

Effects of Asymmetries in Owner–Intruder Conflicts

OLOF LEIMAR

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

AND

MAGNUS ENQUIST

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

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A common situation when animals compete for resources is that there is an owner–intruder asymmetry. Many studies show that owners win most of these conflicts. We investigate how various asymmetries between contestants that might be present in owner–intruder conflicts will affect the outcome and nature of such interactions. A mathematical model is used to represent a fight between an owner and an intruder. A fight in this model consists of a sequence of behaviours; at each step in the sequence the contestants assess their relative strength and each of them decides whether to give up or to continue to fight on the basis of these assessments. For such contests it is shown that the role asymmetry inherent in an owner–intruder conflict can give rise to an ESS where the individual in one role is less willing to continue fighting than the individual in the other role. We also consider that the resource might be more valuable for an owner than for an intruder and that owners might be stronger on the average. Asymmetry in average strength will appear when a resource typically is contested several times and strong individuals have an advantage in such contests. This process of accumulation of strong individuals as owners is studied in some detail. ESS's for contests with these different types of asymmetries are computed numerically. A common feature is that owners will be more persistent than intruders and from this some predictions follow, e.g., owners will win more also when opponents are of equal strength, contests won by the owner will tend to be shorter than those won by the intruder, and the longest contests will be those where the intruder is slightly stronger.

1. Introduction

Many contests in nature are between an owner, an animal in possession of a resource, and a challenger or intruder. Several field studies have shown that the owner wins considerably more than half of these interactions (see

TABLE 1
Data from various field studies on the outcome of interactions between owners and intruders

Species	Resource	Number of interactions observed	Percent won by owner
A damsel fly <i>Hetaerina americana</i>	Territory	63	71%
A digger wasp <i>Philanthus multimaculatus</i>	Perch site	37	86%
A bee <i>Xylocopa hirsutissima</i>	Mating territory	25	81%
Iguana <i>Iguana iguana</i>	Nesting burrow	580	80%
Speckled wood butterfly <i>Pararge aegeria</i>	Encounter site	210	100%
A fiddler crab <i>Uca pugilator</i>	Burrow	403	87%
A fiddler crab <i>Uca pugnax</i>	Burrow	365	88%
Dung fly <i>Scatophaga stercoraria</i>	Female	199	72%
Fulmar <i>Fulmarus glacialis</i>	Food	1383	78%

Johnson, 1962
 Alcock, 1975
 Velthuis & DeCamargo, 1975
 Rand & Rand, 1976
 Davies, 1978
 Hyatt & Salmon, 1978
 Hyatt & Salmon, 1978
 Sigurjónsdóttir & Parker, 1981
 Enquist, Plane & Röed, 1985

Table 1). It is also evident from studies of territorial animals that owners are able to defend their territories for long times, which implies high success for owners in territorial contests. Effects of ownership or prior residence have also been demonstrated in several experiments (Braddock, 1949; Kummer, Götz & Angst, 1974; Figler, Klein & Peeke, 1976; Riechert, 1978; Yasukawa & Bick, 1983). Some of these experimental results indicate that the owner wins more often also when there are no differences in fighting ability between the contestants (Riechert, 1978; Yasukawa & Bick, 1983).

That owners win more than intruders must be due to some asymmetry between them and there are several asymmetries that are likely to be present in owner-intruder conflicts. First of all, if there is a variation in fighting ability among individuals in a population and if a resource typically lasts long enough to be contested several times then strong individuals will accumulate as owners. Secondly, the value of the resource may be higher for owners, e.g. an owner of a territory with progeny in some stage would be more motivated to fight than an intruder. Finally, even if there are no asymmetries in fighting ability or resource value the role asymmetry inherent in an owner-intruder conflict might be used by the contestants as a cue for settlement. The possibility of such a conventional settlement has been pointed out by Maynard Smith (1974).

Of these suggested explanations of the phenomenon the last one is certainly the most surprising and it has received a lot of interest. Several models of conflicts where conventional settlement is evolutionarily stable have been investigated (Maynard Smith & Parker, 1976; Hammerstein, 1981; Hammerstein & Parker, 1982) and studies have also been carried out in order to test if this type of settlement of conflicts occurs in nature (Davies, 1978; Barnard & Brown, 1982; Krebs, 1982; Yasukawa & Bick, 1983).

