Evolution of Fighting Behaviour: Decision Rules and Assessment of Relative Strength

MAGNUS ENQUIST

Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden

AND

OLOF LEIMAR

Department of Genetics, University of Stockholm, S-106 91 Stockholm, Sweden

(Received 12 December 1982)

A mathematical model of fighting behaviour is developed. The contestants belong to a population with varying fighting abilities and the fights consist of the repetition of one type of interaction. At each interaction in the sequence the opponents acquire some information about the true fighting abilities. The fights are seen as a motion of each opponent through a causal factor space; the current position of an animal in the space represents all information obtained by the animals so far. A decision rule (strategy) is a specification of what action to take at each point in the causal factor space. Evolutionarily stable strategies are calculated numerically and are found to be pure and unique. The distribution of fighting times and the probabilities of winning are calculated for pairs of contestants from a population using the ESS. Expected utilities are also computed and in the situations investigated they are fairly close to the maximum value that would obtain if the contested resource were divided equally between the contestants without any cost.

1. Introduction

The present understanding of the evolution of aggressive behaviour in animals is primarily due to Maynard Smith's application of the theory of games to animal conflicts (Maynard Smith & Price, 1973; Maynard Smith, 1974). The concept of an evolutionarily stable strategy or ESS (Maynard Smith, 1974), the key result of these theoretical studies, has provided ethologists with a general method of analysis of conflict situations.

A number of mathematical models of fighting behaviour have been developed (e.g. Maynard Smith & Price, 1973; Maynard Smith & Parker, 1976; Parker & Rubenstein, 1981). The approach has been to simplify the

0022-5193/83/110387+24 \$03.00/0

© 1983 Academic Press Inc. (London) Ltd.

biological situation so that an ESS can be found and analysed without too much effort. In this way one hopes to gain a qualitative understanding of real fighting behaviour and to elucidate basic questions such as the effect of asymmetries. However, the fact that these models are simplified makes it hard to apply them to cases where it is possible to test them. The main problem is that they are behavioural models only to a limited extent. Fights generally consist of a sequence of behaviours, each preceded by an active decision by the animals involved. In making such a decision an animal should take into account all relevant information, e.g. concerning the opponent's fighting ability, obtained so far during the fight. We believe that the next step in the study of fighting strategies must be to develop models based on plausible behavioural mechanisms.

The idea that information about fighting ability is transmitted during a contest and that this information will influence the behaviour of the contestants and thus the outcome was discussed by Parker (1974). Two attempts have been made to model information acquisition (Maynard Smith & Parker, 1976; Parker & Rubenstein, 1981). Due to the complexities of such an analysis the simplifying assumptions involved were quite drastic, making application to real fighting difficult. The importance of these attempts is that they provide a conceptual framework for information acquisition during a fight. An animal's state of knowledge of differences in fighting ability between itself and its opponent is represented as a probability distribution over the *a priori* possible values of this difference. As the fight progresses this distribution changes, being a conditional probability distribution for the difference in fighting ability given the observations made by the animal so far.

The aim of this paper is to develop a model that focuses on plausible behavioural mechanisms, evolutionary stability, and on how information about fighting ability is transmitted between opponents during a fight. An important concept will be that of a causal factor space (McFarland & Sibly, 1975). A causal factor is a variable that is available to the animal for observation and that is of relevance for the animal's decisions. In principle, all relevant observable variables should be included in the causal factor space, but in practice one must choose a few believed to be the most basic. There is, however, a criterion of consistency that can be applied to the choice made. The values of the causal factors at a given time should represent the animal's state at this time, in the sense that they provide sufficient information for the animal to base a decision on. Thus a knowledge of the causal factors before this time, which necessarily must be available to the animal, should not give any additional information.

2. Biological Background

In this section we present our hypothesis concerning fighting behaviour in a non-mathematical manner. By a fight we mean an aggressive interaction over a valuable resource such as a breeding territory or a high rank position. The effect achieved by an animal, A, that shows fighting behaviour towards another animal, B, is that a cost is inflicted on B and that information is gained by B and possibly also by A about the cost associated with continued fighting. If animal B has little to gain by staying near A it should leave in order to avoid costs caused by aggressive behaviour from A, but if B also could benefit from the same resources as A then B might stay and a fight will occur.

In order to understand the evolution of fighting behaviour there are several aspects that one should consider. Natural selection will act on ability to inflict cost (i.e. fighting ability) but also on ability to assess relevant asymmetries in a conflict and on decision rules (strategies) based on these assessments. There will be an interaction between these forms of adaptation, e.g. it has been suggested (Maynard Smith & Price, 1973) that evolution of strategies may limit the adaptive value of ability to inflict cost. We will leave the question of evolution of ability to inflict cost aside and concentrate on the other two aspects.

We assume that the contestants generally will differ in fighting ability but that prior to a fight they have incomplete information about the difference. Additional information could be gained during the fight, first of all from the effect of potentially dangerous behaviour, since the success of an attempt to injure the opponent necessarily carries information about the likelihood of success in further attempts. Furthermore, the assessment of factors like differences in size or strength could provide the contestants with estimates of the cost of continued fighting. Associated with any attempt at assessment there will be an uncertainty or error of observation, which can be decreased by further observation. We propose that information about the difference in fighting ability is accumulated during the fight in a way that can be compared with statistical sampling. If the fighting proceeds in stages with varying intensity, the most informative but also most costly sampling will take place during the final escalated phase.

Another way for a contestant to gain some knowledge of the relative fighting ability is to try to estimate the opponent's estimate. This information will be available only to a very restricted degree, but in a case where an animal believes itself to be much stronger, the fact that the opponent is still fighting may indicate that the estimate is too optimistic. Concerning prior information, the least that can be assumed by the opponents is that they are a pair randomly drawn from a population with known distribution of fighting abilities. If an animal has experience of fighting it will have an idea about its own ability to inflict costs compared with others, and if two animals have fought each other one or several times before and recognize this fact they have a particularly high amount of prior information.

