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The Role of Asymmetries in Animal Contests

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I. Introduction

Maynard Smith and Price (1973) showed that game theory may be used for a functional analysis of animal contest behaviour. They introduced the concept of an evolutionarily stable strategy (ESS) with the particular intention of explaining the conventional aspects of such behaviour in terms of individual selection. Maynard Smith and Parker (1976) analyzed contest situations in which animals were supposed to find themselves having different roles such as "owner" and "intruder" in a territorial dispute. They draw an important conclusion for conflicts in which escalation is dangerous and information about an opponent's role is perfect: There will be one of two distinct roles, such that the player in that role is always the winner. This was shown even for contests with a "payoff irrelevant" asymmetry, in which the role difference does not bias either the value of the resource competed for or the probability of winning an escalated fight.

Can an asymmetry of this kind still be used for settling the contest, when other more "relevant" differences, such as in fighting ability, exist? Should we for example expect a smaller owner of a territory to defend it against a larger intruder if size indicates fighting ability and if the territory is of the same or almost the same value to both of the opponents? For contests having several asymmetric features the obvious problem arises: which of them may or must be used for settlement by an ESS? The present paper proposes some simple mathematical models suggesting answers to this question. It also demonstrates an easy method of analyzing a class of contests with perfect information. This method is closely related to the work done by Prof. R. Selten (1978), to whom I am greatly indebted for helpful comments and advice.

It will be shown that individuals "playing" an ESS may base their behaviour on a payoff irrelevant aspect of a contest situation, while ignoring a difference relevant to fighting ability. This is possible under the assumption that there is a risk of injury in an escalated contest which is considerable when compared to the payoff of obtaining the resource under competition. If the difference in fighting ability exceeds a critical value, the behaviour must be based on this relevant asymmetry.

A particular question for cases with a difference in more than one payoff relevant aspect will be: What can be said about contest situations in which the value of the resource is not the same to the two opponents who, in addition, differ in fighting ability? Should for example a territory be defended in cases where the owner has much more to gain (lose) than an intruder? It is demonstrated here that the difference in value of the resource is not the crucial factor determining whether a strategy of the type "ignore small differences in fighting ability but respect ownership" may be evolutionarily stable. As long as the owner stands a relatively high risk of injury, the ESS's are nearly the same, as they would be if the ownership asymmetry were payoff irrelevant. If the risk of injury (in view of the difference in fighting ability) is compensated for by the significance the resource has for the owner's reproductive success, defense becomes the only behaviour an ESS may ascribe to the owner's role. Again this condition does not take into account the difference in value of the resource. On the other hand, an intruder having sufficient advantage in fighting ability must ignore ownership regardless of what this strategy would prescribe if he were the owner. This may lead to cases in which a smaller owner must engage in a nearly hopeless fight against the escalating intruder.

The same argument which explains the evolutionary stability of strategies in which relevant asymmetries are ignored may be used to demonstrate that behaviour relying on "bluff" has a chance to be maintained under selection. The behaviour may even persist if bluff is detectable by the individuals of a population. The word bluff here refers to characteristics which increase apparent fighting ability without considerably altering the chance of winning an escalated contest.

In the following, the class of models as well as the concepts used are specified. Roles are defined as a combination of variables, e.g. relative size and ownership status ("larger owner"). These variables are referred to as aspects of a role. A contest situation is characterized by a pair of roles. It is called asymmetric if in at least one aspect a difference exists. Throughout this paper contest situations are assumed to be asymmetric: Two opponents may not have the same information situation.

Selten (1978) proved a general theorem stating that as a consequence of this assumption an ESS must be a pure strategy, i.e. it allows for no randomized choice of actions. The theorem was formulated for a general class of contest models including those with incomplete information about the asymmetry. Selten's approach will be adopted here but it will be restricted to conflicts with perfect information, for which roles are unambiguously paired. This restriction has the advantage that the considerably large "evolutionary games" which arise when more than one aspect is considered, are decomposable into small subgames. The latter will be called "situation games" as they correspond to single contest situations in which two opponents can choose between the "local strategies" available in their particular roles.

A strategy in the evolutionary game must provide an individual with a specification of what the local strategies for all roles are. With the assumptions made an ESS is characterized as a combination of strong equilibrium pairs of local strategies for the situation games. The notion of an equilibrium pair (Nash 1951) is the central tool used in noncooperative game theory for the analysis of conflicts between two individuals.

A more explicit form of the characterization of an ESS p is now given. For each pair of roles (A,B) which may appear with nonzero probability as a contest situation, the local strategies p_A and p_B, which p ascribes to A and B, must have the following property: p_A is the only best reply to p_B in the situation game of (A,B) and vice versa. A best reply strategy is defined by maximizing a player's payoff against a fixed strategy of the opponent.

II. DEFINITIONS AND BASIC CONCEPTS

1. Situation games

Let (A,B) denote a contest situation with roles A and B which is likely to appear in a population. Suppose there are choices of actions $a_1,\dots,a_n$ and $b_1,\dots,b_m$ available in roles A and B. The situation payoffs a_{ij} and b_{ij} describe the consequences to the individuals in role A and B of choosing a_i, b_j respectively. They are thought to be measured as changes in expected fitness resulting from a particular contest. A situation payoff matrix defines a finite not necessarily symmetric two person game in "normal form" which is called here a situation game (for example: Figure 1).

Choices in role B

Choices in role A	b_1	b_2	b_3
a_1	a_{11} b_{11}	a_{12} b_{12}	a_{13} b_{13}
a_2	a_{21} b_{21}	a_{22} b_{22}	a_{23} b_{23}

Fig. 1. A situation game

A strategy p_A for "player A" in this game ascribes probabilities to the choices of the available actions a_i. The way in which the expected payoffs $E_A(p_A,q_B)$ to A and $E_B(p_A,q_B)$ to B are defined when the players choose p_A, q_B respectively is well known.

p_A is called a best reply strategy to q_B in the situation game for (A,B) if

$$E_A(p_A,q_B) \geq E_A(r_A,q_B) ,$$

for all strategies r_A available in role A.

If it has the analogous property, q_B is called a best reply to p_A.

The pair (p_A, q_B) is called an equilibrium pair if p_A is a best reply to q_B and if conversely q_B is a best reply to p_A. The term strong equilibrium pair is used when both strategies are the only best replies to each other.

2. The evolutionary game

A finite set of roles which are unambiguously paired is considered, i.e. to every role A exactly one opposite role B exists which may occur. In cases with perfect information about roles this can be assumed without loss of generality. Furthermore all contest situations are supposed to have the information asymmetry property $A \neq B$. These two assumptions can be restated as follows:

There are 2n mutually distinct roles $A_1, \ldots, A_n$, $B_1, \ldots, B_n$ such that the only likely contest situations are the pairs (A_i, B_i).

A strategy of the evolutionary game is a "list" containing, for each role, a local strategy for the situation game. A local strategy is simply a role strategy as defined in the last section. This definition corresponds to what is called a behaviour strategy in the context of games in "extensive form". In sociobiology the term conditional strategy is also used (Dawkins 1976). .

Role determination is assumed to be independent of the strategies under investigation. A randomly chosen individual finds itself with the "basic probability" w_i in roles A_i, B_i respectively. Let behaviour strategies p, q be defined by their local strategies p_R, q_R for roles R. The total expected payoff to the individual playing p in a randomly chosen contest between strategies p and q is then

$$E(p,q) = \sum_{i=1}^{n} w_i \left(E_{A_i}(p_{A_i}, q_{B_i}) + E_{B_i}(q_{A_i}, p_{B_i}) \right).$$

An evolutionary game of the class considered here is defined by the set of behaviour strategies and the total payoffs $E(p,q)$. It is already specified by situation games and basic probabilities w_i.

