Negotiation may lead selfish individuals to cooperate: the example of the collective vigilance game

Etienne Sirot*

Laboratoire Ecobio, UMR CNRS 6553, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes, France

Game-theoretical models have been highly influential in behavioural ecology. However, these models generally assume that animals choose their action before observing the behaviour of their opponents while, in many natural situations, individuals in fact continuously react to the actions of others. A negotiation process then takes place and this may fundamentally influence the individual attitudes and the tendency to cooperate. Here, I use the classical model system of vigilance behaviour to demonstrate the consequences of such behavioural negotiation among selfish individuals, by predicting patterns of vigilance in a pair of animals foraging under threat of predation. I show that the game played by the animals and the resulting vigilance strategies take radically different forms, according to the way predation risk is shared in the pair. In particular, if predators choose their target at random, the prey respond by displaying moderate vigilance and taking turns scanning. By contrast, if the individual that takes flight later in an attack endures a higher risk of being targeted, vigilance increases and there is always at least one sentinel in the pair. Finally, when lagging behind its companion in fleeing from an attacker becomes extremely risky, vigilance decreases again and the animals scan simultaneously.

Keywords: antipredator behaviour; cooperation; evolutionarily stable strategies; game theory; negotiation; vigilance

1. INTRODUCTION

Evolutionary game theory is a dedicated approach of studying strategies involved in interactions among organisms and their shaping by natural selection. It has been highly influential in evolutionary biology, particularly in the field of animal behaviour [1]. The main concept of evolutionary game theory is the evolutionarily stable strategy (ESS); that is, a strategy which, once implanted in a population, may not be supplanted by any mutant strategy [2]. ESSs are used as theoretical landmarks to better understand real strategies.

In general, game-theoretical models of animal behaviour consider that each individual decides what action to take before noting its opponents’ behaviour. For example, in models of conflicts, each protagonist chooses its level of aggressiveness [2] and in models of parental care, each parent decides how much to invest in feeding young ones [3]. However, interactions between individuals often spread over long periods, allowing each individual to continuously adapt its behaviour to the attitude of others. Natural selection should then favour efficient ways to respond to the attitude of others and, thereby, efficient ways to manipulate others’ behaviour through one’s own attitude. To take this negotiation process into account, it is thus necessary to focus on evolutionarily stable responding rules, instead of considering that attitudes are fixed [4,5].

Negotiation affects the outcome of evolutionary games in a complex way. In particular, the resulting level of cooperation between individuals is rather unpredictable. Through negotiation, each individual may indeed try to exploit its partners by reducing its own effort [4], which corresponds to a defecting attitude. However, the tendency to cooperate with other cooperative individuals may also prove to be evolutionarily stable, so negotiation may promote cooperation through the process of reciprocity [5].

In groups of prey, the survival probability of each individual depends on its own vigilance towards predators and on the vigilance of its companions [6,7], which makes collective vigilance a dedicated subject of study for evolutionary game theory [8–10]. In general, scanning for predators is perceived as a cooperative attitude, as the information gleaned by scanning individuals may benefit other group members. Such collective vigilance does indeed allow members of large groups to detect predators more easily than members of small groups or isolated individuals [7,11]. However, individuals that do not detect a predator by themselves may also fail to detect the flight of a companion [12], or flee with a significant delay [13,14]. Indirect detection is thus less valuable than direct detection. Furthermore, individuals that only benefit from indirect detection may, because of an inappropriate reaction, become preferential targets for the predator [13]. Scanning for predators then becomes a defecting attitude that exposes non-vigilant companions to a higher risk of being targeted [15,16]. Collective vigilance is thus a complex and polymorphous game.

Several elements suggest that it could be the object of a negotiation process within groups of prey. Bouts of antipredator vigilance do indeed spread over long periods dedicated to their activities, such as feeding or resting, propitious for reciprocal influences between group members. In addition, individuals in groups do often observe the attitude of their neighbours ([17–20] but see [21,22]) and the information thus gleaned influences their own vigilance behaviour [20,23,24].