We can now loosely identify three sets of causal factors: The *a priori* distribution of fighting abilities, a sequence of observations of some factor related to fighting ability, and the opponent's behaviour. A strategy is a rule specifying which action to take for each combination of causal factors. The relative merits of different strategies played against a given strategy will be based on their expected marginal contribution to the player's fitness (expected utility), the optimal strategy yielding the highest expected utility. Note that adding more variables to the causal factor space will increase the utility of an optimal strategy, or leave it constant if the added variables are irrelevant. Thus evolution will typically tend to enlarge the causal factor space, e.g. proceeding from a situation where only severe physical damage is assessed and successively including the assessment of more factors related to fighting ability such as relative size and strength.

3. The Model

To illustrate and also to extend the discussion in the previous section we now study a particular mathematical model. Let the contested resource have equal value V (in fitness units) to the two animals involved. Assume that the fight consists of the repetition of one potentially dangerous interaction such as an exchange of blows. This would best fit the case of a fight with only one intense phase. We thus have a sequence of steps terminating when one of the contestants gives up. For a given pair of animals, A and B, the cost per step for A, c_A , will depend not only on the size and strength of B but also on the size and strength of A. The ratio c_A/c_B describes the opponents' relative abilities to inflict costs on each other, but we choose to use the quantity

$$\theta_{AB} = \ln \left(c_B / c_A \right) \tag{1}$$

as a measure of the relative fighting ability since it has the nice property that $\theta_{BA} = -\theta_{AB}$. For the opponents, it will be important to try to estimate not only the ratio but also the magnitudes of the costs. To keep things simple we make the arbitrary assumption that for all pairs A and B the relation $c_A c_B = c^2 = \text{constant holds}$. Both costs can then be expressed as

functions of $\theta = \theta_{AB}$:

$$c_A = c \exp(-\theta/2), \quad c_B = c \exp(\theta/2).$$
 (2)

In general both c and θ will vary for different pairs of contestants but taking c constant in equation (2) is a first approximation in the sense that it seems plausible that c will vary much less than θ . In order to identify θ in an experiment one must find a functional relationship between the ratio of costs and the physical characteristics of the animals.

During the *i*th step of the fight the costs c_A and c_B are inflicted on A and B respectively and each opponent samples the relative fighting ability θ with a certain error of observation. Animal A observes

and B observes

$$v_i^B = -\theta + z_i^B$$

 $v_i^A = \theta + z_i^A$

 z_i^A and z_i^B are the errors of observation. We assume that they are independently drawn from a normal distribution with mean zero and standard deviation σ . After *n* steps *A* and *B* can make the estimates

$$x_n^A = \frac{1}{n} \sum_{i=1}^n y_i^A$$
 and $x_n^B = \frac{1}{n} \sum_{i=1}^n y_i^B$.

The sampling error is now reduced and has a standard deviation σ/\sqrt{n} . We can identify two causal factors here: the estimate of relative fighting ability and the uncertainty associated with the estimate. In a causal factor space (Fig. 1) we can represent how these factors change during the fight.



FIG. 1. A causal factor space with an evolutionarily stable switching line and a fight lasting eight steps. The cost parameter c is 0.005 and the standard deviation of sampling σ is 1. The causal factors are the sampling average (x) and the uncertainty of the sampling average $(1/\sqrt{n})$.

Initially the uncertainty is high, but as the fight progresses it decreases and the trajectories representing A and B execute a random motion as shown. Note that the decrease per step of the uncertainty becomes successively smaller, σ/\sqrt{n} reaching zero only after an infinite number of steps. In Fig. 1 we have drawn a boundary or switching line which represents a decision rule. When an animal's trajectory goes below the switching line that animal gives up.

We make this a bit more formal so that we can compute the strategy (switching line) that is optimal against an opponent using a given strategy. We assume that the contestants only have a minimal amount of prior information, i.e. before the fight they only know that θ has a given probability density $\beta(\theta)$ that is symmetric around $\theta = 0$. Since the prior information will be the same for all individuals it is not necessary to include any parameters of this distribution in the causal factor space. For our computations we choose

$$\boldsymbol{\beta}(\boldsymbol{\theta}) = \exp\left(-\boldsymbol{\theta}\right) / (1 + \exp\left(-\boldsymbol{\theta}\right))^2. \tag{3}$$

The distribution was arrived at by assuming that $c_B/c_A = m_A/m_B$, where m_A and m_B are the weights of A and B, and that A and B are a randomly drawn pair from a population with exponentially distributed weights. The particular form of equation (3) is however not crucial as long as it has a spread that approximates the range of variation of relative fighting ability in the population.

Now let $\Theta, Z_1^A, Z_2^A, \ldots, Z_1^B, Z_2^B, \ldots$ be independent stochastic variables, Θ having probability density β and $Z_i^{A,B}$ normal with mean zero and standard deviation σ . Formally the contestants are represented by the stochastic processes

$$X_{n}^{A} = \Theta + \frac{1}{n} \sum_{i=1}^{n} Z_{i}^{A}$$
 and $X_{n}^{B} = -\Theta + \frac{1}{n} \sum_{i=1}^{n} Z_{i}^{B};$ $n = 1, 2, ...$
(4)

If B plays strategy $S = \{S_1, S_2, \ldots\}$, i.e. B gives up after step n if $X_1^B > S_1, \ldots, X_{n-1}^B > S_{n-1}, X_n^B \le S_n$, then we want to find a strategy S' for A that maximizes A's expected utility U(S', S). Define the stochastic variable (stopping time) T_A as the smallest n for which $X_n^A \le S'_n$ and similarly T_B , the smallest n for which $X_n^B \le S_n$. T_A or T_B may be infinite but the variable $T = \min(T_A, T_B)$, giving the duration of the fight, should be finite. Should both A and B give up after the same step we assume that they "flip a coin" to decide the winner. The expected utility for A is then

$$U(S', S) = V \Pr(T_B < T_A) + \frac{1}{2} V \Pr(T_B = T_A) - E(T_C \exp(-\Theta/2)).$$
 (5)

