

THE LOGIC OF ASYMMETRIC CONTESTS

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Abstract. A theoretical analysis is made of the evolution of behavioural strategies in contest situations. It is assumed that behaviour will evolve so as to maximize individual fitness. If so, a population will evolve an ‘evolutionarily stable strategy’, or ESS, which can be defined as a strategy such that, if all members of a population adopt it, no ‘mutant’ strategy can do better. A number of simple models of contest situations are analysed from this point of view. It is concluded that in ‘symmetric’ contests the ESS is likely to be a ‘mixed’ strategy; that is, either the population will be genetically polymorphic or individuals will be behaviourally variable. Most real contests are probably asymmetric, either in pay-off to the contestants, or in size or weapons, or in some ‘uncorrelated’ fashion; i.e. in a fashion which does not substantially bias either the pay-offs or the likely outcome of an escalated contest. An example of an uncorrelated asymmetry is that between the ‘discoverer’ of a resource and a ‘late-comer’. It is shown that the ESS in asymmetric contests will usually be to permit the asymmetric cue to settle the contest without escalation. Escalated contests will, however, occur if information to the contestants about the asymmetry is imperfect.

I. Introduction

This paper discusses the question, ‘How would we expect animals to behave in contest situations?’ It attempts to combine two previous approaches to the problem. Maynard Smith (1974) defined an ‘evolutionarily stable strategy’, or ESS, and argued that natural selection, acting between individuals, would produce such a strategy. The concept was, however, applied mainly to symmetric contests between equally matched opponents. Parker (1974a) discussed the consequences of the fact that most contests between animals are not symmetric. The present paper is mainly concerned with applying the concept of an ESS to asymmetric contests.

A contest between two individual animals may be ‘asymmetric’ in any of three ways:

(i) Pay-off Asymmetry. One contestant may have more to gain by winning (or, equivalently, more to lose by accepting defeat). For example, the owner of a territory may have invested time and energy in exploring the territory, settling boundaries with neighbours, building a nest, etc. and therefore will suffer a greater loss of fitness than an interloper by retreating from the territory.

(ii) Asymmetry in Fighting Ability, or in ‘RHP’ (= ‘Resource Holding Potential’). Individuals may differ in some intrinsic feature such as size, weapons, etc. or there may be extrinsic circumstances favouring one contestant (for example, ‘postural’ advantages in contests between insects, as discussed by Parker (1974a)).

(iii) Uncorrelated Asymmetries. That is to say asymmetries which do not affect either the

pay-offs or the RHP’s of the contestants. No example can be given, since it is unlikely that any actual asymmetry is completely without effect either on pay-off or RHP. It is, however, important to analyse contests which are uncorrelated in the above sense, because if it can be shown that completely uncorrelated asymmetries can settle contests, then the argument that differences in pay-offs or RHP are too small to explain the conventional settling of disputes is irrelevant. Thus it is no part of our argument that differences in pay-off and RHP do not exist, only that they need not exist for contests to be settled conventionally.

In all cases we shall look for an ‘evolutionarily stable strategy’ or ESS. This concept is defined mathematically in the next section, and methods of finding ESS’s discussed. Briefly, however, a strategy is an ESS if a population of individuals adopting that strategy cannot be ‘invaded’ by an initially rare mutant adopting an alternative strategy. A few explanatory points are:

(i) A ‘strategy’ is a specification of what an individual will do in all the situations it may find itself in; if contests are asymmetrical, it must specify what a contestant would do in either ‘role’ (e.g. if owner of a territory and if interloper).

(ii) A strategy may be ‘pure’, e.g. in situation *A*, always do *a*, or ‘mixed’, e.g. in situation *A*, do *a* with probability *p* and *b* with probability *q*.

(iii) If an ESS is a mixed strategy, it might be realized genetically in one of two ways. The members of a population might be genetically identical, each individual adopting different pure

strategies on different occasions, with probabilities corresponding to the ESS. Alternatively, each individual might be fixed in its behaviour, the population being genetically polymorphic, with the frequencies of different genotypes corresponding to the ESS.

(iv) If it is asserted that some strategy I is an ESS, this can be shown only for some specified set of alternative strategies.

There are two features of asymmetric contests which must be made explicit in any analysis:

(i) Given that there is an asymmetry, are both contestants fully informed about its nature? Clearly, if neither contestant has any information, the asymmetry is irrelevant to their strategy; if two animals differ in size, but neither has any information as to whether it is larger or smaller than its opponent, then their strategy is unaffected by the size difference, although the outcome may be affected. Contests in which there is perfect information available to both contestants are in general rather easy to analyse; almost always there are two possible ESS's, the contestant in one or other of the two 'roles' being treated conventionally as the winner. Much greater difficulties arise when only partial information exists.

(ii) It will be assumed that different behaviours or strategies have different genotypes. A genotype may specify a 'mixed' strategy, so that an individual with that genotype may behave differently on different occasions. There will also be genes which influence the likelihood of an animal playing a particular 'role' in an asymmetric contest. For example, an individual with genes for early maturation might be more likely to be an 'owner' than an 'interloper' in a territorial contest; genes will also affect RHP. It is assumed in this paper that the genetic determination of strategies is independent of the genetic determination of roles. To put the matter another way, it is assumed that individuals may find themselves playing different roles, and it is asked, what strategies appropriate to these roles will evolve?

This paper is mainly concerned with the evolution of strategies. It may be, however, that physical characteristics uncorrelated with RHP, for example skin colour, are used to settle asymmetric contests. Then some animals will usually have the more favoured role, others the less favoured one, and selection for the helpful physical feature will proceed. One aspect of this problem is analysed in section V, on 'bluff'. By

bluff we mean the possession of physical characteristics, such as manes or crests, which increase apparent RHP without conferring an equivalent increase in actual RHP in an escalated contest.

II. Notation and Definitions

Suppose I and J are strategies. Then $E_J(I)$ means the expected gain or pay-off to an individual adopting strategy I against an opponent adopting strategy J . The pay-off is measured in terms of Darwinian fitness, i.e. as a change in the expected number of offspring consequent on adopting strategy I . We shall be concerned not with absolute values of these pay-offs but with relative values. Thus if J is 'stay and fight it out in a given territory' and I is 'retreat and look for an alternative territory elsewhere' we shall be concerned with the values of $E_J(I) - E_J(J)$, which is supposed to be interpreted as the gain in the expected number of offspring to an individual who retreats, compared to the number it would have had if it had stayed to fight it out (of course, this 'gain' may be negative).

Suppose now that a population consists of a fraction p adopting I and q adopting J where $p+q=1$, then

$$\text{average 'fitness' of } I = \bar{W}_I = pE_I(I) + qE_J(I)$$

and

$$\text{average 'fitness' of } J = \bar{W}_J = pE_I(J) + qE_J(J).$$

I will then be an ESS if $\bar{W}_I > \bar{W}_J$ for all alternative strategies J when the 'mutant' strategy J is rare, i.e. when $0 < q \ll 1$. That is, I is an ESS if, for all alternative strategies J , either

$$E_I(I) > E_I(J) \quad (1a)$$

or

$$E_I(I) = E_I(J) \text{ and } E_J(I) > E_J(J). \quad (1b)$$

If I is a pure strategy and an ESS, it is usually the case that (1a) will be satisfied for all or almost all J . But if I is a mixed strategy, composed of strategies $I_1 I_2 \dots I_n$ with frequencies $p_1 p_2 \dots p_n$, it is easy to see that $E_I(I_i)$ must be the same for all i (otherwise, I_i would increase or decrease in frequency relative to other strategies); stability then depends on satisfying (1b). If therefore one suspects the existence of a mixed ESS, the procedure is first to seek for probabilities $p_1 \dots p_n$ (or in the 'continuous' case, for a probability density function) such that each component pure strategy has the same expectation against the mixed strategy. This establishes

that the mixed strategy is an equilibrium strategy; condition (1b) will then show whether it is a stable equilibrium.

