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EVOLUTIONARY EQUILIBRIUM  
STRATEGIES

By

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## 1. INTRODUCTION

The last decade has seen a growing use of game theory to explain the evolution of genetic mechanisms and hence the behaviour of animals and insects. However, the Nash equilibrium concept used in the analysis of non-cooperative human interaction is not directly applicable since it attributes rational decisionmaking capabilities to the conflicting agents.

Building on the early work by Fisher (1930), and a paper by Hamilton (1967), Maynard Smith (1974, 1976) in collaboration with Price (1973), has proposed an alternative 'evolutionary equilibrium' concept. Maynard Smith's particular interest in developing this concept was to explain the nature of conflict both within and among species. It is therefore to such conflicts that we shall periodically refer.

In the following section it is argued that when interaction is between pairs of agents drawn at random from a *finite* population, a strategy which satisfies Maynard Smith's conditions may not be protected against invasion by a mutant strategy. Indeed for certain mutant strategies it is possible that the agents using what Maynard Smith has called an "evolutionarily stable strategy" will be completely eliminated!

Given such an unsatisfactory conclusion two alternative definitions of evolutionary stability are then proposed. If a mutant has a lower fitness when its numbers are very small the strategy of the initial population is described as being *strongly evolutionarily stable* with respect to this mutant. If a mutant has a lower fitness only when its numbers are sufficiently large, the strategy of the initial population is described as being *weakly evolutionarily stable* with respect to this mutant.

The problem with Maynard Smith's definition of equilibrium is that it only ensures weak stability with respect to all feasible mutants. Thus the number

of players required before the mutant has a lower fitness may exceed the total population.

Section 3 considers the implications for the simply "war of attrition" discussed by Smith (1976) and developed more completely by Hines (1977) and Bishop and Cannings (1977). As the latter have established there is a unique "evolutionary equilibrium" in which animals compete (for food or territory) by trying to wait out their opponent according to an exponential mixed strategy. It is shown first that this is only a evolutionary quasi-equilibrium and that for any integer  $n$ , there is some mutant which has a higher fitness until its population exceeds  $n$ .

The nature of mutant strategies for which  $n$  is large are then examined. It is shown that only those mutant strategies which are similar to the weakly stable strategy can invade to any significant extent. Therefore, for a large finite population the unique weakly stable strategy can only be eliminated by a mutant strategy which is almost certain to be empirically indistinguishable.

It is tempting to draw the conclusion that the weakly stable strategy is "approximately" viable. However, the indistinguishable mutant is not itself weakly stable. Therefore, once the players of the weakly stable strategy have been eliminated there exist further mutations which have a higher fitness.

It is shown that these second round mutant strategies will in general be very unlike the evolutionary quasi-equilibrium strategy. Thus, after a long period in which the behaviour of the great majority of some population changed only imperceptably, it would be possible to observe quite different behaviour spreading throughout.

In the final section it is shown that these stability problems can be avoided by altering the underlying model to take account of a natural

informational asymmetry. Instead of adopting a mixed strategy each agent uses a pure strategy which is conditioned on its own information. The precise form of the strong evolutionary equilibrium strategy is then derived for the war of attrition.

## 2. EVOLUTIONARILY STABLE STRATEGIES IN SYMMETRIC GAMES

The essential features of an evolutionary equilibrium are most readily described when the conflicting agents are identical except, possibly, in the strategies they adopt. Let

$r(v|\mu) \equiv$  the expected return to adopting strategy  $v$  when the opponent adopts strategy  $\mu$ .

Then each agent has the following matrix of possible expected payoffs.

		opponent's strategy	
		$v$	$\mu$
own strategy	$v$	$r(v v)$	$r(v \mu)$
	$\mu$	$r(\mu v)$	$r(\mu \mu)$

Suppose that the number of agents in the population is  $N + 1$ . Of these  $M$  use the 'mutant strategy'  $\mu$  and the remainder use the strategy  $v$ . If a particular agent is among the former, the probability that a random encounter will be with another of the same type is  $(M - 1)/N$ . The expected return or "fitness" of the agent is therefore

$$(1) \quad r(\mu) = (1 - \frac{M-1}{N})r(\mu|v) + \frac{M-1}{N}r(\mu|\mu)$$

Similarly, if the agent uses strategy  $v$ , the probability that a random encounter will be with an agent using the mutant strategy is  $M/N$ . The expected return is then

$$(2) \quad r(v) = (1 - \frac{M}{N})r(v|v) + \frac{M}{N}r(v|\mu)$$

Suppose that the environment will support only a fixed population and that the number of mutants rises whenever the fitness associated with the mutant strategy

is higher. We then seek some strategy,  $v$ , which is protected from invasion by any mutant in the set,  $S$ , of feasible strategies. That is, we seek some strategy,  $v$ , satisfying,

$$(3) \quad r(v) - r(\mu) > 0 \quad \text{for all } \mu \neq v, \mu \in S.$$

Subtracting (2) from (1) yields

$$(4) \quad \begin{aligned} r(v) - r(\mu) = & (1 - \frac{M}{N})[r(v|v) - r(\mu|v)] \\ & + \frac{M}{N}[r(v|\mu) - r(\mu|\mu)] \\ & + \frac{1}{N}[r(\mu|\mu) - r(\mu|v)] \end{aligned}$$

