Abstract

Descriptions of interactions between ants and their 'guests' serve to illustrate the thesis that Ewald's theory of the 'evolution of virulence' not only applies to interactions between micro-organisms causing infectious diseases and their hosts, but also to interactions between individuals belonging to differing species. For instance, the prediction is put forward and discussed that guests of army ants are, relative to guests of other species of ants, more often parasitic. A key variable in Ewald's theory is 'transmissibility'. It shows some resemblance to similar variables used in micro-economic theory and in Emerson's sociological Power-Dependence Relations theory. In this article, this variable is called 'outside opportunities'. In an A–B relation, an outside opportunity for A is anything which constitutes an alternative to what B can provide. It is concluded that in A–B interactions, the more outside opportunities are available to A, the more costs are incurred by B. Differences and similarities between this idea and Game Theory are discussed.

Keywords: Evolution of virulence; Game theory; Guests of army-ants

1. Introduction: The initial question

Why do ant colonies participate in many symbioses and are sometimes largely dependent upon them, whereas honeybee colonies have no known symbionts but many parasites? The answer given by Axelrod and Hamilton (1984), based on Game Theory, will be discussed further on in this article. Here, Ewald’s theory of the ‘evolution of virulence’ is used to construct an alternative explanation, and to provide additional predictions about ants and their guests. A description of Ewald’s theory now follows.

2. The evolution of virulence

Micro-organisms living in or on hosts use resources of the host to reproduce themselves. As organisms are designed by natural selection to reproduce maximally, one would at first sight expect extensive replication by the micro-organism. Extensive replication by a micro-organism in or on a host results in depletion of the host’s resources, which may cause the host to get sick. How sick? Some micro-organisms have quite severe effects, while others rarely inflict any damage beyond a cold or a sore throat. Why are some parasites more dangerous than others?

Ewald argued that the ‘transmission mode’ of micro-organisms living in or on hosts is a key variable with regard to their evolution. An example of rather benign parasites are the Rhinoviruses, causing the common cold. An exhausted and very sick host would not increase, but rather decrease the chance of infecting new hosts, since the host must somehow get near potential new hosts, (sneeze in their vicinity, touch their hands or other objects which will soon be touched by potential hosts), in order to infect them. A strain of Rhinoviruses so virulent that infected patients stay in bed for days in a row, means that few new hosts will be infected. So virulent strains are out-reproduced by Rhinoviruses which keep the patient mobile and relatively healthy. In the case of Rhinoviruses, natural selection favors parasites that are relatively benign to their hosts.

Quite the contrary holds if the health of the host is largely irrelevant to the micro-organism’s ability to transmit to new hosts. This is the case when the micro-organism
is transported to new hosts by a ‘vector’, for instance a mosquito, a syringe, or a sewer leaking into drinking water. In Ewald’s words: “Even if a pathogen reproduces so extensively that it causes its host to become gravely sick, its host-impairing instructions may still win over the less damaging instructions of less aggressive competitors. The more virulent pathogen would achieve this success if its increased replication led to a level of transmission into new hosts that exceeded the loss of transmission resulting from the host’s illness or death.” (Ewald, 1993, p. 56). The general idea is thus that the ‘easier’ it is for the micro-organism to infect other hosts, (or the more ‘opportunities’ the micro-organism has outside the present relation between host and micro-organism to get to new hosts), the more damaging it will be to the host.

Ewald’s theory explains variations in virulence; and also why there is some truth in the old idea that commensalisms is the evolutionary end product of host–parasite interactions, supposedly because harm to the host decreases the parasite’s long-term survival (Hoeprich, 1977). An extremely virulent and lethal variant of a pathogen, killing a large proportion of its hosts, will often find it increasingly difficult to transmit to new hosts, since these will get scarce and more thinly distributed. Hence, natural selection will start favoring milder variants of this pathogen. But if for some reason hosts do not become more scarce (for instance because at a hospital new patients, potential hosts, arrive every day at the place of the outbreak of the infectious disease), then this automatic natural selection of milder variants of the pathogen will not occur.