* Author for correspondence (sirot@univ-ubs.fr).
In the present study, I derive evolutionarily stable responding rules for antipredator vigilance within a pair of foraging animals. In other words, I consider that natural selection acts on individual responsiveness to the attitudes of other prey, instead of acting on vigilance levels only. I analyse the resulting patterns of vigilance and study to what extent selfish responding rules may lead flock companions to cooperate.

2. MODEL DESCRIPTION

I consider a pair of animals foraging under predation threat. At any moment in time, each member of the pair may either be feeding or vigilant. The reward for feeding is a gain in energy and the reward for vigilance is an increased probability of escaping, should an attack occur. A vigilance strategy is described by two probabilities, \( P_{vf} \) and \( P_{vf} \) corresponding to the probabilities of choosing to be vigilant when one’s companion is feeding and when it is vigilant, respectively. Individuals make their decisions in turn, so that each one responds to the decision immediately taken by its partner and, reciprocally, influences its next decision. The objective is to derive the evolutionarily stable values of \( P_{vf} \) and \( P_{vf} \) which govern the proportions of time spent in vigilance by both individuals and the level of overlap between their respective scanning bouts.

When individual A plays strategy \( \{ P_{vf}; P_{vf} \} \) and individual B strategy \( \{ P_{vf}; P_{vf} \} \), the resulting proportions of time during which A is vigilant and B feeding, B is vigilant and A feeding, A and B are vigilant, and A and B are feeding, determine the levels of risk endured by each individual. They are denoted by \( W_{vf}, W_{fv}, W_{vv} \) and \( W_{ff} \) respectively. To make the responding process possible, we consider time as a series of infinitely small moments when A can switch its activity which alternate with moments when B can switch. \( W_{ff} \) is the proportion of moments when A is in state i and B in state j, among the moments when A can switch its activity. Reciprocally, \( W_{ff} \) is the proportion of moments when A is in state i and B in state j, among the moments when B can switch its activity. These proportions are linked by the following transition equations, which are solved analytically:

\[
\begin{align*}
W_{vf} &= P_{vf}W_{vf} + P_{vf}W_{fv} \\
W_{fv} &= P_{fv}W_{vf} + P_{fv}W_{fv} \\
W_{vv} &= (1 - P_{vf})W_{vf} + (1 - P_{vf})W_{fv} \\
W_{ff} &= (1 - P_{vf})W_{vf} + (1 - P_{fv})W_{fv},
\end{align*}
\]

and

\[
\begin{align*}
W_{vf} &= P_{vf}W_{vf} + P_{vf}W_{fv} \\
W_{fv} &= (1 - P_{vf})W_{vf} + (1 - P_{fv})W_{fv} \\
W_{vv} &= P_{fv}W_{vf} + P_{fv}W_{fv} \\
W_{ff} &= (1 - P_{vf})W_{vf} + (1 - P_{fv})W_{fv}.
\end{align*}
\]

Finally, the overall proportion of time when A is in state i and B in state j is \( W_i = (W_{vf} + W_{fv})/2 \).

