

Biological modelling / Biomodélisation

Cooperation strategies, signals and symbiosis

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Abstract

The authors of models concerning cooperation found an interesting application point in mutualism and symbiosis. Phenomena which are to be found in symbiosis are integrated by the various models in relation to the ‘Prisoner’s Dilemma’: ‘cost–benefit’ ratio components, signals, neighbourhood interaction or reciprocity. Reciprocal altruism is found in symbiosis, but others strategies seem more to reflect human societies, where choice is unrestricted. It is very difficult to give a value to cost and benefit equilibriums. The biological environment interferes and a model based on a dominant strategy is often limited or insufficient to report on the living system’s evolution. **To cite this article:** *O. Perru, C. R. Biologies 329 (2006).*

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Résumé

Stratégies de coopération, signaux et symbiose. Les auteurs des modèles de coopération ont trouvé un point d’application intéressant dans le mutualisme et la symbiose. Des phénomènes que l’on retrouve dans les symbioses sont intégrés par les divers modèles en rapport avec le « dilemme du prisonnier » : composantes du rapport « coût–bénéfice », signaux, interactions de voisinage ou réciprocité. L’altruisme réciproque renvoie à l’évolution d’une symbiose, mais d’autres stratégies semblent refléter davantage les sociétés humaines où le choix est libre. Il demeure difficile de donner une valeur à des équilibres « coût–bénéfice ». L’environnement biologique interfère et ces modèles sont souvent limités ou insuffisants pour rendre compte de l’évolution d’un système vivant. **Pour citer cet article :** *O. Perru, C. R. Biologies 329 (2006).*

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1. Introduction

Models related to cooperation and based on successive variations of the ‘Prisoner’s Dilemma’ (IPD) were studied intensely between 1980–1990, in biology and economy, and more particularly in human and animal

societies. Their authors occasionally touched on the relationship between these models and mutualism or symbiosis. Some cases of symbiosis, where the apparently mutual initial benefit tends towards unidirectionality, may represent an illustration of one of these strategies. However, the application of IPD models to biological phenomena remains uncertain for reasons that we are going to speak about. Signalisation has also been an issue of theoretical considerations; it implies that the

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other player has recognised the adversary's game in order to adapt its strategy. However, in most strategic cooperation models, this remains implicit: often the model does not take the signal into account.

Axelrod and Hamilton speak about both cooperation and exploitation as sources of payoffs in mutualistic systems. Payoffs are measured by the effect of interactions between partners concerning fitness (survival and fecundity). Therefore, it is almost like a game (the famous 'Prisoner's Dilemma'), in which strategies of cooperation or non-cooperation with the other proponent alternate: "The problem is that while an individual can benefit from mutual cooperation, each one can also do better by exploiting the cooperative efforts of others." [1] The dilemma lies in this choice. Christopher Stephens criticises the position of Axelrod and Hamilton on this point, because although cases exist where it is more beneficial for one partner to exploit the other than to cooperate, cases may also exist where the best strategy for both is an alternating exploitation of the other's possibilities [2]. Stephens considers this strategy as a form of cooperation.

The complexity of the modelling already stems from the fact that in theory, the two partners' behaviour is never predetermined; another unknown factor concerns the recognition of this behaviour, i.e. concerning its signalisation. Each partner must make its behaviour known through signs, of which the modelling is only a remote echo of the biological phenomena. Therefore, stability and recognition of cooperation would be two essential conditions.

In the field of symbiosis, Axelrod and Hamilton quote the example of *Rhizobium*: bacteria can live freely in the soil or in legume nodules, which they supply with nitrogen that they have fixed. The authors write: "In the light of theory to follow, it would be interesting to know whether these parasitised legumes are perhaps less beneficial to free living *Rhizobium* in the surrounding soil than are those in which the full symbiosis is established." [3] In other words, the authors are querying whether, from the bacteria's point of view, a beneficial effect results from being placed inside the plant rather than in the neighbouring environment, even close by. Yet, the reply to this question is not settled; the legume may seem to be a parasite of the *Rhizobium* bacteria, it controls its development and uses it as a supplier of organic nitrogen. Furthermore, the 'Prisoner's Dilemma' does not only make an issue of interest-linked relationships, but also and above all is concerned with the relationship's establishment and continuity in time, this is what interests biologists and economists. If the establishment of cooperation based on reciprocity is never

obvious, when this exists, it is highly probable that it will last: "Once cooperation based upon reciprocity is established, no player can do any better than to cooperate as well, provided the chance for future interaction, w , is high enough." [4] Therefore, from a cooperation point of view, symbiosis is a phenomenon that could, *in all probability*, give rise to this type of modelling.

