



An ESF Exploratory Workshop



The evolution of cooperation and cheating in Nature

Montpellier, France, 12--15 May 2003 Tel. 04 67 61 32 51

Scientific Report

Marie Charlotte ANSTETT

Introduction

The workshop was held in Montpellier with 30 attendants. Cooperation theory fails to explain how mutualisms evolved from antagonistic interactions and how they persist in the face of invasion by specialized parasites that purloin benefits. This theory also fails to explain the persistence of mutualism against temptation for cheating behaviour in the mutualists themselves. The goal of the workshop was to work toward filling this gap by contrasting and synthesizing both theoretical and empirical work on a variety of model systems, by researchers using different empirical techniques.

On the first two days the participants had the opportunity to present their results and their questions about the subject of the workshop. In spite of the extremely high diversity of study systems, with different focal points, ranging from molecules to community ecology, and with a high diversity of scientific questions, much common ground was perceived and many fruitful discussions began with a lot of interaction between specialists in different fields. No important contradictions were perceived between the participants. However, broadly accepted generalizations about mutualisms are still difficult to advance since counter examples of each theory are frequent. The first part of this report is a synthesis of these scientific presentations. On the third day of the workshop, small groups auto-organized for free discussion or building of possible cooperations. This was followed by a restitution and synthesis of the emergent questions. The last day of the meeting was a synthetic discussion by the group on open questions on mutualism, and on those now considered solved. The main scientific results are presented in the second part of this report

Synthesis of the scientific presentations

A total of 22 presentations, each one half hour in length were given (see programs and summaries in the annex). Talks were grouped according to the type of study system, since each study system is associated with some more or less specific techniques and a more or less specific explanation for the stability of the study system.

The session on plant-rhizobia interactions underlined the importance of plant sanctions in the stability of this mutualism. New results were presented by F. Denison and T. Kiers on the level of plant sanctions against cheating nodules, plants being able to retaliate against individual cheating nodule. These results could influence our thinking about the stability of this mutualism. Another aspect of this association is partners recognition at the time of the initiation of the interaction. Bacteria must recognise compatible host plants and host plants have to attract compatible bacteria. The impact of plant domestication on symbiotic specificity was also discussed.

The second session treated interactions between animals and their associated micro-organisms, these interactions ranging from true mutualism to parasitism. In a parasitic system (malaria), the influence of different vaccines strategies on the virulence of the parasite and on consequences on the host population was detailed by M. McKinnon. The integration of both field data and mathematical models on the evolution of virulence leads to the surprising conclusion that vaccines can lead to a higher mortality rate in the host population. This kind of counter-intuitive result underlines the importance of interdisciplinarity in understanding complex systems. The two other systems concerned symbionts of animal digestive tracts. Symbionts in locust gut form a community of different organisms, showing no impact on the animal in laboratory conditions. The advantage given by the symbionts seems to be a better resistance to diseases. This opens the question of a possible regulation of the gut flora by the host. In this case, the gut symbionts form a community and have to be considered as such, with evolutionary consequences quite different from a one to one interaction such as the examples presented by A. Douglas. In these more specific and more co-evolved cases, the interaction between the aphid and its digestive symbionts is obligate, opening the possibility for the host plant of the aphid to target its defences against the symbiosis itself. Since these interactions are costly, it entails the possibility of cheating by both partners.

The third session concerned interactions between “microbes”, a family of study systems with very short generation time for both organisms, allowing direct observation of on going evolution. Velicer experimentally studied the destabilizing force of cheaters in an example of cooperation within species. Dionisio then presented the case of the evolution of antibiotic resistance, which, from the point of view of the bacteria constitutes the evolution of symbiosis with a plasmid. The persistence of conjugative plasmids is still not understood, since they transfer horizontally. JB Ferdy developed the result of a modelling study on the impact of the mode of transmission on the evolution of cooperation between plasmid and chromosome. He underlined the importance of the shape of the trade-off between vertical and horizontal transmission of plasmids. In this case, the stability of a cooperative plasmid depends on the existence of a non cooperative plasmid, showing that the stability of mutualism might depend on the existence of pathogens. S. Brown tickled the concept of mutualism with evidence showing that parasites may help their host in competitive interactions and thereby become mutualists.

