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Calculating the ESS level of information transfer in aggressive communication

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Summary

We present a model of aggressive communication that demonstrates the use of evolutionarily stable ambiguous threat displays. We use stochastic dynamic programming to solve a game in which two contestants of differing fighting ability communicate using cost-free threats. These contestants use communication strategies that supply information of varying reliability to the opponent. The results demonstrate that communication does not need to be either costly or unambiguous to be evolutionarily stable.

Keywords: communication; threat; cost; honesty; aggression

Introduction

Current models of animal conflict rely heavily on the theory of games (Maynard Smith, 1982). The first theoretical analyses of animal contests made use of two games: the war of attrition (Maynard Smith and Parker, 1976; Bishop and Cannings, 1978) and the hawk–dove game (Maynard Smith and Price, 1973; Maynard Smith and Parker, 1976; Maynard Smith, 1982). The hawk–dove game demonstrated that contests may be resolved by conventional displays, while the war of attrition demonstrated the evolutionary instability of displaying information about intended actions.

However, not all information exchange is necessarily communication of intent. There remains information about ability, for example visual (e.g. Robinson, 1985; Enquist and Jakobsson, 1986; Enquist *et al.*, 1987) or auditory (e.g. Davies and Halliday, 1978) cues of body size, condition (e.g. Clutton-Brock and Albon, 1979) or status (e.g. Rohwer, 1977; Rohwer and Rohwer, 1978). Theoretical speculation was that unequally matched contestants should communicate their resource holding potential (RHP (Parker, 1974) or ability to win an all-out fight (Maynard Smith, 1979)).

Current theoretical work on the communication of RHP revolves around Enquist and Leimar's (1983) sequential assessment game. Communication in this game is modelled as repeated updating of estimated relative fighting ability (the difference between the opponents' RHPs). The actor engages a reactor in a bout of some potentially risky nature and this interaction provides the actor with a sample of relative ability. This sample is combined with the actor's current estimate, producing a new information state (DeGroot, 1970; Enquist, 1984). The sequential assessment game is one example of a communication system that is not driven by the inherent costs of displays. There is widespread belief (Zahavi, 1975, 1977, 1993; Grafen, 1990) that evolutionary stability requires such costs. Enquist (1985) has demonstrated signalling of motivation using cost-free conventional signals; we present below a demonstration of the cost-free signalling of fighting ability.

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Here we present a sequential threat game in which the uncertain element is placed in the reactor. An actor makes a threat prompting a response ('fear' or 'no fear') from the reactor. The actor processes information using a Bayesian updating procedure that calculates the probability of each possible opponent RHP level. The only stochastic element in the exchange lies in what type of reply the reactor produces when threatened. The probability of returning a 'fear' sample is a function of the threatened individual's perception of the RHP asymmetry. This function is the reactor's communication strategy.

We demonstrate that while a non-communicating ESS does exist, so do several others which use information of intermediate clarity, being neither maximally informative nor non-communicating.

The model

Basic overview

The model describes competition over a non-divisible resource by two strangers. We will refer to these players as A and B. The player acting at any given time is called 'ego', and the player not acting is called 'opponent'. The ego and opponent roles switch in the middle of each turn, so that both players move every turn. Much of the model is best understood in terms of ego and opponent, rather than players A and B.

In each turn both players must choose one of the three behavioural options: quit, threaten or fight. Possible outcomes for each contestant are win, lose without sustaining an injury and lose with an injury. Losing with injury returns no fitness, uninjured losers collect a residual fitness, V_r and winners receive the residual fitness plus the prize value, V_k.

In choosing to quit, a contestant ensures that it will lose without injury, while the opponent wins. By choosing to fight, a contestant attempts to take the resource and the probabilities of success and injury are determined as a function of the difference between ego and opponent RHP values. Both quit and fight are end-points, in that the contest is resolved in favour of one of the contestants when one of these behaviours is selected.

Threat returns either a 'fear' or 'no fear' response from the opponent. The probability of a fear sample being returned is based on the opponent's assessment of the differences in fighting ability between the contestants. This assessment is crucial to the strategy because the estimated chances of winning a fight and the probability of injury, are derived from it. With each threat, the actor improves its assessment of the opponent's RHP.

