Should Co-operative Groups be More Vigilant than Selfish Groups?

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We develop four simple models of group vigilance that illustrate the conditions under which co-operative groups should be more or less vigilant than selfish groups. In the first model, prey individuals that directly detect the predator have a lower chance of being captured than those that were not vigilant at the time of the attack; but the predator's choice of a specific individual is not influenced by the prey's behavior. In this case, the expected level of vigilance in a co-operative group always equals or exceeds that in a selfish group. In the second model, the predator always attacks an individual that was not vigilant at the time of the attack. Co-operative vigilance can now be lower than selfish vigilance, providing that being warned by a vigilant flockmate has a sufficiently small effect on the chances of escape by a nonvigilant group member. The third model is a generalization of the first two models for the case of small groups. It can be used to consider all situations in which the predator bases its selection on the prey's behavior at the time of its attack. It reveals a variety of conditions in which selfish groups are expected to be more vigilant than co-operative groups. In the fourth model, the predator assesses the vigilance levels of each prey prior to its attack and attacks the individual that it judges to be least vigilant. If the predator is sufficiently accurate in assessing the least vigilant prey, selfish groups are always more vigilant than co-operative groups. In this case, there are circumstances where a selfish population will be expected to undergo endless cycles in its level of vigilance.

Introduction

Group living can confer significant protection against predation. The most important advantage of grouping is the dilution effect. This occurs when a predator is no more likely to locate a large group than a small one and can only capture a single individual at a time (e.g. Hamilton, 1971; Inman & Krebs, 1987). However, further benefits from grouping are possible when each group member devotes some time to vigilance. If the entire group learns of the presence of a predator whenever any group member detects it, the time that each individual must devote to vigilance is expected to decrease as group size increases (Pulliam, 1973; Lendrem, 1986).

The effects of vigilance by one individual on the fitness of other group members has thus become the subject of considerable interest. Two recent models have pointed out that because an individual's vigilance may enhance its companions' chances of escaping predation, the expected levels of vigilance shown by each individual will reflect the outcome of an evolutionary game (Pulliam *et al.*, 1982; Parker & Hammerstein, 1985). Such a game can be viewed from two perspectives. In a co-operative

game, each individual is expected to be vigilant at a rate that gives the highest fitness if all group members play the same strategy. This is the Pareto optimum, and is evolutionarily stable if group members are genetically identical (Grafen, 1979). In a selfish game, each individual is vigilant at the rate that gives a higher fitness when played against itself than any alternative vigilance rate would gain against it. This is the Nash optimum; it is evolutionarily stable when groups are composed of unrelated individuals (Maynard Smith, 1982).

According to previous models the level of individual vigilance in a co-operative group is expected to be higher than in a selfish group: the vigilance of one individual increases its companion's chances of escaping predation (and vice versa), and thus a relatively high level of vigilance enhances the fitness of both. A selfish mutant that showed a lower level of vigilance would take advantage of its companion's vigilance, but without paying similar costs from devoting time to vigilance. It would be informed of the presence of a predator by the responses of more vigilant companions and could spend more of its own time feeding. Thus low levels of vigilance should prevail in a group of nonrelatives; but as group members become more closely related, the individual (Nash) optimum will move toward the co-operative optimum (Grafen, 1979).

Both Pulliam *et al.* (1982) and Parker & Hammerstein (1985) conclude that field data more often conform to the co-operative rather than to the selfish optimum. Pulliam *et al.* (1982) suggest that co-operative vigilance could evolve through some form of reciprocity where co-operators protect themselves against cheating by non-vigilant companions. However, excessive vigilance occurs in species that form large, temporary flocks of unrelated companions and reciprocity is most likely to evolve when the chances of further interaction are high (Axelrod & Hamilton, 1981) and when group size is very small (Boyd & Richerson, 1988). Further, it seems particularly unlikely that an individual could successfully monitor the vigilance of its companions *while it is not being vigilant itself* and thus be able to detect and punish non-co-operators.

Using a dynamic optimization approach, Lima (1989) has recently considered an alternative explanation for co-operative vigilance. If risk of predation is sufficiently high and individuals could not easily move from one group to another, each individual would increase its own long term survival by acting in ways that guaranteed the continued survival of its companions. Preserving a partner for future encounters would thus confer long term selfish advantages from the dilution effect and co-operative vigilance would not have to be based on reciprocity. However this explanation would again be most compelling for small stable groups.

Because of the difficulties in explaining apparently co-operative levels of vigilance it is now necessary to re-examine previous models. These had assumed that (1) predators were equally likely to attack vigilant and nonvigilant individuals and (2) all group members were equally likely to escape as long as at least one member detected the predator. Data from several recent studies suggest a more complex picture. First, Elgar *et al.* (1986) showed that nonvigilant individuals in flocks of house sparrows were slower to react during alarm flights. A vigilant bird might therefore be more likely to escape an attack. Second, FitzGibbon (1989) found that

individual Thompson's gazelle that had spotted a nearby cheetah did not always act in a way that informed the rest of the herd of the cheetah's presence, and the cheetah usually focussed its stalk on a relatively inattentive individual in the herd.

We show here that the difference between selfish and co-operative vigilance depends on how an individual's probability of survival is affected by the vigilance of other group members. This effect is determined by two factors: (1) the extent to which the chance of survival is improved by being warned of an attack by another group member, and (2) the criterion by which the predator bases its selection of a specific group member.

We present four alternative models of group vigilance that illustrate the importance of these two factors. In the first model, each group member has an equal probability of being attacked by the predator, but those individuals that detect the predator's attack by their own vigilance have a greater probability of escape than the rest of the group. This model focusses exclusively on how personal advantages of vigilance affect the expected levels of vigilance in a selfish group compared to those in a co-operative group.

