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Evolution of Fighting Behaviour: The Effect of Variation in Resource Value

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A number of empirical studies have shown that animals adjust their fighting behaviour when resource value is changed. We apply evolutionary game theory to investigate how variation in resource value influences the evolution of fighting behaviour. Although no completely general predictions can be made concerning the cost of fighting and the probability of victory, for most situations of biological relevance the cost of fighting will increase when resource value increases and the probability of victory for an animal will increase when resource value is increased only to that animal. In order to study the effect of variation in resource value when differences in fighting ability exist and are assessed, sequential assessment games are developed for two situations. In the first situation, contestants do not know each other's subjective resource value. In the second situation, there is an owner-intruder asymmetry where the owner is better informed about the value of the resource than the intruder. The models give predictions for fight duration, cost, and probability of victory. The predictions are compared with empirical data, and a good qualitative agreement is found.

Introduction

Apart from fighting ability, resource value is likely to be the most important non-strategic variable in fighting behaviour, Resource value may vary among contests and animals for several reasons. For instance, the amount or quality of a resource may vary from contest to contest, internal physiological states (hunger, thirst, etc.) may vary among contestants, and contestants may vary in their information about a particular resource, leading to different estimates of its value. Intuitively we expect contestants to be more willing to take risks the higher is the value of the resource. We also expect an animal with more to gain to be more likely to win. Such relationships between fighting behaviour and resource value have been demonstrated in several studies (see the final section for references to this literature).

The aim of this paper is to analyse the action of selection on fighting behaviour in relation to variation in resource value. We will do so by applying evolutionary game theory (Maynard Smith, 1982). The effect of variation in resource value has been given some attention in game theory modelling of fighting behaviour. There has, however, been no systematic study of this matter, and several situations of biological importance have not been analysed. Some existing models also lack elements likely to be of importance in nature, in particular variation in fighting ability and assessment of fighting ability. In the first section of this paper we outline the problem in some detail and identify situations of biological interest. In parallel,

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we discuss existing models of contest behaviour dealing with resource value. After that, we consider some general properties of ESS's for games with variation in resource value. We then study the joint effect of variation in resource value and variation in fighting ability in two examples of sequential assessment games (Enquist & Leimar, 1983; Leimar & Enquist, 1984). The first example can be regarded as an extension of the war of attrition with random rewards (Bishop *et al.*, 1978) to cases where differences in fighting ability exist and are assessed by the contestants. The second example deals with owner-intruder interactions where the amount (or quality) of the resource varies from contest to contest, but only the owner is informed about the particular amount. Finally, we discuss the qualitative predictions from game theory models on the effect of variation in resource value in relation to empirical studies.

Informational Situations in Games With Variation in Resource Value

For most game theory models of fighting behaviour developed the utility (U) for an animal of using a given strategy in a contest situation can be written as

$$U = pV - C$$

where p is the probability of winning, V the value of the resource, and C the cost of an interaction. The value of the resource might depend on factors like properties of the resource, the physiological state of the animal, and the expected availability of the particular type of resource in space and time. We will sometimes refer to the value that the resource represents to an animal as subjective resource value, to indicate that resource value depends on internal factors like the animal's physiological state and information about the environment, and may thus vary among contestants.

In the expression for the utility given above one assumes that V does not depend on the animal's strategy. This form for the utility has the advantage of mathematical simplicity but does not describe all cases that could occur in nature. For instance, an animal's use of strategy could affect the probability of injury and thus its ability to utilize the resource. Another example which requires a different expression for the utility is the information asymmetric owner-intruder conflict analysed below.

When analysing how selection will act on fighting behaviour in situations with variation in resource value, one must consider the informational situation in detail i.e. what information is available to the animal, prior to and during the contest, about the value of the resource and about the opponent's use of strategy. We can indentify several situations of biological importance. When subjective resource value only depends on factors, typically properties of the resource, equally available to both contestants, there will be no uncertainty about which local strategy an opponent will use (with respect to subjective resource value). This case has the property that each resource value is an independent game, and the effect of variation in resource value can be analysed by determining ESS's for different resource values. This has been done in several studies, yielding the result that the cost of an interaction tends to increase when resource value increases (e.g. Maynard Smith, 1982; Enquist & Leimar, 1983).

The situation will be different if some factors influencing subjective resource value cannot be observed by an opponent. This might be the case when subjective resource value is determined by physiological states or depends on information about the resource gained prior to the interaction. An animal that does not "know" exactly the opponent's subjective resource value will, for a given prior information about the opponent, play against opponents differing in subjective resource value, and thus probably in the use of local strategy, according to some probability distribution. This also means that an individual's own use of strategy may not be perfectly "known" to an opponent. Note that an animal's subjective resource value *per se* has no economic consequences for an opponent. Even if subjective resource value varies, the use of strategy might not.

One attempt to investigate a case where an individual in unaware of the opponent's subjective resource value is the war of attrition with random rewards (Bishop *et al.*, 1978). In this game each contestant's resource value is independently drawn from some distribution of resource values. Variation in fighting ability and transmission of information about fighting ability during a contest are not incorporated into the model. The main qualitative predictions from an ESS of this game are that an animal with higher resource value will always win (at equal values the probability of winning is 0·5), and the cost and duration of a contest will increase if the value of the resource to the contestants increases.

If there is a role asymmetry, such as an owner-intruder asymmetry, additional elements are introduced. There may be differences between roles with respect to fighting ability, subjective resource value, and available information (information asymmetry). The role asymmetry *per se* can also influence the choice of local strategy, thus introducing a conventional element (Maynard Smith & Parker, 1976; Maynard Smith, 1982; Leimar & Enquist, 1984).