Stochastic dynamic programming (Mangel and Clark, 1988) is used to derive the set of optimal behaviours under all possible combinations of state. Forward iteration (Mangel and Clark, 1988) is then used to calculate the expected fitness of each RHP and role combination.

Two versions of the model are presented. In the first model, all contestants use the same function for determining the probability of responding to a threat with fear. In the second, players use one of several possible functions for determining how to respond to threats.

Model dynamics

The solution proceeds through successive time intervals $t = 1, 2, 3 \ldots T$ and terminates (if neither contestant has yet chosen to quit or fight) at $T = 10$. Contestants alternate in each time interval, with player A being ego first and player B second.

Contestants are assigned an RHP state, which does not change during a contest. A player's state is also described by the number of times, n, that the opponent has responded to a threat with 'fear' and, t, the number of turns elapsed. Since threat is the only non-end-point behavioural option, the number of 'no fear' samples must equal $t - n$.

Contestants know the present values of n and t as well as their own fighting ability (RHP_e) and the population distribution of fighting abilities (Υ_{RHP}). The contestants do not know their opponent's fighting ability, RHP_o, nor do they know the number of fear samples, n_o, collected by their opponent, but probabilistic estimation of these opponent state variables is possible.

Decisions

We let Φ_e denote the fitness of ego as a function of RHP_e, n, t and T (potentially confusing symbols are explained in Table 1). If ego's behaviour, B_e, is to quit ('Q') then a pay-off equal to residual fitness, V_r (lose without injury) is returned,

$$\Phi_e(RHP_e,n,t,T,B_e \mid B_e = 'Q') = V_r \tag{1}$$

The pay-off to a fight behaviour ('F') against an opponent of known RHP is

$$\Phi_e(RHP_e,n,t,T,a,B_e \mid \mathrm{B_e} = '\mathrm{F}') = (1 - \omega(a))(V_r + \pi(a)V_k) + \omega(a) \cdot 0 \tag{2}$$

where, a is the asymmetry in RHPs, $a = RHP_e - RHP_o$, $\omega(a)$ is the probability of getting injured as a function of a, and $\pi(a)$ is the probability of winning as a function of a.

Parameter values are shown in Table 2.

Since ω and π are both functions of a, a contestant must have an estimate of RHP_o to calculate the expected pay-off of fighting. The estimate is made by threatening the opponent and observing the response. The mechanism behind this estimation procedure is presented below (see Estimating opponent state).

With increasing numbers of threats made, the accuracy of the estimates of the opponent's RHP increases. Since threat is not an end-point, the opponent will reply with a behaviour of it's own. It is necessary to know what the opponent's next behaviour, B_o, will be to evaluate the threat pay-off. Finding this reply is a matter of checking the opponent's optimal behaviour set for the opponent state (the combination of opponent's RHP, t and n) under consideration. Ego must do this for each possible RHP and n, to calculate a probability of each combination.

If the opponent's next move is to quit then the pay-off for threatening ('T') the opponent is

$$\Phi_e(RHP_e,n,t,T,a,B_e,B_o \mid \mathrm{B_e} = '\mathrm{T}',B_o = '\mathrm{Q}') = V_k + \mathrm{V_r} \tag{3}$$

If the opponent's next behaviour is fight, then the pay-off for threatening is

$$\Phi_e(RHP_e,n,t,T,a,B_e,B_o \mid \mathrm{B_e} = '\mathrm{T}',B_o = '\mathrm{F}') = (1 - \omega(a))(V_r + \pi(a)V_k) \tag{4}$$

If the opponent's next behaviour is threat, then the pay-off for threatening is

$$\begin{aligned}\Phi_e(RHP_e,n,t,T,a,B_e,B_o \mid \mathrm{B_e} = '\mathrm{T}',B_o = '\mathrm{T}') &= \Psi_{S_e}(a)\Phi_e(RHP_e,n + 1,t + 1,T) \\ &+ (1 - \Psi_{S_e}(a))\Phi_e(RHP_e,n,t + 1,T)\end{aligned} \tag{5}$$

where Ψ is ego's estimated probability of the opponent responding with 'fear' to a threat, as a function of a.

