John Maynard Smith, Evolution and the Theory of Games (Cambridge U.P., 1982).

3 *The war of attrition*

In the last chapter, I assumed that two 'Doves' competing for a resource worth V could share the resource. There will be many cases in which it will not be worth while to share a resource. For example, suppose two animals compete for a territory, and that there is no asymmetry, such as prior ownership, which can settle the matter.

Let N = expected offspring to the owner of the territory,
kN = expected offspring to the owner of half the territory ($k < 1$),
n = expected offspring to an animal who does not compete but instead sets up a territory in a less satisfactory habitat ($n < N$).

If $n > kN$, it would not pay either contestant to share the territory. The payoff V for obtaining the territory is $N-n$; note that it is *not* the expected fitness of an owner of the territory, but the *change* in fitness for winning.

Suppose, then, that $V = N-n$, and that the contest is settled without escalation. That is, the contestants display, and the owner is the one which persists longest. For how long should a contestant persist? If displaying cost nothing, the contestant should persist for ever, which is clearly absurd. In practice, to display must cost something, if only because to display for a long time is to delay the start of breeding.

I assume, therefore, that the cost of displaying increases with the length of the contest and is the same for the two contestants. The only choice open to an individual is to select a length of time for which he is prepared to continue and an associated cost, m, he is prepared to pay. Thus if the two contestants, A and B, select costs m_A and m_B, respectively, the winner will be the one selecting the higher cost; however, he will not have to pay that cost, because the length of the contest is determined by the loser. Thus the payoffs are

	Player A	Player B
$m_A > m_B$	$V-m_B$	$-m_B$
$m_A = m_B$	$(V/2)-m_B$	$(V/2)-m_B$
$m_A < m_B$	$-m_A$	$V-m_A$.

This assumes that in the (infinitely unlikely) event that $m_A = m_B$, the contest is decided randomly. Given these payoffs, what choice of m is evolutionarily stable?

Before answering this question, one biological point must be made. In assuming that the only possible choice of strategy is a choice of m, made before the contest, I have assumed that no relevant information (e.g. about what would happen in an escalated contest) is obtained during the contest. The problem of information transfer is crucial; it is discussed further on p. 35 and in later chapters.

Clearly, no pure strategy can be an ESS. Thus suppose the members of a population play M. Their average payoff is $(V/2)-M$. A mutant playing $M+\delta M$ would have an average payoff $V-M$, and could invade. If $M > (V/2)$, a mutant playing 0 could also invade.

Hence, if there is an ESS, it must be a mixed one. Let I be a strategy defined by the probability density function $p(x)$. That is, the probability of accepting a cost between x and $x+\delta x$ is $p(x)\delta x$. To find $p(x)$, we make use of the Bishop–Cannings theorem (Appendix C), which in the present context states that, if m is a pure strategy in the 'support' of I (i.e. $p(m) \neq 0$), then $E(m,I)$ is constant.

Now

$$E(m,I) = \int_0^m (V-x)p(x)\mathrm{d}x - \int_m^\infty m\,p(x)\mathrm{d}x.$$

We have to find $p(x)$ such that $\partial E(m,I)/\partial m = 0$, subject to the constraint $\int_0^\infty p(x)\mathrm{d}x = 1$. It is easy to confirm that

$$p(x) = (1/V)\mathrm{e}^{-x/V} \tag{3.1}$$

is the required function. This shows that $I = p(x)$ is an equilibrium strategy; to show that it is stable, we must also show that

$$E(I,m) > E(m,m). \tag{3.2}$$

This can easily be done if m is a pure strategy (Maynard Smith, 1974); it has been proved by Bishop & Cannings (1978) for the case when m can be any mixed strategy different from I.

The negative exponential form of equation (3.1) is intuitively appealing for the following reason. Since no information is exchanged, a contestant who has continued for time t, and whose opponent is still displaying, is in exactly the same state as far as *future* gains and losses are concerned as he was at time zero. Logically, therefore, he should make the same choice of future expenditure at time t as at time zero; this requires a negative exponential distribution.

