2 The basic model

This chapter aims to make clear the assumptions lying behind evolutionary game theory. I will be surprised if it is fully successful. When I first wrote on the applications of game theory to evolution (Maynard Smith & Price, 1973), I was unaware of many of the assumptions being made and of many of the distinctions between different kinds of games which ought to be drawn. No doubt many confusions and obscurities remain, but at least they are fewer than they were.

In this chapter, I introduce the concept of an 'evolutionarily stable strategy', or ESS. A 'strategy' is a behavioural phenotype; i.e. it is a specification of what an individual will do in any situation in which it may find itself. An ESS is a strategy such that, if all the members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection. The concept is couched in terms of a 'strategy' because it arose in the context of animal behaviour. The idea, however, can be applied equally well to any kind of phenotypic variation, and the word strategy could be replaced by the word phenotype; for example, a strategy could be the growth form of a plant, or the age at first reproduction, or the relative numbers of sons and daughters produced by a parent.

The definition of an ESS as an uninvadable strategy can be made more precise in particular cases; that is, if precise assumptions are made about the nature of the evolving population. Section A of this chapter describes the context in which an ESS was first defined by Maynard Smith & Price (1973), and leads to the mathematical conditions (2.4a, b) for uninvadability. The essential features of this model are that the population is infinite, that reproduction is asexual, and that pairwise contests take place between two opponents, which do not differ in any way discernible to themselves before the contest starts (i.e. 'symmetric' contests). It is also assumed that there is a finite set of alternative strategies, so that the game can be expressed in matrix form; this assumption will be relaxed in Chapter 3.

Still using this model of pairwise contests, I then contrast the concept of an ESS with that of a population in an evolutionarily stable state. The distinction is as follows. Suppose that the stable strategy for some particular game requires an individual to do sometimes one thing and sometimes another – e.g. to do I with probability P, and J with probability $1 - P$. An individual with a variable behaviour of this kind is said to adopt a mixed strategy, and the uninvadable strategy is a mixed ESS. Alternatively, a population might consist of some individuals which always do A and others which always do B. Such a population might evolve to a stable equilibrium with both types present – that is, to an evolutionarily stable polymorphic state. The question then arises whether the probabilities in the two cases correspond; that is, if the mixed ESS is to do I with probability P, is it also true that a stable polymorphic population contains a proportion P of individuals which always do I? This question is discussed in section A below, and in Appendix D, for the case of asexual (or one-locus haploid) inheritance; the more difficult but realistic case of sexual diploids is postponed to Chapter 4.

Section B reviews the assumptions made in the model, and indicates how they might be relaxed or broadened. Section C considers a particular extension of the model, in which an individual is 'playing the field'; that is, its success depends, not on a contest with a single opponent, but on the aggregate behaviour of other members of the population as a whole, or some section of it. This is the appropriate extension of the model for such applications as the evolution of the sex ratio, of dispersal, of life history strategies, or of plant growth. The conditions for a strategy to be an ESS for this extended model are given in equations (2.9).

A The Hawk–Dove game

Imagine that two animals are contesting a resource of value V. By 'value', I mean that the Darwinian fitness of an individual obtaining the resource would be increased by V. Note that the individual which does not obtain the resource need not have zero fitness. Imagine, for example, that the 'resource' is a territory in a favourable habitat, and that there is adequate space in a less favourable habitat in which losers can breed. Suppose, also, that animals with a territory in a

favourable habitat produce, on average, 5 offspring, and that those breeding in the less favourable habitat produce 3 offspring. Then V would equal $5-3=2$ offspring. Thus V is the *gain* in fitness to the winner, and losers do not have zero fitness. During the contest an animal can behave in one of three ways, 'display', 'escalate' and 'retreat'. An animal which displays does not injure its opponent; one which escalates may succeed in doing so. An animal which retreats abandons the resource to its opponent.

In real contests, animals may switch from one behaviour to another in a complex manner. For the moment, however, I suppose that individuals in a given contest adopt one of two 'strategies'; for the time being, I assume that a particular individual always behaves in the same way.

