A Note on Vigilance Behavior and Stability Against Recognizable Social Parasites

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Vigilance for predators while feeding seems to present an evolutionary problem: whereas vigilance confers a common benefit to all the group members, its cost is borne only by the vigilant individual itself. Pulliam *et al.* (1982, *J. theor. Biol.* **95**, 89) and Parker & Hammerstein (1985, Game theory and animal behaviour: In: *Evolution: Essays in honour of John Maynard Smith*, pp. 73-94.) demonstrated that in cases of diminishing returns with regard to feeding time, an evolutionarily stable vigilance strategy, represented by a positive probability of being vigilant at each time unit, can exist. Thus, if this strategy is the prevailing one in the population, any individual which defects from vigilance duty suffers a reduction in fitness. But what happens if the non-vigilant defector can be recognized as such by the other group members? This work attempts to answer this question and to shed some more light on the evolutionary stability in the vigilance game.

1. Introduction

Vigilance for predators while feeding, also known as scanning behavior, has recently received much attention in the literature, both in field observations (for a review, see Barnard & Thompson, 1985) and in theoretical models (Pulliam *et al.*, 1982; Hart & Lendrem, 1984; Parker & Hammerstein, 1985; Lima, 1987; Motro & Cohen, in press).

From a theoretical point of view, vigilance behavior seems to present an evolutionary problem because a scanning individual gives up feeding. In choosing not to scan, the individual gains a personal benefit (through increased feeding), whereas scanning yields a benefit to all the individuals in the group. In other words, for ego it is clearly more beneficial that others will do the scanning, and that ego will spend all its time feeding. Since such argument applies to all other group members as well, it seems that natural selection will always favor the pure strategy of not scanning at all.

In their models, Pulliam *et al.* (1982) and Parker & Hammerstein (1985) used a game theory approach in order to study the evolution of scanning behavior. Under the plausible assumption of diminishing returns to scale with regard to feeding effort, each model finds a unique evolutionarily stable vigilance strategy, represented by the probability of being vigilant at each time unit. Since it is assumed that even a single vigilant individual is sufficient to avoid predators' success, it is not surprising

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that in both models the evolutionarily stable vigilance probabilities decrease as group size increases.

In this note we wish to shed some more light on the stability of these evolutionarily stable strategies. We will also demonstrate how, by exposing themselves, social parasites can sometimes have an advantage over any individual adopting the prevalent ESS. For that purpose we use the more simple model of Parker and Hammerstein, with a small modification.

2. Parker and Hammerstein's Vigilance Model

Consider a group of n individuals, which expect an attack by a predator, but have no knowledge about its timing. During the fixed time that the game is played (e.g., one day) only one attack will occur, and the instance of its occurrence is uniformly distributed over that time interval. The predator is successful only if no group member is vigilant at the time of the attack, and in that case, each group member has an equal probability of being captured.

The vigilance strategy of an individual is represented by a probability v of being vigilant in a given time unit, and it is assumed that behavior in distinct time units is independent.

The fitness of an individual is its survival probability times its gains through feeding. The survival probability depends on the strategies of the other group members as well, while gains through feeding depend solely on the individual's own vigilance strategy. The simplest case is that in which gains through feeding (g) decrease linearly as a function of the vigilance probability v (i.e., $g = 1 - v$). In that case, the only ESS in groups consisting of at least two members is that of no vigilance at all. However, there are plausible biological reasons to expect diminishing returns to scale with regard to feeding effort, and by considering the function $g = 1 - v^2$, Parker and Hammerstein show that a unique ESS $v^* > 0$ exists, which is a decreasing function of the group size n. Moreover, the total vigilance effort of the group (nv^*, which is the expected number of vigilant individuals at any given time unit) is also a decreasing function of n.

Other decreasing and concave functions $g = g(v)$ can be considered, and it is easier to illustrate our point by choosing the function $g(v; k) = (1-v)/(k+1-v)$, $k > 0$. The parameter k has the nice interpretation of being the proportion of time needed for feeding in order to get "half satiation", i.e., in order that the gains through feeding will be equal to $1/2$.