The per time unit probability of a predator attack is denoted by \( \mu \). An attacking predator is detected by each vigilant individual with probability \( D \) and is not detected by feeding individuals. Although animals feeding in a head-down posture may retain limited detection capacities [25], the assumption that they cannot detect predators does not influence the qualitative predictions of the model. If both individuals detect the predator or neither of them detects it, each individual is targeted with probability \( 1/2 \). If one individual detects and the other not, the first individual immediately flees. Its companion benefits from the information and takes flight, but suffers from an increased probability of drawing the predator’s attention [13,15]. The probability of being targeted is then \( \alpha/(1 + \alpha) \) for the detector and \( 1/(1 + \alpha) \) for the non-detector, where decreasing values of \( \alpha (0 \leq \alpha \leq 1) \) indicate that the probability of being targeted decreases for the detector and increases for its companion [16,26]. \( k_1 \) denotes the probability of being killed in an attack for a targeted detector, \( k_2 \) the probability of being killed when targeted for a non-detecting individual, when its companion has detected the predator, and \( k_3 \) the probability of being killed when targeted by an undetected predator, with \( k_1 \leq k_2 \leq k_3 \), because of imperfect collective detection. For individual A, the per time unit probability of being killed is thus \( P_{killed} = \mu \left( W_{vf}(Dk_1/2 + (1 - D)ak_1/(1 + \alpha)) + (1 - D)(Dk_2/(1 + \alpha) + (1 - D)(k_2/2) + W_{fv}(Dk_1/2 + (1 + \alpha) + (1 - D)k_2/2) + W_{vf}(Dk_1/2 + (1 + \alpha) + (1 - D)k_2/2) + W_{fv}(k_3/2) \right) \) and the probability of surviving over the whole foraging bout, of duration \( T \), is \( P_{survival} = \exp(-P_{killed}T) \). The total time spent feeding by A is \( (W_{vf} + W_{fv})T \). The reward for the possible responses to the trade-off between vigilance and feeding is measured by the product of these quantities [8,27]: \( R = P_{survival}W_{vf} + P_{killed}T \). For each set of parameters, the evolutionarily stable responding rule is the set of \( \{ P_{vf}; P_{vf} \} \) values which does better against itself than any other strategy. This means that, when adopted by virtually all members of the population, hereafter called the residents, this strategy cannot be outcompeted by any other mutant strategy.

Concurrently, the cooperative solution to the game is computed as the set of \( \{ P_{vf}; P_{vf} \} \) values that ensure maximum fitness to both animals when played by both of them [8]. This cooperative solution may not be evolutionarily stable, as it does not consider the possible arrival of mutants. It is used as a reference to estimate the level of cooperation achieved when individuals adopt the evolutionarily stable responding rules.

3. ANALYSIS

The evolutionarily stable values of \( P_{vf} \) and \( P_{vf} \) and the resulting proportion of time spent in vigilance by each individual in the pair are represented as a function of \( \alpha \) (figure 1). The expected proportion of time spent in vigilance by an isolated individual is also presented, for comparison. Individuals always scan less when in pairs than when isolated, but different types of situation emerge (figure 2).

(a) Collective vigilance as a war of attrition between reluctant sentinels

When predators select their prey at random (\( \alpha \) close to 1), an individual will never accept to be vigilant when its partner is already scanning (\( P_{vf} = 0 \); figure 1). The reason is that, in this situation, a vigilant individual offers protection to its companion. Thus, in a population where individuals tend to imitate vigilance, a defector
which would immediately resume feeding would let its companion carry alone the burden of vigilance and would finally do better than the residents. The proportions of time spent in vigilance are relatively low, because, in a population with a high propensity to initiate vigilance (high value of \( P_{\text{vig}} \)), residents would also be exploited by defectors. Collective vigilance thus takes the form of a war of attrition [2], with, as consequence, a relatively low level of individual vigilance and a high proportion of time during which no one is vigilant, in spite of an absence of overlap between individual scans (figure 2a). By avoiding simultaneous scans, individuals achieve higher fitness than if they behaved independently of one another. The coordination of vigilance that derives from negotiation thus denotes a tendency to cooperate. This tendency is limited, however, because the selection of a reluctance to scan induces lower levels of vigilance than in the cooperative scenario (figure 2b).

When \( \alpha \) takes lower values, the war of attrition over vigilance still prevails, but the cost for being the only sentinel decreases because of an increased probability of escaping for a sole detector. As a consequence, the evolutionarily stable tendency to initiate vigilance (\( P_{\text{vig}} \)) increases, leading to higher levels of vigilance and to a reduced proportion of time with no sentinel. When this tendency becomes extreme (\( P_{\text{vig}} \) close to 1), a sentinel is almost always present in the pair. The absence of overlap between scans leads to perfect vigilance coordination, each individual ensuring half of the vigilance time (figure 2b). Interestingly, perfect coordination prevails for a certain range of values for \( \alpha \) (figure 1), but still denotes a limited tendency to cooperate, as the individuals are less vigilant than in the cooperative scenario (figure 2b).