If cost is a linear function of time, then the times for which an individual is prepared to display will be distributed as a negative exponential. A stay time with this distribution, however, is not particularly strong evidence for a mixed ESS, since all that is needed to generate such a distribution is that the individual should have a constant probability of leaving per unit time. It must also be shown that the constant probability has the correct value – 'correct' here means the value which equalises the fitnesses of individuals with different stay times, as is true for the distribution given by equation (3.1). The work of Parker (1970*a*,*b*) and of Parker & Thompson (1980) on the dung fly *Scatophaga stercoraria* affords two examples, one of which may be a mixed ESS, and the other certainly is not.

Female dung flies come to fresh cowpats to lay their eggs. The males congregate at cowpats, and attempt to mate with arriving females. For how long should a male stay at a cowpat? Many females arrive at a fresh pat, and progressively fewer arrive as the pat grows stale. Therefore, a male which stays too long will meet few females. However, if most males stay only for a short time, a male which stays for a longer time will have a better chance of mating with those females which do arrive. Hence, if other males move it pays to stay, and vice versa. The contest is a frequency-dependent one similar, but not mathematically identical, to the war of attrition.

Parker (1970*a*) found that male stay times are exponentially distributed. Further, if female arrival rates are measured, it is found that male stay times are so distributed as to give the same expected success to males adopting different strategies (Figure 2). To get equal success rates, Parker had to suppose that the time required to find a

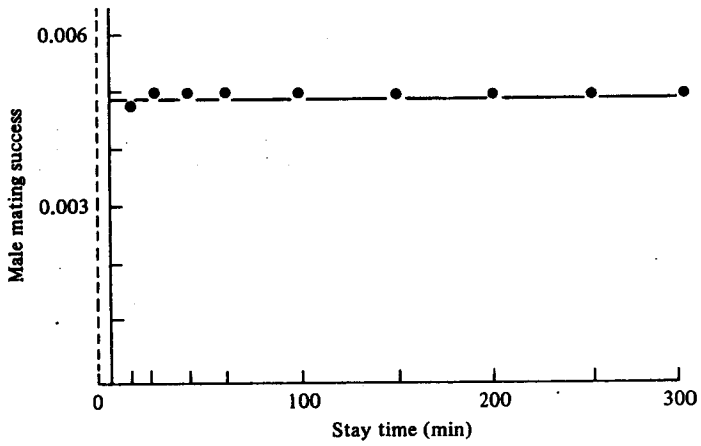

Figure 2. Estimated mating success of male dung flies, as a function of their stay times at cowpats, assuming it takes four minutes to find a fresh pat. (After Parker, 1970*a*.)

new pat, after leaving an old one, was four minutes. This was not an arbitrary choice made only to get a good fit; four minutes is the average time it takes males to arrive at a freshly deposited pat. Parker's data, therefore, provide a striking fit with the theory.

The mechanism by which this is achieved, however, is not known. There are at least three possibilities. First, the population may be genetically variable, with each male having a different genetically determined stay time. Secondly, all males may be alike, with an individually flexible stay time; since the distribution is, approximately, a negative exponential, all that this requires is that each male should have the same constant probability of leaving per unit time. Thirdly, and perhaps most plausible, males may adjust their stay times in the light of experience. It will be shown in Chapter 5 that learning can take a population to the ESS frequencies in a single generation, without genetic evolution. A learning mechanism would have the advantage of enabling males to adjust their behaviour as the density of cowpats changes.

It may not be accidental that Parker's data refer to a contest in which individuals are playing the field. In pairwise contests, asymmetries of size, ownership, sex, age etc. are likely to be perceived and to

influence strategy choices. An example, also from Parker's dung fly study, will now be given, but first we must derive an expression for the lengths of contests to be expected in a war of attrition.

The expression $p(x) = (1/V)\exp(-x/V)$ gives the length of time for which an individual is prepared to continue (or, more precisely, the cost it is prepared to accept). Often, what we can actually observe is the duration of the actual contest. How are these durations distributed? Perhaps the easiest way of seeing the answer is as follows. In a time interval δt, the chance that a particular contestant will leave is $\delta t/V$. Since the two contestants are independent, the chance that one or other will leave is $2\delta t/V$. Hence the distribution of contest length is

$$P(x) = (2/V)e^{-2x/V}. \tag{3.3}$$

Thus contest lengths are also exponentially distributed, but with mean $V/2$ instead of V.

Parker & Thompson (1980) derived this result and applied it to a later stage of the contest between male dung flies. After mating, females stay on the dung laying eggs. The male remains on the back of the female during this period. In this way, he prevents a second male from copulating with the female; if a second copulation does occur, the second male's sperm fertilise 80% of the eggs laid subsequently.