Except for small populations, the first term on the right hand side of (4) tends to dominate the other two for small  $M$ . Therefore a natural requirement for  $v$  to be an equilibrium strategy is

$$\text{Condition N: } r(v|v) \geq r(\mu|v), \text{ for all } \mu \in S.$$

This is precisely the Nash equilibrium condition for non-cooperative games among rational agents.

However, to ensure the viability of an evolutionary strategy it must be shown that it has a higher fitness than alternative strategies. Maynard Smith argued that when the proportion of mutants in the population was  $p$ , the net advantage of strategy  $v$  could be expressed as

$$(4)' \quad \begin{aligned} r(v) - r(\mu) = & (1 - p)[r(v|\mu) - r(\mu|v)] \\ & + p[r(v|\mu) - r(\mu|\mu)]. \end{aligned}$$

The right hand side of (4)' has the sign of the first bracket for small  $p$ .

Furthermore, if the first bracket is zero the right hand side of (4)' takes on the sign of the second bracket. This led Maynard Smith to propose the following definition of an evolutionarily stable strategy.

DEFINITION 1: (Maynard Smith) Evolutionary Equilibrium Strategy.

Strategy  $v$  is evolutionarily stable if, for all feasible alternatives  $\mu$

EITHER  $r(v|v) > r(\mu|v)$ ,

OR  $r(v|v) = r(\mu|v)$  and  $r(v|\mu) > r(\mu|\mu)$ .

Comparing (4) and (4)' it is apparent that the two are formally equivalent only for infinite populations. We now show that, for finite populations, the analysis of stability is very different. As the first step, suppose the mutation has just occurred so that  $M = 1$ . Substituting into (4) we have

$$\begin{aligned} r(v) - r(\mu) &= [r(v|v) - r(\mu|v) + \frac{1}{N}[r(v|\mu) - r(v|v)]] \\ &= \frac{1}{N}[r(v|\mu) - r(v|v)], \text{ if } v \text{ satisfies condition N.} \end{aligned}$$

Therefore strategy  $v$  is protected from any invasion if it fares better in conflict with a mutant, than in conflict with itself.

This suggests the following definition of a stable strategy.

DEFINITION 2: Strategy  $v$  is *strongly evolutionarily stable* with respect to the alternative  $\mu$ , if it has a higher fitness when the proportion adopting  $\mu$  is small.

From the above argument, if strategy  $v$  is a Nash equilibrium and, in addition  $r(v|\mu) > r(v|v)$ , then  $v$  is strongly evolutionarily stable with respect to the mutant strategy  $\mu$ . All this leads naturally to the following definition of equilibrium.

DEFINITION 3: Strategy  $v$  is a *strong evolutionary equilibrium* strategy if it is strongly evolutionarily stable with respect to all feasible alternative strategies.

Unfortunately, as will be shown in the next section, there may be no such strategy. We therefore seek some weaker stability requirement. Returning again to expression (4), we have, for any Nash equilibrium strategy  $v$ ,

$$(5) \quad r(v) - r(\mu) \geq \frac{1}{N}(M[r(v|\mu) - r(\mu|\mu)] + r(\mu|\mu) - r(\mu|v))$$

If the first bracket on the right hand side of (5) is positive, the entire expression is positive for sufficiently large  $M$ . Thus when the number of invaders adopting the mutant strategy exceeds some absolute number,  $M(\mu)$ , strategy  $v$  yields a higher fitness. Strategy  $v$  is therefore protected from invasion beyond the level  $M(\mu)$ . Formally, we have the following definitions.

DEFINITION 4: If strategy  $v$  is a Nash strategy, and, in addition

$$r(v|\mu) > r(\mu|\mu),$$

then  $v$  is *weakly evolutionarily stable* with respect to the alternative  $\mu$ .

DEFINITION 5: Strategy  $v$  is an *evolutionary quasi-equilibrium* strategy if it is weakly evolutionarily stable with respect to all feasible alternative strategies.

If  $v$  is weakly evolutionarily stable against all alternatives, it is protected against any particular alternative  $\mu$ , beyond some level  $M(\mu)$ . Then the largest encroachment by any mutant is  $M^* = \max_{\mu \in S} M(\mu)$ .

However, in the absence of further specification of  $S$  and  $N$ , there is no assurance that  $M^*$  is exceeded by  $N$ , hence the expression "quasi-equilibrium."