2. Cooperation strategies and biological phenomena

Going back to the mathematical point of view of the cooperation problem, in so far as this can participate in biological applications; the 'Prisoner's Dilemma' was clarified in a spectacular article published in *Science*, in March 1981, by Robert Axelrod and William D. Hamilton. Its interest is to demonstrate that, in certain hypotheses, cooperation strategies appear more beneficial in the long term than purely 'egoistical' ones. In the 1980s, the theory of selection of groups seemed to fade away in favour of the idea of reciprocal altruism as a motor for relationships between living beings. This at least corresponds to Hamilton's opinion and underlines the fact that the 'Prisoner's Dilemma' takes root in the theory of altruistic genes. Another origin of this model is Robert Axelrod's reflection in political sciences, which may bring us to be wary of certain anthropomorphism in the application of the model to interaction between living 'non-human' beings. Initially, in economical and political sciences, the authors of strategies are supposed to be free and autonomous, conscious of their choices. Axelrod and Hamilton quote symbioses as examples of the field of application of cooperation strategies, but without really defining a distinction between symbiosis and mutualism, nor between the various types of symbiosis. Thus, in this model, relationships resulting from symbiosis or the various relating genotypic and phenotypic parameters are not really taken into account. We can simply establish a connection between this model and biological parameters (such as the fitness of one 'player' creating the probability of descendants, the contribution of the symbiosis to the host would be evaluated in terms of nutrition). The players' winnings are expressed in abstract values, R (recompense for a mutual cooperation, $R = 3$), T (winnings of the defecting player – the egoist – when the other player cooperates, $T = 5$), P (winnings of the two partners when they both refuse to cooperate, $P = 1$), S (salary of the cooperating player when the other player defects, $S = 0$). Therefore, the basic hypotheses of the dilemma are $T > R > P > S$ and $2R > T + S$. If the egoist's winnings are the highest, on the

Table 1
Axelrod and Hamilton's model

Situation	Winnings	Strategies of the players
Mutual Cooperation (C)	$R = 3$ 'Reward' (for the two partners)	'Always Cooperate' and 'Tit for Tat' (if opponent's prior play is C)
A player defects (D), the other cooperates (C)	$T = 5$ 'Temptation' (for the defector) $S = 0$ (for the cooperator)	'Always Defect' (one player) 'Always Cooperate' (the other) or 'Tit for Tat' (decision to defect if the opponent has defected in its precedent move)
Mutual Defection (D)	$P = 1$ 'Punishment' (for the two partners)	'Always Defect' and 'Tit for Tat' (if opponent's prior play is C)

contrary, the sum of the cooperating players' winnings are higher than $T + S$, sum of the winnings obtained in a unilateral exploitation relationship. These fundamental hypotheses have been taken up and discussed by nearly all authors. Initially the dilemma appears to be between R and P : should one player cooperate, hoping that, if the other player cooperates, the winnings obtained will be higher than if both players do not cooperate? In this type of issue that was asked in the 1980s, it was a question of proving that even if the initial theories favoured the 'egoist', cooperating behaviour tends to spread when interactions are repeated between the same proponents and the number of interactions is not necessarily known beforehand. Axelrod and Hamilton define the establishment of the 'Tit for Tat' strategy if, and only if, $w \geq (T - R)/(R - S)$, w representing the probability of future interaction. On a biological level, knowledge of biological interactions implies the necessity of a signal, of the mediation that makes interaction 'known' (cf. Table 1).

Signal may be simple exchanged information between the two partners. This information means a defection or a cooperation. It produces a reaction in the partner's organism. For instance, in the weevil *Sitophilus orizae*, Heddi has demonstrated that enzymatic activities are the highest on mitochondria isolated from symbiotic strains [5]. Primary endosymbiont increases mitochondrial energetic metabolism by a nutritional way. So, it improves the physiological traits of the insect. This improvement signals benefits obtained from cooperation. However, we find it difficult to define this strategy as 'Tit for Tat'. As we shall see later, the reciprocity between weevils and bacteria is uncertain. Weevils may exploit their symbionts.

