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# THE ASYMMETRIC WAR OF ATTRITION

by

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## ABSTRACT

The paper, which has an informal discussion at the end, provides a game theoretical analysis of the asymmetric "war of attrition" with incomplete information. This is a contest where animals adopt different roles like "owner" and "intruder" in a territorial conflict, and where the winner is the individual prepared to persist longer. The term incomplete information refers to mistakes in the identification of roles. The idea by Parker & Rubenstein (1981) is mathematically worked out and confirmed that there exists only a single evolutionarily stable strategy (ESS) for the model with a continuum of possible levels of persistence and no discontinuities in the increase of cost during attrition. The ESS prescribes to settle the conflict according to "who has more to gain or less to pay for persistence". The only evolutionarily stable convention is thus to give the player access to the resource who has the role which is favoured with respect to payoffs. By contrast, it was shown earlier (Hammerstein, 1981) for various asymmetric versions of the "Hawks-Doves" model that an ESS can exist which appears paradoxical with respect to payoffs. The nature of this contrast is further analyzed by introducing elements of discreteness in the asymmetric war of attrition. It turns out that some conditions must be satisfied in order to have the possibility of an alternative ESS which is not of the above simple commonsense type. First, a decision to persist (or escalate) further in a contest must typically commit a contestant to go on fighting for a full "round", before he can give up without danger. Second, such a "discontinuity" must occur at a level of persistence where the contest is still cheap, and, finally, errors in the identification of roles must be rare.

## I. INTRODUCTION

To give a functional explanation of conventional settlement in animal contests poses problems which are due to the involved frequency dependent nature of selection. Evolutionary game theory (e.g. Maynard Smith, 1979) has proved useful in overcoming these difficulties and in deriving results which are not immediately obvious. Maynard Smith & Parker (1976) and Hammerstein (1981) have stated a particular set of such results, the essence of which may be characterized as follows. Suppose that a type of conflict between two individuals over an indivisible resource has usually the feature that there exist perceivable differences between the opponents. When playing an evolutionarily stable strategy (ESS), the contestants must under a wide range of conditions base their behaviour on at least one of these differences. The individual having the conventional winning role then usually obtains the resource without major dispute. It may even be possible that this role, which is defined by a "historical" convention, is not the one in which there is more to gain or in which an escalated fight is less costly. An important message of the above papers consisted therefore in pointing out that the winning role need not necessarily be the role which is favoured with respect to payoffs.

However, Parker and Rubenstein (1981) proposed that the latter property does not hold if the conflict under consideration may be best described as a war of attrition, i.e. as a contest in which, when escalation occurs, the winner is determined by persistence rather than by a risky use of weapons. They argued that the winning role must always be that favoured with respect to payoffs. The present paper is an attempt to analyze the nature of this divergence of opinions and also to present a complete mathematical deduction of the ESS-solution for the asymmetric war of attrition. We are able to confirm that the former approach by Parker and Rubenstein, which was of a rather heuristic character, has led to a result which is a limiting case of the true solution provided that errors in role assessment are rare. In fact, although the structure of the problem turns out to be more complex than reflected in the original argument, we are able to confirm the following: in the asymmetric war of attrition it is typically the case that only one of the two roles can be a "winning role", in the sense that the contestant in that role usually gains the resource. With some caveats given in the discussion, this role can be characterized in a simple way: the individual in that role is able to persist longer than the opponent before his contest costs exceed the value of the resource. This rule was proposed by Parker (1974) in a non-game-theoretical setting.

Can then an ESS exist which appears paradoxical with respect to payoffs? The approach of Maynard Smith and Parker (1976) and Hammerstein (1981) clearly suggests that this is possible for models related to the well known "Hawks-Doves" game. In contrast, the continuous case of the war of attrition appears not to generate this result. A major aim of the present paper is to explain this difference in terms of controllability of risk: in the Hawks-Doves paradigm we are faced with the extreme case of decision only between low- and high degree of risk taking, whereas the expected cost against an escalating opponent can be finely tuned in the continuous case of a war of attrition. These model features can be shown to be the crucial key for reestablishing a coherent picture of the theory of asymmetric contests, with the two types of models as the extreme cases.

A word must be said about the exact notion of "asymmetry" and about the history of the problem. The first approach to the asymmetric war of attrition (Maynard Smith, 1974) was based on the idealizing view that there is always a perceivable difference between the opponents in the contest. Selten (1980) called this the assumption of "information asymmetry" and showed for a general class of models that an ESS must then be a pure strategy, i.e. it assigns definite instead of randomized choices to situations. The first solution to the problem, offered by Maynard Smith, accords with Selten's theorem: the animal in one role should be prepared to persist for a long time, up to a certain cost which is higher than the value of winning. The animal in the "complementary" role should give up immediately. A population playing this strategy, however, is not stable against invasion by a type of contestant that chooses a different maximal level of persistence in the winning role. By random drift, the population might even reach a state where it pays also to escalate in the former "losing role". The original answer to the problem is therefore not an ESS in the strict sense for the specified model, there does not even exist an ESS.

One way out of this dilemma (see also Parker & Rubenstein, 1981), by giving selection a fair chance to operate, consists in weakening the assumption that there must always be a perceivable difference (information asymmetry). Inaccuracies in the assessment of the difference between individuals are sufficient to ensure that two contestants will perceive themselves to be in the same role even in the context of an asymmetric contest. An essential feature of the present model is that with small probabilities two opponents may have the same role. Therefore, our results, which are mixed strategies, do not contradict Selten's theorem.

## II. THE MODEL WITH A CONTINUUM OF CHOICES

1. Contest situations: Conflicts between two individuals over an indivisible resource are considered. The characteristic feature of the model is that the opponents usually have a different concept of the situation they find themselves in. We call an animal's concept of its situation a role. It is assumed that only two roles A and B exist for the class of conflicts under investigation. A contest situation is described as a pair consisting of the opponents' concepts of their situations, i.e. as a pair of roles. We do not necessarily have to invoke the idea of a "real" contest situation as opposed to this "subjective" contest situation for the following reason: an animal's strategic choice can only be made in dependence of its perceived image of the state of affairs. It is therefore quite natural to refer mainly to those states in a strategic analysis.

We introduce the model artefact of randomly calling one of the involved animals in a conflict "player 1", the opponent "player 2". A contest situation is then more exactly a pair of roles, the first of which is assigned to player 1, the second to player 2. There are four contest situations (A,B), (A,A), etc. one may think of. Let $w_{AB}$ denote the probability that player 1 has role A and player 2 has role B in a randomly chosen contest. We call $w_{AB}$ the basic probability of the contest situation (A,B) and clearly must require $w_{AB} = w_{BA}$, since roles are assigned randomly to each opponent. We assume that there is at least a small positive probability that both opponents have the same role in a contest, i.e. $w_{AA} \neq 0$ and $w_{BB} \neq 0$. Here, we are introducing the notion of "incomplete information" which may be justified, for example, by assuming that animals make mistakes in the perception of a true asymmetric situation. Such an interpretation of the model will be discussed in detail in section V.

2. Strategic choices and situation dependent payoffs: The strategic choices in a role are the same as in the well known "war of attrition" model for a symmetric conflict (Maynard Smith, 1974). A player's decision in this game is simply a choice of how long

he would continue the dispute if the opponent did also continue. The winner is the individual prepared to persist longer. Both have a linear cost for their actually exhibited persistence time. It should be emphasized that in the present model, decisions are made depending on roles, and that the value of the resource under competition as well as the time rate of cost may depend on the contest situation. These parameters will be called $V_{AA}$, $V_{AB}$, etc. (value of winning) and $C_{AA}$, $C_{AB}$, etc. (cost rate). Thus $V_{AB}$, for example, is the expected value of winning to a player when he estimates his role as A and the opponent estimates himself B.

We now describe the payoff to a player having role A in a conflict against B if he chooses a persistence time x and the opponent chooses y. This value $a_{AB}(x,y)$ will be called payoff dependent on situation (A,B):

$$(1) \qquad a_{AB}(x,y) = \begin{cases} V_{AB} - C_{AB}y & \text{if } x > y \\ V_{AB}/2 - C_{AB}x & \text{if } x = y \\ -C_{AB}x & \text{if } x < y \end{cases}$$

Note that the persistence times x and y are each chosen from the continuum of non-negative real numbers, and that we do not assume there to be an upper limit. For the three remaining functions $a_{AA}$, etc. replace the subscript AB by AA, etc. in (1) wherever it appears.

<u>3. Strategies:</u> A local strategy $p_A$ for a role A is a prescription how to behave in this particular role. It may assign a definite choice of persistence time to that role, but a local strategy is more generally defined as a probability distribution over the set of available choices (persistence times). To play $p_A$ in role A means to randomize the choice according to this distribution. The assignment of a definite persistence time x to A is a special case in which $p_A$ gives x the probability 1. Due to the infinite set of choices, this clearly requires an appropriate technical specification of the term "probability distribution" which will be presented in section III.

Whereas a local strategy represents only a partial aspect of strategic behaviour, the notion of a strategy requires a complete prescription, how to act in all situations of the considered game. A strategy p is therefore defined here as a pair $p = (p_A, p_B)$ of local strategies for each role. It is called pure if it assigns definite choices to both roles. Otherwise, p is called a properly mixed strategy.

4. Expected payoffs: Let $p_A$ and $q_B$ be local strategies for the roles A and B. The expected value of the payoff to an individual playing $p_A$ in role A against an opponent playing $q_B$ is denoted by $E_{AB}(p_A, q_B)$.

Let $q = (q_A, q_B)$ be a strategy. We call the following expression local expected payoff for playing $p_A$ in role A against q:

$$E_A(p_A, q) = w_{AA}E_{AA}(p_A, q_A) + w_{AB}E_{AB}(p_A, q_B) \ .$$

Finally, the expected payoff for playing a strategy $p = (p_A, p_B)$ against q in the actual evolutionary game is

$$E(p,q) = E_A(p_A, q) + E_B(p_B, q).$$

Note here that the evolutionary game is a symmetric one (despite the asymmetric conflict!) in which a random move of role assignment preceeds the players' decisions.

5. Best replies and evolutionarily stable strategies: Consider a local strategy $q_A$ and a strategy p. We call $q_A$ a local best reply to p if

$$E_A(q_A, p) \geq E_A(r_A, p)$$

for all local strategies $r_A$. Analogously, a strategy q is called a best reply to p if for all r:

$$E(q,p) \geq E(r,p) \ .$$

A strategy p is called evolutionarily stable (ESS) if the following two conditions are satisfied:

(2) Equilibrium condition: p is a best reply to p.