In this paper we will attempt to illustrate how the asymmetries mentioned above will affect the probability of take-over of a resource by an intruder and we also discuss the nature of evolutionarily stable strategies given these asymmetries. As a model of owner-intruder interactions we will mainly use the kind of fighting studied by us previously for the case when there are no asymmetries known to the contestants prior to an interaction (Enquist & Leimar, 1983). Henceforth that type of fighting will be referred to as a sequential assessment game. Regarding the question of conventions we will show that for the sequential assessment game with a role asymmetry that is uncorrelated with fighting ability and value of the resource "conventional" ESS's exist having the property that the player in one role will be less willing to persist than the player in the other role.

2. Accumulation of Strong Individuals as Owners

To get some quantitative estimates of the rate at which strong individuals accumulate as owners and the resulting probability of take-over of a resource by an intruder we construct a simple model. The basic assumptions behind the model are that a group of individuals compete for a limited number of resources and that fighting abilities vary among the individuals. Let m_k be some trait of individual number k , such as the weight or size, that measures the individual's fighting ability. Assume that the probability of victory for individual k when in the role of intruder in a contest against individual l in the role of owner is a function of the relative fighting ability defined as

$$\theta_{kl} = \ln(m_k/m_l). \quad (1)$$

Denote this function by $p(\theta_{kl})$. A natural requirement is that $p(\theta)$ should grow from zero to one when θ goes from large negative to large positive. It is, however, not necessary that $p(0) = 0.5$ since owners and intruders might use different strategies. An example of a possible $p(\theta)$ is given in Fig. 1.

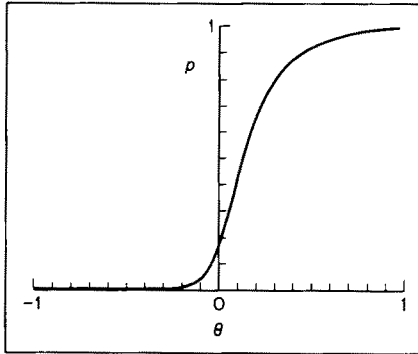


FIG. 1. Probability that the intruder wins as a function of the relative fighting ability (θ) between intruder and owner. The curve is derived from an ESS of a sequential assessment game with an asymmetry in the prior distribution of relative fighting ability.

For convenience, let $u_k = \ln(m_k)$ denote the fighting ability of k so that $\theta_{kl} = u_k - u_l$. The distribution of fighting abilities in the entire population will be given by a probability density $f(u)$ and similarly let $g(u)$ and $h(u)$ be the distribution among owners and intruders respectively. If α is the proportion of owners in the population (number of resources/population size) it then follows that

$$\alpha g(u) + (1 - \alpha)h(u) = f(u). \quad (2)$$

We now ask how g and h change when individuals are interacting. Set the

time scale so that there is on the average one fight per resource per unit time. Assuming that fights are between randomly chosen owners and intruders the fraction of fights in a unit time between intruders with fighting ability in the interval $(u, u+du)$ and owners in $(v, v+dv)$ will be $h(u)g(v) du dv$. A fraction $p(u-v)$ of these fights will result in take-over and thus change the distributions. There might be other processes besides fights that change g and h . For instance, resources might disappear and new resources appear at other locations as could be the case with items of food, or owners might be removed by predation. To model this we assume that a random owner is replaced by a random intruder at the rate r . An equation for the change in time of g can now be written

$$\frac{\partial}{\partial t} g(u) = \int [g(v)h(u)p(u-v) - g(u)h(v)p(v-u)] dv + r\{h(u) - g(u)\}. \quad (3)$$

If the overall distribution $f(u)$ is assumed to be constant in time then from equation (2)

$$\frac{\partial}{\partial t} h(u) = -\frac{\alpha}{1-\alpha} \frac{\partial}{\partial t} g(u). \quad (4)$$

Equations (3) and (4) can easily be intergrated numerically for specified initial conditions. The take-over probability is then calculated as

$$p_T = \iint g(u)h(v)p(v-u) du dv.$$

As an example, take $f(u)$ to be a normal distribution with variance 0.15 and let the initial condition be that $g = h = f$, i.e. that the resources are initially occupied by random individuals. The relative fighting ability will

