(Reprinted from Nature, Vol. 279, No. 5712, pp. 419-421, May 31 1979)
© Macmillan Journals Ltd., 1979

2

An evolutionarily stable strategy approach to indiscriminate spite

AN individual behaves spitefully when it harms itself in order to harm another individual more[1]. Hamilton[1,2] predicted that spite may evolve if it is expressed only in those encounters that occur between individuals of less than average relatedness. More recently Verner[3] suggested that territory size may become super-optimal because of a selective advantage arising from the spiteful exclusion of others from limited resources. His model is essentially different from Hamilton's in that spite is directed at individuals indiscriminately with respect to relatedness. Recently Rothstein[4] has shown analytically that the initial spread of spiteful traits will be very slow in all but the smallest populations. He also argued verbally that indiscriminate spite can never be evolutionarily stable even if it should spread (see also Davies[5]). The question of evolutionary stability is clearly important, but its resolution requires an analytical approach. We report here an approach based on Maynard Smith's[6] concept of the evolutionarily stable strategy (ESS), a strategy which, when common, does better than any alternative strategy played by a rare mutant. We show that spite can be an ESS, but that the magnitude of spite will be small in large populations.

Consider a territorial species with non-overlapping generations in which individuals compete for a finite number of resource units essential for reproduction. The resource units are distributed in patches, each of which has a pool of competitors for the resource units. At each patch individuals settle at random, one by one, out of the pool until no more resource units are available.

Let: R = the number of resource units in a single patch; P = the number of patches; X = the number of resource units defended by an individual; X_p = the strategy for resource use (the number of resource units defended) established in the population; X_m = the strategy played by a single mutant in one of the P pools of competitors; $f(X)$ = the fitness of an individual defending X resource units ($0 \leq f(X) \leq 1$), expressed as the product of gross benefit ($b(X)$) and cost ($c(X)$); X_{opt} = the strategy which maximises individual fitness ($b(X)c(X)$); V = a constant that converts $f(X)$ into the number of surviving offspring produced by an individual; $n(X_p)$ = the number of individuals in generation $t+1$ competing for the R resource units of each patch when the population strategy of generation t was X_p; we assume here that $n(X_p) = f(X_p)VR/X_p$; W_X = the mean fitness of individuals playing strategy X.

We wish to find a value for the strategy X_p such that the mean expected fitness of individuals playing X_p ($\bar{W}_{X_p}$) exceeds the expected fitness of a mutant individual playing any alternative strategy X_m ($\bar{W}_{X_m}$). Figure 1 shows how $\bar{W}_{X_p}$ and $\bar{W}_{X_m}$ can be precisely calculated for specific cases. Unfortunately, although general formulations for $\bar{W}_{X_p}$ and $\bar{W}_{X_m}$ can be obtained in terms of R, X_p and X_m, they are mathematically intractable. For this reason we have used the following approximations (written in a form parallel to the precise examples in Fig. 1):

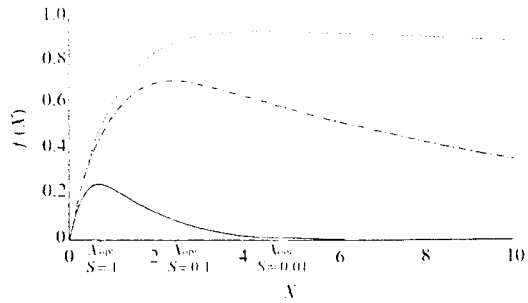

Fig. 2 The relationship between the number of resource units defended and individual fitness for three fitness functions. X_{opt} is the value of X which maximises the number of surviving offspring produced ($f'(X_{opt}) = 0$). Solid line, $S = 1$; dash-dot line, $S = 0.1$; dotted line, $S = 0.01$. $f(X) = b(X)c(X) = (1 - \exp(-X))(\exp(-SX))$.

$$\bar{W}_{X_p} = \Bigg[\overbrace{\underbrace{\left(\frac{R/X_p}{n(X_p)}\right)}_{\text{prob.}}\underbrace{\left(\frac{R - X_m}{X_p}\right)f(X_p)}_{\text{total payoff}}}^{\text{1 patch, mutant gets in}} + \overbrace{\underbrace{\left(\frac{n(X_p) - R/X_p}{n(X_p)}\right)}_{\text{prob.}}\underbrace{\left(\frac{R}{X_p}\right)f(X_p)}_{\text{total payoff}}}^{\text{1 patch, mutant does not get in}} + \overbrace{(P-1)\underbrace{1}_{\text{prob.}}\underbrace{\left(\frac{R}{X_p}\right)f(X_p)}_{\text{total payoff}}}^{P-1\text{ patches, no mutant}}\Bigg] \Big/ \underbrace{(Pn(X_p) - 1)}_{\text{No. individuals playing } X_p} \tag{1}$$

$$\bar{W}_{X_m} = \overbrace{\underbrace{\left(\frac{R/X_p}{n(X_p)}\right)}_{\text{prob.}}\underbrace{f(X_m)}_{\text{payoff}}}^{\text{1 patch, mutant gets in}} \Big/ \underbrace{1}_{\text{No. individuals playing } X_m} \tag{2}$$

(assuming $n(X_p) \geq R/X_p$, $n > 1$, $R \geq X_p$, $R \geq X_m$, prob. = probability).