In the second model, the predator always selects one of the individuals that was not vigilant at the start of its attack. The analysis shows that if an individual that has been selected by a predator has a low chance of escaping, the predator's selectivity can result in selfish groups being more vigilant than co-operative groups.

The third model generalizes the first two and allows the chances of escape of both vigilant and nonvigilant individuals to depend on the number of vigilant and nonvigilant companions. Co-operative strategists will often be expected to be less vigilant than selfish ones in situations where vigilance by one individual increases the chance that another vigilant individual will be captured.

The fourth model assumes that the predator bases its selection according to the vigilance level of each prey prior to the attack. In this case, the predator first assesses the relative vigilance of each group member and then attacks the individual that it judges to be least vigilant. This results in the most extreme excess of selfish vigilance over co-operative vigilance. It can also result in cycles of vigilance levels in the prey population.

The Models

We base our analysis on the models of Pulliam *et al.* (1982) and Parker & Hammerstein (1985); which share the same basic structure. Both assume that a predator takes only one individual during a single hunt, the predator is always successful when all group members are simultaneously inattentive, the vigilance of each group member is independent of that of its companions and the timing of the predator's attack is random with respect to the behavior of the prey. Pulliam *et al.* assume that when at least one group member is vigilant, the predator's chances of success are reduced. Parker & Hammerstein assume that the predator always fails in such cases. Pulliam *et al.*, allow the attack rate to vary, whereas Parker & Hammerstein allow only one attack per game.

The most important contrast between the two is in their view of the costs of vigilance. Pulliam *et al.*, assume that there are no constraints on the organism's time

budget. A bird eventually gains its feeding requirements in a day, and an increase in vigilance results in more time spent in a feeding area where it is vulnerable to predation. Thus an optimal vigilance rate minimizes predation risk by balancing the risk of predation per unit time against the time spent at risk. However, when the chances of escaping a detected predator are sufficiently low, the predicted vigilance rate would exceed available time.

In contrast, Parker & Hammerstein view the costs of vigilance as being time diverted from feeding: an animal can increase its vigilance only at the cost of reducing time spent feeding. They analyze two specific relationships between vigilance and feeding.

We follow Parker & Hammerstein in assuming a tradeoff between vigilance and feeding and only one hunt per game. We investigate various forms of the tradeoff function between feeding and vigilance; and derive many results without any assumptions about its specific form. However, as with Pulliam *et al.*, we allow intermediate chances of escape when the group detects the predator. We also vary the assumption that an individual is always captured from a group in which all members are simultaneously inattentive.

Following Parker & Hammerstein we measure vigilance as x, the proportion of potential foraging time devoted to vigilance. The probability that a given individual will detect an attacking predator is assumed to equal x. In addition, prey individuals are assumed to scan independently of one another (Caraco, 1982; but see Hart & Lendrem, 1984). Thus at any given time, the mean proportion of individuals that are vigilant is x, and the probability that at least one member of a group of n prey detects the predator is $1-(1-x)^n$. While these assumptions are simplistic, conclusions about the relative values of the optimal selfish and co-operative levels of vigilance do not appear to be very sensitive to these assumptions. In more realistic models, a description of vigilance behavior would include the length of time taken by a single scan; the distribution of times between scans; the length of time between the point when a predator is first detectable and when escape is no longer possible; the probability of capture as a function of the time when the predator is detected; the behavioral rules used by the predator to time its attack; and the possibility that vigilance and feeding are not mutually exclusive. No vigilance model has yet considered all these features, but some are discussed by Pulliam *et al.*, (1982), Ward (1985), Hart & Lendrem (1984), Lendrem (1986), and Lima (1987, 1988).

The general methods for finding and comparing the selfish and co-operative optima are presented with the analysis of Model 1.

MODEL 1. THE PREDATOR CHOOSES PREY AT RANDOM FROM THE GROUP; EACH PREY'S CHANCE OF ESCAPE DEPENDS ON WHETHER IT IS VIGILANT AT THE START OF THE ATTACK

In a group of n prey, each individual has a $1/n$ probability of being selected by the predator. The predator is always successful when all group members are non-vigilant at the start of its attack. However, if at least one group member is vigilant,

the predator's success depends on the behavior of the individual prey that it selects from the group. If it selects an individual that is vigilant at the start of the attack it is successful with a probability of b; if it selects a nonvigilant individual, it succeeds with probability c. Thus if a particular individual, "ego", is vigilant when the predator attacks, ego's chance of being killed is b/n. If the attack occurs when ego is not vigilant, ego has a $1/n$ chance of dying if no one else is vigilant or a c/n chance of dying if at least one other group member is vigilant.

In this case an individual prey animal has the following probability (q) of surviving the attack:

$$q = (1-b/n)x + (1-x)[(1-1/n)(1-x^*)^{(n-1)} + (1-c/n)(1-(1-x^*)^{(n-1)})],$$

    n = group size,
    x = probability that ego is vigilant,
    x^* = probability that each other individual in the flock is vigilant.

Fitness is given by the product sq; s is fitness from feeding and is a decreasing function of x.

The expression for q may be understood as follows. The probability that ego detects an attack is x and its probability of surviving the attack is $(1-b/n)$. The probability that ego does not directly detect the attack is $(1-x)$. Ego's probability of survival then depends on whether another group member detects the attack. The probability that no other member of the group detects the predator is $(1-x^*)^{(n-1)}$ and ego's probability of survival is then $(1-1/n)$. The probability that at least one other member of the group does detect the predator is $[1-(1-x^*)^{(n-1)}]$, and ego's probability of surviving is then $(1-c/n)$. Note that all previous models assumed that $b = c = 0$.