'Hawk': escalate and continue until injured or until opponent retreats.

'Dove': display; retreat at once if opponent escalates. If two opponents both escalate, it is asumed that, sooner or later, one is injured and forced to retreat. Alternatively, one could suppose that both suffer some injury, but for the moment I am seeking the simplest possible model. Injury reduces fitness by a cost, C.

Table 1. *Payoff Hawk–Dove game*

	H	D
H	$\frac{1}{2}(V-C)$	V
D	0	$V/2$

Writing H and D for Hawk and Dove, it is now possible to write down the 'payoff matrix' shown in Table 1. In this matrix, the entries are the payoffs, or changes of fitness arising from the contest, to the individual adopting the strategy on the left, if his opponent adopts the strategy above. Some further assumptions were made in writing down the matrix, as follows:

(i) *Hawk v. Hawk* Each contestant has a 50% chance of injuring its opponent and obtaining the resource, V, and a 50% chance of being injured. Thus it has been assumed that the factors,

genetic or otherwise, determining behaviour are independent of those which determine success or failure in an escalated contest. Later, in Chapter 8, I discuss contests in which differences, for example in size, which influence success in an escalated contest can be detected by the contestants.

(ii) *Hawk v. Dove* Hawk obtains the resource, and Dove retreats before being injured. Note that the entry of zero for Dove does *not* mean that Doves, in a population of Hawks, have zero fitness: it means that the fitness of a Dove does not alter as a result of a contest with a Hawk.

In the imaginary example, described above, of a contest over a territory, the fitness of a Dove, after a contest with a Hawk, would be 3 offspring.

(iii) *Dove v. Dove* The resource is shared equally by the two contestants. If the resource is indivisible, the contestants might waste much time displaying; such contests are analysed in Chapter 3.

Now imagine an infinite population of individuals, each adopting the strategy H or D, pairing off at random. Before the contest, all individuals have a fitness W_0.

Let p = frequency of H strategists in the population,

$W(H)$, $W(D)$ = fitness of H and D strategists respectively,

and $E(H,D)$ = payoff to individual adopting H against a D opponent (and a similar notation for other strategy pairs).

Then if each individual engages in one contest,

$$\left.\begin{array}{l} W(H) = W_0 + p\,E(H,H) + (1-p)\,E(H,D), \\ W(D) = W_0 + p\,E(D,H) + (1-p)\,E(D,D). \end{array}\right\} \quad (2.1)$$

It is then supposed that individuals reproduce their kind asexually, in numbers proportional to their fitnesses. The frequency p' of Hawks in the next generation is

$$p' = p\,W(H)/\bar{W}, \quad (2.2)$$

where $\bar{W} = p\,W(H) + (1-p)\,W(D).$

Equation (2.2) describes the dynamics of the population. Knowing the values of V and C, and the initial frequency of H, it would be a simple matter to calculate numerically how the population changes in time. It is more fruitful, however, to ask what are the stable states, if any, towards which the population will evolve. The stability criteria will first be derived for the general case, in which more than two strategies are possible, and then applied to the two-strategy Hawk–Dove game.

If I is a stable strategy,* it must have the property that, if almost all members of the population adopt I, then the fitness of these typical members is greater than that of any possible mutant; otherwise, the mutant could invade the population, and I would not be stable. Thus consider a population consisting mainly of I, with a small frequency p of some mutant J. Then, as in (2.1),

$$\left.\begin{array}{l} W(I) = W_0 + (1-p)\,E(I,I) + p\,E(I,J), \\ W(J) = W_0 + (1-p)\,E(J,I) + p\,E(J,J). \end{array}\right\} \quad (2.3)$$

Since I is stable, $W(I) > W(J)$. Since $J \neq I$,

either $E(I,I) > E(J,I)$ $(2.4a)$

or $E(I,I) = E(J,I)$ and $E(I,J) > E(J,J)$. $(2.4b)$

These conditions were given by Maynard Smith & Price (1973).