Representation of possible outcomes			Probabilities: 1 Patch 1 mutant	Probabilities: $P-1$ Patches no mutants	Total payoffs to players of: X_p	Total payoffs to players of: X_m	Expected fitnesses of strategies
First	Second	Third					
X_m	X_p	X_p	$\frac{1}{n}$	0	$f(2)+f(1)$	$f(3)$	$\bar{W}_{X_p} = \Big[\Big(\frac{f(2)+f(1)}{n} + \frac{f(2)+f(1)}{n} + \frac{2f(2)}{n}\Big)$
X_p	X_m	X_p	$\frac{1}{n}$	0	$f(2)+f(1)$	$f(3)$	$+\frac{(n-6/2)3f(2)}{n} + (P-1)3f(2)\Big]\Big/(Pn-1)$
X_p	X_p	X_m	$\frac{1}{n}$	0	$2f(2)$	$f(2)$	$\bar{W}_{X_m} = \Big[\frac{f(3)}{n} + \frac{f(3)}{n} + \frac{f(2)}{n}\Big]\Big/1$
X_p	X_p	X_p	$\frac{n-(6/2)}{n}$	1	$3f(2)$	0	

Fig. 1 The possible outcomes when individuals settle out at random from a pool of n competitors to fill patches with 6 resource units. In one patch competitors consist of $n-1$ individuals who play $X_p = 2$, and a single mutant individual who plays $X_m = 3$. In the remaining $P-1$ patches all competitors play the strategy X_p. A particular individual, say the mutant in one patch, may settle first, second, third or not at all. Note that the last individual to settle takes either the number of resource units dictated by its strategy or the number left in the patch, whichever is smaller. The mean expected fitness of an individual playing a particular strategy is equal to the total expected payoffs to all individuals playing the strategy divided by the number of individuals playing the strategy.

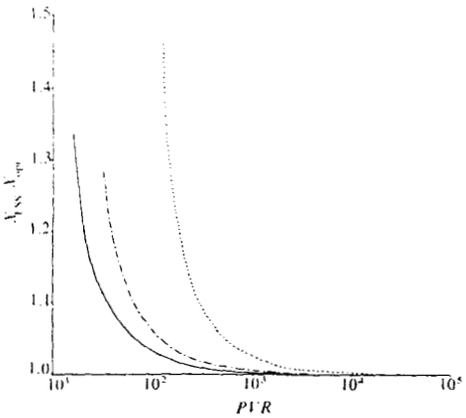

Fig. 3 The degree of spite, expressed as a ratio of the ESS number of resource units defended to the 'optimal' number, as a function of the cost of spite (as modified by the shape constant, S) and potential population size (PVR) using the same fitness functions as in Fig. 2. For each fitness curve, the ESS is equal to R (that is, 'take the entire patch') whenever PVR is below the range of values for which the ratio is plotted. Solid line, $S = 1$; dash-dot line, $S = 0.1$; dotted line, $S = 0.01$.

We now solve for the ESS, using the technique described by Parker and Macnair[7], as follows. If X_{ESS} is the ESS for the number of resource units taken, then it must be more fit when common than any single mutant which takes $X_{ESS}Y$ resource units ($Y > 0$). Thus if we subtract the expected fitness of a single mutant taking $X_{ESS}Y$ units from the mean expected fitness of individuals taking X_{ESS} units, the result is positive except when $Y = 1$, when the result is zero.

$$\therefore \text{ when } Y = 1, \quad \frac{\mathrm{d}}{\mathrm{d}X_{ESS}Y}[\bar{W}_{X_p = X_{ESS}} - \bar{W}_{X_m = X_{ESS}Y}]\Big|_{X_{ESS}} = 0 \tag{3}$$

Substituting equations (1) and (2) into equation (3) gives: when $Y = 1$,

$$\frac{\mathrm{d}}{\mathrm{d}X_{ESS}Y}\Bigg[\Bigg[\left(\frac{R/X_{ESS}}{n(X_{ESS})}\right)\left(\frac{R - X_{ESS}Y}{X_{ESS}}\right)f(X_{ESS}) + \left(\frac{n(X_{ESS}) - R/X_{ESS}}{n(X_{ESS})}\right)\left(\frac{R}{X_{ESS}}\right)f(X_{ESS}) + (P-1)\left(\frac{R}{X_{ESS}}\right)f(X_{ESS})\Bigg]\Big/(Pn(X_{ESS}) - 1) - \left(\frac{R/X_{ESS}}{n(X_{ESS})}\right)f(X_{ESS}Y)\Bigg]\Bigg|_{X_{ESS}} = 0 \tag{4}$$

Differentiating, holding X_{ESS} constant, and then substituting $Y = 1$ eventually resolves to:

$$X_{ESS} = \frac{-f(X_{ESS})}{f'(X_{ESS})(Pn(X_{ESS}) - 1)} \quad \text{or} \quad f(X_{ESS})\left[PVR + \frac{1}{f'(X_{ESS})}\right] \tag{5}$$

(as we assume that $n(X_{ESS}) = f(X_{ESS})VR/X_{ESS}$).

