

ROLE ASSESSMENT, RESERVE STRATEGY, AND ACQUISITION OF INFORMATION IN ASYMMETRIC ANIMAL CONFLICTS

BY G. A. PARKER* & D. I. RUBENSTEIN

King's College Research Centre, King's College, Cambridge CB2 1ST

Abstract. It was formerly argued that alternative evolutionarily stable strategies (ESSs) are possible for animal contests characterized by some asymmetry that can be perceived with perfect accuracy. Where roles *A* and *B* refer to the asymmetry between opponents, ESSs are: 'fight when *A*, retreat when *B*', and vice versa. Either can be an ESS, but only if the 'reserve strategy' (= what an animal does when it fights) is sufficiently damaging. We examine the 'war of attrition' (winner = opponent that persists longer). In a population at either ESS, reserve strategy is never normally shown; it is therefore subject to drift unless the selective action of rare individuals which break the convention is considered. These could arise either by mutation or by mistakes in role assessment. When mutations and mistakes simply specify that occasionally an animal fights when it 'should' retreat, selection adjusts reserve strategy to a level where only one ESS (the 'commonsense' ESS) is possible, if the asymmetry is relevant to payoff. Thus for asymmetries in fighting ability or resource value, the individual with the lower score will retreat. However, we are particularly concerned with cases where *both* payoff-relevant aspects (fighting ability and resource value) are asymmetric. If opponents sustain contest costs at rates K_A and K_B , and their resource values are V_A and V_B , an 'optimal assessor' strategy defined by the interaction between the two asymmetries, is a unique ESS. It obeys the rule 'fight on estimating role *A*, where $V_A/K_A > V_B/K_B$; retreat in *B*'. If mistakes can occur in both roles, but are very rare, the ESS is not fundamentally altered though there will be infinitesimal tendencies for persisting in role *B*. Selection to improve assessment abilities intensifies as abilities improve, but is weak if roles *A* and *B* are rather similar. Over a range of similarity between roles, an 'owner wins' convention may be adopted if ownership correlates positively with role *A* and an individual cannot tell when it would otherwise pay him to break the convention. We also examine a contest in which information about roles can be acquired only during a contest itself, and at a cost. Much depends on the rate at which information is acquired relative to the rate at which costs are expended, and on whether contests normally escalate in intensity, remain at the same level, or de-escalate. Selection favours short contests when costs are high relative to resource value, where the outcome of a round contains much information about fighting ability, and where the actual disparity in fighting ability is large.

Introduction

J. Maynard Smith's pioneering approach to the evolutionary theory of animal fighting created a landmark in sociobiology (Maynard Smith 1972; Maynard Smith & Price 1973). It also instigated the development of the evolutionarily stable strategy (ESS) concept, an idea that has major implications for the whole of evolutionary biology. A strategy is an ESS if, when fixed in a population, it cannot be invaded genetically by any alternative strategy.

In early models of animal contests, two identical opponents were assumed to be in dispute over a resource of equal value to each individual (Maynard Smith 1972; Maynard Smith & Price 1973; Maynard Smith 1974). The game is thus assumed to be symmetric. But in most competi-

tive situations asymmetries play a major role in determining the outcomes of contests.

Two sorts of asymmetries are of importance in animal fights (Parker 1974; Maynard Smith & Parker 1976).

(i) **Asymmetry in fighting ability or 'resource holding potential' (RHP).** Individuals may differ in some intrinsic features (e.g. size, strength, weaponry, etc.) or in some extrinsic feature (e.g. 'postural' differences to do with the relative placing of the two opponents). RHP asymmetries affect the probable allocation of contest costs.

(ii) **Asymmetries in resource (reward) value.** The contested resource may be worth (in terms of fitness units) more to one opponent than the other.

Maynard Smith (1974) noted that an asymmetry that is entirely uncorrelated with either of

*Present address: Department of Zoology, University of Liverpool, Liverpool L69 3BX.

the above ('uncorrelated asymmetries') might be important in settling disputes. The commonplace adoption of 'owner wins' conventions (or 'bourgeois strategies'; Maynard Smith 1976) is often taken as evidence that uncorrelated asymmetries exist in nature. However, it is not clear how such conventions can be maintained by selection, especially when there exist asymmetries in RHP or resource value.

Our present aims are twofold. We are firstly concerned with how animals should behave in contests in which both resource value and RHP are asymmetric: i.e. where there are interactions between these asymmetries. We show that the 'assessment strategy' model (Parker 1974) is correct, although it was not originally developed by ESS techniques. Secondly, we examine further the problem of obtaining information about roles (see also Maynard Smith & Parker 1976). Will abilities for obtaining better information (better assessment) spread when populations obey 'assessor' rules? We also consider the problem of acquiring information during a contest (see also Maynard Smith & Parker 1976), because it is clear that accurate assessment of RHP can often be obtained only after engaging in combat. How long should an animal engage in combat, and at what level, to obtain better information about his role?

The Structure of Conventional ESSs based on Asymmetries that are Accurately Perceived

Maynard Smith & Parker (1976) showed that if contests are characterized by the asymmetric roles A and B , then either of the conventions: 'when in A , be prepared to escalate to cost Z ; when in B , retreat without contesting' or 'when in B , be prepared to play Z ; when in A , retreat' can be an ESS if $Z > V$, where V is the value of the resource. Examining contests in which either RHP or resource value were asymmetric, they defined a 'commonsense' ESS as one where the individual with lower RHP or with least to gain retreats, and a 'paradoxical' strategy as the reverse (the bigger animal, or the one with more to gain, is the one that retreats). In general, commonsense ESSs were much more likely to be found in nature, though the possibility of paradoxical ESSs could not be entirely eliminated. In an extension of Maynard Smith & Parker's analysis, Hammerstein (1981) has stressed the formal possibility of paradoxical strategies. An important assumption in these models is that opponents have perfect information about the

asymmetries — they always 'know' which role they occupy.

The stability of conventional strategies of the above type depends critically on Z , the level of damage an animal is prepared to play to when it is challenged by an individual that breaks the convention. We shall call this (Z) the 'reserve strategy'; we argue that correct deductions about reserve strategy are the key to modelling asymmetric contests in which role assessment is almost perfect. In a population in which all individuals observe a given convention and never make mistakes about roles, then the reserve strategy is never shown. If $Z > V$, a mutant that fails to retreat and breaks the convention always experiences a fitness less than mean population fitness, and hence cannot invade. But so, of course, do the individuals he fights against. Thus recurrent mutation for convention-breaking can exert selection to reduce reserve play. Perhaps even more important, we shall see that rare mistakes about roles will also exert selection on the reserve strategy. We argue that the result of such selection, in animal contests that obey the rules of the 'war of attrition' (Maynard Smith 1974), is generally to adjust reserve strategy to such a level that only commonsense conventions are possible. We find that paradoxical conventions can exist only temporarily as a result of drift to a maladaptively high reserve strategy level. Rare mistakes about role, and recurrent mutation for convention-breaking, will often erode the reserve strategy by selection to a level where the paradoxical convention is invadable.

Interactions between Asymmetries: Can Assessment Evolve?

The central idea of assessment strategy in animal contests is that individuals are expected to monitor relative RHP and relative resource value. As a result it was suggested that disputes will generally be settled without escalation by a convention set by an interaction between the asymmetries in RHP and V . The interaction proposed (Parker 1974) was simply that the individual with the lesser score for

resource value V

rate of cost accrual if both escalate

(1)

should be prepared to retreat, but not his opponent. We attempt to show that a convention based on (1) is not only an ESS: it approximates to the only ESS for the case where opponents can assess their roles accurately before beginning an

escalated contest, and where the costs of an escalated contest would rise continuously at fixed rates. We call a strategy based on a (1) an 'assessor' strategy because it defines which individual would have the expectation of being the first to enter a range where payoff from the particular interaction becomes negative if both were to continue to fight indefinitely.

We define interactions between RHP and V asymmetry as two types:

(i) **Non-contradictory.** The opponent with higher RHP also has most to gain (higher V) from the contest. Alternatively, either RHP or payoff may be symmetric, with opponents differing in only one respect. Non-contradictory interactions of the latter type were studied by Maynard Smith & Parker (1976), and apart from providing further evidence for the implausibility of paradoxical strategies, we add little to their conclusions for cases where information about roles is perfect.

(ii) **Contradictory.** Here the opponent with higher RHP has least to gain from the contest, and vice versa. Such forms of interaction were not investigated by Maynard Smith & Parker (1976) and they generally present more problems for the development of assessor strategies than non-contradictory asymmetries.

Is it important to investigate contradictory interactions? We believe that it may be very important. Resource value is the difference in fitness between obtaining the disputed resource (not counting contest costs) versus leaving to search for an alternative, 'takeable' resource (Maynard Smith 1974; Parker 1974). If some commonsense convention involving RHP is adopted, then V will increase as RHP decreases, since an individual of low RHP must search longer than one of high RHP before he can find a resource occupied by an individual of lower RHP. This inverse correlation between RHP and V will generate contradictory interactions. The specific form of the relationship will not be investigated here as it is complex and depends on the distribution of RHP and on how non-random the tenureship of resources is, with respect to RHP (see simple model in Parker 1974). The important point is that most interactions between the two important forms of asymmetry may be contradictory.

A Model with Contest Costs Increasing Continuously at Fixed Rates

In Parker's (1974) model, each individual has a 'fitness budget' (= resource value), which we

shall call V_A for individual A and V_B for individual B . During a contest, costs rise continuously but asymmetrically for each opponent at rates K_A and K_B . In fact, it makes no difference whether contest costs involve energy loss or small discrete injuries, so long as the mean expectation for cost accrual rates stays constant. It was assumed that the type of assessment likely to be favoured by selection would be one of: 'withdraw only if you will run out of fitness budget before your opponent will, otherwise persist' (see (1)). This is equivalent to the rule: 'withdraw if in B , persist if in A ;' where A and B are defined by

$$\frac{V_A}{K_A} > \frac{V_B}{K_B} \quad (2)$$

1. Success of Assessor Mutants

Firstly, can an assessor as defined by rule (2) always invade into a population that ignores the asymmetry?