Changing the strategy S' will change the distribution of T_A and thus of T. Qualitatively, lowering the S'_n will increase the probability of winning but also the expected cost. The distribution of the stopping times can not be calculated analytically, so one must resort to computer simulation. We must then formulate the optimization problem in a form suitable for numerical analysis, at the same time gaining some conceptual insight. Consider a point in time immediately after the *n*th step, assuming that the fight is still going on. Animal A has observed $X_n^A = x$ and must decide whether or not to give up, not yet knowing B's decision at this step. A's observation can be formalized as the event

$$O_{n,x} = \{X_n^A = x, T_B > n-1\}.$$
 (6)

Define $U_n(x)$ as A's expected (future) utility given $0_{n,x}$. The two alternatives, to give up or to continue to fight with the best possible strategy, will in general give different utilities and A should choose the alternative with the highest utility. The optimal switching point S'_n will be located at the x-value where the two alternatives give equal utility. We can now write equation (5) as

$$U(S',S) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} (U_1(x) - c \exp(-\theta/2))\gamma(x|\theta) \, \mathrm{d}x \,\beta(\theta) \, \mathrm{d}\theta \qquad (7)$$

where $\gamma(x|\theta) dx = \Pr(X_1^A \in (x, x + dx)|\Theta = \theta)$. For $x \le S_1$ we have $U_1(x) = \frac{1}{2}V \Pr(T_B = 1|O_{1,x})$, but for $x > S'_1$, $U_1(x)$ will depend on S'_i , $i \ge 2$. Continuing the iteration we get

$$U_{n}(x) = \begin{cases} \frac{1}{2} V \Pr(T_{B} = n | O_{n,x}); & x \leq S'_{n} \\ V \Pr(T_{B} = n | O_{n,x}) + \left\{ \int_{-\infty}^{\infty} U_{n+1}(z) \gamma_{n}(z | x) dz & (8) \\ -E(c \exp(-\Theta/2) | O_{n,x}, T_{B} > n) \right\} \Pr(T_{B} > n | O_{n,x}); & x > S'_{n} \end{cases}$$

where $\gamma_n(z|x) dz = \Pr(X_{n+1}^A \in (z, z+dz)|0_{n,x}, T_B > n)$. Condensing the notation, equation (8) becomes

$$U_{n}(x) = \begin{cases} \frac{1}{2} V \alpha_{n}(x); & x \leq S'_{n} \\ V \alpha_{n}(x) + \left\{ \int_{-\infty}^{\infty} U_{n+1}(z) \gamma_{n}(z|x) \, \mathrm{d}z - C_{n}(x) \right\} (1 - \alpha_{n}(x)); & x > S'_{n}. \end{cases}$$
(9)

The two alternatives, giving up or continuing, have equal utilities when

$$\frac{1}{2}V\frac{\alpha_n(x)}{1-\alpha_n(x)} + \int_{-\infty}^{\infty} U_{n+1}(z)\gamma_n(z|x)\,\mathrm{d}z - C_n(x) = 0. \tag{10}$$

Intuitively it is clear that each of the three terms on the left hand side of equation (10) is an increasing function of x, implying a unique solution $x = S'_n$ as the optimal switching point for specified S'_i , i > n. Note further that using the iteration of equation (9) from high *n*-values downwards there is a stability in the sense that the factor $(1 - \alpha_n(x)) < 1$ and the substraction of the cost $C_n(x)$ will reduce the contribution from the "distant future". This is an expression of the fact that in an optimal case it is highly unlikely that the fight will continue for a very long time, so that what happens in such a case should not influence present decisions. We then have a clear indication, confirmed by the computer studies, that there is a unique best strategy S' against S. This means that there will be no mixed evolutionarily stable strategies in this situation.

For the consistency of the model it is important that the observations $O_{n,x}$ by A contain all relevant information available to A to predict the future. A has observed the entire "history" X_i^A , $i \le n$ and one could wonder if more information could be gained. This is not the case, due to the fact that the distribution of Θ given $O_{n,x}$ is the same as the distribution given $T_B > n-1$, $X_1^A = x_1, \ldots, X_n^A = x$ (see appendix A). We stress this point to illustrate the concept of an animals state. That state should be a collection of all variables available to the animal that are relevant for predicting future events. These variables are then the causal factors. In our case the event $O_{n,x}$ specifies the causal factors.

To find a stable strategy we compute a sequence S, S', S'', \ldots converging to a strategy S^{∞} that is optimal against itself. In appendix B some more details are given regarding the computational algorithm. Numerically we have only found one ESS for specified parameters c and σ , indicating that the ESS is unique.

4. Results

The model presented in the previous section contains two parameters, c and σ . As can be seen from equation (2), c is related to the cost of obtaining a sample of the relative fighting ability θ , a higher value of c corresponding to a more dangerous fight. The other parameter, σ , is the standard deviation of the sampling error. These two parameters are not independent of each other, since an interaction that yields a very reliable estimate of the relative fighting ability is likely to be very costly. In order to specify a functional relationship between c and σ one needs, however, to understand the detailed mechanism of the interaction. We have studied several combinations of values of the parameters numerically, determining the evolutionarily stable strategy and then characterizing the fights of

individuals using this strategy. We have chosen the unit of fitness so that the value of the contested resource, V, equals one. Thus c measures the expected cost of an interaction relative to V and will be a function of the mechanism of interaction and of the resource value. Let us first look at the case c = 0.005 and $\sigma = 1$. In Figs 1 and 2 the same switching line is presented using two different choices of causal factors, the uncertainty of the sampling average, σ/\sqrt{n} , in Fig. 1 and the fighting time, n, in Fig. 2.