Any strategy satisfying (2.4) is an 'evolutionarily stable strategy', or ESS, as defined at the beginning of this chapter. Conditions (2.4a, b) will be referred to as the 'standard conditions' for an ESS, but it should be clear that they apply only to the particular model just described, with an infinite population, asexual inheritance and pairwise contests.

We now use these conditions to find the ESS of the Hawk–Dove game.

Clearly, D is not an ESS, because $E(D,D) < E(H,D)$; a population of Doves can be invaded by a Hawk mutant.

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*The distinction between a stable strategy and a stable state of the population is discussed further on pp. 16–17 and Appendix D.

H is an ESS if $\frac{1}{2}(V-C) > 0$, or $V > C$. In other words, if it is worth risking injury to obtain the resource, H is the only sensible strategy.

But what if $V < C$? Neither H nor D is an ESS. We can proceed in two ways. We could ask: what would happen to a population of Hawks and Doves? I shall return to this question later in this chapter, but first I want to ask what will happen if an individual can play sometimes H and sometimes D. Thus let strategy I be defined as 'play H with probability P, and D with probability $(1-P)$'; when an individual reproduces, it transmits to its offspring, not H or D, but the probability P of playing H. It does not matter whether each individual plays many games during its life, with probability P of playing H on each occasion, the payoffs from different games being additive, or whether each individual plays only one game, P then being the probability that individuals of a particular genotype play H.

Such a strategy I, which chooses randomly from a set of possible actions, is called a 'mixed' strategy; this contrasts with a 'pure' strategy, such as Hawk, which contains no stochastic element.

Is there a value of P such that I is an ESS? To answer this question, we make use of a theorem proved by Bishop & Cannings (1978), which states:

If I is a mixed ESS which includes, with non-zero probability, the pure strategies $A, B, C, \ldots$, then

$$E(A,I) = E(B,I) = E(C,I) \ldots = E(I,I).$$

The reason for this can be seen intuitively as follows. If $E(A,I) > E(B,I)$ then surely it would pay to adopt A more often and B less often. If so, then I would not be an ESS. Hence, if I is an ESS, the expected payoffs to the various strategies composing I must be equal. A more precise formulation and proof of the theorem is given in Appendix C. Its importance in the present context is that, if there *is* a value P which makes I an ESS of the Hawk–Dove game, we can find it by solving the equation

$$E(H,I) = E(D,I),$$

therefore

$$P\,E(H,H) + (1-P)\,E(H,D) = PE(D,H) + (1-P)\,E(D,D), \quad (2.5)$$

therefore

$$\tfrac{1}{2}(V-C)P+V(1-P) = \tfrac{1}{2}V(1-P),$$

or $P = V/C.$ (2.6)

More generally, for the matrix:

	I	J
I	a	b
J	c	d,

there is a mixed ESS if $a < c$ and $d < b$, the ESS being to adopt I with probability

$$P = \frac{(b-d)}{(b+c-a-d)}.$$ (2.7)

If there is an ESS of the form $I = PH+(1-P)D$, then P is given by equation (2.6). We still have to prove, however, that I satisfies equations (2.4b). Thus $E(H,I) = E(D,I) = E(I,I)$, and therefore stability requires that $E(I,D) > E(D,D)$ and $E(I,H) > E(H,H)$. To check this:

$$E(I,D) = PV+\tfrac{1}{2}(1-P)V > E(D,D).$$

and $E(I,H) = \tfrac{1}{2}P(V-C) > E(H,H),$ since $V < C.$

Thus we have shown that, when $V < C$, a mixed strategy with $P = V/C$ is evolutionarily stable. The first conclusion from our model, then, is that, in contests in which the cost of injury is high relative to the rewards of victory, we expect to find mixed strategies. The model is so oversimplified that the conclusion must be treated with reserve. Field data bearing on it are discussed in Chapters 6 and 7, after some possible complications have been analysed theoretically.

