

THE HAWK-DOVE GAME PLAYED BETWEEN RELATIVES

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Abstract. Maynard Smith (1978) has raised the problem of the hawk-dove game played between relatives. Here, the evolutionarily stable state of the population is found as a function of the average relatedness of a player to his opponents. Surprisingly, the continuous or 'mixed' strategy case and the discrete or 'pure' strategy case must be treated separately. It is claimed that previous published analyses of the evolutionarily stable state are invalid. The errors committed are discussed, and ascribed to the use of the concept of 'fitness', rather than the less confusing notion of gene frequency.

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The two-strategy linear ESS game has been used to shed light on some interesting problems in recent biological theory, including intra-specific aggression and mating systems (Maynard Smith & Price 1973; Maynard Smith 1977). Maynard Smith (1978) has raised the problem of the outcome of such games when they are played between relatives. Here I present the solution to this problem in both the continuous or 'mixed' strategy case and the discrete or 'pure' strategy case. That these cases have different solutions shows that Maynard Smith's (1978) original analysis is invalid, and this can be attributed to his use of a fitness approach, rather than a gene frequency approach. This strengthens Dawkins's (1978) case in favour of the latter. Although the arguments are general, I will refer to the two-strategy linear ESS game as the hawk-dove game for the rest of the paper.

In the simple hawk-dove game, the population consists of a very large number of unrelated 'hawks' and 'doves', each of whom plays an indefinitely large number of bouts against opponents drawn randomly from the population. The game payoff is the sum of the payoffs from each bout. These depend on the strategy played, and that of the opponent. Let us use *H* for hawk and *D* for dove, and let $E(I, J)$ be the payoff to *I* in a bout against an opponent playing *J*. For brevity we define *a*, *b*, *c*, *d* as follows:

$$\begin{matrix} E(H, H) = a & E(H, D) = b \\ E(D, H) = c & E(D, D) = d \end{matrix} \quad (1)$$

This is the game matrix. If a proportion '*t*' of the population play *H*, and the rest *D*, then the average payoff in each bout to *H* is given by

$$E(H, tH + (1-t)D) = tE(H, H) + (1-t)E(H, D)$$

An individual playing *H* a proportion *s* of the time, and *D* the rest, against a population playing *J*, will have average payoff

$$E(sH + (1-s)D, J) = sE(H, J) + (1-s)E(D, J)$$

The crucial point about the hawk-dove game, simple or between relatives, is that we can work out the proportions of the various strategies in the next generation if we know the proportions in this generation. Each individual supplies offspring to the next generation in proportion to his average payoff, and offspring play the same strategy as their parents. For this to make sense, all payoffs must be non-negative. Considering the case where there are only two strategies, *I* and *J*, let $G(I, J)$ be the average payoff to *I* against *J*, let *p* be the proportion of *I* in this generation and *p'* the proportion in the next. The number of *I* in the next generation is proportional to $pG(I, pI + (1-p)J)$, since there are *p* of them in this generation, and the population plays ' $pI + (1-p)J$ '. The number of *J* in the next generation is likewise proportional to $(1-p)G(J, pI + (1-p)J)$, and so

$$p' = \frac{pG(I, pI + (1-p)J)}{pG(I, pI + (1-p)J) + (1-p)G(J, pI + (1-p)J)} \quad (2)$$

This simplifies at equilibrium, where *p'* must equal *p*, to

$$G(I, pI + (1-p)J) = G(J, pI + (1-p)J) \quad (3)$$

In the simple hawk-dove game $G(I, J) = E(I, J)$ so (3) becomes

$$pa + (1-p)b = pc + (1-p)d$$

This is solved for *p* to give the standard solution for the hawk-dove game:

$$p = -\frac{b-d}{a-b-c+d} \quad (4)$$

Equation (4) gives the ESS only if it is sensible, that is if p lies between 0 and 1, and the solution is stable. It is stable if $a-b-c+d < 0$. If (4) does not give the ESS, then the ESS may be all hawks or all doves or both may be ESSs, depending on the circumstances. The same remarks and the same stability condition apply to both the other game solutions in this paper.

Maynard Smith (1978) raised the problem of the game when it is played between relatives. This could be of interest if the game was played between parents and offspring, or between neighbours in a species with low dispersal. If the average relatedness was ' r ', then with chance ' r ' an individual plays someone who plays the same strategy as he does because they are related, and with chance ' $1-r$ ' he plays against the strategies in their population proportions. Thus the average payoff to I in a population playing J can be denoted $F(I, J)$ where

$$F(I, J) = rE(I, I) + (1-r)E(I, J) \quad (5)$$

In the simple hawk-dove game, a population where all individuals play a mixture of H and D need not be distinguished from a population polymorphic for H and D in the same proportion. In the hawk-dove game between relatives it is necessary to make this distinction, and to treat the continuous strategy case separately from the discrete strategy case. This is because the following is *not* true, as can easily be shown:

$$F(pH + (1-p)D, J) = pF(H, J) + (1-p)F(D, J)$$

In this discrete case, each individual plays either always hawk or always dove. The equilibrium proportion p of hawks must occur, by (3), where

$$F(H, pH + (1-p)D) = F(D, pH + (1-p)D)$$

Using (1) and (5), we can write this as

$$ra + (1-r)(pa + (1-p)b) = rd + (1-r)(pc + (1-p)d)$$

Solving for p we obtain

$$p = -\frac{b-d + r(a-b)}{(1-r)(a-b-c+d)} \quad (6)$$

This is the solution to the discrete strategy case.

