

Evolutionarily stable strategies in competition for resource intake rate maximization

I. The model

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Summary. Many animals exploit resources distributed in separate patches. It is commonly assumed that the aim of individuals travelling between patches and exploiting them is to maximize their rate of resource intake, and that the costs of searching for resources are one obvious constraint in fitness maximization. This paper also takes into account some asymmetries between competitors. Conflicts between individuals take the form of either competition by exploitation or of overt contests for resource items. A simple model is developed to answer the question: Which animal should withdraw and when (thereby leaving his opponent within a patch)? It was found that evolutionarily stable strategies (ESS's) are based not only on existing asymmetries but also on current population density. It is possible for conventional and paradoxical ESS's to occur when a patch exists for a sufficiently long period of time in relation to the time of travelling between patches. These strategies can be expected when resources are not overcrowded or when the costs associated with joint exploitation of patches are high. This result is compared with the existing models of animal conflicts for distinct indivisible resources. Some topics concerning optimal foraging and migration decisions are discussed, and empirical evidence is examined.

Introduction

The concept of the evolutionarily stable strategy ESS has been widely and successfully applied in studies of animal conflicts. Two theoretical models in particular, the Hawk-Dove model (Maynard Smith and Price 1973) and the "war of attrition" (Maynard Smith 1974), inspired many theoretical and empirical studies. They were designed to pre-

dict the outcome of animal contests over indivisible resource particles, and the decision making was assumed to be restricted to a *single contest* only. In a sense, in the described approach the history of a given competitor is atomized into distinct events of independent conflicts.

In this model, I will attempt to answer two questions. First, should the cost of a single contest be regarded as the main determinant of animal conflicts? Second, is indivisibility of resources a necessary condition for a game between individuals? Here, animals compete by exploitation and their decision basically consists in deciding to share a patch of resource with others or to leave it and look for a free one. Nevertheless, this does not necessarily exclude the possibility of fights. In this type of competition, time obviously becomes one of the crucial factors, because the aim of animals is to maximize their *intake rate*. The density of a population is another important factor, because it may influence the chances of success in searching for an unoccupied patch and, therefore, markedly change the subject of choice. Finally, individual differences between competitors, whether or not correlated with size or resource value, are also supposed to play some role in animals' decisions. Broadly speaking, my approach emphasizes the importance of ecological factors (such as population density) for determining ESS's. I will consider, in particular, whether high costs of a fight are a necessary condition for the existence of conventional and paradoxical ESS's.

The presented model resembles the Hawk-Dove model for asymmetric contests (Maynard Smith and Parker 1976). To find evolutionarily stable strategies, I make use of the theoretical results of Selten (1980), and I follow some methods of Hammerstein (1981). Their main assumption is that the models have the information-asymmetry

property. This means that opponents never find themselves in possession of the same information about each other. As Selten (1980) proved, if the condition about information-asymmetry holds, then an ESS must be a pure strategy, i.e., in every possible contest situation, it ascribes definite choices, giving probability 1 to each role. In this paper I start with an analysis of a particular game of this class, and I reach an analogous result in the end.

The model

Imagine that competition for scattered resources is taking place, e.g., animals are foraging on distinct feeding areas, males are waiting for mates at especially attractive points, females are laying eggs at their oviposition sites, filtrating animals are settled in narrowings of a stream, etc. Thus, a "patch" either consists of a portion of a divisible resource or is an area with increased probability of encountering indivisible resource items. In this model both the number of resource patches that are used by animals and the population density are assumed to be constant in time. Each patch provides an opportunity for the intake of V resources per unit time. Travelling between patches costs C per unit time. Both V and C are measured in terms of individual fitness. It is assumed that one patch can be occupied by no more than two animals (this simplified assumption is discussed more thoroughly later).