A strategy p is called evolutionarily stable if the following conditions are satisfied:

(i) p is a best reply to p, i.e.

$E(p,p) \geq E(r,p)$, for all behaviour strategies r.

(ii) For every alternative best reply q to p ($q \neq p$) the following inequality holds:

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

The definition of an ESS given here characterizes monomorphic population states which are stable under a process of frequency dependent selection. This is discussed in more detail by Maynard Smith and Parker (1976), Maynard Smith (1978) and Selten (1978).

One important objection to the above definition of an ESS should be stated: it is not a suitable approach for conflicts between relatives. Extended concepts for such games were first proposed by Treisman (1977) and Mirmirani and Oster (1978). A different approach was recently formulated by Grafen (in press) and Hines and Maynard Smith (in press).

3. Fundamental results

The assumed information asymmetry $A \neq B$ for all contests (A,B) has an important consequence which does not depend on the particular situation games considered later:

An ESS must be a pure strategy, i.e. it ascribes definite choices with probability 1 to each role. For a strategy p to be an ESS the following condition is necessary and sufficient:

(i) p is the only best reply to p.

Selten (1978) stated this theorem for a more general class of conflict models in which a player's information situation was defined as a role together with an inaccurate image of the opponent's role. The information asymmetry is then satisfied if roles or images differ between the opponents.

In the present paper games with perfect information are considered. The obvious advantage is that knowing an individual's role one is already informed about which of the situation games is played. It is easy to show that the following requirement (ii) is then equivalent to the condition (i) of the above theorem:

(ii) For every contest situation (A,B), which may appear, the pair of local strategies (p_A, p_B) is a strong equilibrium pair in the situation game of (A,B).

ESS's can therefore be identified with the combinations of strong equilibrium pairs of strategies for the situation games, written as

$$p = ((p_{A_1}, p_{B_1}), \ldots, (p_{A_n}, p_{B_n})).$$

This decomposition property allows for separately analyzing the different situation games which are subgames in the context of games in "extensive form".

The basic probabilities w_i for role assignment appear in the just stated characterization of an ESS only insofar as those roles (subgames) are exclusively taken into account which have a nonzero probability of occurrence in the population. Therefore the w_i need not be specified in the following models.

III. MODELS

1. Payoff irrelevant roles

An aspect of a role is called payoff irrelevant if payoffs are defined independent of this aspect: Two opponents' choices lead to the same situation payoffs if they are made with roles altered in the irrelevant aspect. Corresponding to this definition a role is called payoff irrelevant if all its aspects have this property. A simple model suggested by Maynard Smith and Parker (1976) is useful for understanding the significance payoff irrelevant roles may have, and for demonstrating how evolutionary games are constructed and solved in this paper.

Contest situations and choices: Only one pair of roles (A,B) is considered. A and B could be interpreted as "discoverer of a resource" and "latecomer" or as "owner" and "intruder". Individuals are assumed to be fully informed about the asymmetry, and for each role they have the choice between "escalate" and "display". Roughly, the first of the alternatives refers to a dangerous way of fighting which is not given up before the individual is injured or the opponent retreats; the second refers to behaving in such a way that a considerable risk of injury is avoided.

Model parameters:
V = Expected utility of getting the resource without cost.
-D = Expected cost of injury.
-T = Expected cost of a protracted but not escalated contest.

Payoffs: The chance of winning an escalated contest is supposed to be independent of the roles A and B. Furthermore the simplyfying assumption (it will be relaxed later in III.4) is made that the winner is not injured in an escalated fight. When both opponents choose to escalate, they therefore each have the expected payoff 1/2(V-D). If both contestants display, they are supposed to win with equal chances, both having cost -T. Their expected payoff is 1/2V-T.

The evolutionary game has one single situation game (Fig. 2) which in its structure coincides with the well known "Hawks" and "Doves" model.

Fig. 2 (payoff matrix; in each cell the upper left entry is the payoff to the player in role A, the lower right entry is the payoff to the player in role B):

Choices in role A		Choices in role B: Escalate	Choices in role B: Display
	Escalate	1/2(V-D) / 1/2(V-D)	V / 0
	Display	0 / V	1/2V-T / 1/2V-T

Fig. 2. Situation game for the pair of roles (A,B)

<u>Strategies</u>: The four pure strategies of the evolutionary game (Fig. 3) can be identified with the pairs of choices for situation (A,B).

Pure strategies		Role A	Role B
	S_1	Escalate	Escalate
	S_2	Escalate	Display
	S_3	Display	Escalate
	S_4	Display	Display

Fig. 3. Pure strategies of the evolutionary game

It is worth pointing out that a (behaviour) strategy of the evolutionary game cannot be thought of as a "mixture" of these pure strategies, i.e. as a probability distribution over the set of pure strategies. Several such mixtures of pure strategies would represent the same mixed behaviour strategy. Consider for example the decision rule: in either situation escalate with probability 1/2. It would be realized by two distinct mixtures of pure strategies, namely (1/4, 1/4, 1/4, 1/4) and (1/2, 0, 0, 1/2).

<u>Analysis</u>: According to the theoretical results stated, the ESS's can be identified with the strong equilibrium pairs for the situation game. A numerical example (Fig. 4) will be used for illustrating how they are calculated. The head of the arrows

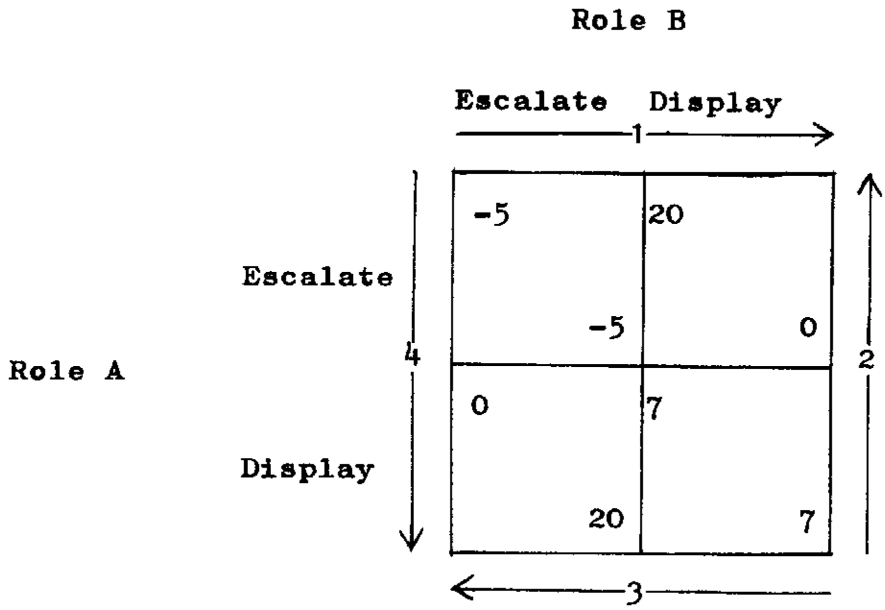

Fig. 4. Numerical example ($V = 20$, $D = 30$, $T = 3$)

points to the strategy which is the best reply. Arrow 1 for example indicates that if A escalates, B's only best reply is to display. This is simply a consequence of the payoff relation $0 > -5$.

