



Mafia Behaviour and the Evolution of Facultative Virulence

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Some organisms enforce “maladaptive” behaviours on others of the same or different species by imposing costs in the absence of compliance. Such enforcement is used by the enforcer to obtain benefits in the possession of the enforced individual. This mechanism is known as mafia behaviour in humans, but may be widespread in parasite–host relationships in nature, from the cellular level to societies. In this paper we describe the evolution of such mafia mechanisms, and we propose a fuzzy logic model where the mafia mechanism is based on enforcement of hosts by exponentially increasing the cost of resistance to the parasite. The benefits of host resistance can be counteracted by parasite virulence, or even a decrease in response to an increment in its resistance. This parasite response to the host defence increment can be used for the parasite to teach the host that it is better to pay part of its benefits than increase its extremely costly defence. This model differs from others because it takes into account the evolution of host defence related to the evolution of parasite virulence (host–parasite coevolution) and points out an optimum in host defence related to the facultative virulence of the parasite. We provide several potential examples of facultative virulence depending on the antiparasite responses of hosts, and we suggest that this kind of mafia behaviour may be a widespread mechanism in biological processes at a number of different levels.

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1. Introduction

Mafia behaviour is well-known and widespread in humans and is defined by the Oxford English dictionary as “a network of persons regarded as exerting hidden influence”. The mafia behaviour could also be defined as an enforcement by the mafioso individual to the rest or part of the population to pay, to the enforced, part of their benefits (generally money in the human mafia) or to cooperate with the mafia system. This mechanism of enforcement is based on learning the fact that it is less costly to pay part of your assets and maintain some than lose all. This is the case because punishment is more likely for avoiders of the enforcement than for those who accept the enforcement and pay their interest to the mafia. Of course, it is the mafia that controls punishment, thereby increasing the cost of

avoiding the system. Therefore, the mafia system is evolutionarily stable due to maintenance of the relationship between mafioso and host at equilibrium by the mafioso, who could change its pressure on the host depending on host defences.

Zahavi (1979) first suggested that a brood parasitic bird could force its host to incubate and rear parasitic chicks even when the host was able to discriminate against parasitic eggs. This is possible because the host could learn that if it ejected the parasitic eggs, the probability of having its nest depredated (by the parasite-mafioso) would increase. Therefore, the optimal behaviour of the parasitized bird is to rear the parasitic chick and, simultaneously, attempt to rear some of their own chicks because of the high cost of ejection (Soler *et al.*, 1995). However, Guilford & Read (1990) pointed out that a predatory behaviour would be needed to ensure maintenance of facultative

virulence among parasites. Recently, it has been shown that such predatory behaviour exists in two different families of brood parasites *Clamator glandarius* (Soler *et al.*, 1995), *Molothrus ater* (Arcese *et al.*, 1996). The host, after suffering predation can reneest, but it will run a renewed risk of being parasitized. In these two bird families of brood parasites it has also been shown that parasitized host nests suffer less from predation than non-parasitized ones, because brood parasites do not depredate host nests in which they have laid their own eggs (Soler *et al.*, 1995; Arcese *et al.*, 1996). Parasite individuals which have depredated a host nest an benefit from forcing the host to reneest in order to (1) increase future opportunities for parasitism (Soler *et al.*, 1995; Arcese *et al.*, 1992); (2) synchronise own laying with the efforts of the host (Arcese *et al.*, 1992); and (3) increase the cost of reproduction of the host rendering the fitness benefits of parasitized and non-parasitized hosts more similar (Soler *et al.*, 1995). Even if the host reneests, it will be for a seasonal breeder the last opportunity to breed that year and, as the predation rate of unparasitized nests is very high, it may be relatively beneficial for the host to be parasitized (the mafia mechanism). Soler *et al.* (1995) provided experimental evidence for this mafia mechanism in a brood parasite and its host; we found that (1) magpie (*Pica pica*) nests, in which we simulated host ejection of a parasite egg by removing the egg of the great spotted cuckoo, suffered significantly higher predation rates than those in which parasite eggs had not been removed; (2) the reproductive success of parasite ejector host was not different from that of hosts which accepted the cuckoo egg; and (3) observational data confirmed that the same great spotted cuckoo individual which parasitized a host nest was indeed responsible for the destruction of host clutches with an experimentally ejected parasite egg.

In this paper we suggest that this kind of mafia-like behaviour may be a widespread mechanism in biological processes at a number of different levels, and that this “hidden” enforcement can be useful for understanding “maladaptive” behaviour of some organisms “exploited” by others. We also propose a general model based on fuzzy logic (Zadeh, 1996; Mendel, 1995) and a graphical model explaining the relationships between mafiosos and host individuals, not only for brood parasites and their host, but for general host–parasite relationships.