The presentations of the next morning concerned plant/insect mutualisms. In some ant /plant interactions, the plant seems to sanction non cooperative ants by stopping the production of the reward (in this case the domatia in which ants nest). Whether this sanction is a coevolved trait or a direct result of herbivory is still an open question. McKey explained the coexistence of cooperating and cheating strategy of two ant species on one plant by niche differences. The mutualist species adopts a space-perennial strategy and is disadvantaged by disturbance. Modification of the disturbance regime, especially by human activities, can possibly favour the cheating species. Another cheating strategy for ants is to castrate their host plant, resulting in diversion of resources from reproduction to growth, favouring the ants. Ghazoul showed that floral ant repellents are widespread among plants and repel most ant species. This could be a pre-existing trait preventing ants from parasitizing plant-pollinator mutualisms.

The obligate pollination system between *Trochilus* and *Chiastocheta* was studied from both theoretical and experimental approaches. This is the kind of integration of different disciplines this workshop wanted to promote. In this case too, the partitioning of resources in several niches seems to be central to explaining the coexistence of both mutualists and cheaters. The importance of the level of benefit was also underlined by Després, who show that the outcome of the interaction may dramatically change between for example individual and population levels. Kjellberg detailed the evolution and extinction of some traits of mutualism by analysing the phylogenies of figs and fig wasps. He also underlined the impossibility of defining a mutualism by a cost-benefit analysis in the case of an obligate mutualism. Such mutualisms must be defined at a higher level. Mazancourt also questioned classical definitions of mutualism, by discussing for example the evolved dependency of grazed plants on their grazers.

The last session concerned a synthesis of different theoretical models of mutualisms and their relation to intra specific models of cooperation. Dionisio showed that cooperation may increase or decrease with group size depending on the kind of benefit involved in the interaction. He also pointed out the importance of determining the meaning of relatedness in models from the social sciences. The two last talks concerned intra-specific cooperation, showing how this kind of interaction can lead to divergence, even possibly to speciation, and to the structuring of communication.

Synthesis of the round tables

DEFINITION OF MUTUALISM

The definition of mutualisms based on the matrix of ecological interactions found in most text books is definitely outdated. It has been replaced by the cost benefit framework, but this now also must be modified, since it cannot apply to obligate mutualisms. The level at which the costs and benefits of the interaction are defined is central to the way we perceive host-symbiont interaction and perhaps also to its functioning.

There is a difference between the operational/ecological/proximate definition and the evolutionary/ultimate definition of the mutualism but the link between these two components of the concept still needs to be developed.

A special feature of mutualism is the bi-directional control of the partners and the fact that each partner is the niche of the other, with the potentiality for each partner to select its symbiont and thus modify its niche. For this aspect, we have to invite community ecologists to future meetings.

EXPLAINING MUTUALISM

The question “Are the current theoretical approaches (including the ones developed to understand intra-specific cooperation) adequate for explaining mutualisms?” was followed by a quite lengthy discussion showing that the answer is probably “not yet”. However, the participants agreed on a number of statements/mechanisms that are important.

There is not a single set of rules to explain mutualism. We do know some general conditions that prevent mutualism but we do not know the sufficient conditions to have a mutualism.

There is a conditional dependence of the outcome of the interaction in evolutionary and ecological time.

Most mutualisms are asymmetric (e.g. in generation time, selective pressures) but most models involve symmetric players.

Mutualisms are now explained by individual selection and inclusive fitness. “Naïve group selection” is now excluded from the field but the importance of interdemic and species selection is still open.

The field of mutualisms is rich with handy metaphors that can hide the diversity of phenomena. For example sanction /host regulation; escape from mutualism/reversibility; cheat/parasitism; addiction/dependency.

In the future, patterns of death and migration (and thus geographical pattern) of the interaction are probably central to the understanding of mutualisms and care must be taken to consider the whole life cycle of each interactor.

The study of mutualisms has to be placed in the context of the community; especially when the partner is a community (e.g. gut symbionts). In these cases is a cow rumen different from an island? Or in other words does the fact that the environment is a living organism change the structure and the evolution of the community?