The following example in which there are only two feasible strategies,  $S = \{v, \mu\}$ , illustrates the different concepts.

		opponent's strategy	
		v	μ
own strategy	v	$r(v v)=0$	$r(v \mu) = -1+c$
	μ	$r(\mu v)=0$	$r(\mu \mu) = -1$

Suppose that all agents initially use strategy  $v$  in situations of conflict. Then one is replaced by an agent using the mutant strategy. Since the mutant only meets non-mutants, its expected return is zero. The non-mutants also achieve an expected return of zero against other non-mutants. In addition each has a probability of  $1/N$  that its opponent is the mutant. If  $c > 1$ ,  $r(v|\mu) > 0$  and the non-mutants are made better off by the arrival of the mutant. The latter is therefore at an evolutionary disadvantage, and the initial state is a strong evolutionary equilibrium.

However, if  $c < 1$  the arrival of the mutant lowers the expected return of the non-mutants below that of the mutant. The mutant therefore has the evolutionary advantage. Now suppose all but one of the  $N + 1$  agents use the mutant strategy. The expected return of each mutant is

$$r(\mu) = \frac{1}{N}r(\mu|v) + (1 - \frac{1}{N})r(\mu|\mu) = -1 + \frac{1}{N}$$

Since the non-mutant meets only mutants, its expected return is simply  $r(v|\mu) = -1 + c$ . If  $c$  is negative, strategy  $v$  remains at an evolutionary disadvantage, regardless of the population size. If  $c$  is positive,  $v$  is an evolutionary quasi-equilibrium strategy. Moreover, Maynard Smith's conditions for evolutionary stability are satisfied. However, unless  $c$  exceeds  $1/N$ , the agents using strategy  $v$  are again at an evolutionary disadvantage, regardless of their proportion in the population.



### 3. THE WAR OF ATTRITION

In the original model analysed by Maynard Smith, two members of a population both wish to obtain the same object. Each, in effect, makes a sealed bid. The higher bidder wins and *both* must pay the low bid.<sup>1</sup>

Suppose the value of the object to either agent is  $V$ . Maynard Smith conjectured that, for such a game, the exponential mixed strategy of bidding  $x$  or more with probability  $\frac{1}{V}e^{-x/V}$ , satisfied his requirements for evolutionary stability. This has since been formally demonstrated by Bishop and Canning (1977). In this section we begin by showing that the exponential strategy is only a quasi-equilibrium strategy.

First of all, it is easy to see that no strategy which involves making any bid,  $b$ , with finite probability, can be stable. If  $b$  were less than the value of the prize, a mutant would obtain a higher expected return by bidding slightly higher than  $b$  with the same probability. Similarly if  $b$  were greater than or equal to  $V$ , a mutant would obtain a higher expected return by bidding zero with the same probability.

Suppose, therefore, that the quasi-equilibrium strategy  $v$ , is to bid  $b$  or less with probability  $F_v(b)$ . Without loss of generality, we may normalize and set the value of the prize equal to unity. If the mutant's bid,  $a$ , exceeds  $b$ , it wins the contest and receives a net return of  $1 - b$ . If the mutant's bid is the low bid it loses  $a$ . The net return to the mutant for different values of  $b$  is, therefore, as depicted in Figure 1.

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<sup>1</sup> Maynard Smith suggests the following model of the animal world. Two doves desire the same food source or territory. Each chooses to "display" for some length of time. The longer the display, the higher the price each dove is paying. Eventually one dove ends its display and departs. The other then collects the resource.

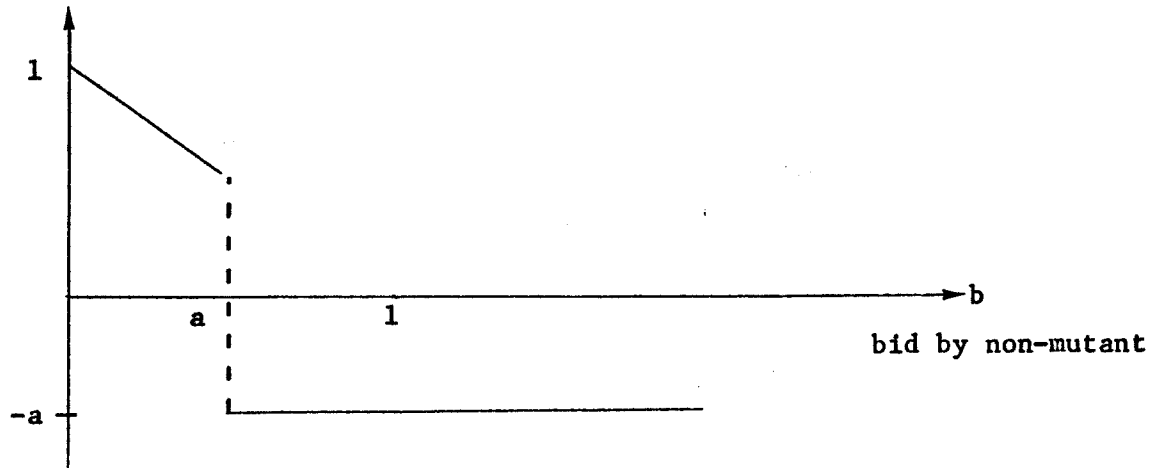


Figure 1: Net Return to Mutant Bidding a

Multiplying by the probability density associated with each bid  $b$ , the expected return is

$$r(a|v) = \int_0^a (1 - b) f_v(b) db - a \int_a^\infty f_v(b) db$$

Then writing

$$(6) \quad T(a) = \int_0^a F(b) db,$$

and integrating by parts, we have,

$$(7) \quad r(a|v) = F_v(a) - a + T_v(a).$$

This is the expected return to following the pure strategy of always bidding  $a$ .