The selfish optimum is found by taking the derivative of fitness, sq, with respect to x, setting it equal to zero, and then substituting $x^* = x$. This gives:

$$0 = (ds/dx)q + s[(1-(b/n)) - (1-(c/n)) + ((1-c)/n)(1-x)^{(n-1)}]. \qquad (1)$$

The co-operative optimum is found by first setting $x = x^*$, taking the derivative of sq with respect to x, and setting it equal to zero:

$$0 = (ds/dx)q + s[(1-(b/n)) - (1-(c/n)) + (1-c)(1-x)^{(n-1)}]. \qquad (2)$$

The right hand side of eqn (2) is the derivative of group fitness with respect to vigilance. If this quantity is positive at the selfish optimum x, then group fitness would be increased by increasing vigilance above the selfish optimum level. Assuming that group fitness is a unimodal function of x (which is true for the s functions that we have investigated), this implies that the co-operative optimum x is greater than the selfish optimum x. Conversely, if the right hand side of (2) is negative when evaluated at the selfish optimum, then the co-operative optimum will be smaller than the selfish. Whenever fitness is given by the product sq, the derivative of group fitness evaluated at the selfish optimum is given by $s(dq/dx^*)$. Thus, the relative

values of the two optima are determined by the effects of vigilance by other individuals on the survival of ego (i.e. by the sign of dq/dx^*). If ego's probability of survival is increased when companions show vigilance at a level greater than the selfish optimum, then the co-operative optimum is greater than the selfish. If it is decreased, the co-operative optimum is lower than the selfish.

In Model 1, the expression for dq/dx^* is:

$$[(n-1)/n](1-x)^{(n-1)}(1-c). \qquad (3)$$

Expression (3) is positive in all cases except when $c = 1$, at which point it is equal to zero. Therefore the co-operative level of vigilance should always be higher than the selfish, except when $c = 1$. In the latter case, one individual's vigilance has no effect on its companions' chances of escaping predation, and thus there is no difference between co-operation and selfishness.

Comparisons of selfish and co-operative maxima for different values of c are shown in Fig. 1 for the case of $s = 1 - x^2$. Figure 1 shows that for a given group size an increase in c increases the selfish optimum, but decreases the co-operative optimum.

This figure also illustrates the fact that individual vigilance is expected to decline with increasing group size purely as a result of the dilution effect. Vigilance should decline with increasing group size even when the vigilance of one individual has
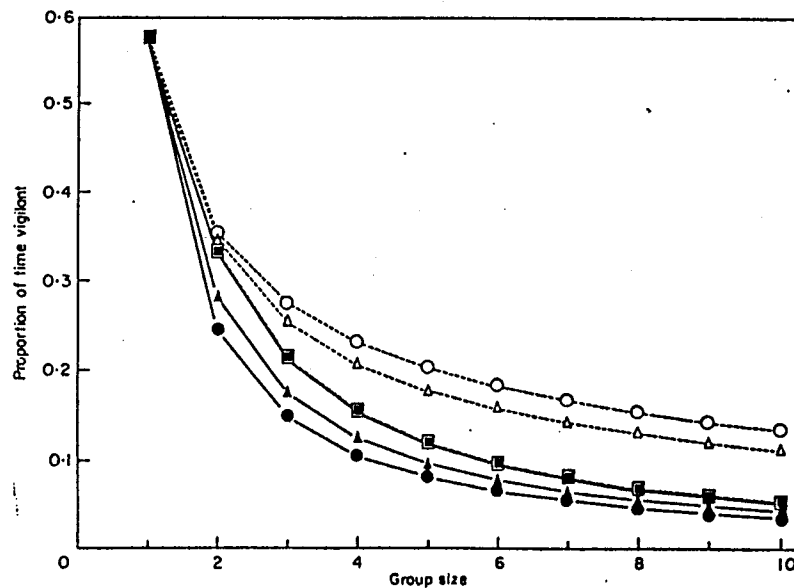

FIG. 1. Optimal levels of vigilance from Model 1 for co-operative groups and selfish groups for differing values of c, where $s(x) = 1 - x^2$ and $b = 0$. Selfish: $c = 0$ (—●—); $c = 0.5$ (—▲—); $c = 1$ (—■—). Co-operative: $c = 0$ (--○--); $c = 0.5$ (--△--); $c = 1$ (--□--).

no effect on its companions' chances of escaping predation ($c=1$). In all cases examined, increasing group size from 1 to 2 has a greater effect on both the cooperative and selfish optima than does decreasing c from 1 to 0 at any given group size.

MODEL 2. THE PREDATOR ONLY ATTEMPTS TO CAPTURE AN INDIVIDUAL THAT IS NOT VIGILANT AT THE START OF THE ATTACK

Again assume that the predator is always successful if it is undetected by the entire group. Because predators do not select vigilant individuals, the parameter b is no longer applicable. If one or more group members are vigilant at the start of its attack, the predator has chance c of catching the nonvigilant individual that it selects. Each prey's probability of dying now depends not only on the presence of a vigilant companion but also on the number of vigilant companions. Ego will only be selected when it is not vigilant. If no one else is vigilant, ego's chance of dying is $1/n$. If everyone else is vigilant, ego's probability of dying is c; if all but one of its companions are vigilant its probability is $c/2$; and so on.

The probability of a specific individual surviving is now:

$$q = x + (1-x)\left\{(1-1/n)(1-x^*)^{(n-1)} + \sum_{j=1}^{n-1}(1-c/(n-j))\binom{n-1}{j}x^{*j}(1-x^*)^{(n-1-j)}\right\}.$$

Where j denotes the number of vigilant individuals' among ego's $n-1$ companions.

By this model there are still conditions where the co-operative optimum level of x exceeds the selfish; however, there are also conditions where the selfish exceeds the co-operative optimum. The relationship between individual and group fitnesses is very complex and depends on c, n, and s. Figure 2 illustrates the general result that the optimal level of vigilance in a co-operative group is higher than the selfish level for a given value of c only when c is small; the selfish level exceeds the co-operative level when c is large.