MUTUALISM AND PARASITISM

The evolution of parasitism towards mutualism seems to be more frequent than the reverse and we have to explain why. What determines whether a mutualist can return to a free living stage? If a symbiont gains control of its host, does it become a parasite? Is mutualism managed virulence? Do mutualists that evolved from parasites and commensals have different traits? Do mutualists always have complementary resources, or do they also under circumstances compete for the same resource?

OPEN QUESTIONS

Vertical transmission of symbionts (from the host to its offspring) is central to the explanation of cooperation since it is similar to kin selection at the intra-specific level. However, it does not matter if vertical transmission is theoretically beneficial if developmental constraints are barriers to prevent it. The mode of transmission is also linked to the expected diversity of symbionts, with horizontal transmission having the same effect as sexual reproduction of increasing the diversity and the vertical transmission having the same effect as asexual reproduction of decreasing the diversity.

How does mutualism stability vary with diversity of symbionts?

The reason why so many mutualisms are horizontally transmitted is still under debate.

There are many interactions between symbiosis and sex with many symbionts giving up sexual reproduction. The idea that they have lost sex because they are in a perfect and stable environment still remains to be tested.

CONCLUSION

During the round tables, confrontation of different aspects of the study of mutualisms gave rise to many theoretical questions. The science of mutualism is at the interface between many scientific fields and we need to integrate all these disciplines to understand the ecology and evolution of mutualism. This workshop was a first step in this direction and the participants found a great interest in the interdisciplinarity of the workshop. We decided to build a web site to promote further interactions of the group (broadening these interaction to include other participants as well) and to keep open the possibility of cooperation between scientists. The web site will be published before the end of July. We also decided to apply for funding of an ESF network on the subject, to try to produce a general theory of mutualism that is still lacking.



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FINAL PROGRAMME

May 12. Small Things

- 9:00** Registration in CEFE
9:30 Welcome address (M.-C. Anstett & D. Yu)
9:30 Presentation of ESF & LESC (R. Verheyen)

Rhizobia, Chair D. Yu

- 9:40-10:10** R. Denison. Why don't symbiotic cheaters displace cooperators sharing the same individual host?
10:10-10:40 T. Kiers. Evidence for legume host sanctions against rhizobial cheaters
10:40-11:10 P. Young. Genetic variation in host specificity in the rhizobium-legume symbiosis

11:10-11:40 Coffee

Microbes in animals, Chair R.F. Denison

- 11:40-12:10** A. Buckling. The diversity of locust gut symbionts determines disease susceptibility
12:10-12:40 M. Mackinnon. Malaria - a parasite behaving as it should
12:40-1:10 A. Douglas. Co-operation and the breakdown of co-operation in animal-microbial symbioses

1:10-2:30 Lunch

Bacteria things, Chair A. Buckling

- 2:30-3:00** G. Velicer. Competitive fates and population-level effects of *Myxococcus* developmental cheaters
3:00-3:30 F. Dionisio. Spread of conjugative plasmids among different bacterial strains and species
3:30-4:00 S. Brown. Indirect host/parasite mutualism: virus-carriers invade resident bacteria

4:00-4:30 Coffee

- 4:30-5:00** James Cook. Two for the price of one: Co-pollinators of figs
5:00-5:30 JB Ferdy. Conjugation and the evolution of cooperation between plasmids and chromosome in bacteria

May 13. Animal-Plant interactions and General Theory

Ants & plants, Chair M.-C. Anstett

- 9:30-10:00** D. Yu. Host coercion in ant-plants
10:00-10:30 D. Mckey. Dispersal polymorphism in a mutualist plant-ant and it's specific parasite : the ghost of colonisation past?
10:30-11:00 J. Ghazoul. Repellent flowers make plants more attractive: the resolution of ant-plant conflicts over pollinators

11:00-11:30 Coffee

Globeflowers & figs, Chair J. Cook

- 11:30-12:00** B. Godelle. A plurispecific model of mutualism evolution
12:00-12:30 L. Despres. Evolutionary stability of mutualism between globeflowers and globeflower flies
12:30-1:10 F. Kjellberg. Greed: the evolution of active/passive pollination in the *Ficus*-Agaonid wasp mutualism