In 1964, Hamilton suggested that altruistic behaviour was a type of cooperation, that this could be observed

between similar beings [6]. Thus, the selection of an 'altruistic' gene would affect all similar beings which possess this gene. The theory of reciprocal altruism is based on the 'Prisoner's Dilemma' and particularly on the TFT strategy (in the 'Tit for Tat' strategy, one plays what the partner played in the previous round, either $C =$ cooperation, or $D =$ defect). For Axelrod and Hamilton, this strategy is stable from an evolutionary point of view. Concerning this, Martin A. Nowak and Karl Sigmund wrote a remarkable article in 1993 called *Chaos and the evolution of cooperation* [7]. The authors write that the TFT strategy really consists in repeating what the adversary played in its preceding move. "This led Axelrod and Hamilton to use the IPD for explaining the evolution of cooperation in biological interactions on the basis of reciprocity." [8] In fact, the problem of TFT strategy applicability remains. The authors assert: "While reciprocal interactions abound in nature, it is usually difficult to find clear-cut empirical evidence for the implementation of the TFT strategy." [9] What is interesting here is that the authors acknowledge that the model is fragile in a biological environment. Indeed, it takes interactions between 'players' into account, but not the environment. Yet, the biological environment may provoke errors. A recorded defection may be accidental and result from an environmental factor, the presence of a predator, etc., but, depending on the model it risks creating a series of 'reprisals'. Therefore 'vulnerability to error' exists due to the biological environment which is not reproduced in the simulation conditions of a computer game. For example, environmental disruptions may provoke different responses. At the end of the 19th century, we already knew that marine invertebrates' response to symbiosis differed, depending on whether surroundings contain the necessary nutritional elements or not. Some animals become non-symbiotic in a rich environment and receive symbionts when the nutritional surroundings do not contain the elements they need. In this case, the environment appears as a determining factor of the cooperation relationship between host and symbiont. Multiple control mechanisms also exist, which may result in rejecting the symbiont. In this situation, how should the reciprocal cooperation model be expressed – which in fact is a model of mutual benefit and stabilisation – in biological realities which rarely guarantee mutual benefit of egalitarian and fair anthropomorphic modes. In the case of mutualism, the mutual benefit defines the nature of the biological phenomena, but in the case of symbiosis, this benefit may be very unequal, or even almost unidirectional. Then, the model which simulates the higher total advantage for the two cooperating partners is not necessarily adapted.

We may think that in certain symbiosis relationships, the advantage of one of the partners wins: resulting in discussions still going on today concerning the difficulty of specifying a limit between ‘mutualistic’ symbiosis, symbiosis that cannot be strictly considered as mutualistic, and parasitism. For example, a symbiont that has a transovarial transmission would be expected to shift from mutualism to parasitism if conditions change in any way. In *Hydra vulgaris* and *Hydra attenuata*, algal symbionts are transmitted by an infective way (horizontally). Pathological symptoms are a sign of a definite parasitism by the algae. This signal produces a reaction from the animal: it may reject the symbiont. Between algae and *Hydra vulgaris*, impermanence of association destabilises symbiosis. On the opposite side, specialised insect endosymbionts are able to circumvent host defences [10]. So, they give a signal of cooperation and stabilise the symbiosis.

A persistent problem found in nature is the coexistence of cooperation and exploitation, notably in viruses and bacteria. In an article from 1999 in *La Recherche*, Nowak and Sigmund give the example of two viruses, the phages $\Phi H2$ and $\Phi 6$ [11]. The virulence of these phages can be measured with a genetic marker. The phage $\Phi 6$, which produces more proteins, cooperates with the host bacteria and therefore enables the other phage, $\Phi H2$ (non-cooperating) to benefit from a higher virulence level than cooperating phages: $T > R$. In other words, the benefit of the ‘egoist’ (T) then becomes higher than the benefit collected by the cooperating phage. In this position, “the mutant $\Phi H2$ only appears when the infection rate is high, i.e. when the host bacterium is invaded by numerous phages” [12]. Thus, exploitation only pays off for the mutant virus $\Phi H2$ if cooperation existed between the bacterium and the phage $\Phi 6$ previously. Therefore the dominating form is the cooperating virus in so far as not only does it favour the development of the exploiting one, but also the durability of its own clone. It becomes indispensable. The exploiter’s strategy pays off better in the short term, but it presupposes the durability of a population of beings that cooperate and its biological description. Can we rely on the same type of reflection for endosymbionts? Concerning vitaminised nutrition, the *Sitophilus Oryzae* weevil exploits the symbiotic bacterium, which cooperates and depends on the weevil. But there is no doubt that the total weevil population depends on the presence of symbionts and an initial cooperation between weevils and bacteria.