Individuals compete for the divisible resources previously mentioned in a way that is graphically presented in Fig. 1. The possibility of a choice appears when a second individual arrives at a patch in which there already is one individual. For each opponent two moves exist: "share" the resource or "leave" and look for a free patch. In every encounter there are two roles called A and B , where A is "larger", or rather, more efficient, and its expected share is x ($0.5 < x < 1$). It is supposed that phenotypic differences do exist and contestants are perfectly informed about their roles. In addition to the asymmetry in size an asymmetry uncorrelated with size (e.g., different images of ownership) can also appear. Competitors use this information in contest settlement. They are not expected, however, to perceive their absolute sizes and to "know" the distribution of phenotypes in a population.

Payoffs

Figure 2 explains how the payoffs of competitors are calculated. While together, competitors with role A and B get xV and $(1-x)V$, respectively.

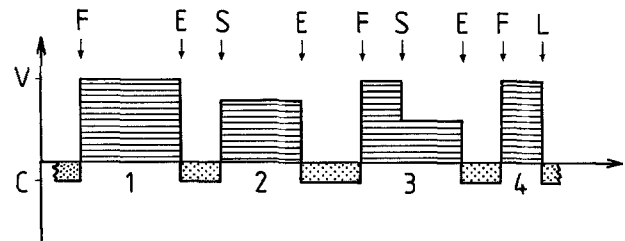


Fig. 1. A hypothetical route of an individual (horizontal axis) and its rewards after particular choices (vertical axis). Every animal always takes free patches (F) and gives up those that end naturally (E), as shown in patch 1. It may decide to enter and stay (S) in a patch that is already occupied by a competitor (patch 2). It may also decide to stay (S) when another individual joins its patch (patch 3), but it will leave (L) when the arriving opponent is too large (patch 4)

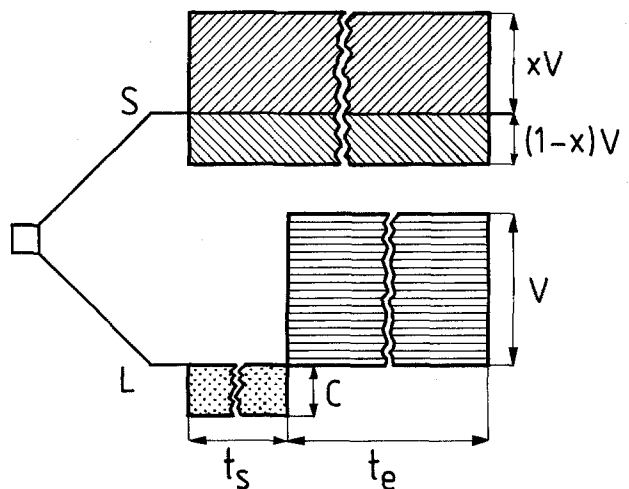


Fig. 2. Decision diagram for an individual faced with the presence of another. Two choices are possible, either to stay or to leave, as was shown in Fig. 1. When A and B share a patch (S) they take xV and $(1-x)V$ respectively. After leaving (L), each competitor pays C in t_s units of time during searching for a free patch; then it takes V in a free patch until another appears, i.e., during t_e units of time. It is important that the expected reward after leaving a patch is constant. This is so, because it is assumed that the population density per one patch is constant. Thus, at every moment of time, the expected gains from joint exploitation can be compared with the average reward after leaving. Consequently, it does not matter which choice (L or S) is associated with the longer period of time

The average rate of resource intake after the alternative choice (leave), l , is identical for each competitor. It can be defined as a proportion of the maximum rate of exploitation, V , by the equation:

$$l = \frac{1}{V} \frac{Vt_e - Ct_s}{(t_e + t_s)} \quad (1)$$

where t_e is the expected time of patch exploitation by a solitary individual before the next competitor

arrives, and t_s is the expected time necessary to find a free patch.