The attainment of a mixed ESS depends on the assumption that a genotype can exist which specifies the mixed strategy and which can breed true. I now return to the question: what would happen to a population of pure Hawks and pure Doves? We have already seen that, if $V < C$, there can be no pure ESS. There may, however, be a stable genetic polymorphism; i.e. there may be a mixture of pure-breeding Hawks and Doves which is genetically stable.

Consider, then, a population consisting of H and D in frequencies p

and $1-p$. At equilibrium, the fitnesses $W(H)$ and $W(D)$ must be equal. That is

$$pE(H,H)+(1-p)E(H,D) = pE(D,H)+(1-p)E(D,D). \quad (2.8)$$

Equation (2.8) is identical to equation (2.5), with p replacing P. Thus if P gives the frequency of H in a mixed ESS, and p the frequency of H in a population at genetic equilibrium, then $p = P$. This conclusion holds also if there are more than two pure strategies. But is the genetic polymorphism stable? When there are only two pure strategies, if the mixed strategy is stable then so is the genetic polymorphism; thus, for the Hawk–Dove game, a genetic polymorphism with a frequency of $p = V/C$ of pure Hawk is stable.

Unhappily, if there are more than two pure strategies, this simple conclusion no longer holds. It is possible for a mixed ESS to be stable but the corresponding polymorphism to be unstable, and vice versa. The problem of stability is discussed further in Appendix D; it is mainly of mathematical interest, if only because the stability of a polymorphism in an asexual population is a problem different from that of the stability of a sexual diploid population (see Chapter 4, section A).

I want now to extend the Hawk–Dove game by including more complex strategies. It will be convenient to replace the algebraic payoffs V and C by numerical ones; since only inequalities matter in determining qualitative outcomes, this makes things easier to follow without losing anything. Taking $V = 2$ and $C = 4$, there is a mixed ESS with $P = \tfrac{1}{2}$; the payoff matrix is

	H	D
H	−1	2
D	0	1.

Suppose now that we introduce a third strategy, R or 'Retaliator'. R behaves like a Dove against another Dove, but, if its opponent escalates, R escalates also and acts like a Hawk. The payoff matrix is shown in Table 2a.

This more general version of the Hawk–Dove game and, in particular, the stability of retaliation is treated in more detail in Appendix E, which, I hope, corrects some of the errors I have made in earlier discussions of this problem. The game is discussed here to

Table 2. *The Hawk–Dove–Retaliator game*

	a				*b*		
	H	*D*	*R*		*H*	*D*	*R*
H	−1	2	−1	*H*	−1	2	−1
D	0	1	1	*D*	0	1	0.9
R	−1	1	1	*R*	−1	1.1	1

illustrate how games with more than two strategies can be analysed. The matrix in Table 2*a* is awkward to analyse because, in the absence of Hawk, *D* and *R* are identical. It is shown in Appendix E that the only ESS is the mixed strategy, $I = \frac{1}{2}H + \frac{1}{2}D$.

The payoff matrix in Table 2*b* may be more realistic; it assumes that, in a contest between *D* and *R*, the Retaliator does, at least occasionally, discover that its opponent is unwilling to escalate, and takes advantage of this, so that, in *D* v. *R* contests, *R* does a little better and *D* a little worse. It is easy to see that *R* is now an ESS, because $E(R,R)$ is greater than either $E(D,R)$ or $E(H,R)$. Hence neither *D* nor *H*, nor any mixture of the two, could invade an *R* population. In general, if any entry on the diagonal of a payoff matrix is greater than all other entries in the same column, then the corresponding pure strategy is an ESS.

But is there any other ESS? In particular, what of $I = \frac{1}{2}H + \frac{1}{2}D$? Following the usual rules:

$$E(H,I) = -\tfrac{1}{2} + \tfrac{1}{2} \cdot 2 = \tfrac{1}{2},$$
$$E(D,I) = \tfrac{1}{2} \cdot 0 + \tfrac{1}{2} = \tfrac{1}{2},$$

and hence $E(I,I) = \frac{1}{2}$. Note that, as required of a mixed ESS, $E(H,I) = E(D,I)$.