Axelrod and Hamilton make some interesting remarks about symbiotic bacteria. These bacteria are very sensitive to certain factors of their environment. There-

fore they can reply differently to surrounding organisms, they may implement strategies that put them in contact with certain organisms. This behaviour is inherited and influences each partner’s fitness and can indeed be noticed in endosymbiosis: depending on the host’s reactions (cooperation, defence, control, exploitation...), we can consider that a series of strategies exists, which results in the establishment of stable interactions. The initial model of Axelrod and Hamilton admits that symbiotic bacteria such as *Rhizobium* may gain less benefit from legumes than those that live in the surrounding soil [13]. This remark is very interesting in so far as, in general, we tend to look at the benefit of symbiosis for the plant and not for the bacteria. The model foresees a symbiosis cost for both partners, but does not indicate how life stability is initially established. It simply lists the symbiosis cases in which the association is stable, the *Chlorohydra viridissima* hydra living in symbiosis with green alga for example... The paradigm of the ‘Prisoner’s Dilemma’ implies that in return for a minimum fitness gain, it is not unrealistic that biological individuals establish cooperation strategies in order to survive.

3. Mathematical and biological models for cooperation

3.1. The works of Nowak and Sigmund: the various possible strategies and their evolution

In *Chaos and the evolution of cooperation* (1993), Nowak and Sigmund demonstrate that the coexistence of strategies in a population can lead to chaos, resulting in the necessity for evolution to favour one or two strategies. Sixteen possible strategies exist, from which we will retain: ‘Always defect’, ‘Always cooperate’, ‘Tit for Tat’ or again ‘Generous TFT’, ‘GRIM’, or ‘PAVLOV’. ‘Generous TFT’ is a strategy that consists in cooperating with a certain probability when the adversary defects. In the ‘GRIM’ strategy, after a single defection by the adversary, cooperation no longer occurs. When the algal symbionts cause pathological symptoms in hydras, they may be rejected: It is a case of ‘GRIM’ strategy. Paradoxically, this strategy is stable: the host chooses to keep or not its symbionts. Cooperation may occur with other symbiotic individuals. In the ‘PAVLOV’ strategy, “players cooperate each time they choose the same action as in the previous move.” [14] These strategies are defined by probabilities of cooperation in four different situations: after receiving the mutual cooperation salary R , one cooperates with a probability p_1 ; after receiving the partner’s defection salary S , one cooperates with a

Table 2
Nowak and Sigmund's model (cf. [14])

Previous round			Strategies			
Last move	Opponent's move	Winnings	Always cooperate	Always defect	TFT	PAVLOV
C	C	$R = 3$	C	D	C	C
C	D	$S = 0$	C	D	D	D
D	C	$T = 5$	C	D	C	D
D	D	$P = 1$	C	D	D	C

probability p_2 ; after receiving the salary further to one's own defection T , one cooperates with the probability p_3 ; after receiving salary further to both partners' defection P , one cooperates with the probability p_4 . Obviously, the $T > R > P > S$ rule is maintained. The game implies an iterative process described in this article [15] (cf. Table 2).

The simulations' conclusion is stability of the strategies 'Always defect' or 'GRIM', in which non-cooperation predominates. The coexistence of the other strategies leads to chaos. But the authors underline the advantage of the 'Generous TFT' strategy, where cooperation exists even if the partner defects, with the probability $q = \min\{1 - (T - R)/(R - S), (R - P)/(T - P)\}$. The formula demonstrates that this strategy takes into account the importance of the difference in payoff between the four situations. According to this formula, small relative differences between R and T and between R and P will stimulate cooperation. The strategy amounts to the integration of a cost–benefit ratio and therefore seems adapted on a biological level (at least as concerns simulation). In the scope of symbiosis, this would signify a slight discrepancy between a mutualistic type of cooperation situation between the two partners, and a more unidirectional or autonomous situation for each partner, in relation to each other. The relative advantage drawn from the reciprocal relationship is hardly distinguishable from total autonomy interests or from a unidirectional benefit for one of the partners. Therefore, it is a question of a strategy that inaugurates a symbiotic relationship. When the symbiont enters into contact with the host, the discrepancies in autonomy for each partner do not clearly appear as yet; a relative reciprocity in the advantages obtained through symbiosis may exist, and the host's search for optimal exploitation of the symbiont's capacities is not yet obvious. This should be confirmed by examples, but in all events, the symbiosis evolves in the same way as these strategies. The GTFT strategy is an initiation strategy for a cooperating relationship. One could say that one of the partners is 'flirting' with the other, which supposes a signalisa-

tion strategy of advantages. It is not absurd to imagine its application to symbiosis cases known by biologists, but the correspondences between simulated strategy and biological behaviour would have to be clearly specified for each form of symbiosis.

