frequencies, independently each time? I know I could not. Not using a randomizing device is giving an advantage to an opponent who does so—action anathema to all serious games players.

## Games animals play

Everyone knows the central place of mathematical models in physics. Their use in biology is less well appreciated. But the operation of Mendel's laws is best seen mathematically, and great advances in biological understanding came through the models developed by R. A. Fisher, J. B. S. Haldane, and Sewell Wright. More recently, game theory has been used to understand animal behaviour.

One prototype is a model of contests between two animals who are disputing ownership of food, territory or mating rights—anything that will aid their success in passing on their genes to the next generation. The simplest idea is that just two types of behaviour can be used, Hawk or Dove. A Hawk is always willing to start a fight, and will fight back if attacked; it will retreat only when too severely injured to continue. A Dove will posture, but not begin a real fight; if attacked, it retreats before it suffers any damage. Two contesting Doves will huff and puff for some time, wasting time and energy, before one tires and concedes the prize.

The prize is measured in what biologists would call 'added fitness', a way of describing the extra average number of offspring they obtain from victory. Losers have offspring too; the prize just gives extra offspring, who can be expected to follow their parents' successful tactics. So if Hawk does better than Dove in these contests, we can expect the frequency of Hawks to increase, and vice versa.

To draw up a payoff table, we need some scale and reference point to describe the values of the prize being contested, the loss of fitness through injury in an escalated fight, and the loss of fitness through wasting time on display. Take the value of the prize as ten units, and assume that in Dove–Dove or Hawk–Hawk contests, either player is equally likely to win, so either gains five units, on average, from the contest. In a Dove–Hawk contest, the Hawk wins all ten units, the Dove wins nothing, but suffers no damage either. In Dove–Dove contests, deduct two units from each player to account for the fruitless time they seek to stare the other out, but assume Hawk–Hawk contests are so fierce that the average loss to both



exceeds their average gain of five—make the net value −2. The payoffs to the player using the tactic in the left column are

| | Hawk | Dove |
|---|---|---|
| Hawk | −2 | 10 |
| Dove | 0 | 3 |

This contest is quite different from all the contests we have looked at so far. We are seeking to discover which of the two available *tactics* does better, not how Rows should compete against Columns. The new approach is to assume that the population contains some proportion, $p$, of players who use Hawk, so that a proportion $1 - p$ will use Dove, and see how well each tactic does in such a population. If one tactic does better than the other, the use of the favoured tactic can be expected to increase.

When a Dove decides to enter a contest, the chance it picks a contest with a Hawk is $p$, with another Dove it is $1 - p$. So the average outcome to the Dove is

$$(0) \times p + (3) \times (1-p) = 3 - 3p.$$

Similarly, the average payoff to a Hawk is

$$(-2) \times p + (10) \times (1-p) = 10 - 12p.$$

This means the two tactics do equally well, on average, when $3 - 3p = 10 - 12p$, which is when $p = 7/9$. When the proportion of Hawks exceeds 7/9, the average payoff to Hawks is less (they get involved in too many damaging fights), so Hawk numbers reduce. But when the proportion of Hawks is less than 7/9, Hawks are favoured and their numbers tend to increase.

A population can collectively play Hawk 7/9 of the time in many ways. At one extreme, 7/9 of the population play Hawk all the time, and 2/9 play Dove. At the other extreme, every individual uses the mixed strategy (7/9, 2/9) all the time. In either case, an interloper has probability 7/9 of facing a Hawk, and 2/9 of facing a Dove, and that is all the information we used to compute this neutral position. Suppose a population does collectively use this strategy in some manner, but that a small mutant population playing Hawk at a different frequency arises. Can this mutant survive?

The mutants use Hawk and Dove in some proportions $(x, 1 - x)$, where $x$ can take any value except 7/9. When they are present in only small numbers, virtually all their battles are against the indigenous population. But since each of Hawk and Dove do equally well, on average, these mutants also gain the same average benefit from the games they play. They are at no advantage, or disadvantage, so sheer random chance determines whether their numbers increase or decrease. Sometimes random chance eliminates them anyway.