(b) Overbidding for vigilance between selfish sentinels

For even lower values of \( \alpha \), being vigilant tends to concentrate predator attacks on the companion. Vigilance thus becomes a defecting attitude. The war of attrition over vigilance does not exist any more and, as a consequence, there is always at least one sentinel in the pair. At the same time, each individual starts to imitate the vigilance of its companion (\( P_{\text{vig}} > 0 \)), leading to a further increase in vigilance and some overlap between the scans of the two individuals (figure 2c). The reason is that, in a population with no tendency to imitate vigilance, a mutant inclined to imitate vigilance would manipulate the residents. This mutant would indeed often copy the vigilance of its companion, then become the only sentinel when this companion resumes feeding, thereby achieving a very high chance of survival. Interestingly, the evolutionarily stable responding rule, driven by a tendency to avoid letting the partner be the sole sentinel, now leads to higher levels of vigilance than the cooperative scenario (figure 2c).

The tendency to imitate vigilance further rises when \( \alpha \) decreases, leading to ever increasing levels of vigilance, until the evolutionarily stable responding rules suddenly switch to the diametrically opposite situation where individuals have both a very low tendency to initiate vigilance (\( P_{\text{vig}} \) close to 0) and a very high tendency to copy vigilance (\( P_{\text{vig}} \) close to 1). Such behaviour results in an alternation of long periods of simultaneous feeding and long periods of simultaneous scanning (figure 2d). Concurrently, the individual level of vigilance abruptly declines (figure 1). The reason for this switch is that an ever increasing tendency to imitate vigilance, together with a total tendency to initiate vigilance, progressively leads both individuals to forsake feeding. In a population displaying such extreme vigilance behaviour, a mutant reluctant to initiate vigilance, but inclined to imitate it, would finally do better than the residents by dedicating more time to feeding and limiting the time when it feeds while its companions are vigilant. Ultimately, the evolutionarily stable responding rule has a very low tendency to initiate vigilance and a very high tendency to copy it, which results in a moderate level of vigilance for both individuals and a high proportion of time without any sentinel (figure 2d). The level of vigilance further declines when \( \alpha \) tends towards 0 because the probability of being killed in an attack rises when both individuals are vigilant.
Parameter values are the same as figure 1. To detect the predator, when its companion has detected it. Thus, they denote a cooperative attitude. The cooperative scenario also predicts this switch in behaviour. Moreover, the evolutionarily stable responding rule now matches the cooperative solution (figure 2d). The reduced level of individual vigilance and the total synchronization of activities indirectly engendered by negotiation do indeed reduce the level of risk endured by the companion. Thus, they denote a cooperative attitude.

(c) Influence of collective detection and predation risk
In the preceding sections, I show how vigilance patterns in the pair of prey switch from coordination to synchronization, as the tendency of predators to preferentially target non-detectors increases. Increasing the probability of being killed for a targeted non-detector, when its companion has detected the predator (i.e. parameter $k_2$), leads to similar results. Low values of $k_2$, corresponding to efficient information transfer between a detector and a non-detector, do indeed induce vigilance coordination, whereas high values of $k_2$, corresponding to inefficient collective detection, make vigilance a defecting attitude and induce synchronization.

By contrast, increasing the overall level of predation risk, $\mu$, leads to higher levels of individual vigilance but does not modify the switching conditions between coordination and synchronization.

Thus, the expected level of individual vigilance increases with the level of risk endured, while temporal patterns of vigilance (i.e. coordination or synchronization) essentially depend on the parameters that govern risk-sharing in the pair.

4. DISCUSSION
When animals in a group continuously interact with each other, a process of negotiation naturally takes place, whereby each individual responds to the attitude of its companions and influences them through its own behaviour [4]. Here, I use a game-theoretic model to study how such responding rules can shape patterns of vigilance within a pair of foraging prey.