The parameters of equation (1) can be measured in field experiments. In the model, the simplest expressions are chosen to define parameters t_e and t_s as a function of population density d . This density in turn is defined as the number of animals divided by the total number of patches. Now, assume that the fraction of free patches, p_0 , decreases exponentially as the density increases, i.e., $P_0 = e^{-\alpha d}$ ($\alpha > 0$) and that the time of searching (t_s) is inversely proportional to the fraction of free patches. If the average time of travelling between patches is T_s , then $t_s(d) = T_s e^{\alpha d}$. On the other hand, the expected time of solitary exploitation (t_e) must decrease when density increases. Therefore, if T_e is the average time left to the natural end of a patch, then $t_e(d) = T_e e^{-\beta d}$ ($\beta > 0$). Substituting these terms into (1) yields:

$$l(d) = \frac{VT_e e^{-\beta d} - CT_s e^{\alpha d}}{V(T_e e^{-\beta d} + T_s e^{\alpha d})} \quad (2)$$

Let us set both α and β to 1, which is not very unrealistic, and considerably simplifying the equations. This yields the definition of $l(d)$ as follows:

$$l(d) = \frac{1 - SEe^{2d}}{1 + Se^{2d}} \quad (3)$$

where $S = T_s/T_e$ (time of travelling between two neighboring patches in relation to average time of patch existence) and $E = C/V$ (cost of travelling in relation to maximal rate of exploitation).

Now, we are able to gather our results in a payoff matrix (M1) for bigger (A) and smaller (B) competitors:

		Role B	
		share	leave
Role A	share	xV	$(1-x)V$
	leave	$l(d)V$	$[1+l(d)]V/2$

(M1)

where the expressions below the diagonals refer to role A and those above the diagonals to role B . Notice that all payoffs are expressed as fractions of the maximal intake rate V . They depend on relative differences in size (when an individual decides to share a resource) and on population density (when it leaves). Thus, the problem for com-

petitors is to make such choices that result in the highest intake rates in all possible situations, i.e., for all combinations of x and d .

Evolutionarily stable strategies

To start the analysis of this game, two terms are defined: a "best reply" and a "strong equilibrium pair". In every game the payoff for a given individual after its particular move is determined by the move of its opponent. The move that would hypothetically be the most profitable for the role in question will be called the "best reply". For example, when A leaves, then the best reply for B is always to share (see M1). (Of course, competitors do not know what their opponents will do. They only recognize their roles.) When both choices are the best replies to each other, then such a pair of choices is called an "equilibrium pair". A "strong equilibrium pair" appears when both replies are the only best replies to each other. In the above example, "leave" is not always the best reply for A when B chooses "share". "Leave" for A and "share" for B are a strong equilibrium pair when $l(d)V > xV$ (see payoff matrix M1).

The crucial step in searching for ESS's is to find strong equilibrium pairs in every contest situation determined here by the difference between animals, x , and population density, d (Selten 1980; Hammerstein 1981). The reason is as follows. Imagine a strategy that consists of such choices for both roles where in each contest situation they form a strong equilibrium pair, i.e., the strategy that is the only best reply to itself. It is an ESS

because any different "mutant strategy" would not reply in the best way, at least on some occasions. Therefore, the mutant strategy would pay less than the established strategy, this being a sufficient condition for the latter to be an ESS (Maynard Smith 1974).

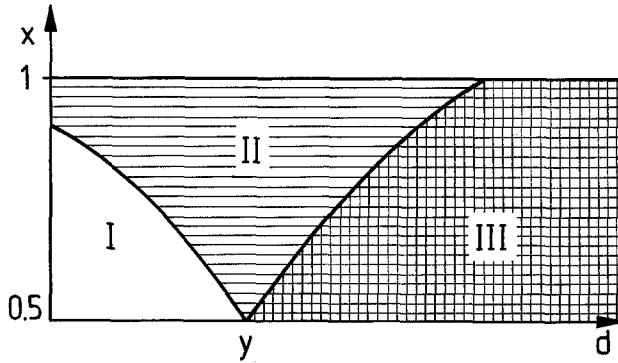


Fig. 3. All possible contest situations (population density as the abscissa and size difference as the ordinate) are divided into three domains by the threshold function (5), where $E=0.1$ and $S=0.1$. In the zone with horizontal lines, role A always play "share" no matter what its opponent is doing. The analogous zone for role B is marked by vertical lines. See the text and Table 1 for more details