A word must be said about the inheritance of behavioural strategies, and the corresponding stability criteria. There are three possibilities:

(i) Each strategy, pure or mixed, can reproduce itself without genetic recombination with others. The 'fitness' of strategy I would be $K + E_I$, where K is a constant and E_I the expected pay-off to strategy I , played against itself and the other strategies weighted by their frequencies in the population; K is introduced because E_I may be negative. With this type of inheritance, conditions (1a, b) are necessary and sufficient to ensure that a population playing I is in a genetically stable equilibrium.

(ii) As (i), but only pure strategies can reproduce. If the ESS is a mixed strategy, it can be achieved only by a genetically polymorphic population. In this case, if there are more than two pure strategies in the ESS, conditions (1b) are neither necessary nor sufficient to ensure the stability of the equilibrium. They do, however, appear to be a good indicator of stability. The only two equilibria of this type considered in this paper are the distributions for the 'war of attrition' and the 'graduated risk' games. Both have been simulated on a computer and found to be stable for this type of inheritance.

(iii) Bisexual inheritance with genetic recombination. Nothing general can be said. There are cases (e.g. the 'war of attrition') in which the ESS calls for a frequency distribution which could not be maintained under sexual reproduction with most types of genetic determination. In such cases, simulation suggests that the genetic equilibrium will approach as close to the ESS as the genetic system allows.

III. Symmetric Contests

(i) The 'War of Attrition'

Maynard Smith (1974) analysed a 'war of attrition', in which only display is possible. Clearly, contests can only be settled because a long contest is disadvantageous, in wasting time and energy. Winning consists in the opponent 'backing down'. Let the value of winning be V . Suppose that two contestants, A and B , are prepared to continue for periods m_A and m_B , where m_A and m_B equal the loss of fitness associated with a contest of that length, measured on the same scale as V . Then if $m_A > m_B$, the pay-off to A is $V - m_B$ and to B is $-m_B$. In this situation,

no pure strategy can be stable. It can be shown that the ESS is to play $m = x$, where

$$p(x) = \frac{1}{V} \exp(-x/V). \quad (2)$$

That is, in the 'war of attrition', individuals will vary in their persistence as shown in Fig. 1. The strategy could be realized by a genetically uniform population whose members had a constant probability $k\delta t$ of giving up per time δt during a contest, where $k = 1/V$; natural selection would adjust k to the appropriate value.

(ii) 'Hawks' and 'Doves'

Consider now a contest in which two pure strategies are possible: (a) Escalate, and continue until either opponent retreats, or until injured. (b) Display; retreat if opponent escalates.

It is supposed that if both contestants display, then the contest can be settled without excessive waste of time, each contestant having an equal chance of winning. If the value of winning is $+V$ and of injury is $-D$, the pay-off matrix is

	Escalate	Display
Escalate	$\frac{V-D}{2}$	V
Display	0	$V/2$

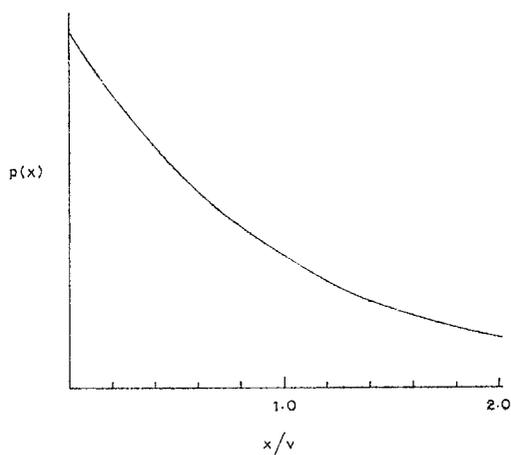


Fig. 1. Evolutionary stable strategy for 'war of attrition'. V is the value of winning and x the price an individual is prepared to pay.

In the matrix, the pay-offs are to the left-hand-side individual. Allowing for mixed strategies, the possible strategies are, 'always escalate', or 'always display', or 'escalate with probability P '.

Let strategy I be the ESS, and suppose that it is a mixed strategy, escalate with probability P . Since I is an equilibrium, the expected gain of an individual who escalates against I must equal the expected gain of one who displays. That is

$$P \frac{V-D}{2} + (1-P)V = (1-P) \frac{V}{2}$$

or

$$P = \frac{V}{D} \quad (3)$$

Let J be an alternative strategy, escalate with probability P' . Then since I is stable,

$$E_J(I) > E_J(J) \text{ for all } P'.$$

$$E_J(I) - E_J(J)$$

$$= (P - P') \left[P' \frac{(V-D)}{2} + (1-P') \frac{V}{2} \right],$$

and for $P \neq P'$ this expression is always positive, so that the strategy $P = V/D$ is an ESS. Clearly, if $V > D$, the ESS is $P = 1$. If the advantages of winning outweigh the risks of injury, contestants will always escalate. If $V < D$, the ESS is given by (3).

(iii) Retaliator

Maynard Smith & Price (1973) analysed this case further, with $D > V$, but allowing for more complex strategies, in which an individual could modify its behaviour in the light of its opponent's behaviour. They concluded that the ESS is to display, but to escalate if one's opponent escalates, i.e. to 'retaliate'.

It has since been pointed out by Gale & Eaves (1975) that 'retaliation' is not the only ESS for the set of strategies considered; there is an alternative, mixed, ESS composed of a mixture of Hawks, and 'Bullies' (i.e. escalate, but retreat if one's opponent escalates in return). This is an interesting example of the fact that the same preconditions (weapons, advantages to be gained, etc.) can lead to two different evolutionarily stable patterns of behaviour. Which ESS in fact evolves in any particular species will depend on the initial conditions; that is to say, on the behaviour patterns of the

ancestral species. This possibility of two stable strategies should not cause any surprise. Analogous bistable or multistable situations are familiar to anatomists; for example, ostriches, antelopes and kangaroos have solved the problem of rapid locomotion on open plains in quite different ways.

(iv) The 'Graduated Risk' Game

Consider now one final symmetric contest. Suppose that each contestant can select a 'level' to which he is prepared to escalate the contest; let A select level m_A and B select level m_B , where $m_A > m_B$. Then the contest will actually escalate up to level m_B . At or before this stage, one or other contestant may be injured, in which case the other is left as victor; alternatively, if neither is injured, A (who is willing to continue) wins. Let x_B be the probability that *neither* contestant is injured (x_B will be a decreasing function of m_B); then $\frac{1}{2}(1-x_B)$ is the probability that a particular contestant is injured, and hence

$$\text{expected pay-off to } A = Vx_B + \frac{V-D}{2}(1-x_B),$$

$$\text{expected pay-off to } B = \frac{V-D}{2}(1-x_B).$$

A 'strategy' consists of a choice of m_B and hence of x_B . Suppose that the ESS is a mixed strategy I , given by the probability distribution $p(x)$.

To find $p(x)$ we first find a distribution such that $E_I(k) = E_I(I)$ for all fixed k .