2. Fuzzy Logic Systems

A fuzzy logic system is unique in that it is able to simultaneously handle numerical data and linguistic

knowledge. It is a nonlinear mapping of an input data (feature) vector into a scalar output, i.e. it maps numbers into numbers. It can be expressed mathematically as a linear combination of fuzzy basis functions (Mendel, 1995). The fuzzy basis function expansion is very powerful because its basis functions can be derived from either numerical data or linguistic knowledge, both which can be cast into the form of IF–THEN rules. To date, a fuzzy logic system is the only approximation method that is able to incorporate both types of knowledge in a unified mathematical manner (Mendel, 1995). Computers with words can be seen as a branch of fuzzy logic. The point of departure in computing with words is the concept of a granule. In essence, a granule is a fuzzy set of points having the form of a clump of elements drawn together by similarity (Zadeh, 1996). A granule “g” which is the denotation of a word “w” is viewed as a fuzzy constraint on a variable. A pivotal role in this methodology is played by fuzzy constraint propagation from premises to conclusions. A basic assumption in a computer with words is that information is conveyed by constraining the values of variables.

Words serve as the values of variables and play the role of fuzzy constraints. In this perspective, the use of words may be viewed as a form of granulation, which in turn may be regarded as a form of fuzzy quantification (Zadeh, 1996).

Computing with words is used when (1) the available information is too imprecise to justify the use of numbers, and (2) there is a tolerance for the imprecision which can be exploited to achieve tractability, robustness, low solution cost, and better consistence with reality (Zadeh, 1996).

Basically, a computer with words may be viewed as a bi-influence of two related streams: fuzzy logic and test-score semantics, with the latter based on fuzzy logic. The point of contact is the collection of canonical forms of the premises, which is assumed to be proportionally expressed in a natural language. The function of canonical forms is to explicate the implicit fuzzy constraints which are resident in the premises. With canonical forms as the point of departure, fuzzy constraint propagation leads to conclusions in the form of induced fuzzy constraints. Finally, the induced constraints are translated into natural language through the use of linguistic approximation [for further information on fuzzy logic system, see also Zadeh, (1994)].

In this article we only defined a model of host–parasite relationships based on fuzzy logic, but we did not use semantic scores. Due to real data on host

defense and parasite counter-defence being scarce, we defined the model using linguistic approximation.

3. A Simple Model of Mafia Behaviour

3.1. SCENARIO

Parasitism, in general, can be viewed in an ecological community sense, where animals requiring a similar kind of resources are competing for those resources (Keller & Lloyd, 1992), with the peculiarity that parasites are exploiting resources obtained for other individuals. In that ecological community we can define resources as nutrients used for individuals (hosts) in their activities that can also be used by other individuals (parasites) when those energetic materials become available. The total amount of resources in host individuals is that which can be used by both host and parasite. Therefore, low accessibility to the host resource for a parasite would result in a small proportion of resources used by the parasite and, therefore, most of the resources will be used by the individual who collected them (the host).

Defence mechanisms of hosts are predicted to evolve in order to reduce parasite accessibility to host resources, while mechanisms increasing parasite accessibility to host resources are predicted to evolve in parasites. Therefore, a sequence of host defences and parasite counter-defences is predicted to occur in any host–parasite system (arms race hypothesis; Dawkins & Krebs, 1979).

Host defence is costly, since some resources are spent in this host activity (time and errors in parasite recognition for hosts of brood parasites; the immune system as a defence against pathogens). Parasite counter-defences are also costly (time and punishment for brood parasites, and production of substances reducing parasite detectability for general pathogens). Costs of parasite counter-defences are not only paid by parasites, but indirectly by hosts, because parasites are using host resources. Therefore, any increment in host defence and parasite counter-defence will result in a reduction of the total amount of resources which could be used by both host and parasite in order to increase their fitness.

Under this scenario, the condition for host defences and parasite counter-defences being adaptive is that the benefits (accessibility to resources) of those strategies exceed their costs (Ridley, 1993).