We are now able to formulate the ESS's in this game explicitly. As in the last example, we first look for the best replies for both roles (Table 1). To simplify the analysis of conditions from Table 1, the threshold function $f(d)$ is given:

$$f(d) = \begin{cases} l(d) & \text{if } d \leq Y \\ 1-l(d) & \text{if } d > Y \end{cases} \quad (4)$$

where

$$Y = \frac{1}{\alpha + \beta} \ln \frac{1}{S(1+2E)}$$

or, when $\alpha = \beta = 1$

$$Y = \frac{1}{2} \ln \frac{1}{S(1+2E)}$$

The parameter Y is such a density (d) when both functions constituting $f(d)$ intersect, so that $l(d) = 1/2$ (Fig. 3). Note that any value of α and β cannot alter the possibility of the existence of domain I, although they do influence its range. So far, we have divided all contest situations in the game into three domains between which the best replies can change (Fig. 3). To find the ESS, we will use this division and the concept for a strong equilibrium pair. We can decompose the game because animals

are assumed to be always fully informed about their situation and can change their moves according to this information.

Consider first, domain III. A glance at Table 1 and Fig. 3 assures us that both A and B have to share and that this is the only possible strong equilibrium pair. The biological meaning of this statement is that it is hard to find a new patch. In domain II A is sufficiently larger and its share exceeds the expected gain after deciding to look for a free patch; however, that is not the case for B , which must leave. The situation is more interesting in domain I. Generally, when one of the contestants makes a given choice, the other is forced to make a complementary one. For example, when A plays share that only best reply of B is leave, but the paradoxical solution, B (weaker) persists and A leaves, is possible as well (see Table 1). The reason is simple. When switching to another patch is sufficiently cheap, then staying together with any other individual (even a smaller one) would be the worse choice.

Suppose now that a conventional asymmetry, such as ownership, also exists. When can this information be used to settle a contest, i.e., to decide which animal leaves (intruder or owner)? It is impossible in domain III where both have to persist and also in domain II where size determines the outcome. Thus, it is possible only in the domain of complementary choices, i.e., in domain I. A paradoxical strong equilibrium pair, i.e., intruder remains, owner leaves, is also possible. Table 2 summarizes our results.

These three domains are quantitatively demarcated by the threshold function (4). It shows what ecological circumstances are necessary to promote the evolution of paradoxical strategies. The domain of complementary choices can appear only when $S(1+2E) < 1$. The cheaper the switch to another patch (low values of E and/or S) the bigger is this domain, because in such cases Y is higher (4). The time of travelling between patches must be shorter than the time of patch existence ($S < 1$). On the other hand, the cost of travelling between patches can be higher than the income rate within a patch ($E > 1$), provided that S is sufficiently low.

Table 1. Hypothetical best replies (BR) after the opponent's choice derived from the payoff matrix M1

A "shares"	then BR for B is "leave"	if $l(d)V > (1-x)V$ so that $x > 1-l(d)$
A "leaves"	then BR for B is "share"	always
B "shares"	then BR for A is "leave"	if $l(d)V > xV$ so that $x < l(d)$
B "leaves"	then BR for A is "share"	always

Table 2. Four different ESS's that are combinations of strong equilibrium pairs. Strategies (2) and (4) are called "paradoxical". In strategies (3) and (4), it is assumed that when contestants can base their decisions both on size and ownership asymmetries, the ownership asymmetry is used regardless of the fact which contestant is bigger

Strategies	Domains		
	I	II	III
Based on size	(1) larger shares smaller leaves		
	(2) larger leaves smaller shares	larger shares smaller leaves	larger shares smaller shares
Based on ownership and size	(3) owner shares intruder leaves		
	(4) owner leaves intruder shares		