For a role asymmetry with subjective resource value being determined by the role, there will be no uncertainty about an opponent's local strategy, and the informational situation is thus similar to the first one discussed above. The effect of resource value is analysed by determining ESS's for pairs of resource values. This type of situation was studied by Maynard Smith & Parker (1976) by incorporating a role asymmetry into the war of attrition and considering that the value of the resource may be unequal for the two roles. They concluded that a conventional settlement will be stable, i.e. that the individual in one of the roles will get the resource without a fight. The winning role could be either the high resource value role, referred to as a "common sense" ESS, or the low resource value role, referred to as a "paradoxical" ESS, but they argue that a paradoxical ESS is unlikely to appear in evolution. Hammerstein & Parker (1982) made the further assumption that animals may make mistakes about what their role is and obtained a unique ESS for this game. With this ESS, an individual in the high resource value role will win most contests. If the value of the resource to either role is increased, the contests will tend to be longer and more costly.

A similar but more realistic situation was studied by Leimar & Enquist (1984) using a sequential assessment game with a role asymmetry. In a sequential assessment game, contestants may vary in fighting ability, and information about the relative fighting ability is obtained by the contestants during a fight. If the value of the resource is higher for one role (the favoured role), the common sense ESS for this game has the property that an individual in the favoured role will be more persistent in fighting than an individual in the other role, so that the favoured role will win most fights. If the disparity in resource value between the roles is not too great, the game also has a paradoxical ESS where the favoured role is less persistent; however, such an ESS has a small basin of attraction. An increase of the resource value for either role has the effect, both for the common sense and the paradoxical ESS, that that role wins more fights.

An individual's subjective resource value might not be completely specified by the role. An interesting situation of this kind is an information asymmetry, i.e. when the individual in one role has more information. This could be the case in many owner–intruder interactions, since the owner may be better informed about the resource than the intruder (Sigurjónsdóttir & Parker, 1981).

General Properties

A common, although not universal, finding for games with variation in resource value is that an ESS will prescribe more costly strategies when resource value increases. The increased cost may result from increased persistence of the animal and/or from the use of more costly behaviour patterns. For instance, in the Hawk-Dove game (Maynard Smith & Parker, 1976) where the ESS is to play Hawk with probability q and Dove with probability $1-q$ (the Hawk strategy is more costly than the Dove strategy), increasing the resource value will change the ESS so that q increases until $q=1$. On the other hand, if there is a role asymmetry with resource value being determined by the role and if the subjective resource value to one role is increased, an ESS may change in such a way that the cost of an interaction decreases (Leimar & Enquist, 1984). The reason for this is that, although the favored role increases in persistence, the other role may become cautious and even decline to fight.

In order to clarify to what extent the effects of variation in resource value that are suggested by theoretical models and empirical results are general consequences of evolutionary game theory, we will consider three different (and somewhat idealized) informational situations. First, in a symmetric situation where resource value is the same for both contestants, each resource value results in an independent game. Let $S(V)$ be an ESS for the game when resource value is V and assume that $S(V)$ varies gradually with V. One would expect that the cost of a contest where $S(V)$ meets itself should increase with V. However, from game theory alone it is not possible to derive such a result. What can be shown is that if $S(V)$ has the additional property of continuous stability, it will become more "daring" as V increases (the concept of a continuously stable strategy was introduced by Eshel (1983) and entails that if a population uses a strategy that is close to the ESS, then evolution tends to move the population closer to the ESS). Namely, in a contest between $S(V_1)$ and $S(V_2)$ with V_1 slightly greater than V_2, $S(V_1)$ will win more than half the fights and take a higher cost than $S(V_2)$ against itself, i.e. $S(V_1)$ is more effective and more costly than $S(V_2)$ in contests against $S(V_2)$. See Appendix

A for a derivation of this result. If the mechanisms of interaction are such that a more effective and costly strategy will impose a higher cost on the opponent, it follows that $S(V_1)$ is more costly against itself than $S(V_2)$ against itself, and most aggressive interactions in nature clearly seem to be of this kind, but there may be exceptions to this.

Second, consider contests with a role asymmetry and with resource value being determined by the role. Let V^A and V^B be the resource values (A and B denote the roles) and S^A and S^B the local strategies that yield an ESS for the game with these resource values. As already mentioned, no general prediction as to changes in costs when the resource value to one role is increased can be made. Concerning probabilities of winning, one would intuitively expect that if, say, V^A is increased, then role A should win more fights. This, however, does not follow generally from evolutionary game theory. Proceeding as in Appendix A, assuming continuous stability, one can show that role A becomes more "daring" as V^A increases, but in principle it is possible that role B also becomes more "daring", leading to a decrease in the number of fights won by role A. Since we have not found any biologically realistic situation where this happens, we will not go into details. In conclusion, when resource value to one role is increased, the typical consequence is that that role will win more fights, but there might be exceptions where the opposite is true.

Third, consider a case where there is variation in subjective resource value among contestants but no correlation between the resource values of a pair of contestants. Assume in addition that the only means by which an individual can get information about an opponent's use of local strategy based on subjective resource value is to observe the opponent's behaviour during a contest. It is then possible to give general predictions regarding changes in probabilities of winning and costs when an ESS prescribes variation in local strategies as subjective resource value varies. Namely, if an increase in subjective resource value results in the use of a different local strategy, then both the probability of winning and the cost of an interaction will increase. A proof of this statement is given in Appendix B (see Enquist *et al.* (1985) for a graphical demonstration).