The direction of the arrows 1,...,4 would be unchanged for another choice of parameters, provided, the condition $V < D$ is satisfied. If $V \geq D$, the arrows 1 and 4 have reversed direction.

The strong equilibrium pairs of the situation game correspond to points where arrow heads meet. We are therefore now able to state the solutions:

Case 1: $V < D$ (injury is relatively serious).
There are two strong equilibrium pairs. They correspond to the strategies S_2 and S_3 which "respect" the asymmetry:

Escalate - Display,
Display - Escalate.

Case 2: $V \geq D$.
Only one strong equilibrium pair exists which corresponds to the strategy S_1:

Escalate - Escalate.

The model shows that, provided injury is relatively serious, a payoff irrelevant role asymmetry, perfectly known to the opponents, must be used for settling the contest. In a population playing one of the two ESS's, a deviant strategy involves a risk of injury which is not compensated for by the value of the disputed resource. Therefore it has lower expected fitness than the population strategy.

2. Contests asymmetric in two aspects

Suppose that roles have two aspects, one of them being payoff irrelevant, as in the previous example, the other payoff relevant. May an ESS ignore the asymmetry in the latter aspect but respect a difference in the former?

Basic assumptions: A model is considered now, in which roles are defined by ownership status and relative size of some of the individual's feature. As an extreme case, ownership status in this section is thought to be payoff irrelevant, whereas relative size is associated with fighting ability. For simplicity only two sizes may appear in the population, "large" and "small". It is assumed that size assessment is unambiguous and without cost, and that two opponents never consider themselves as having identical ownership status. All contest situations then have the information asymmetry property, and roles are unambiguously paired. The model therefore fits into the theoretical framework outlined earlier.

Contest situations: There are three pairs of roles which may appear as contest situations:

larger owner - smaller intruder
smaller " - larger "
equal " - equal "

A possible objection here could be that not only relative size but also some information about absolute size may be taken into account by the individuals in conflict. This would lead to a greater number of contest situations. The last stated pair of roles would be replaced by "small owner - small intruder" and "large owner - large intruder". It will be assumed throughout this paper that only information about relative size is available to the contestants. By relative size any measure which monotonically increases with the difference in size is meant (the models are easily reinterpreted with another notion of relative size).

Parameters: In addition to the parameters already introduced in the previous section, the difference in fighting ability for size asymmetric situations must be reflected:

x = Probability that the larger individual wins an escalated fight ($x > 0.5$).

Situation games: The evolutionary game has three situation games associated with the three pairs of roles. They are derived from the previous model.

(1) Equal owner - equal intruder: The payoff matrix is supposed to be the same as in the last section (Fig. 2).

(2) Larger owner - smaller intruder: Due to the bias in fighting ability, the consequences of an escalated fight are not the same to the opponents (Fig. 5).

LARGER OWNER \ SMALLER INTRUDER	Escalate	Display
Escalate	$xV-(1-x)D$; $(1-x)V-xD$	V ; 0
Display	0 ; V	$1/2V-T$; $1/2V-T$

Fig. 5. Situation game for the pair of roles: larger owner - smaller intruder

(3) Smaller owner - larger intruder: The payoff matrix is constructed analogously. It will be shown later in this section (Fig. 8).

<u>Strategies</u>: In spite of the simple assumption of having only two sizes, the number of pure strategies, $2^6 = 64$, is considerable. Two examples are given in Figures 6 and 7, where the rows correspond to one aspect of a role and the columns to the other. The entries show the behaviour prescribed to the roles: The "Bourgeois" strategy ignores size asymmetry and respects ownership. The "Assessor" strategy respects differences in fighting ability and respects ownership in size symmetric cases.

	Owner	Intruder
Larger	Escalate	Display
Smaller	Escalate	Display
Equal	Escalate	Display

Fig. 6. The Bourgeois strategy

	Owner	Intruder
Larger	Escalate	Escalate
Smaller	Display	Display
Equal	Escalate	Display

Fig. 7. The Assessor strategy

<u>Analysis</u>: It will turn out that the conditions for which particular strategies are evolutionarily stable may be stated in terms of the ratio D/V. Therefore the following definition is made: The ratio

$$\alpha = D/V$$

is called <u>index of relative seriousness of injury</u>.

The ESS's are the combinations of strong equilibrium pairs for the subgames. The contest situation "smaller owner - larger intruder" will be analyzed explicitly: Its payoff matrix (Fig. 8) is shown with arrows indicating best reply strategies under the following two conditions (i) and (ii):

(i) Injury is relatively serious, i.e. $\alpha>1$.

(ii) The probability of winning for the larger individual does not outweigh the risk of injury, i.e. $xV-(1-x)D<0$, or equivalently $x<\alpha/(1+\alpha)$.

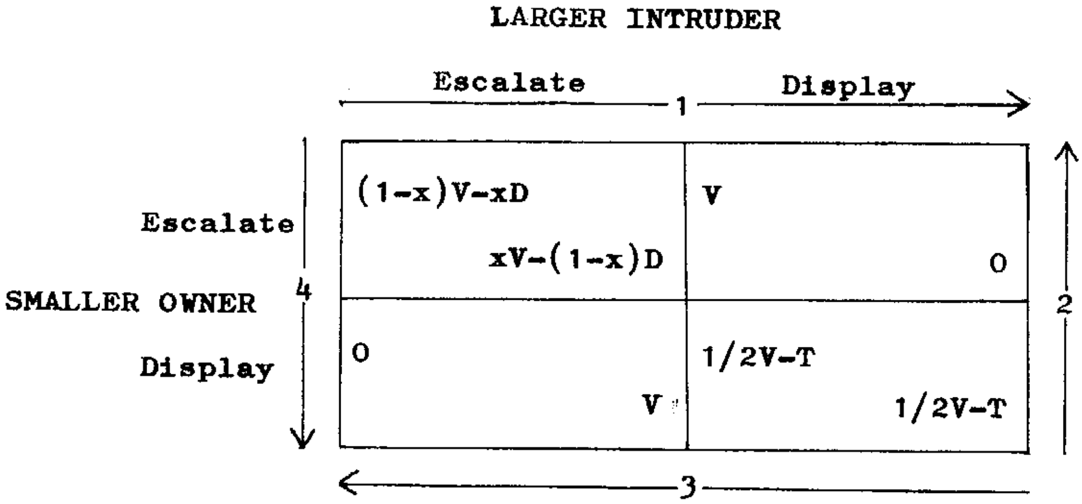

Fig. 8. The subgame: Smaller owner - Larger intruder

There are two strong equilibrium pairs: The first can be associated with the Bourgeois strategy, the second with the Assessor strategy:

Escalate - Display,
Display - Escalate.

If the assumption (ii) is not satisfied, i.e. if the probability of winning outweighs the risk of injury for the larger individual, the direction of arrow 1 is reversed and only the second equilibrium pair which corresponds to the Assessor strategy exists.

Consider now all choices of parameters with $\alpha\leq 1$. The first equilibrium pair above which corresponds to a respecting of the payoff irrelevant aspect may never appear because arrow 1 points to the left. The second equilibrium pair does not exist for $x<1/(1+\alpha)$, where it is replaced by

Escalate - Escalate.

