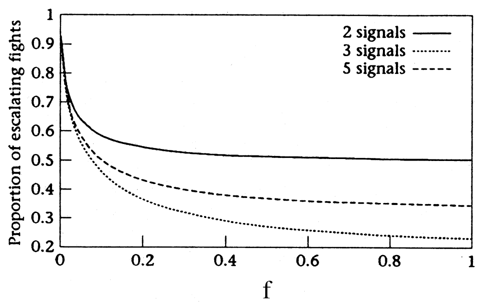

Figure 4: Proportion of interactions ending in a physical fight as a function of f when the players do not have the option to give up. The plotted lines refer to repertoire sizes of two, three or five signals. The number of escalating fights decreases when the players are allowed to use more signals (cf. Fig. 2).

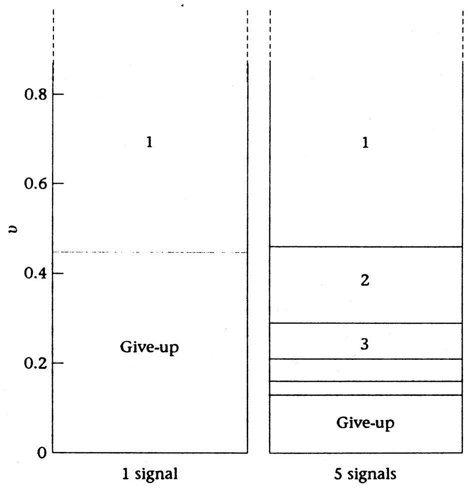

Figure 5: Use of signals as a function of subjective resource value in the case of an exponential distribution of resource value, $g(v) = \exp(-v)$. The initial cost is 0.3, and the solution for repertoire sizes of one and five signals are shown. The threshold beyond which the most effective threat is used changes from $v_0 \simeq 0.449$ to $v_0 \simeq 0.461$.

case. We have obtained the same results for a number of other distributions. A technical reason for this consistency is that only the cumulative distribution function, $G(v) = \int_{v_m}^{v} g(\xi)\mathrm{d}\xi$, enters the equations (see Appendix 1), and all cumulative functions share some important structural properties.

3 Discussion

The model studied in this paper, originally described by Enquist (1985), shows that if a physical fight entails a minimum cost (i.e. a cost that can not be avoided), then discrete conventional signalling of a continuous trait becomes possible in fighting behaviour despite the opposing interests of the players. In addition, the model suggests that conventional signalling will be important in deciding contest outcome when the value of the resource is of equal or lesser magnitude than the cost of an attack.

How do these predictions compare with reality? Most animal conflicts are not characterized by signalling in the narrow sense portrayed here. Instead, fights are dominated by activities which communicate information about relative fighting ability through the performance of acts such as pushing or pulling, which are unbluffable (see e.g. Dawkins & Krebs, 1978). These activities are typically repeated many times and there is an escalation during the fight (e.g. Enquist & Leimar, 1990). The number of distinct threat displays used is small. We know of no observations indicating that prolonged fights are settled by conventional signalling alone. Fights tend to be longer and more costly when the subjective resource values increase for both opponents (e.g. Enquist & Leimar, 1987) . Hence, fights over valuable resources are not settled by conventional signalling. If, however the resource is only valuable to one of the contestants a simple threat display may be decisive. For instance, if an animal happens to cross another animal's territory a threat display from the owner is usually enough to cause the intruder to retreat (Davies, 1981).

What about when the resource is of low value to both opponents? The richest and most flexible use of signals we know of is in contests between birds over resources such as a few seeds or a temporary resting site (P. L. Hurd & M. Enquist, unpublished data). The signals used in these situations are discrete in their nature. Intermediate forms of the displays do occur, but typically behaviour patterns fall into distinct categories with little variation within each one (Morris, 1957). That subjective resource value influences choice of signal in fighting behaviour has been shown by Enquist et al. (1985), Senar (1990) and Popp (1987).

Another study with results consistent with our model concerns aggressive signalling in the parrots genus *Trichoglossus* (Serpell, 1982). In this genus, species with larger beaks (presumably capable of inflicting more cost in a single attack) employ larger repertoires of signals and have lower tendency to attack their mirror images.

In conclusion, existing data on aggressive signalling are consistent with our results. It must be recognized, however, that the existing empirical information does not allow a satisfactory evaluation of the model. For instance, we need studies of groups other than birds, and experimental data on how subjective resource value influences choice of agonistic signals.

The only game-theoretical model that we are aware of that produces discrete conventional signalling from an underlying continuous variation is the cheap talk model by Crawford & Sobel (1982; see also Gibbons 1992). In this model a sender can be in different states (varying continuously along a single dimension). This state determines which receiver response is most preferable to both the sender and to the receiver. The players' interests may not coincide perfectly but there is, however, a degree of common interest that can varied by changing a parameter. The sender can signal its state to the receiver. The following solution is obtained: when the players interests are not exactly the same, the sender will not provide perfect information but rather use a set of discrete signals, each indicating a set of states. For each degree of common interest there is an upper bound to the number of signals that yield an equilibrium solution. When the common interest increases more signals are possible and when all conflicts are removed the state can be communicated with arbitrary precision.

We recognize several similarities, as well as differences, with the model dealt with in this paper. In both models, the degree to which the state of the individual can be communicated by signalling decreases when the conflicts between the players increase. However, in contrast with the cheap-talk model, our model has no upper bound for the number of signals but in practice only a finite number of signals have any likelihood to be used.