In the following, we will give two examples of sequential assessment games with variation in resource value. For both these examples, the informational situation will be of the third type above.

The Sequential Assessment Game With Variation in Resource Value

A sequential assessment game models a contest that proceeds in steps, each step entailing a certain cost or risk for a contestant. Contestants vary in their ability to inflict and avoid costs during a fight, i.e. in their fighting ability. Prior to an interaction, a pair of competing individuals have poor information about their relative fighting ability, but during the interaction they gain more information and use this information to decide whether to give up or to continue fighting.

Subjective resource value may vary among contestants. There might be a positive correlation between the subjective resource values (prior to a contest) of two contestants, and in that case an individual could gain information about an opponent's subjective resource value (and choice of local strategy) from its own subjective resource value. In order to simplify the contest situation, we assume that no such correlation is present. Furthermore, we assume that an individual can get information about an opponent's subjective resource value only through observation of the opponent's behaviour during an interaction. Such observation of the opponent can result in changes in an individual's subjective resource value during a contest by providing information about the resource. In principle, an individual could also gain information about the resource through direct observation of the resource during the interaction, but we neglect this possibility.

We now give a short presentation of the variables and parameters in a sequential assessment game (for more details, see Enquist & Leimar (1983), Leimar & Enquist (1984), and Appendix C). Denote a pair of opponents by A and B, and let c_A and c_B be the costs per step for A and B, respectively. It is important for, say, A to estimate both these costs, and in order to reduce the number of variables that are estimated during the fight, we assume that the relation $c_A c_B = c^2$ holds with the same c for all pairs of contestants (the parameter c measures how costly the mechanisms of interaction that make up a step in the contest are). Only one variable then remains to be estimated by the contestants, and we choose that variable as $\theta = \theta_{AB} = \ln(c_B/c_A)$. θ is referred to as the relative fighting ability, and it has the property that $\theta_{AB} = -\theta_{BA}$. Prior to a fight, contestants only have limited information about the relative fighting ability, and this information can be expressed as a prior distribution, $\beta(\theta)$, of the relative fighting ability (in the examples we give below, $\beta(\theta)$ is the same for all contestants and is symmetric around $\theta = 0$). At each step of the fight, A assesses θ_{AB} and B assesses θ_{BA}. There is some inaccuracy in these assessments, and the errors of observation for A and B are assumed to be independent and normally distributed with mean zero and standard deviation σ. As the fight progresses, the contestants can get better estimates of θ by forming the average of the observations obtained so far; let x_n^A and x_n^B be the average of the n first observations by A and B, respectively.

We use the term local strategy to denote a contestant's decision rule given the information that is available prior to the contest. Of greatest interest is prior information that may vary among contestants, and here we will only take into account subjective resource value and, for contests with a role asymmetry, the role. A global strategy then consists of a local strategy for each subjective resource value (prior to the start of a contest) and, when appropriate, role. We only consider local strategies where a decision whether or not to continue interacting is based on the average, x_n, of the so far obtained samples of relative fighting ability and on the number, n, of samples taken. Specifically, a local strategy S is given by a level (switching point) S_n for each n; if x_n goes below S_n the player gives up at step n. In a two-dimensional causal factor space with x and n as casual factors, A's and B's local strategies are given by switching lines, and a fight can be represented as the random motion of A's and B's trajectories, x_n^A and x_n^B, through this space. A fight ends when one of the trajectories crosses the corresponding switching line and that individual gives up (if both individuals cross simultaneously, one of them is randomly assigned as winner).

A numerical iteration is used to find ESS's for the game: starting from an initial strategy, a sequence of best replies are computed until convergence to an ESS is obtained. More details on this procedure are given in Appendix C. The procedure does not guarantee that all ESS's for the game will be found, but ESS's having a large basin of attraction can be found in this way, and such ESS's are the most likely ones to appear in evolution.

The informational situation with respect to subjective resource value delineated above makes it possible to apply the theorem in Appendix B. Thus, if an ESS specifies different local strategies for different subjective resource values, the probability of winning and the cost of an interaction will increase with an individual's subjective resource value. For a sequential assessment game, it is possible to extend this result somewhat. Consider the local strategies (switching lines):

$$S' = (S'_1, S'_2, \ldots), \qquad S'' = (S''_1, S''_2, \ldots).$$

If $S'_n < S''_n$ for all n we say that S' is more persistent than S''. Using the theorem in Appendix B one can show that if an ESS has the property that different local strategies are used as subjective resource value varies, then progressively more persistent local strategies will be used as subjective resource value increases.

First Example: Sequential Assessment Game With Random Rewards

We now consider contests between animals that vary in fighting ability according to some distribution and independently vary in subjective resource value according to some other distribution. Two contesting animals are to be independently drawn from these distributions. There is no role asymmetry, and the only information an individual has about an opponent prior to an interaction is that the opponent is drawn from the above mentioned distributions. As a contest proceeds, an individual will get information about the opponent's subjective resource value, but this information is assumed not to change the individual's own subjective resource value. This contest situation might correspond to contests over food items with variation in subjective resource value being due to varying degrees of hunger.