1:10-2:30 Lunch

Theory, Chair M. Mackinnon

- 2:30-3:00** C. de Manzacourt. What is mutualism?
3:00-3:30 F. Dionisio. Public goods dilemma, the tragedy of the commons and evolutionary biology

3:30-4:00 Coffee

More theory, Chair S. Gandon

- 4:00-4:30** M. Hochberg. Socially-mediated genetic divergence
4:30-5:00 M. van Baalen. Common Language or Tower of Babel: on the evolutionary dynamics of signals and their meaning
5:00-5:30 M. Dufaÿ. Conflicts of interests and partners encounter in the mutualism between the dwarf palm and its specific pollinator

May 14 - Round Tables

- 9:30** Round tables
11:00 **Coffee**
11:30 Round tables
1:30 **Lunch**
2:45 Round tables
4h00 **Coffee**
4:30-5:30 Synthesis of the results of the day

8:00 **Conference Diner – Le Petit Jardin**

May 15 – Round Tables

9:30	Round tables
11:00	Coffee
11:30	Round tables
1:30	Lunch
2:45	Synthesis
4:00	Coffee
4:30-5:30	Synthesis

SUMMARIES

Sam Brown: Indirect host/parasite mutualism: virus-carriers invade resident bacteria

Parasites have been suggested to be determining agents in the success or failure of biological invasions. Indirectly-mutualistic interactions have been proposed to modify the invasibility of parasite/host couples. Here, we parameterised the direct interaction-costs of a parasite (temperate bacteriophage virus) on two lineages of bacterial host (phage-carriers and susceptibles). We then modelled the indirect consequences of these interactions, and confirmed these results in competition experiments. We show that whereas phage are a direct burden to their carriers due to probabilistic host lysis, by killing competitor bacteria they may indirectly benefit bacteria made immune by carrying isogenic phage. This is similar to previously described colicin-mediated effects involving release of colicins [killer proteins] upon cell death of producers and kin immunity via antidote production. However, unlike colicin-proteins, phage can amplify on susceptible competitors which become factories producing more viruses. This amplification makes phage-carriers able to invade well-mixed susceptibles even faster when rare, whereas colicin-producers can only win when abundant, as we expect to be the general case in the altruistic provision of public goods. Thus, whereas bacteriocins are only beneficial as a resident strategy, phage-carrying favors invasion.

Angus Buckling: The diversity of locust gut symbionts determines disease susceptibility

Decreasing species diversity has been shown to increase community susceptibility to invasion by foreign species. It follows that the diversity of symbiotic gut microflora may also affect the invasibility and hence virulence of pathogens. We tested this hypothesis by measuring the ability of an insect pathogen to invade and kill locusts that differed in gut microflora diversity. Locusts with diverse gut microflora were invaded less well by the pathogen and had lower mortality rates.

Mathilde Dufay: Conflicts of interests and partners encounter in the mutualism between the dwarf palm and its specific pollinator.

Mutualisms are ubiquitous in nature, but according to current theory the conflicts of interest between mutualists should make these interactions unstable. Studies based on game theory have underlined the importance of the process of partner encounter in determining the evolutionary stability of mutualisms. The aim of this study was to understand, using an experimental approach, how the conflicts of interest between partners in a horizontally transmitted mutualism, and the emission of signals facilitating partner encounter in each new generation, interact to affect the evolutionary stability of the mutualism.

We studied the mutualism between the palm *Chamaerops humilis* and its specific pollinator *Derelomus chamaeropsis*, which reproduces inside the inflorescences of its host plant. In this mutualism, female plants are “cheaters”: they kill the eggs of their pollinator, leading to a phenomenon of pollination by deceit, imposing high costs on the pollinator and constituting a potential source of instability for the interaction. Our study of the mode of pollinator attraction by *C. humilis* has revealed a unique system, previously unknown in angiosperms. The pollinators are attracted by volatile

compounds emitted by leaves, and not by flowers. Furthermore, the chemical signal released shows sexual dimorphism in the total quantities of volatile compounds emitted by plants. This difference leads the pollinator to encounter male plants more frequently and to visit them more often. However, we showed that the chemical composition of the signal was extremely variable among individuals, excluding any possibility of qualitative distinction between signals emitted by male and female plants and preventing the evolution of an active choice behaviour by the pollinator. Our results contradict predictions from theory and show that the inability of a partner to “punish cheaters” can paradoxically stabilise a mutualism.