$$E(R,I) = -\tfrac{1}{2} + 1 \cdot 1 \times \tfrac{1}{2} = 0.05.$$

The matrix in Table 2*b*, then, has two ESS's, $I = \frac{1}{2}H + \frac{1}{2}D$ and *R*. A population could evolve to either, depending on its initial composition.
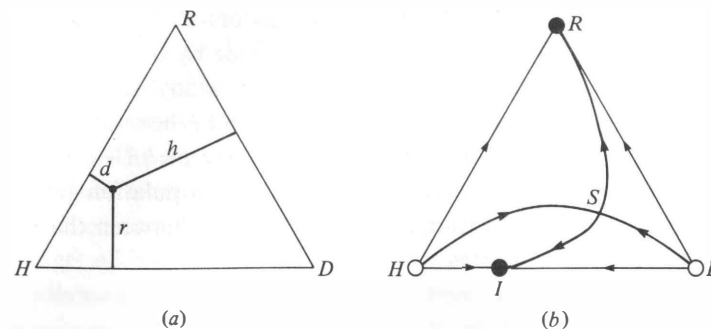

(*a*)   (*b*)

Figure 1. The Hawk–Dove–Retaliator game. (*a*) Representation of the state of a polymorphic population; *h*, *d* and *r* are the frequencies of pure *H*, *D* and *R* respectively. (*b*) Flows for the *H*–*D*–*R* game given in Table 2. There are attractors at *I* and *R* and a saddle point at *S*.

In picturing the dynamics of a game with three pure strategies, it is convenient to plot the state of the population as a point in an equilateral triangle, and then to plot the trajectories followed by the population, as in Figure 1. Of course, such a diagram can only represent the frequencies of the three pure strategies in a polymorphic population. In this case, however, there is a correspondence between the stable states of the polymorphic population and the stable strategies when mixed strategies are possible. Thus there are two stable states: pure *R*, and a polymorphism with equal frequencies of *H* and *D*, the latter corresponding to the mixed ESS, $I = \frac{1}{2}H + \frac{1}{2}D$.

A game with only two pure strategies always has at least one ESS (Appendix B); but if there are three or more pure strategies, there may be no ESS. Consider, for example, the matrix in Table 3. This

Table 3. *The Rock–Scissors–Paper game*

	R	*S*	*P*
R	−ε	1	−1
S	−1	−ε	1
P	1	−1	−ε

describes the children's game, 'Rock–Scissors–Paper' (R–S–P), with the proviso that a small payment ε be made by both players to the bank if there is a draw. It also represents any game with three strategies, such that R beats S, S beats P and P beats R. It is easy to check that, for ε positive, the mixed strategy $I = \frac{1}{3}R + \frac{1}{3}S + \frac{1}{3}P$ is an ESS. However, the genetically polymorphic population $\frac{1}{3}R, \frac{1}{3}S, \frac{1}{3}P$ is unstable; this is an example of a discrepancy between the stability criteria in the two cases.

Suppose that ε is small and negative; i.e. there is a small positive payoff for a draw. In this case there is no ESS, pure or mixed. In the absence of an ESS, the population will cycle indefinitely, $P \rightarrow S \rightarrow R \rightarrow P \rightarrow \ldots$. I cannot decide whether there are intraspecific contest situations likely to lead to such indefinite cycles; comparable cycles, in asymmetric games, are discussed on p. 130 and Appendix J.

B A review of the assumptions

An infinite random-mixing population

If, as will commonly be the case, individuals do not move far from where they were born, this will alter the model in various ways.

First, opponents will have some degree of genetic relatedness. An analysis of games between relatives is given in Appendix F. The problem turns out to be far from straightforward. At a qualitative level, however, the conclusion is the commonsense one, that animals will behave in a more Dove-like and less Hawk-like manner.

Secondly, an individual may have a succession of contests against the same opponent. If there is no learning from experience, this will not alter the conclusions. If there is learning, then the 'strategies' which have to be considered when seeking an ESS are no longer fixed behaviour patterns, but 'learning rules'; the evolution of learning rules is discussed in Chapter 5.