To give an example of an ESS for this situation, we have analysed a case with a discrete distribution of subjective resource values with 11 classes ranging from $V = 0{\cdot}5$ to $V = 1{\cdot}5$ with increment $0{\cdot}1$ and with the same relative frequency for each class. The prior distribution of relative fighting ability ($\beta(\theta)$) is normal with mean zero and standard deviation $0{\cdot}5$. The standard deviation of the sampling error (σ) is put to $0{\cdot}5$ and the cost parameter (c) is $0{\cdot}05$. We have found only one ESS for the game. This ESS is shown in Fig. 1 as switching lines representing local strategies for each subjective resource value.

Note from Fig. 1 that the local strategies have the property that the level (S_n) where one gives up becomes higher as n increases; this is related to the fact that a contestant's estimate of relative fighting ability becomes more accurate as the interaction proceeds. It is also clear that animals with higher subjective resource value are more persistent.

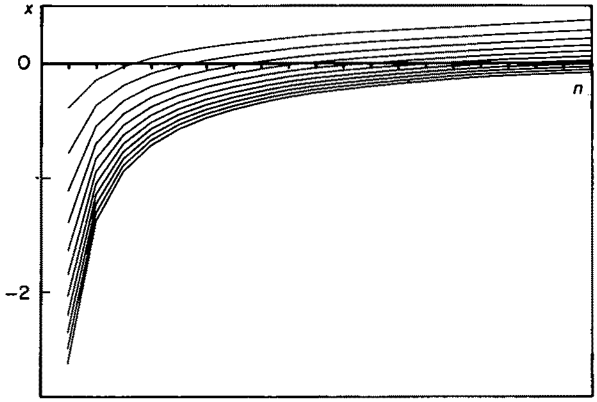

FIG. 1. An ESS for a sequential assessment game with random rewards (first example in the text). The ESS is shown as local strategies (switching lines), one for each subjective resource value. During a fight, an individual uses its estimate of relative fighting ability (x) at the current step (n) to make decisions. The individual continues fighting as long as x is above the switching line (and the opponent continues). Subjective resource value varies from 0·5 to 1·5 with increment 0·1. The topmost line corresponds to $V=0{\cdot}5$, and as V increases the lines move downwards to the bottommost line corresponding to $V=1{\cdot}5$.

The increase in persistence with subjective resource value has a number of consequences. For instance, an individual with higher V than the opponent will on average (with respect to relative fighting ability) win more than half the interactions. Considering contests of individuals with a given V against the population, the probability of winning will increase with V. Furthermore, both fight duration and cost increases when an individual's and/or an opponent's V increases. Further consequences of variation in persistence are that for contests where an individual, A, has a greater V than an opponent, B, the longest contests will be those where

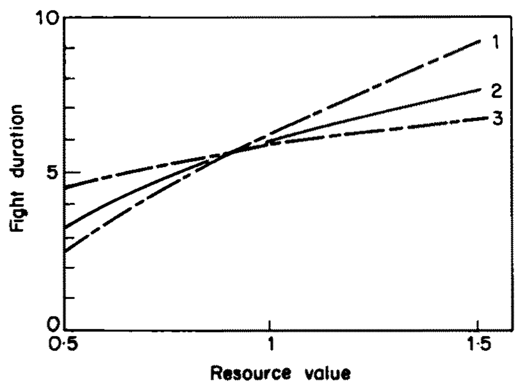

FIG. 2. Expected fight duration for an individual, as a function of the individual's subjective resource value, for the ESS of the sequential assessment game with random rewards shown in Fig. 1. Curve 1 refers to fights lost by the individual, curve 2 to all fights, and curve 3 to fights won by the individual.

B is slightly stronger, and contests won by B will tend to be longer than those won by A. In Fig. 2 we illustrate how this affects the expected length of contests between an individual with subjective resource value V and a random opponent.

If the cost of acquiring information about relative fighting ability is decreased, either by decreasing σ or c, the ESS changes so that the switching lines come closer together in the causal factor space. The effect of this will be that the outcomes of fights will be more determined by relative fighting ability than by asymmetries in subjective resource value. Increasing σ and/or c will have the reverse effect of instead spreading out the switching lines more, but for sufficiently large σ or c the ESS changes qualitatively, and individuals with small V will decline to fight (e.g. this will happen if σ is increased to 1·0 in our example). Increasing the range of variation of subjective resource value in the population or decreasing the range of variation of relative fighting ability has a similar effect on the ESS, making the outcomes of fights more determined by asymmetry in subjective resource value than asymmetry in fighting ability.

Second Example: Information Asymmetry

A common contest situation where one can expect information asymmetries is an owner–intruder interaction. The owner, having spent some time at the resource, will often be better informed about the resource than the intruder. To study this, let us consider a situation where there are no differences among animals regarding their physiological state, but where the amount of resource varies among contests. The owner knows the exact value of the resource, whereas the intruder does not have this information. For a sequential assessment game, this means that the intruder can base its decisions only on two causal factors (apart from the role), namely, estimate of relative fighting ability (x) and fighting time (n). An owner can, however, also base its decisions on the value of the resource. Thus, there will be only one local strategy with respect to resource value for intruders, whereas there might be one for each amount of resource for owners. This does not mean that the intruder will get no information about the resource during a fight, but that this information will come only through estimate of relative fighting ability and fighting time. For simplicity, we will in our example exclude several other asymmetries that are likely to occur in nature (for instance, differences in average fighting ability between owners and intruders; see Leimar & Enquist (1984)). Note that in this case the expected resource value for the intruder depends on the intruder's strategy. A cautious intruder only wins resources of low value whereas a persistent intruder also wins valuable resources.