Claire de Manzacourt: What is mutualism?

A mutualism is defined as a mutually beneficial interaction between individuals of two species. However, the benefits depend on which genotypes are involved in the interaction, notably differential adaptation to partner species. The *proximate response* measures the short-term benefit or cost incurred by the addition or removal of the partner species, without allowing for any adaptation. By contrast, the *ultimate response* measures the long-term effect of adding or removing the partner species over evolutionary time, thus allowing for the focal species to adapt to the absence or presence of its partner. While in the former case the *same genotypes* are compared with and without the partner, in the latter *different genotypes* are compared with and without the partner. Either response can be used as a criterion to measure the benefit of an interaction, leading to two different definitions that we call *proximate mutualism* and *ultimate mutualism*. Finally, *mutualistic evolution* is defined as investment in a mutualistic partner. In the mutualism literature, different authors tend to use different criteria for defining mutualism, leading to important consequences for our understanding of mutualism. Examples from the plant-herbivore debate highlight a need for distinguishing between these alternative criteria. I will discuss mechanisms that lead to the differences between different definitions of mutualism, present the advantages and the problems associated with each, and point at the new questions resulting for the study of mutualisms.

Ford Denison: Why don't symbiotic cheaters displace cooperators sharing the same individual host?

Potentially mutualistic microbial symbionts often share individual hosts with other symbionts that may vary in cost and benefit to the host. Examples include mycorrhizae and the symbiosis between legumes and N₂-fixing rhizobia. Within-host symbiont diversity creates a potential Tragedy of the Commons in which making significant investments in the welfare of the host does not appear to be evolutionarily stable. Host sanctions targeted at individual strains, based on monitoring their actual symbiotic performance, could reduce the temptation to cheat and thereby explain the evolutionary persistence of mutualism. The legume-rhizobium symbiosis is especially suitable for experimental work on mutualism because of its practical importance, experimental tractability, and apparent diversity of host and symbiont strategies. For example, Rhizobium evolution is apparently shaped by individual selection in some legume hosts and by kin selection in others.

Laurence Despres; Evolutionary stability of mutualism between globeflowers and globeflower flies

I document costs for globeflower (*Trollius europaeus*) to breed its pollinating flies (*Chiastocheta spp.*) in 26 populations sampled throughout the altitudinal and latitudinal range of this arctic-alpine European plant, during several years. Despite considerable variability in ecological conditions and fly densities, the percentage of seeds lost to pollinators remains strikingly stable over time and space. Both plant and insect traits are involved in stabilising the interaction, but these traits are not necessarily coevolved. Density-dependent competition among larvae co-developing in globeflower fruits appears to be the most important stabilising mechanism of this mutualism. Fly density is maintained at levels optimizing net seed production at the plant population level, while breeding larvae always decreases individual plant fitness. In this context, plants killing larvae should be selected. However, the red queen is likely to run faster for short-lived parasitic insects than for long-lived plants, resulting in an asymmetrical arm race between the parasite and the plant.

Francisco Dionisio: Spread of conjugative plasmids among different bacterial strains and species.

Mutualistic relationships between plasmids and bacteria have been studied mainly with non-conjugative plasmids (plasmids that are not able to transfer to other cells). However, the ability of conjugative plasmids of self-transfer makes them interesting entities to study mutualistic relationships. In this workshop I'll discuss 1) the role of some bacteria in the spread of conjugative plasmids among other strains; 2) the effect of co-evolution of plasmid-bacteria and the behaviour of the evolved plasmid in new bacteria. In this second point, it will be discussed why, contrary to previous works, competition with other bacteria may have an important effect in the evolution of plasmid-bacteria co-evolution.

Francisco Dionisio: Public goods dilemma, the tragedy of the commons and evolutionary biology

The development of Evolutionary Biology has profited both from economical and environmental sciences. The most important example is, perhaps, the adaptation of Game Theory into Evolutionary Game Theory. Meanwhile, expressions such as "tragedy of the commons" and "collective action" have slowly invaded evolutionary biology papers to discuss issues such as the evolution of virulence. In this workshop I purpose to discuss the differences and similarities between the "tragedy of the commons" and the "logic of the collective actions". Then, I'll discuss some consequences to evolutionary biology.

