Interaction between individuals: from cooperation to cheating

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Communication to the 6th Ecology & Behavior Meeting
Tours 12-16 April 2010

Full text 20 April 2010
Modified 03/05/2010

> « Avant Darwin, le monde était simple, harmonieux et facile à comprendre. Tel que Dieu l'avait fait. » (Cavanna, Les grands imposteurs, 1991 – "Before Darwin, the world was simple, harmonious and easy to understand. Like God made it.")

Evolution has favoured many interactions between individuals of the same species and between species. The degree of interaction varies from simple parasitism to cooperation (mutualism). The persistence of cooperation is an evolutionary paradox as selection should favour those individuals that exploit their partners (cheating) obtaining benefits without providing a reward in return, resulting in the breakdown of cooperation. To prevent this, mechanisms avoid or retaliate against exploitation by cheaters, maintaining the stability of mutualisms. Such conflict is seen in biological systems at every level from individual genes within a cell to individuals within societies. Most works have focused on maintenance of cooperation within a single species through mechanisms such as kin selection but aiding non related individuals of another species has also evolved in many cases.

Intraspecific cheating

The social amoebae *Dictyostelium discoideum* have been studied using the kin selection theory of social insects. They are clonal organisms that can form very large patches as it has been discovered in a cattle pasture in Texas, but these patches are very unstable and disappear rapidly when conditions are not good (Gilbert et al. 2009). When starved from their bacterial food, they aggregate in multicellular slimes. The slimes transform in a fruiting body where cells from the stalk (25% of the cells) dye by apoptosis (programmed cell death) while the other ones become a hard resistant reproductive spore. In the laboratory, when two strains are mixed to form the fruiting body, some behave as selfish cheaters: they prefer to take the good place to become spores. These cheaters cannot invade the population as they need the presence of altruists (models using game theory). Actual conflict may be rather low in the field, generally the strains are able to discriminate kin and do not mix with non-kin during fruiting, preventing the development of cheaters (Mehdiabadi and al. 2006). Genetic studies have began on different strains to understand how the cheater mutants modify prestalk cells differentiation (Khare and Shaulsky 2010). A similar fruiting behaviour exists also in the bacterium *Myxococcus* (Velicer et al. 2000).

In *Pristomyrmex punctatus*, a parthenogenetic ant species, reproductive cheaters have been discovered. The larger ants lay more eggs and hardly take part in cooperative division of labour. They form a genetically distinct lineage, isolated from cooperators by parthenogenesis. Cheaters were discovered in the field in 1984 and the system is stable with a long-term coexistence (Dobata et al. 2009). Other cheaters will probably be discovered in ants. We discovered reproductive cheating in non-parthenogenetic ants: workers of *Aphaenogaster senilis* are able to lay haploid eggs in the absence of the queen; but some can escape the queen inhibition and lay in the presence of the queen. These cheating workers are attacked by other workers that make police for the queen and their eggs are eaten (Ichinose and Lenoir 2009). It has also been observed in *A. cockerelli* (Smith et al. 2009).

Interspecific cheating

Cleaning behaviour

Interspecific cooperation is well-known in vertebrates, for examples in cleaner reef fishes. Some cleaner will try to feed directly on the client mucus instead of parasites. Various strategies will limit the spread of cheating behaviour: clients observe cleaners and will avoid more frequently cheaters, a process called "image-scoring" of cleaners (Bshary and Grutter 2006); but cheaters also use altruism with smaller clients (stimulation of the dorsal area of their clients) to improve their image and deceive their image-scoring (Bshary 2002). Cleaner-fishes (*Garra rufa*, Cyprinidae, called "the doctor fish") from Turkey are used in human therapy for psoriasis. In the natural habitat *G. rufa* grazes on aquatic plants and mainly feeds on plant materials that mostly consist of benthic chrysophytes and phytoplankton (Yalcin-Ozdilek and Ekmekci 2006). Interestingly, the fish specialize and tear, pierce or polish the skin (Larrochelle 1010). They may be a good model for studies on the evolution of alternatives strategies in cooperation and cheating.

Cleaning behaviour has been discovered in ants where a small species (*Dorymyrmex*) licks the bigger harvester ant (*Pogonomyrmex maricopa*) in Arizona desert. The harvester ant adopts a cleaning posture. We suppose that the benefit of the client is prophylactic (Moffett 2010). We studied myrmecophile beetles *Sternocoelis hispanus*, which enter the nest of the host ants *Aphaenogaster senilis* using chemical mimicry. They are tolerated as they have the host colony odour. Are they simple guests? We observed that they spend considerable time licking the ants and the larvae. This may be also an example of cleaning behaviour (A. Lenoir, unpublished).

Mutualistic communities

Fungus-growing ants are a good model for studies in mutualism. 45 million years ago, they have domesticated a fungus used to feed their larvae. There is a fungus parasite (*Escovopsis*) which can destroy very efficiently the garden and kill the colony. The ants defend as they have actinomycete (*Pseudonocardia* in *Acromyrmex* or *Mycobacterium* and *Microbacterium* in *Atta*) bacteria on their cuticle providing an efficiency antifungal (Mueller et al. 2008; Oh et al. 2009). This antifungal was considered to be ideal as the parasite fungus did not develop resistance. It was impossible if we think Darwinian evolution with arms race between host and parasites (The red queen). In fact, it appeared that some *Escocopsis* strains are more or less sensitive. The symbiosis is much more complicated as yeasts have been recently discovered; which feed on good bacteria, and render more difficult the fight against the parasite (Little and Currie 2007; Youngsteadt 2008). Metagenomics now permits to discover new bacteria which degrade cellulose in termites showing that the symbiosis is very complex (Warnecke and al. 2007). These bacteria probably exist also in fungus-growing ants. The symbiosis in fungus-growing ants is a stable mix of cooperation and conflicts.