The fear – no fear mechanism

The parameter S is used to track which Ψ function an individual is playing. Players cannot change their Ψ strategy, while S is treated as a state variable for computational puposes, it is not dynamic. Ψ_{S_e} is ego's Ψ and Ψ_{S_o} is the opponent's. All $\Psi_S\,(a)$ functions are linear, differ in slope and are given by

Table 1. Symbols used

Equation	Symbol	Interpretation
1	$\Phi_e(RHP_e,n,t,T,B_e \mid \mathrm{B_e} = \text{'Q'})$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to quit
2 and 9	$\Phi_e(RHP_e,n,t,T,a,B_e \mid \mathrm{B_e} = \text{'F'})$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to fight an opponent when the RHP asymmetry is a
3	$\Phi_e(RHP_e,n,t,T,a,B_e,B_o \mid B_e = \text{'T'},B_o = \text{'Q'})$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to threaten an opponent whose next behaviour is to quit, when the RHP asymmetry is a
4	$\Phi_e(RHP_e,n,t,T,a,B_e,B_o \mid \mathrm{B_e} = \text{'T'},B_o = \text{'F'})$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to threaten an opponent whose next behaviour is to fight, when the RHP asymmetry is a
5	$\Phi_e(RHP_e,n,t,T,a,B_e,B_o \mid \mathrm{B_e} = \text{'T'},B_o = \text{'T'})$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to threaten an opponent whose next behaviour is to threaten, when the RHP asymmetry is a
5	$\Phi_e(RHP_e,n + 1,t + 1,T)$	The maximum expected fitness for ego when its RHP is RHP_e, has received $n + 1$ fear samples on turn $t + 1$
5	$\Phi_e(RHP_e,n,t + 1,T)$	The maximum expected fitness for ego when its RHP is RHP_e, has received n fear samples on turn $t + 1$
5,6,7,8,15,16,17	$\Psi_{S_e}(a)$	What ego estimates to be the probability that the opponent will respond with fear to a threat as a function of the perceived RHP asymmetry, a. S denotes one of five functions (see Fig. 1)
6	$\Psi_S(a)$	The probability that the opponent returns a fear sample as a function of their RHP asymmetry, a. S denotes one of five functions (see Fig. 1)

Table 1. Symbols used

7	$Pr(RHP_o \mid t,n)$	The probability that the opponents RHP is RHP_o given that ego has received n fear samples on turn t
8	$Pr(n_o \mid t,a)$	The probability that the opponent has received n_o fear samples on turn t given that the asymmetry is a
9	$\Phi_e(RHP_e,n,t,T,B_e \mid \mathrm{B_e} = \text{'F'})$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to fight an opponent
10	$\Phi_e(RHP_e,n,t,T,B_e \mid \mathrm{B_e} = \text{'T'})$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to threaten an opponent
10	$\sum_{n_o=0}^{n_{max}}$	Sum across all possible values of n_o. If player A is ego then B will still act this turn and the maximum n_o is equal to t. If B is ego then A will act in the next turn, when the maximum n_o will be $t + 1$
11	$\Phi_e(RHP_e,n,t,T)$	The maximum expected fitness for ego when its RHP is RHP_e, has received n fear samples by turn t
11	$\Phi_e(RHP_e,n,t,T,B_e)$	The expected fitness for ego when its RHP is RHP_e, has received n fear samples and on turn t decides to use behaviour B_e
15,16 and 17	Ψ_{S_o}	What the opponent believes to be the probability that ego will respond with fear to a threat
15 and 17	$W(\Psi_{S_e} \mid \mathrm{R}, RHP_e, \Psi_{S_o})$	The expected fitness when player R (A or B) is ego, has a RHP equal to RHP_e, and is playing strategy Ψ_{S_e} against an opponent playing strategy Ψ_{S_o}
15 and 16	$P(t,n \mid \Psi_{S_e}, \Psi_{S_o})$	The proportion of the ego population which, by turn t, has not quit and has had n fear samples returned to it, given that ego is using Ψ_{S_e} and the opponent is using Ψ_{S_o}