Thirdly, it is possible that the population whose evolution is being considered is not only finite but small. If so, the basic model must be altered, because mutants cannot be very rare. Finite population games have been considered by Riley (1978).

Asexual reproduction

Most species whose behaviour is of interest are sexual and diploid,

whereas the model outlined above assumes asexual reproduction. This discrepancy is unlikely to matter in practice. When reasoning about the function of some behavioural trait, some assumption must be made about the range of phenotypes possible to the species; i.e. the 'strategy set'. This may be based in part on knowledge of the range of actual variability in the species or in related species and in part on guesswork or common sense. It is most unlikely to be based on a knowledge of the genetic basis of the behavioural variability. Therefore a simple assumption of 'like begets like' is often more sensible than a detailed assumption about the genetic basis. A case where there seems no escape from detailed genetic hypotheses is discussed in Chapter 10, section D.

It is, however, important to be able to show, for simple model situations, that the results of parthenogenesis and of diploid inheritance are similar. This is done for a particular case by Maynard Smith (1981), and in Chapter 4, section A. Briefly, an infinite random-mating diploid population plays a game with two pure strategies; P^* represents the frequency of one strategy at the ESS (i.e. P^* is given by equation 2.7). The actual frequency with which an individual adopts that strategy is determined by two alleles, A and a, being P_0, P_1 and P_2 in AA, Aa and aa, respectively.

If $P_0 \geqslant P_1 \geqslant P_2$ (i.e. no overdominance), then the population will evolve to the ESS provided P^* lies between P_0 and P_2. If P^* lies outside that range, then obviously the population cannot evolve to P^*, but it will become fixed for the homozygote lying closest to the ESS. If there is overdominance, things are more complex, but it is still true that the population will usually evolve to an ESS if the genetic system permits, and otherwise approaches it as closely as it can. Eshel (1981b) has shown that a diploid population will evolve to the ESS for a wide range of genetic structures, although it is not true for the most general ones.

In general, as the number of loci, or number of alleles per locus, increases, it becomes more likely that a population will reach an ESS (Slatkin, 1979). If the ESS requires a range of phenotypes, achievable only by a genetic polymorphism and not by a mixed strategy, then the genetic system may prevent the phenotypes existing in the appropriate frequencies. As an example, the ESS for the 'war of attrition' discussed in the next chapter requires a phenotypic distribution

which could not easily be generated by a polygenic system. Of course, no difficulty arises if an individual can adopt a mixed strategy.

Symmetric and asymmetric contests

The Hawk–Dove game analysed above is symmetrical. That is to say, the two contestants start in identical situations: they have the same choice of strategies and the same prospective payoffs. There may be a difference in size or strength between them, which would influence the outcome of an escalated contest, but if so it is not known to the contestants and therefore cannot affect their choice of strategies.

Most actual contests, however, are asymmetric. They may be between a male and a female, between an old and young, or a small and large individual, or between the owner of a resource and a non-owner. An asymmetry may be perceived beforehand by the contestants; if so, it can and usually will influence the choice of action. This is most obviously so if the asymmetry alters the payoffs, or affects the likely outcome of an escalated contest. It is equally true, although less obvious, that an asymmetry which does not alter either payoffs or success in escalation can determine the choice of action.

Table 4. *The Hawk–Dove–Bourgeois game*

	H	D	B
H	−1	2	0.5
D	0	1	0.5
B	−0.5	1.5	1.0

Thus, consider a contest between the owner of a territory and an intruder. In practice, the value of the territory may be greater to the owner because of learnt local knowledge, and it is also possible that ownership confers an advantage in an escalated contest. For simplicity, however, I shall ignore these effects. Let us introduce into the Hawk–Dove game a third strategy, B or 'Bourgeois'; i.e. 'if owner, play Hawk; if intruder, play Dove'. The payoff matrix is shown in Table 4.

Note that it is always the case, when two B strategists meet, that one is the owner and the other intruder. I have assumed in filling in

the matrix that each strategy type is owner and intruder equally frequently. That is, genes determining behaviour are independent of the factors, genetic or environmental, determining ownership.