We have analysed a case with a discrete distribution of amount of resource with eleven classes corresponding to resource values varying from $V=0{\cdot}5$ to $V=1{\cdot}5$ with increment 0·1 and with equal frequency for each class. The prior distribution of relative fighting ability ($\beta(\theta)$) is normal with standard deviation 0·5 and other parameter values are $\sigma=1{\cdot}5$ and $c=0{\cdot}05$. Only one ESS was found, and this ESS is shown in Fig. 3 (we were not able to find alternative ESS's, as for instance something like a paradoxical ESS).

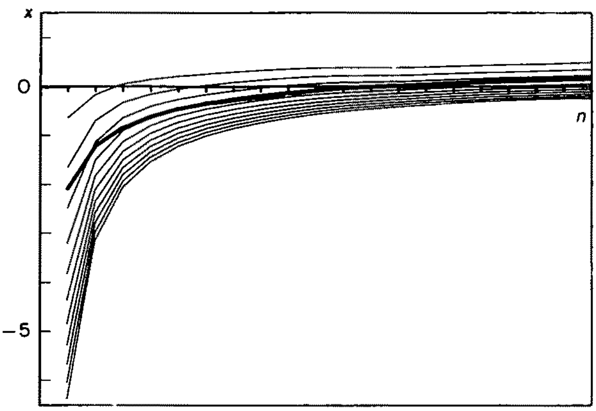

FIG. 3. An ESS for an owner–intruder game with information asymmetry (second example in the text). The ESS is shown as switching lines: the heavy line is the intruder's strategy, and the light lines are the owner's local strategies (one for each amount of resource). Resource value varies from 0·5 to 1·5 with increment 0·1. The topmost fine line corresponds to resource value $V=0{\cdot}5$ (for the owner), and as V increases, the owner becomes more persistent.

As shown, the owner will become more persistent as the value of the resource increases. This has the effect that the intruder, not having perfect information about the resource, tends to win the "wrong" fights. The intruder will take over most of the resources of low value but few of the resources of high value (see Fig. 4). This is further demonstrated in that the owner will win no more than 55% of the interactions, but the overall utility for an owner is 0·26 (ranging from 0·02 for $V=0{\cdot}5$ to 0·57 for $V=1{\cdot}5$) compared to only 0·10 for intruders.

The shape of the intruder's switching line differs from the owner's lines in that it is more flat (see Fig. 3). This is connected to the fact that there is information about resource value in the owner's behaviour. From the intruder's point of view,

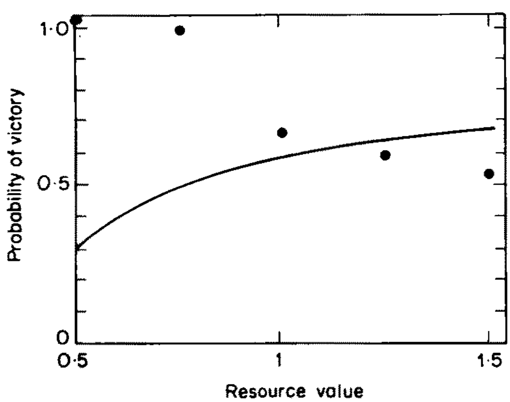

FIG. 4. The curve illustrates the probability that the owner wins as a function of resource value with the ESS for the owner–intruder game with an information asymmetry shown in Fig. 3. For comparison, data for an owner–intruder game with an uncorrelated role asymmetry (no information asymmetry) are given as dots.

the proportion of owners defending a valuable resource will increase with n, since these owners are the least likely to give up, and thus the intruder's expected resource value will increase with n. The intruder's estimate of relative fighting ability also affects the expected resource value. If an intruder has estimated a high x and the owner continues fighting, the owner is likely to be using a persistent local strategy, i.e. to defend a valuable resource. The intruder's expected resource value as a function of n and x is illustrated in Fig. 5.

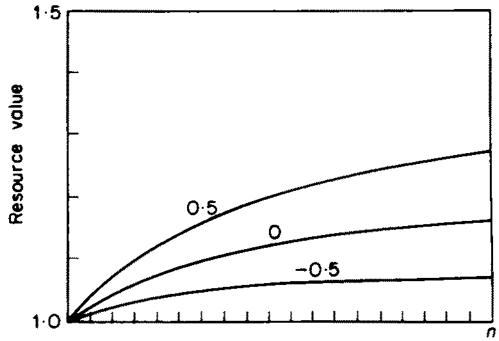

FIG. 5. The intruder's expected resource value as a function of fighting step (n) and estimate of relative fighting ability (x) for the ESS for the owner-intruder game with an information asymmetry shown in Fig. 3. The three curves refer to three particular x-values.

The ESS determined for the present situation, role asymmetry with an associated information asymmetry, yields several predictions that can be tested: (i) the owner's probability of winning will increase with resource value, (ii) fight duration will increase when resource value increases, (iii) the cost of a contest (both for owners and intruders) will increase with resource value, and (iv) when resource value increases fight duration will increase faster in fights leading to take-overs than in fights not leading to take-overs. Predictions (i) and (iii) follow from the theorem in Appendix B and (ii) is selfevident from the local strategies depicted in Fig. 3. Prediction (iv) is less obvious intuitively, and we have no general proof. A numerical illustration of this prediction for our example is given in Fig. 6 (cf. Fig. 2).