It is clear that the above game in symmetric form corresponds exactly to Maynard Smith's (1974) 'war of attrition', in which victory goes to the opponent that persists longest. Thus a strategy consists of a choice of maximum persistence time that an individual is prepared to play in a contest. The ESS to this game (with RHP and V equal for both opponents) is to play strategy Q which selects a persistence time x from a probability distribution $p(x)$ such that if costs rise linearly = Kx ,

$$p(x) = \frac{K}{V} \exp(-Kx/V) \quad (3a)$$

(see Maynard Smith 1974; and Norman et al. (1977) and Bishop & Cannings (1978) for more general solutions with non-linear costs). The distribution $p_o(x)$ of actual contest lengths expected if individuals select bids in accordance with (3a) can be shown to be:

$$p_o(x) = \frac{2K}{V} \exp(-2Kx/V) \quad (3b)$$

(Parker & Thompson, 1980). The mean persistence time is therefore $V/2K$ and hence mean costs $V/2$. Since each opponent wins V exactly half the time, then $E(Q, Q)$, the mean payoff of Q played against Q , = 0 (Maynard Smith 1974; Bishop & Cannings 1978).

For the parallel asymmetric game in which opponents have no information about roles A or B , then the ESS must be as in (3) in which

$$\frac{K}{V} = \frac{\bar{K}}{\bar{V}} = \frac{K_A + K_B}{V_A + V_B}$$

Suppose a mutant assessor I arises that can estimate correctly that it is in A or B with probability P ; it is therefore incorrect with probability $(1 - P)$. It spreads if its payoff against Q , $E(I, Q) > E(Q, Q)$ the payoff of Q against itself, i.e. if

$$\frac{P}{2} \left[\frac{V_A}{2} - \frac{K_A}{2} \left(\frac{V_A + V_B}{K_A + K_B} \right) \right] + \frac{(1 - P)}{2} \left[\frac{V_B}{2} - \frac{K_B}{2} \left(\frac{V_A + V_B}{K_A + K_B} \right) \right] > 0 \quad (4)$$

estimates correctly that
is in role A

really in B , estimates
 A incorrectly

A few words of explanation are necessary about (4). We assume that: (i) the mutant strategy finds itself in roles A and B equally often (RHP and V are environmentally induced; or if genetic, are unlinked to the mutant gene); (ii) I fights exactly as does Q when it is in A , but retreats when it is in B . This second assumption is equivalent to a plausible unitary genetic change coding for dropping out of contests when some cue is observed that correlates imperfectly with role B . When the mutant estimates A , it persists for a mean time $\bar{V}/2\bar{K}$ and sustains a cost accrual rate K_A if it is really in A , and a rate K_B if it is really in B . Mean contest costs are thus $K_A\bar{V}/2\bar{K}$ in A and $K_B\bar{V}/2\bar{K}$ in B , though 'bids' will be selected after (3a).

Equation (4) reduces to:

$$(2P - 1) \frac{V_A}{K_A} > (2P - 1) \frac{V_B}{K_B} \quad (5)$$

From (5) it is clear that if $P > \frac{1}{2}$ (the assessor can do better than simply to guess its role), then the mutant will always spread. The 'paradoxical' mutant playing 'contest the resource when you estimate B ' can spread only if it is deluded most of the time (i.e. $P < \frac{1}{2}$), in other words, when it is actually commonsense! Where $V_A/K_A = V_B/K_B$, a mutant that drops out in response to any cue is selectively neutral and the trait will drift.

The conclusion is that even if information about roles is very poor, tendencies to drop out

of contests when in B will always spread. This conclusion is interesting, because in reality there will be a vast array of possible disparity between V_A/K_A , producing a vast payoff matrix. Starting from a population with zero information, assessor strategies can always invade provided there is a real disparity as in (2), but paradoxical strategies cannot. By reduction it must always be possible to find a cell of the matrix in which opponents have no information about roles A and B , whatever the current level of discriminatory powers. The deduction that only a commonsense assessor can invade a population ignoring the asymmetry is equivalent to the similar finding

of Maynard Smith & Parker (1976) for contests with perfect information in which resource value was asymmetric: we have shown that perfect information about roles is not necessary for spread.

2. Selection Acting on the Reserve Strategy; and the Stability of Assessor Strategies with Accurate Role Assessment

Consider now exactly the same asymmetric contest, but in which the opponents can estimate their roles accurately. For this game, Maynard Smith & Parker (1976) have argued that retreat is favoured in one role and escalation in the other, as we have discussed above. Note that in this hypothetical population, the reserve strategy (escalation) is never used. Thus although it is reasonable to argue that reserve strategy might be set by an ancestral population that ignored the asymmetry, this may not give a good indication of its current value, because the reserve strategy will now be subject to drift. We argue here that reserve strategy can never be entirely buffered from the action of selection, and that selection should maintain it at a constant level. In the analysis that follows, we assume that role assessment is perfect or near perfect and that an ESS will approximate to a convention in which there is escalation in one role and retreat in another (following Maynard Smith & Parker 1976). In fact, imperfect role assessment will always generate some escalation in the 'retreating' role, but simulations have shown that this becomes infinitesimal as role assessment approaches perfection. A more extensive analysis

of this problem will be published later. There are essentially two causes of selection on reserve strategy, and these have rather different effects:

(i) **Recurrent mutation for convention-breaking.**

In this section we examine whether there can exist a conventional ESS (escalate in one role, retreat in the other) when reserve strategy is set by recurrent mutation for convention-breaking. To do this, we first assert that there are two possible ESSs, commonsense and paradoxical, and establish what the reserve strategy must be for each case. We then see whether these can truly be ESSs against convention-breaking mutants.

First assume that the convention 'escalate in *A*, retreat in *B*' has become established. Every so often, rare mutants arise that fail to obey the convention to retreat when in *B*. The simplest assumption is that such mutants differ only in this single respect from other members of the population, so that they fight using the reserve strategy of the rest of the population. These mutants will exert selection on the reserve strategy. It is easy to show that in such contests, the only stable reserve strategy is that which plays $p(x)$ as in (3) but with mean V_A/K_A , assuming that the convention is to persist only in *A*. This is the only strategy that gives a zero expectation against the mutant strategy. A reserve strategy with a higher mean is under selection to reduce, since it has a negative payoff against the mutants; a reserve strategy with lower mean is under selection to increase, since this gives a greater chance of winning. On the other hand, if the population is playing the paradoxical strategy 'persist in *B*, withdraw in *A*' then it follows that the reserve strategy will be eroded to 'play $p(x)$ with mean V_B/K_B '. Note that the mean escalation cost would be higher for the commonsense strategy than for the paradoxical strategy.

How stable are these strategies? Consider first the commonsense case where animals escalate in *A* with

$$p(x) = \frac{K_A}{V_A} \exp(-x K_A/V_A)$$

and retreat in *B*. Can one of the convention-breaking mutants (called *J*) spread? We shall assume that *J* contests with probability p_B when in *B*, by using the same strategy as the reserve strategy of *I*.

$$\text{Then } E(I, I) = \frac{V_A}{2}$$

$$E(J, I) = \frac{V_A}{2} + p_B \left(\frac{V_B}{2} - \frac{K_B}{2} \cdot \frac{V_A}{K_A} \right)$$

and so $E(I, I) > E(J, I)$ if, for any p_B , $V_A/K_A > V_B/K_B$.

By a similar technique, it is possible to show that the paradoxical strategy can always be invaded by the convention-breaking mutant if $V_A/K_A > V_B/K_B$. Only the commonsense assessor can be an ESS.

The above analysis is simplistic in its assumption that escalation is allowed only in one role. Simulations in which a set of persistence times could be played in either role showed that the above conclusions are largely unaffected, provided that recurrent mutation generates rare individuals of two sorts: those that always play as if they were in *A*, and those that always play as if they were in *B*, whatever their role. If recurrent mutation generates only individuals that always play as if *A*, a form of paradoxical ESS (but with some escalation in *A*) is possible if the starting condition is essentially a paradoxical convention. This is because reserve strategy in *B* is not being tested. A more detailed account of this problem will be published elsewhere.

(ii) **Mistakes about role.** Now suppose that information about roles *A* and *B* is slightly imperfect, so that opponents occasionally make mistakes about which role they are in. We shall again make the restrictive assumption that when such mistakes are rare, an ESS must consist of a state in which an animal escalates on estimating itself to be in one role, and withdraws on estimating itself to be in the other role. This assumption is *not* correct, because if mistakes can occur in both roles, then an ESS will consist of some escalation in both roles. But if mistakes are rare it is a good approximation, because the amount of escalation in one role must approximate to zero and consequently exerts a minor effect on the strategy played in the 'escalating' role. This strategy (= the reserve play) is consequently tested mainly by the mistakes.

Let P = the probability that an individual is correct about its role; $(1 - P)$ = the probability that it is incorrect. If assessments are generally correct ($1 > P \gg \frac{1}{2}$), it may seem that an escalating animal is normally in the escalating role. In fact, it only thinks it is, and there is an equal probability = $P(1 - P)/2$ that it is really in *A* or *B*. So when escalation actually occurs, individuals have no information as to which is correct. For the reserve play to be stable, escalation must

yield a zero expectation. Calling ϕ = the mean of the exponential distribution $p(x)$ of selected bids ($\phi/2$ = the mean of observed bids), we require that:

$$\frac{P(1-P)}{2} \left(\frac{V_A}{2} - \frac{K_A \phi}{2} \right) + \frac{P(1-P)}{2} \left(\frac{V_B}{2} - \frac{K_B \phi}{2} \right) = 0$$

probability times payoff when really in *A* probability times payoff when really in *B*

$$\therefore \phi = \frac{\bar{V}}{\bar{K}}; p(x) = \frac{\bar{K}}{\bar{V}} \exp(-\bar{K}x/\bar{V})$$

Because both individuals are in the same information situation when they escalate then they must play in accordance with the ESS for a population that ignores the asymmetry. Remember that this conclusion is an approximation that holds only when mistakes are rare.

Will a strategy *I* that has this reserve play in its escalating role be stable against *J* that escalates (using the same reserve play) in either role? It is easy to show that exactly equivalent conditions apply here to the case of recurrent mutation. Only the commonsense 'assessor' that escalates in *A*, where *A* has $V_A/K_A > V_B/K_B$, can be an ESS. The paradoxical strategy, that escalates in *B*, is invadable.