It is clear that B is an ESS, and easy to check that it is the only ESS of this game. Thus an asymmetry of ownership will be used as a conventional one to settle the contest, even when ownership alters neither the payoffs nor success in fighting. The same is true of any other asymmetry, provided it is unambiguously perceived by both contestants. Asymmetric contests are discussed in detail in Chapters 8–10.

Pairwise contests

The Hawk–Dove model, and more complex models expressed in payoff matrix form, suppose that an individual engages in one or more pairwise contests; if more than one contest occurs, payoffs are assumed to be combined additively. Such a model can be applied to agonistic encounters between pairs, or, in asymmetric form, to contests between mates or between parent and offspring. There are many situations, however, in which an individual is, in effect, competing not against an individual opponent but against the population as a whole, or some section of it. Such cases can loosely be described as 'playing the field'. Examples include the evolution of the sex ratio (Fisher, 1930; Shaw & Mohler, 1953; Hamilton, 1967), of dispersal (Fretwell, 1972; Hamilton & May, 1977), of competition between plants (since each plant competes against all its neighbours, not against a single opponent), and many other examples. In fact, such contests against the field are probably more widespread and important than pairwise contests; it therefore seems appropriate to discuss them under a separate head.

C An extended model – playing the field

We can extend the concept of an 'unbeatable strategy' (Hamilton, 1967) or an 'evolutionarily stable strategy', to cases in which the payoff to an individual adopting a particular strategy depends, not on the strategy adopted by one or a series of individual opponents, but on some average property of the population as a whole, or some section of it.

Table 5. *Fitness matrix for the extended model*

		Population	
		I	*J*
Mutant	*I*	$W(I,I)$	$W(I,J)$
	J	$W(J,I)$	$W(J,J)$

Table 6. *Fitness matrix for the sex ratio game*

		Population	
		$s_1 = 0.1$	$s_2 = 0.6$
Mutant	$s_1 = 0.1$	1.8	0.967
	$s_2 = 0.6$	5.8	0.8

How should an ESS be defined when individuals are playing the field? This question has been treated by P. Hammerstein (personal communication), and I have followed his proposal. Let the fitness of a single *A* strategist in a population of *B* strategists be written $W(A,B)$. Clearly, *I* will be an ESS if, for all $J \neq I$, $W(J,I) < W(I,I)$. But what if $W(J,I) = W(I,I)$? We then need that $W(J) < W(I)$ in a population of *I* strategists containing a small proportion *q* of *J* strategists. We define $W(J,P_{q,J,I})$ as the fitness of a *J* strategist in a population *P* consisting of $qJ + (1-q)I$. The conditions for *I* to be an ESS then are, for all $J \neq I$,

either $W(J,I) < W(I,I)$

or $W(J,I) = W(I,I)$

and, for small *q*,   (2.9)

$$W(J,P_{q,J,I}) < W(I,P_{q,J,I}).$$

If only two strategies are possible, *I* and *J*, we can draw up the fitness matrix in Table 5.

If $W(J,I) < W(I,I)$, then *I* is an ESS; if $W(I,J) < W(J,J)$, then *J* is an ESS. If neither of these inequalities hold, then the ESS is a mixture of *I* and *J*. It would be wrong though, to think that the proportions of the two strategies at the ESS are necessarily given by equation (2.7). This would be true only if the fitness of an individual *I* in a population consisting of a mixture *I* and *J* in proportion *P* to $1-P$ were given by the linear sum $PW(I,I) + (1-P)W(I,J)$, and this is not necessarily so.

These points can best be illustrated by considering the simplest form of the sex ratio game, in which a female can produce a total of *N*

offspring, in the ratio *s* males to $(1-s)$ females. If we measure 'fitness' as expected number of grandchildren, then in a random-mating population of sex ratio s', we have

$$W(s,s') = N^2 \left[1 - s + s \frac{(1-s')}{s'} \right],$$

and $W(s',s') = 2N^2(1-s').$ (2.10)

If we then consider a population containing two types of female, producing sex ratios $s_1 = 0.1$ and $s_2 = 0.6$, we have the fitness matrix in Table 6.