(3) Stability condition: for every alternative best reply q to p with $q \neq p$, the following inequality holds:

$$E(p,q) > E(q,q).$$

A strategy which satisfies (2) will be referred to as an equilibrium strategy. The use of game theoretical language in this paper follows closely the proposals made by Selten (1980).

6. Parameter relations: For a given contest situation (A,B), the relative value of the resource as compared to the time rate of cost is $V_{AB}/C_{AB}$ and $V_{BA}/C_{BA}$ for the two opponents. We call a role A "favoured with respect to payoffs" if $V_{AB}/C_{AB} > V_{BA}/C_{BA}$. The restriction will be made on the relation between parameters that such an inequality implies

(4) $$\frac{V_{AB}}{C_{AB}} > \frac{V_{BB}}{C_{BB}} \quad \text{and} \quad \frac{V_{BA}}{C_{BA}} < \frac{V_{AA}}{C_{AA}} \quad .$$

This obvious restriction is, in particular, compatible with the interpretation presented in section V.

## III. THE ESS FOR THE CONTINUOUS MODEL

The continuous asymmetric war of attrition with linear costs was introduced in the previous section. This model has the notable property that the risk in contests against escalating opponents is finely controllable, since the expected cost can be chosen from a continuum. It will be shown in the present section for the continuous model that only a role which is favoured with respect to payoffs can be a "winning role" if an ESS is played. We directly state the central theorem, a proof of which is subsequently given in a series of separate steps.

Theorem 1. "Continuously controllable risk. The unique ESS": Suppose that one of the two roles which we call A is favoured in the sense that the value of the resource under competition relative to the time rate of cost is higher in that role:

(5) $$\frac{V_{AB}}{C_{AB}} > \frac{V_{BA}}{C_{BA}} \quad .$$

Suppose further that symmetric contest situations, where both opponents have the same role A or B, are sufficiently rare, such that the following two inequalities hold:

(6) $$w_{AB}V_{AB} > w_{BB}V_{BB} \quad ,$$

(7) $$w_{BA}C_{BA} > w_{AA}C_{AA} \quad .$$

The latter set of inequalities (6), (7) will be referred to as the weak asymmetry condition.

Under these assumptions, there exists only a single strategy $p = (p_A, p_B)$ which is an ESS. Moreover, p is the only equilibrium strategy. A separation value $s > 0$ partitions the set of choices (persistence times) such that, according to p, all values greater than s are likely to be played in role A, all smaller values in role B. The exact form of the mixed local strategies is defined by the following probability density functions:

$$(8)\qquad p_A(x) = \begin{cases} 0 & \text{if } 0 \leq x < s \\ \frac{C_{AA}}{V_{AA}} \exp\left(\frac{C_{AA}}{V_{AA}}(s-x)\right) & \text{if } x \geq s \end{cases}$$

$$(9)\qquad p_B(x) = \begin{cases} \frac{1}{V_{BB}}\left(\frac{w_{BA}C_{BA}}{w_{BB}} + C_{BB}\right) \exp\left(-\frac{C_{BB}}{V_{BB}}x\right) & \text{if } 0 \leq x < s \\ 0 & \text{if } x \geq s \end{cases}$$

The separation value s is defined as

$$(10)\qquad s = -\frac{V_{BB}}{C_{BB}} \ln\left(\frac{w_{BA}C_{BA}}{w_{BA}C_{BA} + w_{BB}C_{BB}}\right) .$$

<u>Remark on the weak asymmetry condition:</u> The smaller the probabilities $w_{AA}$, $w_{BB}$, the more we are inclined to call the type of conflict asymmetric. A more precise delimitation can only be justified by its technical convenience. The theorem shows that a surprisingly low degree of asymmetry suffices in order to guarantee that p is an ESS and that no alternative ESS exists. If role A is favoured in a twofold sense, i.e. if $V_{AB} > V_{BA}$ and $C_{AB} < C_{BA}$, the weak asymmetry condition (6), (7) does not even require role asymmetric situations to be more frequent than symmetric ones. The case with $w_{AA} = w_{AB}$ and $w_{BB} = w_{BA}$ is then included, where roles are paired at random as in the "war of attrition with random rewards". This model was analyzed by Bishop, Cannings & Maynard Smith (1978) for more than two roles, but with equal cost rates. They found also non-overlapping ranges of values that are "permitted" in the different roles. This is according to our analysis not always true if there are differences in both the value of winning and the time rate of cost (see concluding remark in this section).

Remark on payoff irrelevant asymmetries: By the assumption of the preceding theorem, the interesting case is excluded, where the relative value of the resource is equal in both roles:

$$\frac{V_{AB}}{C_{AB}} = \frac{V_{BA}}{C_{BA}} \quad . \tag{11}$$

This may appear to be an important loss of generality. However, any solution for this case would be drastically altered by arbitrarily small changes in the parameter values which turn (11) into an inequality. Due to this structural instability, it would not be sensible to assume that any strategy in this case may be really stable even if it satisfied formally the ESS-conditions.

Completion of the definition of a local strategy: A local strategy was introduced in the last section as a probability distribution over the set of choices (persistence times) in a role. For reasons of its rather technical nature, the necessary specification of this slightly ambiguous notion is placed behind theorem 1, though being part of its premises. As local strategies we consider, in particular, probability distributions which have piecewise continuous density functions with a finite number of discontinuities (in order to get a unique representation, only those densities are used which are in addition continuous to the left). More generally, as local strategies we admit also convex combinations of such a distribution with point measures that assign probability 1 to single choices. If we did not, pure strategies and finite mixtures of them could not be realised.

Use of language. "Possible choices and supports": Consider, for example, the local strategy $p_A$. Had we only a finite set of choices, we would call a persistence time "possible according to $p_A$" if $p_A$ assigned a non-zero probability to this choice. The infinite number of persistence times requires here the following analogous definition: a choice (persistence time) is called "possible according to $p_A$" if $p_A$ assigns either a non-zero probability to this choice, or probability zero and positive density. The set of all such choices is called "support of $p_A$" and denoted by $S(p_A)$. The support corresponds, in other words, to the set of those pure local strategies that appear in the "mixture" $p_A$. It is convenient to include into $S(p_A)$ all points on its boundary.

Guide through the proof of theorem 1: An ESS is in particular an equilibrium strategy, i.e. a best reply to itself. Using the fundamental local characterization (Lemma 1) of an equilibrium strategy $p = (p_A, p_B)$, we first derive necessary conditions on the structure of the supports of $p_A$ and $p_B$ (Lemma 2 to 7). It turns out (Lemma 8) that only one support structure is not excluded, for which the possible choices according to $p_B$ are all persistence times smaller than a separation value, whereas for the favoured role A, the support of A consists of all greater choices. For the specific support structure, the existence of an equilibrium strategy can after all be established by a rather straight forward procedure (Lemma 9), again using the fundamental characterization. Only one question remains then unanswered, whether this equilibrium strategy satisfies the stability condition (3). Here, the argument (Lemma 10) is similar to the one used for the "war of attrition with random rewards" in the above cited paper.

Lemma 1."Fundamental local property of an equilibrium strategy": For a strategy $p = (p_A, p_B)$, the following three statements (i), (ii) and (iii) are equivalent:

(i) p is a best reply to p.

(ii) For every role R = A, B, the local strategy $p_R$ is a local best reply to p.

(iii) For every role R = A, B, the local strategy $p_R$ satisfies the following two conditions:

(12) $$E_R(x,p) = E_R(p_R,p) \qquad \text{f.a.} \quad x \in S(p_R) ,$$

(13) $$E_R(x,p) \leq E_R(p_R,p) \qquad \text{f.a.} \quad x \notin S(p_R) .$$

The equivalence between (i) and (ii) means verbally that in order to be best against p one must do best in each situation. This is so, since the players may get into all of the considered information situations (roles), irrespectively of their strategies. The equivalence between (ii) and (iii) expresses the well known game theoretical fact that if a mixed (local) strategy is a (local) best reply, so is every pure (local) strategy that can be realized when playing the mixture.

The following Lemma allows us to identify the local strategies $p_A$ and $p_B$ with density functions of the above defined type from now on in this section.

Lemma 2. "No atoms of probability": Let p be an equilibrium strategy. Neither of its local strategies may assign an atom of probability to any of the choice values.

The proof is analogous to that for the symmetric war of attrition as given by Bishop & Cannings (1978). It is easy to show that if, for example, $p_A$ assigned an atom of probability to a choice x, one would yield higher payoff against p by playing $x+\varepsilon$ in role A than by playing x, for sufficiently small $\varepsilon > 0$. According to the preceeding Lemma, there cannot be such a difference in local payoffs if $p_A$ is a local best reply. The argument clearly bases on the assumption of continuously rising costs, and it would not hold for an upper limit of persistence time if it existed.

Lemma 3."No gaps in the support of A": Let p be an equilibrium strategy. Suppose that role A is favoured with respect to payoffs (5) and that the weak asymmetry condition (6), (7) holds. The local strategy $p_A$ has then the following property: if two choices a, b with $a < b$ belong to the support of $p_A$, every intermediate value x with $a < x < b$ also belongs to this support. Furthermore, the union of both supports for the roles A, B may in the analogous sense not have a gap.

Proof: It is easy to see first without reference to the asymmetry condition that the union of both supports $S = S(p_A) \cup S(p_B)$ may not have a gap. If there were an interval (a,b) not belonging to S and if, for example, $b \in S(p_A)$, every strategy "play x" with $a \leq x < b$ would in role A be a better local reply to p than "play b". The argument is here that x wins if b wins and loses if b loses, but at a lower cost. On the other hand, we know from Lemma 1 that $E_A(x,p) \leq E_A(b,p)$ if $x \notin S(p_A)$ and therefore conclude: all persistence times between a and b belong to the union S of the supports. Note that the given reasoning depends critically on the already established fact that there cannot be an atom of probability at b.

It is less trivial to exclude the possibility that the support of $p_A$ has a gap (a,b), but this interval belongs to the support of $p_B$. We now treat this case and refer to the weak asymmetry condition, as well as to the fact that role A is favoured with respect to payoffs. The argument will be indirect.