What is Nowak and Sigmund's opinion? Their conclusion is that "this success of GTFT is surprising because 'Always defect' and 'GRIM' are still the only evolutionarily stable strategies, and GTFT can be invaded by 'Always Cooperate' [...]. It seems that very small repeated invasion attempts can twist this system from defection to cooperation" [16]. The theoretical results obtained in 1993 leave us in doubt: does cooperation have a chance in this simulation of evolution in so far as the systems can be chaotic, and where cooperating populations (TFT, 'Always cooperate' or GTFT) meet with a certain success, but with no stability of evolution? Despite the sophistication of these simulations, uncertainty remains concerning the environment's role in biological applications. From a strategic point of view, there are several ways of interpreting complexity in symbiotic interactions. In insect intracellular symbionts, the TFT strategy seems to be used in the control of symbiont populations. Symbionts depend on the host's genome for their reproduction (activation) but they induce production of bacteriocytes by specific signals. These intracellular bacteria live sheltered from environmental fluctuations within their host but they always synthesise vitamins for the host [17]. Is it the strategy 'Tit for Tat' or 'Always cooperate'? It seems difficult to model.

The same authors endeavoured to reply in later texts. In *The arithmetics of mutual aid*, Nowak, May and Sigmund recall the book by the anarchist Kropotkin *Mutual aid* (1902) [18]. This book was intended to fight and disprove social Darwinism of the end of the 19th century and the exaggeration of 'struggle for life'. At the time, this argument was already directly in line with biologists and ecologists who had recorded the fundamental character of mutualism in animal societies and symbiosis. "But at the same time, the ubiquity of cooperation seems to have become ever more paradoxical. The Russian anarchist has failed to see how threatened it is by exploitation. What prevents mutualists from turning into parasites?" [19] Here, we are at the heart of the symbiosis issue: one of the partners, the host for example, may play at cooperating for several generations, and then non-cooperating behaviour may turn out to be more beneficial. This is how we could describe the transformation of cooperation into exploitation by the host's progressive control of the symbiont. The ambiguity of the game is that the alternative to cooperation, defection, does not have its own signification content:

we can talk about either unidirectional benefit or autonomisation. In actual fact, the host may not cooperate, but control, dominate the symbiont. Therefore defection would encompass multiple forms of exploitation which may be more or less intense. Modelling the complexity of ‘host–symbiont’ relationships, their costs and benefits, appears difficult in these strategies. We could imagine that these strategies throw light on a prior adaptation of each partner in relation to the other.

Nowak et al. (1995) describe those strategies that are supposed to work best in nature and human societies, notably ‘GTFT’ and ‘PAVLOV’. But they specify: “Furthermore, the strategies discussed will only work if benefits from future encounters are not significantly discounted as compared with present. Again this expectation may be reasonable for many of the activities humans conduct, but for most simple organisms delayed payoffs in the form of future reproductive success may count for little: if life is short and unpredictable, there is scant evolutionary pressure to make long-term investments.” [20] Therefore, it is difficult to model cooperation without further specifying what it provides. Here, we come up against the problem of predictability. The difficulty of integrating benefit in the model and the multiplicity of interactions (environment, other individuals, etc.) makes generalisation of the ‘IPD’ model difficult for cooperation in life phenomena. On a biological level, how the various signals can participate in system regulation remains to be modelled. This does not work in the same way in animal society or association relationships. Nowak, May and Sigmund queried the realism of the cooperation model: “But what of the creatures, such as many invertebrates, that seem to exhibit forms of reciprocal cooperation, even though they often cannot recognise individual players or remember their actions?” [21] In other words, what happens when we cannot call on a minimum amount of conscience to simulate cooperation? Do biological regulation signals exist, enabling cooperation to continue? In the case of endocytobiosis, can we imagine that cooperation implies, in each partner, a genetic possibility of interaction between species, a sort of prior adaptation? In this type of subject and from a philosophical point of view, we could perhaps formulate a very Bergsonian question concerning the various forms of conscience from animals to humans and their incidence on the variety of cooperation forms.

The solution suggested by Nowak et al. (1995) for modelling and universalising cooperation is cellular automats. Players occupy fixed positions and only interact with their closest neighbours [22]. In this way, games organised in space can simulate biological cooperating

relationships, themselves situated and particularised in space, without calling on memory or conscience. This is the case in the neighbourhood geographical structure imagined by Albin and Foley; this neighbourhood acts as a launch signal [23]. The resemblance with Conway’s game of life is clear. However, “it may well be that the results generated by any one of our spatial versions of the Prisoner’s Dilemma – be they irregular patterns or symmetrical Persian carpets – are intrinsically unpredictable and chaotic in the sense that no algorithm can possibly predict what will occur.” [24]