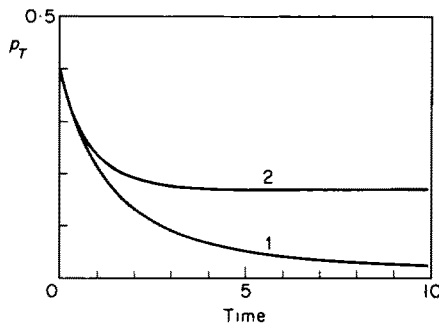


FIG. 2. Decay of the probability of take-over of a resource (p_T) from an initial state where resources are occupied by random individuals. Time is measured as number of interactions per resource. For curve 1 the rate of random take-over (r) is 0 and for curve 2 it is 0.18.

then also be normally distributed initially with mean zero and variance 0.30. Using the function $p(\theta)$ shown in Fig. 1 and $\alpha=0.5$ the resulting decrease of p_T is given in Fig. 2 and the equilibrium distribution of relative fighting ability in Fig. 3 for the two cases of $r=0$ and $r=0.18$. As can be seen the take-over probability falls off rapidly at first and after five to ten interactions per resource it is fairly close to the equilibrium value. Note that since $p(\theta)$ in Fig. 1 gives the owners an advantage p_T is less than 0.5 initially.

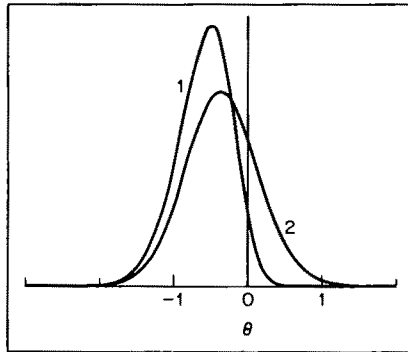


FIG. 3. Equilibrium distribution of the relative fighting ability (θ) between intruder and owner for the two cases shown in Fig. 2 (Curve 1: $r=0$; curve 2: $r=0.18$).

To get a more complete picture consider the following class of functions

$$p(\theta) = \frac{1}{1 + \exp(-s(\theta/d - a))}$$

The parameter d in this expression is the standard deviation of the distribution of relative fighting ability for a pair randomly drawn from the entire population; d is introduced to give a scale on which to measure relative fighting ability in relation to its variation in the population. The parameter s describes the steepness of the increase of p from zero to one and a is referred to as the advantage for owners since an intruder must have $\theta = ad$ in order to have 50% chance of winning. We have computed equilibrium take-over probabilities for combinations of s and a and the result is presented in Fig. 4 in the form of lines of constant p_T in an (s, a) parameter space. As initial condition for equations (3) and (4) $g = h = \text{normal}$ was used and the parameters α and r were chosen as $\alpha = 0.5$ and $r = 0$. From Fig. 4 it is seen that the effect of accumulation becomes noticeable for $s \geq 1$. The steepness s can be regarded as a measure of how effective the fights are in

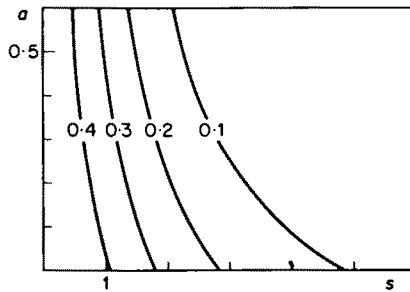


FIG. 4. Lines of constant equilibrium take-over probability in an (s, a) parameter space. The parameter s is the steepness and a is the advantage for owners for the function $p(\theta)$ given in the text. The rate of random take-over (r) is zero.

discriminating relative fighting ability. With $a = 0$ and $s = 1$ we get $p(d) = 0.73$ and $p(2d) = 0.88$; $\theta = d$ can be considered a "typical" amount of asymmetry in fighting ability for a pair of contestants and $\theta = 2d$ a very strong individual against a very weak one. The not very surprising conclusion is that accumulation of strong individuals as owners will be an important effect when there is enough variation in fighting ability to give the strongest individuals a major advantage in contests against the weakest.