Angela Douglas: Co-operation and the breakdown of co-operation in animal-microbial symbioses

Symbiotic micro-organisms co-operate with their animal hosts, apparently against their immediate selective advantage. In particular, they provide the host with nutrients that would otherwise support elevated microbial proliferation. The proximate and evolutionary determinants of these co-operative traits will be considered, using the symbioses between bacteria and herbivorous insects and between micro-algae and corals as examples. The collapse of these co-operative nutritional interactions may contribute to the breakdown of symbioses, as observed in coral bleaching and in symbioses of herbivorous insects as the primary target of plant defences.

Bernard Godelle: A plurispecific model of mutualism evolution

Plant/seed-eater pollinators mutualisms involve pollinator which larvae eat a fraction of the seeds produced by the plant. Among the very few reported cases of such mutualisms is the globeflower-globeflower flies symbiosis, which is unique in that it involves several congeneric fly species (*Chiastocheta* genus) coexisting within a single host plant species, *Trollius europaeus*. These flies exhibit contrasted oviposition behaviors that result in a more or less beneficial outcome for the plant. We designed an adaptive dynamics model to investigate how morphological traits of globeflower could affect the evolution of oviposition in its pollinating flies. Whatever the shape of the flower, we found that evolutionary branching occurs for the age of flowers in which flies choose to lay their eggs. This corresponds to a specialization of flies on different ecological niches. Once this specialization is established, we found that the closed shape of the corolla is likely to increase competition between larvae in one of the niches. The result is that the fly occupying this niche is selected to reduce the number of eggs it lays per flower. This can be seen as a first step in the evolution of a mutualistic behavior. Flies in other niches retain their parasitic behaviour. In addition, if the globe shape of the flowers permits such a manipulation of competition, it can be positively selected because it decreases parasitic loads within flowers. We found that this evolutionary step stabilizes the mutualism association between globeflower and flies.

Michael Hochberg : Socially-mediated genetic divergence

I present a simple model to show that social selection can lead to genetic divergence. The evolution of social discrimination causes the congealing of phenotypically similar individuals into different, spatially distinct tribes despite the presence of cheaters. Genetic tribal formation is only obtained, however, for certain types of social behavior: altruistic and selfish acts can produce tribes, whereas spiteful and mutualistic behaviors never do. Moreover, reduced hybrid fitness at genotype borders leads to the selection of mating preferences, which then spread to the core areas of the respective genetic tribes. Unlike models of resource competition, the model generates genetic divergence isolation in an ecologically homogeneous environment. This theory provides a framework for how individual-level interactions mold lineage diversification, with parapatric speciation as a possible end product.

E. Toby Kiers: Mutualism Stability: Experimental evidence for legume host sanctions against rhizobial cheaters

Explaining mutualistic cooperation between species remains one of the greatest problems for evolutionary biology. We have proposed that cooperation can be enforced by the active rewarding of cooperation or the punishing of less cooperative behavior. Here we provide experimental evidence that legume plants use such sanctions to enforce cooperative fixation of atmospheric N_2 by symbiotic rhizobia bacteria within their root nodules. We forced normally mutualistic rhizobia to "cheat" from symbiotic cooperation by replacing the usual atmosphere ($N_2:O_2$) with an N_2 -free atmosphere ($Ar:O_2$). Our results from a series of experiments at three spatial scales (individual plants, half root systems and individual nodules) showed that such cheating significantly decreased the reproductive success of rhizobia, suggesting that plants withhold resources to uncooperative rhizobia or reduced their fitness in some other way. Furthermore, we provide evidence consistent with a specific mechanism: plants impose sanctions by decreasing the permeability of the nodule to O_2 . Statistically significant decreases in internal O_2 concentration and O_2 permeability of nonfixing nodules was demonstrated within 48 hours.

