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## CHAPTER THREE

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# Selfish cooperation in social roles: the vigilance game in continuous time

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### 3.1 INTRODUCTION

Social interactions in nature often involve conflict to a certain extent. Game theory can sometimes provide us with insight and tools to improve our understanding of how natural selection has resolved such conflicts. Undoubtedly, the major conceptual tool in this field is the concept of **evolutionarily stable strategies** (ESS), which was introduced by Maynard Smith and Price (1973). A strategy, in an evolutionary context, is one of a set of possible alternative behavioural programmes that an individual in a population can adopt. It is usually assumed that these are genetically determined. An ESS is a strategy which, when adopted by a large enough fraction of the population, cannot be invaded by any alternative rare ('mutant') strategy. A rare ESS strategy can invade a non-ESS population.

A certain class of evolutionary games consists of games having two pure strategies: 'defection', which yields only a personal benefit, and 'cooperation', which yields a common benefit to all the individuals in the group. Clearly, if the personal benefit from defection is greater than the personal benefit from cooperation, the evolutionarily stable strategy is defection. What happens, however, if the benefit from cooperation is the greater? In such cases it is more advantageous to cooperate, but even more advantageous to defect if other individuals in the group will nonetheless cooperate, thus enjoying both the personal benefit from one's own defection and the common benefit from cooperation performed by other individuals. Since this argument applies to all individuals in the group, it may seem that natural selection will always favour the selfish strategy of defection.

We shall briefly refer to three examples which will illustrate the ESS of

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these evolutionary games, namely the three brothers' problem, the conflict involved in dispersal, and the vigilance game.

### **3.2 THE THREE BROTHERS' PROBLEM**

The theory of kin selection was introduced by Hamilton (1964) and has been developed further in many other papers; it is described in terms of help directed from one relative (the donor) towards another (the recipient). Let us consider the more complex situation in which an individual needs help, and this help can be provided (with some risk to the donor) by each of several relatives. In such a situation, even if Hamilton's condition for altruism between two relatives is satisfied, it is easy to see the advantage of standing by and waiting for another relative to take the risk and provide the necessary help. It is true, though, that if all are passive, Hamilton's original argument again holds and any potential helper can increase its own inclusive fitness by exclusively taking the risk and saving the relative in need. However, this entails an even greater increase in the inclusive fitness of the relatives which decided not to offer their help. It seems, therefore, that if there is any altruistic relative in the vicinity natural selection will always favour the other selfish relatives.

The analysis of situations involving more than one potential helper reveals that if Hamilton's condition for one-to-one altruism does not hold, the pure strategy of absolute selfishness is the only ESS, independent of the number of potential helpers. If, on the other hand, Hamilton's condition is satisfied, the ESS is a mixed strategy of altruism and selfishness represented by an evolutionarily stable probability of providing the needed help. This probability decreases to zero as group size increases. This is true both for cases where immediate help is needed (Eshel and Motro, 1988) and for cases of delayed help (Motro and Eshel, 1988). The former are situations in which each potential helper has to instantaneously decide whether or not to offer its help, without knowing what the other potential helpers are doing. In cases of delayed help, no immediate help is mandatory (yet any delay increases the risk to the individual in need) and, at any moment, each potential helper has full information on what the other potential helpers have done and on the situation of their distressed relative.

### **3.3 THE CONFLICT INVOLVED IN DISPERSAL**

Upon dispersal of the parental site, a dispersing offspring leaves more room for its siblings (with which it shares, to a certain degree, the same genes), thus increasing their survival chances. Dispersal, on the other hand, is more risky for the dispersing individual than staying at home. Hence, whenever the decision whether to disperse or to stay in the parental site is made by the

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offspring itself, there is a conflict: the strategy of staying at home confers a personal benefit, whereas the strategy of dispersing yields a benefit to the other siblings (and, via the kinship component of the inclusive fitness, a smaller benefit also to the dispersing individual).

It turns out that if dispersal is too risky (i.e., if the survival chances of the dispersers are below a certain level), the only ESS is the pure strategy of staying at home. If, on the other hand, the survival chances of the dispersers are above that level, a mixed strategy, represented by a probability of leaving the parental site, is the only ESS. This probability increases as the risk involved in dispersal decreases (Hamilton and May, 1977; Motro, 1983).

### **3.4 THE VIGILANCE GAME**

Vigilance for predators while feeding, also known as scanning behaviour, represents a similar evolutionary problem because a scanning individual gives up feeding. In choosing not to scan, an individual gains a personal benefit through increased feeding, whereas scanning yields a benefit to all individuals in the group. In other words, for an individual it is clearly more beneficial that others will do the scanning, and that it will spend all its time feeding. Again, since such an argument applies to all other group members as well, it seems that natural selection will always favour the pure strategy of not scanning at all.