If strategy  $v$  is the exponential mixed strategy it is readily shown that

$$r(a|v) = 0, \quad \forall a \geq 0$$

Therefore, regardless of the mixture of bids chosen by  $\mu$  its expected return

$$\begin{aligned} r(\mu|v) &= \int_0^\infty r(a|v) f_\mu(a) da \\ &= 0. \end{aligned}$$

Since this is true for all  $\mu$  it is true for  $\mu = v$ . Thus condition N is satisfied and the exponential strategy,  $v$ , is a Nash equilibrium strategy.

Bishop and Canning establish that, in the war of attrition, the exponential strategy is evolutionarily stable in the sense of Maynard Smith. Moreover, we have seen that

$$r(\mu|v) = r(v|v), \quad \text{for all } \mu \in S.$$

Therefore, from definition 1, it must be the case that

$$(3) \quad r(v|\mu) > r(\mu|\mu), \quad \text{for all } \mu \in S.$$

It follows immediately from definitions 4 and 5, that strategy  $v$  is an evolutionarily quasi-equilibrium strategy.

Inequality (8) also demonstrates that for all  $\mu \neq v$ , strategy  $\mu$  cannot be a Nash equilibrium. Hence strategy  $v$  is the *unique* evolutionary quasi-equilibrium strategy.

We now show that strategy  $v$  is not strongly evolutionarily stable. Suppose a mutant were to appear in the population playing the alternative mixed strategy,  $\mu$ , with associated cumulative distribution function  $F_\mu(a)$ . Utilizing (7)

$$r(b|\mu) = F_\mu(b) - b + T_\mu(b)$$

Thus the expected return to playing the exponential mixed strategy  $v$  against an agent playing  $\mu$  is

$$\begin{aligned} (9) \quad r(v|\mu) &= \int_0^\infty e^{-b} [F_\mu(b) - b - T_\mu(b)] db \\ &= \int_0^\infty e^{-b} F_\mu(b) db - \int_0^\infty b e^{-b} db - \int_0^\infty e^{-b} T_\mu(b) db \end{aligned}$$

Integrating by parts, the second integral equals unity and the third integral,

$$\int_0^\infty e^{-b} T_\mu(b) db = [-T_\mu(x) e^{-x}]_0^\infty + \int_0^\infty e^{-b} F_\mu(b) db.$$

From (6)

$$\begin{aligned} T_{\mu}(x) &= \int_0^x F_{\mu}(b) db \\ &\leq \int_0^x db \quad \text{since } F_{\mu}(b) \leq 1 \\ &= x \end{aligned}$$

Therefore  $\lim_{x \rightarrow \infty} T_{\mu}(x)e^{-x} = 0$ . Collecting terms it follows that (9) can be rewritten as

$$(10) \quad r(v|\mu) = 2 \int_0^{\infty} e^{-b} F_{\mu}(b) db - 1$$

In particular suppose the mutant strategy  $\mu$  is of the form,

$$(11) \quad F_{\mu}(b) = \begin{cases} 0 & b < \ln \lambda; \lambda \geq 1 \\ 1 - \lambda e^{-b} & b \geq \ln \lambda \end{cases}$$

Substituting (11) into (10) we have

$$(12) \quad r(v|\mu) = \frac{1}{\lambda} - 1$$

Moreover, the expected return to a mutant when it plays another mutant is given by

$$(13) \quad r(\mu|\mu) = \int_0^{\infty} f_{\mu}(b) [F_{\mu}(b) - b - T_{\mu}(b)] db$$

For the particular mutant strategy given in (11) we can integrate by parts to obtain

$$(14) \quad r(\mu|\mu) = -\ln \lambda.$$

Finally we note again, that for the exponential strategy  $v$ ,

$$(15) \quad r(\mu|v) = r(v|v) = 0$$

Let  $M$  be the number of agents using the mutant strategy. Substituting (12), (14) and (15) into (4), the net advantage of strategy  $v$  is

$$r(v) - r(\mu) = \frac{1}{N} \left\{ M \left( \frac{1}{\lambda} - 1 + \ln \lambda \right) - \ln \lambda \right\}$$

This is positive if and only if

$$(16) \quad M > M(\lambda) = \frac{\ln \lambda}{\frac{1}{\lambda} - 1 + \ln \lambda}$$

For all  $\lambda \geq 1$  the right hand side of (15) exceeds unity. Moreover, applying L'Hôpital's rule,

$$\lim_{\lambda \rightarrow 1^+} M(\lambda) = \lim_{\lambda \rightarrow 1^+} \left\{ \frac{\frac{1}{\lambda}}{\frac{1}{\lambda} - \frac{1}{\lambda^2}} \right\} = \infty$$

Therefore, in the war of attrition there are mutant strategies which have a net advantage over the unique evolutionary quasi-equilibrium strategy for *any* finite population.