FIG. 2. The same switching line as in Fig. 1 drawn in a space with the sampling average (x) and the number of steps (n) as causal factors. A fight lasting 39 steps is shown.

The switching line in Fig. 1 is approximately straight. The most obvious characteristic of the ESS is that early in the fight the sampling average, x, must be quite low before an animal gives up. The expected utility prior to the fight, $U(S^{\infty}, S^{\infty})$, for an individual in a population using this strategy is 0.451. Since the value of the contested resource is one and the prior probability of winning 0.5, the expected cost of fighting will be 0.049, which is quite small compared to the benefit obtained by the winning animal, and we conclude that assessment of fighting ability results in good fighting economy. In Figs 1 and 2 the trajectories representing two different fights are plotted. The fight in Fig. 1 is between unequal opponents; the weaker animal gives up after eight steps.

The opponents in Fig. 2 have equal fighting abilities ($\theta = 0$) which tends to give a longer fight. The most probable x-coordinates for the contestants are $x = \theta$ and $x = -\theta$ respectively, but the randomness involved in the sampling can lead to that the stronger animal gives up first.

At the switching line the expected utility of continued fighting, $U_n(x)$, is approximately zero. We have drawn curves of constant $U_n(x)$ in Fig. 3. As *n* increases the curves come closer together, which means that the change from low to high expected utility with increasing *x* is more abrupt at high values of *n*. Thus the predictive value of the causal factor *x* becomes greater as the fight progresses.



FIG. 3. Curves of constant utility in the causal factor space. The utility can vary between zero and one. At the switching line the utility is approximately zero. Parameters: c = 0.005, $\sigma = 1$.

As mentioned above the *a priori* probability of winning is 0.5 and the expected cost 0.049. These are the values obtained given that θ is distributed according to equation (3), but an observer that is able to measure θ before the fight can use this extra information to get different estimates. These estimates are plotted in Figs 4 and 5. The graph in Fig. 4 shows the accuracy of the fight to discriminate between the weaker and the stronger animal. When the absolute value of θ is greater than 0.5 the discrimination is almost perfect but for more closely equal opponents some "mistakes" do occur. Figure 5 illustrates the fact that it is more costly to meet an opponent of equal strength than one that is stronger. This is due to the assessment taking place during the fight. A weaker animal will quickly realize that the situation is unfavourable and give up.

Let us now investigate what the effects of different values of c and σ are. The evolutionarily stable switching lines for various combinations of



FIG. 4. The probability of victory as a function of the relative fighting ability θ for the ESS with parameters c = 0.005 and $\sigma = 1$.

c and σ are plotted in Figs 6 and 7. Varying σ (Fig. 6) influences the strategy most strongly in the beginning of the fight. A high uncertainty of sampling will cause the contestants to be unwilling to give up early, and they will take the cost of continued sampling in order to get a more accurate estimate of the relative fighting ability. This can be seen also from the expected utilities and costs given in Table 1. Increasing σ and keeping c constant will make the fights more costly, since it is more expensive to get



FIG. 5. Expected total cost as a function of relative fighting ability for the ESS with parameters c = 0.005 and $\sigma = 1$.



FIG. 6. Evolutionarily stable switching lines for c = 0.005 and σ varying from 0.5 to 1.5.

a certain amount of information when σ is high. The total amount of information gathered is however less for high σ than for low, in the sense that the accuracy of the fight to discriminate between the stronger and the weaker animal is lower for high σ . Varying c (Fig. 7) will affect the ESS somewhat differently. When c is high the contestants will be more cautious in all stages of the fight, requiring a higher sampling average x in order to continue fighting. As can be seen from Fig. 7 the switching line will intersect the line x = 0 when c is high, the intersection occurring for a smaller value



FIG. 7. Evolutionarily stable switching lines for $\sigma = 1$ and c increasing from 0.0025 to 0.02 (increasing cost of interaction or alternatively decreasing value of resource).

TABLE 1

Expected utility and expected cost prior to the start of the fight for different values of c and σ in a population adopting the evolutionarily stable strategy

σ	с	Expected utility	Expected cost
0.5	0.005	0.471	0.029
$1 \cdot 0$	0.005	0.451	0.049
1.5	0.005	0.437	0.063
1.0	0.0025	0.466	0.034
$1 \cdot 0$	0.005	0.451	0.049
1.0	0.01	0.435	0.065
1.0	0.02	0.405	0.095

of *n* the higher *c* is. There might be an intersection also for small *c* but we have not studied the switching line beyond n = 100. When *x* is positive at the switching line the information that the opponent is still fighting will have a major influence on the estimate of relative fighting ability, since the contestants know that they both have a positive sampling average. It might seem strange that an animal should give up having sampled itself as stronger, but since additional information accumulates very slowly for high *n*-values, the expected time until the opponent gives up will be long. Thus, an aspect of the ESS will be to avoid extreme fighting times when the contestants have similar fighting abilities.



FIG. 8. Average fighting times measured in number of steps, as a function of relative fighting ability. The three curves refer to the stable strategies for c = 0.005 and different values of σ .

If one wants to test this model empirically one will face the problem of determining the strategy actually used by the animals in question. Since an animal's position in the causal factor space (or even the exact nature of the space) is not readily available to an outside observer, one may not be able to estimate directly the location of a switching line. There are however several quantitative predictions of the model that can be tested. One such prediction is the distribution of fighting times. In Figs 8 and 9



FIG. 9. Average fighting times measured in number of steps, as a function of relative fighting ability. The four curves refer to the stable strategies for $\sigma = 1$ and different values of c.

average fighting times as a function of θ are shown for different parameter values. The form of the curves can be understood from the discussion of the strategies in the previous paragraph. A larger sampling error (Fig. 8) will increase the fighting times of unequal opponents. For opponents of identical fighting ability one finds, somewhat surprisingly, that the average fighting time is independent of σ . From the point of view of the mathematics of our model this is due to the fact that, for small |x| and high *n*, varying σ basically amounts to a change of scale of the *x*-axis. Rescaling *x* and σ in the same way will affect the prior distribution of θ and the dependence of the costs on θ , but this will have a small effect on the utilities estimated by the contestants when |x| is small and *n* large. In contrast, the average fighting time for $\theta = 0$ depends sensitively on *c* (Fig. 9), illustrating the importance of avoiding excessive costs for matched opponents.