Table 2. Parameter values used

RHP	Υ_{RHP}	a	$\pi(a)$	$\omega(a)$	$\Psi_1(a)$
1	0.1	−4	0.1	0.3	0.1
2	0.2	−3	0.2	0.25	0.2
3	0.4	−2	0.3	0.2	0.3
4	0.2	−1	0.4	0.2	0.4
5	0.1	0	0.5	0.15	0.5
–	–	1	0.6	0.1	0.6
–	–	2	0.7	0.05	0.7
–	–	3	0.8	0.02	0.8
–	–	4	0.9	0.01	0.9

Υ is the population distribution of RHPs, a is RHP asymmetry ($RHP_e - RHP_o$), $\pi(a)$ is the probability of winning a fight, $\omega(a)$ is the probability of injury in a fight, $\Psi_1(a)$ is the probability that the opponent returns a fear sample, $\Psi_1(a)$ is that used in the simple model. V_r was 0.333 and V_k was 0.667, meaning that the maximum fitness was 1.0.

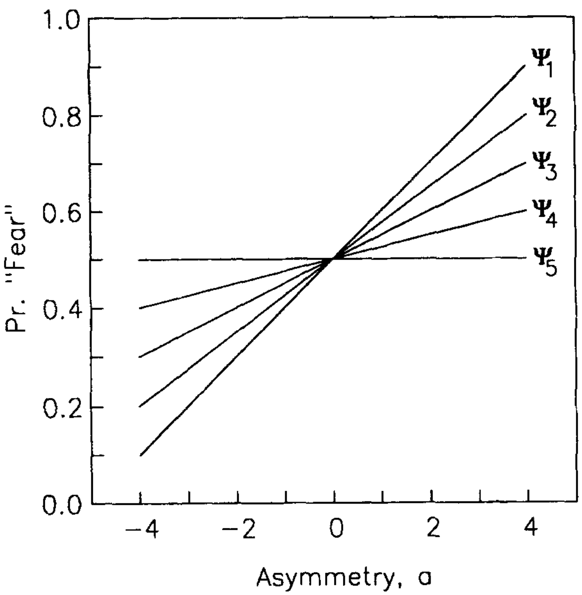

Figure 1. Strategy sets, $\Psi_s(a)$ functions. Pr. "Fear" is the probability that the opponent will return a 'fear' sample as a function of the asymmetry. The asymmetry is $RHP_e - RHP_o$. Note that the simple model used Ψ_1 exclusively.

$$\Psi_s(a) = \left(\frac{S}{2S_{max}} + a + RHP_{max} - 1\right)\left(0.1 - \frac{0.1(S-1)}{S_{max}}\right) \tag{6}$$

where S_{max} is the number of strategies available, five.

Functions with a low slope are less reliable indicators of RHP (see Fig. 1). Thus, strategy 1, Ψ_1 (a), is the most informative and strategy 5, Ψ_5 (a), is the least informative. The Ψ function used in the simple model was (Ψ_1 (a)).

Estimating opponent state

Estimation of the pay-offs to the fight and threat options requires that the actor have an estimate of RHP_o and n_o. Pay-offs for each opponent state are weighted by the estimated probability that the opponent is actually of that state. The Bayesian updating function (DeGroot, 1970) gives the probability that the opponent has a given RHP level conditioned on t and the number of samples returned,

$$Pr(RHP_o \mid t,n) = \frac{\Upsilon(RHP_o)\binom{t}{n}\Psi_{S_e}(a)^n(1 - \Psi_{S_e}(a))^{t-n}}{\sum_{RHP_i=1}^{RHP_{max}} \Upsilon(i)\binom{t}{n}\Psi_{S_e}(RHP_{e-i})^n(1 - \Psi_{S_e}(RHP_{e-i}))^{t-n}} \tag{7}$$