The results of a complete analysis of all subgames are given in the following. A threshold function $t(\alpha)$

$$t(\alpha) = \begin{cases} 1/(1+\alpha) & \text{if } \alpha \leq 1 \\ \alpha/(1+\alpha) & \text{if } \alpha > 1 \end{cases}$$

is used which gives rise to three areas in the x-α-plane, called zone 1,2,3 respectively (Fig. 9). The strong equilibrium

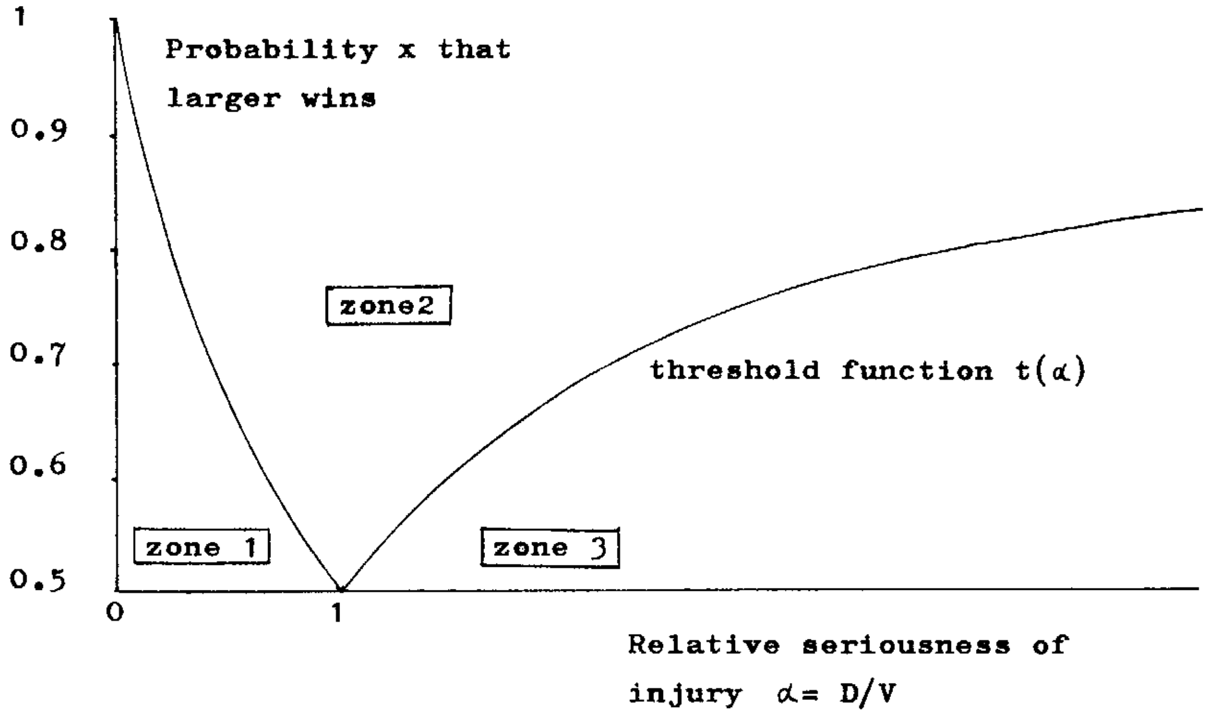

Fig. 9. The threshold function $t(\alpha)$

SUBGAMES

		Smaller owner – Larger intruder	Larger owner – Smaller intruder
(α,x) located in zone	1	Escalate – Escalate	Escalate – Escalate
	2	Display – Escalate	Escalate – Display
	3	Escalate – Display Display – Escalate	Escalate – Display Display – Escalate

Fig. 10. Strong equilibrium pairs for size asymmetric situations

pairs of strategies for subgames associated with size asymmetric contest situations are shown in Figure 10. The solutions for the size symmetric subgame are known from the previous section (Fig. 11).

		Equal owner - Equal intruder
	$\alpha \leq 1$	Escalate - Escalate
Relative seriousness of injury	$\alpha > 1$	Escalate - Display Display - Escalate

Fig. 11. Strong equilibrium pairs for size symmetric situations

Evolutionarily stable strategies: The possible combinations of strong equilibrium pairs for the different conditions are summarized now.

Case 1: Injury is of relatively low cost ($\alpha \leq 1$).

The payoff irrelevant aspect is decision irrelevant for an ESS. If the difference in fighting ability is below a critical value ($x < 1/(1+\alpha)$), then the only ESS is "always escalate". Beyond the threshold, differences in size must be respected, as in the Assessor strategy.

Case 2: Injury is relatively serious ($\alpha > 1$).

The Assessor strategy is always an ESS. The Bourgeois strategy is an alternative ESS if the following condition is satisfied: The difference in size (fighting ability) is smaller than a threshold value ($x < \alpha/(1+\alpha)$) which depends only on the index of seriousness of injury . The payoff irrelevant aspect may therefore within limits be used for conventional settlement of a contest, despite the existence of a payoff relevant asymmetric aspect.

For the same conditions which allow the Bourgeois strategy to be evolutionarily stable, "paradoxical" ESS's also exist, as for example the paradoxical assessment strategy "escalate if smaller, display if larger" or the strategy paradoxical with respect to ownership "escalate if intruder, display if owner".

3. A model with a distribution of relative size

So far relative size has been assumed to have two discrete possible values: larger and smaller. Now suppose that it varies over a finite but arbitrarily large number of values d. A randomly chosen individual finds itself with a probability f(d) in a contest situation with relative size d. The distribution f is symmetric around d = 0 and there is a maximal value d_{max}, to which f assigns a positive probability of occurring.

The probability x_d that the larger individual wins an escalated contest is supposed to be an increasing function of its relative size d (Fig. 12).

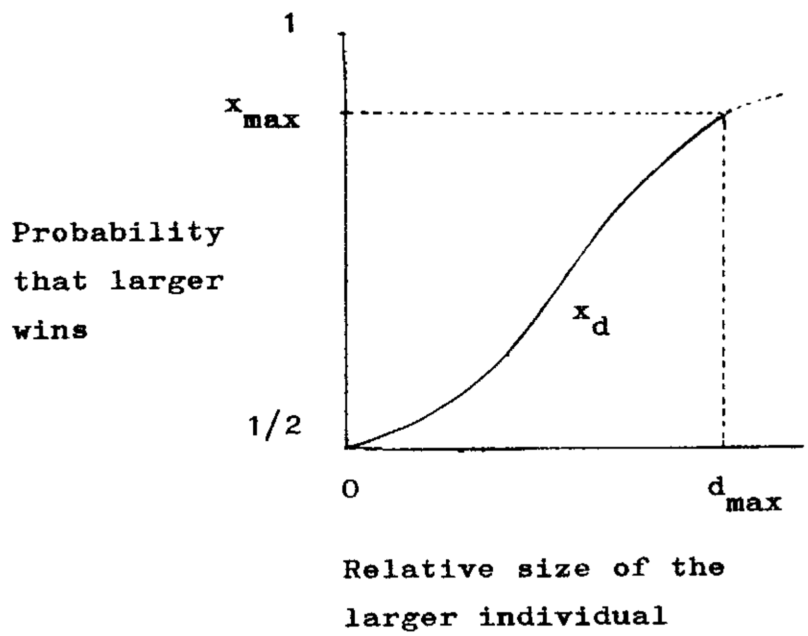

Fig. 12. The relation between fighting ability and relative size

Every value of relative size d gives rise to two pairs of roles:

Owner, rel. size d - Intruder, rel. size -d,
Owner, " -d - Intruder, rel " d.

Here, the associated situation games must be introduced. They are defined as in the previous model, with x replaced by x_d.

The number of pure strategies proves to be immense. The analysis of the many subgames however is simple, as it can always be done for classes of subgames. In fact the reasonning is analogous to the previous model. The threshold function $t(\alpha)$ may be used to define a critical relative size $d(\alpha)$:

$$x_{d(\alpha)} = t(\alpha).$$

Suppose $\alpha > 1$ (injury relatively serious). There are then three classes of subgames for which the sets of strong equilibrium pairs are invariant, shown in Figure 13.