In brood-parasite host systems, host defence increases in relation to the duration of sympatry with parasites (Soler & Møller, 1990). Simultaneously, the level of parasite counter-defence increases in relation to host defences (Brooke & Davies, 1988). A similar

relationship appears in host–pathogen systems in relation to the duration of coevolution (Schrag & Wiener, 1995). Therefore, for a certain duration of sympatry, host defences have reached a specific level and, if the parasite has evolved counter-defences, its level would be related to that of host defence (fixed parasite virulence). However, due to host defences and parasite counter-defences being costly, consuming resources that could otherwise be used by host and parasite (see above), for host–parasite systems where hosts and parasites have reached high levels of defence and counter-defence, respectively, a high level of counter-defence is not beneficial for a parasite because it considerably reduces access to host resources resulting in a decrease in the availability of resources for parasites (Frank, 1996a). But, since an increase in host defence differentially will reduce parasite accessibility to host resources, it will only in the case when the host increases its costly level of defence be beneficial for the parasite to increase its level of counter-defence, resulting in a facultatively virulent strategy for the parasite. Therefore, the parasite may either have a fixed strategy allowing host-resource accessibility (independent of the level of host defence), or the parasite may be phenotypically plastic and able to increase its negative effects on the host depending on the level of host defence.

3.2. MODELS

In order to define the model based on fuzzy logic we are going to consider nine different steps in the outcome of the relationship between parasite and host related to the level of host defence and negative effects of the parasite (facultative virulent) on hosts (counter-defence).

In order to simplify the model, we assume that the parasite can only use resources from the host and only one parasite genotype infects each host (avoiding competition within hosts).

3.3. PARASITE WITH A CONSTANT VIRULENCE (FIG. 1)

If the parasite is not phenotypically plastic and, thus, is unable to increase its counter-defences or virulence in relation to an increment in host defence:

(1) at the beginning of the infection, the host has not activated its defence yet and, therefore, parasite accessibility to, and consumption of, host resources very quickly reach a maximum. This results in a large reduction of host resources (at the same rate as resource accessibility for the parasite increases). This outcome will be the same when considering a brood parasite or pathogen parasitizing a new host (Soler & Møller, 1990; Ebert & Herre, 1996);

(2) in a second step, host defences start to reduce parasite accessibility to host resources and thus reduce the rate of parasite consumption of host resources. Presuming that an increase in host defence has an exponential effect on parasite accessibility to host resources (Frank, 1996a), this increment will result in an exponential decrease of the rate of parasite consumption of host resources. At the end of this step parasite consumption of host resources will reach its maximum. On the other hand, because host defence is costly, and thus the host spends some resources in defence mechanisms, the total amount of resource available for both host and parasite decreases proportionately to the level of host defence;

(3) after the maximum parasite consumption of host resources, any increment in host defence will result in a negative rate of resource consumption by the parasite, and therefore an exponential increase of available resources for the host;

(4) it would be advantageous for the host to follow increasing defences against parasites up to the level when the benefits and the costs of defence mechanisms become similar, maximising resource availability for the hosts and therefore minimising parasite accessibility to host resources. This scenario may result in parasite extinction;

(5) the negative-exponential relationship between host defence and its resource availability will reach the asymptote when the percentage of available resources used by the host equals that of non-parasitized individuals. For the parasite the asymptote is equal to zero because host defences result in inaccessibility to host resources for a parasite.

Because hosts and parasites are sharing the same amount of resources or energy, the curves of parasite and host benefits related to host defences should be symmetric. Therefore, in a host-parasite system where the host is able to increase its defence but the parasite is unable to increase its counter-defence, it is always beneficial for a parasitized host to increase its level of defence.

3.4. PARASITE WITH A FACULTATIVE VIRULENCE (FIG. 2)

If parasite's counter-defences were phenotypically plastic and, therefore, the parasite was able to increase the cost of host resistance by exponentially increasing its negative effect on hosts, the relationship between parasite and host benefits (resource accessibility) would be the same up to the level of host defences when parasites started to increase their negative effects on the host population, by increasing their counter-defences and, therefore, reducing the proportion of resource available for the host. This is

also the case when parasite and host are involved in an arms-race coevolutionary process and both host and parasite are able to evolve an improved system of defence and counter-defence, respectively.

Due to parasite counter-defence being costly (see Section 3.1), just when the parasite costs due to host defences overcome the possible cost for the parasite to increase its negative effects on the host, this behaviour will be beneficial for the parasite. Therefore, steps 1, 2 and 3 will be the same as when the parasite had fixed counter-defences. Thus, in order to simplify the model, we assume that the parasite starts to increase its negative effect on the host when the increment in host benefits, due to host-defence mechanisms, is maximised (consuming 50% of the resources in Fig. 1). However, depending on the cost for the parasite of increasing its negative effect on the host that point could vary inside the area delimited by step 3 (Fig. 2):

(4) parasite benefits are decreasing due to defence mechanisms of the hosts but, in this case, parasite counter-defences are phenotypically plastic and the parasite is able to increase its negative effects on the host population. When parasite benefits exceed the cost of this behaviour, the parasite starts to increase its negative effects on the hosts. This behaviour results in a reduction of host defence benefits compared with those expected due to its level of defence. On the other hand, a decrease of the value of the negative slope is expected for the parasite benefits-host defence relationship;