The same technique may also be used to determine whether X_{ESS} can invade any population playing $X_{ESS}Y$ (an ESS unable to do so is less likely to be found in nature as its ability to become established is more dependent on the starting conditions). In this case when $Y = 1$,

$$\frac{\mathrm{d}}{\mathrm{d}X_{ESS}Y}[\bar{W}_{X_p = X_{ESS}Y} - \bar{W}_{X_m = X_{ESS}}]\Big|_{X_{ESS}} = 0 \tag{6}$$

This also gives equation (5) as a solution, indicating that the ESS can invade a population playing an alternative strategy.

Examination of equation (5) and Figs 2 and 3 helps in understanding the biological meaning of these results. First, equation (5) shows that in populations of finite size X_{ESS} must be greater than X_{opt} (where $f'(X) = 0$) because only when $f'(X_{ESS})$ is negative can X_{ESS} be positive and thus biologically meaningful. Second, note that when the cost of spite is lowered (that is, $f(X)$ is increased and $|f'(X)|$ is decreased for values of X above the optimum; dotted lines, Fig. 2), the ESS level of spite is increased, as expected (Fig. 3). Third, as the number of competing individuals per patch $n(X_{ESS}) = f(X_{ESS})VR/X_{ESS}$) or the number of patches (P) increases (that is, as total potential population size increases), the ESS approaches the 'optimal' level, because $f'(X_{ESS})$ must get closer to zero as $Pn(X_{ESS}) - 1$ increases if the equality in equation (5) is to remain satisfied. Thus in populations of infinite size spite will never evolve (Fig. 3).

The ESS model presented above is only an approximation. First, it makes the following assumptions: (1) Any rare mutant which secures a place in a patch always takes the full number of resource units dictated by the strategy it is playing (that is, it is never forced to take less, as in the third outcome of Fig. 1). (2) The last X_p-playing individual to enter a patch, if forced to take some fraction α of X_p, has a fitness of $\alpha f(X_p)$ (a value which may be higher or lower than the true fitness $f(\alpha X_p)$). We compared some of the results presented in Fig. 3 with those obtained using iterations based on precise formulations which do not make these assumptions, however, and found that the differences between the two were generally less than 1% (manuscript in preparation). When the discrepancies were larger, then the approximate solutions were usually a conservative estimate of the degree of spite which can be evolutionarily stable. Second, there are no explicit genetic constraints on the models we have presented for the stability and spread of the ESS. We used the technique of Parker and Macnair[7] to show that our results are unaffected by assumptions of dominance or recessiveness in single locus diploid models (unpublished results). No attempt has been made to model other types of genetic control, however.

In conclusion, we have provided an ESS model for the evolution of spite which considers a continuous strategy set in populations of finite size. Like Rothstein[4], we found that highly spiteful behaviour is generally unlikely to occur, except in small populations, but our models contrast with his in indicating that some degree of indiscriminate spite can be an evolutionarily stable strategy.

We thank D. Rubenstein for criticisms and S. Rothstein for a preview of his manuscript. N.K. held a NATO Post-doctoral Fellowship, and G.A.P. held a King's College Fellowship while on leave from the University of Liverpool.

N. KNOWLTON*

Sub-Department of Animal Behaviour, Madingley, Cambridge University, Cambridge, UK

G. A. PARKER

King's College Research Centre, King's College, Cambridge, UK

Received 23 January; accepted 18 April 1979.

* Present address: Department of Biology, Yale University, New Haven, Connecticut 06520.

1. Hamilton, W. D. *Nature* **228**, 1218–1220 (1970).
2. Hamilton, W. D. in *Man and Beast: Comparative Social Behavior* (eds Eisenberg, J. F. & Dillon, W. S.) 59–91 (Smithsonian Institution Press, Washington, D.C., 1971).
3. Verner, J. *Am. Nat.* **111**, 769–775 (1977).
4. Rothstein, S. I. *Am. Nat.* **113**, 317–333 (1979).
5. Davies, N. B. in *Behavioural Ecology: An Evolutionary Approach* (eds Krebs, J. R. & Davies, N. B.) 317–350 (1978).
6. Maynard Smith, J. & Price, G. R. *Nature* **246**, 15–18 (1973).
7. Parker, G. A. & Macnair, M. R. *Anim. Behav.* **26**, 97–110 (1978).

Printed in Great Britain by Macmillan P