Should the mutants increase their numbers, more of their contests are against other mutants. Their fate will depend on a comparison of how well a mutant fares against another mutant with how well the indigenous population fare against mutants. And the arithmetic shows that the originals do *better*; as soon as the mutants begin to increase in numbers, they become at a disadvantage, and so can make no headway. They are inevitably eliminated, whatever the proportion who play Hawk.

John Maynard Smith coined the term *evolutionarily stable strategy*, ESS for short, to denote any strategy that will resist all invasions. Much more can be read about the use of game theory to comprehend animal behaviour in his *Evolution and the Theory of Games*. In this example, if Hawk and Dove are the only tactics available, then using them in proportions 7:2 is an ESS for this table of payoffs.

Change the numbers in the payoff table, and a different population composition may emerge. Make the item being contested less valuable, but suppose the Hawks fight more fiercely and inflict more damage on each other. The new numbers may be:

| | Hawk | Dove |
|---|---|---|
| Hawk | –4 | 6 |
| Dove | 0 | 2 |

Using the same argument as before, the average payoffs to Hawk and Dove are $6 - 10p$ and $2 - 2p$ respectively, which are equal when $p = 1/2$. Once again, any mutant sub-population that tried to use Hawk and Dove in proportions other than 50:50 would be at a disadvantage as soon as it gained a toehold, and would be eliminated. Equal numbers of Hawks and Doves is an ESS.

But suppose Hawks were less aggressive, settling contests with less damage to each other, while still beating Doves at no cost. The payoffs might be:

| | Hawk | Dove |
|---|---|---|
| Hawk | 1 | 6 |
| Dove | 0 | 2 |



and now the average returns to Hawk and Dove are $6 - 5p$ and $2 - 2p$. But $p$ is a proportion, and must be between zero and one, so the former *always* exceeds the latter. Hawks inevitably do better than Doves, so any Doves are eliminated, and the entire population uses Hawk all the time. No mutant using Dove at any frequency can invade—Hawk is an ESS.

By contrast, suppose Hawks were really brutal, and the average outcome of a contest between two Hawks was a payoff of –100 to each. Even here, Hawks are not driven to extinction, merely to a very low frequency. They survive at a low frequency because they meet few other Hawks, but still terrorize the Doves to gain fitness. Check that if you replace the '1' in the last table by –100, Hawks and Doves do equally well if the population plays Dove 25 times for every once it plays Hawk. Once again, no mutant using a different mixture can invade, so (1/26, 25/26) is an ESS.

In any of these games with two strategies, there is an easy way to see whether there is some mixed strategy that is an ESS. Set out the table of payoffs as we have shown, and look down each of the two columns. There will be an ESS, provided that in the first column it is the second number that is higher, and in the second column it is the first number that is higher. That is, Dove does better against Hawk than Hawk does against Hawk; and Hawk does better against Dove than Dove v. Dove. When these conditions hold finding the ESS is immediate, and uses the same method as finding Colin's best mixed strategy against Roy in games such as that of Table 6.2. Subtract the numbers in the second row from those in the first. The first will always be negative, the second positive. Ignore the minus sign, and swop the answers round. This gives the two proportions. In the first game introduced, with payoffs:

| | Hawk | Dove |
|---|---|---|
| Hawk | –2 | 10 |
| Dove | 0 | 3 |

this subtraction leads to (–2, 7). Ignoring the minus sign and swapping, the proportions are (7, 2), which corresponds, of course, to the answer we found. In the second table, the subtraction leads to (–4, 4), and so in one more step to equal use of Hawk and Dove. If we followed the recipe for the third set of payoffs, the subtraction step gives (1, 4); the first entry is not negative, so there is no mixed ESS.