Suppose that $a,b \in S(p_A)$ with $a < b$ and $(a,b) \cap S(p_A) = \emptyset$, but $(a,b) \subset S(p_B)$. According to Lemma 1, "play a" and "play b" are local best replies in both roles, and therefore

(14) $$\Delta E_A = E_A(a,p) - E_A(b,p) = 0 \ ,$$

(15) $$\Delta E_B = E_B(a,p) - E_B(b,p) = 0 \ ,$$

where

$$\Delta E_A = w_{AA}k_{AA} + w_{AB}k_{AB} \ ,$$

$$\Delta E_B = w_{BA}k_{BA} + w_{BB}k_{BB} \ .$$

Here, the following abbreviations are used:

(16) $$k_{AA} = C_{AA}(b-a) \int_b^\infty p_A(x)\,dx \ ,$$

(17) $$k_{BA} = C_{BA}(b-a) \int_b^\infty p_A(x)\,dx \ ,$$

(18) $$k_{AB} = C_{AB}(b-a)\int_b^{\infty} p_B(x)\,dx + \int_a^b [C_{AB}(x-a) - V_{AB}]\,p_B(x)\,dx,$$

(19) $$k_{BB} = C_{BB}(b-a)\int_b^{\infty} p_B(x)\,dx + \int_a^b [C_{BB}(x-a) - V_{BB}]\,p_B(x)\,dx.$$

As $k_{AA}$ and $k_{BA}$ are positive, it follows from (14) and (15) that $k_{AB}$ and $k_{BB}$ are negative.

We now derive the following inequality which contradicts the pair of equations (14),(15) and which therefore concludes the proof:

(20) $$\Delta E_B > \Delta E_A \,.$$

As an immediate consequence of the weak asymmetry condition (7) we get

(21) $$w_{BA}k_{BA} > w_{AA}k_{AA} \,.$$

It is less obvious that (5) and (6) imply

(22) $$w_{BB}k_{BB} > w_{AB}k_{AB} \,.$$

Looking at the expressions (18) and (19), for $k_{AB}$ and $k_{BB}$, we may assert that there exist positive numbers $\alpha$, $\beta$ such that

$$k_{BB} = \alpha C_{BB} - \beta V_{BB} \,,$$

$$k_{AB} = \alpha C_{AB} - \beta V_{AB} \,.$$

The inequality (22) is equivalent to the following:

(23) $$w_{BB}V_{BB}\left(\alpha\frac{C_{BB}}{V_{BB}} - \beta\right) > w_{AB}V_{AB}\left(\alpha\frac{C_{AB}}{V_{AB}} - \beta\right) .$$

It is easy to see that this holds, since $w_{BB}V_{BB} < w_{AB}V_{AB}$ and

$V_{AB}/C_{AB} > V_{BB}/C_{BB}$ . Note here that both sides of (23) are negative, which follows from $k_{AB} < 0$ and $k_{BB} < 0$. To summarize, we have shown the two inequalities (21), (22), and thus get the contradictive statement (20).

Lemma 4. "Supports cover the set of choices": Every persistence time belongs to at least one of the supports of an equilibrium strategy p.

Proof: Consider the minimal persistence time x which is a possible choice according to at least one of the local strategies of p. To play x against p in a role has the consequence that one loses with probability one. "Play x" is a local best reply for one of the roles, and there cannot be another way of always losing which involves a lower cost. Therefore, zero is the minimal value of the union S of the supports. On the other hand, assume there exists a maximal possible choice y, and let, without loss of generality, $y = \max S(p_A) \geq \max S(p_B)$. It is easy to show that "play y" is then a better reply to p in role A than "play $y-\varepsilon$", for small $\varepsilon > 0$. This contradicts the fundamental property of an equilibrium strategy (Lemma 1), since we know from Lemma 2 that there cannot be an atom of probability at y and thus $y-\varepsilon \in S(p_A)$ if $\varepsilon$ is chosen small enough. Now, having no upper bound and no gap, S must contain all persistence times.

Lemma 5. "No overlap if support of B is bounded": Let p be an equilibrium strategy, with all the assumptions made in theorem 1. If the support of $p_B$ has an upper limit, there is only a single point overlap between the supports for the different roles.

Proof: Suppose there were an overlap and let $x = \max S(p_B)$. The value x and for small $\varepsilon > 0$ the value $x-\varepsilon$ belong then to both supports. From the fundamental property of an equilibrium strategy (Lemma 1) we derive:

$$(24) \qquad E_A(x,p) - E_A(x-\varepsilon,p) = E_B(x,p) - E_B(x-\varepsilon,p) = 0 .$$

When looking at the explicit expressions, it is easy to derive from (24) the contradictive statement that the payoff difference for role A is greater than that for role B. This follows in particular from the fact that role A is favoured with respect to payoffs. For reasons of similarity to the procedure used in the proof of Lemma 3, details are omitted.

Remark: The following result is an important step in order to understand why there do not exist paradoxical ESS's. The proof is therefore more explicitly presented.

Lemma 6."High values must be played in the favoured role A": Let p be an equilibrium strategy and assume that role A is favoured as stated in theorem 1. The support of $p_A$ has then no upper bound.

Proof: Suppose that $s = \max S(p_A)$. Consider a value $x > s$. We may calculate $\Delta E_A = E_A(x,p) - E_A(s,p)$ and $\Delta E_B = E_B(x,p) - E_B(s,p)$:

$$\Delta E_A = w_{AB}\{ \int_s^x (V_{AB} - C_{AB}(y-s))p_B(y)\,dy - C_{AB}(x-s) \int_x^\infty p_B(y)\,dy\} ,$$

$$\Delta E_B = w_{BB}\{ \int_s^x (V_{BB} - C_{BB}(y-s))p_B(y)\,dy - C_{BB}(x-s) \int_x^\infty p_B(y)\,dy\} .$$

As x and s belong to the support of $p_B$, the fundamental property of an equilibrium strategy (Lemma 1) tells us that $\Delta E_B = 0$, and therefore

$$\frac{\Delta E_A}{w_{AB}C_{AB}} = \frac{\Delta E_A}{w_{AB}C_{AB}} - \frac{\Delta E_B}{w_{BB}C_{BB}} = (\frac{V_{AB}}{C_{AB}} - \frac{V_{BB}}{C_{BB}}) \int_s^x p_B(y)\,dy .$$

Knowing role A to be favoured in the sense $V_{AB}/C_{AB} > V_{BB}/C_{BB}$, we get $\Delta E_A > 0$. This means x is a better reply to p than s in role A which contradicts the fundamental property of best replies.

<u>Lemma 7. "Support of B has an upper bound":</u> With the assumptions made in theorem 1, no equilibrium strategy can exist, for which the supports of $p_A$ and $p_B$ are both above unlimited.

<u>Proof:</u> We assumed that the probability density functions $p_A$ and $p_B$ can only have a finite number of discontinuities. This was done with the intention to exclude from the analysis absurd strategies of great complexity which we do not expect to be realised as an animal's behavioural program. For the proof of the present Lemma we make use of this assumption, since it is helpful to know that the support of $p_B$ may only have a finite number of "gaps".

Suppose that the supports $S(p_A)$ and $S(p_B)$ of an equilibrium strategy p have both no upper bound. Let z be a value of overlap between them, such that all persistence times greater z belong also to both supports, i.e. $[z,\infty) \subset S(p_A) \cap S(p_B)$. We know (Lemma 1), there are two constants $k_A$ and $k_B$, such that all local strategies "play x" with $x \geqq z$ yield in the same role the same payoff $k_A$, $k_B$ respectively against p:

$$(25) \qquad E_A(x,p) = k_A \quad \text{and} \quad E_B(x,p) = k_B \qquad \text{f.a.} \quad x \geqq z.$$

This means that the pair of density functions $p = (p_A, p_B)$ solves for $x \geqq z$ a set of two integral equations, the first of which has the following explicit form:

$$(26) \qquad w_{AA}\left\{ \int_0^x (V_{AA} - C_{AA}y)p_A(y)\,dy - C_{AA}x \int_x^\infty p_A(y)\,dy \right\} +$$

$$w_{AB}\left\{ \int_0^x (V_{AB} - C_{AB}y)p_B(y)\,dy - C_{AB}x \int_x^\infty p_B(y)\,dy \right\} = k_A.$$

The second equation for role B is the analogous one with A and B exchanged in the subscripts wherever they appear. Clearly, p must also be a solution of the differentiated form of (26) which is

$$(27) \quad p_A(x) = \frac{C_{AA}}{V_{AA}} \int_x^\infty p_A(y)\,dy + \frac{w_{AB}}{w_{AA}V_{AA}} \left( C_{AB} \int_x^\infty p_B(y)\,dy - V_{AB}p_B(x) \right)$$

and the corresponding equation for B. It is easy to see that $p_A$ and $p_B$ are differentiable, and that after differentiating (27) with respect to x, we get a linear differential equation

$$(28) \qquad \dot{p}(x) = A\,p(x) \quad ,$$

where p is considered as a column for the moment, and A is a 2x2-matrix. The coefficients of A are

$$a_{11} = \left( \frac{w_{AB}^2 V_{AB} C_{BA}}{w_{AA} w_{BB} V_{AA} V_{BB}} - \frac{C_{AA}}{V_{AA}} \right) / M ,$$

$$a_{12} = \frac{w_{AB}}{w_{AA}V_{AA}} \left( \frac{V_{AB}C_{BB}}{V_{BB}} - C_{AB} \right) / M ,$$

with $M = 1 - (w_{AB}^2 V_{AB} V_{BA}) / (w_{AA} w_{BB} V_{AA} V_{BB})$, as well as $a_{21}$ and $a_{22}$, which are yield from $a_{12}$, $a_{11}$ respectively by role reversal in the subscripts.

The matrix A has the following structure which will be used in the remainder of the proof. Either, $a_{11}$ and $a_{12}$ are positive and $a_{21}$ is negative (case 1), or $a_{11}$ and $a_{12}$ are negative and $a_{21}$ is positive (case 2). Furthermore, if $a_{11}$ and $a_{22}$ are both negative, the inequality $a_{11} < a_{22}$ holds. We omit the check of these statements which rely on the assumptions made in theorem 1. It will be shown now that no pair of probability densities $p = (p_A, p_B)$ exists which satisfies the differential equation (28) for $x > z$.

If p is a pair of probability densities, its trajectory in the phase space of (28) must asymptotically approach the origin and also remain within the positive quadrant. However, the following study of the eigenvalues and corresponding eigenvectors of A shows that this is impossible for a solution of (28).

A necessary condition for a solution of (28) to be of the just outlined type is that the matrix A has a negative real eigenvalue, with the additional property that the corresponding line of eigenvectors intersects the positive quadrant. The eigenvalues
$\lambda = (a_{11} + a_{22})/2 \pm \sqrt{(a_{11} - a_{22})^2/4 + a_{12}a_{21}}$ give rise to eigenvectors $v = (1, y)$ which satisfy

(29) $$a_{11} - \lambda + a_{12}y = 0 ,$$

(30) $$a_{21} + (a_{22} - \lambda)y = 0 .$$

We show that the necessary condition is violated in both cases of parameter relations mentioned above. Consider case 1 first with $a_{11} > 0$, $a_{12} > 0$ and $a_{21} < 0$. If $a_{22} > 0$, no negative eigenvalue exists. On the other hand, if $a_{22} < 0$, we get $\lambda > a_{22}$. From (30) it follows that $y < 0$. Thus, the line of corresponding eigenvectors does not intersect the positive quadrant as required in the necessary condition. Consider case 2 now with $a_{11} < 0$, $a_{12} < 0$ and $a_{21} > 0$. If $a_{22} > 0$ and $\lambda < 0$, it follows trivially from (30) that $y < 0$. Finally, if $a_{22} < 0$, we get $\lambda > \min(a_{11}, a_{22})$. Now, since $a_{11} < a_{22}$ in this case, we have $\lambda > a_{11}$ and conclude from (29) that $y < 0$. This completes the proof that the necessary condition is violated.