Changes of the proportion of owners, α , has very little effect on the equilibrium p_T . The parameter r in equation (3) is more important. Since it takes typically five to ten interactions per resource for the equilibrium to be attained there will be less accumulation if, e.g., the resource disappears before this time. If the fights discriminate relative fighting ability strongly there will however be a reduction in p_T even if $r = 1$. As an example, with $s = 3$ and $a = 0$ the equilibrium p_T is 0.18 for $r = 0$, 0.37 for $r = 0.5$, and 0.42 for $r = 1$. Finally we note that with accumulation a role assessment will give contestants a considerable amount of information about relative fighting ability prior to a contest. For the cases shown in Fig. 4 the average θ for an intruder will be less than $-d$ for $s \geq 2.5$.

3. The Sequential Assessment Game

A summary of this model will be given with some straightforward generalizations to cover asymmetric situations (for more details see Enquist & Leimar, 1983). A pair of contestants, A and B , compete for a resource having the expected value V_A for A and V_B for B . A fight consists of the repetition on one potentially dangerous interaction such as an exchange of blows. The expected cost of each step in the sequence is c_A for A and c_B

for B . As a measure of the fighting ability of A relative to B the quantity

$$\theta = \theta_{AB} = \ln (c_B/c_A) \quad (5)$$

will be used. This would be the same as the relative fighting ability defined in equation (1) if one assumes that $c_B/c_A = m_A/m_B$. In order to keep the number of variables to a minimum an assumption regarding the costs is introduced, namely that the relation $c_A c_B = c^2$ will hold with c constant for all pairs of contestants. The costs per step can now be expressed as functions of c and θ

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

Prior to a contest A and B will have some information about the relative fighting ability. Assume that this information is the same for both contestants and that it is given by a probability density $\beta(\theta_{AB})$. From equation (5) it then follows that θ_{BA} has the probability density $\beta(-\theta_{BA})$. At each step in the fight A assesses θ_{AB} and B θ_{BA} ; let y_n^A and y_n^B be the observations at step n . There will be some inaccuracy in the assessments and the errors of observation for A and B are assumed to be independent and normally distributed with mean zero and variance σ^2 . As the fight progresses the contestants can get better estimates of θ by forming the average of the observations obtained so far. Thus, after n steps A and B can make the estimates

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

Immediately after each observation a contestant can choose either to give up or to continue. Such a decision will be based on the so far observed sequence y_1, \dots, y_n and the prior information. Using the term local strategy to denote a decision rule given a certain prior information, a general local strategy would be a specification for each n and sequence y_1, \dots, y_n of a probability of continuing. An analysis of the game in this general strategy space would, however, be extremely complicated. For this reason we restrict attention to those pure local strategies where a choice at step n is determined by the current average x_n . This restriction is also motivated by the fact that x_n actually contains all information available in the sequence to predict the behaviour of an opponent (Enquist & Leimar, 1983). Furthermore, we assume that a local strategy is given by a specification of a level S_n for each n ; if x_n goes below S_n the player gives up at step n . In principle there could be ESS's with paradoxical local strategies not conforming to this assump-

tion; we have not investigated this matter. Consider now the local strategies

$$S^A = (S_1^A, S_2^A, \dots), \quad S^B = (S_1^B, S_2^B, \dots).$$

If $S_n^A > S_n^B$ for all n we say that B is more persistent than A . This does not mean that A always gives up first but for matched opponents ($\theta = 0$) it will mean that B has more than 50% chance of winning.

In the model there are two kinds of asymmetries that could be known to the contestants prior to a fight and thus affect their local strategies. The prior distribution $\beta(\theta)$ might not be symmetric around $\theta = 0$ and V_A might be different from V_B . If there is a role asymmetry, such as owner-intruder, which is unambiguously perceived and if β and V are specified by the role then an ESS must have the form of a strong equilibrium pair of local strategies (Selten, 1980), i.e. a pair of strategies, S' and S'' , with the property that S' is the only best reply in one role to S'' played in the other role and S'' is the only best reply in the other role to S' played in the first role. For the sequential assessment game it appears to be the case that a best reply to a local strategy of the kind described above is a unique local strategy of the same type. We have used the following numerical method to find ESS's. A local strategy is initially assigned to one role and the best reply to this for the other role is computed. Successive best replies are then computed until the process converges to an equilibrium pair. The procedure for determining best replies is described in Enquist & Leimar (1983). A potential problem with this method is that there is no guarantee that all equilibrium pairs for the game can be found in this way. However, if one wants to find an ESS that is likely to be of biological interest it is reasonable to assume that such an ESS could be arrived at through evolution starting from a fairly wide range of initial strategies. An iteration of best replies can be thought of as a rather crude way of modelling an evolution (see sections 5 and 6 for further comments on this). In conclusion, we have not been able to perform a complete game theoretical analysis of the sequential assessment game but have instead made assumptions that allow results of potential biological interest to be derived.