If $E_I(k) = E_I(I)$, then $E_I(k)$ is the same for all k , and in particular $E_I(k) = E_I(k + \delta k)$, therefore

$$\begin{aligned} & \int_0^k p(x) \frac{V-D}{2} (1-k) dx + \\ & \int_k^1 p(x) \left[Vx + \frac{V-D}{2} (1-x) \right] dx \\ &= \int_0^{k+\delta k} p(x) \frac{V-D}{2} (1-k-\delta k) dx + \end{aligned}$$

$$\int_{k+\delta k}^1 p(x) \left[Vx - \frac{V-D}{2}(1-x) \right] dx$$

which simplifies to

$$Vk p(k) = \frac{D-V}{2} \int_0^k p(x) dx. \tag{4}$$

The solution of (4), subject to the constraint

$$\int_0^1 p(x) dx = 1,$$

is

$$p(x) = \frac{D-V}{2V} x^{(D-3V)/2V}$$

or writing $D/V = \alpha$, a measure of the 'riskiness' of fighting,

$$p(x) = \frac{\alpha-1}{2} x^{(\alpha-3)/2}. \tag{5}$$

If there is to be a mixed ESS, given by $p(x)$, then (5) must be satisfied. It is also necessary to show that the equilibrium given by (5) is a stable one. Stability is suggested by the fact that

$E_k(I) > E_k(k)$ for all fixed k (the proof is straightforward and is not given here), and has been confirmed by computer simulation.

It is easier to interpret (5) if we put $y = \frac{1}{2}(1-x)$, and plot $p(y)$ as a function of y . We can interpret y as follows. In selecting a maximum level of escalation m , an animal also selects a maximum probability, $(1-x)$, that one or other contestant will be seriously injured. Hence y is the risk of serious injury an individual is prepared to run. Note that $y > 0.5$, since even in a contest between two 'hawks' the risk of injury to each contestant is only 0.5.

$p(y)$ is given as a function of y in Fig. 2. We reach the common-sense conclusion that the greater the damage, the smaller on average the risk an animal will run of incurring that damage.

It is interesting that, provided $\alpha > 1$, the ESS is a mixed one. If $\alpha < 1$, (5) cannot be satisfied, and no mixed strategy can be an equilibrium. In this case, it is always worth while to escalate to the limit.

IV. Asymmetric Contests

(i) Uncorrelated Asymmetry with Perfect Information

Suppose that whenever a contest takes place, it is between a 'discoverer' and a 'latecomer', or has some other similar asymmetry. It is assumed that the asymmetry makes no difference to the pay-offs to the contestants, or to their RHP's. This is what we mean by 'uncorrelated'. It is also assumed that the contestants have complete

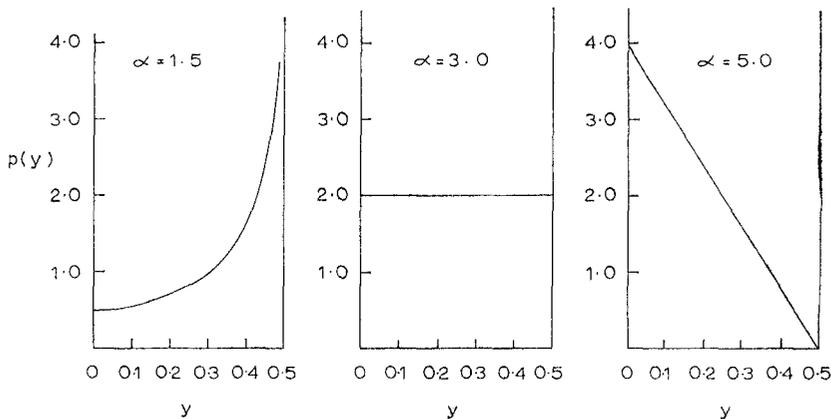


Figure 2. Evolutionarily stable strategy for 'graduated risk game'. y is the risk of serious injury an individual is prepared to run, and $\alpha = D/V$, where V is the value of winning and D the price of serious injury.

information about their roles, i.e. an individual 'knows' that he is an owner and his opponent an interloper, or, of course, vice-versa.

Maynard Smith (1974) analysed the 'war of attrition' contest when associated with an uncorrelated asymmetry. If we refer to the roles as *A* and *B* (i.e. *A* might mean 'discoverer' and *B* 'late-comer') then it was shown that there are two ESS's. The first is 'If *A*, play *M* (where $M > V$); if *B*, play 0', and the second is 'if *A*, play 0; if *B*, play $M > V$ '. Here, *M* represents the cost in fitness terms that a contestant is prepared to suffer from a prolonged contest. That is, the members of an evolutionarily stable population persist in one role, and retreat immediately in the other. These two alternative ESS's are stable against the mixed strategy given by (2), which ignores the asymmetry. The reason is that members of a stable population have a high expected gain against each other, since they win half the contests they engage in, and are never involved in a long contest.

This conclusion is not unique to the 'war of attrition'. A similar conclusion can easily be established for the 'hawks and doves' contest. If $V < D$, the strategy (3) is no longer an ESS; instead, the ESS's are 'escalate if *A*, retreat if *B*', and 'retreat if *A*, escalate if *B*'. In fact, it is typically the case that a contest with an uncorrelated asymmetry has two alternative ESS's.

In practice, as mentioned earlier, an asymmetric contest is unlikely to be completely uncorrelated. We next consider contests in which there is a difference either in pay-off or RHP. These contests also tend to have two alternative ESS's, but these are no longer equivalent. One, the 'common-sense' ESS, is for the contestant with the most to gain or the higher RHP to persist and his opponent to retreat. However, there is sometimes also a 'paradoxical' ESS, in which the contestant with the least to gain or the lower RHP persists. Some reasons are given why such paradoxical ESS's are unlikely to occur in nature, although their occurrence cannot be completely ruled out.

(ii) Contests with Unequal Pay-offs and Perfect Information

Suppose that in a contest between, say, an owner, *A*, and an interloper, *B*, the owner has more to gain (or lose); let the value of victory to the owner be V_A and to the interloper be V_B , where $V_A > V_B$. Suppose further that the contest is a 'war of attrition', victory going to the contestant who continues longer. It follows from the

analysis in the last section that if we permit only strategies which ignore the role of the contestants, then the ESS, which we will call strategy *I*, is to continue for a time *x* distributed as

$$p(x) = \frac{1}{\bar{V}} \exp(-x/\bar{V})$$

where $\bar{V} = (V_A + V_B)/2$.

Consider two alternative strategies, *J* and *K*, as follows:

strategy *J*; play 0 when *B*, play *M* when *A*; the 'common-sense' strategy;

K; play *M*' when *B*, play 0 when *A*; the 'paradoxical' strategy.

We show first that both strategy *J* and *K* can be an ESS. Consider first strategy *J*:

$$E_J(J) = \frac{1}{2}V_A,$$

$$E_J(I) = \frac{1}{2}V_A + \frac{1}{2} \left\{ \int_0^M -\frac{x}{\bar{V}} \exp(-x/\bar{V}) dx + \int_M^\infty \frac{V_B - M}{\bar{V}} \exp(-x/\bar{V}) dx \right\}$$

$$= \frac{1}{2}V_A + \frac{1}{2}V_B \exp(-M/\bar{V}) - \frac{1}{2}\bar{V}(1 - \exp[-M/\bar{V}]).$$

Hence $E_J(J) > E_J(I)$ if $\bar{V}(1 - \exp[-M/\bar{V}]) > V_B \exp(-M/\bar{V})$. Thus *J* is an ESS against *I* provided that

$$\exp(-M/\bar{V}) < \frac{V_A + V_B}{V_A + 3V_B}.$$

There is therefore always a value of *M* which will make *J* stable against *I*; in the extreme case $V_B = 0$, any positive *M* makes *J* stable. It is easy to show that *J* is also stable against *K*.