Lemma 8."Interim balance": Let p be an equilibrium strategy and suppose that the assumptions of theorem 1 are satisfied. The support structure of $p = (p_A, p_B)$ is then necessarily of the following type: there exists a persistence time $s > 0$, such that all values $x \leq s$ are the choices which are possible according to $p_B$, and all values $x \geq s$ are the choices which are possible according to $p_A$. Formally, this summarizing of Lemma 2 to 7 means: $S(p_B) = [0,s]$ and $S(p_A) = [s,\infty)$.

Lemma 9."Existence of a unique equilibrium strategy": With the assumptions of theorem 1, there exists exactly one equilibrium strategy p. It is of the form defined in theorem 1.

Proof: We only have to deal with strategies of the type introduced in the preceeding Lemma. An equilibrium strategy is characterized by the conditions (12), (13) stated as fundamental local property of an equilibrium strategy. It will first be shown that among all candidates $p = (p_A, p_B)$ there exists a unique solution to (12), i.e. satisfying the equations

$$(31) \qquad E_B(x,p) = 0 \qquad \text{f.a. } 0 \leq x < s\ ,$$

$$(32) \qquad E_A(x,p) = k_A \qquad \text{f.a. } x \geq s\ ,$$

where $k_A$ is some constant. We demonstrate first how (31) is solved which has the explicit form

$$(33) \quad w_{BB}\left\{ \int_0^x (V_{BB} - C_{BB}y) p_B(y)\,dy - C_{BB}x \int_x^s p_B(y)\,dy \right\} - w_{BA}C_{BA}x = 0\ .$$

Note that $p_B$ is a probability density having integral 1. The equation is therefore equivalent to

$$\int_0^x (V_{BB} - C_{BB}(y-x)) p_B(y)\,dy = x\left(\frac{w_{BA}C_{BA}}{w_{BB}} + C_{BB}\right)\ .$$

This Volterra equation of the first kind can be restated in differentiated form which reveals the simple nature of the problem:

$$(34) \qquad p_B(x) = \frac{w_{BA}C_{BA}}{w_{BB}V_{BB}} + \frac{C_{BB}}{V_{BB}} \int_x^s p_B(y)\,dy\ .$$

The only probability density satisfying (34) is

$$(35) \qquad p_B(x) = \left(\frac{w_{BA}C_{BA}}{w_{BB}V_{BB}} + \frac{C_{BB}}{V_{BB}}\right) \exp\left(-\frac{C_{BB}}{V_{BB}}x\right) \quad \text{f.a. } 0 \leq x < s,$$

where s is uniquely defined by the model parameters:

$$(36) \qquad s = -\frac{V_{BB}}{C_{BB}} \ln\left(\frac{w_{BA}C_{BA}}{w_{BA}C_{BA} + w_{BB}C_{BB}}\right)\ .$$

The local strategy $p_A$ can be similarly deduced. Its characterizing equation (32) reads after some rearrangements as follows, where $\bar{x}_B$ denotes the expected persistence time when $p_B$ is played:

(37) $$\int_s^x (V_{AA} - C_{AA}(y-x))\, p_A(y)\, dy = C_{AA}x + \frac{k_A - w_{AB}(V_{AB} - C_{AB}\bar{x}_B)}{w_{AA}} .$$

The constant $k_A$ must be chosen such that the r.h.s reduces to the expression $C_{AA}(x-s)$. Differentiation with respect to x yields:

$$p_A(x) = \frac{C_{AA}}{V_{AA}} \int_x^\infty p_A(y)\, dy .$$

Clearly, this is solved by

(38) $$p_A(x) = \frac{C_{AA}}{V_{AA}} \exp\left(\frac{C_{AA}(s-x)}{V_{AA}}\right) \quad \text{f.a. } x \geqq s.$$

It remains to show that this strategy $p = (p_A, p_B)$ also has the following two properties of a best reply which correspond to (13):

(39) $$E_B(x,p) \leqq E_B(s,p) \qquad \text{f.a. } x > s ,$$

(40) $$E_A(x,p) \leqq E_A(s,p) \qquad \text{f.a. } x < s .$$

The inequalities (39), (40) can be established even in their strict form. The argument which demonstrates (39) corresponds with reversed roles to the reasoning already used in the proof of Lemma 6: knowing that $E_A(x,p) - E_A(s,p) = 0$, one derives here analogously the payoff difference in question:

$$E_B(x,p) - E_B(s,p) = w_{BA}C_{BA}\left(\frac{V_{BA}}{C_{BA}} - \frac{V_{AA}}{C_{AA}}\right) \int_s^x p_A(y)\, dy .$$

The expression is negative if role A is favoured, as the bracketed term is then negative. Therefore, the strict form of (39) holds.

In order to show (40), we differentiate the local payoff function $E_A(x,p)$ with respect to x. After some calculation one gets for $x < s$:

$$(41)\qquad \frac{dE_A(x,p)}{dx} = w_{AB}p_B(x)(V_{AB} - \frac{V_{BB}}{C_{BB}}C_{AB}) + \frac{w_{BA}^2 C_{BA}C_{AB}}{w_{BB}C_{BB}} - w_{AA}C_{AA}.$$

With the help of (34), the greatest lower bound for (41) can be written as follows:

$$(42)\qquad \lim_{x\uparrow s} \frac{dE_A(x,p)}{dx} = \frac{w_{AB}^2 C_{BA}V_{AB}}{w_{BB}V_{BB}} - w_{AA}C_{AA}.$$

This expression is positive, because it follows from the weak asymmetry condition that $w_{AB}^2 C_{BA}V_{AB} > w_{AA}w_{BB}C_{AA}V_{BB}$. On the interval $(0,s)$, the local payoff $E_A(x,p)$ is therefore a strictly increasing function of x. It is also continuous at the bounds 0 and s, since p does not assign an atom of probability to those values. We have thus derived (40) as a strict inequality which completes the proof of this Lemma.

In order to complete the proof of theorem 1, there remains a final question to be answered: does the equilibrium strategy just derived also satisfy the stability condition (3) which qualifies it as an ESS? The following Lemma shows that this is the case if we remember that the inequalities (39) and (40) where shown to be valid in their strict form.

Lemma 10. "Stability against alternative best replies": Let p be a strategy with nonoverlapping supports $S(p_A)$, $S(p_B)$ that are separated by a value s, i.e. with $S(p_A) \geq s$ and $S(p_B) \leq s$. Furthermore, assume that $E_A(x,p) < E_A(p_A,p)$ f.a. $x \notin S(p_A)$ and $E_B(x,p) < E_B(p_B,p)$ f.a. $x \notin S(p_B)$. If p is an equilibrium strategy and $q \neq p$ an alternative best reply to p, the following inequality then holds: $E(p,q) > E(q,q)$.

Proof: We make use of the idea by Bishop & Cannings (1978) to consider the function

$$T(p,q) = E(p,p) - E(p,q) - E(q,p) + E(q,q)$$

and show the following: if p is an equilibrium strategy with the properties listed above and if q is a best reply to p, the value $T(p,q)$ is negative for $p \neq q$ and zero for $p = q$.

We omit the vast explicit expression for $T(p,q)$ in terms of expected situation dependent payoffs like $E_{AB}(p_A, q_B)$ etc. This expression can be reduced to a simpler one by exploiting the particular properties of p listed above. From $E_A(x,p) < E_A(p_A,p)$ for $x \notin S(p_A)$ it follows that $S(q_A) \subset S(p_A)$ for a best reply q to p, and analogously we get $S(q_B) \subset S(p_B)$. Knowing also that $S(p_B) \leq s \leq S(p_A)$, a number of pairs of situation dependent payoffs turn out to be identical, as, for example, $E_{AB}(p_A, p_B)$ and $E_{AB}(q_A, p_B)$. These identical payoffs appear in the expression for $T(p,q)$ with opposite sign and thus disappear. Therefore, we get

$$T(p,q) = w_{AA} T_{AA}(p_A, q_A) + w_{BB} T_{BB}(p_B, q_B) \ ,$$

with $T_{AA}(p_A,q_A) = E_{AA}(p_A,p_A) - E_{AA}(p_A,q_A) - E_{AA}(q_A,p_A) + E_{AA}(q_A,q_A)$, and with $T_{BB}$ defined analogously.

It is known from the analysis of the symmetric war of attrition (Bishop & Cannings, 1978) that the function $T_{AA}(p_A,q_A)$ takes negative values for $p_A \neq q_A$ and zero for $p_A = q_A$ and that $T_{BB}(p_B,q_B)$ has the corresponding property. Therefore, $T(p,q)$ is of the desired type.

<u>Concluding remark. "Necessity of an asymmetry condition":</u> Forgetting about the problem of uniqueness, one may ask, whether the solution p of theorem 1 is also an ESS if the weak asymmetry condition is violated. A brief review of the proof, especially of (42), shows that this is only the case if $w_{AB}^2 C_{BA} V_{AB} > w_{AA} w_{BB} C_{AA} V_{BB}$. Otherwise, no ESS exists with the support structure of two non-overlapping ranges. The argument holds, in particular, for the already mentioned war of attrition with random rewards. Note that the necessary condition just stated for the support structure of p can be violated if, for example, $V_{AB} > V_{BA}$ and $C_{AB} > C_{BA}$.

## IV. THE MODEL WITH ELEMENTS OF DISCRETENESS

The model, thus far considered, has the extreme feature that a player can select his maximal expected cost from a continuum of values when making his choice of persistence time. In this section, we discuss alternative approaches to the war of attrition, taking seriously the idea that discontinuities may be involved in the rise of cost which is associated with an increase in the level of persistence.

The simplest such model has the additional feature to the already considered one that there is always some initial cost of engaging at all in the process of attrition. This means there is no cost for both opponents if one of them retreats immediately, but if they persist to any degree, both have an initial cost plus expenses which increase with the duration of the contest. The formal description deviates here from the continuous model in section II only insofar as the linear cost function which appears in the situation dependent payoff (1) has to be replaced by the discontinuous function

$$\text{(43)} \qquad \text{cost}_{AB}(x) = \begin{cases} 0 & \text{if } x = 0 \\ C_{AB}x + I_{AB} & \text{if } x > 0 \end{cases}$$

where x is the actual duration of the contest, $I_{AB} > 0$ the initial cost and $C_{AB}$ the rate of time dependent cost. We will call this model the "war of attrition with initial expenses".