It might be of some interest to compare the example given here with a situation where the intruder is fully informed about the value of the resource. Such a situation with an uncorrelated role asymmetry was studied in Leimar & Enquist (1984) (the same parameter values were used). For the uncorrelated role asymmetry, an ESS was found with the property that one role (which we arbitrarily refer to as owner) was more persistent. A qualitative difference from a situation with information asymmetry is that for an uncorrelated role asymmetry, the owner's probability of winning will decrease with resource value (illustrated in Fig. 4). This is due to a weaker impact of the uncorrelated role asymmetry when resource value is high.

If we modify our example with an information asymmetry so that also the owner is unaware to the exact value of the resource (subjective resource value will then

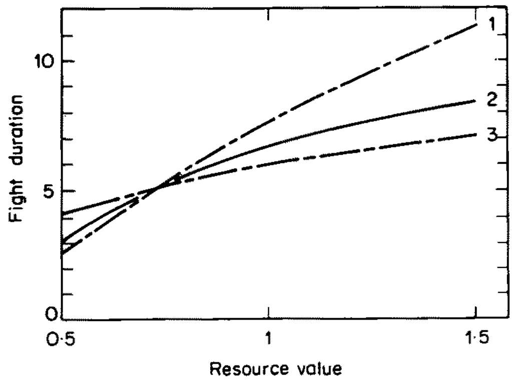

FIG. 6. Expected fight duration as a function of resource value for the ESS for the owner–intruder game with an information asymmetry shown in Fig. 3. Curve 1 refers to fights won by the intruder, curve 2 to all fights, and curve 3 to fights won by the owner.

be 1·0 both for owners and intruders) we obtain a situation with an uncorrelated role asymmetry. Intuitively, it would seem that such a situation is less asymmetric and more favourable to intruders than when owners are more informed about the resource. However, comparing the owner's probability of winning and overall utility between the information asymmetric case studied here and the situation with an uncorrelated role asymmetry studied in Leimar & Enquist (1984), one obtains that the owner has a higher probability winning and a higher utility with the ESS for the uncorrelated role asymmetry. This indicates that information asymmetry per se has a rather small importance when it comes to explaining why in nature owners tend to win most owner–intruder interactions. It also shows that intuition can sometimes be a poor guide to the solution of game theory problems.

Comparison With Empirical Data

Effects of resource value on contest behaviour have been demonstrated in several studies, and we now discuss to what extent results from such studies are in agreement with predictions from game theory. The behavioural parameters usually analysed in relation to variation in resource value are fight duration, frequencies of various behaviour patterns, and, in asymmetrical situations probability of victory. The data we have found in the literature on relationships between these variables and resource value are summarized in Table 1.

In those studies where they have been analysed, both fight duration and the frequency of potentially dangerous behaviour patterns (offensive behaviour in Table 1) increase when resource value increases. The cost of fighting has been measured directly in a study of male bowl and doily spiders competing for females (Austad, 1983). The cost was estimated as the relative frequency of fatal injuries, and was shown to increase with the value of the female. The results on fight duration and use of offensive behaviour patterns in Table 1 also suggest that the cost of fighting

TABLE 1

Empirical data on the relationship between subjective resource value and fighting behaviour

Species	Resources	Variable	Effect of subjective resource value on† Fight duration	Offensive behaviour	Probability of victory	Reference
A hermit crab	food	time of deprivation			+	Hazlett, 1966
A spider crab	food	time of deprivation			+	Hazlett & Estabrook, 1974
A cray fish	food	time of deprivation		+	+	Hazlett *et al.*, 1975
Funnel web spider	web	quality of web site	+	+	owner+	Riechert, 1979, 1984
Bowl and doily spider	female	copulation time	+		owner+	Austad, 1983
A digger wasp	nesting burrow	no. of katydids provisioned	+		+	Dawkins & Brockman, 1980
Dung fly	female	copulation time	+		owner+	Sigurjonsdottir & Parker, 1981
Dung fly	female	female size (fecundity)	+		owner−	Sigurjonsdottir & Parker, 1981
Red-spotted newt	female	female size (fecundity)	+			Verrell, 1986
Iguana	nesting burrow	depth of burrow		+	owner+	Rand & Rand, 1976
Fulmar	food	time feeding		+	+	Enquist *et al.*, 1985
Bald eagle	food	time feeding		+	+	Hansen, 1986
Grey-breasted silver eye	food	time feeding			+	Kikkava, 1968
Starling	food	no. of nestlings		+		Kacelnik, pers. com.
Starling	food	expected delivery from a feeder		+	+	Kacelnik, pers. com.
White rat	food	time of food deprivation			+	Bruce, 1941
Red deer	harem	size of harem	+			Clutton-Brock *et al.*, 1979
Red deer	harem	receptivity of females	+			Clutton-Brock *et al.*, 1979
Common shrew	feeding site	expected food availability			+	Barnard & Brown, 1984
House cat	food	time of food deprivation		+		Cole & Shaffer, 1966
Chimpanzee	food	time of food deprivation			+	Nowlis, 1941

† Increase: +, decrease: −.

increases when resource value increases. The studies in Table 1 also show that when the subjective resource value of one of the contestants increases (without a similar increase for the opponent) then that individual will win more often.

The model of owner–intruder conflicts with an information asymmetry presented in the previous section yeilded four predictions. Several studies of contests with an information asymmetry between owner and intruder support these predictions (these studies are also included in Table 1).

Rand & Rand (1976) studied female iguanas competing for nesting burrows, a situation in which the owner was likely to be better informed about the value of the resource than the intruder. They showed that the intruder's probability of winning declined with resource value (prediction (i)) and that the resident's choice of action was related to the resource value but the intruder's was not.