The sampling errors introduced into the model lead to a considerable random variation in fighting times even when the relative strength of the animals is specified. The standard deviation, given in Fig. 10 for c = 0.005and $\sigma = 1$, is of the same order of magnitude as the average. It is often assumed that variation in behaviour of identically treated animals in an experiment is due to either undetected differences between animals or imperfect control of the test environment. In the model presented here there will always remain a certain amount of variation, regardless of how carefully the animals are selected, resulting from the imperfect nature of the observations used by the animals as a basis for decisions.



FIG. 10. Standard deviation of fighting times as a function of relative fighting ability. The parameters of the ESS are c = 0.005 and $\sigma = 1$.

5. Evolutionary Stability and Assessment

Several models of fighting without assessment have been presented in the literature. Among these are the war of attrition (Maynard Smith, 1974), the graduated risk game (Maynard Smith & Parker, 1976), and the generalized war of attrition (Bishop & Cannings, 1978). A common feature of these models is that the ESS is a mixed strategy and that the expected utility of fighting prior to the fight is zero. A zero expected utility will be a feature of any mixed ESS where one of the pure component strategies is not to fight at all, since all component strategies must have equal expected utility against the ESS. The models mentioned above all assume symmetry

between the opponents. To see how the possibility of assessment affects this picture, consider the type of fighting assumed in our model but without any assessment taking place. The contest will then be symmetric in the sense that the expected cost per step will be the same for both opponents before and during the fight. The ESS will be a version of the war of attrition with discrete time steps. This strategy will result in long fighting times, on the average using up the entire resource value, and will be unstable against an assessor mutant that gives up fast when weaker and persists longer when stronger. Although the type of situation that the war of attrition is intended to describe is not the more intense fights of our model, the argument still illustrates that when differences in ability to inflict cost exist evolution will favor the assessment of such differences. Note that the costs assessed in an early non-escalated stage of a fight might be the costs of fighting in a later escalated stage. Since in practice there will always be differences in fighting ability between individuals in a population, this suggests that fighting strategies occurring in nature will generally be pure and yield a positive expected marginal contribution to the individual player's fitness.

Apart from factors correlated with fighting ability, other asymmetries between contestants could be assessed and used as criteria for decisions. This leads to strategies based on conventions, which means that the outcome of conflicts is partly determined by some difference between the contestants that is unrelated to the expected cost of an interaction. In the extreme case all fights are settled by a role asymmetry without any cost. The example commonly used is an owner-intruder convention where ownership settles the conflict (Maynard Smith, 1974; Maynard Smith & Parker, 1976). Conventional fighting will mean less aggression in the population and it thus has the attractive feature of high expected utility of fighting. The question is whether or not "irrelevant variables" will be included in the causal factor space during the course of evolution. We will here argue that this is unlikely in all cases where differences in fighting ability exist and are assessed. Consider first a convention mutant attempting to invade a population using the ESS of our model. Denote the roles by A (owner) and B (intruder) and let S be the original ESS and C the convention to give up without fighting when in role B and fight according to S when in role A. The expected utility of S against itself, U(S, S), is positive (see Table 1) so that the utility of C against S,

$$U(C, S) = \frac{1}{2} \cdot 0 + \frac{1}{2}U(S, S),$$

will be strictly smaller than U(S, S) and the mutant cannot invade. The stability of a convention that somehow has been established against a mutation that ignores the role asymmetry is a more delicate matter. If the

assignment and assessment of roles are perfect, players of the convention strategy can prevent invasion by persisting long enough when challenged in role A, so that all opponents will receive a negative expected utility. However, if mistakes about roles occur the situation changes. Let p_A , p_B be probabilities of being in role A and B respectively and let $p_{A|A}$, $p_{A|B}$, $p_{B|A}$, and $p_{B|B}$ be conditional probabilities of a role given the opponents role. The kind of mistakes we are interested in is when both contestants are in role A, so let us assume that $p_{A|A} > 0$ and (for simplicity) $p_{B|B} = 0$. Compare the strategies C, using S when challenged, and C', using some other strategy S' when challenged.

$$U(C', C) = p_A(p_{B|A} \cdot 1 + p_{A|A} \cdot U(S', S)) + p_B \cdot 0$$
$$U(C, C) = p_A(p_{B|A} \cdot 1 + p_{A|A} \cdot U(S, S)) + p_B \cdot 0$$

We see that if S is an ESS when no convention exists then C will be stable against C'. But C is not stable against S:

$$U(S, C) - U(C, C) = p_A(p_{B|A} + p_{A|A}U(S, S)) + p_BU(S, S)$$
$$-p_A(p_{B|A} + p_{A|A}U(S, S))$$
$$= p_BU(S, S) > 0.$$

The argument above deals with one often used example with an "irrelevant variable" and does not show that in general no such variables will be part of the causal factor space. It does however indicate that these variables are less likely to play a role when assessment is taken into account. The discussion in this section in some ways parallels that in Parker & Rubenstein (1981). We have used the words convention and role in a more restricted sense than in that paper, not considering that the role could be correlated with fighting ability or value of the contested resource, because the point we wish to make is that only "relevant" variables should be included in the causal factor space. Concerning the question of when a conflict will be settled without fighting one could heuristically argue as follows. If the assessment of a role asymmetry conveys such information about fighting ability as to place either opponent below the switching line (see Fig. 1) in the causal factor space then no fighting will occur. The role assessment is then regarded as an initial sampling of relative fighting ability.