3. Analysis of the Slightly Different Model

The survivial probability p of an individual is 1 if at the moment of the attack at least one group member was vigilant, and is $1 - 1/n$ if no one was vigilant. If the prevailing strategy in the population is v^*, the survival probability of an individual having a different strategy v is

$$p = 1 - (1-v^*)^{n-1}(1-v) + (1-1/n)(1-v^*)^{n-1}(1-v)$$
$$= 1 - (1-v^*)^{n-1}(1-v)/n.$$

Hence the fitness W of that individual is

$$W(v, v^*) = [1 - (1 - v^*)^{n-1}(1 - v)/n] \frac{1 - v}{k + 1 - v}. \qquad (2)$$

v^* is an ESS if for all $v \neq v^*$ either $W(v, v^*) < W(v^*, v^*)$ or, if $W(v, v^*) = W(v^*, v^*)$, then $W(v^*, v) > W(v, v)$ (Maynard Smith & Price, 1973; Maynard Smith, 1982). Thus, in order to find the ESS v^*, we consider the eqn

$$\frac{\partial}{\partial v} W(v, v^*)\Big|_{v=v^*} = 0 \qquad (3)$$

i.e., the eqn

$$(1 - v^*)^n (2k + 1 - v^*)/n - k = 0. \qquad (4)$$

If $n \geq 2 + 1/k$, eqn (4) has no solution in the interval $0 < v^* \leq 1$, and $v^* = 0$ is the only ESS in that case. If $n < 2 + 1/k$, eqn (4) has a single solution in $(0, 1]$, which is a decreasing function of n, and this positive solution v^* is the ESS.

Table 1 gives the ESS v^* for $k = 0 \cdot 25$ and for $k = 0 \cdot 10$ as a function of group size n. The table also gives nv^*, which is the total vigilance effort of a group adopting the ESS. Except for a possible initial increase, nv^* decreases as n increases. (For small values of k (not shown), this initial increase of nv^* occurs over a wider range of n. Thus, for small k the model predicts that in small groups the expected number of vigilants at any given time unit will, indeed, increase with n.) Another total

TABLE 1

(a) $k = 0 \cdot 25$

group size (n)	1	2	3	4	5	6
v^*	0·6910	0·3427	0·1732	0·0834	0·0317	0·0000
nv^*	0·6910	0·6854	0·5195	0·3335	0·1584	0·0000
$1 - (1 - v^*)^n$	0·6910	0·5680	0·4347	0·2941	0·1487	0·0000
W^*	0·3820	0·5680	0·6232	0·6470	0·6595	0·6667

Remark: $v^* = 0$ for $n \geq 6$
$\qquad\quad W^* \to 0 \cdot 8000$ as $n \to \infty$.

(b) $k = 0 \cdot 10$

group size (n)	1	2	3	4	5	6	7	8	9	10	11	12
v^*	0·7683	0·4748	0·3053	0·2039	0·1396	0·0966	0·0665	0·0449	0·0288	0·0167	0·0037	0·0000
nv^*	0·7683	0·9497	0·9158	0·8158	0·6980	0·5793	0·4657	0·3590	0·2595	0·1669	0·0806	0·0000
$1 - (1 - v^*)^n$	0·7683	0·7242	0·6647	0·5984	0·5285	0·4562	0·3824	0·3074	0·2315	0·1549	0·0777	0·0000
W^*	0·5367	0·7242	0·7765	0·7992	0·8114	0·8187	0·8236	0·8269	0·8292	0·8310	0·8323	0·8333

Remark: $\quad v^* = 0$ for $n \geq 12$
$\qquad\qquad W^* \to 0 \cdot 9091$ as $n \to \infty$.

$v^* =$ Evolutionarily stable scanning probability.
nv^* and $1 - (1 - v^*)^n =$ Total vigilance.
$W^* =$ ESS fitness.
$n =$ group size.

vigilance measure, namely $1-(1-v^*)^n$, which is the probability that at least one group member will be vigilant at the time of attack, is also shown to be a decreasing function of n. The fitness W^* of each individual in an all-v^* group is an increasing function of group size.

4. More on the ESS

The ESS v^* satisfies the first ESS condition. Thus, if the prevailing strategy is $v^* > 0$, any mutant (we assume that vigilance behavior is genetically determined) with a different strategy $v \neq v^*$ has a lower fitness, in particular a mutant adopting the pure selfish strategy $v = 0$ of not scanning at all. It is true, however, that the fitness of this selfish mutant is larger than the fitness of each of the other $n-1$ members of its own group, since all have the same survival probability, whereas the mutant has larger gains through feeding. What should be compared is the fitness of that mutant with the fitness of an individual adopting the strategy v^* in a similar all-v^* group. In other words, our defecting mutant (actually, any mutant in an all-v^* group) could do better by conforming with the prevailing ESS. It is in this sense that v^* is evolutionarily stable.