The strategies mentioned so far all imply that at least one step in the sequence will be taken by the contestants. There is one more local strategy, namely not to fight at all, that should be taken into account. If, for instance, intruders receive a negative pay-off from contests with owners they should avoid these contests. In a situation where, as we have assumed, the role asymmetry is assessed without errors, a strategy where intruders avoid contesting owners cannot be an ESS. This follows from the fact that any owner strategy resulting in a negative pay-off for challenging intruders will provide an equilibrium pair. Of course, respecting ownership can still be

selected for and remain stable once it is established, but the strategy owners would use if they were challenged cannot be predicted from a game theoretical analysis (cf. the discussion of reserve strategy in Parker & Rubenstein, 1981).

4. Asymmetry in Average Fighting Ability or Resource Value

We now give some examples of stable strategies for the sequential assessment game with an owner-intruder asymmetry that is associated with differences in average fighting ability or resource value. Consider first a case where the prior distribution $\beta(\theta)$ has a mean different from zero but where the value of the resource (V) is the same for both roles. Let A be in the role of intruder and B in the role of owner. Using for $\beta(\theta_{AB})$ a normal distribution with standard deviation 0.5 and mean -0.35 (i.e. intruders are weaker on the average) and with the standard deviation of sampling (σ) equal to 0.5 and the cost parameter c given by $c/V = 0.04$ we have computed an equilibrium pair S^A and S^B of local strategies. This pair has the property that $S_n^A > S_n^B$ for all n , i.e. the owner is more persistent. The resulting probability of victory for the intruder given θ_{AB} is shown in Fig. 1. With matched opponents ($\theta = 0$) the intruder, being less persistent, will win only 16.7% of these fights. The average probability of take-over is 16.6% and this is partly due to that owners are stronger on the average and partly to that they are more persistent. The assumed prior distribution $\beta(\theta_{AB})$ is well approximated by the equilibrium distribution shown in Fig. 3 for the case $r = 0.18$ and that is the reason why we gave that particular example (note that we are identifying equations (1) and (5)). It illustrates a situation that is consistent in the sense that the equilibrium accumulation of strong owners results in decision rules that produce this equilibrium. The expected pay-off per contest is in this case $0.72V$ for the owner and $0.04V$ for the intruder. With a more extreme accumulation of strong owners the pay-off for intruders will be negative and they will not challenge owners. It appears that, in the context of the models presented here, if r is small and fights discriminate relative fighting ability accurately then accumulation will proceed to a stage where ownership is respected. Concerning the average length of contests the following should be noted. The longest contests will be those where the intruder is slightly stronger and furthermore the contests won by the intruder will tend to be longer than those won by the owner. For the example the greatest average length is 7.0 steps occurring for $\theta = 0.10$. Given that the intruder wins the average contest length is 5.9 steps and given that the owner wins it is 2.2 steps. Let us finally see what would happen if two individuals somehow are made to consider themselves the owner of the

same resource. Assume that this means that they will both use the persistent owner strategy S^B from our example (this will not give an equilibrium pair of strategies). A contest for such opponents will then be longer on the average; if the opponents are taken at random from the owner group (or the intruder group) it will be 2.5 times longer than the contests with a clear owner-intruder asymmetry.

Next we consider a situation where the prior average of θ is zero and the resource represents a higher value for owners ($V_B > V_A$). For the model presented here there is a qualitative difference between asymmetry in average θ and asymmetry in V in that θ is assessed during a contest whereas V_A and V_B are known prior to the start of a fight. From our numerical computations it appears that asymmetry in resource value has a stronger effect on the local strategies used in the different roles. If the previous example is modified so that the prior average of θ is zero and the value of the resource to the owner (V_B) is increased from V , then for $\ln(V/V_B) \leq -0.3$ an iteration of best replies leads to progressively less persistent intruder strategies, eventually yielding a negative pay-off, and no convergence to an equilibrium pair is obtained. Presumably ownership will be respected in this case. With smaller asymmetry the iteration converges to an ESS having the property that intruders are less persistent than owners, e.g., with $V_B = 1.2V$ intruders will win 19% of the fights between matched opponents. As in the example above with asymmetry in the prior average of θ the contests won by the intruder will tend to be longer than those won by the owner and the longest contests will be those where the intruder is slightly stronger; these effects are a consequence of the greater persistence of owners.