6. Discussion

A difference between this work and earlier attempts at modelling fighting behaviour is that our model incorporates a more detailed mechanism of interaction. For this reason we believe that, although we have dealt mainly

404

with functional aspects of fighting, the model also sheds some light on the problem of causation. The control of aggressive and sexual behaviour is often regarded as non-regulatory and believed to differ from the control of behaviour associated with homeostatic systems like drinking or feeding (e.g. Grossman, 1967). The recent contributions to the study of motivation through the application of control theory (McFarland, 1971, 1978; Toates, 1975) have with few exceptions dealt with behaviour attached to homeostatic systems. There are some quantitative models of sexual behaviour (Houston, Halliday & McFarland, 1977; Freeman & McFarland, 1974; Toates & O'Rourke, 1978; Toates & Archer, 1978) and attempts have been made to develop quantitative models of aggressive mechanisms (Heiligenberg, 1976; Archer, 1976; Toates & Archer, 1978). One major distinction between behaviour belonging to homeostatic systems and behaviour controlled in other ways is that the main causal factors for feeding, drinking, etc. are well known physiological variables, whereas the causal factors for aggression and sexual behaviour are harder to identify. Secondly, for a homeostatic system, the purpose of which is the regulation of a physiological state, the effect of behaviour on the causal factors is fairly direct and easy to understand. In order to attack problems of "nonregulatory" control, the following questions should be kept in mind: what are the causal factors, how does the causal factor state determine the behaviour, and how does behaviour feed back on the causal factors? If one uses a careful quantitative examination of function as a starting point these questions are highly interrelated. Take the kind of fights studied above as an example. A "complete causal factor state" would be a detailed specification of all that in principle could be observed by an animal during (and prior to) the fight, up to the present time. In our simplified situation the sampled sequence x_1, \ldots, x_n would be part of the complete state. The feedback of behaviour on such a complete state is of course trivial, the state being merely a specification of what has happened. Functionally, a fight is a matter of costs and benefits, and only those causal relationships between the state and behaviour that do affect expected utilities will have evolutionary significance. This means that the causal factor state can be contracted to the minimum number of variables that are sufficient to make an equally good prediction of future costs and benefits as can be made from the complete state. In our example the sampling average x and the number of samplings n sum up the functionally relevant information contained in the sequence. Identification of causal factors of aggressive behaviour thus essentially boils down to the problem of understanding the predictions (of costs and benefits) that the mechanisms of interaction will allow an animal to make. The information present in an interaction could be perceived by sight, hearing, painreceptors, pressure receptors, etc. The result of these perceptions might combine to something like degree of confidence, but note that no "aggressive drive" needs to be included.

The method whereby an animal obtains information that was chosen in the present model is just one of many possible. No detailed investigations exist that show how information about fighting ability is obtained in the last and most escalated phase of a fight. A few papers treat this subject for phases prior to the last phase (Geist, 1966; Davies & Halliday, 1978; Clutton-Brock & Albon, 1979). We have assumed that the information is obtained simultaneously by the two opponents in clearly separated acts of one type. The error in the estimate is not due to any randomness in the outcome of the interaction itself but caused by imperfect perception of the result. This means that, given the true value of the relative fighting ability, no correlation exists between the two opponents' observations. One can, however, easily imagine a situation where there is a correlation. For instance, the outcome could be uncertain and the result perfectly observed. The mechanisms can differ in many other ways. The information could be obtained successively by the two opponents instead of simultaneously. The animal might use several different methods to gain information at the same stage of the fight. In many cases the information is not obtained in separated acts but rather in rounds like the antler fighting in deers and mouthfighting in cichlid fish. We feel that investigation of mechanisms for obtaining information should be an important part of the study of animal communication in the future.

In this connection we want to emphasize that the only information transmitted between the opponents in our model is information about fighting ability. The action or act itself means nothing. It is the success of the attack or the information obtained about fighting ability that matters. For example, tailbeating, where a fish with the tail shoots a wave of water against the opponent, is an important pattern in many fish fights, and could carry information about fighting ability. A tailbeat from a strong fish would then carry a very different information than a tailbeat from a weak fish. This means that it is not enough to study aggressive communication by simply recording the sequence of acts, which is the method commonly used by ethologists investigating behaviour. Although this argument primarily concerns fighting behaviour and not aggressive interactions where threat displays play a major role, similar arguments will apply to that case also.

At the present time no data exist in the literature that allow a quantitative test of the model presented in this paper. The predictions that are most easily tested are perhaps the dependence of the probability of victory and the average fighting time on the relative fighting ability (see Figs 4, 8 and

9). Qualitatively these results agree with what is known. That size differences, which probably are correlated to relative fighting ability, affect the outcome of fights has been demonstrated in several studies (e.g. Hazlett, 1968; Hyatt & Salmon, 1978; Reichert, 1978; Caldwell & Dingle, 1979; Sigurjónsdóttir & Parker, 1981). Hazlett (1968) also shows that the probability of victory for the larger animal increases with size difference. That average fighting time increases with decreasing difference in fighting ability has been shown for the cichlid *Nannacara anomala* by Enquist & Jakobsson (in preparation). In order to make a very rough quantitative comparison we have pooled data from two somewhat different studies of the fighting behaviour of this species, carried out at the department of Zoology in Stockholm. The mean and dispersion of fighting times as a function of relative weight are given for this material in Fig. 11. We have also plotted



FIG. 11. Average (wide bars) and standard deviation (narrow bars) of fighting times measured in seconds, for contestants in different relative weight classes. For comparison a curve of average fighting times according to the model are given.

the "predicted" fighting times by making the identification $\theta = \ln (m_A/m_B)$ (see discussion following equation (3)) and choosing the parameters c and σ to achieve a good fit. The observed dispersions, being of the same order of magnitude as the means, agree fairly well with the prediction. Since several of the assumptions of the model do not apply in this case, the test should not be taken too seriously, and we have not tried to motivate further our choice of dependence of θ on m_A and m_B . The most important deviation is probably that these fish fight in two phases whereas the model assumes fighting in one phase. Note also that only the variation of mean fighting times with θ is compared with the prediction and not the magnitude of the means.