Now consider the paradoxical strategy *K* (paradoxical because contestants play high when they have least to gain).

$$E_K(K) = \frac{1}{2}V_B \text{ and } E_K(J) = \frac{1}{4}V_B - \frac{M}{2}$$

if $M' > M$ and $= \frac{1}{4}V_B + \frac{1}{2}(V_A - M')$ if $M' < M$.

Hence *K* is stable against *J*, even if $M > M'$, provided that $M' > V_A - (V_B/2)$.

Considering the stability of *K* against *I*, an argument identical to that used for strategy *J*

leads to the conclusion that K is stable provided

$$\exp(-M'/\bar{V}) < \frac{V_A + V_B}{3V_A + V_B}$$

This condition can also be satisfied, although it requires larger values of M' than was required of M . We therefore conclude that either the common-sense strategy J or the paradoxical strategy K can be an ESS.

We will now show that although strategy K is an ESS, a population initially adopting strategy I , which ignores differences in pay-off, would evolve to strategy J but not to K . This follows, because an I population can be invaded by a mutant J but not by a mutant K . Considering first invasion by J ,

$$E_I(J) = \frac{1}{2} \left\{ \int_0^M (V_A - x) \frac{1}{\bar{V}} \exp(-x/\bar{V}) dx - \int_M^\infty \frac{1}{\bar{V}} \exp(-x/\bar{V}) dx \right\} = \frac{V_A - \bar{V}}{2} (1 - \exp[-M/\bar{V}]).$$

Since $E_I(I) = 0$, it follows that $E_I(J) > E_I(I)$ for any M , provided that $V_A > V_B$, as has been assumed. Hence a J mutant can invade an I population. The same argument shows that a K mutant cannot invade an I population.

We conclude that in contests with unequal pay-offs, and perfect information, the common-sense strategy, play high when you have more to gain and zero when you have less to gain, is an ESS. The converse, paradoxical, strategy is also an ESS, but a population will not evolve the paradoxical strategy if it starts from a strategy which ignores the difference in pay-offs.

(iii) Contests with Unequal RHP's and Perfect Information

We suppose that in each contest there is an asymmetry, which can be thought of as a difference in size, which affects the chances of victory if escalation takes place. Contestant A is 'large', and has a probability $x \geq 0.5$ of victory; B is 'small' and has probability $(1-x)$ of victory.

The pay-off matrix (M1) then is:

		B	
		escalates	displays
A	escalates	$V(1-x) - Dx$	0
	displays	$Vx - D(1-x)$	V
		V	$V/2$

(M1)

A strategy is defined by (p_1, p_2) where p_1 is the probability of escalating when A , and p_2 the probability of escalating when B .

We first show that no mixed strategy, with p_1 and/or p_2 in the open interval 0 to 1, can be an ESS. Let I, J , and K be the strategies (p_1, p_2) , (p'_1, p_2) and (p_1, p'_2) .

$$E_I(I) = \frac{1}{2} \left\{ p_1 p_2 [Vx - D(1-x)] + p_1(1-p_2)V + (1-p_1)(1-p_2)\frac{V}{2} \right\} + \frac{1}{2} \left\{ p_2 p_1 [V(1-x) - Dx] + p_2(1-p_1)V + (1-p_2)(1-p_1)\frac{V}{2} \right\} \quad (6)$$

If I is an ESS, then

$$E_I(I) \geq E_I(J)$$

and

$$E_I(I) \geq E_I(K).$$

Hence

$$(p_1 - p'_1) \left\{ p_2 [Vx - D(1-x)] + (1-p_2)\frac{V}{2} \right\} \geq 0 \quad (7A)$$

and

$$(p_2 - p'_2) \left\{ p_1 [V(1-x) - Dx] + (1-p_1)\frac{V}{2} \right\} \geq 0. \quad (7B)$$

If $0 < p_1 < 1$, then $(p_1 - p'_1)$ can be positive or negative, and hence

$$p_2[Vx - D(1-x)] + (1-p_2)\frac{V}{2} = 0$$

putting $D/V = a$, we obtain

$$\text{if } 0 < p_1 < 1, \text{ then } p_2 = \frac{1}{1 + 2a(1-x) - 2x}$$

and

$$\text{if } 0 < p_2 < 1, \text{ then } p_1 = \frac{1}{2x + 2ax - 1}. \quad (8)$$

It is clear that if one of these equations is satisfied, both must be. Since

$$p_1 < 1, 2x + 2ax - 1 > 1,$$

or

$$x > 1/(1+a).$$

We now show that the equilibrium strategy (8) is unstable. Consider the alternative strategy J , ($p_1 = 1, p_2 = 0$). We already know that $E_I(I) = E_I(J)$, so that stability of I requires $E_J(I) > E_J(J)$. From (6), this becomes

$$\frac{p_1}{2} - \frac{1}{2} + p_2[1 - x(1+a)] > 0 - \quad (9)$$

Since $x > 1/(1+a)$, the

$$LHS < (p_1/2) - \frac{1}{2} + p_2(1-1) < 0,$$

so that inequality (9) cannot be satisfied. Thus we have shown that no mixed ESS can be stable.

It follows that only the pure strategies (0,0) (1,0) (0,1) and (1,1) need be considered. It is then easy to show that if $a > (1-x)/x$ (i.e. injury relatively serious), then $(p_1 = 1, p_2 = 0)$ is an ESS, and if $a < (1-x)/x$ (i.e. injury not serious), then $p_1 = p_2 = 1$ is an ESS.

If $a > x/(1-x)$ (and hence, since $x > 0.5, a > 1$), the 'paradoxical' strategy ($p_1 = 0, p_2 = 1$) is also an ESS.

The first two strategies are common-sense, but a word of explanation is needed for the third. Note that it requires: (a) damage is serious ($a > 1$); (b) a contestant knows for certain that he is larger (or smaller) than his opponent; (c) Size is an uncertain guide to the results of a contest.

Therefore a population adopting the paradoxical ESS will be stable, because they will never be involved in escalated fights with each other, and a mutant hawk runs a non-negligible risk ($1-x > 0$) of serious injury. The weakness of the model lies in the assumption that the estimate of size is certain. If information is not perfect, then things are more complex. An individual may estimate (correctly or otherwise) that he is an A , and therefore escalate, only to find that his opponent has also estimated himself to be an A , the result being an escalated contest.

A particular case of a contest with incomplete information is analysed in the next section.

(iv) A Contest With Incomplete Information

Suppose that a population consists of individuals of different sizes, and that size differences affect the outcome of an escalated contest. Suppose further that a contestant estimates, with greater or lesser accuracy, the difference in size between himself and his opponent. How will strategy depend on this estimate?

Ideally, one would like to analyse a model in which size was continuously distributed and in which the error of estimates was similarly distributed. We have been unable to do this. The model which follows is much simpler, but gives qualitatively interesting results.

Suppose that there are only two equally frequent classes of individual, say 'large' and 'small', and that in an escalated contest a large individual has a probability $x \geq 0.5$ of winning. An individual is assumed not to 'know' his own size, but to estimate whether his opponent is larger (+), equal (0), or smaller (-) than himself. An individual makes a correct estimate with probability P ; if he makes a wrong estimate, he will not make the 'double' error of estimating that a larger opponent is smaller, or vice-versa.

With these assumptions the relative frequencies of different types of contest are as shown in matrix (M2).

We define the ESS, (J), as (p_1, p_2, p_3) , where

p_1 = probability of escalating if estimate opponent is (-),

p_2 = probability of escalating if estimate opponent is (0),

p_3 = probability of escalating if estimate opponent is (+).