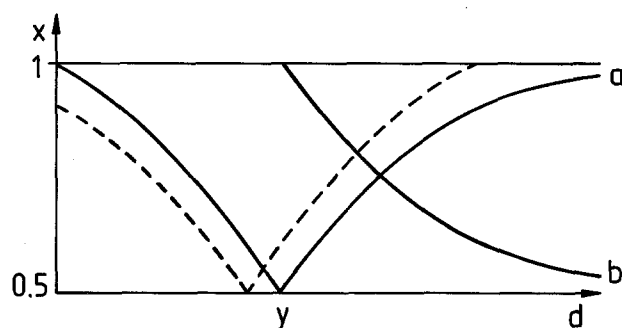


Fig. 4. In the same environment as in Fig. 3 (dotted line), costs of staying together are introduced. When these costs are not very big, $Z/V=0.1$, then domain I is moderately enlarged (a). When costs slightly exceed the critical value, $Z/V > (1+2E)/2$, only domains I and II exist (b). As costs increase, domain I becomes increasingly larger

Some extensions

(a) It is possible that not only the necessity of sharing a resource with another animal lowers the resource intake, but there may also be some expenses, Z , associated with size assessment, fights, or other reasons. In this case in the payoff matrix M1, expressions xV and $(1-x)V$ would be replaced by $xV-Z$ and $(1-x)V-Z$. Y , defined previously by (4), which now gives the following equation:

$$Y = \frac{1}{2} \ln \frac{1+2Z/V}{S(1+2E)-2SZ/V}$$

Thus, domain I is enlarged. When the costs of staying together are very high, $Z/V > (1+2E)/2$, then domain III disappears (Fig. 4).

(b) So far, it has been assumed that, at most, two animals can be found in one patch. The interpretation might be that patches are small or that the presence of more competitors would drastically lower fitness. However, the qualitative conclusions can be maintained when more individuals occupy each patch. The assumptions about resource sharing and environmental properties would remain exactly the same. Perhaps it would be more difficult for animals to perceive adequate information about asymmetries between them. Nevertheless, some social agreements can exist, e.g., newcomers may never withdraw or smaller individuals may leave first.

Discussion

Theoretical conclusions

A more general and formal analysis of possible ESS's in information-asymmetry contests was provided by Hammerstein (1981). Recently, other authors (e.g., Gardner et al. 1987; Grafen 1987) also focused on ESS's applied by individuals under different environmental conditions. In this paper the principle of resource intake maximization is introduced. New features of the model include attempts to describe the situations where the gains are obtained by sharing of resource patches and where the costs of travel between patches are explicitly considered. The gains and the costs are linked to patch stability and population density.

Some predictions can be derived from the model. The first one refers to general rules of animal contest settlement. Parker and Rubinstein (1981), as well as Hammerstein and Parker (1982), argued that there is an essential difference between animal conflicts where a considerable risk of injury exists and those where the costs of the contest consist mainly of controllable energetic expenses. The former may be associated with the Hawk-Dove game, the latter with the war of attrition. According to these authors, conventional and paradoxical strategies can appear only in the first one, i.e., in conflicts where both opponents have to undertake actions that are dangerous and cannot be finished at any moment. As was shown above, in a game with asymmetry in the rate of resource exploitation, paradoxical solutions can be evolutionarily stable despite the fact that individuals may not be aggressive at all, although aggressiveness can reinforce this effect. Still, the fundamental reason remains similar; the choice "share" or "leave" is a sharp distinction, and it irreversibly determines the reward in the immediate future. Conventional

settlement of contests should not be expected when animals are able to continuously control the level of involvement in a conflict and when they have incomplete information about their roles (Parker and Rubenstein 1981; Enquist and Leimar 1983).

Another feature of this game is that the ESS's predict different outcomes of conflicts between the same pair of competitors when population density changes. I believe that this result is more realistic than conclusions based on the assumption that costs and benefits are fixed. We should remember that contests are only one of many factors determining the intake rate of competitors.