5. Uncorrelated Role Asymmetry

The fact that conflicts in nature are usually settled without a very costly "total war" between the contestants was referred to as the conventional nature of contests by Maynard Smith & Price (1973). For contests with a role asymmetry Maynard Smith (1974) suggested that an animal's role might be used as a conventional cue for settlement, thus reducing the cost of contests. The simplest model where conventional settlement is evolutionarily stable is the "Hawks" and "Doves" game (Maynard Smith & Parker, 1976) with a sufficiently high cost of injury in an escalated fight to make the pay-off from such a fight negative. This model has been extended by Hammerstein (1981) through the introduction of a continuously distributed size asymmetry between the contestants. The size asymmetry is assumed to determine the probability of winning an escalated fight and to be perfectly known to the contestants after some initial phase of assessment. Stable

strategies for this game have the property that if the size asymmetry is large enough to give the bigger individual a positive pay-off from an escalated fight then size must be respected but for smaller size asymmetry any unambiguous difference between contestants could be used as a cue to settle the contest. These examples show that when the cost of an escalated fight is high then the introduction of a role asymmetry might give rise to new ESS's not present in a situation without this role asymmetry. For a sequential assessment game it turns out that this can happen also when the expected benefit of an escalated fight is positive. Before going into that we give a more general discussion of how a role asymmetry can introduce stable strategies in addition to those that ignore the roles.

Consider a contest where some quantity related to relative fighting ability is assessed by the opponents. To simplify we make the restrictive assumption that the best reply to a given strategy is always unique. Let $S' = \omega(S)$ be the best reply in one role to the local strategy S used in the other role. An ESS ignoring the roles will be a solution to the equation

$$\omega(S) = S \tag{6}$$

and an equilibrium pair $S, \omega(S)$ will correspond to a pair of solutions to

$$\omega(\omega(S)) = S \tag{7}$$

(if S is a solution then $\omega(S)$ is also a solution). Solutions to equation (6) will also satisfy equation (7) and additional solutions to equation (7) have the property that the role is used as a cue for the selection of a local strategy. An individual's decisions in a contest will partly be based on estimates of the quantity related to relative fighting ability and we can call a local strategy more daring or persistent than another if a player of the second strategy requires a higher estimate of relative fighting ability in order to continue than a player of the first strategy. Now, increasing the persistence of S will typically decrease the persistence of the best reply $\omega(S)$. This gives a kind of structural robustness to equation (6). In contrast, increasing the persistence of S will typically increase the persistence of $\omega(\omega(S))$ so that this mapping might be close to the identity (this is the case for the sequential assessment game), making solutions to equation (7) sensitive to small changes in ω . This problem becomes acute for models, such as the "Hawks" and "Doves" game with a size asymmetry mentioned above, where the contestants have perfect information about some continuous variable. Since this variable could be used as a cue for settlement instead of the role equation (7) will have a continuum of solutions and will be structurally unstable with respect to the introduction of slight uncertainty for each opponent of the other's estimate of the variable. The effect of such a

perturbation depends on how the uncertainty is introduced; we have made some calculations for the "Hawks" and "Doves" case with the result that only a role-ignoring solution to equation (7) remained, but since this does not appear to have any generality we will not present the details.

Using the method described in section 3 (with some modifications, see below) we have looked for equilibrium pairs for the sequential assessment game with an uncorrelated role asymmetry. It appears that equation (7) has three solutions, one of which is a solution to equation (6) and the other two corresponding to an equilibrium pair with the property that the player in one role is more persistent than the player in the other role. An example of these equilibrium pairs is given in Fig. 5. The difference in persistence