There are other ways of introducing elements of discreteness. Assume, for example, that it is not at every given moment possible to withdraw without taking the risk of an additional harm, as it may result from giving up in an unfortunate position. Especially, when contests typically consist of a sequence of bouts, the strategic choices can sometimes better be idealized in terms of "engaging in the next round" than by referring to a continuum of possible contest durations. Here, the discrete war of attrition is intuitively more appealing which was analyzed for symmetric conflicts by Bishop & Cannings (1978). This model allows the players to choose only from a discrete set of persistence times. We calculated evolutionarily stable strategies for numerical examples of the asymmetric war of attrition with a finite number of choices in each role. This was done by applying an algorithm which is an extension of the procedure suggested by Haigh (1975) and by Bishop & Cannings (1976), for games in "normal form", to games considered here in the "restricted extensive form". We do not state all the results explicitly, but give a brief account of the most interesting trait. It turns out that if we choose the probabilities $w_{AA}$ and $w_{BB}$ of role-symmetric encounters sufficiently small and the cost steps between the discrete levels of persistence high enough, the following feature emerges which contrasts the characteristic property of the continuous model: an ESS exists which makes the role that is favoured with respect to payoffs a "losing role". The solutions for such a numerical example are presented in Fig. 1. Clearly, an alternative ESS exists here also which makes the favoured role a "winning role".

How can we get more analytical insights in the consequences of discretization, and what are here more precisely the essential causes for the existence of evolutionarily stable strategies which appear paradoxical with respect to payoffs? An examination of the following model throws some light on the latter problem, in providing us with information about where we minimally need a discontinuity in the set of choices (costs), how big this step must be and how sharp the notion of asymmetry must be, in order to get paradoxical solutions. We simply take up the continuous war of attrition, as defined in section II, but "cut off" a small interval from the set of potential peristence times. The values within this interval cannot be chosen now by a player. Let a,b with $a < b$ be the boundary points of this cut off piece. The set of choices is then more exactly thought to consist of all persistence times x with either $0 \leq x \leq a$ or $x > b$. We will call this the model with a single discontinuity in the rise of cost. It is easy to see that the above war of attrition with initial cost can formally be described in this way if the initial cost $I_{AB}$ is proportional to the situation dependent time rate of cost $C_{AB}$. Here, the length of the cut off interval has to be the constant of proportionality. Analogously, we can treat such jumps in the cost function which do not appear at the start of the contest. The following theorem states now conditions which guarantee

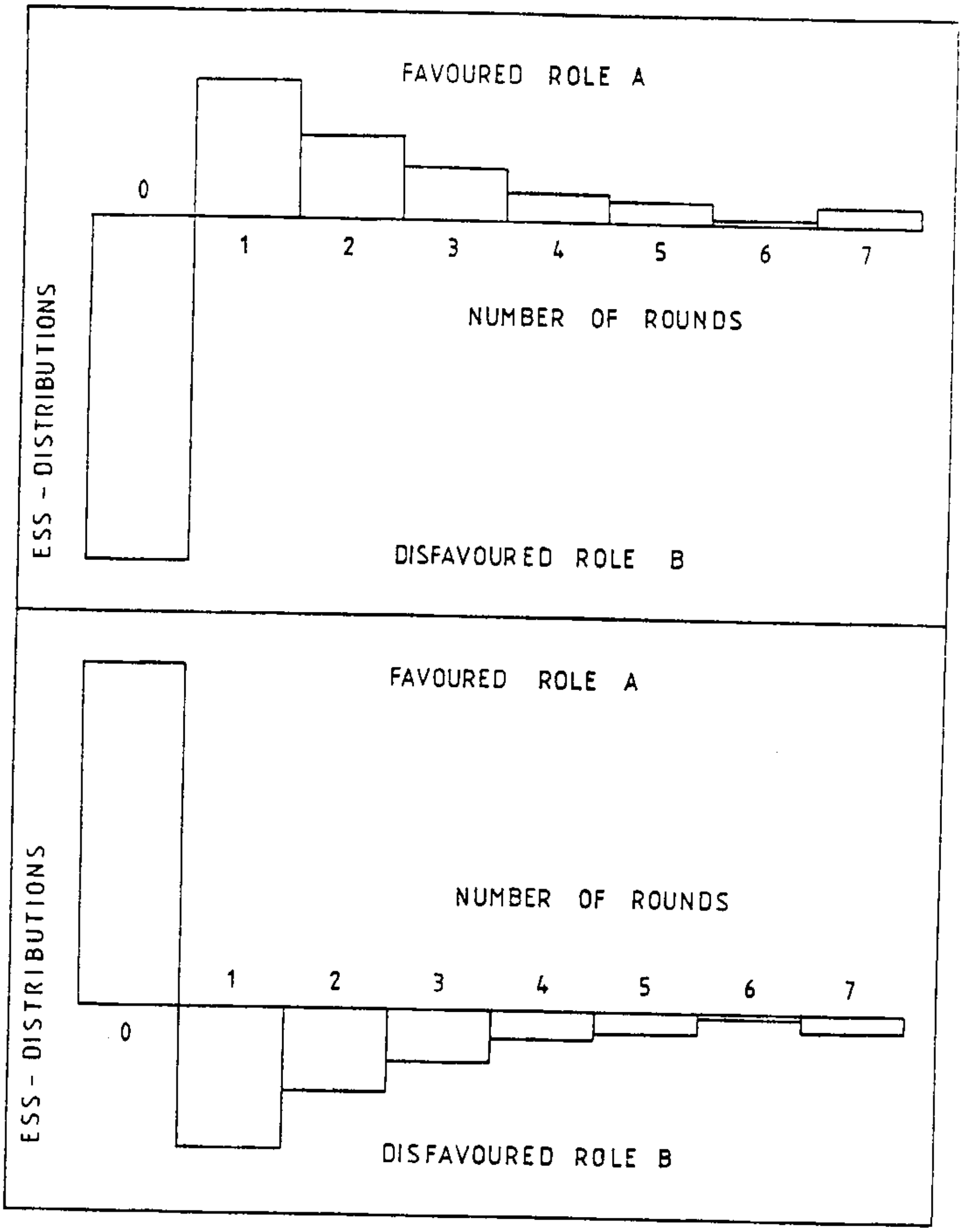


Fig. 1. Two alternative evolutionarily stable strategies for the discrete war of attrition with eight levels of persistence. Role A is favoured with respect to payoffs. Therefore, the above ESS is a commonsense solution, whereas the alternative ESS below appears paradoxical with respect to payoffs. The parameters are $w_{AB} = 0.49$, $V_{AB} = 2.2$, $V_{BA} = 1.4$, cost of a round = 1.

the existence of a paradoxical ESS.

Theorem 2."The disfavoured role as a winning role": Consider the asymmetric war of attrition with a single discontinuity in the rise of cost, i.e. where the players are not allowed to choose persistence times x with $a < x \leq b$. Let role A be favoured with respect to payoffs or let the asymmetry be payoff irrelevant, i.e. $V_{AB}/C_{AB} \geq V_{BB}/C_{BB}$. Suppose that the length $d = b-a$ of the "cut off" interval is greater than the difference in the relative values of the resource:

$$(44) \qquad d > \frac{V_{AB}}{C_{AB}} - \frac{V_{BB}}{C_{BB}} .$$

Suppose also that the persistence time

$$(45) \qquad s = -\frac{V_{AA}}{C_{AA}} \ln\left(\frac{w_{AB}C_{AB}}{w_{AB}C_{AB} + w_{AA}C_{AA}}\right) ,$$

known from theorem 1 (with reversed roles ) as "separation value" falls within the "cut off" interval (a,b]. Finally, suppose that the probability $w_{AA}$, of role-symmetry for role A, is small enough, such that the following inequality holds:

$$(46) \qquad \frac{w_{AB}}{w_{AA}} > \frac{V_{AA}}{2C_{AB}D} ,$$

with D standing for the difference between l.h.s. and r.h.s. in (44).

Under these assumptions, there exists, in particular, an ESS $p = (p_A, p_B)$ with the following property: the local strategy $p_A$, for the favoured role A, places all mass of probability into the range of persistence times between zero and the point a, the local strategy $p_B$ places all mass of probability onto the range of persistence times greater b. The explicit form of $p_B$ is given by the density function:

(47) $$p_B(x) = \frac{C_{BB}}{V_{BB}} \exp\left(\frac{C_{BB}}{V_{BB}}(b-x)\right) \qquad \text{for } x > b.$$

The local strategy $p_A$ assigns probability 1 to the persistence time a if $w_{AA}V_{AA}/2 > a(w_{AB}C_{AB} + w_{AA}C_{AA})$, i.e. if a is relatively small. However, if the opposite strict inequality holds, it assigns an atom of probability smaller than 1 to a. In the latter case, the remaining mass of probability is distributed over the persistence times between zero and a limit $z < a$. The explicit form of this residual distribution is given by a truncation of the probability density which is known from theorem 1 (there with reversed role indices), where it is played in the "losing role":

(48) $$\tilde{p}_A(x) = \frac{1}{V_{AA}}\left(\frac{w_{AB}C_{AB}}{w_{AA}} + C_{AA}\right)\exp\left(-\frac{C_{AA}}{V_{AA}}x\right) \quad \text{f.a. } 0 \leq x \leq z.$$

<u>Discussion of theorem 2:</u> In order to get the existence of the above strategy p, which makes the disfavoured role a winning role, three important assumptions were made in the theorem: the first one about the length of the interval of impossible choices (44), another about the position of this interval within the set of choices (45) and a final one about the proportion of role-symmetric contest situations (46). We now discuss these assumptions. Note that the length of the interval of impossible choices can be written as a ratio which expresses the size of the cost step at the discontinuity relative to the elsewhere valid linear time rate of cost. One may therefore restate the first assumption (44) as follows: the relative size of the cost step is greater than the difference in relative values of the resource. It is, however, intuitively easier to understand the following two special cases. If the time rates of cost are equal for all contest situations, the condition just discussed states that the size of the cost step must be greater than the difference $V_{AB} - V_{BB}$ in the values of the resource. If, on the other hand, the values of the resource are all equal to a value V, the cost step must be greater than the expression $V(1 - C_{AB}/C_{BB})$. Therefore, a jump in the rise of cost which is very small compared to the order of magnitude of the values of the resource can be great enough to "generate" a paradoxical ESS. To conclude the discussion of this first assumption, we would like to emphasize that it is also a necessary condition for the evolutionary stabi-

lity of the above strategy p, and that it is trivially satisfied if the asymmetry is payoff irrelevant.