Evolutionarily stable responding rules produce lower levels of individual vigilance in pairs than in isolated individuals. Although adapting the present approach to larger groups would involve important adjustments, we can expect negotiation to also operate in such groups, between each individual and the neighbours with which it interacts [28]. The propensity of each individual to be vigilant does indeed depend on its proportion of vigilant neighbours [20,23,24], so the individual may, in turn, influence the behaviour of its companions by modifying its own attitude.

In general, the model reveals subtle interactions between the two types of decision involved in antipredator vigilance, namely, the proportion of time dedicated to vigilance by each individual and the amount of temporal overlap between individual scanning bouts. A demonstrative example is the situation where the individual that takes flight after its companion in an attack endures a higher risk of being targeted by the predator. When such conditions prevail, each individual naturally tends to become vigilant when its companion is already scanning, to avoid straggling behind in an attack. We described this effect in a preceding theoretical study that ignored negotiation and predicted that such copying tendency, which engenders long periods of simultaneous scanning, would make the level of individual vigilance rise [16]. By contrast, the present model does not predict an increase in vigilance in such conditions. Instead, it shows that, when stragglers endure a higher chance of being targeted, the tendency to imitate the vigilance of the others should be balanced by a strongly reduced tendency to initiate vigilance. Through negotiation, group members should thus be able to maintain moderate levels of vigilance, even when conditions make them inclined to imitate the vigilance of their companions.

This point is of particular importance, because significant tendencies for vigilance synchronization have been demonstrated in a wide range of mammalian and avian prey species (e.g. rodents [29]; marsupials [30]; ungulates

Figure 2. Proportions of time when 0, 1 or 2 individuals are vigilant in the pair. The figure presents the proportions of time when 0, 1 or 2 individuals in the pair are vigilant, in the negotiated scenario (black bars) and in the cooperative scenario (white bars). Parameter $\alpha$ takes decreasing values over panels (a–d), which indicates an increasing probability of being targeted in an attack for an individual that failed to detect the predator, when its companion has detected it. Parameter values are the same as figure 1.

Proc. R. Soc. B
varying with the proximity of such cover. So should thus stimulate field studies that simultaneously launched influences both predator targeting behaviour the distance from obstructive cover from which attacks are

ator selects its target, with respect to departures spread out lance synchronization, and may contribute to explain why sharing between detectors and non-detectors is thus likely, with important disadvantage of living in groups for prey [35].

contribute to limit these effects, thereby countering an cohesiveness [35,36]. Negotiation over vigilance could thus produce such effects.

Moreover, periods of alertness resulting from vigilance contagion can facilitate false alarms and superfluous flights, through informational cascade effects, with important consequences for the energy budget of the animals and for group cohesiveness [35,36]. Negotiation over vigilance could thus contribute to limit these effects, thereby countering an important disadvantage of living in groups for prey [35].

In the wild, the hasty departure of a few individuals does not always trigger collective flight [21,37,38] and, even when it does, the delay between the first and the last departures is sufficient to influence individual chance of escape, should the threat be real [13,14]. Unequal risk-sharing between detectors and non-detectors is thus likely, which, according to the present model, should favour vigilance synchronization, and may contribute to explain why this pattern is so common. However, the moment the predator selects its target, with respect to departures spread out over time, varies with ecological conditions. In particular, the distance from obstructive cover from which attacks are launched influences both predator targeting behaviour and risk perception by prey [39]. The present model should thus stimulate field studies that simultaneously measure how vigilance levels and coordination patterns vary with the proximity of such cover.

I thank Judith Christie, Innes Cuthill, Sasha Dall, Vlastimil Krivan, Graeme Ruxton and two reviewers for helpful comments on previous versions of the manuscript.

REFERENCES

25 Lima, S. L. & Bednekoff, P. A. 1999 Back to the basics of antipredatory vigilance: can nonvigilant animals detect