(5) if the host continues to increase its defence against the parasite, it will be beneficial for the parasite to continue increasing its negative effects on the hosts. Therefore, this scenario will result in an absence of a relationship between host or parasite benefits (in percentage of available resources) and level of host defence due to parasite counter-defences counteracting the effects of host defence. In that step the benefits of host defence reach the maximum (in percentage of available resources) that is possible in a host-phenotypically plastic parasite system;

(6) due to phenotypically plastic parasites being able to continuously increase their negative effects on the hosts in relation to host defences, any increment in host defence will not result in an increment of the percentage of resource available for the host, but a relative high cost will appear for hosts that increase their level of defence. Meanwhile parasite benefits, due to the increment of their negative effect, will be maintained or increased;

(7) in the scenario where the hosts continued to increase their level of defence and, as a consequence

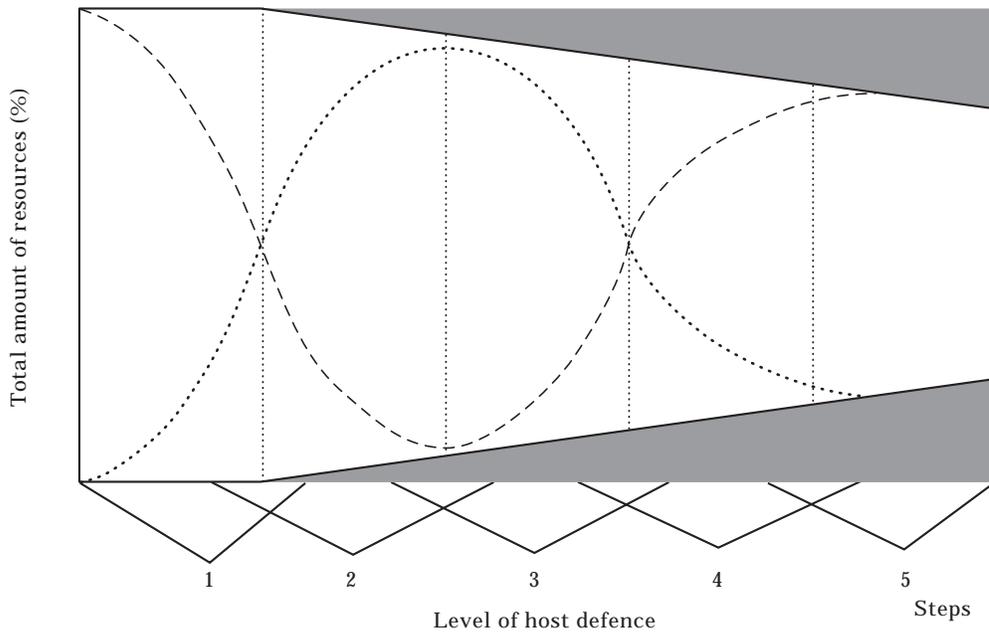


FIG. 1. Crisp function of the percentage of resources used by the parasite (.....) and the host (---) in relation to the level of host defence against the parasite, which has a constant negative effect on the host. The proportion of resources used by the host for defence mechanisms (■) is also represented. Steps are not assumed to be fixed and a confidence interval of 25% represented. The model can be viewed either as a parasitism or coevolutionary process.

parasites increased their negative effects on hosts, host benefits would decrease exponentially (with the power of the curve being proportional to the negative value of the increment in defence). As a consequence of that reduction in host benefits, available host resources decrease and thus, because parasite fitness depends on host resources, parasite benefits will also decrease with the same rate as host benefits;

(8) if hosts and parasites continued to increase their defences and counter-defences, respectively, the benefit for both would decrease. As in the previous step this reduction of benefits would depend inversely on the increment in host defence because it provokes a reduction in available host resources (and therefore host benefits), which results in a reduction of parasite benefits;