3. Transmissibility and cooperation or parasitism

Why do ant colonies participate in many symbioses, whereas honeybee colonies have no known symbionts but many parasites? Honey bees do not display territoriality in their feeding areas. A honey bee worker may visit many flowers, perhaps carrying a guest (like a mite) with her, and the guest may drop off at a flower and subsequently climb onto a worker of another colony. Honey bees forage for nectar and pollen resources which may be more than 10 km away from the hive (Seeley, 1985; Beekman and Ratnieks, 2000). This implies that sources within an area of several hundreds of square kms may be exploited. In this area many other colonies live. Estimates run from two colonies to more than a hundred colonies per square km in the Amazon basin (Taylor, 1985). Therefore, foragers from many colonies will use the same flower patches as food source, and guests have good opportunities to switch host colony. In addition, when floral resources are scarce, foragers will often steal stored honey from relatively weak or dying colonies (Gary, 1966), also increasing opportunities for guests to switch host colony. It seems, therefore, that guests can easily transfer from one colony of honeybees to another. Applying Ewald’s reasoning, guests of honeybees should evolve to become parasitic.

Despite immense variety among the 12,000 or so known species of ants, certain aspects of their general behavior and physiology do not particularly favor the transmission of guests from one colony to another. In the first place, and as in contrast to honeybees, worker ants cannot fly, and do not go from one flower to another. So it is unlikely that the locality at which a worker ant drops off a guest, would quickly be visited by a worker ant of another colony. Furthermore, ants are generally sessile (rooted to a nest site) as well as territorial, where a territory is defined as an area occupied more or less exclusively by an animal group by means of repulsion (Hölldobler and Wilson 1990, p. 400). It is thus unlikely that guests could easily transfer to other colonies of ants. Again, following Ewald, guests of ants would be expected to be benign and to cooperate with their hosts, as is often found in ants.

A further prediction about different ant species and their guests is possible. As noted, ants are sessile, but army ants do not have a permanent place of abode. They frequently change the location of their bivouacs, and as the army ants move on, guests may stay behind, and be picked up by, or follow the trail of another colony (Hölldobler and Wilson 1990, p. 490). So Ewald’s theory would predict parasitic rather than cooperative guests in army ants.

It is beyond dispute that cooperation between ants and guests exists. Ants ‘milk’ aphids, cultivate fungus gardens, protect acacia-trees, and so on. No such cooperation is found in army ants. By contrast, there are many species of parasites associated with army ants, and several of them can be found in a single colony. Mites travel on the army ants while sucking their blood, some of them especially adapted to cling to the ants’ legs. Parasites attack adult army ants, the injured or sick, the larvae, or steal food. Some parasites mimic the army ants in appearance as they march along beside them, apparently to avoid predation by vertebrates like birds, who follow the legion and prey on beetles though usually not on ants. And there are also cases where army ants and their guests seem indifferent to each other. For instance, butterflies feed on droppings of birds that follow the raiding swarm. However, there appears to be no single case cited in Hölldobler and Wilson (1990) where the relation between army ants and their guests is associated with benefit to the ants. Given the spectacular array of guests found in very large (sometimes up to twenty million individuals) colonies of army ants, this is remarkable. So, the prediction of more parasitism in army ants is supported.

3.1. More on ants and their guests

One aspect of transmissibility (and hence virulence) of a micro-organism causing an infectious disease is its capacity to stay alive outside of and reproduce independently of the
Table 1

Two behavioral differences between ‘generalized’ and ‘specialized’ staphylinid beetles (Hölldobler and Wilson 1990, p. 489), guests of army ants

<table>
<thead>
<tr>
<th>Generalized staphylinids</th>
<th>Specialized staphylinids</th>
</tr>
</thead>
<tbody>
<tr>
<td>• Attack adult ants but usually kill only injured or weak workers</td>
<td>• Do not attack adult ants</td>
</tr>
<tr>
<td>• Can tolerate a wider range of ecological conditions; live with a few or no ants for a day to weeks</td>
<td>• Can tolerate only a narrow range of ecological conditions; usually die within a few hours of removal from colony</td>
</tr>
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The word ‘guest’ is used here in the neutral sense of one organism living with an organism of another species. Hölldobler & Wilson employ the word ‘symbiont’ in this neutral manner, but Axelrod and Hamilton use it to refer to a cooperative and non-parasitic guest. Here we adopt the latter usage.

current host. The virus causing the common cold can live outside its host for little more than 2 days (Walther and Ewald 2004, p. 858), so this is an incentive to keep the host mobile. But a pathogen that can live outside a host for weeks or even years, like the virus which causes smallpox, waiting for a new host to come along, will be malicious to its hosts. The same rule seems to apply to the guests of ants. Hölldobler and Wilson list some behavioral differences between what they call “generalized” and “specialized” guests (staphylinid beetles) of army ants. Here are two of those differences between the categories (Table 1).