Owner's value of d		Owner - Intruder
	$d \geq d(\alpha)$	Escalate - Display
	$-d(\alpha) < d < d(\alpha)$	Escalate - Display Display - Escalate
	$d \leq -d(\alpha)$	Display - Escalate

Fig. 13. Strong equilibrium pairs for $\alpha > 1$ $(D > V)$

<u>The structure of an ESS for $\alpha > 1$</u>: For all subgames such that d falls within the "ambiguous zone" between $-d(\alpha)$ and $d(\alpha)$, an ESS can only be characterized by the term <u>complementary</u>. That is, if one of the two available choices Escalate or Display is ascribed to role A, the alternative choice must be assigned to the opposed role B. Outside the ambiguous zone size must be respected by an ESS (Fig. 14).

It is worthwhile to point out the intuitive meaning of the critical value $d(\alpha)$ which defines the ambiguous zone. Below this value, the higher probability of winning for a larger individual does not outweigh the risk of its injury in an escalated contest because $x_d V - (1 - x_d) D < 0$.

<u>Examples of ESS's $(\alpha \geq 1)$:</u>

(1) The "Assessor strategy with decision criterion c" (Fig. 15) coincides for small size differences $(|d| < c)$ with the Bourgeois strategy. For large size differences $(|d| \geq c)$ it cannot be distinguished from the Assessor strategy.

The introduced strategy is an ESS if the decision criterion c falls within the ambiguous zone.

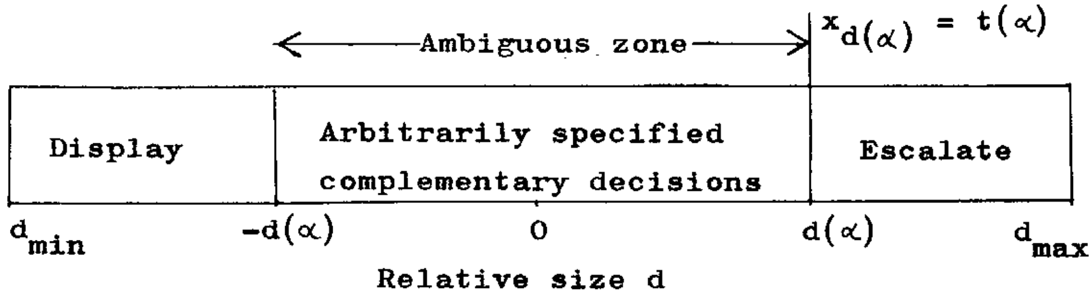

Fig. 14. The structure of an ESS for $\alpha > 1$ $(D > V)$

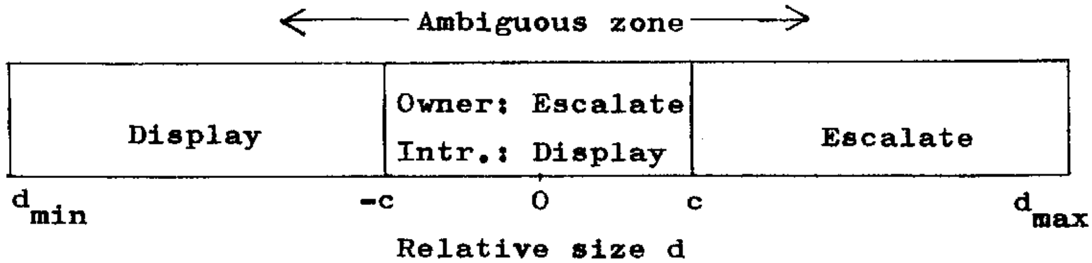

Fig. 15. Example of an ESS: the Assessor strategy with decision criterion c

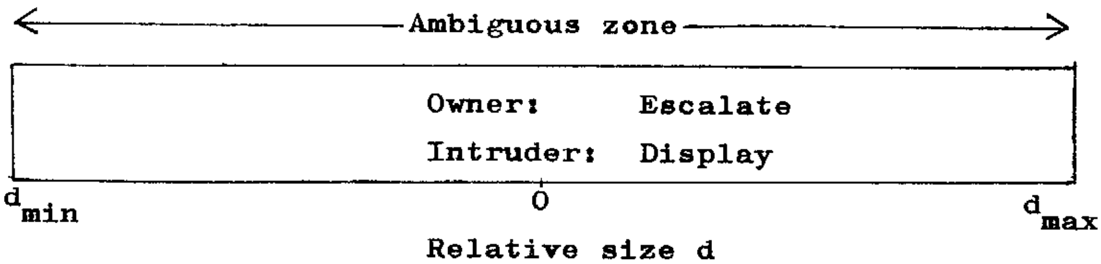

Fig. 16. Example of an ESS for $d(\alpha) > d_{max}$: The Bourgeois strategy

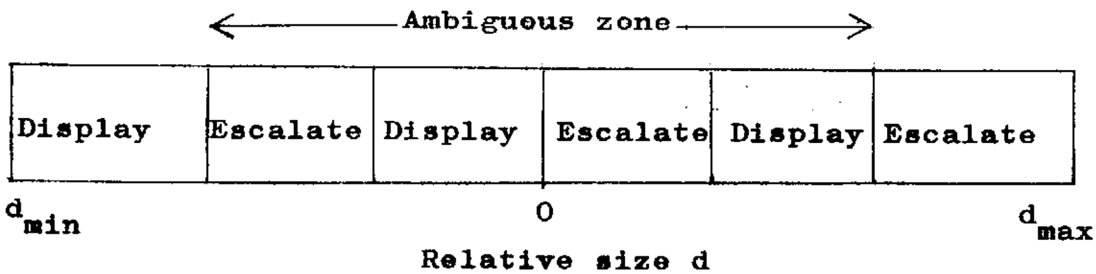

Fig. 17. Example of a paradoxical ESS

(2) The Bourgeois strategy may be considered as a special case of (1) with $c > d_{max}$. It is evolutionarily stable if $x_{d_{max}} < t(\alpha)$ as shown in Figure 16. It is worth mentioning that this result depends on the range of the distribution f(d) of relative size, but not on its shape.

(3) Paradoxical strategies are also evolutionarily stable. This follows from the relatively undetermined structure of an ESS within the ambiguous zone (Fig. 17).

The ESS for $\alpha \leq 1$: If $V \geq D$, a unique ESS exists which is to "escalate for small size differences and make the decision dependent on size for large differences", with the threshold $d(\alpha)$.

Conclusions: The model yields analogous results to the previous one: First, the intuitive view is confirmed that a difference relevant to fighting ability cannot be ignored if this difference is relatively large, that is, if a critical value is exceeded. Second, the more counterintuitive result is stated that, within limits, payoff relevant role aspects may be ignored in favour of payoff irrelevant aspects.

The ambiguous zone gives rise to the general prediction that an arbitrary "complementary" convention, once introduced in the evolutionary course of a population, must be maintained for all contest situations in which no other asymmetry of strong relevance exists.

4. The winner's risk of injury

The winner's risk of injury in an escalated contest has not been taken into account in the models thus far considered. Suppose that the winner has an expected cost of injury which is a fraction q of the loser's cost $-D$, with $0 \leq q \leq 1$. One of the situation games is shown in Figure 18.