Bacteria and eukaryotic hosts

Some bacteria are endosymbiontic that live inside host cells and reproduce along with them. Acquiring functionality by adopting a bacterium intracellularly has happened repeatedly in insects, particularly those that ingest plant sap. *Buchneria aphidicola* produces amino acids for its aphid host (Wernegreen and Moran 2001). In carpenter ants *Camponotus* these bacteria are known since one century, their role has been confirmed only a few years ago: they also have a nutritional function (Feldhaar et al. 2007). We discovered that they also stimulate the immune system of the host (de Souza et al. 2009). *Buchnera* has a tiny genome, under 650 kb, specialized on what aphids cannot make, while many gene products needed by the symbiont are now made by the aphid. The interests of both bacteria and host are therefore bound and little conflict occurs. More and more data will appear in the next years concerning endosymbiotic bacteria; see 2 talks in this meeting (Dedeine 2010; Giron 2010).

Micro-organisms are a superb model for evolutionary studies due to their rapid reproduction (one generation every 30 minutes in bacteria).

Quorum sensing: decision-making process used by decentralized groups to coordinate behaviour. Many species of bacteria use quorum sensing to coordinate behaviour according to the local density of their population. Similarly, social insects use quorum sensing to make collective decisions about where to nest.

Bacteria

The growth and survival of bacteria depend upon excreted products ("**public goods**") that perform a variety of functions such as scavenging nutrients, communication, defence, formation of biofilms and movement. For example, bacteria use diffusible chemical signals to coordinate group behaviour through governing gene expression of the receptor cell (a quorum sensing process). A use of a public good is a dilemma for the maintenance of cooperation (Trisos and Brown 2010).

The pyocyanic bacillus *Pseudomonas aeruginosa* is a dangerous pathogen for mammals (nosocomial infections in humans). When injected to mice they multiply and at a certain density they kill them in a few days. They produce siderophores (molecules fixing iron, here a pyoverdin), available for the secretory cell but also for neighbours. It represents a cost for the producer which is altruistic. Cheater mutants do not produce siderophores, but profit of those produced by neighbours and exploit kin selection. Here also mutant cannot invade the population as cooperation is favoured by relatedness (Griffin et al. 2004; Diggle et al. 2007). A great discover was that in mice mortality is lower when a mixture of wild and cheaters was injected. May be in a few years we will treat infections by injection of cheating strains?

Resistance to antibiotics in bacteria represents a massive challenge for the treatment of infectious disease in humans and animals as 70% of bacteria are resistant to at least one antibiotic. It is predicted that cheating bacteria will limit the spread of resistance genes in antibiotic free environments.

Interactions between different bacteria species appear to be more and more common, forming very complex communities which are now studied and called "**Microbiomes**". Trillions of microbes live harmoniously in the mammalian gut but the composition can be altered contributing to obesity (Li and Hotamisligil 2010). The human skin is a large, heterogeneous organ that protects the body from pathogens while sustaining a lot of microorganisms that influence human health and disease. Skin harbours very complex bacterial communities studied by metagenomics with already 205 different genera (Grice and al. 2009). Cooperation can evolve between microbial species and permit to observe this evolution in the lab in real time. For example, the banal *Escherichia coli* and the dangerous *Salmonella enterica* (responsible of typhus) interact. *Salmonella* feeds on the waste byproducts excreted by the colibacillus. A colibacillus mutant was constructed, unable to synthesize methionine. When the mutant and *Salmonella* are cultured in a special nutritional minimal media (only with lactose), they are unable to grow together because there was insufficient methionine for *E. coli* and thus insufficient sugar byproducts for *Salmonella*. In *Salmonella* populations some mutants excrete spontaneously small amounts of methionine and these cooperative mutants rapidly increase from 1% to more than 80% in only 10 generations. It allows the met-E. coli mutants to growth normally (Harcombe 2010).

Conclusion

In conclusion, mutualisms present a challenge for evolutionary theory. How is cooperation maintained in the face of selection for selfishness and cheating? See the review by (West et al. 2007). When variability is introduced into organisms each generation, in the form of less cooperative individuals, choice is maintained. This suggests that the presence of cheaters and cheater species in many mutualisms is central to the maintenance of partner choice and, paradoxically, cooperation itself (Foster and Kokko 2006).

A new concept: “organismality”

In their famous article in Nature (Szathmary and Maynard Smith 1995) described the major evolutionary transitions: cell, organism and the superorganism of eusocial animals. Social insects, some squids and naked mole-rat are considered to form superorganisms and it is the choice of Hölldobler and Wilson to give this name to their last book (Hölldobler and Wilson 2009). But a new concept just appeared, the concept of “organismality”: assemblages of multi-species with commonality of interests, extensive cooperation and very little conflict that when combined, makes for an optimum level of adaptation and are nearly free of conflicts (Queller and Strassmann 2009). These entities are subject to natural selection which can either be always the theatre of conflicts or attain stability. One very recent example was that polysaccharides are degraded in the human gut by bacteria providing the enzymes. Japanese are able to degrade a sugar (the porphyrane) from red algae used in sushi, but the bacteria are absent in occidental people. It indicates that selection populations can evolve with different bacterial flora according to their alimentary regime (Anonymous 2010; Hehemann et al. 2010). Gene transfer between the organisms in these assemblages are probably much more frequent that it could be hypothesized; see for example one recent paper showing carotenoid horizontal gene transfer between a fungus and the pea aphid (Fukatsu 2010; Moran and Jarvik 2010) or the shift of transposons across the *Rhodnius* and mammals (opossum, squirrel monkey) or pond snails (Gilbert et al. 2010). It appears that this new research field will be promising for behavioural ecologists.

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