Just as Ewald’s theory predicts, guests able to live longer outside an ant colony are more malicious. There are many other examples of the same phenomenon. If there are more ‘outside opportunities’ for the guest, that is ways to transfer to other colonies of hosts and to reproduce independently of the current host, then the guest will be more parasitic. If such outside opportunities are absent or virtually absent, then there will be mutualism. Two other examples will now briefly be discussed.

The leafcutting ant Atta sexdens (and many other ant species of the New World) strips leaves from trees and plants, and carries them to its nest. After being laboriously processed by the ants, they pluck tufts of the fungus Leucocoprinus gongylophora, growing elsewhere in the underground gardens, and plant them on the chewed up fragments of the leaves. The fungus will eventually form ‘kohlrabi-like structures’, which are then eaten by both adult ants and larvae.

The ants apparently do not permit the fungus to form mushrooms or other spore-bearing bodies. In any case, the fungus does not depend on windborne spores to transfer to other nests, because even in the absence of ants it rarely forms sporophores. Before departing on her nuptial flight a virgin queen packs a small wad of the fungus in a special locality in her body. Following the nuptial flight, she casts off her wings and excavates a little nest in the soil. It might be the beginning of a new colony and a new fungus-garden. There is close to perfect cooperation and commensalism between ant and fungus.

It is a different story with the fungus Cordyceps subdiscoidea. After it has infected an ant it sprouts from the body of the ant (which will soon die) a club-shaped organ on a stalk that protrudes as much as 10 cm outside the body of the host. As Hölldobler and Wilson (1990, p. 554) write: “It is a startling experience to encounter a large ant, dead yet standing rigidly at attention with a Cordyceps sporophore raised above it like a flag.” Apparently, this fungus has evolved to transmit itself as quickly as possible to other ants, at the expense of its current host. It illustrates Ewald’s mechanism: More transmissibility means more parasitism.

Another example of the same mechanism. As early as 1922, it was reported (Hölldobler and Wilson, 1990, p. 532) that acacia trees in Zaire devoid of the ant Pseudomyrmex nigropilosa suffer great damage from attacks by herbivores, and also tended to be overgrown by other trees. The acacia is normally occupied by the ants, who find shelter in hollow thorns, and feed on extra floral nectarines and food bodies provided by the tree. With this arrangement the tree possibly saves energy by not having to produce toxins and other defenses. The ants are extremely aggressive toward intruders of all sizes, and their stings are painful. If there are several ant colonies in one tree, the dominant one will eventually wipe out all competitors and take possession of the entire tree. Evidently, tree and ants cooperate.

Not all species of ants follow the same strategy though. The ant Pseudomyrmex nigropilosa occupies the hollow thorns, eats the nectar and food bodies, but provides no protection at all for the acacia. It produces males and queens earlier in the life of the colony than is the case with the mutualistic species, so it can disperse before the host dies as a result of lack of protection (Hölldobler and Wilson 1990, p. 553). By reproducing early, the ant Pseudomyrmex nigropilosa creates ‘outside opportunities’ for itself, and this is associated with costs for the host.

3.2. A similarity between three theories

Ewald’s theory applies to infectious diseases, but apparently also to ants and their guests. Why not to still other fields like for example human interactions? It will now be demonstrated that ‘outside opportunities’ as a variable is used both in micro-economic theory and in Richard Emerson’s sociological Power-Dependence Relations theory (see Emerson 1962, 1967a, b; Cook and Emerson 1978). What follows is a brief description of a part of Emerson’s theory. It is used to illustrate the similarities between the three theories just mentioned.
Human social relations involve the transfer of valued items (i.e. the provision of information, gossip, affection or approval, advice or promises, or more tangible things like goods and services). In his effort to analyze human social relations, Emerson started with the simplest possible form, that between two persons, the actors A and B. He used the concepts of power and dependence to understand why valued items are transferred between them. The power of an actor A over an actor B, denoted \( P_{AB} \), is defined as the amount of resistance on the part of B which can be potentially overcome by A. If actor A has power over B, he can induce or coerce B to transfer something to A which A wants. Why does actor A have power over B; and how much power? Emerson’s answer is that A’s power over B is equal to, and based upon the dependence of B upon A, denoted \( D_{BA} \). In other words, \( P_{AB} = D_{BA} \).