The evolutionary aspects of vigilance behaviour are studied in several game theory models (Pulliam, Pyke and Caraco, 1982; Parker and Hammerstein, 1985; Motro and Cohen, 1989; refer to Hart and Lendrem, 1984 and Lima, 1987 for different approaches). Under the plausible assumption of diminishing returns with regard to feeding effort, a single evolutionarily stable vigilance strategy, represented by the probability of being vigilant at each time unit, is found to exist in each of the game theory models. This positive probability is a consequence of absolute selfish, short-term considerations, without any further assumptions concerning kinship, reciprocity, the gaining of prestige and so forth. Since it is assumed that even a single vigilant is sufficient to avoid predation, it is quite reasonable to find that in all the models the evolutionarily stable vigilance probabilities decrease as group size increases.

A common feature of these models is that at any time unit, the actual performance of each individual is independent of that of the other group members. Thus, at any moment, the number of simultaneous vigilants is a random variable which can be 0, 1, 2 or more. This model is an appropriate description in many natural cases (e.g., flocks of waders or winter groups of other small birds).

There are many cases, however, where each individual usually has full information on the current vigilance situation in the group (e.g., certain

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barbets and babblers (Wickler, 1985; Zahavi, personal communication), the dwarf mongoose (Rasa, 1986)). If a single sentinel is sufficient to avoid predators' success, we expect to find, in such cases, no more than one vigilant individual at a time.

In the next section we present and analyse such a model, that is, a continuous time, full-information vigilance game.

### **3.5 THE VIGILANCE GAME WITH FULL INFORMATION**

Consider a group of  $n$  ( $n \geq 2$ ) individuals, which expect an attack by a predator, but have no knowledge about its timing. If the attack has not yet occurred until time  $t$ , there is some probability,  $\theta dt$ , that the predator will appear during the time interval  $(t, t + dt)$ . Hence the time passed until the predator's appearance is exponentially distributed, with expectation  $1/\theta$ .

The predator is successful only if there is not a vigilant group member at the time of the attack. In that case, each group member has an equal probability of being captured. In any case, the game terminates after the appearance of the predator.

The vigilance strategy of an individual is represented by  $v$ , such that for any given time  $t$ , the probability of this individual starting a vigilance shift during the time interval  $(t, t + dt)$  is  $v dt$  (provided that the predator has not yet appeared until time  $t$  and no group member was vigilant at that time).

A vigilance shift has a fixed duration, and let  $r$  be the probability that the predator will appear during the shift. The vigilant individual bears a cost  $c$  ( $c > 0$ ), which reflects the deprivation from feeding while being on guard, and the extra risk of predation of the vigilant, especially while rejoining its moving, foraging group (Rasa, 1986).

In order to find the ESS, we assume that the prevailing strategy in the population is  $v$ , and consider the fitness  $W(x, v)$  of a mutant having the strategy  $x \neq v$ . The fitness of the mutant is the weighted sum of its fitness in the three possible events:

1. the predator attacks before any of the group members go on guard;
2. one of the other  $n - 1$  group members goes on guard before the predator comes;
3. the mutant goes on guard before the predator comes.

As given in the Appendix, the fitness of the mutant is given by

$$W(x, v) = \frac{(1 - 1/n)\theta + (n - 1)rv + (r - c)x}{\theta + (n - 1)rv + rx} \quad (3.1)$$

The definition of the ESS,  $v^*$ , requires that the fitness of a mutant  $W(x, v^*)$

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is a maximum with respect to the mutant strategy  $x$  at  $x = v^*$ . We find the maximum by solving the equation

$$\frac{\delta}{\delta x} W(x, v^*) \Big|_{x=v^*} = 0$$

We get that the ESS  $v^*$  is

$$v^* = \frac{\theta(r/n - c)}{(n-1)rc} \quad (3.2)$$

if  $n < r/c$

$$v^* = 0 \quad \text{if } n \geq r/c$$

Not surprisingly, the ESS  $v^*$  is a decreasing function of the group size,  $n$ . Moreover,  $nv^*$  is a decreasing function of  $n$  (i.e.,  $1/nv^*$ ), which is the expected time without vigilance between shifts, is an increasing function of  $n$ ). Thus, a larger group increases the probability of a successful attack by the predator. These results are concordant with those of the non-information models.