SMALLER OWNER, REL. SIZE −d	LARGER INTRUDER, REL. SIZE d: Escalate	LARGER INTRUDER, REL. SIZE d: Display
Escalate	$(1-x_d)(V-qD)-x_dD$ $x_d(V-qD)-(1-x_d)D$	V 0
Display	0 V	1/2V−T 1/2V−T

Fig. 18. A situation game

Consider the threshold function

$$t_q(\alpha) = \begin{cases} \alpha/(1+\alpha(1-q)) & \text{if } \alpha > 1/(1+q) \,, \\ (1-\alpha q)/(1+\alpha(1-q)) & \text{if } \alpha \le 1/(1+q) \,. \end{cases}$$

For q = 0 this is the already known function $t(\alpha)$. The interesting effect of introducing $q \neq 0$ is to enlarge the zone 3 which gave rise to the ambiguous zone of d-values (Fig. 19).

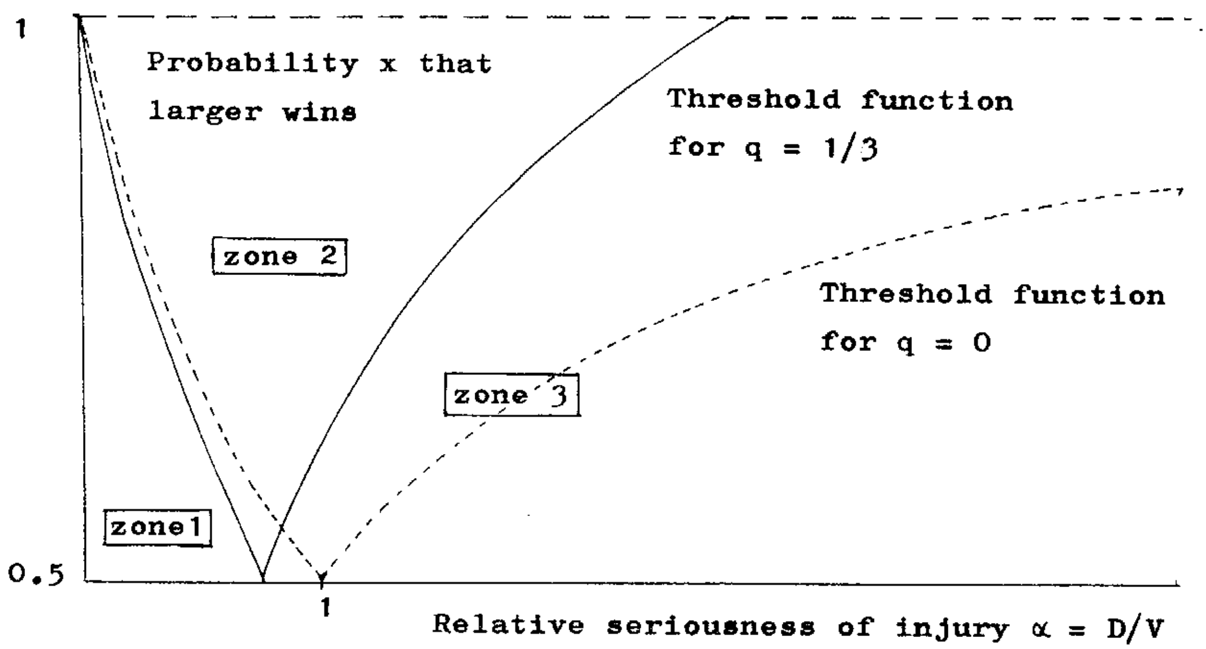

Fig. 19. The threshold function $t_q(\alpha)$

All results from the former analysis are valid for this model if the threshold function $t(\alpha)$ is considered as a special case of $t_q(\alpha)$ with $q = 0$, and if the condition $\alpha > 1$ is replaced by $\alpha > 1/(1+q)$. The effect a higher value of q has on the resulting ESS's is mainly to extend the ambiguous zone.

5. Payoff relevant ownership asymmetry

Suppose the resource under competition is of unequal value to the opponents in contest:

$$V_O > V_I ,$$

where V_O, V_I stand for the value of victory to owner, intruder respectively. Taking up the model of section 3, the situation games are slightly modified, as shown in Figure 20. The arrows indicate best reply strategies under the subsequent two conditions:

(i) Injury is relatively serious to the owner, i.e. $V_O < D$.

(ii) The intruder's probability of winning does not outweigh its risk of injury, i.e. $x_d < t(\alpha_I)$, with $\alpha_I = D/V_I$, or equivalently: $x_d V_I - (1-x_d)D < 0$.

SMALLER OWNER, REL. SIZE -d \ LARGER INTRUDER, REL. SIZE d	Escalate	Display
Escalate	$(1-x_d)V_O - x_d D$; $x_d V_I - (1-x_d)D$	V_O ; 0
Display	0 ; V_I	$1/2 V_O - T$; $1/2 V_I - T$

Fig. 20. Situation game with a smaller owner

A smaller owner may therefore respect either ownership or relative size if (i) and (ii) are satisfied.

The variation of the structure of an ESS which accompanies an increase of V_0 is shown in Figures 21 to 24.

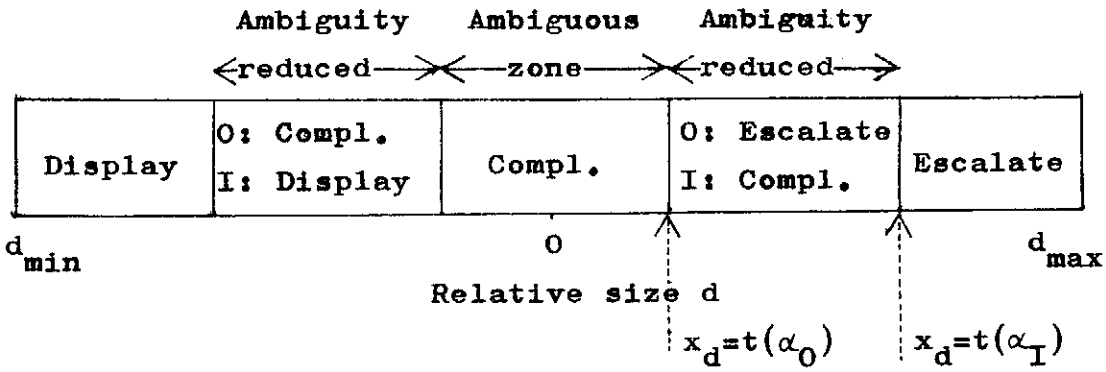

Fig. 21. Structure of an ESS for $V_I < V_0 < D$
(O = Owner, I = Intruder, Compl. = Arbitrarily specified complementary decision)