While a female paired in this way is laying eggs, unmated males attempt to displace the male in possession (Parker, 1970*b*). Usually, an approaching male is deflected by the owner without a struggle. If, however, the approaching male manages to touch the female, a struggle often ensues, in which the intruder attempts to displace the owner. Parker & Thompson (1980) analyse these struggles. The durations are, approximately, exponentially distributed. Further, the relation between mean duration and estimated costs is at least consistent with a 'war of attrition' interpretation, although costs cannot be measured with any precision. The authors point out, though, that it would be quite wrong to interpret the contests in this way. Thus if, as in Figure 3, a distinction is made between those won by owners and by intruders, the contests are seen to be quite different, and the latter are far from exponential in distribution. Yet in the symmetric war of attrition the two distributions should be the same,

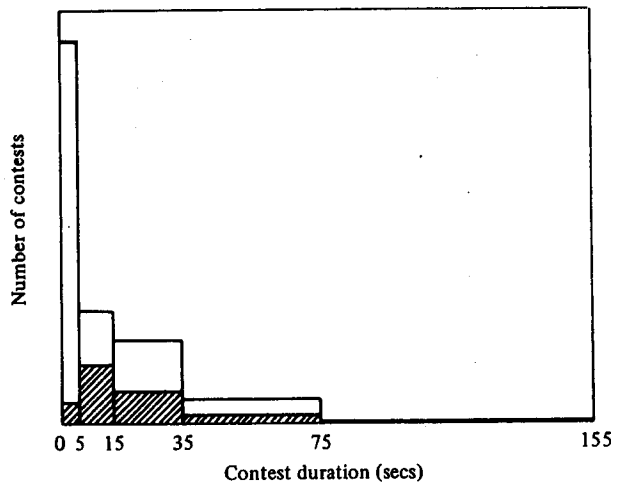

Figure 3. Observed lengths of contests between male dung flies. Open histogram, all data; cross-hatched histogram, contests in which the attacking male won. (After Parker & Thompson, 1980.)

and both exponential. The contest, clearly, is an asymmetric one, and should be analysed as such; this will be done on p. 121. It has been mentioned here as a warning; an exponential distribution of contest durations is an insufficient reason for regarding a contest as a symmetric war of attrition.

It may be that cost is not a linear function of time. If so, the contest can still be analysed in the same way, but its duration will no longer be exponentially distributed (Norman, Taylor & Robertson, 1977). Thus suppose the cost Q is some function $q(x)$ of the time x for which the contest lasts. The contestants can be thought of as choosing an acceptable cost, and, by exactly the same argument as that leading to equation (3.1), the stable distribution of choices will be

$$p(Q) = (1/V)e^{-Q/V}. \tag{3.4}$$

What, then, will be the distribution of x? The probability that an individual will select a time between x and δx is the same as the probability that it will accept a cost between $q(x)$ and $q(x+\delta x)$. That is

$$p(x)\delta x = p(Q)\delta Q$$

or

$$p(x) = p(Q)\frac{dQ}{dx}.$$

For example, suppose costs were proportioned to the square of the duration; i.e. $Q = kx^2$. Then

$$p(x) = p(Q)\cdot 2kx = (2kx/V)e^{-kx^2/V}$$

This gives a very different form for the expected duration of contests (see Figure 4). This is a further reason for not treating the distribution of contest durations as evidence for or against a war of attrition interpretation. The critical evidence required is an equality of payoffs for different choices, as shown for dung flies in Figure 2.

Bishop & Cannings (1978) point out that the war of attrition model can be applied in a wide range of contexts, provided that:

(i) No relevant information is received during the contest, so that an action (i.e. a persistence time) can in effect be made at the start.

(ii) The winner is the contestant prepared to accept the higher cost.

(iii) The actual cost to both contestants is equal to the cost acceptable to the loser.

(iv) The range of possible actions must be a continuous one; the significance of this is discussed further on p. 105.

For example, cost might be measured by injury received during the contest. Such injury might be proportional to the length of the contest; alternatively, the strategy choice might be of a level to which the contestant would escalate, the amount of injury increasing as the level was raised. It need not even be the case that actual injury received is a function of duration or level of escalation, provided that the *risk* of injury (i.e. the 'expected' injury) is such a function. It is, however, a necessary feature of the model that injury should not be so great as to prevent a contestant from continuing. A crucial difference between the war of attrition and the Hawk–Dove game is that, in the former, an animal can almost guarantee victory by choosing a sufficiently high risk (although, of course, it cannot guarantee a positive payoff), whereas a Hawk meeting another Hawk has only an even chance of victory.