The contrast between Models 1 and 2 can be readily seen by considering groups of two. In Model 1, the effect of a companion's vigilance on ego's survival (dq/dx^*) is $[(1-c)/2](1-x)$. This is positive whenever c is less than one. Under Model 2, the corresponding formula for (dq/dx^*) is $[(1-2c)/2](1-x)$. This is only positive when $c<1/2$ (i.e. when the chance of being caught despite being warned by a vigilant companion is less than 1/2). When $c>1/2$ the benefit of being warned is overridden by the cost of always being selected in the presence of a vigilant companion. In the latter case, the co-operative optimal level of vigilance is less than the selfish optimum.

By Model 2, there is a value of c for each group size above which the co-operative optimum no longer exceeds the selfish optimum. However, for groups of three or more this value of c depends on the selfish optimum x, which in turn depends on the feeding function s. Figure 3 shows the critical value of c for groups of two to ten individuals for a variety of s functions. This critical value may increase or decrease with group size.
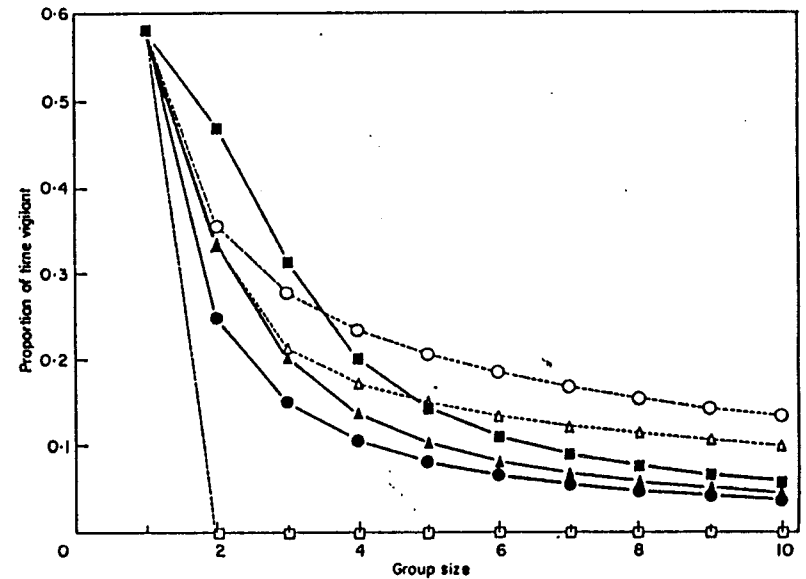
FIG. 2. Optimal levels of vigilance from Model 2 for selfish groups and co-operative groups for differing values of c, where $s(x)=1-x^2$. Key as for Fig. 1.

The results for Model 2 imply that, in general, selfish groups should be more vigilant than co-operative groups when being warned by a flockmate does little to increase an individual's chance of escape. The difference between Models 1 and 2 emphasizes the importance of prey selection by the predator. In Model 1 the vigilance of one individual can never decrease the fitness of its companions. In Model 2, the advantage of being informed of an impending attack by vigilant companions may be outweighed by an increased probability of being singled out by the predator.

MODEL 3. CHANCES OF ESCAPE OF BOTH VIGILANT AND NONVIGILANT INDIVIDUALS DEPEND ON THE NUMBER OF VIGILANT COMPANIONS

In the previous two models an individual escaped with a constant probability if it was vigilant at the time of the attack. In this model we allow this probability to depend on the vigilance levels of the other group members. This is designed to investigate situations in which the predator can catch prey that have detected its attack, but prefers to chase individuals that were not vigilant at the time of the attack. A vigilant individual may then have a *lower* probability of surviving if most other group members were also vigilant than if most were non-vigilant at the time of the attack. Because of the computational complexity of the problem, results are presented only for the case of a group of two. The Appendix shows how the results
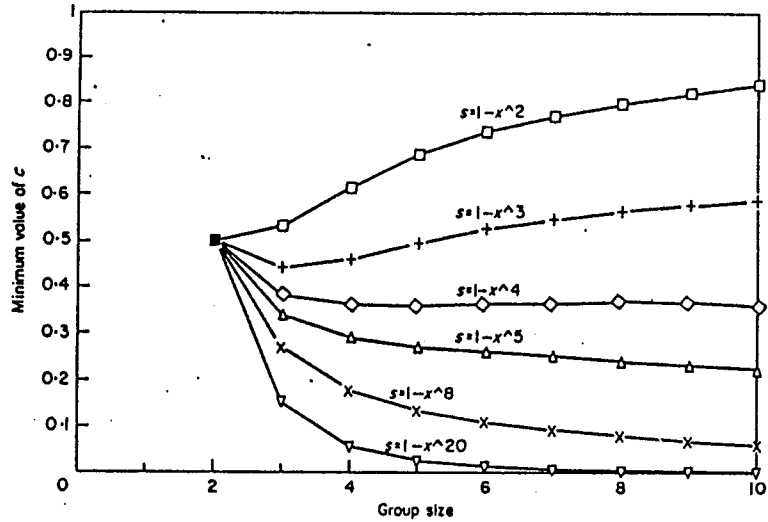
FIG. 3. The value of c where the selfish level of vigilance is equal to the co-operative optimum for each group size. The selfish optimum is always greater than the co-operative for higher values of c, and less than the co-operative at lower values. The critical values of c are plotted for different functions of $s(x)$. The figure does not show critical c values for $s = 1 - x$; in this case, both the selfish and co-operative optima are equal to 0 when $c > 1/n$; otherwise the co-operative optimum is greater than the selfish.

can be extended to larger group sizes.

$p_2 =$ the probability of each individual dying when both were vigilant at the time of the attack,

$p_b =$ the probability of an individual dying when it is vigilant at the time of the attack, but its companion is not vigilant,

$p_c =$ the probability of an individual dying when it is not vigilant at the time of the attack, but its companion is vigilant,

$p_0 =$ the probability of each individual dying when neither were vigilant at the time of the attack.