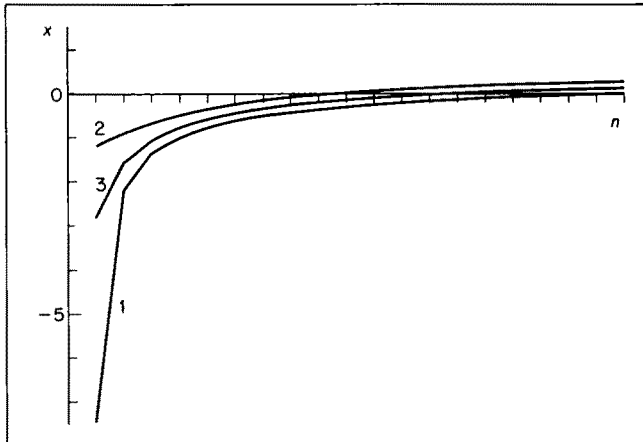


FIG. 5. The three curves illustrate local strategies which define two different ESS's for a sequential assessment game with an uncorrelated role asymmetry. The curves have meaning only for integer number of steps (n) and show the level S_n of the estimate (x) of relative fighting ability below which a contestant gives up. One ESS is given by the equilibrium pair (3, 3) and ignores the roles and the other ESS is given by the equilibrium pair (1, 2). The local strategy 1 is associated with the persistent role.

between the roles depends on the parameters of the model. This difference increases when the ratio of the standard deviation of sampling (σ) to the standard deviation of the prior distribution is increased and also when the relative cost c/V is increased. For the example in Fig. 5 $\beta(\theta)$ has standard deviation 0.5, σ is 1.5, and c/V is 0.05. In this case the overall probability of winning is 66% for the persistent role and for matched opponents it is 74%. If σ is reduced to 0.5 the corresponding figures are 53 and 61%. This is to some extent in agreement with the results from the "Hawks" and "Doves" game, in the sense that both increasing σ and c/V will tend to

lower the pay-off for a contest where a role-ignoring ESS is used. Also, the region between curves 1 and 2 in Fig. 5 could loosely be interpreted as a region where the role is used as a cue for settlement. There is however a qualitative difference. The expected pay-off from a fight where the roles are ignored does not have to be negative for the role to be used as a cue. The pay-offs for the strategies in Fig. 5 are 0.35 V for 1 against 2, 0.05 V for 2 against 1, and 0.15 V for 3 against itself.

When there is a role asymmetry the nature of the stability is different for the two equilibrium pairs depicted in Fig. 5. The role-ignoring ESS is not continuously stable (this concept was introduced by Eshel, 1983), i.e. if the population deviates slightly from the ESS evolution will tend to remove it further from this point, whereas the other equilibrium pair is stable in this sense. If, however, there is no role asymmetry then the solution to equation (6) is continuously stable. A technical comment might be in order here. The role-ignoring ESS is not an attractor for the iteration described in section 3. A numerical trick, mimicking a gradual evolution with no role asymmetry changes this. If instead of using the best reply to the "present" strategy as the next step in the iteration a weighted average of the "present" strategy and its best reply is used, then, with sufficient weight on the "present" strategy, the iteration will converge towards a solution to equation (6).

The above results undermine the basis of an argument put forward by us previously (Enquist & Leimar, 1983) concerning the possibility of having conventions when differences in fighting ability exist and are assessed. The main point of that argument was that with efficient assessment the pay-off from an escalated fight should be positive, but it implicitly assumed that a role-ignoring strategy would be used in such a fight.

6. Paradoxical and Common-sense Strategies

Extending the discussion in the previous section to sequential assessment games where an animal's role is correlated with fighting ability or resource value equation (7) must be changed to

$$\omega''(\omega'(S)) = S. \quad (8)$$

Here $\omega'(S)$ is the best reply in one role to the local strategy S used in the other role and $\omega''(S)$ is the analogous mapping when the roles are reversed. If, starting from a symmetric situation, one role is gradually made more favoured with respect to fighting ability or resource value the solutions to equation (8) will change continuously starting from the solutions to equation (7). The continuously stable equilibrium pair will split up into two pairs, one where the favoured role is more persistent and one where it is less

persistent. Using the notation of Maynard Smith & Parker (1976) these strategies will be called respectively common sense and paradoxical. Presumably the continuously unstable pair can also be extended; it can however not be located numerically and should not be of any practical importance. The examples given in section 4 are common sense solutions to equation (8). There are good reasons for believing that paradoxical ESS's will be quite uncommon in evolution (Maynard Smith & Parker, 1976). It appears that a paradoxical ESS has a much smaller basin of attraction than the corresponding common sense ESS, i.e. it can evolve only from a very restricted set of "initial" strategies. We have located paradoxical ESS's numerically starting from a symmetric situation and then gradually favouring the less persistent role. As the asymmetry increases the paradoxical ESS becomes less attracting and thus harder to locate and it seems likely that beyond a certain degree of asymmetry only the common sense solution remains.