But what happens if the other $n-1$ members of the group can recognize the non-scanning mutant? In this case v^* is no longer an ESS, and another strategy λ^*, which is the solution of

$$\frac{\partial}{\partial \lambda} \left\{ [1 - (1 - \lambda^*)^{n-2}(1 - \lambda)/n] \frac{1 - \lambda}{k + 1 - \lambda} \right\} \Bigg|_{\lambda = \lambda^*} = 0, \tag{5}$$

will be favored by natural selection. This strategy is the ESS for the $n-1$ player game in our situation, i.e., if λ^* is adopted by the non-defectors, any one of them which changes its strategy decreases its own fitness. (It is not surprising that knowing there are fewer potential vigilants increases the evolutionarily stable scanning probability to $\lambda^* > v^*$). Also, if λ^* is adopted by the $n-1$ non-defectors, their fitness $\hat{W}$ is larger than their fitness $\tilde{W}$ had they stuck to v^* (see Table 2). Moreover, $\hat{W}$ in a group of size n is larger than W^* in a group of size $n-1$. Hence, given there is a defector in the group, it is advantageous for the others, because of Hamilton's dilution effect (Hamilton, 1971), not to expel the defector (provided there is no intra-group exploitative competition).

As for the fate of the recognizable defector, its fitness W' is also shown in Table 2. It turns out that its fitness is *larger* than W^*, which is the fitness of a v^*-player in an all-v^* population. (This is true provided k is not too small, e.g., for $n = 2$, k has to be at least $0 \cdot 02$).

5. Conclusions

If the evolutionarily stable vigilance strategy $v^* > 0$ is the prevailing strategy in the population, any non-recognizable defector which devotes all its time to feeding and does not participate in the vigilance activity always suffers a reduction in fitness. If, however, the defector can be recognized, v^* is no longer an ESS, and a different strategy will be evolutionarily stable in the $n-1$ player game. If that strategy is adopted by the other group members, the defector can have a larger fitness.

TABLE 2

(a) $k = 0 \cdot 25$

group size (n)	2	3	4	5	6
W^*	0·5680	0·6232	0·6470	0·6595	0·6667
$\tilde{W}$	0·4864	0·5929	0·6344	0·6550	0·6667
$\hat{W}$	0·5000	0·6059	0·6416	0·6579	0·6667
W'	0·6000	0·6424	0·6566	0·6632	0·6667

(b) $k = 0 \cdot 10$

group size (n)	2	3	4	5	6	7	8	9	10	11	12
W^*	0·7242	0·7765	0·7992	0·8114	0·8187	0·8236	0·8269	0·8292	0·8310	0·8323	0·8333
$\tilde{W}$	0·6195	0·7335	0·7764	0·7977	0·8100	0·8179	0·8232	0·8269	0·8297	0·8317	0·8333
$\hat{W}$	0·6417	0·7528	0·7894	0·8066	0·8161	0·8221	0·8260	0·8288	0·8307	0·8322	0·8333
W'	0·7462	0·7967	0·8134	0·8212	0·8255	0·8282	0·8300	0·8313	0·8322	0·8328	0·8333

W^* = The fitness if all play v^*.
$\tilde{W}$ = The fitness of a non-defector if all $n-1$ non-defectors play v^*.
$\hat{W}$ = The fitness of a non-defector if all $n-1$ non-defectors play λ^*.
W' = The fitness of the defector if all $n-1$ non-defectors play λ^*.

Thus, in such cases, it is advantageous for a defector to *advertize* its parasitic strategy, and for the other group members it is advantageous to *receive* that message and act accordingly. (No doubt, if the possibility of bargaining is incorporated into our game, the outcome can be even more complicated. We are dealing, however, with a genetically determined trait, where the probability of having an immediate counter-mutation against any mutant is really negligible.)

The advantage of the recognizable defector is, of course, frequency dependent. (For example, if $n = 2$, this advantage persists as long as the frequency of the defector is smaller than $0 \cdot 2424$ for $k = 0 \cdot 25$ or $0 \cdot 1052$ for $k = 0 \cdot 10$.) Hence, in such cases, an evolutionary process can be envisaged, leading eventually to a stable polymorphism, in which both the recognizable social parasites and the co-operative individuals co-exist together.

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