		B is large; estimates A is:			B is small; estimates A is:		
		+	0	-	+	0	-
A is large;	+	$\frac{(1-P)^2}{4}$	$P\frac{(1-P)}{2}$	$\frac{(1-P)^2}{4}$	0	0	0
estimates B is:	0	$P\frac{(1-P)}{2}$	P^2	$P\frac{(1-P)}{2}$	$P(1-P)^*$	$(1-P)^2$	0
	-	$\frac{(1-P)^2}{4}$	$P\frac{(1-P)}{2}$	$\frac{(1-P)^2}{4}$	P^2	$P(1-P)$	0
(M2)							
A is small;	+	0	$P(1-P)$	P^2	$\frac{(1-P)^2}{4}$	$P\frac{(1-P)}{2}$	$\frac{(1-P)^2}{4}$
estimates B is:	0	0	$(1-P)^2$	$P(1-P)$	$P\frac{(1-P)}{2}$	P^2	$P\frac{(1-P)}{2}$
	-	0	0	0	$\frac{(1-P)^2}{4}$	$P\frac{(1-P)}{2}$	$\frac{(1-P)^2}{4}$

The expression for $E_I(I)$ is complex, containing a term corresponding to each entry in the table, the first such term being

$$\frac{1}{4} \frac{(1-P)^2}{4} \left[p_3^2 \frac{V-D}{2} + p_3(1-p_3)V + (1-p_3)^2 \frac{V}{2} \right]$$

and the term corresponding to the entry $P(1-P)^*$ being

$$\frac{1}{4} P(1-P) \left\{ p_2 p_3 [Vx - D(1-x)] + p_2(1-p_3)V + (1-p_2)(1-p_3) \frac{V}{2} \right\}$$

and so on.

If I is an ESS, then $E_I(I) \geq E_I(J)$, where J is the strategy (p'_1, p_2, p_3) ; two other inequalities are obtained from comparing I with (p_1, p'_2, p_3) and (p_1, p_2, p'_3) . Putting $D/V = a$, the ratio of the risk to the value of winning, these inequalities reduce to

$$\begin{aligned} & (p_1 - p'_1) \{ (1-P)^2 [2 - p_1 a - p_3 a] + \\ & + 2P(1-P) [2 + p_2(2x - 2a(1-x) - 1 - a)] \\ & + 2P^2 [p_3(2x - 2a(1-x) - 1) + 1] \} \geq 0 \end{aligned} \quad (10A)$$

$$\begin{aligned} & (p_1 - p'_2) \{ P(1-P) [4 - p_1 a - p_3 a \\ & + p_3(2x - 2a(1-x) - 1) \\ & + p_1(2(1-x) - 2ax - 1)] \\ & + 2[P^2 + (1-P)^2] (1 - p_2 a) \} \geq 0 \end{aligned} \quad (10B)$$

and

$$\begin{aligned} & (p_3 - p'_3) \{ (1-P)^2 [2 - p_1 a - p_3 a] \\ & + 2P^2 [1 + p_1(2(1-x) - 2ax - 1)] \\ & + 2P(1-P) [2 + p_2(2(1-x) - 2ax - 1 - a)] \} \geq 0. \end{aligned} \quad (10C)$$

Case (i) $x = 1, p = \frac{2}{3}$.

To get some feel for these inequalities, consider the simple case in which $x = 1$ (large individuals always win escalated contests) and $P = \frac{2}{3}$ (a substantial probability, $\frac{1}{3}$, that a contestant's estimate of size difference is faulty).

We proceed by asking for what range of values of a the strategy $(p_1 = 1, 0 \leq p_3 \leq 1, p_3 = 0)$ is an ESS. The inequalities reduce to

$$18 - a + 4p_2(1-a) > 0, \quad (11A)$$

$$(p_2 - p'_2)(16 - 6a - 10ap_2) \geq 0, \quad (11B)$$

$$10 - 17a - 4p_2(1+3a) < 0. \quad (11C)$$

Inequality *B* leads to the conditions

$$(i) \quad \alpha > \frac{8}{3}, \quad p_2 = 0,$$

$$(ii) \quad 1 < \alpha < \frac{8}{3}, \quad p_2 = \frac{8-3\alpha}{5\alpha},$$

$$(iii) \quad \alpha < 1, \quad p_2 = 1.$$

If $p_2 = 0$, condition *A* is satisfied provided $\alpha < 18$. If $p_2 = 1$, condition *C* is satisfied provided $\alpha > \frac{6}{29}$. Hence the strategy $p_1 = 1, p_3 = 0$ is an ESS for $\frac{6}{29} < \alpha < 18$, with

$$p_2 = 1 \text{ if } \frac{6}{29} < \alpha < 1$$

$$p_2 = \frac{8-3\alpha}{5\alpha} \text{ if } 1 < \alpha < \frac{8}{3}$$

and

$$p_2 = 0 \text{ if } \frac{8}{3} < \alpha < 18.$$

It follows that if the outcome of a fight between large and small individuals is certain, the strategy 'escalate if estimate opponent is smaller, display if estimate opponent is larger' is stable for a very wide range of $\alpha = D/V$. When a contestant estimates that his opponent is equal, the stable strategy may be pure escalate, mixed, or pure display, depending upon α .

Is it possible that the reverse 'paradoxical' strategy, $p_1 = 0, p_3 = 1$, could be an ESS? Analysis shows that there is no value of α for which *A* and *C* can simultaneously be satisfied if $p_1 = 0$ and $p_3 = 1$. No paradoxical ESS exists in this case.

It makes surprisingly little difference if $x \neq 1$; that is, if size difference is only an imperfect indicator of victory. For example, if $x = \frac{2}{3}$ and as before $P = \frac{2}{3}$, a calculation similar to that above shows that the strategy

$$(p_1 = 1, 0 \leq p_2 \leq 1, p_3 = 0)$$

is stable for $\frac{2}{3} < \alpha < 18$, with p_2 taking an intermediate value for $\frac{13}{11} < \alpha < \frac{26}{7}$. The main difference is that if size difference is a certain indicator of the outcome of an escalated contact, $p_3 = 0$ is stable to a lower value of α ; that is, the risk of injury must be lower before

individuals estimating that their opponent is larger will escalate.

A more important difference is that the paradoxical strategy $p_1 = 0, p_3 = 1$ is now an ESS, for $2.3 < \alpha < 18$.

To conclude concerning contests with imperfect information, it is important to distinguish two sources of uncertainty: (i) uncertainty concerning the cue used to estimate the outcome ($P \neq 1$), and (ii) the cue is an uncertain predictor of the outcome of an escalated contest ($x \neq 1$).

Provided that the cue (e.g. size difference) can be estimated accurately, it will be used as a conventional means of settling contests, even if it is a poor predictor of the outcome. No paradoxical ESS will exist, and escalated contests will be rare, unless α is small (injury not serious). If the cue cannot be estimated reliably, escalation will be more frequent, and there is a theoretical possibility of a paradoxical ESS.

(v) Information Acquired During a Contest

One last type of contest will be considered, because it introduces an element of realism missing from previous examples, and because it illustrates the general argument rather well. Suppose that two contestants differ in RHP, but that information about this difference is only obtained in the course of a contest. For simplicity, the contest is divided into a series of 'rounds'; it can be imagined as a butting match between two rams. Each round is 'won' by one contestant. The probability that contestant *A* wins each round is constant and equal to x , where $0.5 \leq x \leq 1$. Thus the result of each round provides both contestants with some information about the likely outcome of subsequent rounds. If $x = 1$ this information is perfect; a contestant who loses one round is sure to lose the next. If $x = 0.5$, the contest is symmetric, and no relevant information is conveyed. The loser of each round also suffers some damage, or loss of fitness. A strategy is then simply a choice of when to retreat after losing a round rather than enter the next.