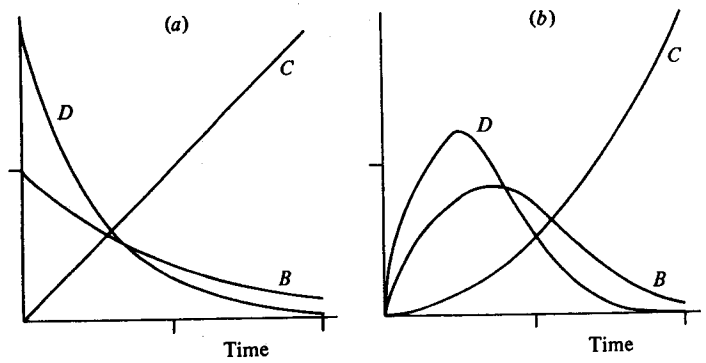

Figure 4. The war of attrition. Distribution of acceptable durations (B), and durations of contests (D), when (a) cost, C, is proportional to time, and (b) cost is proportional to the square of the time.

When discussing the persistence times of male dung flies at cowpats, the point was made that this is a contest in which each individual is playing the field, and that the reasonable fit with the war of attrition model is probably dependent on this fact; in pairwise contest, information transfer is likely to influence behaviour. The time has now come to discuss information transfer. It is convenient to start by considering two extreme models.

(i) There are no differences in size or weapons which can be detected by the contestants. There are, however, differences in motivation, leading contestant A to choose cost m_A and B to choose cost m_B, where $m_A > m_B$, say. Would it not pay them both to signal the level they have chosen, and for B then to retreat at once? Indeed, both would be better off; A would gain V instead of $V - m_B$, and B would gain 0 instead of $-m_B$. Unfortunately, this signalling behaviour is not proof against 'lying'. Thus suppose we start with a population of individuals which select a value of m according to equation (3.1), signal it accurately, and retreat at once if their opponent signals a higher value. A mutant which signals a large value M, but retreats if its opponent does not retreat at once, can invade such a population. Soon the population would consist of individuals signalling high values of M which did not correspond to their actual future behaviour. At this stage, a mutant which ignored the signal it

received, which gave no signal, and which followed equation (3.1), could invade the population. That is, we end with a population not giving any information.

(ii) Now consider a model in which there are detectable differences of size, such that the larger animal would certainly win an escalated contest. It would be evolutionarily stable for animals to convey information about their size, and to retreat if smaller than their opponents. Thus a mutant which either ignored information it received, or which did not itself transmit information, would engage in unnecessary fights. The essential difference between this and the preceding model is that I am now assuming that it is impossible for an animal to give false information about its size.

This distinction is crucial to an understanding of animal contests in general, and information transfer in particular. In the first model, it is possible for an animal to transmit any signal, at little or no cost, except in so far as there might be a cost exacted in the subsequent course of the contest. In the second model, it is impossible for an animal to transmit false information about its size, although there will certainly be selection for animals to appear as large as possible. Also, since larger animals win contests, there will be strong selection for increased size. There are also likely to be counteracting disadvantages to large size. An analysis of this situation is given in Chapter 11.

The problems of information transfer are discussed further in Chapters 9 and 12. For the present, the essential point is to distinguish two cases:

(i) Information about 'motivation' or 'intentions'. Because any message about motivation can be sent, with little cost, there is no reason why such messages should be accurate, and therefore no advantage in paying attention to them.

(ii) Information about 'Resource-Holding Power', or RHP (Parker, 1974*b*); RHP is a measure of the size, strength, weapons etc. which would enable an animal to win an escalated contest. It can be evolutionarily stable to transmit information about RHP, and to accept such information to settle a contest, provided two things are true. It must be impossible to transmit false information about RHP, and it must be expensive to acquire high RHP in the first place.

