17TH-20TH APRIL, 2011
MONTE VERITA, ASCONA, SWITZERLAND

SOCIAL DECISION MAKING
BRIDGING ECONOMICS AND BIOLOGY

Conference Programme

Timetable

SUNDAY 17TH APRIL.

12.30 - 16.30 Locano station shuttle

13:00 - 17:00. Arrival and registration

17.00-19.00. Welcome Session
17:00 - 17:20. Welcome

17:20 - 18:20. Alan Grafen

18.20-18.40 Samir Okasha
18.40-19.00 Christine Clavien

19.00 - 21.00. Dinner

MONDAY 18TH APRIL.

09:00-11:00.
Peyton Young & David W. Stephens

11:00 - 11:30. Coffee

11:30 - 12:30. Contributed Talks Session 1
11.30-11.50 – Andrew King
11.50-12.10 – Andrew Mell
12.10-12.30 – Redouan Bsary

12:30 - 14:00. Lunch

13:50 - Conference photo

14:00 - 15:50. Contributed Talks Session 2
14.00-14.20 – Roman Zakharenko
14.20-14.40 – Sam Yeaman
14.40-15.00 – Joanna Masel
15.00-15.20 – Michal Arbilly
15.20-15.40 – Tamas David-Barrett

15:40 - 16:20. Coffee

16:20 - 18:00. Contributed Talks Session 3
16.20-16.40 – Aimee Dunlap
16.40-17.00 – Shakti Lamba
17.00-17.20 – Nichola Raihini
17.20-17.40 – Sinead English
17.40-18.00 – Rahul Bhui

19:00 - 21:00. Dinner

TUESDAY 19TH APRIL.

09:00 - 11:00.
Arnon Lotem & Colin Camerer

11:00 - 11:30. Coffee

11:30 - 12:30. Contributed talks Session 4
11.30-11.50 – Max Burton-Chellew
11.50-12.10 – Riccardo Pansini
12.10-12.30 – Mikael Puurtinen

12:30 - 14:00. Lunch

14:00 - 16:40. Contributed Talks Session 5
14.00-14.20 – Livio Riboli-Sasco
14.20-14.40 – Silvia de Monte
14.40-15.00 – Eric Dickson
15.00-15.20 – Marco Archetti

15:20 - 16:20. Poster Session and Coffee

16:20 - 17:40. Contributed Talks Session 6
16.20-16.40 – Ralph Dobler
16.40-17.00 – John Lazarus
17.00-17.20 – Jean Baptiste André
17.20-17.40 – Mike Cant

17.40 - 19.30. Free Time.

19:30 - 21.30. Dinner

WEDNESDAY 20TH APRIL.

09:00 - 11:00.
Paul Seabright & John McNamara

11.00 - 11.30. Closing discussion.

11:30 - Conference close.

11:30 - 3.30. Locano station shuttle

Please be seated 5 minutes before a session is due to start.

We will strictly adhere to the 15 minute time limit for contributed talks.

Plenary Talks

Contributed Talks

Sunday 17th April

Monday 18th April

Contributed Talks Session 3

Tuesday 19th April

Contributed Talks Session 4

Contributed Talks Session 5

Contributed Talks Session 6

Posters

15:20-16:20 Tuesday 19th April

Plenary Talk Abstracts

Sunday 16.00
The chasm between biology and economics
Alan Grafen

The similarities between biology and economics in their study of behaviour have been very fruitfully explored. However, there are also very deep differences between the two approaches, and it is useful to try to bring them into sharp focus. In particular, the biological maximand is (at least roughly) number of offspring, and this has strong formal properties that can be very un-economic. The sophistication of inclusive fitness on the biological side also has strong implications for how social decision-making can easily be framed.