This research was supported by a grant from the Swedish Natural Research Council.

REFERENCES

- ARCHER, J. (1976). In: Perspectives in Ethology. Vol. 2. (Bateson, P. P. G. & Klopfer, P. H. eds), London: Plenum Press.
- BISHOP, D. T. & CANNINGS, C. (1978). J. theor. Biol. 70, 85.
- CALDWELL, R. L. & DINGLE, J. (1979). Behaviour 69, 255.
- CLUTTON-BROCK, T. H. & ALBON, S. D. (1979). Behaviour 69, 145.
- DAVIES, N. B. & HALLIDAY, T. R. (1978). Nature 274, 683.
- FREEMAN, S. & MCFARLAND, D. J. (1974). In: Motivational Control Systems Analysis (McFarland, D. J. ed.). London: Academic Press.
- GEIST, V. (1966). Behaviour 27, 175.
- GROSSMAN, S. P. (1967). A Textbook of Physiological Psychology. New York: John Wiley & Sons.
- HAZLETT, B. A. (1968). Z. Tierpsychol. 25, 608.
- HEILIGENBERG, W. (1976). In: Simpler Networks and Behaviour (Fentress, J. C. ed.). Sunderland, Massachusetts: Sinauer.
- HOUSTON, A. I., HALLIDAY, T. R. & MCFARLAND, D. J. (1977). Med. Biol. Eng. Comput. 15, 49.
- HYATT, G. W. & SALMON, M. (1978). Behaviour 65, 182.
- MAYNARD SMITH, J. (1974). J. theor. Biol. 47, 209.
- MAYNARD SMITH, J. & PARKER, G. A. (1976). Anim. Behav. 24, 159.
- MAYNARD SMITH, J. & PRICE, G. R. (1973). Nature 246, 15.
- MCFARLAND, D. J. (1971). Feedback Mechanisms in Animal Behaviour. London: Academic Press.
- MCFARLAND, D. J. (1978). In: Hunger Models: Computable Theory of Feeding Control (Booth, D. A. ed.). New York: Academic Press.
- MCFARLAND, D. J. & SILBY, R. M. (1975). Phil. trans. R. Soc. B. 270, 265.
- PARKER, G. A. (1974). J. theor. Biol. 47, 223.
- PARKER, G. A. & RUBENSTEIN, D. I. (1981). Anim. Behav. 29, 221.
- REICHERT, S. E. (1978). Behav. Ecol. Sociobiol. 3, 135.
- SIGURJÓNSDÓTTIR, H. & PARKER, G. A. (1981). Behav. Ecol. Sociobiol. 8, 219.
- TOATES, F. M. (1975). Control Theory in Biology and Experimental Psychology. London: Hutchinson Educational.
- TOATES, F. M. & ARCHER, J. (1978). Anim. Behav. 26, 368.
- TOATES, F. M. & O'ROURKE, C. (1978). Med. Biol. Eng. Comput. 16, 98.

APPENDIX A

We prove our statement that $O_{n,x}$ contains all information available to A to predict the behaviour of B. Let the sequence sampled by A be

$$y_1 = \theta + z_1^A, \dots, y_n = \theta + z_n^A; \qquad x = \frac{1}{n} \sum_{i=1}^n y_i$$

The conditional probability density for Θ given this sequence and that $T_B > n-1$ is

$$p(\theta|y_1, \dots, y_n, T_b > n-1) = \frac{p(\theta, y_1, \dots, y_n, T_B > n-1)}{p(y_1, \dots, y_n, T_B > n-1)}$$
$$= \frac{p(y_1, \dots, y_n|\theta) \operatorname{Pr} (T_B > n-1|\theta) \beta(\theta)}{\int_{-\infty}^{\infty} p(y_1, \dots, y_n|\theta) \operatorname{Pr} (T_B > n-1|\theta) \beta(\theta) d\theta}$$
(A1)

We have used small ps as a general notation for a probability function, e.g.

$$p(y_1, \dots, y_n, T_B > n-1) \, dy_1 \dots dy_n$$

= Pr (Y₁ \epsilon (y₁, y₁+dy₁), ..., T_B > n-1)

where Y_i is the stochastic variable $\Theta + Z_i^A$. Equation (A1) follows from Bayes' theorem and the observation that given $\Theta = \theta$ the stochastic processes representing A and B are independent. Using the fact that the variables Z_i^A are independent and normally distributed we get

$$p(y_1, ..., y_n | \theta) = \frac{1}{(2\pi\sigma^2)^{n/2}} \exp\left(-\frac{1}{2\sigma^2}(y_1 - \theta)^2\right) ... \exp\left(-\frac{1}{2\sigma^2}(y_n - \theta)^2\right)$$
$$= \frac{1}{(2\pi\sigma^2)^{n/2}} \exp\left(-\frac{n}{2\sigma^2}(x - \theta)^2\right) \exp\left(-\frac{1}{2\sigma^2}(y_1^2 + \dots + y_n^2 - nx^2)\right)$$

The last factor does not contain θ and thus cancels in the last member equation (A1):

$$p(\theta|y_1, \dots, y_n, T_B > n-1) = \frac{\exp\left(-(n/2\sigma^2)(x-\theta)^2\right) \Pr\left(T_B > n-1|\theta\right) \beta(\theta)}{\int_{-\infty}^{\infty} \exp\left(-(n/2\sigma^2)(x-\theta)^2\right) \Pr\left(T_B > n-1|\theta\right) \beta(\theta) \, d\theta}$$
(A2)

This shows that the conditional distribution of Θ depends on y_1, \ldots, y_n only trough x. But the information available to A to predict the behaviour of B is the knowledge of the distribution of Θ and the fact that B is still fighting. Thus $O_{n,x}$ contains that information.