7. Discussion

It is clear that, in the context of the sequential assessment game, either accumulation of strong owners, higher resource value for owners, or an uncorrelated role asymmetry could lead to low probability of take-over of a resource by an intruder. If we exclude paradoxical strategies from consideration and assume that the pay-off from a fight is positive for an intruder so that fighting will take place then the nature of observed fights will be quite similar in each of these cases. The most notable similarities are: (i) owners will win more also for matched opponents, (ii) the longest interactions will occur when the intruder is slightly stronger, (iii) interactions won by the intruder will tend to be longer than those won by the owner, and (iv) if both contestants (by mistake or through manipulation) consider themselves as owner then a long interaction will be observed.

Although owner-intruder interactions in nature are likely to involve many factors beyond those considered here it seems that results derived from the sequential assessment game have at least some generality. The predictions (i)-(iv) above are in accordance with observation in several studies of conflicts with a role asymmetry, e.g.; (i) and (iii) were shown by Riechert (1978) for contests over webs in the funnel web spider *Agelenopsis aperta*; (i) was shown by Yasukawa & Bick (1983) for contests between residents and non-residents in the dark-eyed junco *Junco hyemalis*; and (iv) was shown by Davies (1978) for speckled wood butterflies *Parage aegeria* competing for sunspot territories.

For a sequential assessment game with an uncorrelated role asymmetry using the role as a cue in an ESS, but, as was discussed following equation

(7), this might be highly dependent on the details of the model. It is thus difficult to determine whether or not such conventions will be commonly occurring in nature. This is further complicated by the fact that conflicts with a completely uncorrelated role asymmetry might be rare. The remarks made about the sensitivity of solutions to equation (7) apply also to equation (8). It is quite possible that a small asymmetry in motivation and/or average fighting ability will have considerable effect on the strategies used in the different roles.

An example where an ownership convention seems to be operating is provided by Davies's (1978) study of territoriality in the speckled wood butterfly. Davies studied this species during a warm summer in England and described conflicts over sunspots (mating sites) as being settled by ownership. The interactions lasted a few seconds only. In a study of the same species in Sweden during the cold spring much longer interactions were described and interpreted as fights (Wickman & Wiklund, 1983). A tentative explanation is that the cold weather and the limited amount of sunspots in the Swedish locality made these areas more valuable than those in England. This interpretation is further supported by the finding that the average contest length decreased in the Swedish locality as temperatures increased towards the summer. Furthermore, during cooler weather longer interactions were also observed at the English locality (Davies, 1979). Such an explanation is in agreement with results for the sequential assessment game. As was pointed out above, for contests with an uncorrelated role asymmetry the difference in persistence between roles increases with increasing c/V , and as a consequence of this the average contest length will decrease with decreasing V (this will happen also if the role is correlated with fighting ability or resource value).

The conditions needed to produce an accumulation of strong individuals as owners are not very restrictive, which means that this phenomenon should be quite common. That owners on the average have higher fighting ability than animals without a resource has been shown to be the case in field studies of territorial behaviour in three Hymenoptera species: the wasp *Hemipepsis ustulata* (Alcock, 1979) and the bees *Anthidium maculosum* (Alcock, Eickwort & Eickwort, 1977) and *Anthidium manicatum* (Severinghaus, Kurtak & Eickwort, 1981). In a study of male mating behaviour of the bee *Centris pallida* (Alcock, Jones & Buchmann, 1977) the process of accumulation can be seen in greater detail. The contested resource consists of buried females emerging from the ground to mate. Males of this species employ two different mating strategies; patroller-diggers locate sites at which a buried female is about to emerge and dig through the soil to uncover the female, hoverers wait for females not captured by patrollers. A male digging

at a site will frequently be attacked by other patrollers and take-overs do occur. The last occupant of a site has a high probability of mating with the female. The study showed a marked difference in average size between mating males and patrollers in general, indicating that the average fighting ability of an owner increased due to take-overs during the time of activity at a site.

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