Further work to be published separately, showed that the true ESS for the case of imperfect role assessment is in fact to play two non-overlapping distributions of persistence times, a higher one in *A* and a lower one in *B*, without a gap between distributions. (A rather similar ESS has been obtained analytically by Bishop et al. (1978) for a contest in which an opponent 'knows' only his resource value (*V*) but not that of his opponent.) This converges towards the assessor ESS as information tends towards perfection. Forms of paradoxical ESS can be maintained only if animals make no mistakes in role *B*.

3. Imperfect Information: Selection Acting on Assessment Abilities

We know that assessor mutants will spread where previously there was no information about roles, even if the assessor is rather poor at assessment. We also conclude that where role

assessment is perfect (except for rare mutants lacking role perception) or where role assessment is almost perfect, a strategy approximating to the assessor strategy is the only ESS. We now

ask whether selection can act to increase abilities to assess roles.

One way to approach this problem would be to find the ESS at a particular level of ability *P* to assess roles, then to examine the success of a mutant with better assessment ability (has $P' > P$), assuming that it retains the same strategies on estimating *A* and *B* as the rest of the population. Though we have established by simulation that there is only one ESS at any particular *P*, this approach will be possible only when the ESS is formulated analytically. Instead, we have investigated an alternative scenario. We simply assume that it is rather difficult, in evolutionary terms, to adjust $p(x)$, but relatively easy to evolve a decision to drop out of a contest immediately in response to particular cues. Thus we shall allow only the choice of two strategies: withdraw, or contest with a fixed $p(x)$. The fixed $p(x)$ chosen is 'play negative exponential with mean $\phi = \bar{V}/\bar{K}$ ' as in (3a), since this is the ESS to the game in which there is no information about roles *A* and *B*. This is assumed to be the starting point for $p(x)$; it also approximates to the end point if assessment approaches perfection. An opponent can play a mixed strategy for contesting/withdrawing (p_A = probability of contesting on estimating *A*, p_B = probability for *B*).

We find that although it will always pay to contest when role *A* is estimated (see Appendix I. 1), when role *B* is estimated and information is not very good, there should be a mixture of tendencies to contest and to withdraw (see Appendix I.2). In short, the assessor strategy need not fixate in the population. Provided that what animals do in contests remains fixed as $p(x)$ with $\phi = \bar{V}/\bar{K}$, then at any given level of information about roles that is poorer than a level we shall call P^* , there exists a stable proba-

bility p_B ($0 < p_B < 1$) = the probability of contesting when B is estimated. This has:

$$p_B = \{[P(V_A K_A - V_A K_B + 3V_B K_A + V_B K_B) + V_A K_B - V_B K_A] / (V_A K_A + V_A K_B + V_B K_A + V_B K_B) - P^2\} / P(1 - P); P \in [\frac{1}{2}, P^*] \quad (6)$$

However, we again emphasize that this condition is not the true ESS, which as discussed, consists of two truncated and adjoining distributions of persistence times. It is simply a plausible transient population state in which we shall examine the success of a mutant with better assessment abilities.

Suppose then that ϕ remains fixed; what will be the relationship between p_B and P ? From (6) and Appendix I.2, it is easy to deduce that $p_B = 1$ only if

$$\frac{V_A}{K_A} (2P - 1) \leq \frac{V_B}{K_B} (2P - 1) \quad (7)$$

Since by assumption $V_A/K_A > V_B/K_B$, the strategy for always contesting in B can occur only if $(2P \leq 1)$, i.e. animals can do no better than guess their role ($P = 0.5$), or are usually incorrect ($P < 0.5$). Alternatively, for $p_B = 0$ requires that:

$$P(V_A K_A - V_A K_B + 3V_B K_A + V_B K_B) + V_A K_B - V_B K_A \leq P^2(V_A K_A + V_A K_B + V_B K_A + V_B K_B) \quad (8)$$

As we would expect, this inequality can never be satisfied if $P \leq \frac{1}{2}$, but if P approaches 1, then

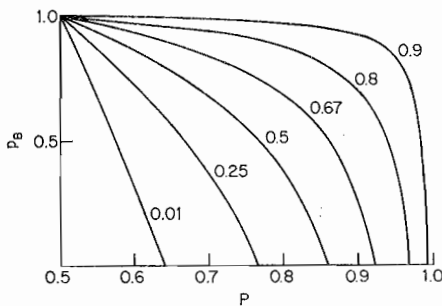


Fig. 1. Transient stable values for p_B (probability of contesting when in role B) at any given state of information P about roles, assuming that if both individuals contest they will do so with a negative exponential distribution of persistence times selected from $p(x)$ with mean $\phi = \sqrt{V/K}$ (and observed mean = $\sqrt{V/2K}$). This is not an ESS at a given P (see text) but gives a minimum likely p_B value, obtained from equation (8). Values on the curves are for $\mu = (V_B/K_B)/(V_A/K_A)$. For a given μ , P^* is the intercept on the P axis.

it requires simply that $V_A/K_A > V_B/K_B$. Equations (7) and (8) establish the range of mixed

strategy, $0 < p_B < 1$, for $P \in [\frac{1}{2}, P^*]$. At higher information levels $P \in [P^*, 1]$ the assessor strategy $p_B = 0$ will fixate; at $P \in [0, \frac{1}{2}]$ the stable strategy is $p_A = 1, p_B = 1$. The critical determinant of p_B within the mixed range is the ratio $\mu = (V_B/K_B)/(V_A/K_A)$; Fig. 1. The closer μ approaches to its maximum value of 1.0, the higher the tendency p_B to contest at a given $P \in [\frac{1}{2}, P^*]$, and the greater the value of P^* . Contradictions between asymmetries are most likely to generate high values for μ because of the compensatory effects of the two asymmetries, but exactly the same effects can be generated by very weak non-contradictory asymmetries. Strong non-contradictory asymmetries yield lowest μ and hence lowest tendencies for contesting when in B .

We now ask whether abilities for improved role assessment will spread when the transient state in (6) is operative. Call the transient strategy I . Let us first assume that p_B is achieved by genetic monomorphism, so that a mutant J arises that deviates only in its role assessment and not in p_B . The full payoff matrix becomes as shown in M1:

		Against opponent that:		
		contests	retreats	
Half contests estimates A	Correctly	$P'(1-P+p_B)\left(\frac{V_A}{2} - \frac{K_B\phi}{2}\right)$	$P'(1-p_B)V_A$	(M1)
	Incorrectly	$(1-P)\left[p + (1-p)p_B\right]\left(\frac{V_B}{2} - \frac{K_B\phi}{2}\right)$	$(1-p)(1-P)(1-p_B)V_B$	
Half contests estimates B	Correctly	$Pp_B\left[p + (1-p)p_B\right]\left(\frac{V_B}{2} - \frac{K_B\phi}{2}\right)$	$Pp_B(1-P)(1-p_B)V_B$	
	retreats	0	$P'(1-p_B)^2(1-P)V_B/2$	
	contests	$(1-P)p_B\left[1-P+p_B\right]\left(\frac{V_A}{2} - \frac{K_B\phi}{2}\right)$	$(1-P)p_B P(1-p_B)V_A$	
	retreats	0	$(1-P)(1-p_B)^2 P V_A/2$	

After extensive manipulation, (M1) can be used to show that:

$$E(J, I) - E(I, I) = (P' - P) \left[V_A K_A \left(\frac{P}{2} - \frac{3Pp_B}{2} + Pp_B^2 \right) + V_A K_B \left(\frac{P}{2} - Pp_B + \frac{p_B^2}{2} (P - 1) + \frac{1}{2} \right) \right]$$

$$\begin{aligned}
 &+ V_B K_A \left(\frac{P}{2} + p_B (1 - P) + \frac{P p_B^2}{2} - 1 \right) \\
 &+ V_B K_B \left(\frac{P}{2} + p_B (1 - P) + \frac{P p_B^2}{2} (P - 1) - \frac{1}{2} \right) \quad (9)
 \end{aligned}$$

We were able to confirm that the square-bracketed part of (9) is always positive if $P > \frac{1}{2}$ and p_B follows (6). This means that a mutant J with better role assessment abilities ($P' > P$) will always spread. Further, if it can spread it is likely to fixate if p_B remains temporarily unchanged (the likely case if the population is monomorphic for p_B), since increased P demands a lower ESS p_B than will currently be available. After fixation of J , p_B will re-adjust (following mutation) to its new reduced level, to be re-invaded by a new mutant J' with even better abilities, and so on until role assessment approaches perfection (assuming infinite time and infinitesimal costs of perfecting assessment).

This leads to consideration of the case in which p_B is achieved by genetic polymorphism between individuals that always drop out of contests when they estimate B , and those that always contest in both roles. From previous arguments, if the population starts at $P = \frac{1}{2}$ with $p_B = 1$, a mutant assessor K that retreats when estimating B will spread to frequency $(1 - p_B)$. It follows that a second mutation in K to K' that has improved role assessment ($P' > P$) will invade. Though we have not established it analytically, it seems likely that this mechanism would also drive role assessment abilities towards perfection.

Let the part of (9) in square brackets = S ; it gives a measure of selection intensity acting on abilities to improve assessment. Figure 2 shows that S increases exponentially with increasing P (the assessment abilities currently prevalent in the population) until P^* , after which S increases linearly. Selection intensity is weakest when assessment abilities are poorest ($P \approx \frac{1}{2}$). Remembering that when $P = \frac{1}{2}$, p_B must = 1, and substituting $p_B = 1$ into (9), gives a zero within the square brackets (this has to be so because if $p_B = 1$ there is no difference in strategies when A or B is estimated). But we know from previous arguments that an escalating, role-ignoring population will be invaded by a mutant that tends to drop out of contests

when in B , so that there is no major impediment to getting role assessment started from a condition of no information.

When there is a strong contradiction between asymmetries but V_A/K_A is not much greater than V_B/K_B (curve 1, Fig. 2), then $S(P)$ increases very little until it rises dramatically at a very high value of P . Where increasing information has costs, it is quite possible that role assessment will not here develop. Alternatively, strong non-contradictory asymmetries can generate steeply increasing $S(P)$ curves (Fig. 2).