The second assumption about the position of the discontinuity (45) means in terms of cost roughly that it has to be at a stage of the contest where little cost has been accumulated yet if the probability $w_{AA}$ is small. It is easy to see that an ESS which is similar to the above one cannot exist if the cut off interval is placed beyond the critical value s.

The third assumption (46) about the probability $w_{AA}$ is, in general, a much sharper notion of asymmetry than the weak asymmetry condition which was used for the analysis of the continuous war of attrition. It requires a high degree of "role asymmetry" especially if the size of the cost step is not considerably greater than the difference in the relative values of the resource.

<u>Proof of theorem 2:</u> The arguments needed here are closely related to those which were already used in the proof of theorem 1 about the continuous war of attrition. The most interesting question to be answered is: why does it not pay to play larger persistence times in role A? We know in analogy to Lemma 6 that for $x > b$:

$$E_A(x,p) - \lim_{y \downarrow b} E_A(y,p) = w_{AB}C_{AB}\left(\frac{V_{AB}}{C_{AB}} - \frac{V_{BB}}{C_{BB}}\right)\int_b^x p_B(y)\,dy .$$

Now, if role A is favoured, this difference is clearly positive. However, by contrast to the proof of theorem 1, it does not represent the relevant comparison here which is:

$$\Delta E_A = E_A(x,p) - E_A(a,p)$$

$$= \frac{w_{AA}V_{AA}}{2}\phi + w_{AB}C_{AB}\left\{\left(\frac{V_{AB}}{C_{AB}} - \frac{V_{BB}}{C_{BB}}\right)\int_b^x p_B(y)\,dy - d\right\} ,$$

where $\phi$ denotes the atom of probability assigned to a by $p_A$ and d the length of the cut off interval (a,b]. This payoff difference is positive for great persistence times x if (44) is not satisfied, but it is negative, as required, if (44) and (46) hold.

We know now that against a strategy $p = (p_A, p_B)$, as defined in the theorem, it does not pay to deviate from $p_A$ by playing larger values than a. We still have to check, whether $p_A$ is also a better local reply than other deviant choices and, whether the local payoff is equal for all choices that are possible according to $p_A$. Remember that $p_A$ assigns probability 1 to the choice a if the following inequality holds:

$$(49) \qquad w_{AA}V_{AA}/2 > a(w_{AB}C_{AB} + w_{AA}C_{AA}) \, .$$

It is easy to calculate that "play a" is a better local reply to p in role A than any smaller value x if (49) is satisfied in its strict form ( in case of equality, "play zero" is an alternative best reply).

If instead of (49) the reverse strict inequality holds, the strategy p in theorem 2 is only specified up to the parameter z which indicates the end of the range over which $p_A$ is described by the density $\tilde{p}_A$. Let us call the so parametrized strategy $p^z$. It is trivial that for every z with $0 < z < a$, the values between z and a are worse local replies to $p^z$ than z. To answer the question, whether there exists a value z at all such that $0 < z < a$ and $f(z) = E_A(a, p^z) = 0$, requires more effort. Note that for $0 < z < a$ , the function f(z) is monotonically increasing and continuous. Let f(0) and f(a) be the limits of f. The inequality (49) is here not satisfied and therefore $f(0) < 0$. Furthermore, we know from the construction of $\tilde{p}_A$ (in analogy to Lemma 9) that $E_A(z,p^z) = 0$ for $0 < z < a$, and thus

$$(50) \qquad f(a) = \lim_{z \uparrow a} E_A(a,p^z) - \lim_{z \uparrow a} E_A(z,p^z)$$

$$= \frac{w_{AA}V_{AA}}{2} \left( 1 - \int_0^a \tilde{p}_A(y)\,dy \right) .$$

It should be mentioned here that the expression (50) only makes sense for $a < s$, as assumed in the theorem, since only the strategies $p^z$ with $z < s$ are well defined. We can conclude from (50) that $f(a) > 0$, knowing the integral to be smaller 1. Had we positioned the "cut off" interval further to the right, with $a > s$, it could easily be shown that the in this case maximal value $f(s)$ of the function f is negative. Having, however, $f(a) > 0$ and $f(0) < 0$, there must be exactly one intermediate choice $z < a$ with $f(z) = 0$, $E_A(a,p^z) = 0$ respectively. We have now established the existence of a strategy $p^z$ within the set of candidates, for which $p_A^z$ is a local best reply to $p^z$ ( all values smaller z yield the same local payoff due to the construction of $\tilde{p}_A$, compare with Lemma 9 ).

Furthermore, the argument is analogous to the one used in Lemma 9 for the "winning role" that $p_B$ is a local best reply to p. We have shown now that p is an equilibrium strategy. This would not be true if $a > s$, as argued above. The stability condition (3) is satisfied, because Lemma 10 applies here also, except for the case where (49) is an equality. This is, however, the case only for exactly one position of a and therefore not emphasized in the theorem.

## V. A SPECIAL CASE OF THE MODEL

In the preceeding sections, we avoided to make any explicit assumption about the "objective" contest situation and referred directly to the "subjective" roles and their pairing. Remember, roles were introduced as the animals' concepts of the true situation they find themselves in. What are the objective situations we have in mind? One of the opponents may be greater than the other, or the prior user of the resource (owner), they may be of different sex, age or whatsoever. In other words, the basic idea is that there is usually a real difference between the opponents. We present now a special case of the general model, in order to demonstrate how more basic assumptions about true contest situations and mistakes in role identification can be incorporated in the analysis. The general model allows also more sophisticated interpretations.

Suppose that whenever the considered type of contest takes place, there is an objective asymmetry with one individual being in the true situation A, the other in the true situation B. Consider a contestant in the true situation A. Let $P_A$ be the probability that he identifies correctly his situation and adopts role A, and let $1-P_A$ be the probability of erroneously adopting role B. Conversely, denote by $P_B$ the analogous measure of precision in the perception of state B. For the sake of simplicity of this particular demonstration, suppose that the value of the resource in state A (or B) is fixed, whether or not the animal is correct in its role identification. Let us call this value $V_A$, $V_B$ respectively and the cost rates $C_A$ and $C_B$. Do not confuse these parameters with the earlier used $V_{AB}$, etc. which we have now to construct. The expression $V_{AB}$ is the value of the resource to a contestant, given that he adopts role A and his opponent adopts B.

It is a trivial matter to see first, how the basic probabilities $w_{AA}$, $w_{AB}$, etc. are calculated. Remember that $w_{AB}$ indicates, for example, the probability that a randomly chosen player from a randomly picked out contest has role A and is faced with an opponent who identifies himself B. We get $w_{AB} = P_A P_B/2 + (1-P_A)(1-P_B)/2$, $w_{AB} = P_A(1-P_B)$, etc. Furthermore, it is easy to calculate

$$V_{AB} = \frac{P_A P_B V_A + (1-P_A)(1-P_B)V_B}{P_A P_B + (1-P_A)(1-P_B)} \quad ,$$

$$V_{AA} = V_{BB} = \frac{V_A + V_B}{2} \; .$$

Analogously, one gets $V_{BA}$ and the cost rates $C_{AB}$, etc. We have now constructed a model of the type introduced in section II. A role A is favoured with respect to payoffs if $V_A/C_A > V_B/C_B$. In order to facilitate the comparison with the former analysis of the war of attrition by Parker & Rubenstein (1981), we briefly show how the ESS for the continuous model reads in this specific interpretation of the general model.

$$p_A(x) = \frac{C_A + C_B}{V_A + V_B} \exp\left( \frac{C_A + C_B}{V_A + V_B} (s-x) \right) \quad \text{for } x \geqq s,$$

$$p_B(x) = \frac{(1-P_A)C_A + P_B C_B}{P_B(1-P_A)(V_A + V_B)} \exp\left( - \frac{C_A + C_B}{V_A + V_B} x \right) \text{ for } x < s,$$

where s is the separation value and

$$s = - \frac{V_A + V_B}{C_A + C_B} \ln\left(1 - \frac{P_B(1-P_A)(C_A + C_B)}{(1-P_A)C_A + P_B C_B}\right) \; .$$

For small probabilities of errors in the identification of roles, this solution converges to the one suggested by Parker & Rubenstein, with zero played in role B and with $s = 0$.

## VI. DISCUSSION

1. Basic features of the model: We analyze a type of conflict for which an animal's strategic choice in a role can be described as a level of persistence, or simply as the maximum time a process of attrition will be continued. It is assumed that the contest is over if one of the involved two animals has reached its "preset" level of persistence and therefore gives up. The opponent is then thought to get the resource, and both have a cost which corresponds to the actual final stage of the contest. Thus, only the loser has, in general, to pay fully for his chosen "bid". There are two roles A and B in the model like "owner" and "intruder" in a territorial conflict. It is supposed to be usually the case for the considered interactions that one of the contestants estimates his role as A and the opponent estimates himself B. There is, however, at least a small positive probability that both opponents find themselves having the same role, as it may occur due to mistakes in the assessment of the roles which are only the animals' concepts of their objective situations. When calling this war of attrition an "asymmetric contest", we refer to the prevailing occurence of agonistic encounters with a perceivable difference between the opponents. This notion of an asymmetric contest includes even the extreme cases in which these differences have no effect whatsoever on the payoffs of the game. We call the latter type of asymmetry "payoff irrelevant" or "uncorrelated" and may think of the following interpretation within the context of a territorial conflict: an asymmetry in ownership status would be payoff irrelevant if owner and intruder did, on average, equally "profit" from winning the territory and if they also did equally "suffer" from a war of attrition, with gains and losses measured in terms of change in the expected reproductive success.

The feature of the model just outlined which qualifies the term "war of attrition" is that the winner, in case of escalation, is determined by his longer persistence and not by beating the opponent in a decisive damaging combat. This does, however, not generally exclude biological examples with the characteristic trait that a considerable part of the cost of attrition consists in getting progressively more damaged: these examples may fit into the framework of a war of attrition if the accumulation of injuries does typically not affect the basic ability to continue fighting.

2. The continuous asymmetric war of attrition: We call the model a continuous war of attrition if the variety of strategic choices enables the "players" to tune finely the expected cost they would have when fully "paying for their bid". Mathematically this means: they can choose from a continuum of persistence times, and, in addition, there is no "jump" in the increase of expenses.

The central theorem in this paper (section III) states for the continuous asymmetric war of attrition the existence of exactly one evolutionarily stable strategy, under the assumptions that first, errors occur in the identification of roles, secondly, the asymmetry is not payoff irrelevant and the cost of attrition rises linearly. This ESS causes the contestants to behave in a role differentiating way, and it prescribes, roughly, to respect the asymmetry by giving the player access to the resource who has more to gain or less to lose: the role which is favoured with respect to payoffs is the conventional "winning role" in a population playing the ESS. No other convention is evolutionarily stable. The theorem holds even if the rate of errors in role identification is considerable.