3.2. Roberts and Sherratt’s models: reciprocal altruism, resistance to exploitation and IPD

Reciprocal altruism cooperation was introduced by Gilbert Roberts and Thomas Sherratt by simulation of the ‘Raise the stakes’ strategy [25]. In fact, it’s a case of making the consented cooperating investment or cost higher at each round in the game. Timothy Killingback and Michaël Doebeli consider that a population using the RTS strategy and which is progressively invaded by new mutants using other strategies is condemned to evolve towards a non-cooperation strategy [26]. Therefore, selection would always act for the reduction of initial investment values in ‘RTS’ populations. In reality, Sherratt and Roberts’ reply emphasises the interpretation of the RTS strategy. The initially proposed strategy is discontinuous; we watch its performance in the face of given strategies in specific time periods, whereas Killingback and Doebeli’s criticism concerns the continuous action of natural selection through time. Thus, it is difficult to imagine an increase in mutualistic costs and benefits in a continuous time model, if only because resources are not indefinite [27]. In the RTS strategy, a protagonist consents to cooperate at a higher cost in the next round, but in so far as the investment consented by its partner was also higher than its own in the previous round. We always suppose that these investments are signalled to the partner.

Therefore this strategy aims to establish or re-establish cooperating relationships. We can imagine that illustrations exist in nature. Forms of symbiosis exist in which, during evolution, both partners have consented to higher and higher costs, going as far their species loss of autonomy. Generally, the cost of establishing a cooperation relationship is often high for each partner. The RTS model concerns a discontinuous strategy that ends when the cooperation relationship is established. However, we cannot exclude the appearance of a mutant that has a different strategy, i.e. whose action results in the establishment of a less costly coopera-

tion relationship. In cases of endosymbiosis, sometimes in the same species or type of host, diversified forms of symbionts exist for which the ‘cost’ is more or less high. Once again, the stumbling block here is the difficulty of the abstraction of what the costs and payoffs committed in such and such cooperation represent biologically. However, Sherratt and Roberts write: “Our approach adds a new dimension to this work by examining not just whether cooperation will occur, but how cooperative individuals will be.” [28] (Cf. Table 3.) Sherratt and Roberts present the necessity of modifying the initial conditions presented in the classical form of the ‘Prisoner’s Dilemma’. Notably, the cooperation choice supposes distinct forms of altruism; the choice of non-cooperation is not purely defection. This may also imply, in anthropomorphic language, a form of ‘deceit’ that consists in investing less than the partner. In this way, these authors have explored various possible forms of cooperation, their emergence and resistance to occupation. In the same way, Brauchli and his collaborators introduced a condition of spatial structure in the ‘Tit for Tat’ strategy [29]. According to these authors, inspired by Nowak and May’s works [30], cooperation behaviour may imply stability: “A second situation where cooperative behaviour can be evolutionary stable are models that introduce some kind of spatial structure, so that within a population all interactions are local.” [31] Albin and Foley also speak of neighbouring interactions. This is indeed what happens in the case of insect endocytobiosis. Interactions between bacteria and eukaryotic cells are neighbouring interactions. The same authors affirm that: “The main effect of spatial structures is that in structured populations cooperative strategies can build clusters in which the benefits of mutual cooperation can outweigh losses against defectors.” [32] In the issue that concerns us, such an affirmation remains vague, it seems to be better adapted to problems concerning population dynamics within animal societies in which individuals are supposed to ‘cooperate’ (such as bees or various insect societies).

In the model proposed by Sherratt and Roberts, genes code for altruistic behaviour that is expressed by a cost in favour of the partner. In mathematical modelling, these genes are expressed as ‘generosity values’ that represent this beneficial opening towards the partner. Certain genes sometimes code at a complete loss in favour of the partner, but others code under the condition of an already existent partnership. This would seem to pertinently retranscribe what occurs in endocytobiosis where the symbiont’s genes code for the host’s nutrition, but also react to its behaviour (which once again supposes the mediation of a signal). It is indeed

Table 3
Robert and Sherratt’s model (cf. [28])

Situation of partners	Strategy
First round	Individual’s opening generosity to any partner Investment at some minimal level
Next rounds	1, Individual’s response encountered once before, if the partner has previously cooperated at a given cost c (0–7). 2, General response if individual has recently cooperated with its partner at a given cost c (0–7). The same condition is required from the partner. Each cost c is translated into benefits b to the partner with $b = kc$.
Results	Strategies of cooperation arise very quickly.
Cost effectiveness	“Optimal level of investment depends on the precise ratio of benefits to costs.” (Roberts and Sherratt, 1998, p. 425).
Interaction length	“Generosity increases with the number of rounds.” “Meeting again makes greater cooperative investment possible.” (Roberts and Sherratt, 1998, p. 425).