ESS's have been found for a particular numerical example. The value of winning is $V = 10$. The losses of fitness for losing each of the first five rounds are 1, 2, 4, 8 and 16 respectively; no loser continues after this point. It is assumed (for simplicity of analysis) that an individual decides whether to continue to the next round on the basis of the result of the last round only. Thus only five 'pure' strategies need be considered: *S1* retreats after losing the first round, *S2* after

losing the second round, and so on, up to *S5*, who retreats after losing the fifth round.

Values of x were taken from 0.5 to 1. Before the first round, a contestant does not 'know' whether he is the stronger or weaker contestant, but does 'know' the degree of asymmetry associated with the contest; that is, when finding the ESS for $x = 0.7$, say, it is assumed that individuals are involved in contests in which the chance of winning each round is either 0.7 or 0.3, with equal frequency. The method of analysis was first to compute, for each value of x , a payoff matrix for each of the five strategies played against all the others, and then to seek for the ESS (if necessary by iteration) of each matrix.

The ESS's are given in Table I. If $x \geq 0.7$, the ESS is a pure strategy. When $x = 1$, an individual losing the first round retreats before the next, because the first round is a perfect predictor of the outcome of subsequent rounds. As x falls to 0.7, the damage an individual will risk before retreating increases. For $x \leq 0.65$, the ESS is a mixed strategy. In symmetric contests, $x = 0.5$, 28 per cent of individuals retreat after losing one round and 72 per cent continue for four rounds.

These results illustrate the general theme that symmetric contests usually give rise to mixed ESS's whereas asymmetric contests are settled without appreciable escalation.

V. On Bluff

If some cue such as relative size can be used to settle conflicts conventionally, one might expect animals to evolve features which make them look larger than they actually are. This will only happen if a given increase in apparent size can be achieved more cheaply (in resource cost or other selective disadvantage) by some feature such as a mane or ruff of hair than by actual growth in size. Such a feature will be referred to as 'bluff'. The essential feature of a bluff is that it should increase apparent size (or whatever feature is being used to settle conflicts without escalation) without altering RHP in an escalated contest.

It is not difficult to see that if a bluff cannot be distinguished from an actual increase in size, then bluff will spread through the population.

To illustrate this point, consider a population of non-bluffers. An individual will be the same size as his opponent with probability P , and either larger or smaller with probability $\frac{1}{2}(1-P)$. Suppose that opponents correctly estimate their relative sizes, and that a difference in size

Table I. ESS's for a Multiple-round Contest, Expressed as Proportions of the Constituent Pure Strategies

\bar{x}	Pure strategies				
	S1	S2	S3	S4	S5
0.5	0.28	0	0	0.72	0
0.55	0.29	0	0	0.71	0
0.6	0.14	0.17	0	0.69	0
0.65	0	0.367	0.046	0.587	0
0.7	0	0	1.0	0	0
0.75	0	0	1.0	0	0
0.8	0	0	1.0	0	0
0.85	0	1.0	0	0	0
0.9	0	1.0	0	0	0
0.95	1.0	0	0	0	0
1.0	1.0	0	0	0	0

accurately predicts the outcome of an escalated contest. Let V and $-D$ be the pay-offs for victory and injury respectively, and let $D/V = \alpha$, as before; we consider only cases with $\alpha > 1$, i.e. $D > V$.

From previous sections, the ESS is to escalate with probabilities 1, $p_2 = (V/D)$, and 0 respectively, according to whether a contestant is larger, equal or smaller than its opponent. Call this ESS ' I '. Then

$$E_I(I) = P \left\{ p_2 \left[(1-p_2)V + p_2 \frac{(V-D)}{2} \right] + (1-p_2)^2 \frac{V}{2} \right\} + \frac{1-P}{2} \cdot V$$

which simplifies to

$$E_I(I) = \frac{V}{2} - P \frac{V}{2\alpha}$$

Now consider a mutant 'bluffer', which appears to be one size class larger than it actually is. Consider first an 'optimistic bluffer', *BO*, whose own behaviour corresponds to its apparent

size. $E_I(BO)$ can then be estimated from the following table:

Size relative to opponent:

Actual	Apparent	Frequency	Expected pay-off to mutant
Larger	Larger	$\frac{1-P}{2}$	V
Equal	Larger	P	V
Smaller	Equal	$\frac{1-P}{2}$	$p_2[(1-p_2)V-p_2D] + (1-p_2)^2(V/2)$

It can be calculated that

$$E_I(BO) = \frac{V}{2} \left[\frac{3}{2} - \frac{1}{\alpha} - \frac{1}{2\alpha^2} \right] + \frac{PV}{2} \left[\frac{1}{2} + \frac{1}{\alpha} + \frac{1}{2\alpha^2} \right]$$

Hence

$$E_I(BO) - E_I(I) = \frac{V}{2} \left[\frac{1}{2} - \frac{1}{\alpha} - \frac{1}{2\alpha^2} \right] + \frac{PV}{2} \left[\frac{1}{2} + \frac{2}{\alpha} + \frac{1}{2\alpha^2} \right]$$

Whether *BO* can invade a non-bluffing population then depends on *P*, the frequency of contests between individuals which cannot distinguish their sizes, and α . If $P > \frac{1}{3}$, then the mutant can always invade; if $P = 0$, then the mutant can invade only if $\alpha > 1 + \sqrt{2}$.

The case of a 'pessimistic bluffer', '*BP*', which behaves according to its actual and not to its apparent size, is easier. The relevant table is

Size relative to opponent:

Actual	Apparent	Frequency	Expected pay-off to mutant
Larger	Larger	$(1-P)/2$	V
Equal	Larger	P	$p_2V + (1-p_2)V/2$
Smaller	Equal	$(1-P)/2$	$(1-p_2)V/2$

Note that *BP* never gets into an escalated contest, because if *BP* is willing to escalate, his opponent retreats.

By a calculation similar to that above

$$E_I(BP) - E_I(I) = \frac{V}{2} \left[\frac{1}{2} - \frac{1}{2\alpha} \right] + \frac{PV}{2} \left[1 + \frac{2}{\alpha} \right]$$

which is positive for all values of *P*, and for $\alpha > 1$.

Hence for this particular model, a 'pessimistic' bluffer can always invade, and an 'optimistic' bluffer often can. It is easy to show that bluffing, once established, is evolutionarily stable.

At first sight, this might suggest that bluff will continue to evolve, until the animals were all mane and nobody. It is important to notice, however, that it was assumed that the bluff cannot be detected—short of an escalated contest. This is unlikely to be true. It is more likely that animals could evolve the capacity to distinguish between counterfeit and real size or RHP. This raises a question. Suppose that a population of 'bluffers' has evolved, whose members base their behaviour on apparent size, will a mutant which can distinguish and react to actual size be able to invade it?

It is convenient to write $S = R + B$, where *S* = 'apparent' size, *R* = 'real' size and *B* = bluff component.

Consider a model identical to that just analysed, except that the members of this population base their behaviour on *S*. Let this strategy be *I*.

Consider a mutant, *E*, which can estimate *R* directly, and which bases its behaviour on *R*. There are four situations in which the behaviours of *E* and *I* will differ:

- (i) (*R* + *B*) equal; Mutant *E* has greater *R*.
- (ii) (*R* + *B*) equal; Mutant *E* has smaller *R*.
- (iii) *R* equal; Mutant *E* has greater (*R* + *B*).
- (iv) *R* equal; Mutant *E* has smaller (*R* + *B*).