The next question is: Why is actor B dependent upon actor A, and how great is his dependence? Emerson’s answer: The dependence of B upon A is

1. directly proportional to B’s motivational investment in goals mediated by A, and
2. inversely proportional to the availability of those goals to B outside of the A–B relation.

Much of the work of Emerson and his colleagues concentrated on analyzing networks, predicting the power relations of the actors involved, and testing these predictions (see Cook and Emerson 1978; Cook et al., 1983). One of the things established was that a central position in a network does not always constitute the most powerful position.

Below are three simple networks used here to illustrate the common mechanism operating in both Emerson’s theory, microeconomics, and Ewald’s theory.

In Fig. 1, moving from left to right, and following Emerson’s theory, actor A is expected to have an increasing power-advantage over B, as A’s dependence of B decreases with every additional outside opportunity. Emerson (1967b, p. 67) writes: “To have a power advantage is to use it; (…)”, so it follows that, other things being equal, A will increasingly “overcome resistance” on the part of B. Again moving from left to right, and following standard micro-economic theory, if A is a consumer and B a producer, then A will be able to negotiate the lowest prices in the network at the right of Fig. 1. Being a *Homo economicus* and expected to maximize utility, A will pay lowest prices in the network at the right.

Finally, if A is a pathogen and B a host, then following Ewald’s theory, A maximizes its reproductive success in the situation on the left by keeping the host healthy. But in the situation on the right A may deplete resources of its current host and switch to another one. As long as other hosts are available more virulent strains of A will outcompete less virulent strains because reproductive success of the more virulent strains is higher. As living organisms are expected to behave as if programmed by natural selection to maximize their reproductive success, A will be benign and cooperative in the network on the left, but A will evolve so as to deplete the resources of its current host and thus be malicious on the right. These considerations may be summarized as follows:

In A–B interactions, the more outside opportunities are available to A, the more costs are incurred by B.

This article is not an attempt to evaluate Ewald’s theory (see van Baalen and Sabelis, 1995), Emerson’s theory, or micro-economic theory. Rather, a general proposition in the sense of a ‘covering law’ (Hempel, 1965) is formulated. This ‘covering law’ appears to explain cooperation and parasitism in colonies of ants and honeybees quite well. Game theory also offers an explanation of variations in cooperation and parasitism in ants and honeybees. The two different approaches will now be compared. In brief, the ‘covering law’ (or Ewald’s theory) leads to three predictions about cooperation and parasitism in ants and honeybees. Two are identical to predictions from ‘Game Theory’; the third is different.

4. Game theory and cooperation/parasitism in ants and honeybees

Exchanging ‘altruist’ acts is called ‘reciprocal altruism’ by Trivers (1971), ‘direct reciprocity’ by Alexander (1979, p. 49), and ‘reciprocal cooperation’ by Axelrod and Hamilton (Axelrod and Hamilton 1984, p. 102). Researchers in ‘Game Theory’, particular in their handling of computer-simulated Prisoner’s-Dilemma games, study cooperation between unrelated (*sensu* Hamilton, 1964) individuals with no third party sanctioning. The framework is broad enough to encompass both people and bacteria (Axelrod, 1984, p. 18). The central question is: “Under what conditions will cooperation emerge in a world of egoists without central authority?” (Axelrod 1984, p. 3). In one-shot encounters, actors or players are not expected to cooperate. “When the players will never meet again, the strategy of defection is the only stable strategy”. And: “Apart from being the solution in game theory, defection in a single encounter is also the solution in

![Fig. 1. Three ‘networks’. The solid lines represent interactions. The ‘network’ (dyad) on the left represents interactions solely between A and B. In the middle, A has one ‘outside opportunity’, that is, A can also interact with another B. On the right A has two outside opportunities.](image-url)
biological evolution.” (Axelrod and Hamilton, 1984, p. 92). However, if the game is repeated, that is, if the same players meet again, then defection is not always the best strategy. It appears that for cooperation to emerge, it is not necessary for the two parties to be friends, nor that they are intelligent or have foresight. Important is the probability that after one interaction the same two individuals will meet again, and that they recognize each other and recall how the two of them have interacted so far. Among relevant variables are the average lifespan, the health, and the mobility of the players involved.