In Riechert's (1979, 1984) study of competition for web sites in the funnel-web spider, an owner was better informed than an intruder about the quality of the web-site, i.e., the rate at which suitable prey arrive at the site. Her results agreed with predictions (i), (ii), and (iii).

Sigurjónsdóttir & Parker (1981) studied fights between male dungflies, where a challenging male attempted to displace a copulating male. A copulating male seemed able to estimate how many eggs remained to be fertilized (resource value) at the time of the struggle, and adjusted his behaviour according. The results supported predictions (i), (ii), and (iv). This study is interesting since there was also another factor influencing resource value, namely the total number of eggs produced by the female. The total number of eggs is correlated with female body size, and this information is available to the challenger as well as to the paired male. The study showed that the owner's probability of winning decreased with female size. This result may in part be due to effects of female size on the owners positional advantage, but the informational situation could also lead to more takeovers of bigger females (cf. Fig. 4).

Austad (1983) studied the bowl and doily spider in a situation where a challenging male tried to displace a copulating male. An owner seemed to use the time he had been mating with the female to estimate how many eggs were left to be fertilized (resource value), but the intruder did not have this information. Austad's results support predictions (i) and (iii).

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APPENDIX A

Consider contests with no role asymmetry and the same resource value for both contestants. Let $S(v)$ be a curve through the space of strategies, parametrized by v, with the property that $S(v)$ is an ESS when the value, V, of the resource is equal to v. Let $p(v, w)$ and $C(v, w)$ be, respectively, the probability of winning and the cost for $S(v)$ in a contest against $S(w)$. We will show that if $S(V)$ is continuously stable then $p(v, w)$ and $C(v, w)$ will increase with v at $v = w = V$.

When the value of the resource is equal to V, the utility of $S(v)$ against $S(w)$ is $U(v, w) = p(v, w)V - C(v, w)$. For $S(V)$ to be an ESS, it is necessary that

$$\frac{\partial U}{\partial v} = \frac{\partial p}{\partial v} V - \frac{\partial C}{\partial v} = 0 \tag{A1}$$

at $v = w = V$. Equation (A1) holds identically in $V(v = w = V)$ for some interval of

V-values. Taking the derivative of equation (A1) with respect to V, one obtains that

$$\frac{\partial p}{\partial v}+\frac{\partial^2 p}{\partial v^2}V+\frac{\partial^2 p}{\partial v\,\partial w}V-\frac{\partial^2 C}{\partial v^2}-\frac{\partial^2 C}{\partial v\,\partial w}=0$$

or

$$\frac{\partial p}{\partial v}=-\left[\frac{\partial^2 U}{\partial v^2}+\frac{\partial^2 U}{\partial v\,\partial w}\right] \tag{A2}$$

at $v=w=V$. According to Eshel (eqn (5) in Eshel (1983)), a necessary condition for $S(V)$ to be continuously stable is that

$$\frac{\partial^2 U}{\partial v^2}+\frac{\partial^2 U}{\partial v\,\partial w}\leq 0 \tag{A3}$$

at $v=w=V$. From (A1), (A2), and (A3) one then obtains that

$$\frac{\partial p}{\partial v}\geq 0 \quad\text{and}\quad \frac{\partial C}{\partial v}\geq 0 \tag{A4}$$

at $v=w=V$.

It seems reasonable to interpret (A4) as expressing that the strategy $S(V)$ becomes more "daring" as V increases. In order to show that $C(V, V)$ increases with V one also needs information on the dependence of $C(v, w)$ on w, but such information cannot be obtained from game theory. However, as far as is known, aggressive interactions in nature are of the kind where a more effective and costly strategy will impose a higher cost on the opponent, and if that is the case then $C(V, V)$ will increase with V.

APPENDIX B

If a contest situation with variation in subjective resource value has the property that, given an individual's local strategy, the probability of winning and expected cost are independent of V, one can express the utility of using the local strategy s when resource value is V as

$$U(V, s)=p(s)V-C(s). \tag{B1}$$

The contest situation could be either at the beginning of a fight or at some later stage. In order for (B1) to apply, an individual must contest against the same distribution of opponents, regardless of own subjective resource value.

Consider a pair of subjective resource values, V_1 and V_2, with $V_1>V_2$. Assume that s_i satisfies

$$U(V_i, s_i)=\max\,[U(V_i, s)], \qquad i=1,2 \tag{B2}$$

where the maximum is over the class of local strategies that are appropriate for the contest situation. We now prove the following statements for an optimal strategy, and thus for an ESS

$$p(s_1) \geq p(s_2) \tag{B3}$$

$$C(s_1) \geq C(s_2) \tag{B4}$$

$$p(s_1) > p(s_2) \quad \text{if and only if } C(s_1) > C(s_2). \tag{B5}$$

From (B2) one obtains that $U(V_1, s_1) \geq U(V_1, s_2)$ and $U(V_2, s_1) \leq U(V_2, s_2)$. Subtracting the second of these inequalities from the first one obtains with (B1) that

$$p(s_1)[V_1 - V_2] \geq p(s_2)[V_1 - V_2].$$

Since $V_1 - V_2$ is positive, (B3) follows. Using again that $U(V_2, s_1) \leq U(V_2, s_2)$, one obtains with (B1)

$$C(s_1) - C(s_2) \geq [p(s_1) - p(s_2)]V_2,$$

which together with (B3) yields (B4). This inequality also gives the "only if" part of (B5), and the "if" part follows similarly from $U(V_1, s_1) \geq U(V_1, s_2)$. Finally, if $p(s_1) = p(s_2)$ and $c(s_1) = c(s_2)$ then, although s_1 might differ from s_2, from an economic point of view they are identical in this contest situation, and nothing more can be said.