These animals have no interest in some abstract notion of 'what is best for the population'. It would plainly be 'sensible' to settle all disputes by one toss of a fair coin, thereby removing all the losses through time-wasting posturing and mutual injury. But what matters in the struggle to survive is that you do better than your opponent, *even if*, overall, both of you do worse. Tennyson wrote of 'Nature red in tooth and claw'. But these models show that Hawk and Dove can co-exist, and indicate how changes in the value of resources, or the actions of the players, can lead to Hawk used more often, or less often. If Hawks could settle their contests in ways that led to less damage, they would expect to do better.

Such evolution does occur. Rather than immediately fight, animals might size each other up, through showing off their muscles, or demonstrating their lung capacity with a bellow. This is not Dove–Dove posturing; they really are prepared to fight. However, there are advantages to both animals if they can avoid doing so if it is plain that the contest would be one-sided. An excellent example is the study by Tim Clutton-Brock and his colleagues of the behaviour of red deer. In the mating season, a stag attempts to hold possession of a harem of hinds—success will lead to more offspring. Stags younger than seven years are generally not powerful enough to hold a harem, and fighting ability declines after age 11 or so. But between seven and 11 years, a stag has a reasonable expectation of mating. Stags who dispute a harem do not automatically escalate. Usually, they approach to about 100 metres, and alternately roar at each other; it seems they are attempting to judge who is the stronger. *Loud roars cannot be faked.* If this contest is inconclusive, they often move to within a few metres, and engage in a series of parallel walks, up and down, waving their ferocious antlers, seemingly seeking to persuade the other of the futility of a fight. Observations show that the longer the stags take over these preliminaries, the more likely they are to end up actually fighting. A substantial difference in size would be quickly detected by the roars or the walk; if these are indecisive, it is likely they are equally matched, and serious injury is possible.

The theme of this chapter is games with *few* choices. If there are just two tactics, there is always an ESS; sometimes it is a mixture of the two tactics, at other times there is an ESS when the whole population uses one or other of the two choices. But if there are three or more tactics, there are many more possibilities. Sometimes, there is an ESS that uses all the tactics on offer, but at other times there is no ESS at all.

## The battle of the sexes

Both males and females can measure their reproductive success in terms of how many of their offspring reach maturity capable of passing parental



genes on to the next generation. Having offspring who do not themselves have offspring is a genetic waste. Richard Dawkins offered a simple model in which the two sexes have different strategies. In their efforts to succeed in this game, females can choose between being Coy or Fast, while males opt to be Faithful or a Philanderer.

A Coy female will refuse to mate until she is convinced that the male will share in the offspring's upbringing. Her idea is to have fewer offspring than she is biologically capable of, but to hope that more will reach maturity through the double input into rearing the brood. A disadvantage of her tactics is that she may drive away a succession of suitors not willing to dance to her demands for food, nest-building and so on: she may be left on the shelf.

A Fast female will copulate readily, perhaps with a stream of mates, and have many offspring. She may even find that one of her suitors is a Faithful male who shares the domestic chores, but that would be a bonus: she hopes that a good proportion of her offspring survive.

The units in a payoff table relate to the expected number of offspring *that reach maturity*, or even the expected number of grandchildren. Suppose any birth is worth 15 units to each parent, but it costs a total of 20 units to raise one child to maturity. If males are Faithful, that cost is shared equally. A Faithful male and a Coy female each lose the opportunity for offspring during their courtship, a cost of three units each, say. A Philandering male and a Coy female get nowhere, but waste no courtship time. The table of average payoffs to a female will be:

| | Faithful male | Philanderer |
|---|---|---|
| Coy | 2 | 0 |
| Fast | 5 | –5 |

Suppose the proportion of Faithful males in the population is $x$. If a female is Coy, her average payoff is $2x$; and the average payoff to a Fast female is $5x - 5(1-x) = 10x - 5$. These are equal when $x = 5/8$. So if the proportion of Faithful males exceeds 5/8, it pays to be Fast, while if it is less than 5/8, females are better off being Coy.