In the former two cases, typical members of the population estimate the contest to be equal, whereas *E* knows it is not; in the latter case, typical members estimate the contest to be unequal and settle conventionally, although in fact it is equal.

The expected pay-offs to the two strategies are as follows:

	pay-off to <i>E</i>	pay-off to <i>I</i>
	$E_I(E)$	$E_I(I)$
(i)	V	$p_2V + (1-p_2)^2(V/2)$
(ii)	0	$p_2[(1-p_2)V - p_2D] + (1-p_2)^2(V/2)$
(iii)	$p_2V + (1-p_2)(V/2)$	V
(iv)	$p_2(V - D)/2$	0

If we let the frequency of cases (i) and (ii) be p , and of (iii) and (iv) be p' , it is easy to calculate that from (i) and (ii) there is a net gain to the mutant pV/α , and from (iii) and (iv) a net loss of $p'V(1-1/\alpha)$. Whether the mutant can invade depends on the relative frequencies p and p' of the two types of contests. If $p = p'$, the mutant invades if $\alpha < 2$. It is easy to show that if the mutant becomes established, then a population which bases its behaviour on actual rather than apparent size will be evolutionarily stable.

To conclude, if bluff cannot be distinguished from actual RHP, then it will be established. If however individuals can evolve a capacity to distinguish bluff and reality, most populations will evolve strategies based on actual RHP. It is however possible for a population to evolve a stable strategy in which bluff is extensive, even though the bluff could be detected; this is more likely in species in which serious injury is possible.

VI. Discussion

Two general conclusions emerge from the preceding analysis, one relevant to symmetric and the other to asymmetric contests. In symmetric contests, it will often be the case that the ESS will be a mixed one, as in the 'war of attrition' and 'graduated risk' cases. Escalated contests will occur, but if injury is serious they will be rare. In asymmetric contests, mixed strategies will be the exception. Usually, some asymmetric feature will be taken as a 'cue' by which a contest can be settled conventionally. We shall discuss first whether there is any observational support for these two conclusions. We will then consider the circumstances in which escalated contests may occur. Finally, something will be said about the possibility of 'paradoxical' strategies, and about 'bluff'.

(i) Do Mixed Strategies Occur in Nature?

An example of a mixed strategy which fits the theoretical predictions of this paper is afforded by the dung fly *Scatophaga stercoraria* (Parker 1970, 1974b). The behaviour of males searching for females varies in two ways. A male may stay at a cow pat as it grows stale for a long time, or may leave it and fly upwind in search of a fresh pat. The rate at which unmated females arrive at a pat is greatest when the pat is fresh, and falls off with time. While remaining at a cow pat, a male spends part of its time actually on the pat and part on the grass immediately upwind of the pat. These variations, both temporal and spatial,

can be analysed in terms of success in the number of females successfully mated.

Although the contest is an ' n -person game' rather than a '2-person game', it does have the frequency-dependance characteristic of a contest. Thus the optimal strategy for a male depends on what other males are doing. For example, if most males leave a cow pat as soon as it begins to grow stale, a male who remained at a stale pat would mate all the females arriving at it and so would have a high fitness, whereas if most males stay on a cow pat once found, it would pay to leave and search for a fresh one. When analysed in terms of the observed patterns of female behaviour, it turns out that the actual distribution of male behaviour is such that the fitnesses (i.e. expected number of matings) of males adopting different stay times or spatial positions are equal. That is, the male searching behaviour pattern follows an ESS. The pattern of stay times (Fig. 3) has the expected theoretical distribution for a 'war of attrition'. A distribution of this type requires only that the males should leave at random with constant probability. However, the distribution will only be an ESS if the possibility of leaving per unit time is adjusted by natural selection so that on average the fitness of males leaving early is the same as that of males leaving late, and this seems to be so. Since individual males can be seen to divide their time between the pat and the grass, it seems that in spatial distribution an individual male can adopt a mixed strategy; it is

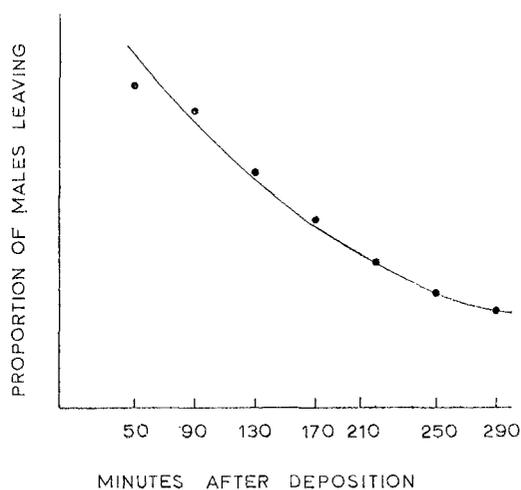


Fig. 3. Relative numbers of male dung flies, *Scatophaga stercoraria*, leaving a cowpat at different times after its deposition.

not known whether the same is true for temporal variations, or whether these reflect genetic differences.

Although searching behaviour of *Scatophaga* can be satisfactorily explained, there is another aspect of male competition which presents more difficulties. A male which has once mounted a female remains mounted until the end of oviposition. A mounted male may be attacked by another; if so, the contest is usually settled conventionally in a few seconds in favour of the 'owner'. Sometimes a more protracted struggle, of very variable duration, ensues; although such struggles are usually won by the owner, they may be won by the attacker. We are not at present able to explain the frequency and duration of contests. The difficulty arises because of the various types of asymmetry associated with the contest, both in pay-off (the owner of an ovipositing female has more to lose) and in RHP (some males are larger than others, and there is a postural advantage to the owner over the attacker).

The case of *Scatophaga* has been considered at some length, because in this case data were collected with the specific aim of seeing whether males adopting different strategies had equal mating success. Until similar investigations have been made of other contest situations, it will not be possible to say how widespread mixed strategies of the kind predicted by the theory will prove to be.

(ii) Are Conventional Cues Used in Nature to Settle Asymmetric Contests?

Although the answer to this question is probably yes, one must be careful before presenting particular cases in support of the theory put forward here. The two best-known situations in which contests are settled without escalation are in territorial behaviour, when an interloper retreats if challenged by an owner, and in dominance hierarchies, when an individual low in the order retreats if challenged by an individual higher in the order. Neither of these cases can be taken as relevant to the present theory because in both cases the behaviour of an individual probably depends on previous experience with the same opponent, a feature of contests which has so far been omitted from our analysis.

This point will be pursued a little further in the case of territory. If two birds hold contiguous territories, and if each retreats when

challenged inside the other's territory, then the behaviour presumably is influenced by previous encounters between the same two individuals. The situation is different when we have to analyse a contest or series of contests between two individuals which determine which of them shall hold a particular territory and which of them shall move away. Such 'decisions' do have to be taken. For example, in great tits breeding success is higher in woodland than in hedgerows. Krebs (1971) showed that when a territory-holding male was removed from a wood, his place was taken by a male from outside the wood. The question therefore arises, why was the original male left in undisputed possession of the territory? One possible answer is that he was there first; if so, this is an example of a, probably largely uncorrelated, asymmetry. Another possibility is that there was some difference in size or age between the males, which was used as a cue to settle ownership; this would be an example of a contest with unequal RHP's. A third possibility, since tits winter in flocks in the area where they breed, is that the territorial contest was settled by prior positions in a hierarchy; if so, this only pushes the problem back to the question of how relative positions in a hierarchy are determined. None of these explanations need be correct. All that can be said is that such contests are settled, and that there are various asymmetries which could be used to settle them.