When a smaller competitor retreats leaving the bigger with a resource, it is usually assumed that the weaker one is forced to withdraw. Analogically, in the models of migration from large populations of different competitors, the smallest ones are expected to emigrate first (e.g., Lomnicki 1978, 1988). We should be more aware, however, when competitors are assumed to be able to play a game based on information asymmetries, as in this model. For example, in domain I every existing asymmetry can serve as a cue to be used in settling contests, and paradoxical solutions are allowed as well. Therefore, it is necessary to know what strategy is fixed in a population in order to predict the outcome of disputes and phenotypic composition of migrants in the whole range of environmental conditions. Similarly, when a game between competing individuals is played, then the ESS must be known in order to predict an optimal way of foraging in domain I. Such prediction becomes a theoretical game rather than an optimization problem. Thus, it is important to realize that in some situations size difference is, in a sense, a conventional cue making it possible to avoid involvement in conflicts that are unprofitable, even for the larger opponent.

Empirical evidence

There are experimental data that seem to support the predictions from the model. In the well known study on the speckled wood butterfly, Davies (1978) found that in disputes between males over sun spots (where females were attracted), the owners always won. These disputes, however, could not be regarded as fights because the contests were brief and harmless. I think that these contests prevent animals from staying together in one small spot, and leaving is not necessarily the worse choice for a given competitor. Indeed, Davies suggests that the loser's alternative, i.e., patrolling tree canopies or waiting for a free spot (in 90% they

were seen later as owners), is not all that bad. Moreover, within bigger spots several males were found that tolerated each other, and in different size spots average male success was found to be identical. Males really behaved optimally and this resulted in an "ideal free distribution" (Fretwell 1972). Sometimes contests are longer and the stronger male remains in a spot (Wickman and Wiklund 1983), but I do not see this as a difficulty. These authors begin the critique of Davies' study with the words: "If Davies' explanation is to have universal applicability to all male-male interactions between speckled wood males...". Such misunderstandings are brought about by the common approach in the studies of animal conflicts where ecological aspects are underestimated. I think that, in this case, the best explanation can be given by the ESS such as strategy (3) in Table 2. This is supported by the fact that conventional settlement appeared when environmental conditions were very favorable (Davies 1979), whereas when it was cold contests were recorded. Therefore, searching outside sun spots was energetically much more expensive (Wickman and Wiklund 1983).

Another example where apparent fights serve as a means of information exchange is the competition in the gall-forming aphid *Pemphigus betae*. Taking a place nearer to the leaf base yields higher reproductive success, and females fight for this by kicking and shoving (Whitham 1979). Usually, the bigger female takes the better place. Whitham suggested that the cost of the conflict might be quite high. However, solitary "basal" mothers had the identical reproductive output as females that won but whose neighbors later died. Therefore, the cost of the fight cannot be significant, because the latter did suffer from the prolonged contests (see Whitham 1986, Fig. 1). On the other hand, staying together significantly lowered the gains of both individuals. Therefore, this contest is rather a signal to the weaker individual that it can emigrate if the payoff after leaving is greater. The bigger one never withdraws; therefore, this strategy can be classified as a size-based one, plus "common sense" (Table 2, line I). Again, ideal free distribution of stem mothers between leaves (Whitham 1980) reveals that animals, in this case losers in fights, make surprisingly appropriate choices in a given population density.

Males of lovebugs form swarms and arriving females are mated mainly by males from the center of the swarm located near the ground (Thornhill 1980). Not all males try to take a place in the center, however, because mating pairs are attacked by other males. Flying males "bump each other

frequently in the swarm", but "these interactions do not appear to represent overt fighting". Consequently, smaller ones take peripheral sites that are less profitable but safe. A similar mechanism occurs in common toads, where bigger males prevail in the pond and smaller ones on the edge (Davies and Halliday 1979). It is known that toads can recognize bigger males by their deeper croaks (Davies and Halliday 1978). Note that in both cases real contests could occur in direct disputes over females. Thus, by choosing a particular place, animals use available information to prevent fights, and contests are not involved in the game.

I have studied oviposition behavior in flour beetles (Korona 1989), and I found that they also can perceive information about their relative sizes. In this case there can be no doubt that this is not a "contest", but an "information transfer", because aggressive interactions between adult beetles were never observed.

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