In conclusion, abilities to assess roles can improve as a result of selection. Where improving assessment costs nothing, abilities to estimate roles A and B (defined as $V_A/K_A > V_B/K_B$) should proceed to a maximal level with selection intensifying as role assessment improves. Where costs of assessment increase as accuracy improves, then this need not be so unless asymmetries in payoff are very strong.

If asymmetries in payoff between the two roles are slight and costs of assessment are high, assessment may not evolve at all.

Acquisition of Information During Contests

For most contests, it is likely that good information, particularly about RHP, can be acquired only during a contest itself, and at a cost. A simple model for such circumstances is given

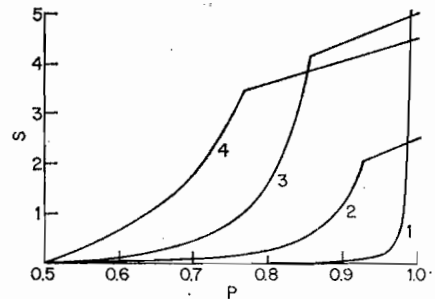


Fig. 2. Function $S(P)$, a measure of selection intensity S acting to improve assessment abilities at any given current level of ability P , assuming that the transient stable state for p_x is as in Fig. 1. Value S is obtained from the part of equation (9) in square brackets, with p_B set by equation (8). Curves are for the following conditions: (1) strong contradiction between asymmetries, $V_A = K_A = 1$, $V_B = 9$, $K_B = 10$. (2) weak contradiction between asymmetries, $V_A = K_A = 1$, $V_B = 2$, $K_B = 3$. (3) non-contradictory asymmetry, $V_A = K_A = 2$, $V_B = 1$, $K_B = 2$. (4) non-contradictory asymmetry, $V_A = K_B = 2$, $V_B = K_A = 1$.

Curves rise exponentially until P^* (see Fig. 1) after which P value they rise linearly; the linear stage is omitted from (1).

by Maynard Smith & Parker (1976). We now attempt a more complex version of their model.

Imagine a contest as a series of rounds. Before round 1, opponents have no information about relative RHP or V . The outcome of each round of the contest conveys some information as to which opponent has higher RHP. Resource value V may be correlated (probably inversely, see p. 223) with RHP, and so the outcome may also convey information about V . Again call the two opponents A and B , but now A is simply the individual with higher RHP. Say that A has probability x of winning a particular round ($\frac{1}{2} < x \leq 1$). Unless $x = 1$, then A may in fact lose, and so it may pay to continue to the next round even after losing. In short, outcomes of rounds convey only imperfect information about RHP unless $x = 1$.

1. The Model

What decision should an animal make if it loses a round? Should it continue to the next round, or withdraw from the contest? We envisage that decision rules will be related to predictions from Bayes theorem. If the probability that B will lose is $P(L/B) = x$, and the prior probability of being the B animal is $P(B)$, then according to the theorem the probability of a loser being B is

$$P(B/L) = \frac{P(L/B) \cdot P(B)}{P(L/B) \cdot P(B) + P(L/A) \cdot P(A)} \quad (10)$$

where L designates a loss. Although we assume that at the start of the contest, $P(A) = P(B) = 0.5$, these prior probabilities will change before the start of each subsequent stage in the contest.

Following Maynard Smith & Parker (1976) we incorporate this iterative process of information gathering into a decision model for animal contests. To make the mathematics more tractable we make a number of simplifying assumptions.

(i) **Stages in a fight.** Contests are divided into three stages or rounds — early, middle, and late (stages 1, 2 and 3).

(ii) **Strategies for retreat.** Three strategies exist, which relate to the stage at which an animal is prepared to give up. These are:

S1 = 'retreat if lose stage 1, or if lose stage 2, otherwise continue';

S2 = 'continue past stage 1, whatever its outcome; retreat if lose stage 2, otherwise continue';

S3 = 'always continue to stage 3 regardless of outcomes of stages 1 and 2'.

(iii) **Fighting tactics.** At any stage in the contest any of three fighting tactics can take place, ranging in intensity from low (L), to medium (M), to high (H). Which tactic occurs at which stage is set quite arbitrarily by conventional rules (we are not initially concerned with the evolution of tactic sequences, though this will be considered later). Each tactic enables an individual to gain a certain amount of information about RHP, but at a cost, as explained below. In Maynard Smith & Parker's (1976) model, contests escalated but information remained constant from stage to stage.

(iv) **Information trade-off from tactics.** Information about roles is assumed to increase as tactic intensity increases. In terms of equation (10), the higher the intensity of the tactic, the higher $P(L/B) = x$, i.e. $x_H > x_M > x_L$. We also assume that information obtainable from a given tactic is not absolute, but increases with the difference in RHP between contestants. To achieve this, we call x_* a theoretical maximum probability that A will win a given round when the tactic employed is at the most intense 'all out' level possible (i.e. most informative level possible). We then allow $P(W/A) = P(L/B) = x$ to vary for L , M , and H tactics as follows:

$$x_L = 0.5 + \left(\frac{x_* - 0.5}{2} \right),$$

$$x_M = x_L + \left(\frac{x_* - x_L}{2} \right),$$

$$x_H = x_M + \left(\frac{x_* - x_M}{2} \right).$$

In other words, L increases information to a point half way between randomness and x_* , M takes it to $3/4$, and H to a point $7/8$ towards x_* .

(v) **Contest costs.** We assume that these are of two types. 'Energetic costs' (e_i) include all costs that are incurred automatically and equally by both opponents, and which therefore carry no information about subsequent outcomes. In contrast, 'damage costs' (D_i) arise from the injury sustained only by the loser of a given stage i . Both types of cost increase equally as tactic intensity increases. Low intensity tactics are

therefore cheap, but their outcome provides little information about roles, and vice versa. Remember also that when opponents are more evenly matched, then costs of a given tactic remain the same but information gained about the outcome of the next stage is poor (see above). Thus to obtain a given amount of information, costs are relatively greater the more evenly matched the opponents.

(vi) **Prior information.** As with Maynard Smith and Parker (1976), we assume that although a contestant does not 'know' his role before the first round, he does 'know' the degree of symmetry associated with the contest. Biologically, x can most easily be interpreted as the *average* value for the symmetry in the population of combatant pairs. Clearly, the model would be more appealing if x were to relate to given contest cases. The immediate reason why x cannot relate to unique contests is that if individuals could assess x before the contest, it is most unlikely that they would be unable to assess roles. However, the model can be given this extended form by making the additional assumption that some feature of round 1 is correlated with the degree of asymmetry x . Most plausibly this could be the time taken for an outcome to be achieved. For example, if damage is inflicted very quickly, the expectation is that x is high for the pair of combatants. The virtue of a cue such as round duration is that it is independent of role. A cue that correlates both with x and with role would act as a confounding variable in the present model, unless its correlation with role is insignificant relative to the cue of losing the round.

Following these specifications, it is now possible to determine ESSs for S1, S2, S3 under a variety of conditions. To this end, we first listed all possible outcomes and their probabilities of occurrence, for each pair of strategies. We then derived general formulae for the expected payoff of each strategy against every strategy (see Appendix II). Finally, we substituted into these equations various numerical values for damage costs (D_i) and energetic costs (e_i), resource value V , and various tactical combinations of x_L , x_M , x_H to determine payoffs for each possible pair of strategies for a given tactical convention. A tactical convention is simply our arbitrary choice of what tactic is always played at what stage of the fight; i.e. it may be for escalating (L \rightarrow M \rightarrow H), or for de-escalating (H \rightarrow M \rightarrow L), or some other permutation.

Finally, it is important to stress again (see (10)) that information about the outcome of a given

stage consists of two components: (i) the prior probability that a given individual is A or B , derived from the previous round; and (ii) the absolute probability of winning the stage for an individual A or B . Both depend critically on the tactical convention. For instance, if the convention is to escalate, (i) is relatively low but (ii) relatively high, and vice versa if the convention is to de-escalate.

2. Some Results for Asymmetries Only in RHP

We first consider the case where $V_A = V_B$ ($\gamma = V_A/V_B = 1$ in payoff equations in Appendix II) so that contestants differ only in RHP. Damage costs are $D_L = 1$, $D_M = 3$, $D_H = 9$, and energetic costs e_i are always $= D_i/2$. A variety of values for $\alpha = D/V$ were obtained by varying V . We checked the accuracy and stability of the solutions below by computer simulation.

Figure 3 shows ESS ranges for contests in which the tactical convention is L \rightarrow M \rightarrow H (escalation); continuous lines in Fig. 3 refer to the case where $V_A = V_B$. α_L and α_H refer to D_L/V and D_H/V respectively. Conclusions are as follows:

(i) For every value of x_* there are zones in which each pure strategy is an ESS. For example when $x_* = 0.9$ (individual A has a theoretical maximum chance of winning = 0.9), losses in stages 1 and 2 will be disregarded as long as resource value V is greater than approximately four times the cost of high intensity damage (D_H). S2 replaces S3 if $4 < \alpha_H \leq 1$; it is in turn replaced by S1 if $\alpha_H > 1$.

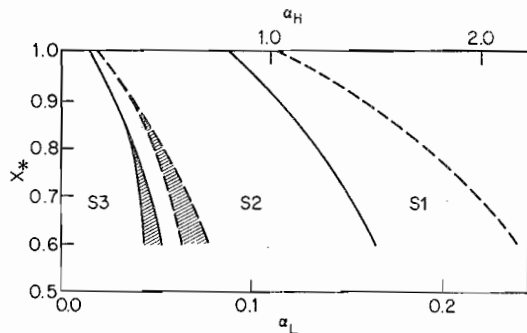


Fig. 3. Threshold values for various ESSs in a population in which the 'tactical convention' is escalated (S \rightarrow M \rightarrow H). Solid lines refer to situations in which both opponents value the resource equally, ($\gamma = 1$), and dashed lines refer to situations in which the less able opponent values the resource more than the more able one ($\gamma = 2$). Hatched areas denote regions where a mixture of S2 and S3 is stable.