APPENDIX B

Our numerical procedure to find the optimal strategy S' against a given strategy S is to choose a reasonable $U_n(x)$ for a large *n*-value (n = 100) and then to use iteration (8), at each step selecting the optimal S'_n as the solution to equation (10). For the iteration we first need to know the distribution of T_B . Put

$$g_n(\theta) = \Pr\left(T_B = n | \Theta = \theta\right). \tag{B1}$$

The $g_n(\theta)$ can be computed on a lattice of θ -values using a pseudo random number generator to simulate random walks. With similar calculations as those in Appendix A the quantities in equation (8) can now be explicitly expressed (the final formula is (B8)):

$$\Pr\left(T_{B}=n|O_{n,x}\right) = \frac{\int_{-\infty}^{\infty} p(X_{n}^{A}=x|\Theta=\theta) \Pr\left(T_{B}=n|\Theta=\theta\right) \beta(\theta) \, \mathrm{d}\theta}{\int_{-\infty}^{\infty} p(X_{n}^{A}=x|\Theta=\theta) \Pr\left(T_{B}>n-1|\Theta=\theta\right) \beta(\theta) \, \mathrm{d}\theta}$$
$$= \frac{\int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^{2}}{2\sigma^{2}/n}\right) g_{n}(\theta)\beta(\theta) \, \mathrm{d}\theta}{\int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^{2}}{2\sigma^{2}/n}\right) \left(1-\sum_{k=1}^{n-1} g_{k}(\theta)\right)\beta(\theta) \, \mathrm{d}\theta} \tag{B2}$$

$$= \int_{-\infty}^{\infty} p(X_{n+1}^{A} = z | X_{n}^{A} = x, \Theta = \theta) p(\Theta = \theta | O_{n,x}, T_{B} > n) d\theta$$

$$= \frac{\frac{(n+1)}{(2\pi\sigma^{2})^{1/2}} \int_{-\infty}^{\infty} \exp\left(-\frac{((n+1)z - nx - \theta)^{2}}{2\sigma^{2}}\right) \exp\left(-\frac{(x-\theta)^{2}}{2\sigma^{2}/n}\right) \left(1 - \sum_{k=1}^{n} g_{k}(\theta)\right) \beta(\theta) d\theta}{\int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^{2}}{2\sigma^{2}/n}\right) \left(1 - \sum_{k=1}^{n} g_{k}(\theta)\right) \beta(\theta) d\theta}$$

$$= \frac{\frac{(n+1)}{(2\pi\sigma^{2})^{1/2}} \exp\left(-\frac{n(n+1)(z-x)^{2}}{2\sigma^{2}}\right) \int_{-\infty}^{\infty} \exp\left(-\frac{(z-\theta)^{2}}{2\sigma^{2}/(n+1)}\right) \left(1 - \sum_{k=1}^{n} g_{k}(\theta)\right) \beta(\theta) d\theta}{\int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^{2}}{2\sigma^{2}/n}\right) \left(1 - \sum_{k=1}^{n} g_{k}(\theta)\right) \beta(\theta) d\theta}$$
(B3)

 $E(c \exp(-\Theta/2)|O_{n,x}, T_B > n)$

$$= \int_{-\infty}^{\infty} c \exp(-\theta/2) p(\Theta = \theta | O_{n,x}, T_B > n) d\theta$$
$$= \frac{\int_{-\infty}^{\infty} c \exp(-\theta/2) \exp\left(-\frac{(x-\theta)^2}{2\sigma^2/n}\right) \left(1 - \sum_{k=1}^{n} g_k(\theta)\right) \beta(\theta) d\theta}{\int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^2}{2\sigma^2/n}\right) \left(1 - \sum_{k=1}^{n} g_k(\theta)\right) \beta(\theta) d\theta}$$
(B4)

The presence of the possibly very small denominators in (B2-B4) causes a numerical problem. This can be taken care of by making the transformation

$$F_n(x) = \left(\frac{n}{2\pi\sigma^2}\right)^{1/2} \int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^2}{2\sigma^2/n}\right) \left(1 - \sum_{k=1}^{n-1} g_k(\theta)\right) \beta(\theta) \,\mathrm{d}\theta \, U_n(x).$$
(B5)

Defining

$$G_n(x) = \left(\frac{n}{2\pi\sigma^2}\right)^{1/2} \int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^2}{2\sigma^2/n}\right) g_n(\theta)\beta(\theta) \,\mathrm{d}\theta \tag{B6}$$

$$D_n(x) = \left(\frac{n}{2\pi\sigma^2}\right)^{1/2}$$
$$\int_{-\infty}^{\infty} c \, \exp\left(-\theta/2\right) \exp\left(-\frac{(x-\theta)^2}{2\sigma^2/n}\right) \left(1 - \sum_{k=1}^n g_k(\theta)\right) \beta(\theta) \, \mathrm{d}\theta \tag{B7}$$

we can write equation (8) as

$$F_{n}(x) = \begin{cases} \frac{1}{2} VG_{n}(x); & x \leq S'_{n} \\ VG_{n}(x) + \left(\frac{n(n+1)}{2\pi\sigma^{2}}\right)^{1/2} \int_{-\infty}^{\infty} \exp\left(-\frac{(z-x)^{2}}{2\sigma^{2}/n(n+1)}\right) F_{n+1}(z) \, \mathrm{d}z \quad (B8) \\ -D_{n}(x); & x > S'_{n} \end{cases}$$

This iteration works well numerically, since the integrands fall off rapidly so that a finite interval of integration can be used. Finally, the expected utility equation (7) is computed as

$$U(S',S) = \int_{-\infty}^{\infty} F_1(x) \, \mathrm{d}x - \int_{-\infty}^{\infty} c \, \exp\left(-\theta/2\right) \beta(\theta) \, \mathrm{d}\theta. \tag{B9}$$