I turn now from the problem of information transfer to discuss cases in which the value of winning is not the same for the two

Table 7. *Supposed breeding success, in offspring successfully reared, of young and old birds*

	Favourable habitat	Unfavourable habitat
First-year bird	2	1
Old bird	4	2

contestants. An example is a contest for food between a hungry and a well-fed animal. To take a more complex example, suppose that two kinds of birds compete for a territory in a favourable habitat, and that the loser can establish a territory in a less favourable habitat without further contests. The two birds may be of different ages: for example, a first-year bird and an older bird. Suppose that expected breeding success is as shown in Table 7. The payoff for winning is then 2 to the older bird and 1 for the first-year bird.

Suppose first that the difference between young and old birds can be recognised unambiguously. Then, as Hammerstein (1981) pointed out, the contest should be analysed as three separate games: young v. young, old v. old, and young v. old. In the first two games, there are no payoff differences to worry about. The third game is a typical asymmetric game of the type discussed in Chapters 8 to 10; almost certainly, the age difference would be used as a cue to settle the contest.

Suppose, however, that the age of an opponent cannot be detected, so that a bird's behaviour can be influenced by its own age status, but not by its opponent's. This is an example of a game of imperfect information (discussed further in Chapter 12); each contestant has some information not available to its opponent. The earlier example of a contest between a hungry and a well-fed bird would be logically similar if a bird knew only its own state of hunger.

The problem of the war of attrition in which an individual knows the value of the resource to itself, but knows only the probability distribution of the value to its opponent, is analysed in Appendix G. Applied to the example of a territorial contest, the conclusions are as follows. Younger birds will select an acceptable cost, m, from a

probability distribution ranging from zero to some threshold value, T, and older birds from a distribution ranging from T to ∞. Thus, old birds will always win against young ones, but symmetric contests will be settled, as in a typical war of attrition, by the chance selection of a value of m from the same distribution.

If there are only two categories of individual, there is a single threshold value T. If there are N categories, for which the values of winning are $V_1 < V_2 < \ldots < V_N$, there will be N non-overlapping probability distributions separated by $N-1$ threshold values. Contests will be won by the animal with the larger value.

What is the average payoff per contest in the war of attrition? For the simple case, with an ESS given by equation (3.1), it is easy to see that the average payoff is zero. Thus the defining characteristic of equation (3.1) is that the payoff for all values of x is the same. This includes the payoff for $x = 0$, which is clearly zero. In other words, the average cost of a contest is equal to $V/2$, the average gain. This may at first sight seem an odd result. It does *not* mean, however, that animals have, on average, zero fitness. Thus suppose, for example, that all territorial contests were symmetric ones between older birds. The value of winning is 2 offspring, so the average cost will be 1 offspring, compared to an average breeding success of 3 in the favourable habitat and 1 in the unfavourable one.

Things are different, however, if the rewards are variable. It is still true that the average payoff is zero for that category with the lowest value for winning; it is positive for all other categories.

The essential feature of the 'variable rewards' model is that animals know the value of the resource to themselves, but not to their opponent. There is one rather strange example which may illustrate this model. This concerns the digger wasp *Sphex ichneumoneus*. Females of this species dig holes, which they then provision with katydids, before laying a single egg and sealing the burrow. Sometimes, instead of digging a burrow, a female will enter a burrow already dug by another wasp. The choice between these strategies is analysed (pp. 74–5) as an example of a mixed ESS. For the present, however, I want to concentrate on the fights which occur if two wasps who are provisioning the same burrow actually meet. Dawkins & Brockmann (1980) analyse Brockmann's data on 23 such fights observed in the field.

For each fight, it is known how long it lasted, who won, which wasp dug the hole, which was larger, and how many katydids each had supplied. Surprisingly, there was no significant advantage for the larger of the two, nor for the owner over the joiner. Eleven wasps fought more than once; there was no significant tendency for some wasps to be winners and others losers. What then does determine the outcome of fights? The hypothesis which best fits the facts is that a wasp fights for a length of time which increases with the number of katydids it has brought to the nest, and hence that the winner is the wasp which has brought most katydids. There is, of course, a correlation between the number of katydids brought by the loser and the total number present, but analysis shows that it is the number brought by the loser which is relevant in determining the length of a fight.

These results are what would be expected from a war of attrition with random rewards, provided that we assume that a wasp knows how many katydids it has supplied (presumably, by monitoring its own activity) but not the total number present. If this is so, then the value of a burrow is indeed an increasing function of what the individual has supplied, and the length of time the individual will fight should likewise increase with the number of katydids supplied.