This would seem to indicate that the quasi-equilibrium concept is too weak to be useful. However, in the above example the number of mutant invaders becomes large only as  $\lambda$  approaches unity. From (11), it follows that the number of mutant invaders becomes large only as their strategy resembles more and more closely the quasi-equilibrium strategy.

We next show that this result holds not only for the special class of mutants described by (11) but for *all* mutant strategies. That is, only if a mutant strategy is in a sense very similar to the exponential mixed strategy can it invade to any significant degree.

Let  $M(\mu)$  be the number of mutants just large enough to eliminate their evolutionary advantage. From (4) and (15) we have

$$(17) \quad r(v) - r(\mu) = M(\mu)[r(v|\mu) - r(\mu|\mu)] + r(\mu|\mu) = 0$$

If  $r(v|\mu)$  is positive it exceeds  $r(\mu|\mu)$ . Then, from definition 2, strategy  $v$  is strongly stable with respect to the mutant strategy  $\mu$ . We therefore restrict our attention to cases in which  $r(v|\mu)$  is negative or zero. From inequality (8) we know that the bracket in (17) is strictly greater than zero for all  $\mu \neq v$ .

Hence

$$(18) \quad r(v|\mu) \leq 0 \rightarrow r(\mu|\mu) < 0; \quad \mu \neq v$$

Moreover, for all  $M > M(\mu)$ ,  $r(v) - r(\mu)$  is strictly positive. Thus  $M(\mu)$  is indeed the upper bound to the extent of the potential encroachment by mutant strategy  $\mu$ . That is for all  $M > M(\mu)$  where  $M(\mu) = (1 - \frac{r(v|\mu)}{r(\mu|\mu)})^{-1}$ , strategy  $v$  is at an evolutionary advantage. Therefore, to solve for the most successful invaders, we seek the solution of

$$\text{Max}_{\mu} \{r(\mu|\mu) | r(v|\mu) = K, K < 0\}$$

From (13)

$$r(\mu|\mu) = \int_0^{\infty} f(b)[F(b) - b - T(b)]db$$

But

$$\begin{aligned} & \int_0^{\infty} f(b)T(b)db \\ &= \int_0^{\infty} f(b) \int_0^b F(a)dad b, \quad \text{from (6)} \\ &= \int_0^{\infty} \int_a^{\infty} f(b)F(a)db da, \quad \text{reversing the order of integration} \\ &= \int_0^{\infty} (1 - F(a))F(a)da \end{aligned}$$

Hence

$$r(\mu|\mu) = \int_0^{\infty} [F(b)f(b) - bf(b) - F(b)(1 - F(b))]db$$

Moreover  $r(v|\mu)$  is given by equation (10). Therefore we seek the solution of

$$\text{Max}_{\mu} \left\{ \int_0^v [F(b)f(b) - bf(b) - F(b)(1 - F(b))]db \mid 2 \int_0^{\infty} e^{-b} F(b)db - 1 = K \right\}$$

This is a fixed endpoint problem in the calculus of variations where the maximand is subject to an integral constraint. Introducing the Lagrange multiplier  $\lambda$ , we apply the Euler condition to the augmented integrand

$$H(b, F, F'; \lambda) = FF' - bF' + F(1 - F) - 2\lambda e^{-b}F$$

It is a straightforward matter to check that

$$(19) \quad F(a; \lambda) = \begin{cases} 0, & a \leq \ln \lambda \\ 1 - \lambda e^{-a}, & a > \ln \lambda \end{cases}$$

satisfies the Euler condition,  $\frac{\partial H}{\partial F} - \frac{d}{db} \left( \frac{\partial H}{\partial F'} \right) = 0$ . Moreover, since  $H$  is strictly concave in  $F$ , (19) defines the unique global maximum. Comparing (19) and (11) it follows that for any given  $K$ , the largest possible invasion is achieved by a mixed strategy with distribution function  $F(a; \lambda(K))$ .