In the continuous strategy case, where each individual can play any proportion of hawk and dove, we wish to find that strategy which once established cannot be invaded by any rival strategy. Let us use for brevity

$$F(q, p) = F(qH + (1-q)D, pH + (1-p)D) \quad (7)$$

$F(q, p)$ is the average payoff to an individual playing hawk ' q ' of the time in a population which overall plays hawk ' p ' of the time. Equations (2) and (3) are easily adapted to give us the condition that any rival strategy q will decrease in the next generation in a population playing p :

$$F(q, p) < F(p, p) \text{ for all } q \text{ except } q = p.$$

Since $F(q, p) = F(p, p)$ when $q = p$, it is clear that provided $0 < p < 1$, $F(q, p)$ reaches a maximum at $q = p$. This means that

$$\frac{\partial F(q, p)}{\partial q} = 0 \text{ at } q = p \quad (8)$$

By (7), (5) and (1) we see that

$$\begin{aligned} F(q, p) &= rE(qH + (1-q)D, qH + (1-q)D) + \\ &\quad (1-r)E(qH + (1-q)D, pH + (1-p)D) \\ &= r\{q^2a + q(1-q)(b+c) + (1-q)^2d\} + \\ &\quad (1-r)\{pqa + p(1-q)c + (1-p)qb + \\ &\quad (1-q)(1-p)d\} \end{aligned}$$

Differentiating with respect to q , according to (8), gives

$$2rq(a-b-c+d) + r(b+c-2d) + (1-r)(pa-pc + (1-p)b - (1-p)d) = 0$$

When $q = p$, this solves for p to give

$$p = -\frac{b-d + r(c-d)}{(1+r)(a-b-c+d)} \quad (9)$$

This is the solution to the continuous strategy case. At this value of p , any rival strategy will decrease in numbers each generation.

There is a less mathematical argument which leads to the same conclusion. Consider a population all playing hawk a proportion ' p ' of the time. For brevity, let us call this strategy, not necessarily the ESS, simply ' p '. We now consider the success of a variant strategy present in very small numbers in the population. The variant strategy is identical to p except that in one bout, chosen randomly, where the individual would have played D , he plays H instead. We consider the two ways in which this change makes the success of the variant strategy different from that of the population strategy. The individual who plays it has his payoff in that bout changed from $E(D, pH + (1-p)D)$ to $E(H, pH + (1-p)D)$. The other way the variant strategy's success is altered is that, with chance ' r ', the individual's opponent also plays

the variant strategy and so the variant strategy's success changes additionally by the difference between $E(pH + (1-p)D, H)$ and $E(pH + (1-p)D, D)$. So on average the effect will be

$$\begin{aligned} & E(H, pH + (1-p)D) - E(D, pH + \\ & (1-p)D) + r\{E(pH + (1-p)D, H) - \\ & E(pH + (1-p)D, D)\} \end{aligned} \quad (10)$$

We have assumed that all opponents play H with probability ' p ' in this bout. This is because the chance that this is also the bout in which an opponent playing the variant strategy plays H instead of D is very small.

Now if (10) is positive the variant strategy does better than ' p ' and so ' p ' is not an ESS. Another variant strategy is to play ' p ', except in one bout to play D instead of H , and the difference between the success of p and its success is easily seen to be minus (10). So if (10) is negative, then this other variant strategy does better than p , and so p is not an ESS. Therefore, if p is an ESS, (10) equals zero. Using (1), this becomes

$$pa + (1-p)b - pc - (1-p)d + r\{pa + (1-p)c - pb - (1-p)d\} = 0,$$

which solves for p to give

$$p = - \frac{b-d + r(c-d)}{(1+r)(a-b-c+d)} \quad \text{as before.}$$

This argument applies only for p between 0 and 1, since otherwise the two variant strategies used will not both exist.

Let us now turn to the solution proposed by Maynard Smith (1978) for both the continuous and discrete cases. His argument ran: in a game between relatives, it is inclusive fitness which should be equal for hawk and dove. So he suggested solving as in (4), except that a , b , c , d should be replaced by $a+ra$, $b+rc$, $c+rb$, $d+rd$. Each of these is the sum of an individual's payoff and ' r ' times that of his opponent, the idea being that these represent the inclusive fitness gained from a bout.

But inclusive fitness involves the weighted sum of all relatives' fitnesses, not just those relatives you happen to play against, and so this method does not give us the inclusive fitness of an individual. By using (4), no account is taken of the fact that an individual is more likely to play against his own strategy than he would if he

played the population at random. The use of (4) also assumed implicitly and, as we have seen, erroneously, that the following is true: that the payoff to playing H ' p ' of the time and D the rest, is equal to ' p ' times the payoff to playing H plus ' $1-p$ ' times the payoff to playing D . Treisman (1977), and Mirmirani & Oster (in press), independently used the same erroneous argument as Maynard Smith in analyses of games between relatives.

This argument amazingly happens to give the correct answer in the continuous strategy case. Hines and Maynard Smith (in preparation), while accepting that the argument is invalid, generalize the equivalence of the results of the invalid argument and the correct argument, arguing that it provides a convenient method of solution.

The results of this paper have been based largely on (3), which is a condition about when the next generation is the same as this one. Arguments using 'fitness' are much more likely to mislead the unwary. Treisman (op. cit.) and Mirmirani & Oster (op. cit.) have been saved from serious error by the algebraic curiosity that an invalid argument happened to give the correct answer for the case they were interested in. Not everyone using fitness arguments can expect to be so fortunate.

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