Another difference is that in the cheap-talk model different interests exist among the senders with respect to the most preferred response. In fighting, the most preferred response is always that the opponent give up. Thus, it is not generally required that senders have different preferences with respect to the receiver's response to allow for a stable conventional signalling strategy. Fundamental to fighting strategies is that cost-inflicting behaviour will be used eventually unless the fight can be settled in some other way. In our model it is a necessary condition for signalling to occur that the cost of an attack be unavoidable. It is this cost that produces the common interest between the players with unequal subjective resource values.

Appendix 1. Solution of the game with n signals

In the case of n signals and a uniform distribution in $[0, v_M]$ of resource value, with fights modelled by the war of attrition, we have to solve the following equations (see Enquist, 1985, for details):

$$\begin{cases} (v_i - v_{i+1})(c + \frac{1}{2}(v_i + v_{i+1})) - c(v_{i-1} - v_i) = 0\,, & i = 1, \ldots, n-2 \\ v_{n-1}\left(\frac{1}{2c} v_{n-1} + 1\right) = v_{n-2} \end{cases} \tag{A1.1}$$

where we recall that $v_0 = v_M$ by definition. By solving the equations for $n = 1, 2, 3$ and so on, one notices that the pattern equation (1) emerges. A more general approach, once this regularity has been discovered, is to look for the conditions in which the thresholds are independent of repertoire size, and then verify that in the case of a uniform distribution of v and war-of-attrition fights, the result equation (1) holds.

The general form of equation (A1.1) is (see Enquist, 1985):

$$\begin{cases} (G(v_i) - G(v_{i+1}))(d(v_i, v_{i+1}) + c) - c(G(v_{i-1}) - G(v_i)) = 0\,, & i = 1, \ldots, n-2 \\ G(v_{n-1})\left(\frac{1}{2c} v_{n-1} + 1\right) = G(v_{n-2}) \end{cases} \tag{A1.2}$$

where $d(v_i, v_{i+1})$ is the cost of physical fight for an individual with subjective resource value v_i fighting against the subpopulation of individuals whose resource values are in the interval $[v_{i+1}, v_i[$, and $G(v)$ is the cumulative function pertaining to the assumed distribution $g(v)$:

$$G(v) = \int_{v_m}^{v} g(\xi)\mathrm{d}\xi \tag{A1.3}$$

v_m being the lower end of the resource interval.

The system equation (A1.2) can be solved, without any assumptions on the function $d(v_i, v_{i+1})$, in the hypothesis that the thresholds are independent of n. To see this, let's consider what happens when going from $n = 2$ to $n = 3$. In the first case we only have one threshold, satisfying:

$$G(v_1)\left(\frac{v_1}{2c} + 1\right) = 1 \tag{A1.4}$$

while in the second case we have to solve:

$$(G(v_1) - G(v_2))(d(v_1, v_2) + c) - c(1 - G(v_1)) = 0 \tag{A1.5}$$
$$G(v_2)\left(\frac{v_2}{2c} + 1\right) = G(v_1)\,. \tag{A1.6}$$

If the thresholds don't move, though, equation (A1.4) is still valid in this case, so that it can be used together with equation (A1.6) to find the thresholds without dealing with the more complex equation equation (A1.5) involving the cost function $d(v_1, v_2)$. This, in turn, poses a constraint on $d(v_1, v_2)$, so that when v_1 and v_2 are linked by equation (A1.6), then equation (A1.5) has to be satisfied. This can easily be generalized to n signals, in which case the thresholds satisfy the following equations:

$$G(v_i)\left(\frac{v_i}{2c} + 1\right) = G(v_{i-1}) \qquad i = 1, \ldots, n-1\,. \tag{A1.7}$$

The relations equation (A1.7) give the expressions equation (1) in the uniform-distribution case, when $G(v) = v/v_M$. By using these expressions in equation (A1.2), we find, after some algebra, that the constraint on $d(v_i, v_{i+1})$ can be written as:

$$d(v_i, v_{i+1}) = c\left(\frac{v_i G(v_i)}{v_{i+1} G(v_{i+1})} - 1\right), \tag{A1.8}$$

where, we recall, there is only one independent threshold in equation (A1.8) due to the relations equation (A1.7). This means that equation equation (A1.8) does not have to hold for arbitrary (v_i, v_{i+1}) pairs, otherwise the function $d(v_i, v_{i+1})$ would be fixed to be the right hand side of equation equation (A1.8), but it must hold only when the relations equation (A1.7) link the different thresholds. At this point it is easy to use the appropriate expressions for a uniform distribution in $[0, 1]$, $G(v) = v$, and for the war of attrition, $d(v_i, v_{i+1}) = (v_i + v_{i+1})/2$, and verify that with these substitutions equation (A1.8) is satisfied when the relations equation (1) hold.

In summary, we have proved that equation (1) holds in the n-signal case when resource value is uniformly distributed and the cost of physical fight can be expressed as a function satisfying equation (A1.8), the war of attrition being a particular case.

Appendix 2. Solution without the 'Give-up' option

When we exclude the specific giving-up option from the model, we have the equation:

$$(G(v_i)-G(v_{i+1}))(d(v_i,v_{i+1})+c)-c(G(v_{i-1})-G(v_i))=0 \qquad \text{(A2.1)}$$
$$i=1,\ldots,n-1$$

that is a straightforward modification of (A1.1): the second equation has simply been removed.

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