From (12)  $r(v|\mu) = \frac{1}{\lambda} - 1$  for the exponential family. Setting this equal to  $K$  we have

$$\lambda = \frac{1}{1+K}.$$

Then from (16), strategy  $v$  is at an evolutionary advantage if and only if

$$M > (1 - K/\ln(1 + K))^{-1}$$

Finally we note that  $r(v|\mu)$  is a natural measure of the difference between the distribution  $F_v(b)$ , associated with the quasi-equilibrium strategy and the distribution  $F_\mu(b)$ , associated with some mutant strategy. Let

$$\begin{aligned} d(\mu, v) &= 2 \int_0^\infty e^{-x} (F_\mu(x) - F_v(x)) dx \\ &= 2 \int_0^\infty e^{-x} F_\mu(x) dx - 2 \int_0^\infty F'_v(x) F_v(x) dx, \text{ since } F_v(x) = 1 - e^{-x} \\ &= 2 \int_0^\infty e^{-x} F_\mu(x) dx - 1. \end{aligned}$$

Comparing this with expression (10) it follows that

$$d(\mu, v) = r(v|\mu).$$

The above results can then be summarized as follows

**THEOREM: MAXIMAL INVASION BY A MUTANT**

Let  $d(\mu, \nu) = 2 \int_0^{\infty} e^{-x} (F_{\mu}(x) - F_{\nu}(x)) dx$  measure the difference between

the cumulative distributions  $F_{\mu}$ ,  $F_{\nu}$  associated with strategies  $\mu$  and  $\nu$ .

Then the exponential mixed strategy

$$F_{\nu}(b) = 1 - e^{-b}$$

is strongly evolutionarily stable with respect to all mutant strategies  $\mu$  for which  $d(\mu, \nu)$  is positive.

Furthermore, among the mutant strategies for which  $d(\mu, \nu)$  is negative, the largest possible invasion is equal to  $[1 - d(\mu, \nu)/\ln(1 + d(\mu, \nu))]^{-1}$ .

That this is a powerful result is easily seen by considering the following table.

$d(\mu, \nu)$	$[1 - d(\mu, \nu)/\ln(1 + d(\mu, \nu))]^{-1}$
-1.0	0
-0.5	2
-0.1	20
-0.01	200
-0.001	2000

Except when  $d(\mu, \nu)$  is extremely close to zero, the upper bound on the number of invaders is low.



#### 4. AN ALTERNATIVE APPROACH

In the previous section it was established that for the war of attrition many mutant strategies have an evolutionary advantage over the unique quasi-equilibrium strategy. However, it was also shown that unless the mutant strategy is very similar to the equilibrium strategy, it cannot encroach upon the latter to any significant extent. This suggests that if the quasi-equilibrium strategy were ever to be established it could survive for a very long period of time. However, suppose an empirically indistinguishable mutant were to invade and eventually replace those using the quasi-equilibrium strategy. From (18), we know that the expected return to this mutant, when in conflict with another of the same type, is negative. It is easy to show that drastically different strategies are now at an evolutionary advantage. For example, the simple strategy of avoiding all conflicts has a larger return (zero).

This raises at least the theoretical possibility that the quasi-equilibrium strategy might eventually be replaced by one or more quite different mutant strategies.

At the very least, the above results make it clear that for the model described by Maynard Smith, partial encroachment is the rule rather than the exception.

However, to this author it is far from clear that the usual formal description of Maynard Smith's model is entirely appropriate. Rather than assume both agents place the same value  $V$  on the desired object, it seems natural that each would value it according to some underlying distribution. For example, if the object is food it is reasonable to suppose that each agent's value is dependent upon the length of time since the last meal.

This introduces an element of informational asymmetry since each agent knows its own valuation of some contested object, but not that of its opponent. As we shall see, adding this asymmetry drastically changes the nature of the evolutionary equilibrium and its stability properties.

To keep things simple, suppose each agent's true value is distributed uniformly over the interval  $[0, \underline{V}]$ . When two agents conflict, both know their own true value but not that of the other agent. Suppose the first adopts the strategy,  $v$ , of bidding

$$(20) \quad b_1 = v_1^2 / 2\underline{V}$$

where  $V_1$  is the agent's true value of the object.<sup>2</sup> If the other agent's true value is  $V_2$ , and it places a bid,  $b$ , its expected return is

$$\begin{aligned} r(b|v) &= (V_2 - b) \Pr\{\text{the first agent wins}\} - b \Pr\{\text{the first agent loses}\} \\ &= (V_2 - b) \Pr\{\text{the first agent wins}\} - b(1 - \Pr\{\text{the first agent wins}\}) \\ &= V_2 \Pr\{\text{the first agent wins}\} - b \\ &= V_2 \Pr\{b_1 < b\} - b \\ &= V_2 \Pr\{V_1 < (2\underline{V}b)^{1/2}\} - b, \quad \text{from (20)} \end{aligned}$$

Furthermore we have assumed that  $V_1$  is distributed uniformly over  $[0, \underline{V}]$ . Thus

$$\Pr\{V_1 < x\} = \begin{cases} x/\underline{V} & x \leq \underline{V} \\ 1 & x > \underline{V} \end{cases}$$

Hence

$$(21) \quad r(b|v) = \begin{cases} v_2 (2\underline{V}b)^{1/2} / \underline{V} - b, & 0 \leq b \leq \underline{V}/2 \\ \underline{V}_2 - b, & \underline{V}/2 < b \end{cases}$$

<sup>2</sup> A constructive derivation of this strategy is provided in the Appendix. For a related discussion of equilibrium strategies for the English and Dutch auctions, see Vickrey (1961).