Note that both p_0 and p_2 must be less than $1/2$ because, in these cases, the predator is equally likely to select either individual.

Ego's probability of survival is given by:

$$q = 1 - [xx^*p_2 + x(1-x^*)p_b + (1-x)x^*p_c + (1-x)(1-x^*)p_0].$$

Using the dq/dx^* criterion, it can be shown that the expected level of vigilance at the co-operative optimum will exceed the selfish level of vigilance whenever:

$$(1-x)(p_0-p_c) + x(p_b-p_2) > 0. \qquad (4)$$

Otherwise the expected level of vigilance will be higher at the selfish optimum. If $p_0 > p_c$ and $p_b > p_2$, then co-operative vigilance will exceed selfish; and if $p_c > p_0$ and $p_2 > p_b$, selfish will exceed co-operative. If these inequalities are mixed, then the magnitude of x determines the sign of expression (4); the magnitude of x is in turn determined by s and the p_i.

In Model 1, we assumed that if $n = 2$, then $p_2 = p_b = b/2$, $p_0 = 1/2$ and $p_c = c/2$. Thus the co-operative optimum always exceeds the selfish optimum except when $c = 1$ in which case $p_0 = p_c$ and they are equivalent. In Model 2, we assumed that $p_2 = p_b = 0$, $p_0 = 1/2$ and $p_c = c$. Whenever $c > 1/2$, $p_c > p_0$ and the selfish level of vigilance can exceed that of the co-operative optimum.

Neither Model 1 nor Model 2 considered the possibility that p_2 could be greater than p_b, i.e. that a vigilant individual could benefit from nonvigilant companions. This would be likely whenever a predator has some chance of capturing a member of a vigilant pair ($p_2 > 0$), but usually selects the nonvigilant member of the pair when only one is vigilant (p_b close to 0). Inequality (4) shows that this condition would greatly increase the circumstances where a co-operative strategist would be less vigilant than a selfish strategist.

MODEL 4. THE PREDATOR ALWAYS CHOOSES THE MEMBER OF THE GROUP THAT IT JUDGES TO BE LEAST VIGILANT

The previous models all assumed that the prey's chances of escaping depended entirely on their behavior at the time of the attack. However, an individual's chances of escaping may depend on its level of vigilance prior to the attack. FitzGibbon's (1989) study suggested that cheetah may monitor their prey for a period of time before they attack and then select the prey that was least vigilant during that period. In this situation an individual with a slightly higher vigilance level may avoid all risks of predation. This situation is similar to Maynard Smith's (1974) "war of attrition": an individual can avoid all risks of predation by devoting slightly more time to vigilance than any of its companions.

In order to investigate such a "war of vigilance", we modify Model 3 to include a function describing a predator's choice between two group members. If the vigilance levels of "ego" and "other" are x and x^*, their respective probabilities of being chosen are given by

$$x^{*m}/(x^m + x^{*m}) \quad \text{and} \quad x^m/(x^{*m} + x^m). \qquad (5a, b)$$

The exponent m represents the accuracy of the predator in selecting the prey with the lower vigilance level. It is affected by both the predator's abilities to measure vigilance levels and its preference for the less vigilant prey. As m approaches 0, its choice approaches random; as m becomes large, it almost always selects the less vigilant prey.

The selection process is incorporated into Model 3 by separating into two components the probability of being killed by the predator: the probability of being selected and the probability of being captured, given that it has been selected. The

three post-selection probabilities of dying are:

p_b = the probability that the selected individual is killed when it is vigilant at the onset of the attack,

p_c = the probability that the selected individual is killed when its companion is vigilant at the onset of the attack, but it is not,

p_0 = the probability that the selected individual is killed when neither are vigilant at the onset of the attack.

Because the predator selects its prey before the attack begins, the partner's vigilance at the time of the attack does not affect ego's probability of dying when ego is itself vigilant. In contrast to Model 3 where the predator may select either individual if both are vigilant, the predator now always chooses the same individual. These p_i differ from the corresponding terms in Model 3 because they refer only to the probability of dying after the predator has selected the individual it will attack. Each p_i may assume any value between 0 and 1.

By these assumptions, ego's probability of surviving an attack is

$$q = 1 - x^{*m}[p_b x + p_c(1-x)x^* + p_0(1-x)(1-x^*)]/(x^m + x^{*m}). \qquad (6)$$

The selfish and co-operative optimum vigilance levels are derived as before and result in the following expressions:

$$0 = (ds/dx)q$$
$$+ (s/4)[p_b(m-1) + p_c(m-mx+2x) + p_0((m/x) - 2m + mx + 2 - 2x)], \qquad (7)$$

for the selfish optimum, and

$$0 = (ds/dx)q + (s/4)[-p_b - 2p_c(1-2x) + 4p_0(1-x)], \qquad (8)$$

for the co-operative optimum. The expression for dq/dx^* is:

$$(1/4)[-p_b m - p_c(1-x)(m+2) + p_0(-(m/x) + 2m - mx - 2x + 2)]. \qquad (9)$$

Co-operation will only result in greater vigilance than selfishness when expression (9) is positive. Expression (9) can be positive or negative, and its sign is not always obvious because the optimum x may be a function of the other parameters. If $m = 0$, the predator attacks a randomly chosen individual and this reduces to Model 3 under the condition that $p_b = p_2$.

Another special case is the situation in which an individual's own vigilance has no effect other than to influence the predator's decision about which individual to attack. An individual's probability of dying is then constant regardless of the vigilance of itself or its partner at the time of the attack ($p_b = p_c = p_0 = p$). This reduces the equations for the selfish and co-operative optima [eqns (7) and (8)] to:

$$(ds/dx)q + smp/(4x) = 0, \qquad (10)$$

$$(ds/dx)q = 0. \qquad (11)$$

Under our assumption that s is non-increasing, eqn (11) can have no solution that maximizes group fitness for $0 < x < 1$. Because vigilance does not influence the probability that the predator will capture a group member, its only effect on group fitness is from reducing foraging time. The co-operative optimum level of vigilance is therefore zero. In contrast, the equation for the selfish optimum, (10), always has a solution for some vigilance level between 0 and 1. Thus in this case, the optimal level of selfish vigilance is always expected to be greater than the co-operative optimum.