Axelrod and Hamilton (1984, p. 101) wrote the following about ants, honeybees and their guests: “(…), conditions of free-mixing, and transitory pairing conditions where recognition is impossible, are much more likely to result in exploitation—parasitism, disease and the like. Thus, where ant colonies participate in many symbioses and are sometimes largely dependent upon them, honeybee colonies—which are much less permanent in place of abode—have no known symbionts but many parasites.” So the explanation proposed by Axelrod and Hamilton for the frequently found cooperation between ants and their guests, in contrast to honeybees and their guests, is that because ants have more permanent nests, the probability that ants and their guests will interact again and hence cooperate is greater than for honeybees and their guests. Presumably, as the location of bivouacs of army ants change, Axelrod and Hamilton would also, as in Ewald’s theory, predict more parasitism in army ants as compared to nonlegionary ants. So the predictions of the two theories are the same. However, if there exists a species of bee which is more permanent in place of abode, then the predictions would not be the same. Game Theory would predict mutualism between bees and guests, but in Ewald’s theory, the permanence of the place of abode is just one way that affects the capacity of guests to transmit themselves to other colonies. Bees with a more permanent place of abode would still be expected to have many parasites, because guests can transfer to other nests via flowers visited by workers of different colonies, or while workers steal honey from other colonies.

4.1. The ability to forego interaction

One reason why Game Theory and Ewald’s theory generate at least one different prediction is that Game Theory, in its attempts to explain the emergence of cooperation between players, uses a model that does not allow players to interact selectively with other players. “A single player may be interacting with many others, but the player is assumed to be interacting with them one at the time.” And: “There is no way to (…) run away from the interaction.” (Axelrod, 1984, pp. 11–12). In other words, players in the Prisoner’s Dilemma game cannot choose to refrain from certain interactions, or initiate new ones.

The ability to initiate some interactions and forego others is essential in micro-economic theory, Emerson’s theory and Ewald’s theory. Following Ewald’s logic, if a guest and its descendents can only reproduce via the current host and its descendents, then the guest is expected to evolve so as to be totally benign to its host. But if there are opportunities for the guest to also reproduce via other hosts, then conflicts of interest and parasitism will emerge, and the guest may even discard of the current host. This is also not possible in Game Theory: “There is no way to eliminate the other player” (Axelrod, 1984, p. 12).

In economic theory, prices and allocation of resources are, other things being equal, the product of consumers and producers making choices, and making choices means interacting with some, but not with others. And in Emerson’s theory, the power of an actor A over B is inversely proportional to the availability outside of the A–B relation of goals wanted by B and mediated by A. To understand the power-relation between A and B, the opportunities they have outside the A–B relation are essential.

So micro-economic theory, Emerson’s theory and Ewald’s theory allow features in their models of interaction that are not present in Game Theory models, causing different predictions.

Finally, a semantic issue is addressed. It seems useful to distinguish between on the one hand defection or cheating, concepts often used in Game Theory, and on the other hand exploitation. Of course, defection or cheating occurs in every sort of network. In Game Theory the word exploitation is sometimes used when defection or a series of defections is meant. This may cause confusion. If an employer pays an employee a scandalously low salary, most people would call that exploitation. Whatever the moral qualification, the employer is certainly not defecting or cheating; in fact, both parties are cooperating. The employer would cheat if the work is done but subsequently no salary is paid, and the employee would cheat if the salary is paid but he or she does not show up for work. Exploitation is a form of reciprocal cooperation.

Acknowledgments

Many thanks to Prof. E. O. Wilson for his comments on an earlier version of this article. Most of what is written here about honeybees comes from Willem Jan Boot, who was also kind enough to give this article a critical scrutiny. Two anonymous reviewers inspired me to reshape my article. Finally, chess-colleague Hamilton McMillan transformed my writing into real English.

References