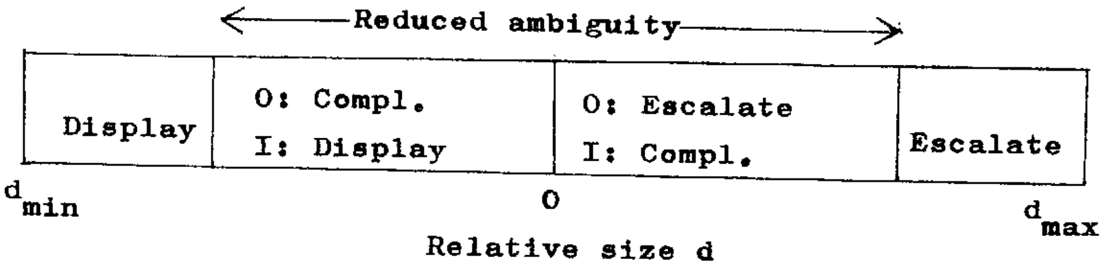

Fig. 22. Structure of an ESS for $V_0 = D$

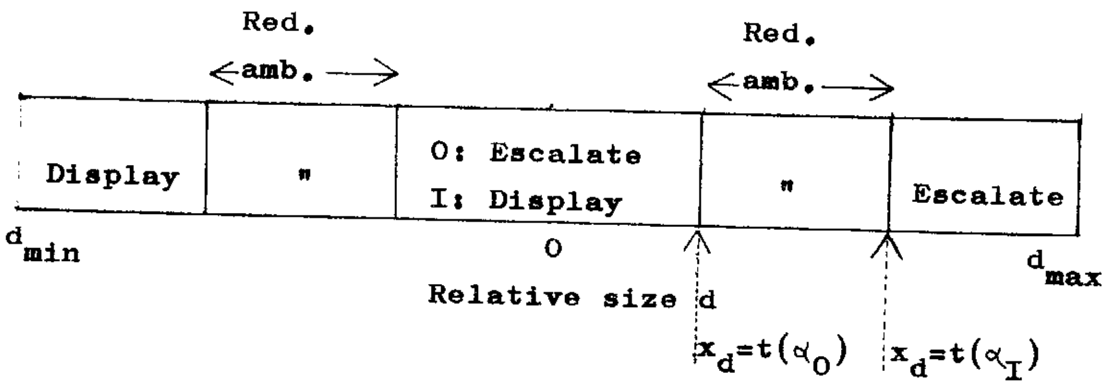

Fig. 23. Structure of an ESS for $V_0 > D$ and $t(\alpha_0) < t(\alpha_I)$

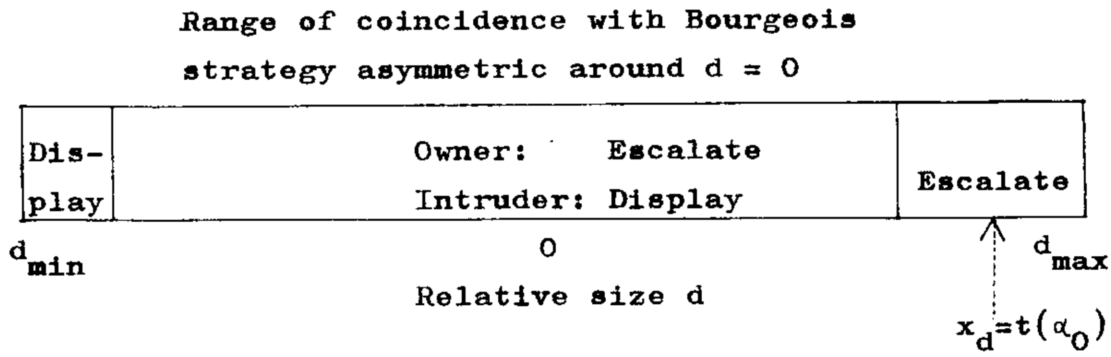

Fig. 24. The unique ESS for $V_0 > D$ and $t(\alpha_0) > t(\alpha_I)$

Conclusions:

(1) Structural stability of the model with a payoff irrelevant aspect: The introduction of a small difference in fighting ability between owner and intruder has only a slight effect (Fig.21) on the structure of an ESS. Therefore the model with payoff irrelevant ownership status is valid as a limiting case of the models considered in this section.

(2) Maintenance of ESS's despite a difference in value of the resource: For arbitrarily large differences in value of the resource between owner and intruder, the following result can be stated: If injury is relatively serious to the owner ($V_0 < D$), the Assessor strategy is an ESS. It must be pointed out that individuals playing Assessor base their behaviour on the role aspect "relative size" in all size asymmetric situations! Furthermore the Assessor strategies with decision criteria c also remain ESS's under the above assumption (Fig. 21).

We conclude that even the introduction of large differences in value of the resource may not affect the set of "non paradoxical" ESS's. There is, however, always a loss in paradoxical ESS's due to the range of reduced ambiguity: A larger owner must escalate for cases in which the decision to display is possible under the condition $V_0 = V_I$.

(3) Coincidence with the Bourgeois strategy: The first important qualitative change of the structure of an ESS appears when the value of the resource to the owner just exceeds the cost of

injury (Fig. 23). For size differences below a certain threshold an ESS now coincides with the Bourgeois strategy. The range of reduced ambiguity becomes smaller with growing V_0 till finally an ESS is uniquely determined by the set of model parameters. The range of coincidence with the Bourgeois strategy becomes asymmetric (Fig. 24) around d = 0. A smaller owner and a larger intruder are then expected to engage in an escalated contest if the values of d fall within the range of non-complementary structure. A smaller owner is therefore, under extreme conditions, expected to be seen in an escalated fight with a considerably low chance of winning.

(4) Thresholds: Whether, for a particular contest situation, an owner must in all ESS's defend its resource, depends only on fighting ability and the owner's index of seriousness of injury α_0. Whether the intruder must escalate depends on α_I. An interesting general aspect of this model is that differences in value of the resource to the opponents are not the essential argument for the evolutionary stability of resource defense.

6. Bluff

Animals may have characteristics which increase size without having a considerable effect on fighting ability. The possession of such characteristics was called bluff by Maynard Smith and Parker (1976). In order to avoid misunderstanding it must be stated that the term bluff used in this sense does not refer to the signaling of intended behaviour.

If "real size" and "apparent size" can be distinguished by the individuals of a population, size gives rise to more than one role aspect (Fig. 25). The discussion of bluff therefore is closely related to the main question asked in this paper: on which of several aspects may or must conflict behaviour be based?

	Difference between own size		opponent's size
Aspect 1	real	-	real
" 2	real	-	apparent
" 3	apparent	-	real
" 4	apparent	-	apparent

Fig. 25. Four possible aspects of a role

<u>The problem</u>: Consider a contest with an ownership asymmetry in which the payoffs to owner and intruder for obtaining the resource do not compensate for their risk of injury in an escalated contest. Suppose a population bases its behaviour on apparent size and plays an Assessor strategy with decision criterion c: "if relative apparent size falls between the limits -c, c, respect ownership, otherwise respect apparent size". Can this be an ESS although bluff can be recognized? If not, there must be a better reply to the population strategy than this strategy is to itself:

(1) Clearly in all roles to which the population strategy ascribes the decision "escalate", it does not pay to deviate. Because of the strategy's complementary structure, this deviation would be to give up an undisputed victory.

(2) Consider now roles to which the population strategy ascribes the choice "display". To deviate involves escalation in such cases. Let B denote the maximum difference of two bluff components' sizes. If the value c+B falls within the ambiguous zone, the difference in real size also falls within this zone. Therefore a deviant's risk of injury in an escalated contest may not be compensated for by the value of winning.

From (1) and (2) it follows that the Assessor strategy with decision criterion c is an ESS (for c+B sufficiently small). The model demonstrates a new aspect of the ambiguous zone: The evolutionary maintenance of behaviour which respects bluff despite its recognition may be possible if the variation of such bluff is not too large.

IV. DISCUSSION: GAMES AND THE THEORY OF ASYMMETRIC CONTESTS

Contest situations are here described by games in which role determination is represented as a "random move" which preceeds the players' choices. This step towards modelling animal conflicts as games in "extensive form" was already implicitly made by Maynard Smith and Parker (1976). It is explicitly formulated by Selten (1978). For contest models having the information asymmetry property (the opponents never find themselves having the same information situation) he stated the characterization of an ESS as a strategy which is the only best reply to itself.