The general condition comparing co-operative and selfish vigilance levels, eqn (9), may also be explored by using calculus to determine the effect of each parameter on its magnitude. Increasing m (the predator's accuracy in assessing vigilance levels), and increasing p_b or p_c (the probability of dying when at least one individual is vigilant), all increase the probability that the selfish optimum will be greater than the co-operative optimum. When m is sufficiently large that the coefficient of p_0 is negative in eqn (9), increasing p_0 has the same effect; but the opposite effect when m is small.

The predator selection function used here introduces a complication that was not present in any of the previous models: a population at the selfish optimum calculated by eqn (7) can sometimes be invaded and displaced by types with very low levels of vigilance. Finding the selfish optimum with calculus specifies a strategy (vigilance level) that is uninvadable by nearby strategies (Maynard Smith, 1982). This does not insure that a significantly different vigilance level would be unable to invade.

Simulations (described below) that assume haploid genetic determination of vigilance levels reveal that a population would be expected to undergo cycles of vigilance levels when the selfish optimum can be invaded by a low vigilance strategy. The maximum average vigilance during the course of such a cycle is always less than the selfish optimum specified by eqn (7). In these cases, the co-operative optimum might instead be more usefully compared with the temporal average of selfish vigilance or the maximum mean vigilance shown by a population during the course of a cycle.

Cycling can be easily understood by again considering the simple case when an individual's probability of dying is constant, given that it has been selected [$p_b = p_c = p_0 = p$ in expression (6)]. An individual with zero vigilance will have the following fitness if it is a rare mutant in a population with the selfish optimum, x_s:

$$s(0)(1-p). \qquad (12)$$

The mutant will survive the attack with probability $q = 1 - p$ because it is always selected by the predator. The mutant will have a greater fitness than the normal type whenever:

$$s(0)(1-p) > s(x_s)(1-(p/2)). \qquad (13)$$

If condition (13) is not satisfied, the selfish optimum specified by eqn (10) is globally stable, and can be used in comparing the vigilance levels of co-operative and selfish strategies. However, when (13) is satisfied, there will be no uninvadable

strategy; and it is also possible to show that no mixture of strategies can be evolutionarily stable (Abrams, in preparation).

Changes in vigilance levels in a population can be simulated by assuming that vigilance is determined by a single locus in a haploid population, and that alleles specifying all possible levels of vigilance are present in the population. (In practice, the simulations assumed 50 or 100 alleles that specified evenly spaced vigilance levels between 0 and 1 or between 0 and x_s.) When (13) was satisfied, cycles of vigilance occurred. Results of one such case are shown in Fig. 4.

The mechanism behind the cycles is as follows. As average vigilance levels increase in the population, the optimum for a selfish individual must also increase to avoid selection by the predator. Eventually, the population can be invaded by types with zero vigilance. Once most of the population has very low vigilance, individuals with slightly higher vigilance have an advantage. This results in another escalation of vigilance levels until nonvigilant individuals can once more invade the population.

The approximate value of the maximum average vigilance that would ever be observed in such a cycle is that which results in the mean fitness of the population being the same as that of a totally nonvigilant mutant. This is found by modifying expression (13) by replacing $>$ with $=$, and replacing x_s with x, and then solving for x.

In this special case (p_i's equal), it is often possible to obtain analytical expressions for the selfish optimum x and the approximation for the largest value of x during the cycles. For example, if $s(x) = 1 - x^2$, then the local evolutionarily stable
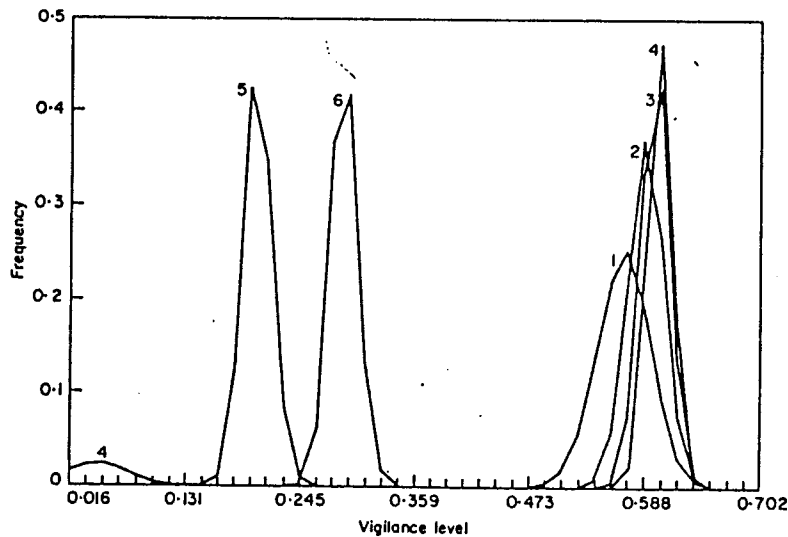

FIG. 4. Cycles of vigilance levels in the "war of vigilance" (Model 4). The numbers next to the peak of each curve represent the number ×100 generations after the beginning of the simulation. In this example, $s(x) = 1 - x^2$, all of the $p_i = 0.5$ and $m = 8$. The iteration was started with equal frequencies of 50 alleles specifying evenly spaced vigilance levels between 0.016 and 0.8.

selfish x is:

$$x_s = [pm/(pm + 8 - 4p)]^{1/2}. \tag{14}$$

This cannot be invaded if;

$$m < (4 - 2p)/(1 - p). \tag{15}$$

If (15) is not satisfied, the population will cycle between vigilance values of 0 and approximately $x = [p/(2 - p)]^{1/2}$. Thus, a large enough value of m or a small enough p will always produce cycles. As noted before, for this case of equal p_i, the co-operative optimum x is always zero and thus the average selfish vigilance over an entire cycle always exceeds the co-operative optimum.