$\Upsilon(RHP)$, the actual population distribution of RHP, serves as the prior. The probability that the opponent has received a given number of samples is

$$Pr(n_o \mid t,a) = \binom{t}{n_o}\Psi_{S_e}(a)^{n_o}(1 - \Psi_{S_e}(a))^{t-n_o} \tag{8}$$

The dynamic programming equation

Combining Equations 2 and 7 gives the expected pay-off of a fight against an opponent of uncertain RHP,

$$\Phi_e(RHP_e,n,t,T,B_e \mid \mathrm{B_e} = 'F') = \sum_{RHP_o=1}^{RHP_{max}} Pr(RHP_o)\Phi_e(RHP_e,n,t,T,a,B_e \mid \mathrm{B_e} = 'F') \tag{9}$$

Similarly, the expected pay-off to threatening an opponent is

$$\Phi_e(RHP_e,n,t,T,B_e \mid \mathrm{B_e} = \mathrm{'T'} =$$

$$\sum_{RHP_o=1}^{RHP_i} Pr(RHP_o) \sum_{n_o=1}^{n_{max}} Pr(n_o)\Phi_e(RHP_e,n,t,T,B_e,B_o \mid \mathrm{B_e} = 'T') \tag{10}$$

where n_{max} is t if ego is 'A' and $t \times 1$ if ego is 'B' (see Table 1). The fitness to ego is thus

$$\Phi_e(RHP_e,n,t,T) = \max_{B_e}\{\Phi_e(RHP_e,n,t,T,B_e)\} \tag{11}$$

Equation 11 provides a solution set of optimal behaviours $B(n,t)$ for each combination of Ψ_{S_e} and Ψ_{S_o}, for players A and B. Implementing the equation for all $_{S_e}$, Ψ_{S_o} yields a $B_{S_e}(n,t, \Psi_{S_e}, \Psi_{S_o})$ for each player. Backward iterations use ego's strategy, Ψ_{S_e}, to generate the optimal behaviour matrix (e.g. Fig. 2) and the forward iterations use the opponent strategy, Ψ_{S_o}, to calculate fitness.

Initialization

Equation 5 (and, thus, Equations 10 and 11 also) requires fitnesses at T to be specified before it can be used to calculate fitnesses at earlier times. These end conditions are calculated using modified versions of the equations above since the rules change slightly at the end of the game. Player B cannot threaten on the very last move of the game and player A's move at T is made with the knowledge that B will not play threat next. The end conditions are given below.

For player B,

$$\Phi_B(RHP_B,n,T,T) = \max_{B_B}\{\Phi_B(RHP_B,n,T,T,B_B)\} \tag{12}$$

where B_B is one of Q or F. For player A,

$$\Phi_A(RHP_A,n,t,T) = \max_{B_A}\{\Phi_A(RHP_A,n,T,T,B_A)\} \tag{13}$$

where B_A can be any of Q, T or F and

$$\Phi_A(RHP_A,n,T,T,B_A \mid \mathrm{B_A} = 'T') =$$
$$\sum_{RHP_B=1}^{RHP_{max}} Pr(RHP_B) \sum_{n_B=0}^{T} Pr(n_B)\Phi_e(RHP_e,n,T,T,B_A,B_B \mid \mathrm{B_e} = 'T') \tag{14}$$

where B_B is one of Q or F.

Calculating fitness

A weighted mean of all possible outcomes was calculated to obtain the expected fitness of each strategy.

The probability of each possible outcome was calculated for each (t, n) state. As end-points were reached, the pay-offs were weighted by the transition densities (Mangel and Clark, 1988) of the states in which they were reached,

$$W(\Psi_{S_e} \mid R,RHP_e,\Psi_{S_o}) = \sum_t^T \sum_n^t P(t,n \mid \Psi_{S_e},\Psi_{S_o}) \times \begin{cases} V_r & \text{if } B_e \text{ is } Q \\ \sum_{RHP_o} \sum_{n_o} \begin{cases} V_r + \mathrm{V_k} \\ \text{if } B_e \text{ is } T \text{ and } B_o \text{ is } Q \\ (1 - \omega(a)V_r \times \pi(a)V_k \\ \\ \text{if } B_e \text{ is } T \text{ and } B_o \text{ is } F \end{cases} \\ (1 - \omega(a))V_r \times \pi(a)V_k & \textit{if } B_e \text{ is } F \end{cases} \tag{15}$$