Monday 9.00
The Dynamics of Social Innovation
H. Peyton Young

Social norms are the building blocks of social institutions, but the mechanisms that induce norm shifts are complex and not well understood.   Changes in norms are typically caused by one of three mechanisms: they can be triggered by idiosyncratic changes in individual perceptions and expectations, by changes in general external conditions (such as prices or technology), and by deliberate experimentation with novel ideas. While these mechanisms differ in some respects, they have similar dynamic effects: change tends to be slow and fitful at first, then accelerates rapidly once a critical threshold is crossed. Of particular importance to norm diffusion is the structure of the social network through which agents obtain information. This paper characterizes the rate at which a social innovation spreads based on three factors: the extent to which agents interact in small clusters, the payoff gain of the innovation relative to the status quo, and the amount of noise in the best response process. The analysis shows why social innovations tend to occur in large jumps rather than through small incremental improvements.

Monday 10.00
Why is social learning special?
David W. Stephens

In many situations, animals seem especially sensitive to social experience. Why should social learning be special? We develop the idea that social learning is special for the same reasons that other privileged forms of learning exist.: because these forms of experience have, in the course of evolutionary history, provided reliable indications about appropriate actions in uncertain situations. To develop this idea, we present a simple model that considers the fitness value of behavioral plasticity that we call the flag model. We show how we have tested this model at both evolutionary and behavioral time scales. Building on this foundation, we explain how the model can be extended to deal with 'prepared learning,' that is to explain why animals may learn some associations both readily than others. We present data from a study using experimental evolution that bears on this point. Finally we ask what this approach might tell us about the 'specialness' of social learning. Notably our approach emphasizes the lawfulness of learning phenomena by stressing the common origins of social learning and other forms of prepared learning.

Tuesday 9.00
Evolution of learning and decision making in a social group: how clever should a sparrow be?
Arnon Lotem

Social animals face complex situations in their everyday life. Sparrows, for example, experience variable outcomes of their foraging behavior and are concurrently involved in frequency-dependent social games. Combining theory and experiments, we investigate how the behavior of social animals could have evolved to produce adaptive decisions. Our experiments demonstrate that learning is involved in both foraging and strategy-choice decisions, and that learning rules are likely to interact with simple conditional responses and phenotypic traits. In light of these results, we use agent-based evolutionary simulations to model the learning process explicitly, testing the adaptive value of different learning rules in the context of social games in finite populations. Applying this approach we can offer possible explanations for: a) the evolution of apparently sub-optimal decision making, b) biases in using social versus private information, and c) stable variation in learning or cognitive abilities in animal societies. More generally, we believe that understanding the evolution of learning and decision making mechanisms can frequently resolve the tension between normative and mechanistic approaches.

Tuesday 10.00
The cognitive neuroscience of strategic thinking
Colin Camerer

Evidence from fMRI, experimental choices and field data suggests that human strategic thinking is typically limited to one to three steps of iterated reasoning. I discuss parametric models of these data and speculate about their biological and evolutionary bases.

Wednesday 9.00
Beyond Reason: the role of the emotions in building economic and social trust
Paul Seabright

A long tradition in economic theory as well as in Western intellectual thought sets reason in opposition to the emotions and hypothesizes that the growth of complex modern societies involves the gradual replacement of emotions by reason in economic exchange, bureaucratic management, political leadership and the administration of justice. This lecture will discuss the contrary evidence that has been accumulating in recent years in psychology, neuroscience and behavioral economics, and propose an alternative view. Far from replacing the emotions, reason is effective by harnessing the emotions in the service of creating social trust. Understanding the cognitive and emotional foundations of social trust is both an exciting research agenda for the future and the source of potentially importance insights for public policy.

Wednesday 10am
Individuality in evolutionary game theory
John McNamara

Within animal populations the behaviour of an individual tends to be consistent in that, given the animal faces the same situation at different times, its behaviour is similar at these times. Behavioural traits such as boldness and aggressiveness also tend to be correlated. In other words animals have different personalities. But why do individuals show this inflexibility in their behaviour? And why are there typically a range of personalities in populations? I will not give any definitive answers to these questions, but highlight general issues and present two mechanisms that help preserve personality differences in populations.