Finn Kjellberg: Greed: the evolution of active/passive pollination in the *Ficus*-Agaonid wasp mutualism

Ficus and agaonid wasps have been engaged in an obligate species-specific mutualism for about 100 million years. The fig is a closed urn-shaped inflorescence the inside of which is lined by uniovulate female flowers and male flowers. The pollen laden wasps enter receptive figs, pollinate and oviposit in some of the ovules and die. Each wasp larvae develops at the expense of one ovule. Some weeks later the wasps emerge, load pollen in their natal fig and leave in search of a new fig. About 2/3 of wasp species pollinate actively. Before leaving their natal fig, they go to the anthers and load pollen into pollen pockets. When they oviposit, they also remove some pollen from the pockets and deposit it on the stigmas. Active pollination seems to have appeared once and has been lost numerous times. The evolutionary trajectory of mode of pollination is the result of a simple conflict, the trees want pollen to go to seeds, the wasps want pollen to go to their galls. This results in a series of coevolved traits that drive the evolution of the association.

Marg Mackinnon: Malaria - a parasite behaving as it should

Malaria parasites, despite having a great evolutionary age, cause much morbidity and mortality in their hosts. Evolutionary theory explains this departure from symbiosis in terms of the parasite's need to extract resources from its host in order to transmit. We have shown using a laboratory model for malaria, *P. chabaudi* infecting mice, that this theory is well justified for malaria. Parasites that multiply faster do transmit more, but also suffer higher morbidity. Data from the field on the human malaria, *P. falciparum*, are also strongly supportive of this hypothesis.

Minus van Baalen : Common Language or Tower of Babel: on the evolutionary dynamics of signals and their meaning

We investigate how the evolution of communication strategies affects signal credibility when there is common interest as well as a conflict between communicating individuals. Taking alarm calls as an example, we show that if the temptation to cheat is low, a single signal is used in the population. If the temptation increases cheaters will erode the credibility of a signal, and an honest mutant using a different signal ('a private code') will be very successful until this, in turn, is cracked by cheaters. In such a system, signal use fluctuates in time and space and hence the meaning of a given signal is not constant. When the temptation to cheat is too large, no honest communication can maintain itself in a Tower of Babel of many signals. We discuss our analysis in the light of the Green Beard mechanism for the evolution of altruism.

Greg Velicer: Competitive fates and population-level effects of *Myxococcus* developmental cheaters

Using the social bacterium *Myxococcus xanthus*, we have tested the short-term competitive fates of mixed cheater and wild-type strains over multiple cycles of cooperative development. Cheater/wild-type mixes underwent several cycles of starvation-induced multicellular development followed by spore germination and vegetative population growth. The population sizes of cheater and wild-type strains in each pairwise mixture were measured at the end of each developmental phase and each growth phase. Cheater genotypes showed several distinct competitive fates, including cheater persistence at high frequencies with little effect on total population dynamics, cheater persistence after

a major disruption of total population dynamics, the self-extinction of cheaters with wild-type survival, and total population extinction. Our results empirically demonstrate that social exploitation can destabilize a cooperative biological system and increase the risk of local extinction events.

Peter Young : Genetic variation in host specificity in the rhizobium-legume symbiosis

We have dissected the microvariation in host specificity in a population of the bacterium *Rhizobium leguminosarum* biovar *viciae*, which forms root nodules on legumes in the tribe Viciae. At the ecological level, we found the majority of strains were able to nodulate all the legume hosts tested, but we also found strains with some specificity in their choice of hosts. At the genetic level, we found polymorphic markers of the nodulation gene region that correlated strongly with host range and host preference. At the biochemical level we found relatively little variation in the Nod factor signals produced by the rhizobia, but indications that differences in specificity may lie in the production of inducers by the hosts and their reception by the NodD protein in the rhizobium. If validated, this will mean that we have traced natural variation in a significant ecological property (host range) back through the biochemical mechanism to the underlying DNA sequence differences.

POSTER

Nigel Raine: Guards versus thieves: antagonistic interactions between two ant species coexisting on the same ant-plant

Despite the great abundance of plant species known to form mutualistic ant associations, to date very few ant species have been discovered that exploit the resources exchanged by co-operating partners. Here we describe the first example of an ant-plant in which both mutualist (*Pseudomyrmex ferrugineus*) and parasitic (*Camponotus planatus*) ant species occur simultaneously on the same individual host (*Acacia mayana*).



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