Before further discussing the form of this solution, we characterize more exactly what determines the winning role. For the model with a linear increase of cost during the war of attrition, it is possible to formulate the required characterizing property simply as follows: in an asymmetric encounter, the contestant has the winning role who can, on average, persist longer than the opponent before his interim balance "value of the resource minus already accumulated cost of persistence" becomes negative. Parker (1974) suggested already in a different formal context that a condition of this kind should define the winner in a conventionally settled animal dispute. A caveat is needed here. Clearly, this rule is formally correct under the assumption of a linear increase of cost. However, it does not reflect in a transparent way the mathematical argument which establishes the ESS under discussion. The argument is based on a more complex "global" comparison of which role would be better off at the various degrees of persistence. It is therefore easy to construct counterexamples with nonlinear cost functions (Fig. 2), such that one of the roles satisfies the stated condition, but an ESS of the discussed type does not exist. How to characterize the winning role then in a more informative way? Let $V_{AB}$ denote the expected value of the resource to a contestant given that he estimates his role as A and that the opponent estimates himself B. Analogously, let $C_{AB}$ denote the time rate of cost for this player. Role A is a winning role if

$$(51) \qquad \frac{V_{AB}}{C_{AB}} > \frac{V_{BA}}{C_{BA}} .$$

With linear rising costs, this inequality is trivially equivalent to the above rule. It was in a similar form first postulated by Parker & Rubenstein (1981). Their preliminary heuristic study of the continuous war of attrition gave rise to the present paper. The reformulated version of what determines the winning role has the advantage that it is apparently also a sensible rule for a class of models with nonlinear costs. Here, the time rate of cost depends on how long the contest has already lasted, and the inequality (51) is thought to be satisfied for all potential durations.

We discuss now the explicit form (Fig. 3) of the ESS. It prescribes that an individual in the winning role, say A, must play only greater persistence times than a critical positive value, and must choose among these "permitted" times at random, with a truncated negative exponential probability distribution. On the other hand, the ESS prescribes that a contestant in the losing role B must play only lower persistence times than the same critical value, also using a truncated negative exponential distribution for randomization. The critical value allows distinction between "low" persistence times that are used in role B and "high" persistence times used in the winning role A. How big this maximal degree of escalation for B is depends on two kinds of parameters. The smaller the probability of making an error in the identification of roles, the closer to zero the critical time is. Conversely, the greater the value of the resource (or: the smaller the time rate of cost), the higher is the critical

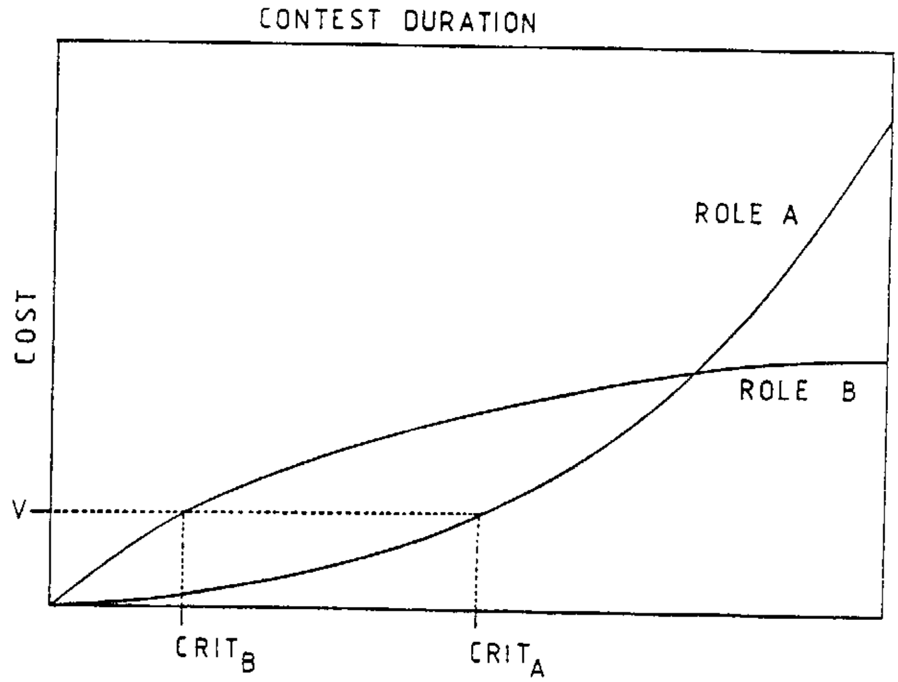


Fig. 2. A type of nonlinear increase of cost, for which no ESS may exist of the simple structure with two nonoverlapping, connected ranges of persistence times that are "permitted" in the two roles. The interim balances "value of the resource minus already accumulated costs" become negative at the critical values $CRIT_A$ and $CRIT_B$ for the two roles. The value V of the resource is, for simplicity, assumed to be identical in both roles.

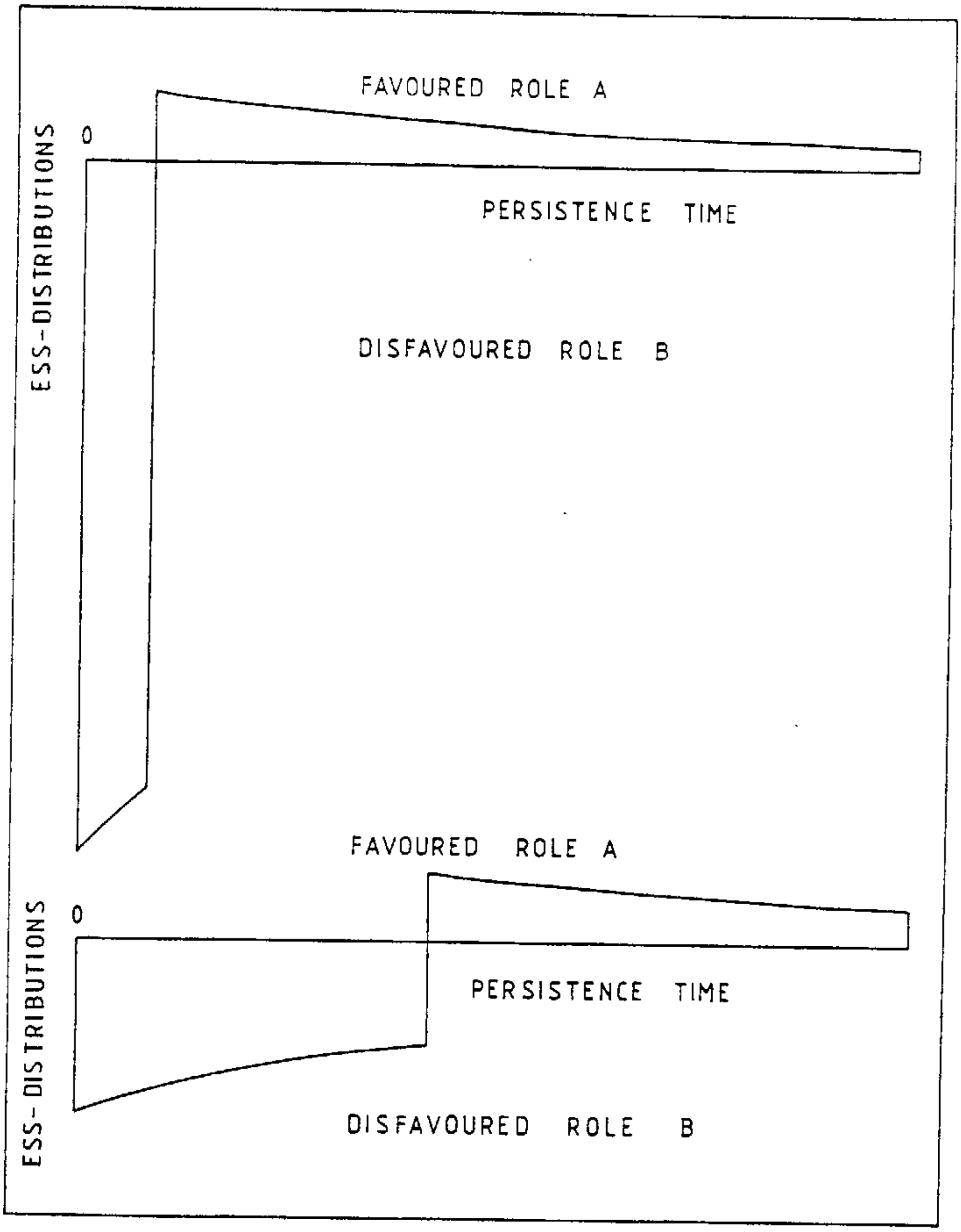


Fig. 3. The ESS for the continuous asymmetric war of attrition. Role A is favoured with respect to payoffs. The two numerical examples differ in the assumed degree of accuracy in role identification which is greater in the upper case. The parameters are $w_{AB}$= 0.45 (upper example), $w_{AB}$= 0.3 (lower example), $V_{AA}$= $V_{BB}$= 0.1 and $C_{AB}$= $C_{BA}$= 1.

degree of persistence.

Note here, in particular, that the solution of the continuous asymmetric war of attrition does not provide a player with the instruction to give up immediately if he estimates his role as B. Why should he persist at all when having the losing role? The term "losing role" must first be given a more careful explanation here. The individual in this role B loses the contest if we are faced with the role-asymmetric situation that the opponent regards himself as A. Such a contest situation is supposed to occur usually but not exclusively in the analyzed game with incomplete information, i.e. with errors in the assessment of roles. Thus, given the event that both opponents estimates themselves B, one of the players clearly wins although he has the conventional losing role. Now, in order to answer the above question, why B should persist at all, consider a different population where the ESS-instructions are only used in role A and where everybody gives up immediately in role B. Suppose, a rare "mutant" strategy arises which prescribes to persist a little in role B. As far as the symmetric encounters are concerned, with both contestants identifying themselves as B, the mutant strategy yields considerably greater situation dependent payoff than the strategy performed by the majority in the considered population: it gets here the resource practically always and without cost. On the other hand, in the more typical situation with the own role being B and the opponent adopting the winning role A, the mutant strategy comes slightly worse off than the population strategy: it loses in this case, unlike the majority's strategy, not comletely without cost. Taking seriously the idea of a continuous war of attrition, a very small degree of persistence can be found, such that the great advantage of the mutant strategy in the rare role-symmetric situations does more than compensate for the minute disadvantage in the frequent asymmetric situation. Therefore, an appropriately chosen mutant strategy can invade the population and, consequently, the ESS cannot prescribe to give up immediately in the losing role B. However, if mistakes are very rare, B must give up almost immediately.