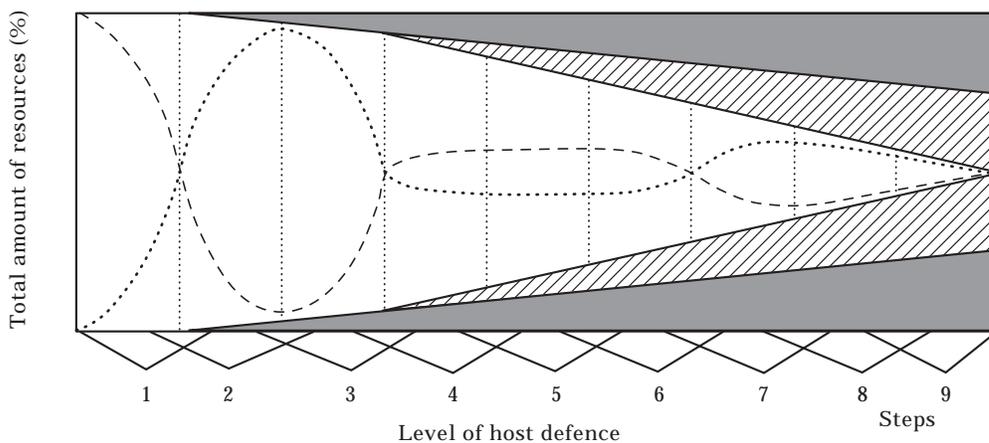


FIG. 2. Crisp function of the percentage of resources used by the parasite (.....) and the host (---) in relation to the level of host defence against the parasite, which facultatively is able to increase its negative effects on the host depending on the level of host defence. The proportion of resources used by the host for defence mechanisms (■) and those used by the parasite for counter-defence (▨) are also represented. Steps are not assumed to be fixed and a confidence interval of 25% is represented. The model can be viewed either as a parasitism or coevolutionary process.

(9) this process, if both hosts and parasites were still increasing the level of their defences and counter-defences, may result in the extinction of both hosts and parasites.

Therefore, the increase in defense mechanism after step 4 would not be beneficial for a parasitized host, but for a facultatively virulent parasite it would not be beneficial to increase its negative effect on the host after step 4 or 5, explaining why most parasites show suboptimal virulence [reviews by Ebert & Herre (1996) and Frank (1996a)]. In the same way when host and parasite have coevolved, after or during step 4, an increment in host defense would not be selectively advantageous if that results in a response by the parasite that increases its negative effect on the host. Therefore, when that is the case a reduction in host defense will be selectively advantageous if that implies a reduction in negative effects of the parasite on the host. Since from the parasite's point of view, an increase in its negative effects on the host will be selectively advantageous only in the case when the host increases its level of defence, for a host-parasite system, where the host decreases its level of defence, a reduction in the negative effect of the parasite on the host is the evolutionary optimum for the parasite.

3.5. DISCUSSION OF THE MODEL

In the case of parasite attacks on a host there can be at least two different outcomes depending on the virulence of the parasite and the resistance of the host:

(a) the parasite may have a constant negative effect on the host and the host may have evolved a defence mechanism (Fig. 1). The stability of the system will depend on (1) individual variability in the negative effects of the parasite on the host and resistance of the host, respectively; and (2) the probability of the host being infected by the parasite. This outcome may exemplify possible individual cheaters (in a mafia system), without facultatively negative effects on the host, where there is no reason for the host to decrease its resistance. Therefore, cheating in a mafia system is not an evolutionarily stable solution;

(b) the parasite may increase its negative effects on the hosts in response to the increment of host defence (facultative virulence). In this case the benefits of host resistance can be counteracted by negative effects of the parasite, or the benefits of the host may even decrease in response to an increment of its resistance (Fig. 2). Therefore, the increment of the negative effects of the parasite on the host in relation to the increment in host defence transforms host resistance into a non-selective trait (Fig. 2) that can be used

(without implying either a conscious decision or a moral sense on the part of the parasite) for the parasite to teach the host that it is better to pay part of the resources than increase its extremely costly defence. In this scenario there is an optimum level of negative parasite effects on the host and host defence, which is likely to be between the host's and the parasite's maximum level of defence and counter-defence, respectively.

The stability of the system will depend on the amount of negative effects that the parasite is able to increase facultatively in relation to the capacity of resistance of the host.

4. Other Models Explaining the Evolution of Parasite Virulence

Evolutionary processes that lead to the maintenance of the harmful effects of parasites are believed to be characterised by the negative impact of the parasite on the host being maintained by genetic correlations with other fitness trait of the parasite (Anderson & May, 1982; Lenski, 1988; Bull, 1994; Read, 1994; Sorci *et al.*, 1997), and, therefore, the parasite evolves an intermediate level of negative effects on their hosts. However, little is known about trade-offs between virulence and other fitness components of parasites, and most arguments rely on plausible suggestions rather than data (Ebert & Herre, 1996). Given the trade-offs between virulence and other parasite fitness parameters, some authors make predictions about the course of the evolution of virulence for different biological scenarios or different ecological conditions. For example, (1) parasites using hosts which are expected to live for a long time can lead to an evolutionary decrement of virulence (Lenski & May, 1994; Kakehashi & Yoshinaga, 1992); (2) host population structure and host density, which increase the number of contacts between a given pair of host individuals and thus limit dispersal of the parasite, will select for a lower level of virulence (Lipsitch *et al.*, 1995); (3) multiple infections are believed to favour the evolution of higher virulence (Bremermann & Pickering, 1983; Nowak & May, 1994; Levin & Pimentel, 1981; van Baalen & Sabelis, 1995); (4) Antia *et al.* (1994) developed the hypothesis that it is the immune system of vertebrates that might be responsible for the maintenance of virulence in microparasites that it controls and clears. In their model, highly virulent parasites kill their hosts, and themselves, too early; and avirulent strains contribute little to parasite transmission before they are cleared by the immune system. As a result selection favours