When males are Faithful, they prefer their mate to be Coy, as they have no interest at all in helping raise someone else's offspring. (This is not quite true: since you share genes with your near relatives, it is in your interest to help your brother's offspring to mature. Haldane famously pointed out that he would be prepared to sacrifice his life for that of two brothers, or eight first cousins. We skip over that glitch.) But should males be Philanderers, Coy females are very bad news. The male's table of payoffs will be:

| | Coy female | Fast |
|---|---|---|
| Faithful | 2 | 5 |
| Philanderer | 0 | 15 |

Male actions are dictated by $y$, the proportion of Coy females. For Faithful males, the average payoff is $2y + 5(1-y) = 5-3y$; a Philanderer gets $15-15y$, and the crossover point is when $y = 5/6$. With fewer Coy females, Philanderers are better off, but when there are more, Faithfulness is favoured.

The scene is set for a permanent merry-go-round, showing how the values of $x$ and $y$ can be expected to vary over time. If ever 5/8 of the males are Faithful, and 5/6 of the females are Coy, at the point marked X in Figure 6.3, there is no pressure to move away. But suppose there are surpluses of both Faithful males and Coy females, somewhere in the rectangle marked A. With so many Faithful males, Fast females are favoured, as they are able to bear many offspring and have someone share the burden of raising them. The genes that favour Fast females will now increase, so the population composition will tend to move into rectangle B.

In the region B, there are few Coy females, but many Faithful males. Philandering males now have the advantage, as nearly all the females are

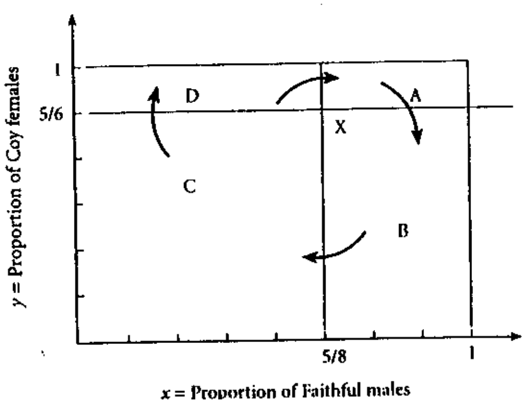


Fig. 6.3 How the population composition cycles.



Fast, so Philanderers have many offspring, and their genes build up in frequency, moving the population composition into region C. Within C, Philandering males are in excess. Fast females normally have to raise their offspring alone, and so the Coy females will increase in numbers because they always have a Faithful partner to help in the upbringing. The pressure is to move the population composition into region D. And here, with many Coy females, the Philanderers do not get a look-in, the few Faithful males increase in numbers, and the population composition returns to region A to begin this cycle again.

There is no single best strategy for either sex; what you should do depends on how the opposite sex behaves (what a surprise!). A female prefers a Faithful male, as the first column of her payoff table dominates the second, and similarly males prefer Fast females. Male behaviour is at the behest of female taste—it was ever thus!

## Postscript

Table 6.5 gives the probabilities that Roy will be ahead by some amount after a series of plays in the game of Table 6.2. It came from simulation, and not from direct calculation. Further details, and an analogy with opinion polls, may be useful. My computer has a built-in random number generator that can be used to choose the plays. In each game, the computer makes the choices of H or T for each player, according to the chosen strategies, and logs Roy's corresponding winnings. To give results for a series of ten games, the computer totals these winnings; at best Roy will be 20 units ahead, at worst he will be 30 units down. To estimate the chance he is ahead, the computer need only note whether this total is positive, zero, or negative. However, as a check on this simulation, it is worth storing the exact total for each game, as we know what the average should be. After ten games, since $10 \times (1/8) = 1.25$, Roy should be about 1.25 ahead on average. This whole process is repeated a large number of times, and the proportion of times the result is positive, zero, or negative then calculated. These proportions will be the estimates of Roy's chances of being ahead, level, or behind after a series of ten games. For longer series, start again and replace 'ten' by 50, 200, or whatever.

How often each series should be repeated depends on how accurate you want your estimates to be. Political opinion polls typically sample about 1500 electors, and warn that the estimates are subject to 'sampling error'.