The expected return  $r(b|v)$  is a strictly concave function of  $b$ , increasing at  $b = 0$ , for all  $v_2 > 0$ , and decreasing outside the interval  $[0, \frac{1}{2}v]$ . Thus there is a unique optimal response,  $b_2$ , and this must lie in the interval  $[0, \frac{1}{2}v]$ . Differentiating  $r(b|v)$  and solving, we have,

$$(22) \quad b_2 = v_2^2/2v, \quad 0 \leq v_2 \leq v$$

Comparing (20) and (22) it follows that the second agent's unique best response is to use exactly the same strategy as the first agent.

Thus, for any alternative strategy,  $\mu$ ,

$$(23) \quad r(\mu|v) < r(v|v).$$

Consider again the net advantage to using strategy  $v$ , given in equation (4). Since the second and third brackets are bounded from below, the first term dominates whenever  $M/N$  is sufficiently small.

From (23), the first bracket is strictly greater than zero for all alternative strategies. Therefore the requirements of Definitions 2 and 3 are satisfied and strategy  $v$  is a strong evolutionary equilibrium.

Finally, it should be noted that this result is not dependent upon the assumption that each agent's value is distributed uniformly on  $[0, v]$ . In the appendix it is shown that if the conflicting agents values are drawn from *any* continuous distribution there exists a strong evolutionary equilibrium strategy.

# Appendix 1: The War of Attrition with Asymmetrical Information

Suppose the values that two agents place on an object can be represented as random drawings from a population with cumulative distribution  $G(V)$ , where  $G'(V)$  is piecewise continuous and  $G(\underline{V}) = 1$ .

Suppose further, that the first agent adopts the strategy of making a bid  $b_1$ , which is a strictly increasing function of  $V_1$ , its own valuation of the object. That is

$$(24) \quad b_1 = h(V_1), \quad h'(\cdot) > 0.$$

We shall refer to this behaviour as strategy  $v$ .

From section 4, if agent 2 makes a bid of  $b$ , its expected return is

$$\begin{aligned} r(b|v) &= V_2 \Pr\{b_1 < b\} - b \\ &= V_2 \Pr\{V_1 < h^{-1}(b)\} - b \quad \text{from (24)} \\ (25) \quad &= V_2 G(h^{-1}(b)) - b \end{aligned}$$

The optimal response of agent 2, is therefore to select the bid,  $b_2$ , that maximizes  $r(b|v)$ .

Since we seek a Nash equilibrium we need consider bids in the interval  $[h(0), h(\underline{V})]$ . Then associated with each possible bid  $b$  is a value

$$(26) \quad \hat{V} = h^{-1}(b).$$

Substituting into (25) we have,

$$(27) \quad r(b|v) = V_2 G(\hat{V}) - h(\hat{V}).$$

Therefore agent 2's optimal response is to select  $\hat{V}_2$  to maximize expression (27).

Differentiating yields

$$\begin{aligned} (28) \quad \frac{d}{d\hat{V}} r(b|v) &= V_2 G'(\hat{V}) - h'(\hat{V}) \\ &= 0 \quad \text{at a local maximum.} \end{aligned}$$

Since  $b_2 = h(\hat{V}_2)$  the optimal strategy of agent 2 is identical to that of agent 1 if and only if  $\hat{V}_2 = V_2$ . Thus for a strategy  $v$  to be a Nash strategy we require

$$v_2 G'(v_2) - h'(v_2) = 0; \quad 0 \leq v_2 \leq \underline{v}$$

Integrating then yields

$$h(v_2) = \int_0^{v_2} 2VG'(V) dV + c$$

Since  $h(0) = 0$  the constant of integration is zero.

Integrating by parts we have finally

$$(29) \quad h(v_2) = v_2 G(v_2) - \int_0^{v_2} 2G(V) dV$$

Note that, since  $G(v_2) \leq 1$ , the optimal bid  $b_2 = h(v_2)$  is never greater than the value of the object.

It remains to check the second order conditions for a maximum.

Differentiating (28) and using (29) we have

$$\begin{aligned} \frac{d^2}{d\hat{v}^2}(r(b|v)) &= v_2 G''(\hat{v}) - h''(\hat{v}) \\ &= -G'(\hat{v}) \\ &< 0, \quad 0 \leq v \leq \underline{v}. \end{aligned}$$

Therefore if the first agent adopts strategy  $v$ , of bidding

$$b = h_v(v) = vG(v) - \int_0^v G(x) dx,$$

any mutant strategy  $\mu \neq v$  yields a strictly lower expected return to the second agent. That is, for all  $\mu \neq v$

$$r(\mu|v) < r(v|v)$$

Strategy  $v$  is thus a strong Nash strategy with respect to all mutant strategies. As already noted in section 4, this implies that  $v$  is a strong evolutionary equilibrium strategy.