(ii) In general, as animals have more to gain from the contest (low α), and where information is poor because opponents are more evenly matched (low x_*), persistence tends to be favoured. As opportunity costs to a loser of wrongly concluding that it is B increase, the less likely it is to retreat. This is despite the fact that (from (10)) the probability of being B has increased from 0.5 to 0.7 after the first loss, and to 0.9 after losing stage 2.

(iii) Only in cases where opponents differ significantly in fighting ability ($x_* > 0.85$) is the ESS necessarily a pure strategy. As opponents become more evenly matched, it is possible for a mixture of strategies S1 and S3 to be evolutionarily stable (cross-hatched zone).

Figure 4 shows the effects on the ESSs of increasing energetic costs (e) whilst holding D_L , D_M , D_H constant as before ($= 1, 3, 9$). This increases the likelihood that animals withdraw if they lose: it makes information relatively more costly to obtain.

Fights need not necessarily follow an escalating convention. Figures 5–7 are for four alternative conventions: 'de-escalation' or $H \rightarrow M \rightarrow L$ (Fig. 5); 'oscillation' or $L \rightarrow H \rightarrow L$ (Fig. 6); and 'constant high' ($H \rightarrow H \rightarrow H$) or 'constant low' ($L \rightarrow L \rightarrow L$) in Fig. 7. The general trend is again that persistence (S3) is most likely to be the ESS when resource value is high (α low) or when opponents are evenly matched (x_* low). But differences in tactical convention can clearly alter the nature of contests quite dramatically.

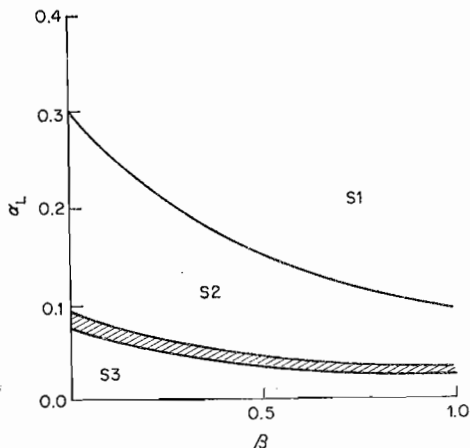


Fig. 4. ESS thresholds corresponding to changes in the energetic costs of the tactics (β). The hatched area corresponds to the region where a mixture of S2 and S3 is stable.

For example when $x_* = 0.9$ and $\alpha_H = 1.0$, the ESS under the escalating convention is S2 whereas it is S1 for the de-escalating and constant high conventions, and S3 for the oscillating and constant low conventions. Examination of Figs 3 and 5 for escalation and de-escalation shows why these differences arise.

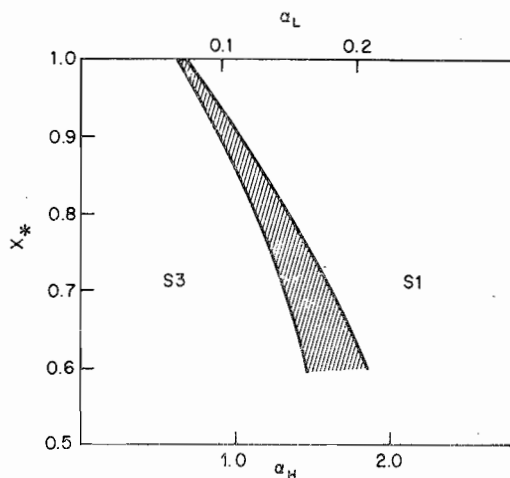


Fig. 5. Threshold values for various ESSs in a population in which the 'tactical convention' is de-escalate ($H \rightarrow M \rightarrow L$). The hatched area denotes the region where a mixture of S1 and S3 is stable.

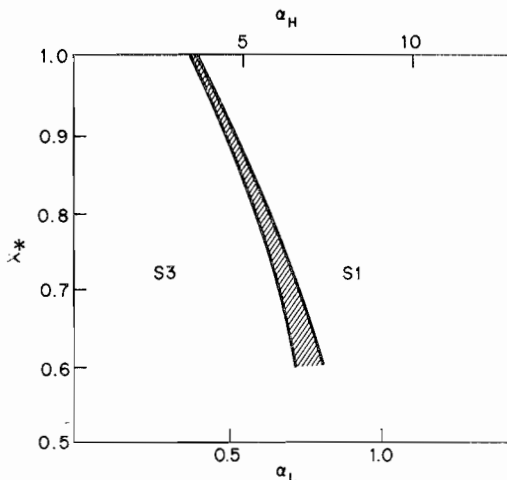


Fig. 6. Threshold values for various ESSs in a population in which the 'tactical convention' is oscillate ($L \rightarrow H \rightarrow L$). The hatched area denotes the region where a mixture of S1 and S3 is stable.

In the escalating convention, strategy S2 is the ESS for a wide range of α . A loss in stage 1 (low intensity) is here such a poor predictor of the outcome of stage 2, that although it will be relatively expensive to gain further information, resource value is sufficiently high to favour continuing after losing. In the de-escalating convention, the situation is more complex: in the same range of α the ESS can be pure S3, pure S1, or mixed S1/S3, but never S2. With de-escalation, a loss in stage 1 conveys very good information about roles *A* and *B* ($P(B/L) = 0.85$ after stage 1), but roles are less important for the outcome of stage 2, and even less for stage 3. Thus given that the first round is unavoidable, it pays to continue to stage 3 for a relatively wider range of α , even though information about roles will be much better than with the escalating convention. Because contest costs are declining as well as roles becoming less important, S2 is never an ESS; it pays either to withdraw after the first loss or to carry on to the end, though there can be a mixed ESS for S1/S3 (cross-hatched zone).

These results indicate that animals will use stages in contests to acquire additional information about roles as long as the costs of doing so

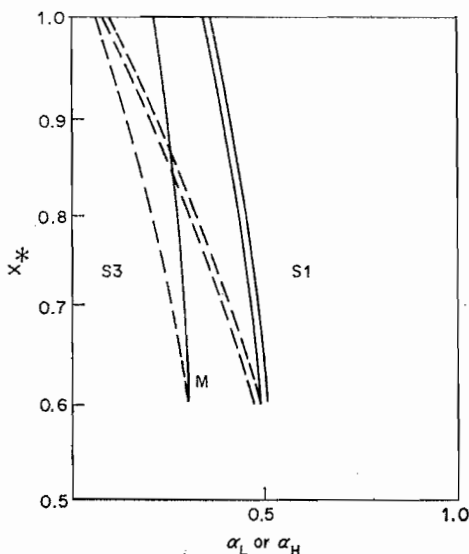


Fig. 7. Threshold values for various ESSs in a constant 'tactical convention' of $L \rightarrow L \rightarrow L$ (solid lines) or $H \rightarrow H \rightarrow H$ (dashed lines). M denotes an area where a mixture of S1 and S3 is stable. The narrow band to the left of S1 is an area where, with recurrent mutation, no pure strategy or mixture of strategies can fixate.

are not high. Where losing a previous bout carries information about success in the next bout, individuals will commonly retreat after losing if the next bout will be very expensive, or if the information acquired is very poor. But even if good information about roles (i.e. which has higher RHP) is obtained, animals will ignore it if roles are not very important in determining victory.

3. Some Results for Asymmetries in Both RHP And V

It will generally be far harder to assess an opponent's resource valuation V than his RHP. However, as we have argued earlier, the two may be correlated (often inversely) so that information about relative RHP may also carry some information about relative V . How will this affect the predictions of the model? This can be ascertained simply by altering $\gamma = V_B/V_A$ in the payoff equations in Appendix II. To do this without changing the relationship between the mean value (\bar{V}) of the resource and the contest costs (D and e), we arranged values of V_A and V_B to give a constant value for $\gamma \neq 1$. This prescribes a new α value, since α is strictly $\alpha_i = D_i/V_A$. In Fig. 3 the broken curves are for the case where $\gamma = 2$ (i.e. the individual with higher RHP, (*A*), has only half the amount to gain as his opponent). The effect is to shift all ESS thresholds to higher values of α . This conclusion is intuitively obvious: when the weaker individual *B* has relatively more to gain, less heed should be paid to losing a bout. Alternatively, when the stronger individual has more to gain ($\gamma < 1$; not included in Fig. 1) all ESS thresholds are shifted to lower values of α : it becomes more valuable to withdraw after losing.

4. Competing Tactical Conventions

What happens if a population adopting one tactical convention is invaded by a subset of another population that follows a different convention? Would one ESS displace the other? The answer to these questions is complex, and depends heavily on what costs are incurred by individuals playing a low intensity tactic against a higher intensity tactic. We envisage two extreme possibilities.

(i) **Ritualized Contests (R)**. Players only incur the energetic costs of their tactic. This seems plausible only for the most ritualized forms of display. The 'winner' is always the higher-intensity player, whatever the true RHP of the two players. Our justification for this assumption

is that animals may monitor an opponent's agility and dexterity in response to its own display.

(ii) **Non-Ritualized Contest (NR).** The lower-intensity player always incurs damage costs at the higher intensity level; energetic costs are again felt by each opponent in accordance with their tactic. This seems appropriate for completely non-ritualized contests in which low intensity actions are inadequate to parry those of a higher-intensity opponent, so that a lower-intensity player always incurs injury. Again, winning or losing is quite independent of RHP roles *A* and *B* unless opponents have matching tactics, in which case all rules are identical to the previous model.