One intention of the present paper is to show how concrete models of asymmetric contests are constructed and solved, such that the structure of the particular problem under consideration remains as transparent as possible. This transparency is obtained here by decomposition into subgames (situation games). The decomposability as such depends on the assumption of perfect information about an opponent's role. The particular form of the solutions, which are considered for the subgames, is a consequence of the above "global" characterization of an ESS.

The central aim of the paper is to discuss whether, according to a functional analysis, animals in contest must or may use an existing asymmetric aspect for settlement. The question will be considered first, whether at least some such aspect must be taken into account by a contestant, and then, which of the aspects may or must be chosen.

Maynard Smith and Parker (1976) convincingly demonstrated the following: In cases where injury is of relatively high cost, a role difference in one aspect, perfectly known to the individuals, must be used for conventional settlement by an ESS (there may be alternative ways of respecting the asymmetry). Selten's characterization of an ESS allows for a brief and general argument on which this result may be based:

Consider a game of a contest with roles A,B, satisfying the role asymmetry A $\neq$ B. An associated "restricted" game may be constructed which contains only those strategies that ignore the roles A, B in assigning to them identical local strategies. The associated game may be interpreted as a model for a symmetric contest, where the differences are not perceivable. We know that ESS's for such symmetric contests tend to be mixed strategies if escalation is dangerous (for example: Bishop and Cannings, 1978). Therefore the statement is of great interest that whenever only mixed ESS's exist in the associated game, the asymmetry cannot be ignored in the original game. This is easy to show:

A strategy which ignores the asymmetry belongs to both games. If it is an ESS for the original game, it is also an ESS for the restricted game. According to its characterization the strategy must be pure. Therefore we get the contradiction that the associated game then has a pure ESS.

The argument is easily generalized to models with various asymmetric role aspects:

(1) General property of asymmetric contests with perfect information: For all contest situations in which the associated symmetric contest has no pure ESS, individuals must base their decision on at least one asymmetric aspect.

We now return to the second question: If some of the aspects have no considerable payoff relevance, but others have, it is not clear from the preceeding argument (1), whether the former may be preferred as conventional cue. The models presented here show that this may be the case if the following condition holds:

(i) Injury is relatively serious compared with the value of the resource under competition.

(2) The range of ambiguity: Suppose (i) and consider contest models of the kind analyzed in this paper. A set of asymmetric contest situations may be found, for which no aspect or combination of aspects favours one of the opponents in such a

way that it would pay him to engage in an escalated fight. This is the range of ambiguity, where animals may base their decisions on payoff irrelevant or relevant aspects: Any convention which is complementary (in assigning the alternative choices to the paired roles), and which therefore leads to an avoidance of escalated contests, is evolutionarily stable.

(3) The range of an aspect's dominance: An asymmetric aspect (or a combination of them) may be of such strong payoff relevance for a contest situation that this particular aspect must be used as cue for settlement. The set of asymmetric contest situations for which this is the case will be called the aspect's range of dominance. Whereas the requirement (i) was necessary for the existence of a range of ambiguity, it is not for the existence of a range of dominance.

Clearly there are asymmetries which cannot be classified as in (2) and (3), but these two classes represent extremes.

(4) Escalation suppression: Suppose that an asymmetry falls within the range of ambiguity or within an aspect's dominance range. In an ideal population playing an ESS, no escalation would be observable, except for encounters with deviant strategies.

(5) Range of two aspects' competing dominance: Two asymmetric aspects of strong payoff relevance which, each alone, would perfectly serve as cue for settlement may have the following property for a range of asymmetries: one of them makes escalation worthwhile for one individual and the other aspect favours the opponent's escalation. The set of such contest situations, for which an ESS does not lead to conventional settlement, will be called the aspects' range of competing dominance. The phenonmenon of competing dominance may appear if injury is not relatively serious for at least one of the opponents.

(6) Results for the particular models: The conclusions for contests with a payoff irrelevant ownership asymmetry and an asymmetry in fighting ability can now be stated in simple terms: If injury is relatively serious, all contest situations belong

either to the range of ambiguity or to the dominance range of fighting ability (III. 3). The greater the winner's risk of injury, the greater is the range of ambiguity (III. 4).

If the resource under competition is of unequal value to owner and intruder, the range of full ambiguity is smaller but still exists, as long as injury is relatively serious to both contestants (III. 5). A third range exists which is less ambiguous because some paradoxical ESS's are excluded. If injury is not relatively expensive for the owner, competing dominance may appear between the role aspects fighting ability and ownership-status.

Finally the discussion of respecting bluff, despite its recognition, shows that such behaviour may be an ESS because the considered asymmetries belong to the range of ambiguity (III. 6).

The question will be discussed now: how far can the theory help us to understand real animal contests? Two examples (7), (8) are given, where the strategy "respect ownership status if the difference in fighting ability is below a critical value, and repect fighting ability for larger differences" seems to be played.

(7) Example (Agelenopsis aperta): Maynard Smith (unpublished) proposes the funnel web spider Agelenopsis aperta as a possible example of an Assessor "player". Riechert (1978) observed agonistic behaviour between females in the field. Encounters were induced at natural web sites. 91% (n=81) of the fights were won by the larger female. However, in 9 of 10 cases with a size (weight) difference less than 10%, the contest resulted in successful defense of the owner. Shaking the web could here be the way of getting rather accurate information about the role aspect "relative weight".

(8) Example (Papio hamadryas): Kummer et al. (1974) discussed evidence which suggests that in Hamadryas baboons pair bonds between a male and a female are protected against "intrusion" of other males by an inhibition of potential rivals. The well known experiments, in which a male-female pair and another

male were brought together, demonstrate the following: Even with a stronger "intruder", the previous "owner" in general remains in undisputed "possession" of the female. For large differences in fighting ability however, rival males did deprive the owner of a female.

The disregarding of ownership seemed to occur mainly between less intimate males. In a recent paper (Kummer et al. 1978), this hypothesis was reversed in view of further experimental data: The degree of intimacy appears to lower the inhibitory effect. The authors suggest a possible explanation: The rival can predict the chance of winning more precisely against an intimate opponent.

The example contains features of the presented models with the role aspects ownership status and relative fighting ability. The last cited results however demonstrate that a discussion also requires the introduction of elements of incomplete information in the models.

<u>(9) Example (Uca pugilator)</u>: Hyatt and Salmon (1978) observed agonistic behaviour between male fiddler crabs (Uca pugilator) in the field. Out of 403 fights, in which burrows were the resource under competition, the owner won in 87% of the cases. In 50 of the remaining 54 cases, the successful intruder was larger. It may be that a main part of the fiddler crab's contest can be interpreted as a process of assessment of relative fighting ability.

The last example (9) makes us aware of a difficulty in interpreting the models: The presented theory assumes an asymmetry to be given, whereas in reality it often appears within the course of a contest. More realistic models should deal more explicitly with the process of assessment and "bargaining". This leads to the discussion of incomplete information and of communication in agonistic interactions which is beyond the scope of this paper. It must be pointed out however that the analysis of communication in contests is one of the interesting problem areas of evolutionary game theory: it stimulates a controversial debate on whether information about intentions may be exchanged (Maynard Smith, unpublished; Caryl, 1979).

A final criticism concerns the "partial analysis" character of the considered models: If we want to discuss the value of a territory, for example, a larger model is needed in which the players are involved in more than a conflict with one single opponent. The value depends on how easily the territory may be successfully defended later against other opponents, etc. The partial analysis was made here in order to maintain the heuristic power of a simple model.

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