For the special case in which actual values are uniformly distributed on  $[0, \underline{v}]$  we have

$$G(V) = V/\underline{V} \quad 0 \leq V \leq \underline{V}$$

Substituting into (25)

$$b = h(V) = V^2/2\underline{V}$$

Then all bids lie in the interval  $[0, \underline{V}/2]$ . Moreover, since  $V$  is distributed uniformly the average gain to agents joining such conflicts is

$$\int_0^{\underline{V}} r(h(V)|v) dG = \int_0^{\underline{V}} (V^2/2\underline{V}^2) dV = \underline{V}/6.$$

Finally, to solve for the average price paid, we note that this is simply the expected value of the lower bid. Since both bids exceed  $V$  with probability  $(1 - G(V))^2$ ,

$$\begin{aligned} \Pr\{\text{lower bid} \leq V\} &= 1 - (1 - G(V))^2 \\ &= 2G(V) - G(V)^2 \end{aligned}$$

Then the expected value of the lower bid is

$$\int_0^{\underline{V}} V[2G' - 2GG'] dV = \underline{V} - \int_0^{\underline{V}} G(V)(2 - G(V)) dV.$$

For the uniform distribution it is a straightforward exercise to show that the latter integral is equal to  $2\underline{V}/3$ . Hence the average price paid is  $\underline{V}/3$ .

## Appendix 2: Evolutionary quasi-equilibrium in the War of Attrition.

For completeness, an alternative proof that the exponential mixed strategy is the unique quasi-equilibrium strategy, is provided below.

In section 3 it was shown that, for the exponential mixed strategy  $v$ , and any alternative  $\mu$ ,

$$r(\mu|v) = r(v|v) = 0.$$

Thus  $v$  is a Nash equilibrium strategy. Also from equations (10) and (13)

$$\begin{aligned} (30) \quad r(\mu|\mu) - r(v|\mu) \\ = \int_0^{\infty} F'_{\mu}(b) [F_{\mu}(b) - b - T_{\mu}(b)] db - 2 \int_0^{\infty} e^{-b} F_{\mu}(b) db + 1 \end{aligned}$$

$$\begin{aligned} \text{Moreover, } \int_0^{\infty} F'_{\mu}(b) T_{\mu}(b) db \\ = \int_0^{\infty} F'_{\mu}(b) \int_0^b F_{\mu}(a) da db \\ = \int_0^{\infty} \int_b^{\infty} F_{\mu}(b) F'_{\mu}(a) da db, \quad \text{reversing the order of integration} \\ = \int_0^{\infty} F_{\mu}(b) (1 - F_{\mu}(b)) db \end{aligned}$$

Substituting into (30) we have

$$\begin{aligned} (31) \quad r(\mu|\mu) - r(v|\mu) \\ = \int_0^{\infty} [F'_{\mu}(F_{\mu} - b) + (1 - F_{\mu})F - 2e^{-b}F_{\mu}] db + 1 \end{aligned}$$

We now ask which mutant strategy  $\mu$  maximizes this difference. Mathematically we seek the distribution function,  $F_{\mu}(b)$ , which maximizes

$$\int_0^{\infty} I(F(b), F'(b), b) db$$

such that  $F(0) = 0$  and  $F(\infty) = 1$  where

$$I = F'(F - b) + (1 - F)F - 2e^{-b}F$$

This is a standard, fixed endpoint problem in the calculus of variation. Among the family of continuous density functions, the Euler necessary condition,

$$(32) \quad \frac{\partial I}{\partial F} - \frac{d}{db} \left( \frac{\partial I}{\partial F'} \right) = 0$$

defines a local maximum. Moreover, since the integrand,  $I$ , is strictly concave in  $F$ , the necessary condition is also sufficient and hence defines the global maximum. Substituting for  $I$  in (32), the maximizing distribution function,  $F_\mu(b)$ , therefore satisfies

$$(1 - 2F_\mu(b) + F'_\mu(b) - 2e^{-b}) - \frac{d}{db}(F_\mu(b) - b) = 0$$

Rearranging we have,

$$F(b) = 1 - e^{-a}$$

But this is the distribution function of the exponential mixed strategy  $v$ . Then, for any  $\mu \neq v$ ,

$$\begin{aligned} r(\mu|\mu) - r(v|\mu) &< \max_{\mu \in S} \{r(\mu|\mu) - r(v|\mu)\} \\ &= r(v|v) - r(v|\mu) \\ &= 0. \end{aligned}$$

It follows that strategy  $v$  is the unique Nash strategy. Moreover the sufficient conditions for weak stability, derived in section 2 are satisfied. Hence the exponential mixed strategy is the unique evolutionary quasi-equilibrium strategy.