the question of simulation of interactions that is asked here. The conclusion imposed on the authors at the end of the algorithm is that: “The optimal level of investment depends on the precise ratio of benefits to costs involved in altruistic acts (the cost effectiveness of altruism).” [33] Admittedly, but it is not very clear how this type of calculation may be applied to our problem. The activation of a gene which is beneficial to the host is certainly a cost, but the biologist is more often incapable of evaluating the ‘cost–benefit’ ratio that the authors speak of. This remains an algorithm in which the simulation of interactions depends on conditions set down initially and is slightly disconnected from the biological knowledge in play. This type of algorithm is not really a model, because it does not integrate parameters referring to a sufficient number of biological variables. In addition, we can suppose that at each stage an autonomous strategy of each partner occurs. Yet, in symbiosis, the phenomenon is much more complex; the symbiont loses its autonomy progressively. Consequently the notion of ‘resistance to exploitation’ is much more difficult to apply in this cooperation equilibrium.

3.3. Mediation of the signal, the neighbourhood, relation to environment

In recent texts, the question of signal or sign mediation in launching cooperation has been broached. As seen by Lotem et al., unconditional altruism is a sign of quality, bringing social acknowledgement and prestige to its author [34]. It is a question of someone’s rep-

utation, in so far as it affects a significant action that signals its personal qualities. This relation between a high-quality subject and development of altruistic activity supposes sign mediation. “If the image, or the reputation, gained by employing certain strategies during reciprocal interactions can also entail addictive signalling benefits due to their effect in other social contexts, it is almost inevitable that these benefits play some part in shaping these cooperative strategies.” [35]

The theory that needs to be validated is that the information concerning the fortunate consequences of reciprocal altruism conditions the formation of cooperation strategies. . . that are then neither disinterested nor altruistic. In human societies, the person’s description or reputation enables the selection of this person in a strategy of reciprocal interest exchanges. Reputation effects are analysable in sociology; analogically, mediation cooperation signals exist in biology. The model’s mathematical expression consists in introducing the supplementary gains, resulting from the description, in the ‘cost–benefit’ matrix. Then we can unroll an evolving simulation made up of three types, which are unconditional altruists, ‘TFT’ altruists, and ‘defectors’, by introducing parameters such as ‘the frequency of low-quality individuals’ (how should this be measured?), or the probability $1 - z$, for a ‘TFT’ individual to help a ‘D’ individual (by mistake, because normally he would not help him). Equilibrium is first obtained with ‘UAH’ individuals (Unconditional Altruism High quality). Is this liberal schema, incorporating a form of altruism in the personal career and in an individual’s reputation, to be reserved to the study of human behaviour? To illustrate cooperation relationships, the biological application of such a schema would appear to lead us to group selection mechanisms. In an insect society, altruists’ behaviour is selected by natural selection, in so far as these are useful to the society’s prosperity, even if they are individually disadvantageous. This issue recurs in the discussion. As a whole, the schema is insufficient to report on relationships in animal societies, in so far as “for social animals who know that numerous opportunities exist to help others, it is highly improbable that all the animals are able to support the cost generated by permanently contributing assistance.” The schema is elitist: the individual selected as ‘unconditional altruist’ is supposed to “permanently invest more in altruism”. Lastly, “the investment in altruism would be similar to an investment in publicity.” [36] The fact of signalling the positive consequences of altruism therefore appears adapted to the description of human behaviour, but also tends to deny any disinterestedness in humans. Furthermore, even if this schema is not immediately applicable

to various cooperation relationships that exist in nature, we may query the existence of signs, biological signs that enable the establishment of a mutualistic or symbiotic type of relationship. In the logic of the text by Lotem et al., the cost of mutualistic behaviour for a living being includes the cost of the potentially mutualistic individual’s signalling. The use of this type of reflection in our work is to integrate the issue of mutual recognition between the host and the symbiont in the establishment of an evolutionary strategy. But we cannot really speak of unconditional altruism in a biological symbiotic relationship, this would not mean anything.

We may wish to modify the initial conditions by trying to modify the number of ‘players’. What may the concerned players be in the biological reality we are concerned with? Spontaneously, we think of the hosts and symbiont’s genes, but we can also imagine the multiplicity of cells present in biological space, which do not necessarily all behave in the same way. As an example we could quote the formation of chimera in embryology.