To conclude the discussion of the continuous model, it is worth describing informally the selective forces which protect a population playing the ESS from invasion by other strategies. Different contest situations enable the selective process to drive out different types of deviant strategies. In a population playing the ESS, the shape of the probability distribution "how to decide between permitted persistence times in the winning role A" is only tested by selection in encounters with both opponents identifying themselves as A. In all other encounters, the actual contest duration never exceeds the minimal time of persistence which the ESS prescribes to A. This form of testing is responsible for the maintenance of the negative exponential distribution, similar to the symmetric war of attrition as analyzed by Maynard Smith (1974) and Bishop & Cannings (1978). Now, what prevents invasion by a strategy that permits lower persistence times in role A than the ESS? Such a deviant has a selective disadvantage, because in contests against B it does not sufficiently "exploit" the opponent's willingness to give up early. Conversely, for the following two reasons it does not pay a deviant to play high values in the losing role B. First, this would be of no advantage in the situations with an opponent also estimating B, since the maximal persistence time which the ESS permits in this role already ensures winning. Secondly, in the typical situation with an opponent who escalates in the opposite role A, it cannot be profitable to escalate beyond the critical value, because A is favoured with respect to payoffs. This latter crucial point is not immediately obvious and we must here refer to the mathematical section (Lemma 9). To summarize, the evolutionary stability of our solution depends essentially on the assumption that errors in the identification of roles cannot completely be eliminated by natural selection. It is this assumption of an inherent basic imperfectness that leads in the asymmetric war of attrition to the existence of an ESS. Whether a meaningful ESS can be found for the continuous model depends also crucially on the assumption of a payoff relevant asymmetry: the continuos war of attrition with a payoff irrelevant (uncorrelated) asymmetry is a pathological structurally unstable model, since arbitrarily small changes in the parameters would lead to fundamentally different solutions.

3. Contrasts in the modelling of asymmetric contests: Our analysis of the continuous war of attrition completes the prospective approach to the problem by Parker & Rubenstein (1981). We provide the game theoretical background which supports their argument that an ESS for this model can only be to respect the asymmetry in a

"commonsense" way, i.e. by giving the individual access to the resource which is stronger or has more to gain. The fact that for the continuous war of attrition, only a commonsense solution can be evolutionarily stable, contrasts strikingly with the greater variety of solutions for other models of asymmetric contests which are derived from the well known "Hawks-Doves" game. The latter way of modelling the game is to idealize an animal's strategic choice in a rather discrete fashion: either engage in a damaging decisive combat and play "Hawk", or avoid a great risk and play "Dove". Maynard Smith & Parker (1976) and Hammerstein (1981) demonstrated that, in such games, an ESS may assign the status of a conventional winner to the contestant who has less to gain or a lower fighting ability, provided these differences between the opponents are not too excessive. Note that not all strategies of this kind merit to be labelled "paradoxical". If, for example, an ESS instructs a weaker owner of a territory to defend it against a stronger intruder, this appears far less counter-intuitive than if an ESS causes a stronger owner to pass the territory without defence to a weaker intruder. Both examples may have the common underlying feature that the winning role "smaller owner", or in the other case "smaller intruder", is disfavoured with respect to payoffs.

A main purpose of this paper is to investigate further the nature of the sort of contrasting conclusions just described that can be drawn for the different model approaches. The reason why in the asymmetric "Hawks-Doves" game a greater number of different evolutionarily stable conventions for the settlement of conflicts exists can easily be described intuitively. A convention-breaking "deviant" strategy that occurs in an ESS-population will sustain an extra expected cost of an escalated contest if it fails to give up in the losing role. Even a fighting advantage can be too small for compensating this cost. The crucial point is now that, by definition of the Hawks-Doves type of the game, selection has no chance to tune the level of how vigorously an animal in the conventional winning role defends the resource against escalating opponents. This level, however, decides over success or failure of convention breaking deviants in their challenge to replace the population strategy. On the other hand, as we have seen in the war of attrition, selection imposes here on the winning role a specific probability distribution over the degrees of escalation. It turns out from the analysis that this distribution does not put sufficient weight on high levels of persistence as would be necessary to allow stability of anything other than commonsense solutions.

Which kind of model is preferable? This is clearly an empirical question rather than a theoretical one. Suppose that the contestants have no physical means of damaging each other, and that all they can do is to prevent themselves from using the resource under competition. This looks like an ideal case for being modelled as a war of attrition. Now, consider examples where escalating animals engage in a dangerous use of weapons. Here, it can typically be the case that a contestant who gives up at an unsuitable moment exposes himself in a dangerous way to the opponents weapons and thus takes an extra risk for giving up at this particular state of the debate. Such a contest has at least features of a more discrete game, an extreme version of which is the Hawks-Doves model.

4. The discrete war of attrition: We now wish to discuss in more detail how elements of discreteness in the sets of strategic choices (or discontinuities in the rise of cost during escalation) may generate in the war of attrition model an ESS which is not of the commonsense type. Suppose that a contest typically consists of a sequence of bouts, and that for reasons above an extra risk is incurred if a contestant gives up within a bout, but not when doing so between two rounds. It appears here more reasonable to describe the levels of persistence in terms of discrete rounds, than by a continuum of persistence times. This is the discrete war of attrition which was analyzed for symmetric contests by Bishop & Cannings (1978). We calculated some numerical examples for the asymmetric case with two roles A and B. The most notable result is that an ESS can now exist which lets the contestant win who has less to gain or more to pay for persistence; the discrete model allows solutions that are paradoxical with respect to payoffs. This result can occur, however, only if role identification is sufficiently accurate and if the expected cost for a single bout is great enough.

To get more analytical insight into the problem, we asked the following question. Considering the continuous asymmetric war of attrition as a "starting point", where do we minimally have to introduce a discrete "step" in the set of persistence times (or in the increase of cost) in order to create an ESS which appears in the above sense paradoxical with respect to payoffs? Furthermore, how big must this step be, and how precise the identification of roles? The answer to the first problem is, roughly, that the step must occur at a level of persistence where little cost has yet been accumulated. This can perhaps best be interpreted as an initial cost of engaging at all in the process of attrition. Note that discontinuities in the increase of cost which occur typically after a long contest do not create an ESS which is paradoxical with respect to payoffs. The minimal size of a step in the possible times of persistence which can generate such an ESS is related to the disparity in the situation dependent parameters: the step size must be greater than the difference $V_{AB}/C_{AB} - V_{BB}/C_{BB}$. With equal cost rates this means that the cost step at the discontinuity must be greater than the difference in value of the resource between the two roles. Finally, to answer the last question, the degree of accuracy in the assessment of roles must be high for the stability of a convention which is paradoxical with respect to payoffs. This is an important difference to commonsense solutions of the war of attrition. Their existence can be established by using only a weak notion of role asymmetry.

5. Discrete versus continuous models: We summarize now the debate on discrete versus continuous models. In a contest where at every stage a decision to go on escalating (or persisting) inflicts no more than an "infinitesimal" risk before the next opportunity to withdraw without extra cost occurs, a conventional settlement of the asymmetric conflict must be a commonsense one, with the winning role characterized by (51). The continuous war of attrition appears a better way of looking at such a problem than a discrete model. On the other hand, if a decision to go on fighting condemns a contestant typically to take a more than vanishingly small "bout risk" before he can give up without danger, this may open the theoretical possibility for other conventions which are not of the commonsense type. It requires, however, some conditions to be satisfied. First, the bout risk must in its consequences be of more weight than the difference in relative values of the resource. Note here, this condition is satisfied for tiny bout risks if the asymmetry is nearly payoff irrelevant. Secondly, the contest must be sharply role-asymmetric, i.e. there must usually be an "objective" dif-

ference between the opponents and a high degree of accuracy in its perception. This is unlikely if there exists only a small difference in fighting ability between two opponents who cannot refer to another easily perceivable asymmetry. Finally, the last condition states that the discussed type of discontinuity must occur already at a level of escalation, or persistence, where the contest is still relatively cheap.

6. Is the asymmetric war of attrition biologically meaningful? We wish to discuss briefly whether there are real biological examples which have some features of an asymmetric war of attrition. Perhaps one of the best such examples was found by Davies (1978) in his field study on the speckled wood butterfly (Pararge aegeria). This well known case of a contest settled by an ownership convention has in the literature rather been considered in the light of the asymmetric Hawks-Doves type of a game (Maynard Smith, 1978). Davies observed how males defend small sunspots they occupy against intruding males. He reported that usually a short spiral flight occurs after which the previous "owner" maintains in possession over the spot. The experiments, performed in the field, provided strong evidence that ownership is really the cue which settles the dispute. Now, when Davies placed a second male into a sunspot, without the butterflies noticing each other, this led after the opponents' mutual discovery to a markedly prolonged spiral flight. He performed here an experiment which probably created the crucial role-symmetric encounter with both contestants identifying themselves as having the winning role. Both the prolonged, as well as the short spiral flight coincide with what would be expected in the asymmetric war of attrition. A problem arises, however, with the interpretation of payoffs. The asymmetric war of attrition yields here only a sensible explanation if an owner had on average a priori an advantage of some kind over the intruder. We cannot decide this question which is an empirical one.

Real asymmetric animal contests clearly pose the theoretician more unsolved problems than can briefly be discussed. One type of open question must suffice in order to demonstrate the need for a more complex account of how roles are paired, i.e. of the "informational structure" of the game. There is some good evidence from empirical work that in a contest between an owner of a resource and an intruder, the owner has rather reliable information about the value of the resource, whereas the intruder has none or little. The same role "intruder" is here typically paired with different roles like owner of a "valuable" or of a "poor" object. Three examples may be given which share the common feature that there is such a bias in the degree of information about resource value. Rand & Rand (1976) suggested that in fights of female iguanas over burrows which they dig for egg laying, the owner is likely to have better information about hole depth than the interloper. Riechert (1976, 1979) was able to measure the value of different web sites to females of the funnel web spider Agelenopsis aperta, by examining how much prey can be caught at a given site. In fights over webs the behaviour varied significantly with the quality of the object if the original owner was involved. However, in induced agonistic encounters between two intruders on a web, no such difference could be found. The third example is the struggle between two male dung flies (Scatophaga stercoraria) over a gravid female (Sigurjonsdottir & Parker, 1981). The value of a female to both males decreases as she lays her eggs. Here, only the guarding male (owner) can have a good information about the number of eggs that remain to be laid. Only contests ending in take over (i.e. which relate to the owner's bid) show a positive correlation between the number of eggs remaining and the length of struggle. These three examples indicate a problem area for future game theoretical research on animal contests which is closely related to the present work.

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