Finally, the evolutionarily stable (ES) fitness  $W(v^*, v^*)$  of any individual in an all  $v^*$  group is

$$W(v^*, v^*) = \begin{cases} 1 - c/r & \text{if } n < r/c \\ 1 - 1/n & \text{if } n \geq r/c \end{cases}$$

Consider now the more typical case in which it is conventional that an individual never performs two consecutive vigilance shifts. That is, after completing a shift, the individual does not take part in the next one. The analysis of this model (carried out in the Appendix) reveals that a single ESS ( $u^*$ ) exists also for this case, and that if  $n < r/c$ ,  $u^*$  is larger than  $v^*$ , and also the ES fitness  $\bar{W}(u^*, u^*)$  is larger than the ES fitness  $W(v^*, v^*)$ . (If  $n \geq r/c$ , both  $u^* = v^* = 0$  and  $\bar{W}(u^*, u^*) = W(v^*, v^*) = 1 - 1/n$ .)

Indeed, it is not very surprising to find that if the one to be last on guard never participates in the next vigilance shift, the evolutionarily stable vigilance strategy implies a greater tendency of the other individuals to go up on guard. Less self-evident, however, is the result that the conventional refraining of any last sentinel from participating in the next vigilance shift increases (at the ESS) the fitness of each group member. The predictions of the two models can be tested by field observations of vigilance behaviour in the two types of social organization.

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Another interesting result of modelling vigilance behaviour is that the ESS in a group with a nonguarding individual is changed if the other group members are aware of the presence of such an individual (Motro and Cohen, 1989). In such a case, the evolutionary stable level of guarding increases. By adopting the new ESS, the guarding individuals suffer a smaller reduction in fitness (compared to the reduction in the case where the nonguarding individual cannot be detected). Over some ranges of the parameters, this increased level of guarding provides a sufficiently high benefit to the detectable nonguarding individual so that its fitness is larger than that of the guarding individuals in the population. Hence, for this range, both declaring the intention to abstain from guard duty and the detection of such an intention will be selected for. Since the advantage of the detectable defector is frequency dependent, the population will stabilize on a polymorphism in which both the guarding and the detectable nonguarding types coexist together.

### **APPENDIX DERIVATION OF THE MUTANT'S FITNESS IN THE VIGILANCE GAME**

We assume that the prevailing strategy in the population is  $v$ , and calculate the fitness  $W(x, v)$  of a mutant having the strategy  $x \neq v$ .

If the predator attacks before any of the group members went on guard (the probability of this event is  $\theta/[\theta + (n-1)v + x]$ ), the conditional fitness of our mutant is  $1 - 1/n$ .

If any of the  $n - 1$  other group members is the first to go on guard before the predator has appeared (the probability of this event is  $(n-1)v/[\theta + (n-1)v + x]$ ), the mutant's fitness is  $r + (1 - r) W(x, v)$ . (With probability  $r$  the predator appears during this shift, and the game is over, and with probability  $1 - r$  we are right back where we started).

Finally, if the mutant is the first to go on guard (the probability is  $x/[\theta + (n-1)v + x]$ ), the fitness is  $r + (1 - r) W(x, v) - c$ .

Hence the mutant's unconditional fitness  $W(x, v)$  satisfies

$$\begin{aligned} W(x, v) &= (1 - 1/n) \frac{\theta}{\theta + (n-1)v + x} \\ &+ (r + (1 - r) W(x, v)) \frac{(n-1)v}{\theta + (n-1)v + x} \\ &+ (r + (1 - r) W(x, v) - c) \frac{x}{\theta + (n-1)v + x} \end{aligned}$$

Rearranging, we get

## Appendix

$$W(x, v) = \frac{(1 - 1/n)\theta + (n-1)rv + (r-c)x}{\theta + (n-1)rv + rx}$$

Now consider the model in which no one individual performs two or more consecutive vigilance shifts. Using a similar (but somewhat more complicated) argument as before, we see that if the prevailing strategy in the population is  $u$ , the fitness  $\tilde{W}(x, u)$  of a mutant having the strategy  $x \neq u$  is

$$\tilde{W}(x, u) = \phi + \frac{ru}{\theta + (n-1)u + x}(1 - \phi)$$

where

$$\phi = \frac{Ax + B}{Cx + D}$$

and

$$A = r - c + (1 - r) \frac{(1 - 1/n)\theta + (n-1)ru}{\theta + (n-1)u}$$

$$B = (1 - 1/n)\theta + (n-2)ru$$

$$C = 1 - (1 - r) \frac{(n-1)(1-r)u}{\theta + (n-1)u} \quad D = \theta + (n-2)ru.$$

The equation  $\delta \tilde{W}(x, u) / \delta x|_{x=u} = 0$  has a positive solution ( $u^*$ ) if and only if  $n < r/c$ . In that case, this solution is unique, and is the ESS. Moreover,  $u^* > v^*$  and also  $\tilde{W}(u^*, u^*) > W(v^*, v^*)$ . If  $n \geq r/c$ , the ESS is  $u^* = 0$  (i.e., the pure strategy of no vigilance).