Two simple cases will be examined:

(A) *Resource value low relative to damage costs (α high).* Here α_H is high enough ($\alpha_H > 5.0$) to ensure that *S1* is the ESS for both constant high and constant low tactic conventions (see Fig. 7). If these conventions were to mix with *S1_L* at frequency *p*, *S1_H* at $(1 - p)$, the expected payoff to *S1_L* for the ritualized and non-ritualized cases would be:

$$\bar{W}_{LR} = p \left\{ \frac{1}{2} [x_L V - (1 - x_L) D_L - e_L] \right. \\ \left. + \frac{1}{2} [(1 - x_L) V - D_L x_L - e_L] \right\} \\ + (1 - p) (-e_L)$$

and

$$\bar{W}_{LNR} = p \left\{ \frac{1}{2} [x_L V - (1 - x_L) D_L - e_L] \right. \\ \left. + \frac{1}{2} [(1 - x_L) V - D_L x_L - e_L] \right\} \\ + (1 - p) (-D_H - e_L)$$

respectively. The expected payoff to *S1_H*, which is the same for both cases, would be

$$\bar{W}_H = p(V - e_H) + (1 - p) \left\{ \frac{1}{2} [x_H V \right. \\ \left. - (1 - x_H) D_H - e_H] \right\} \\ + \frac{1}{2} [(1 - x_H) V - x_H D_H - e_H]$$

By setting $\alpha_L = D_L/V$, $\alpha_H = 9\alpha_L$, $\beta_L = e_L/D_L$, and $\beta_H = 9\beta_L$, we find that the ESS in the ritualized case will be *S1_L* if $\alpha_L > 1/(16\beta_L - 1)$, and *S1_H* if $\alpha_L < 1/(16\beta_L + 1)$. In the range between these values the ESS will be a mixture of *S1_L* and *S1_H* in which the frequency of *S1_L* will be

$$p = \frac{1 - 9\alpha_L - 16\alpha_L\beta_L}{-10\alpha_L}$$

So that at a given β_L , the more serious the damage costs (α_L high), the more likely *S1_L* is to be the pure ESS. For the ritualized case, the situation is more complex. There can be no stable

mixture of *S1_L* and *S1_H*. If $\alpha_L < 1/(16\beta_L - 1)$, *S1_H* is a pure ESS. When $\alpha_L > 1/(16\beta_L - 1)$, either strategy can be a pure ESS, depending on their starting frequencies. If the starting frequency of *S1_L* is

$$p > \frac{1 + 9\alpha_L - 16\alpha_L\beta_L}{8\alpha_L}$$

then *S1_L* fixates; *S1_H* fixates if the sign is reversed. As before, increases in β_L or α_L increase the likelihood that *S1_L* is the ESS. For instance, with $\alpha_L = 0.55$, $\beta_L = \frac{1}{2}$, *S1_L* is the ESS if $p > 0.35$; at these α_L and β_L values *S1_L* is also the pure ESS for the ritualized case.

(B) *Resource value high relative to damage costs (a low).* Let $\alpha_L = 0.25$; damage is not very expensive. Consider now a competition between escalating tactics and constant low tactics. Under the escalating convention *S1* would be the ESS, whereas *S3* is the ESS for constant low tactics. If *p* is now the frequency of *S1* (individuals playing escalating convention) when the two populations meet, the expected payoff of *S1* for both ritualized and non-ritualized cases would be:

$$\bar{W}_{S1} = p.E(S1, S1) \\ + (1 - p) \left\{ \frac{1}{2} [x_L(V - e_L - e_M - e_H) \right. \\ \left. + (1 - x_L)(-D_L - e_L)] \right\} \\ + \frac{1}{2} [(1 - x_L)(V - e_L - e_M - e_H) \\ + x_L(-D_L - e_L)]$$

For *S3* (individuals playing constant low convention) the expected payoffs for the two cases become:

$$\bar{W}_{S3R} = p \left\{ \frac{1}{2} [x_L(V - e_L) \right. \\ \left. + (1 - x_L)(-D_L - 3e_L)] \right\} \\ + \frac{1}{2} [(1 - x_L)(V - e_L) \\ + x_L(-D_L - 3e_L)] \\ + (1 - p).E(S3, S3)$$

$$\bar{W}_{S3NR} = p \left\{ \frac{1}{2} [x_L(V - e_L) + (1 - x_L) \right. \\ \left. (-D_L - D_M - D_H - 3e_L)] \right\} \\ + \frac{1}{2} [(1 - x_L)(V - e_L) \\ + x_L(-D_L - D_M - D_H - 3e_L)] \\ + (1 - p).E(S3, S3)$$

Values for $E(S1, S1)$ and $E(S3, S3)$ can be found in Appendix II. Again by setting $\alpha_L = D_L/V$, $\alpha_H = 9\alpha_L$, $\beta_L = e_L/D_L$, and $\beta_H = 9\beta_L$ we find that *S1* will always be the ESS as long as $\beta_L < 0.25$ (for both ritualized and non-ritualized cases). There can be no stable mix of *S1* and *S3*, but if $\beta_L > 0.25$ the pure ESS depends on the initial conditions. For the ritualized case, *S1* spreads to fixation if its starting frequency $p >$

$(4\beta_L - 1)/(5\beta_L - 1)$. For the non-ritualized case S1 goes to fixation if $p > (4\beta_L - 1)/(5\beta + 5)$. In both cases, as long as energetic costs are small, a strategy of short fights will evolve, with escalation as a reserve play if the winner is then challenged. But as energetic costs increase, a greater proportion of the initial population must follow the escalating convention if the constant low convention (having S3) is to be prevented from successfully displacing it. S1 is more likely to be the ESS in the non-ritualized case, because for any given level of energetic costs (β) the critical p will be smaller. For the present example with $\alpha_L = 0.25$ and $\beta_L = \frac{1}{2}$, S1 would be the the ESS for non-ritualized contests if more than 13% of the initial population were S1. But it would only be the ESS in the ritualized case if over 67% of the initial population were S1.

In conclusion, we can say that it may often be rather difficult to change a given tactical convention, once this has been established in a population, unless the frequency of an alternative convention can suddenly exceed a certain critical threshold (e.g. by drift or by mixing of sub-populations).

Discussion

Our analyses suggest that where animal contests follow war of attrition principles (victory goes to the individual that is prepared to persist longest), selection will favour abilities to acquire information about roles. Contests will obey rules set by an interaction between asymmetries in fighting ability (RHP) and resource value (V). When role assessment approaches perfection, the ESS is likely to be 'commonsense' and will approximate to the form of an optimal assessor strategy as outlined in (1) and (2) (following Parker 1974).

But just because assessment can evolve does not mean that escalated contests will not occur. Contests will be settled entirely peacefully only if reliable estimates of RHP and V can be obtained quickly and cheaply (e.g. by a short assessment phase, or display). This is the assumption of our first model. Because phylogenetic constraints will doubtless limit assessing abilities, animals will occasionally make mistakes about their roles, especially where 'role asymmetries' are weak. We define a role as being set by the interaction between asymmetries in RHP and in V . Hence a weak role asymmetry can arise either because asymmetries in both aspects (RHP and V) are weak, or because asymmetries in both aspects are strong but contradictory, so that their

effects tend to be compensatory. Weak role asymmetry, undetectable by short assessment, will lead to escalation. However, if opponents do escalate into a true contest, role assessment need not have ended. The assumption of our second model is precisely that animals will use the contest itself to increase information.

Despite a vast literature on animal fighting, good evidence for assessment strategy is not easy to obtain (see some examples reviewed by Parker 1974). What evidence there is is often compatible with the prediction that fights tend to escalate or increase in length when opponents are closely matched (e.g. mirror experiments) or where asymmetries in RHP and V are contradictory. For example, in the crayfish *Orconectes virilis*, larger individuals are more likely to attack and defeat smaller individuals (Rubenstein & Hazlett 1974). When size differences are small, fights are significantly longer. Further, when some crayfish were starved for a week (presumably increasing their V), they showed a marked increase in their tendency to attack and win contests against larger crayfish that were well fed (Hazlett et al. 1975). In another example, the pygmy sunfish (*Elassoma evergladei*), small fish tend to be subordinate to large fish. As a result they are usually inactive except when searching for food. If they locate a food item close to a dominant fish, they usually continue searching or return to their retreat if they have fed fairly recently. If, however, the same situation arises after many days of starvation, they almost always strike at the dominant and drive it away from the prey. An intense, protracted fight ensues, but in about 60% of such contests the subordinate gets the prey (Rubenstein 1977).

We see assessment displays primarily as adaptations to obtain information about an opponent; this necessarily produces selection for bluff, or even concealment of cues (Parker 1974; Maynard Smith & Parker 1976). During a contest, an individual may itself convey information by making a probe to obtain information. In a sense, this is a form of (inadvertent) communication. In complete contrast, there can exist contest situations in which selection may have actively favoured specialized signals. For instance, Clutton-Brock & Albon (1979) argue that red deer stags monitor roaring rate as a means of RHP assessment and that this is uncheatable because roaring contests are so exhausting. Escalated contests are very costly. Another example, which is also entirely compatible with an 'assessor' interpretation, is given

by Parker et al. (1974) for the locust *Locusta migratoria*. Here single males attack males paired to females, and take-overs can occur, especially while the female is ovipositing. The interesting feature of these encounters is that the paired male stridulates and performs other signals with the hind legs, which tend to dissuade the attacker from continuing to the next stage of the attack, and tend to cause it to withdraw. Parker et al. (1974) argue that such signals advertise that the paired male is aware of the attacker, and that attacks are much less likely to be successful when this is so because of the paired male's defensive reactions. To be successful, the attacker must insert itself in between the paired male and the female in such a way that, if prepared, the paired male can very effectively kick away the attacker using one of its powerful hind legs. Thus at the moment of perception of the attack (i.e. the moment the signal is given) there is a dramatic change in relative RHP in favour of the resource holder, such that the appropriate assessment for the attacker is to withdraw in response to the signal. This example also indicates why we prefer to use the general term 'RHP' rather than simply 'fighting ability'.

Our models for information acquired during a contest are intended to develop the proposition that role assessment may have costs. Good information about RHP may be obtainable only during some form of trial of strength or weaponry; role assessment may improve as contest costs increase. Behaviour like push-pulling contests (many examples reviewed by Eibl-Eibesfeldt 1970) are plausible candidates for assessment tournaments, but though 'trials of strength' (or weaponry) were commonly discussed in ethological literature, quantitative evidence is not abundant. Much, as we have shown, will depend on how much information can be gained for a given amount of risk or energy expenditure; and much will depend on the current 'tactical convention' of the population. A tactical convention is simply the established format or sequence of fighting tactics during a prolonged contest; it is often assumed or deduced from observation that contests either remain at the same level or gradually escalate to riskier and more damaging levels. Our analysis indicates that tactical conventions will often be difficult to alter because they are often unavoidable by mutants playing different tactics. Changes can often only be achieved by sudden big increases in the frequency of a deviant tactic, e.g. by drift or by mixing of sub-populations.