Albin and Foley (2001) apply co-evolution based on cooperation by several players and local interaction. They affirm their intention: “The present article develops this line of inquiry by introducing the geographical structure of neighbourhoods and the restriction to local interaction in the game and the genetics process of reproduction.” [37] However, it is difficult to apply this model to symbiosis, in so far as it is conceived more for studying animal, or human society, with a limited but already consequent number of partners (400). The matrix model used by Albin and Foley supposes that all partners are alike. In this context, how do we distinguish partners of the symbiosis? Nevertheless, the game is an extension of the cooperation problem as a function of the total number of co-operators. “We assume that in choosing its actions the agent only cares about the total number of co-operators in her neighbourhood.” [38] This supposes that on a biological level, each cell or gene is signalled to its neighbours, each adopting a strategy in view of the number of co-operators or competitors.

In the subject we are interested in, the aim would be to express this in biological terms: the multiplication of interactions between the host and the symbiont’s genome may be extended through time and generations. This is the case for the evolution of endosymbiotic bacteria in mitochondrion, inside the cell. It is also the case for oncogenes. But, can we really speak of cooperation when the host’s genes domesticate the symbiont’s genome, in order to use it? In reality, in the model used, there is a simplification that tends to reduce the fact of

cooperating or defaulting to two binary conditions ‘1’ and ‘0’, depending on whether the elementary unit (for example, the gene) is activated or not. The author’s goal is to measure the relative entropy of a society based on the agents’ neighbourhood.

This entropy is measured in view of the character of the agents present and the proportion of the various characters in the population [39]. The character of an agent is given by a vector that summarises its strategy (cooperating or not) towards other agents. The entropy stabilises quite quickly, but the actual calculation supposes an algorithm which takes both the proportion of the different genetic characters and selection action into account. The authors conclude that the selection action does not invalidate the cooperation contribution. The difficulty of concluding on such studies comes from the ‘black box’ aspect of the simulation undertaken. Here we are indeed concerned by a simulation and not by modelling, at least not in its strict sense.

To summarise: the authors work an algorithm where each character cooperates or not as a function of neighbouring replies; gradually throughout simulation’s progress, the totality of each agent’s replies and therefore the number of each character (defined by agents which have shared the same strategy) is recorded. Therefore, we obtain characters that correspond to more or less cooperative strategies in time. The stabilisation of the entropy after a certain number of generations attests the stabilisation of strategies around cooperation [40]. In fact, this type of simulation seems more adapted to an animal society situation which has strategies constituting genetic characters (or which can be easily linked to genetic characters). Furthermore, this type of simulation seems closer to network calculations, notably in John Holland’s genetic algorithm, than with previous versions of cooperation models. For network models, entropy measures of these agents’ society should therefore be retained as a function of the increase in cooperation strategies (increase which reduces the diversity of strategies and therefore, characters of the population). Further to this result, it would be interesting to ask whether cooperation does not lead to a population’s genetic decline, to a certain uniformity faced with the selective conditions at a given time. The adaptive reply of symbiosis and mutualism, faced with the environmental circumstances, would then imply a new selection unit, quickly stabilised at the cost of considerable impoverishment of the symbiont’s genetic diversity. This hypothesis is worth in-depth study for both modelling and concerning the effective results of molecular genetics.

4. Conclusion

Further to all these considerations, it remains that the algorithms derived from IPD (Iterated Prisoner’s Dilemma) do not constitute immediate models of biological phenomena, because they do not always integrate several parameters referring to a sufficient number of biological variables belonging to living beings and their environment. Moreover, these algorithms suppose that, at each stage, an autonomous strategy of each partner occurs with the possibility of demonstrating ‘altruism’ or ‘egoism’. Yet, in symbiosis, the phenomenon is much more complex; the symbiont gradually loses its autonomy. A fortiori, a parasite’s host is no longer autonomous in the expression of its genetic inheritance, because certain faculties are diminished, dependency exists between the host and the parasite and we cannot really speak of cooperation. The notion of ‘resistance to exploitation’ is much more difficult to apply in the cooperation equilibrium resulting from symbiosis than in human societies.

However, phenomena that can be found in symbiosis are integrated by the various models in relation with the ‘Prisoner’s Dilemma’; this is the case for the various components of the ‘cost-benefit’ ratio; it is also the case for signals that enable the installation of interrelations or again for neighbourhood interaction or reciprocity. Certain cooperating or non-cooperating strategies are found in symbiosis, but others seem more to reflect human societies, where choice is unrestricted. Yet it remains that even if cooperation or defection strategies may be related to certain stages in the installation and evolution of a symbiosis (reciprocal altruism, for example), it remains very difficult to give a value to cost and benefit equilibriums. The biological environment and its multiple signals interfere; a model based on a dominant strategy is often limited or insufficient to report on the living system’s evolution.

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