It is apparent that neither s_1 nor s_2 is an ESS. If, without justification, we were to calculate *P* from equation (2.7), we would conclude, wrongly, that the stable state consisted of 1/25 of s_1 and 24/25 of s_2, giving a population sex ratio of $14.5/25 = 0.58$. In fact, the stable population sex ratio is 0.5.

Supposing that only these two kinds of females existed, the correct way to find the ESS is as follows. Let $\hat{s}$ be the population sex ratio at equilibrium.

Then $W(s_1,\hat{s}) = W(s_2,\hat{s})$, or

$$1 - 0.1 + 0.1(1-\hat{s})/\hat{s} = 1 - 0.6 + 0.6(1-\hat{s})/\hat{s},$$

or $\hat{s} = 0.5,$

requiring

$$0.2s_1 + 0.8s_2.$$

More generally, suppose individual females can produce any sex

ratio between 0 and 1. We seek a sex ratio s^*, which is an ESS in the sense of being uninvadable by any mutant with $s \neq s^*$. That is, $W(s^*, s^*) > W(s,s^*)$ for $s \neq s^*$. Provided that W is differentiable, we can find s^* from the condition

$$[\partial W(s,s^*)/\partial s]_{s = s^*} = 0. \qquad (2.11)$$

Applying this condition to equation (2.10) gives $s^* = 0.5$, as expected. We can use equations (2.9) to check the stability of $s^* = 0.5$, as follows:

Let $s' = qs + (1-q)s^*$, where $s \neq s^*$.

Then from equation (2.10),

$$W(s,s') = N^2 \left[1 - s + s\frac{(1-s')}{s'} \right],$$

and

$$W(s^*,s') = N^2 \left[1 - s^* + s^*\frac{(1-s')}{s'} \right].$$

It is then easy to show that, for $s \neq s^*$, the inequality $W(s,s') < W(s^*,s')$ holds.

To summarise the extended model, a strategy I is an ESS provided that equations (2.9) are satisfied. If, in a game with two pure strategies, I and J, neither satisfies equations (2.9), the ESS will be a mixed strategy; however, the relative frequencies of I and J at the equilibrium cannot be found from equation (2.7), but must be calculated from the equation $W(I, Pop) = W(J, Pop)$, where *Pop* refers to the equilibrium population. If the strategy set is a continuous variable (e.g. the sex ratio, varying continuously from 0 to 1), the ESS can be found from a condition similar to equation (2.11); its stability must be checked by taking the second derivative, or in some other way.

The crucial step in analysing cases in which an individual is playing the field is to write down expressions corresponding to equation (2.10), giving the fitness of a rare mutant in a population of known composition. In the particular case of equation (2.10), the population

is treated as infinite and without structure. This, however, is not a necessary restriction. For example, Hamilton (1967) sought the unbeatable sex ratio, s^*, when the offspring of k females mate randomly *inter se*. The problem reduces to writing down an expression $W(s,s^*)$ for the fitness of an individual producing sex ratio s when in a group with $k-1$ females producing a sex ratio s^*, and then applying condition (2.11). In other words, given that the other females in the group produce the sex ratio s^*, the best thing for the kth female is to do likewise.

To give another example of a structured population, consider competition between plants or sessile animals growing in a pure stand. We would seek a growth strategy I such that, if all the neighbours of an individual were adopting I, the best strategy for the individual is also I. Mirmirani & Oster (1978) considered competition between annual plants which differed in the time at which they switched resources from growth to seed production. To find the evolutionarily stable time, T^*, it would be necessary to find $W(T,T^*)$, the seed production of an individual switching at time T if surrounded by individuals switching at time T^*, and then to solve the equation $[\partial W(T,T^*)/\partial T]_* = 0$. Note that it would not be necessary to work out the fitness of individuals surrounded by a mixture of types.

As a summary of the ideas in this chapter, it might be helpful to read through the 'Explanation of main terms' on p. 204.