When information about roles is being developed during a contest, the outcome of each stage contains some information about the true role of each opponent. In general, contests will be settled quickly when:

(i) contest costs are high relative to resource value, and/or

(ii) an outcome is both a good predictor of RHP (has high information content) and the RHP disparity is big enough to ensure that this information about RHP asymmetry will be important for subsequent outcomes.

In our own model we allow animals to gain better information by more costly tactics: (i) and (ii) above interact in a complex way. If information is poor (or RHPs similar) and costs small, animals may 'gamble' that they will triumph in the last round: it may not pay to withdraw earlier. It becomes difficult to determine whether animals persist through the contest to obtain better information, or because costs are low.

Both models examined in this paper assume that an animal can persist after sustaining damage. In the first model, where mean costs increase in fixed ratio to RHP, an individual can persist to any cost level. In this respect our models differ markedly from 'hawks/doves' games (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Treisman 1977) in which an injured opponent always retreats immediately. The main virtue of hawks/doves models is their mathematical simplicity. Our first approach to the problem of interacting asymmetries began with such a model in which individual A has probability x of winning and V_A is the resource value (B has chance $(1-x)$ of winning V_B). Strategies were 'dove' = 'always retreat if opponent escalates'; 'hawk' = 'escalate, so that if opponent also escalates, one opponent will sustain an injury costing $-D$ fitness units; retreat if injured'. Information about roles is perfect. The analysis (Appendix III) of this game was identical to that of Maynard Smith & Parker (1976) for the same game that is asymmetric only in RHP. As we would expect, only pure ESSs can exist where information about roles is perfect. We also showed (see Appendix III) that a commonsense convention 'escalate when expected benefits exceed expected costs, otherwise retreat' will be an ESS. Calling role B the role in which the value for expected benefit $V_B(1-x)$, minus expected costs Dx , is lowest, this is equivalent to an ESS that escalates in both roles if $V_B(1-x) > Dx$, but retreats in B when the sign is reversed. Paradoxical ESSs also exist.

These conclusions are parallel to those of Maynard Smith & Parker (1976) for RHP asymmetry.

The simple hawks/doves model has some inadequacies. If it pays to escalate, then a mutant that continues to fight when injured will spread, if other individuals normally retreat when they are injured (unless its probability of winning is altered by the injury so that now $V_B(1-x) < Dx$). Also, it seems proper that when two doves meet, the contest follows a war of attrition. However, addition of this continuous strategy set may not alter the properties of the asymmetric game. Selective adjustment of reserve strategy may not here be possible.

Our predictions about selection acting to adjust reserve strategy will generally act to remove the possibility of paradoxical strategies for games that obey war of attrition rules. Recently, Hammerstein (1981) has made an extensive analysis of games with perfect information that obey hawks/doves rules and in which asymmetries relate to RHP, V , and ownership. Reserve strategy in his models is fixed by the pure hawk strategy, with injury at a given cost $-D$. This generates an 'ambiguous zone' (within $\alpha = D/V$, and extent of RHP asymmetry) in which bourgeois (or, incidentally, 'anti-bourgeois') can be an ESS against the RHP asymmetry. This gives the fundamental result that unless 'payoff-relevant aspects' (RHP and V) are relatively strongly asymmetric, they may be ignored in favour of bourgeois, even when this appears paradoxical. There is some impressive evidence that bourgeois conventions do exist in nature. For instance, Davies (1978) found that even very short tenure of a territory was enough to count as 'ownership' in speckled wood butterflies. (Austad et al. (1979) have argued that tenure of the territory may here correlate with RHP.) Three studies (Kummer et al. 1974 for hamadryas baboons; Hazlett et al. 1975, for crayfish; and Riechert 1978, for spiders) appear to conform rather closely with Hammerstein's predictions in that ownership is respected unless size disparity is fairly large. This need not always be so, however. Klingel (1967) narcotized dominant male zebra; the harem was quickly taken by an interloper. But as the faculties of the narcotized male became restored, he immediately displaced the new owner without significant dispute. Perhaps for animals that meet repeatedly and can recognize each other, ownership is respected on a less transient basis than in, say, an insect like the speckled wood butterfly. However, it is

difficult to see reasons why this might not also apply in baboons; and indeed, the most recent work (Kummer et al. 1978) suggests that prior knowledge of opponents does exert a significant influence on whether ownership is respected.

If mistakes about role (or convention-breaking mutants) are rare, we find that paradoxical strategies are apparently unable to persist against an 'optimal assessor' that combines RHP and V asymmetries ('payoff-relevant asymmetries' in Hammerstein's terms) into a single, interactive, role pair. But our conclusions can converge closely towards Hammerstein's conclusions for the hawks/doves game, if on average, bourgeois does not contradict rule (2) for optimal assessor, and provided that within the zone where ownership is respected, individuals have no information when it would pay them to break the bourgeois convention. This simply requires a positive correlation between ownership and V and/or RHP. Reasons why at least long term tenure of territories may be positively correlated with V are discussed by Parker (1974). If major disparity in RHP is always suspected, then on average owners will have higher RHP than interlopers, so that RHP will also correlate with ownership unless resources are very transient. Thus over a range where information about roles A and B is difficult to obtain for an optimal assessor (V_A/K_A close to V_B/K_B), a bourgeois convention may be respected. Ownership is a cue that is available with very good information to both opponents, whereas exact disparities between interacting asymmetries may not be readily available. Nor, as we have shown, will there be intense selection favouring increased assessment ability in conditions where V_A/K_A is close to V_B/K_B . Thus our interpretation necessarily differs from Hammerstein's only by requiring, within the range that bourgeois is respected, that ownership has an expectation of correlating positively with role A , with $V_A/K_A > V_B/K_B$. It may also help to explain why bourgeois, rather than 'anti-bourgeois', is the convention adopted within the range of poor information.

Our arguments about reserve strategy adjustment depend on animals making rare mistakes about their roles, or on the occasional occurrence of (disadvantageous) convention-breaking mutants; though their effects on reserve strategy are slightly different, both adjust it to a level where paradoxical strategies cannot persist even if they could arise by drift in the first place. Though the behaviour of rare mutants is not a

prospect for field study, 'mistakes' about role can sometimes be witnessed in apparent 'bourgeois' strategies. For instance, in a study of the peacock butterfly, Baker (1972) found that although interlopers nearly always retreat when intercepted by an owner as they arrive, sometimes they may settle unchallenged because the owner is preoccupied with some other activity. In this case, they generally refuse to leave the territory.

Selten (1980) has recently argued⁴ that for contests with asymmetric roles $A \neq B$, in which the result of the parallel symmetric game in which individuals ignore (or cannot perceive) the roles would be a mixed ESS, the solution must be a pure ESS that respects the role asymmetry. His analysis makes the assumption that opponents never find themselves in the same information situation. Our arguments are in some respects rather similar to his, but we assume because of adjustment of reserve strategy that only the roles A and B defined by the RHP/payoff interaction can be important, and that individuals can make mistakes about roles. When both contest, it will generally be because one has made a mistake about its role, in which case the opponents are in the same information situation and a mixed ESS seems permissible.

Finally, how feasible is it that animals will be able to estimate roles dependent on the interaction between fighting ability (RHP) and resource value (V)? Accurate assessment of relative RHPs may be possible, but estimations of V_A and V_B may be more difficult. Where V correlates with ownership or RHP, some estimation of resource value may be possible. But where V correlates, say, with some physiological condition such as hunger, it is difficult to see how this could be estimated by an opponent. In the model of Bishop et al. (1978), an individual can accurately estimate his own V , but not that of his opponent. When resource values are drawn from a continuous distribution, the ESS is to play a unique persistence time m such that if $V_A > V_B$, then $m_A > m_B$. If estimation of self's V is possible only within certain categories (e.g. moderately hungry, very hungry, etc.) then the ESS is to play a truncated distribution of persistence times dependent on the estimation of V . There are no gaps between the distributions of adjacent V 's, and distributions are non-overlapping. The ESS for mistakes in role developed in the present paper has two such distributions at a given P , one for estimation of A and one for

estimation of B (paper in preparation). The two models are clearly rather closely related.

Appendix I. The 'Fixed Rates Costs' model, with Imperfect Information

1. Best Strategy when Role A is Estimated, if ϕ Stays Constant as \bar{V}/\bar{K}

An animal estimating itself to be A can contest with probability p_A or retreat with probability $(1 - p_A)$. We shall assume that its opponent (which may or may not be in B) will contest with probability p . We show that at any level of correctness about role better than a random guess ($P > \frac{1}{2}$), it will always pay to contest (play $p_A = 1$) when role A is estimated if $V_A/K_A > V_B/K_B$. When both contest, we assume that escalation (reserve strategy) is set by $\phi = \bar{V}/\bar{K}$.

The payoff matrix for the case where A is estimated is (M1A):

Payoff to individual estimating A :		Against opponent that:		
		contests	retreats	
Correctly	contests	$P p_A p \left(\frac{V_A}{2} - \frac{K_A \phi}{2} \right)$	$P p_A (1-p) V_A$	(M1A)
	retreats	0	$P (1-p_A) (1-p) \frac{V_A}{2}$	
Incorrectly	contests	$(1-P) p_A p \left(\frac{V_B}{2} - \frac{K_B \phi}{2} \right)$	$(1-P) p_A (1-p) V_B$	
	retreats	0	$(1-P) (1-p_A) (1-p) \frac{V_B}{2}$	

Thus, calling the strategy that plays p_A strategy I ,

$$\begin{aligned}
 E(I, I) = & P \left[p_A p \left(\frac{V_A}{2} - \frac{K_A \phi}{2} \right) + p_A (1-p) V_A \right. \\
 & \left. + (1-p_A) (1-p) \frac{V_A}{2} \right] \\
 & + (1-P) \left[p_A p \left(\frac{V_B}{2} - \frac{K_B \phi}{2} \right) \right. \\
 & \left. + p_A (1-p) V_B + (1-p_A) (1-p) \frac{V_B}{2} \right]
 \end{aligned}$$

and a mutant J that has a deviant $p_A' \neq p_A$ spreads if

$$\frac{(p_A' - p_A) [P(V_A - p K_A \phi) + (1-P)(V_B - p K_B \phi)]}{(V_B - p K_B \phi)} > 0 \quad (1A)$$

If $p_A' > p_A$, then in order for J to spread

$$p(V_A - p K_A \phi) + (1-P)(V_B - p K_B \phi) > 0.$$

If this can be true when $p \approx 1$, it must always be true. Substituting $p = 1$ gives the most conservative condition for increasing p_A as:

$$2P(V_A K_B - V_B K_A) > (V_A K_B - V_B K_A),$$

which is always true if role assessment is random ($\frac{1}{2} < P \leq 1$), and role A is defined as $V_A/K_A > V_B/K_B$.