where the transition density, $P(t, n \mid \Psi_{S_o})$, is

$$\begin{aligned} P(t,n \mid \Psi_{S_o}) = {} & P(t-1,n \mid \Psi_{S_o})(1 - \Psi_{S_o}) \mid B_e = 'T') \sum_{RHP_i} \sum_{n_o} Pr(RHP_o)Pr(n_o) \mid B_o = 'T' \\ & + P(t-1,n-1 \mid \Psi_o)(\Psi_o) \mid B_e = 'T') \sum_{RHP_o} \sum_{n_o} Pr(RHP_o)Pr(n_o) \mid B_o = \mathrm{'T'} \end{aligned} \tag{16}$$

This produces a fitness function $W(\Psi_{S_e} \mid R, RHP_e, \Psi_{S_o})$ function, where R is role, either A or B.

Calculating ESSs

Evolutionarily stable strategy (ESS) profiles (a matching pair of Ψ_{S_A} and Ψ_{S_B}) can be determined from the $W(\Psi_{S_e} \mid R, RHP_e, \Psi_{S_o})$ function. All RHP classes of an A or B population are assumed to play the same strategy. The best reply, Ψ_{S_e}, to any opponent strategy is,

$$\Psi^*_{S_e} = \max_{\Psi_{j_e}} \{ \sum_{i=1}^{RHP_{max}} \Upsilon(i) W(\Psi_{j_e} \mid R,RHP_e,\Psi_{S_o})\} \tag{17}$$

We recursively calculated the best replies to opponent strategies, the last iteration $\Psi^*_{S_e}$

becomes Ψ_{S_0} for the next iteration and R alternates between A and B. The iterations stop when a pair of Ψ_{S_A} and Ψ_{S_B} are found that are best replies to each other. We calculated ten such ESSs, one starting from each of the possible player strategies. Many of the equilibrium points were common to different starting points. Since the game is asymmetrical, mixed ESSs cannot occur (Selton, 1980).

Results

Simple model

Sample strategy sets for the basic model are shown in Fig. 2. Early in the contest, the optimal behaviour is threaten, until sufficient threats are made and the optimal behaviour then becomes quit or fight.

The resulting fitnesses for the simple model are shown in Table 3.

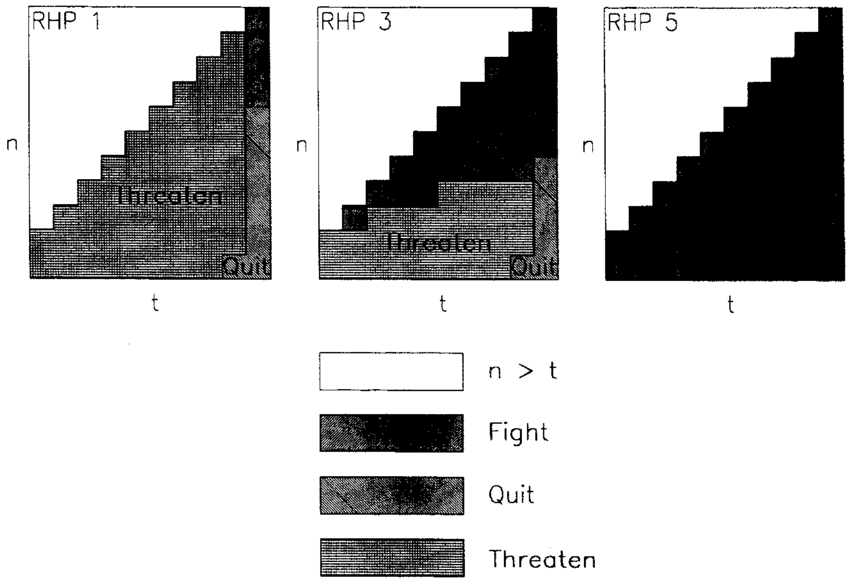

Figure 2. Sample behaviour sets. Some sample excerpts from player B's B_e function from the simple model.