There is one case of territorial behaviour in which there is experimental evidence (Gilbert, personal communication) to show how a contest is settled. The males of the swallowtail butterfly *Papilio zelicaon* in California occupy hilltops, to which virgin females go to mate. Since there are more males than hilltops, there is competition for optimal territories. A strange male arriving at a hilltop is challenged by the occupying male, and retreats without a prolonged contest. Gilbert allowed two males to occupy the same hilltop on alternate days, keeping them in the dark in the intervals. When, after 2 weeks, both males were released on the hilltop on the same day, a prolonged and physically damaging contest ensued before one male ultimately withdrew. This suggests that prior occupancy is the cue which settles contests. Since there is no obvious reason why the owner of a hilltop should have either a higher RHP or a higher pay-off for victory, this is perhaps best regarded as an example of an uncorrelated asymmetry being used to settle a contest.

Asymmetric contests are not confined to territorial situations. Geist (1966) presents evidence that, in *Ovis dalli*, when a strange ram is integrated into a group, his position in the dominance hierarchy is partly determined by relative size (in particular, horn size) without physical engagements, the latter being confined to opponents of approximately equal size. Here the asymmetry is in RHP.

A case of prior ownership settling a contest is described by Kummer (1971) in hamadryas baboons, *Papio hamadryas*, a species in which a single male has permanent ownership of one or several females. Fights between males can be caused in the wild by a procedure analogous to Gilbert's with *Papilio*. If a male is removed from a troop, his females will be taken over by another male or males. If the original male is then reintroduced, ownership is settled by fighting. Kummer brought together a male and female previously strange to one another, and left them for 15 min to form a pair bond. A second male, who had been able to observe the pair, was then introduced into the enclosure; this second male avoided conflict with the first arrival, who was left in possession of the female. On a later occasion the same two males were used in a similar experiment with a second female but with their roles reversed; again the first arrival was left in possession of the female. This seems a clear case of a contest with an almost uncorrelated asymmetry, although it may be that the pay-off for victory is slightly greater to the owner of a female, since he has expended energy in convincing the female of his ownership.

(iii) Escalated Contests

In all likelihood, the settling of contests by prior asymmetries, with or without bias, is widespread, although clear evidence in particular cases is usually lacking. Escalated contests do, nevertheless, occur, and serious injury may be suffered by one or both contestants. There seem to be four situations in which escalated contests are to be expected.

(a) The pay-off for winning is large compared to the loss due to injury. For example, if the loser of a territorial contest has little chance of finding a territory elsewhere, or of surviving to breed next year, then we would expect escalation to be more frequent than if a territory in an alternative habitat is readily available, or if the likelihood of a non-breeder surviving for a further year is high.

It is not clear that this expected correlation occurs. For example, male red grouse establish territories in autumn, and breed in them in spring. There is evidence (Watson & Miller 1971, and references cited) both that more-aggressive males obtain larger territories, and that birds which do not obtain territories usually die in the winter (although they may take over a territory if the owner dies). Yet there is no obvious disadvantage to increased aggression in terms of increased risk of injury. What then is the counterbalancing selection which prevents an indefinite increase in aggression? One possible explanation is that excessive aggression would make pair formation and mating more difficult; yet, in view of the very strong selection in favour of holding a territory, it is hard to believe that birds could not evolve so as to be aggressive to other males but not to females.

(b) The second situation in which we might expect to see escalated contests is when there is no asymmetry which can be used as a cue to settle the contest. The analysis of the 'graduated risk' game suggests that if there are no asymmetries, and if the only choice of strategy open to a contestant is of a 'level of escalation' and an associated probability of serious injury, then escalated contests will occur. Individuals will vary in the level to which they are prepared to escalate; occasionally, two individuals both prepared to escalate to a high level will meet.

There is a way of avoiding escalation in symmetric contests, as suggested by the analysis of 'retaliation' by Maynard Smith & Price (1973). This analysis assumed, however, that two contestants could withdraw from a brief escalation without either contestant having to withdraw from the contest altogether. It also assumed that symmetric contests can be settled by display alone. This leads to a 'war of attrition' type of situation; that is to say, to protracted contests in which the selective cost of the waste in time and energy is of the same order of magnitude as the selective advantage of victory.

It follows that in the absence of some asymmetric cue, the cost of contests, either in the risk of injury or in the cost in time and energy, is likely to be large.

(c) Imperfect information. Even if the contest is asymmetric, escalation is possible if the contestants have imperfect information about the asymmetry. Here it is important to make a distinction between cases in which information about the asymmetric cue is imperfect, and

cases in which the cue is an imperfect prediction of the outcome of a contest. Suppose for example that the 'cue' is the relative size of horns. If the contestants have accurate information about the relative size of their horns, this could in principle be used to settle conflicts without dangerous escalation, even if relative horn size was a rather poor predictor of the outcome of an escalated contest. Indeed, differences of horn size could be used to settle conflicts even if they were uncorrelated with the outcome of escalation (i.e. unbiased asymmetry). But if information about the cue (e.g. relative horn size) is itself imperfect, then escalation is likely; two contestants may both estimate that they are larger, or there may be a range within which discrimination one way or the other is impossible.

(d) The population is not an ESS. This is always a possibility, particularly if the population is the result of recent hybridization, or if it has been domesticated.

(iv) Paradoxical Strategies

One unforeseen outcome of the analysis is that in asymmetric contests, 'paradoxical' strategies may be stable; that is, strategies in which the contestant with the higher RHP or with more to gain gives way, and that with lower RHP or with less to gain wins. Circumstances which favour the existence of a paradoxical ESS are: (a) the possibility of injury which is severe relative to the advantage to be gained; (b) precise information exists about an asymmetric cue; (c) in the case of asymmetry in RHP, the cue is a poor guide to the outcome of escalation.

It is important to bear in mind this possibility, although it is unlikely that paradoxical ESS's occur in nature. First, a contest which permits a paradoxical ESS always permits a 'common-sense' ESS, in which the winner is the contestant with the higher RHP or with more to gain. Further, this common-sense RHP has a larger 'zone of attraction' and hence is more likely to arise. For example, it was shown that in contests with unequal pay-offs, the paradoxical strategy 'give way when you have most to gain' can be stable, but could not evolve from an initial population which ignored the asymmetry, whereas the common-sense strategy 'give way when you have least to gain' could evolve from such a population.

(v) Bluff and the Conveying of Information

It is natural to think that one function of a display is to convey accurate information about the future behaviour of the individual displaying.

In contest situations this need not be the case. In a 'war of attrition' situation, it would be selectively disadvantageous for an individual to convey by its behaviour whether it would continue for a long or a short time (Maynard Smith 1974). In such situations we would expect to see displays of 'typical intensity', although for a reason different from those suggested by Morris (1957).

The situation is somewhat different if contests are settled by an asymmetric cue, for example horn development, which may indicate relative RHP. It is selectively advantageous to an individual not to be involved in escalated contests with equal or superior opponents. The frequency of escalated contests in a population will be lower if the variance of horn size is large (Geist 1966). The problem of course is whether selection at the individual level could bring about such a high variance. It might do so in an animal that grows throughout life, by favouring an allometric relation between body size (and hence RHP) and horn size; animals smaller in size and RHP than the population average would benefit by having unambiguously small horns. However, the problem is not an easy one, and would repay further study.

If contests are settled by asymmetric cues, the possibility of 'bluff' must be considered; that is, the evolution of features which exaggerate apparent size (or whatever feature is used as a cue) without altering RHP in an escalated contest. It seems clear that selection would favour bluff if it could not be detected, particularly if the bluffer were to behave in a way appropriate to his actual and not his apparent RHP. However, it is equally clear that selection will favour individuals capable of distinguishing bluff from actual RHP, and this is likely to limit the extent to which bluff is employed in animal contests.

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