Under the general model described by eqn (6), the condition for the occurrence of cycles [the analog of condition (13)] is:

$$s(0)[1 - p_c x_s - p_0(1 - x_s)]$$
$$> s(x_s)[1 - (1/2)p_b x_s - (1/2)p_c x_s(1 - x_s) - (1/2)p_0(1 - x_s)^2].$$

As in the case of inequality (13), changing this expression to an equality, setting $x_s = x$, and solving for x will yield an approximation for the largest average vigilance levels observed in a cycling, selfish population.

The potential impact of cycles on conclusions about the relative values of selfish and co-operative optima may be explored with two numerical examples. These assume either (i) an individual benefits from its own vigilance, but not from that of its partner ($p_b < p_0 = p_c$); or (ii) an individual benefits equally from the vigilance of either ($p_b = p_c < p_0$). Table 1 shows the results of numerical calculations of selfish and co-operative optima, results of stability analysis, and approximate maximum vigilance in cycles for these two cases when the cost function $s(x) = 1 - x^2$. Repeated cycles of vigilance levels do not change the conclusion outlined earlier for the relationship of the co-operative and selfish optima. Cycles were only observed for parameter values that also resulted in co-operative optima very close to zero. In these cases, the maximum vigilance observed in a selfish cycle would be much larger than the co-operative optimum. The simulations show that the temporal average vigilance is greater than one-half of the maximum vigilance in the cycle. This relationship can be seen in Fig. 4: the rate of change in mean vigilance decreases as mean vigilance increases. Consequently, the temporal average of a selfish cycle is greater than the co-operative optimum.

A similar cycling of strategies was reported by Maynard Smith & Brown (1986) in a model of competition in which larger individuals win contests, but suffer greater mortality before achieving adult size. They note that diploid or polygenic inheritance greatly restricts the conditions under which cycling occurs in their model. The same restriction would probably occur in our model as well, increasing the likelihood that a given population would remain at or near a local optimum.

Finally, it should be noted that these results can be extended to groups containing more than two individuals. In groups of three, the probability that a predator selects an individual with vigilance x_i, when its companions are vigilant at x_j and x_k, is $(x_j x_k)^m / [(x_j x_k)^m + (x_i x_k)^m + (x_i x_j)^m]$. The analysis is algebraically very messy, but

TABLE 1

Comparison of different optimum vigilance levels in Model 4

(a) Case (i): $p_p = p_c > p_b$

m	$p_o = p_c$	p_b	Selfish	Min†	Cycles?	Co-operative
2	0·9	0·8	0·530	0·912	No	0·045
2	0·9	0·5	0·506	0·929	No	0·167
2	0·9	0·1	0·482	0·944	No	0·279
2	0·9	0	0·477	0·947	No	0·299
2	0·5	0·4	0·374	0·599	No	0·033
2	0·5	0·3	0·370	0·620	No	0·066
2	0·5	0	0·360	0·675	No	0·155
2	0·1	0·09	0·160	0·232	No	0·003
2	0·1	0·05	0·160	0·242	No	0·013
2	0·1	0	0·159	0·255	No	0·026
8	0·9	0·8	0·767	0·912	No	0·045
8	0·9	0·5	0·706	0·929	No	0·166
8	0·9	0·1	0·628	0·944	No	0·279
8	0·9	0	0·610	0·947	No	0·299
8	0·5	0·4	0·607	0·599	Yes	0·033
8	0·5	0·3	0·581	0·620	No	0·066
8	0·5	0	0·510	0·675	No	0·155
8	0·1	0·09	0·305	0·232	Yes	0·003
8	0·1	0·05	0·292	0·242	Yes	0·013
8	0·1	0.	0·276	0·255	Yes	0·155

(b) Case (ii): $p_c = p_b < p_o$

m	p_o	$p_c = p_b$	Selfish	Min	Cycles?	Co-operative
1	0·99	0	0·348	0·995	No	0·353
1	0·9	0	0·333	0·948	No	0·333
1	0·5	0	0·252	0·699	No	0·219
2	0·9	0·8	0·515	0·913	No	0·082
2	0·9	0·5	0·454	0·931	No	0·231
2	0·9	0·1	0·393	0·946	No	0·320
2	0·9	0	0·380	0·949	No	0·333
2	0·1	0·09	0·159	0·234	No	0·005
2	0·1	0·05	0·153	0·252	No	0·026
2	0·1	0	0·147	0·275	No	0·050
8	0·9	0·8	0·759	0·913	No	0·082
8	0·9	0·5	0·662	0·931	No	0·231
8	0·9	0·1	0·526	0·946	No	0·320
8	0·9	0	0·494	0·949	No	0·333
8	0·1	0·09	0·301	0·234	Yes	0·005
8	0·1	0·05	0·275	0·252	Yes	0·026
8	0·1	0	0·244	0·275	No	0·050

† "Min" denotes the minimum population vigilance that can be invaded by a type with zero vigilance. If Min is less than the selfish optimum, then there will be cycles of vigilance levels in the population.

two conclusions emerge that are consistent with our analyses of pairs. First, selfish groups may also show cycles of vigilance levels and second, high values of predator selectivity (m) increase selfish optima relative to the co-operative.

In summary, there is a wide range of conditions when selfish individuals will be expected to be more vigilant than co-operative individuals; even when selfish populations show cycles in vigilance levels. Greater levels of vigilance will always

be expected in selfish groups when the predator is a sufficiently good judge of vigilance levels.