APPENDIX C

A brief description of the procedure used to determine ESS's for the sequential assessment games studied in this paper will be given. This procedure is very similar to the one used in Enquist & Leimar (1983) and Leimar & Enquist (1984), and the reader is referred to these papers for further details.

The relative fighting ability between individual A and individual B is regarded as a stochastic variable, denoted Θ, with probability density β. At step i, A observes $Y_i^A = \Theta + Z_i^A$, and B observes $Y_i^B = -\Theta + Z_i^B$, where Z_i^A and Z_i^B (the errors of observation) are independent and normal with mean zero and standard deviation σ. The two players' successive estimates of their relative fighting ability are represented as two stochastic processes, X_n^A and X_n^B, where X_n^A is the average of the n first Y_i^A and similarly for X_n^B.

An individual's strategy is given by a collection of switching lines (local strategies), one for each subjective resource value (only discrete distributions of subjective resource value will be considered). Denote B's switching lines by S^m ($m = 1, \ldots, M$), and let α_m be the prior probability that B uses S^m. We wish to compute the best reply for A to B's strategy. This will be done by computing A's best switching line separately for each initial subjective resource value for A. Let $\bar{V}$ denote a particular initial subjective resource value for A and let S' be the corresponding best local strategy for A. The choice of local strategy by B might contain information about the resource for A, and one can regard A's subjective resource value as a stochastic variable, V, which takes the value V_m when B uses S^m. A's initial subjective resource value then becomes $\bar{V} = \sum_m V_m \alpha_m$.

Introduce the stopping time T_B^m as the first fighting step for which $X_n^B \leq S_n^m$, and define the stopping time T_B as equal to T_B^m when B uses S^m $(m = 1, \ldots, M)$. Consider the following event (A's observation at step n): $O_{n,x} = \{X_n^A = x,\ T_B > n-1\}$. A must decide whether to give up or continue without yet knowing B's decision at this step. This decision should be made so that A's utility is maximized. Let $U_n(x)$ denotes A's utility given the observation $O_{n,x}$. From the relation $c_A c_B = c^2$ it follows that the cost per step for A is $c_A = c\exp(-\Theta/2)$. It is now possible to set up an iteration for $U_n(x)$

$$U_n(x) = \begin{cases} 0{\cdot}5E(V|O_{n,x}, T_B = n)\Pr(T_B = n|O_{n,x}); & x \leq S'_n \\ E(V|O_{n,x}, T_B = n)\Pr(T_B = n|O_{n,x}) + \left[\int_{-\infty}^{\infty} U_{n+1}(z)\gamma_n(z|x)\,\mathrm{d}z \right. & \\ \left. \quad - E(c\exp(-\Theta/2)|O_{n,x}, T_B > n)\right]\Pr(T_B > n|O_{n,x}); & x > S'_n \end{cases}$$

where $\gamma_n(z|x) = p(X_{n+1}^A = z|O_{n,x}, T_B > n)$ (p denotes a probability density). As this iteration proceeds from high n-values downwards, S'_n is determined so that $U_n(x)$ is maximized (this can be done since there is a unique intersection between the upper and lower members of the above equation, viewed as functions of x).

The numerical procedure used to determine the optimal S' is to assume a reasonable $U_n(x)$ for a large n and then to iterate downwards. The distribution of T_B is needed for the iteration. Put

$$g_{n,m}(\theta) = \Pr(T_B^m = n|\Theta = \theta)$$

and

$$g_n(\theta) = \Pr(T_B = n|\Theta = \theta) = \sum_m g_{n,m}\alpha_m.$$

These distributions can be obtained by simulating random walks. A numerically more convenient form of the above iteration is obtained by making the transformation

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

With calculations very similar to the ones given in Enquist & Leimar (1983), the iteration then becomes

$$F_n(x) = \begin{cases} 0{\cdot}5 \sum_{m=1}^{M} V_m G_{n,m}(x)\alpha_m; & x \leq S'_n \\ \sum_{m=1}^{M} V_m G_{n,m}(x)\alpha_m - D_n(x) & \\ \quad + \left(\frac{n(n+1)}{2\pi\sigma^2}\right)^{1/2} \int_{-\infty}^{\infty} \exp\left(-\frac{(z-x)^2}{2\sigma^2/n(n+1)}\right) F_{n+1}(z)\,dz; & x > S'_n \end{cases}$$

where

$$G_{n,m}(x) = \left(\frac{n}{2\pi\sigma^2}\right)^{1/2} \int_{-\infty}^{\infty} \exp\left(-\frac{(x-\theta)^2}{2\sigma^2/n}\right) g_{n,m}(\theta)\beta(\theta)\,\mathrm{d}\theta$$

and

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

The iteration is used to compute the optimal S' for each initial subjective resource value for A. The best reply to A's strategy is then computed, and so on until convergence is obtained. For the first example in the text, an individual's subjective resource value does not depend on the opponents local strategy. All the V_m will then be equal to the initial subjective resource value. For the second example, best replies for one role to the strategy used by the other role are computed, until convergence to an equilibrium pair is obtained. For the intruder, V_m will be equal to the owner's subjective resource value, and for the owner, there is no information about the resource in the intruder's behaviour.