parasites of intermediate virulence; (5) variance in parasite genotypes competing for resources, because, if present, resource competition generates a type of trade-off that can maintain virulence (Ebert & Herre, 1996); (6) the kind of parasite transmission, because the optimal level of virulence is strongly influenced by the relative opportunities for vertical and horizontal transmission, and exclusively vertically transmitted parasites should not harm their hosts because the number of new infections depends on the fecundity of the host (Fine, 1975; Herre, 1993; Axelrod & Hamilton, 1981; Anderson & May, 1981; Bull *et al.*, 1991; Clayton & Tompkins, 1994; Møller, 1996).

A major gap of models of evolution of parasitism concerns the coevolution of hosts and parasites (Ebert & Herre, 1996). Since parasites generally have a high evolutionary rate compared with that of hosts (Fenner & Myers, 1978; Hafner *et al.*, 1994), most authors consider that host evolution may be ignored in a first approximation (Anderson & May, 1982; Bull, 1994), and, therefore, current knowledge of the evolution of diseases comes from systems in which host coevolution appear to have played a minor role in the expression of virulence (see earlier). However, for a better understanding of the evolution of diseases it is essential to know the role played by a host in the coevolutionary process (Ebert & Hamilton, 1996). For a better understanding of the evolution of virulence it is essential to understand the role of genetic recombination in host evolution (Ebert & Hamilton, 1996), because sexual reproduction of hosts is a means to overcome the disadvantage of the low evolutionary rate that an asexual host would have in comparison with its rapidly evolving parasite (Jaenike, 1978; Hamilton, 1980; Lively, 1987). Host diversity hinders evolution towards an optimal level of virulence, and, therefore, virulence should reflect not only the evolution of the parasite to optimize host damage, but also the evolution of the host to minimize damage (Frank, 1993; Read, 1994).

In our model we try to solve this problem and we take into account possible changes in host defences but related to parasite counter-defences. A change in host defence (e.g. immune system) is likely to occur relative to the parasite level of counter-defence, because as Antia *et al.* (1994) suggest, the immune system may impose a selective force that favours virulence in the parasite that it controls and clears, and a high immune response will select for a more aggressive parasite than a low one. Thus, from the hosts point of view, it is possible that, similar to parasite evolution of virulence, a trade-off exists between level of host defence and host fitness (because the differential negative effects of the parasite related

to the increment of host defence), and, therefore, an optimum host defence related to the ability of the parasite to increase its negative effects on the hosts may exist. This optimum in host defence will be controlled by the ability of the parasite to increase its negative effects on the host related to the level of host defence.

In conclusion, the present model differs from previous ones by taking into account the evolution of host defence related to the evolution of parasite virulence (host-parasite coevolution) and point out an optimum in host defence related to parasite facultative virulence. This optimum in host defence results in a constant benefit for the parasite without any increment of its counter-defences and, therefore, the parasite is receiving part of the benefits for doing nothing (just to maintain its optimal level of negative effects) resulting in a mafia system.

5. Potential Examples of Mafia Mechanisms

We have selected from the literature some examples of interactions at different biological levels that may be explained by a mafia mechanism.

5.1. MOLECULAR LEVEL

Retroviral transposable elements are parasitic genetic elements of the genome which cause a reduction in host fitness due to hybrid dysgenesis in offspring of individuals without transposons (Li & Graur, 1991). In other words, individuals that behave aggressively towards the parasitic element, by removing it, are punished in terms of reduced reproductive success.

Zuckerkindl (1986) suggested that the non-random distribution of long and short interspersed repeated elements is the result of need for retrotransposons to be "polite". "Polite" DNA leaves the sequence composition into which it inserts undisturbed. For example an AT-rich transposon will be found in AT-rich regions of the genome, because it prefers this region, and the region is more hospitable towards such a transposon.