Discussion

The models analyzed here show that selfishness will often lead to greater vigilance levels than will co-operation. They clearly illustrate that an optimal vigilance strategy strongly depends on the details of a predator's selection criteria and on the extent to which individuals that are not vigilant at the onset of an attack benefit from being warned by their companions. One of the major limitations of our analysis is that we only consider the consequences of a single attack by the predator. We have analyzed models in which attacks do not always occur, and these do not significantly affect our conclusions. However, games with multiple attacks are more difficult to analyze because of the consequences to each group member from the loss of a companion. If individuals can rapidly and easily replace companions that have been killed by predators, the form of the models is not changed significantly (assuming that the "replacement" companions show a similar distribution of vigilance as the population forming the original groups). Under these assumptions, greater attack rates can be modeled by assuming that s and q measure the fitness loss over a shorter time period. If group members cannot be replaced and members of smaller groups suffer lower fitness, then the selfish optimum would shift toward the co-operative (Lima, 1989).

Selfish vigilance might often be more easily distinguished from co-operative vigilance by testing whether groupmates scan independently. If individuals do scan independently, then individual vigilance levels would have to be used to infer co-operation (as outlined in this paper). However, deviations from random would be more immediately suggestive. Where groupmates tend to scan synchronously (e.g. Bertram, 1980), vigilance is probably not co-operative. Synchronous scanning instead suggests a selfish response to a predator that selects non-vigilant group members (Models 2–4). However, co-operation is strongly implicated when only one group member is vigilant at a time. In this case the group's chances of detecting the predator would be considerably greater than if they were vigilant randomly or synchronously. Recently, McGowan & Woolfenden (1989) presented evidence that small family groups of Florida scrub jays show such a "sentinel" system of asynchronous vigilance. Where such a division of labor has evolved, levels of co-operative vigilance could be even lower than suggested by our models. Of course, such a sentinel system would only be advantageous to a co-operative group when the vigilance of a lone sentinel is very effective in reducing its companions' risk of predation (whenever c or p_c is close to 0).

Although our models justify skepticism that high levels of vigilance indicate co-operation in large temporary groups of nonrelatives, they more clearly emphasize the need for additional information on the consequences of vigilance in foraging groups. The expected levels of vigilance (both co-operative and selfish) are highly sensitive to the prey selection criterion of the predator and to the precise effect of an individual's vigilance on the survival of its companions.

REFERENCES

.XELROD, R. & HAMILTON, W. D. (1981). *Science, Lond.* 211, 1390–1396.
ĴERTRAM, B. C. R. (1980). *Anim. Behav.* 28, 278–286.
ĴOYD, R. & RICHERSON, P. (1988). *J. theor. Biol.* 132, 337–356.
ĴARACO, T. (1982). *Condor* 84, 101–105.
:LGAR, M. A., McKAY, H. & WOON, P. (1986). *Anim. Behav.* 34, 1892–1894.
ĴITZGIBBON, C. (1989). *Anim. Behav.* 37, 508–510.
ĴRAFEN, A. (1979). *Anim. Behav.* 27, 905–907.
ĴAMILTON, W. D. (1971). *J. theor. Biol.* 31, 295–311.
ĴART, A. & LENDREM, D. W. (1984). *Anim. Behav.* 32, 1216–1224.
ĴNMAN, A. J. & KREBS, J. R. (1987). *Trends Ecol. Evol.* 2, 31–32.
ĴENDREM, D. (1986). *Modelling in Behavioural Ecology.* London: Croom Helm.
LIMA, S. L. (1987). *J. theor. Biol.* 124, 303–316.
LIMA, S. L. (1988). *J. theor. Biol.* 132, 127–143.
LIMA, S. L. (1989). *Am. Nat.* 134, 828–834.
MAYNARD SMITH, J. (1974). *J. theor. Biol.* 47, 209–221.
MAYNARD SMITH, J. (1982). *Evolution and the Theory of Games.* Cambridge: Cambridge University Press.
MAYNARD SMITH, J. & BROWN, R. L. W. (1986). *Theor. pop. Biol.* 30, 166–179.
McGOWAN, K. J. & WOOLFENDEN, G. E. (1989). *Anim. Behav.* 37, 1000–1006.
PARKER, G. A. & HAMMERSTEIN, P. (1985). In: *Evolution: Essays in Honour of John Maynard Smith* (Greenwood, P. J., Harvey, P. H. & Slatkin, M., eds) pp. 73–94. Cambridge: Cambridge University Press.
PULLIAM, H. R. (1973). *J. theor. Biol.* 38, 419–422.
PULLIAM, H. R., PYKE, G. H. & CARACO, T. (1982). *J. theor. Biol.* 95, 89–103.
WARD, P. I. (1985). *J. theor. Biol.* 114, 383–385.

APPENDIX

Analysis of Model 3 for Groups of Three Individuals

For three individuals per group, it is necessary to specify the probability of ego dying in six different situations at the time of the attack:

p_0 = no group member is vigilant,

p_1 = ego is the only one vigilant,

p_2 = only ego and one other are vigilant,

p_3 = all three are vigilant,

p_4 = ego is the only one not vigilant,

p_5 = ego and one other are not vigilant.

The fitness of ego is given by:

$$s[1 - p_0(1-x)(1-x^*)^2 - p_1 x(1-x^*)^2 - 2p_2 xx^*(1-x^*) - p_3 xx^{*2}$$
$$- p_4(1-x)x^{*2} - 2p_5(1-x)x^*(1-x^*)].$$

The derivative of group fitness at the selfish optimum is:

$$s[2p_0(1-x)^2 + 2p_1 x(1-x) - 2p_2 x(1-2x) - 2p_3 x^2 - 2p_4 x(1-x) - 2p_5(1-x)(1-2x)].$$

If this quantity is positive, the co-operative optimum will be greater than the selfish optimum.