Table 3. Expected fitnesses for the simple model

Contestant *A*		Contestant *B*	
RHP	Fitness	RHP	Fitness
1	0.628 (0.669)	1	0.694 (0.760)
2	0.605 (0.718)	2	0.695 (0.763)
3	0.644 (0.766)	3	0.725 (0.766)
4	0.696 (0.823)	4	0.781 (0.770)
5	0.829 (0.908)	5	0.849 (0.803)

Expected fitnesses for each contestant and RHP_e combination. With the exception of A at RHP = 2 fitnesses increased with RHP. Numbers in brackets are expected fitness as calculated during the backward iterations.

Table 4. Excerpt from the W (R, RHP_e, Ψ_{S_e}, Ψ_{S_o}) function

	Ψ_{S_B}				
Ψ_{S_A}	Ψ_1	Ψ_2	Ψ_3	Ψ_4	Ψ_5
Ψ_1	0.6949	0.7086	0.7026	0.7025	0.6514
Ψ_2	0.7145	0.7111	0.7042	0.7052	0.6658
Ψ_3	0.7149	0.6997	0.6508	0.6868	0.6900
Ψ_4	0.6886	0.7093	0.6453	0.6490	0.6140
Ψ_5	0.6538	0.6887	0.6960	0.7076	0.6670

This table shows the expected fitnesses for $W(B, 3, \Psi_{S_e}, \Psi_{S_o})$. Maximally informative communication occurs in the top left cell at (S_A = 1, S_B = 1), while no communication occurs in the bottom right corner (S_A = 5, S_B = 5).

Table 5. Expected fitnesses at ESS

Strategy A at ESS (Ψ_{S_A})	Strategy B at ESS (Ψ_{S_B})	Expected fitness A	Expected fitness B
2	2	0.6696	0.7479
3	2	0.6983	0.7419
4	4	0.7743	0.7437
5	1	0.7403	0.7496

Weighted mean expected fitness (collapsed across RHP) for populations A, and B at the four ESS profiles.

Individuals with a higher RHP achieved higher fitness. The exception seen when RHP = 2 for contestant A is a product of retaining opponents who have passed their behavioural end-points in the backward iteration algorithm. Notice that the expected fitnesses from the backward iterations (in brackets) all increase with RHP. First-moving players (A) scored slightly higher fitnesses than second-moving players (B) of the same RHP, but this may also be an artefact of the forward iteration effect, since it differs from the trend seen in the backward iteration results.

Variable strategy model

A sample of $W(R, RHP_e, \Psi_{S_e}, \Psi_{S_o})$ is shown in Table 4. Maximum expected fitnesses were gained under conditions of partial information exchange, in this case when A plays Ψ_2 and B plays Ψ_1. The strategies are highly sensitive to opponent behaviour. Just because player X gains the highest fitness playing strategy I against player Y playing strategy J doesn't imply anything at all about the wisdom of X playing I against Y playing any non-J strategy. The fitnesses in the diagonals, $\Psi_{S_A} = \Psi_{S_B}$, are not particularly good and fitnesses in the corner cells (maximally clear information versus maximally clear information and total ambiguity versus total ambiguity), are poor. This means that simple mutual strategies of equal quality information exchange are not, by and large, communication equilibria.

Calculating ESSs

ESSs profiles were (2,2), (3,2) (4,4) and (5,1), where numbered pairs are (Ψ_{S_A}, Ψ_{S_B}) (Table 5).

Conclusion

The existence of ESS profiles of (2,2) (3,2) and (4,4) for the variable strategy model means that exchange of information can be evolutionarily stable. The (5,1) stable profile for the variable strategy game demonstrates that this is not universally the case. Those cases in which communication was an optimal strategy, did not use the clearest form of communication possible, but provided fairly ambiguous, but on average valid, information, which seemed the best strategy.

Thus, the model demonstrates evolutionarily stable ambiguous communication of fighting ability without inherently costly or perfectly reliable signals.

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