5.2. CELLULAR LEVEL

The cytoplasmic incompatibility phenomenon, which is common in many insects and other invertebrates (Rousset & Raymond, 1991), is caused by rickettsia-like endocellular parasitic micro-organisms such as those belonging to the genus *Wolbachia* (Leu *et al.*, 1989). If the host produces uninfected offspring by not transferring the micro-organisms vertically, such offspring will have a fitness disadvantage, because crosses between uninfected and infected

individuals result in a reduction of offspring production (Rousset & Raymond, 1991). Similar phenomena occur as a result of nucleocytoplasmic male sterility in plants (Saumitou-Laprade *et al.*, 1994).

5.3. ORGANISMAL LEVEL

5.3.1. *Host immune defence vs. parasite virulence*

Some host responses to parasitic infection could be seen as potential examples of mafia mechanisms where the host is forced by the parasite to reduce its level of defence: a well-known, efficient host defence against pathogens is fever, and there is experimental evidence for this claim. However, there is considerable variation in the effectiveness of fever as a defence mechanism: sometimes fever is effective (Kluger, 1991), sometimes not (Banet, 1986; Blatteis, 1986). This polymorphism which has not been explained yet may be related to the mafia mechanism.

A potential example of variation in parasite response depending on host defence level concerns those cases where human immune defence is supplemented with drugs which increases clearance but as a consequence favours greater virulence (Frank, 1996a). Many bacteria such as *Escherichia coli* are typically benign within human hosts (Davis *et al.*, 1990), but highly virulent strains occasionally arise in hospitals causing severe epidemics and high mortality (Ewald, 1994). Ewald (1994) suggested that typically benign pathogens are often highly virulent in hospitals because of the greatly enhanced opportunities for horizontal transmission (trade-off between transmission and virulence). However, the trade-off between clearance and virulence of the parasites may also be important, because rapid clearance by antibiotic treatment tends to favour higher virulence (Frank, 1996a).

5.3.2. *Multiple parasitism of a single host*

The mafia behaviour may also evolve when more than two parasite species are involved in a host-parasite system. An individual of one parasitic species can benefit if provided with some advantage to the host in its fight against another more virulent (costly) parasite. The relatively avirulent parasite may signal to the host that it is beneficial to share resources with this parasite rather than attempt to remove it and increase the probability of being more extensively parasitized by the most virulent parasite. This system differs from commensalism because the parasite receives resources without severely harming the host,

because it is less virulent than the other parasite, and because both parasites are mutually exclusive.

A potential example of this system is: *Cryphonectria parasitica*, a parasitic fungus of the chestnut (genus *Castanea*). The disease is manifested externally as sunken cankers, which eventually kill the host by blocking the exchange of water and nutrients between roots and leaves. However, there is one hypovirulent fungus which provides resistance to the plant against the mortal virus and, when the virulent and the hypovirulent strains come into contact, the virulent strains become hypovirulent (Michalakis *et al.*, 1992).

5.3.3. *Commensalism between different species of insects*

One of the most common examples of commensalism is ants taking care of aphids, defending them against predators, while aphids provide ants with part of the sugar they suck from the plant. However, ants also depredate aphids. Recently, Sakata (1994) pointed out that ant predation on aphids is negatively related to the amount and the quality of sugar that individual aphids provide to the ant. The ants are increasing the costs to aphids of providing little and poor quality sugar. Therefore, the ants will receive more, higher quality sugar from the aphids in the presence of a mafia mechanism than if no punishment of poor providers of low quality sugar occurred.

5.4. INTRASPECIFIC ENFORCEMENT

All previous examples concern enforcement by individuals of one species on individuals of another. Obviously, enforcement of one individual to share resources with the enforcer is a mechanism that may exist intraspecifically.

Recently, punishment in animal societies has been emphasised as an important factor in evolutionary biology (Clutton-Brock & Parker, 1995a, b). It reduces the probability that the victim will repeat a damaging action or will refuse to perform a beneficial one; the victims learn to avoid repeating such behaviour and the dominant individuals continue receiving benefits from the subordinates (Clutton-Brock & Parker, 1995a). In other words, it is more beneficial for individuals of species living in groups to be social than alone because of the advantage of detecting predators or finding resources, and the dominant individual is able to eject anyone from the group due to superior resource-holding-power. If it is much better to be a subordinate member of a group than to be alone, or in a group of reduced size, it is possible that subordinates are forced by the dominant

to remain and fulfil their subordinate role in the group. Therefore, they are forced to provide to the dominant individual security against predators directly because subordinates spend more time scanning for predators, or indirectly because, if a predator appears, subordinates have a higher probability of being chosen as prey than the dominant ones due to their lower physical condition. Alternatively, subordinates may be forced to provide part of their resources to dominants because the latter always have a disproportionate share of the resources due to differential access. If one subordinate does not accept these conditions, the dominant can exclude it from the group, and this option is more costly for the subordinate than to accept the system as predicted by a mafia mechanism. Therefore, punishment behaviour (Clutton-Brock & Parker, 1995a) can be viewed as a particular case of mafia behaviour in societies where enforcement results from punishment of victims.