This implies that the best strategy is always to contest when role A is estimated, even if role assessment is very poor (close to random).

2. Best Strategy when Role B is Estimated, if φ Stays Constant as V/K

Following the same procedure but modifying matrix (M1A) appropriately, it is obvious that a mutant J with a deviant tendency ($p_B' \neq p_B$) to contest when in B can invade only if:

$$(p_B' - p_B) [P(V_B - pK_B\varphi) + (1 - P)(V_A - pK_A\varphi)] > 0 \quad (2A)$$

$$p_B = \frac{[P(V_A K_A - V_A K_B + 3V_B K_A + V_B K_B) + V_A K_B - V_B K_A] / (V_A K_A + V_A K_B + V_B K_A + V_B K_B) - P^2}{P(1 - P)}$$

Note that again p is the tendency of opponents to contest (against now the individual estimating B). Even though the best strategy is to contest if A is estimated, p can never = 1 unless either $P = 1$ or $p_B = 1$.

It is clear from (2A) that if $P \geq \frac{1}{2}$, the best strategy for mutant J depends on p . If $p = 1$ and $P > \frac{1}{2}$, retreat is always favoured (which concurs with previous deductions). Alternatively, if $P \approx \frac{1}{2}$ and $p \approx \frac{1}{2}$ (the minimum possible value for p), then contesting is always favoured. This suggests that over a range $\frac{1}{2} \leq P \leq 1$ there will be a stable equilibrium value for p_B .

To establish the stable p_B at a given P , consider matrix (M2A) for a mutant strategist J that deviates only by playing p_B' when it estimates itself to be in B . Its opponents (I , playing p_B) may have estimated either A or B ; they always contest if they have estimated A .

Payoff to individual estimating B :

Against opponent that:

contests retreats

Correctly	contests	$P p_B' [P + (1-P)p_B] \left(\frac{V_B}{2} - \frac{K_B \varphi}{2} \right)$	$P p_B' (1-P)(1-p_B) \frac{V_B}{2}$
	retreats	0	$P(1-p_B')(1-P)(1-p_B) \frac{V_B}{2}$
Incorrectly	contests	$(1-P)p_B' [(1-P) + P p_B] \left(\frac{V_A}{2} - \frac{K_A \varphi}{2} \right)$	$(1-P)p_B' P(1-p_B) V_A$
	retreats	0	$(1-P)(1-p_B')P(1-p_B) \frac{V_A}{2}$

(M2A)

After some manipulation, it is easy to show that:

$$E(J, I) - E(I, I) =$$

$$(p_B' - p_B) \left[\frac{K_B \varphi}{2} (P^2 p_B - P p_B - P) + \frac{K_A \varphi}{2} (2P + P^2 p_B - P^2 - P p_B - 1) + P V_B + (1 - P) V_A \right] \quad (3A)$$

For p_B to be stable the portion of (3A) in square brackets must = 0, since p_B' can be either positive or negative. Substituting $\varphi = (V_A + V_B)/(K_A + K_B)$ gives:

which = 0 if negative, or 1 if the value exceeds 1.

Note that a strategy playing 'contest with $\varphi = V/K$ when A is estimated, contest with $\varphi = V/K$ at probability p_B' ' cannot be an ESS (see p. 227). It is a transient equilibrium as long as φ and P remain constant.

Appendix II. Payoffs to Strategies Used to Acquire Information During Contests

Below are listed the payoffs of every strategy against every other strategy in terms of $\alpha_i = D_i/V_A$, $\gamma = V_B/V_A$, $\beta_i = e_i/D_i$, and where i represent bouts 1, 2, and 3 of a contest. Tactics low (L), medium (M), and high (H) can be substituted in any combination.

$$E(S_1, S_1) = \gamma - \alpha_1 + x_1(1 - \gamma) - 2\alpha_1\beta_1$$

$$E(S_1, S_2) = \gamma - \alpha_1 - \beta_2\alpha_2 - 2\beta_1\alpha_1 + x_1x_2(1 + \gamma + 2\alpha_2) - (x_1 + x_2)(\gamma + \alpha_2)$$

$$E(S_1, S_3) = \gamma - \alpha_1 - \beta_2\alpha_2 - \beta_3\alpha_3 - 2\beta_1\alpha_1 + x_1x_2x_3(1 - \gamma) + x_1x_2(\gamma - \alpha_3) + 2\alpha_2 - 2\beta_3\alpha_3 + (x_1x_3 + x_2x_3 - x_3)(\gamma + \alpha_3) - (x_1 + x_2)(\gamma + \alpha_2 - \beta_3\alpha_3)$$

$$E(S_2, S_2) = \gamma - \alpha_1 - \alpha_2 - 2\beta_1\alpha_1 - 2\beta_2\alpha_2 + x_2(1 - \gamma)$$

$$E(S_2, S_1) = \gamma - \alpha_1 - \alpha_2 - \beta_2\alpha_2 - 2\beta_1\alpha_1 - x_1x_2(1 + \gamma + 2\alpha_2) + (x_1 + x_2)(1 + \alpha_2)$$

$$\begin{aligned}
 E(S_2, S_3) &= \gamma - \alpha_1 - \alpha_2 - \beta_3\alpha_3 - 2\beta_1\alpha_1 \\
 &\quad - 2\beta_2\alpha_2 + x_2x_3(1 + \gamma + 2\alpha_3) \\
 &\quad - (x_2 + x_3)(\gamma + \alpha_3) \\
 &\quad + (1 - p_A)(1 - p_B) \frac{V_A}{2} \\
 E(S_3, S_3) &= \gamma - \alpha_1 - \alpha_2 - \alpha_3 + x_3(1 - \gamma) \\
 &\quad - 2\beta_1\alpha_1 - 2\beta_2\alpha_2 - 2\beta_3\alpha_3 \\
 &\quad + \frac{1}{2} \left\{ p_A p_B \left[V_B(1 - x) - Dx \right] \right. \\
 E(S_3, S_1) &= \gamma - \alpha_1 - \alpha_2 - \alpha_3 - \beta_2\alpha_2 \\
 &\quad - \beta_3\alpha_3 - 2\beta_1\alpha_1 + x_1x_2x_3(1 - \gamma) \\
 &\quad - x_1x_2(1 + \alpha_3 + 2\beta_3\alpha_3 + 2\alpha_2) \\
 &\quad - (x_2x_3 + x_1x_3 - x_3)(1 + \alpha_3) \\
 &\quad + (x_1 + x_2)(1 + \alpha_2 + \alpha_3 + \beta_3\alpha_3) \\
 &\quad + p_B(1 - p_A) V_B + (1 - p_A)(1 - p_B) \frac{V_B}{2} \\
 E(S_3, S_2) &= \gamma - \alpha_1 - \alpha_2 - \alpha_3 - \beta_3\alpha_3 \\
 &\quad - 2\beta_1\alpha_1 - 2\beta_2\alpha_2 - x_2x_3(1 + \gamma \\
 &\quad + 2\alpha_3) + (x_2 + x_3)(1 + \alpha_3)
 \end{aligned}
 \tag{4A}$$

By a process exactly similar to that given in Maynard Smith & Parker (1976, pp. 165-166) we were able to show that only the pure strategies (0, 0), (0, 1), (1, 0) and (1, 1) can be an ESS. No mixed strategy can persist. This also follows from Selten (1980).

Appendix III. Interaction of Asymmetries with Hawk/Dove Strategies

Hawk plays 'escalate at risk of damage costing -D if opponent escalates, retreat only when injured'.

Dove plays 'retreat if opponent escalates'. If two doves meet, the contest is settled without cost, with each opponent having equal prospects. Individual A has chance x of winning an escalated fight, B has chance (1 - x). Information about this RHP asymmetry, and asymmetry in V, is perfect.

The payoff matrix is:

		Individual in role B:	
		Hawk	Dove
Individual in role A:	Hawk	$V_B(1-x) - Dx$	0
	Dove	$V_A x - D(1-x)$	V_A
		V_B	$\frac{V_B}{2}$
		0	$\frac{V_A}{2}$

Let strategy I be (p_A, p_B) where p_A is the probability of escalating when in A and p_B the probability of escalating when B.

$$\begin{aligned}
 E(I, I) &= \frac{1}{2} \left\{ p_A p_B \left[V_A x - D(1 - x) \right] \right. \\
 &\quad + p_A(1 - p_B)V_A
 \end{aligned}$$

Let strategy I be (1, 1), escalate in both roles. This is an ESS against strategy J (1, 0) for dropping out in B when E(I, I) > E(I, J). From (4A) this is where

$$\begin{aligned}
 &\frac{1}{2} [V_{Ax} - D(1 - x) + V_B(1 - x) - Dx] \\
 &- \frac{1}{2} [V_{Ax} - D(1 - x)] > 0 \\
 &\text{i.e. } V_B(1 - x) > Dx
 \end{aligned}$$

or where the expected benefits to B are greater than its expected losses. J invades if the sign is reversed. It follows that if a positive expectation is possible in both roles if both contestants were to escalate, both will. If a positive expectation is possible in only one role, say A, assuming that B were to escalate, there will be commonsense convention for retreating in role B; no paradoxical ESS exists. But if D ≫ V for both opponents, so that neither could achieve a positive expectation if the other were to escalate, then both commonsense and paradoxical ESSs exist (commonsense = A escalates, B retreats; paradoxical = A retreats, B escalates) in which roles are defined by:

$$V_A x - D(1 - x) > V_B(1 - x) - Dx.$$

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