In an ingenious experiment on keas (*Nestor notabilis*) where cooperation between two individuals were needed to reach food, but only one individual was able to obtain it, Terbich *et al.* (1996) demonstrated that dominant individuals forced their subordinates to open the apparatus holding the food. The suggested benefit for the subordinates was just a reduced risk of being punished by the dominant, as predicted by the mafia model.

In the case of human societies we are aware of several potential examples of mafia-like behaviour other than punishment. One general example concerns the relationship between clients and banks. Clients obtain loans, but pay interest for their loans to the bank that benefits. Payment of interest by clients is profitable for the client in the bank system. The enforcement is based on the fact that each individual that wants to buy a house or start or increase business is forced to ask for money from the bank, accepting banking conditions and paying to the bank the loan and part of the profits. Because of the high level of stability of that enforcement system, and because the bank can ask for a higher interest rate, governments control banks in order to maintain an interest rate that is not "too" high. When the "bank" is illegal, and the government is unable to control interest rates that the "bank" forces its customers to pay, the rate increases considerably, but the system is still stable (part of the human mafia business). If the "customers" intend to leave the bank and, therefore, indirectly damage the bank by no longer paying the interest on loans, the "customer" must pay extra-high interest rates. This obviously prevents or reduces the risk of "customers" leaving or moving to other banks.

6. Discussion

Hosts and parasites will normally have experienced a long period of coevolutionary interaction and some defences and counter-defences will have evolved (Brooks & McLennan, 1993). Anti-parasite resistance of hosts will obviously be adaptive, if the parasite displays obligate virulence, and similarly increased virulence will be adaptive under obligate anti-parasite resistance.

Virulence and anti-parasite behaviour are usually assumed to be genetically determined, obligate responses in models of host-parasite interactions. In other words, a change in virulence or host resistance is caused by a change in genotype frequency (Frank, 1996b). In general, any counter-defence consists of an increase in benefits, but simultaneously this counter-defence is also costly. Therefore, there is an "optimum area" where, if one of the members of the host-parasite system does not increase its costly defence, the other will not increase its costly counter-defence (following step 3, Fig. 2), either in a parasitism or a coevolutionary process. This area (step 4) will be an equilibrium (1) if the parasite is able to decrease the benefits of host defence, even below the level of the benefits reached with a small amount of defence, due to an increase in its virulence (facultative virulence) (following step 4, Fig. 2); (2) if the parasite needs the host for its own survival [which is related to the transmission rate of the parasite to a new host (Ewald, 1994)], then a decrease in host benefits is non-adaptive for the parasite because its benefits depend on host resources, and later the benefits of the parasite will decrease in relation to the decrease in the benefits of the host (following step 7, Fig. 2).

There are two possibilities for the increase of negative effects on the host by the parasite: (1) it could be a direct consequence of resistance (i.e. host induced); or (2) negative effects of the parasite on the host increase because the parasite does so, as a response to host resistance (i.e. parasite induced, the parasite being phenotypically plastic). However, although it is important to distinguish between these alternatives for the study of evolution of such systems, following our mafia model the fact that host benefits do not increase in proportion to increasing resistance is sufficiently important to induce a decrease in the level of host resistance.

Host and parasite responses need not be obligate, but may depend facultatively on the response of the other part in the interaction. Parasitism may be enforced on hosts, and any parasite that behaves relatively avirulent to a host that complies to

parasitism, but shows a high level of virulence to a resistant host, will be at a selective advantage. The reason why facultative virulence of a parasite gives rise to a higher parasite fitness than does obligate virulence is that the mafia parasite tends to harm hosts with high resistance, but is nicer to those with low resistance. Average host resistance in a host population exploited by a mafia parasite will tend to be depressed compared to a host population parasitised by an obligate parasite. Parasitism of a host population with facultative resistance should give rise to an increase in parasite fitness because less energy has to be spent on coping with host resistance. Hosts may benefit from the evolution of facultative virulence by showing low levels of resistance, if they thereby increase their reproductive success relative to resistant hosts that are punished by a facultatively virulent parasite. If we imagine that the cost of host resistance to a parasite is constant, but with a facultatively virulent parasite (a mafia parasite) the benefit to the host is now greater for small and less for large resistances. If both host and parasite responses are facultative, both parties may settle at an intermediate level of virulence and parasite resistance that gives rise to a larger fitness for both host and parasite than under higher virulence and parasite resistance.

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