I will also explore the consequences of the presence of differences. Game theoretical models often ignore differences between individuals. Using a series of examples I will demonstrate that such differences are not innocuous noise, but can fundamentally change the nature of a game. Differences promote the need to have extensive interactions to find out about a partner, so changing the strategy set and hence the outcomes of the interaction. Differences promote choosiness and the need to be socially sensitive. I will illustrate how all of these factors affect how cooperative individuals are likely to be with one another.

Talk Abstracts

Sunday 17th April 2011

Welcome Session

Sunday 18.20
On 'Veil of Ignorance' arguments in Economics and Evolution: Harsanyi meets Mendel
Samir Okasha

This paper explores conceptual and formal links between the famous 'veil of ignorance' argument of Harsanyi and Rawls in social choice theory, and fair Mendelian segregation in evolutionary biology. Harsanyi and Rawls argued that society should choose between alternatives based on how an 'impartial observer', with an equal chance of becoming any individual in society, would choose between them. Harsanyi claimed that this would lead to utilitarianism, i.e. maximisation of total group welfare, a result known as the 'impartial observer theorem'. A number of authors have noted the analogy between Mendelian segregation and the veil of ignorance. Fair meiosis in effect genes are placed behind a veil, with equal chances of being found in any particular gamete. This aligns the interests of all the genes in the genome, ensuring they work for the common good. However this analogy has never been spelled out precisely, which is what I attempt to do. I suggest that fair meiosis means that we can given a biological interpretation to Harsanyi's impartial observer theorem. Interestingly, this biological version of the theorem is free from many of the conceptual difficulties that plague Harsanyi's original.

Sunday 18.40
The many ways experimental economists use the notion of altruism
Christine Clavien

Altruism is a deep and complex phenomenon that has been analysed by scholars of various disciplines, including biology, philosophy and psychology. More recently, experimental economists have started to make extensive use of the notion of altruism. My aim is to investigate what sort of altruism experimental economists have in mind and what conclusions can be drawn from their research.

In their famous book Unto Others, E. Sober and D.S. Wilson made a useful distinction between "evolutionary" and "psychological" altruism. This distinction refers to two separate research contexts in which the notion of altruism has been used: A pressing question for early evolutionary biologists was to explain how "biological altruism" (Abi), that is, behaviours that increase other organisms' Darwinian fitness (measured in terms of expected number of offspring) at a cost to the actor's own fitness come to be selected in evolution. Thanks to the efforts of William Hamilton and others, this difficulty has been resolved. Unaware that altruism could pose a challenge to the theory of evolution, psychologists and philosophers started debate over the possibility of "psychological altruism" (Aps). Their aim is to sort out what kind of primary motives drive helping or moral actions. Primary motives directed towards the needs and well-being of other individuals, earn the label 'altruistic' whereas primary motives aimed at some personal benefit for oneself are considered 'self-interested'.

In this paper, I intend to show that, although one could get the impression that experimental economists investigate on these two notions of altruism, they mostly use two other ones. At times, they cast altruism as a behaviour that benefits other individuals at some cost to the agent, and if there is no way for the agent to reap future benefits from his behaviour. Despite its resemblance with Abi, this notion of altruism – I shall coin it "behavioural altruism" (Abe) – should be differentiated because it fails to fulfil at least two conditions of Abi (calculus in terms of offspring and time span considered). At other times, they define altruism as other-regarding preference and concern for the well-being of others. Again, despite its similarity with Aps, this version of altruism – I shall coin it "preference altruism" (Apr) – does not equate with it.

Monday 18th April 2011

Contributed Talks Session 1

Monday 11.30
Social decision-making and collective behaviour in animal groups: Some examples from sheep, baboons and people.
Andrew King

Have you ever been stood with a group of colleagues following a day of conference talks trying to choose which restaurant to dine at? I expect so, but do you remember how you made your choice, all the while trying to stick together and not lose one another? There are a number of ways you could have arrived at your decision. You may have followed the decision of the group member who set-off purposefully down the High Street, or you all may have agreed to go to the restaurant declared 'the best in town' by the person with local knowledge of the city. Such situations are just as common in the animal world. Swap 'restaurant' to 'foraging patch' and we have a description for the type of foraging decisions faced by almost all social animals, every day of their lives. But these are not trivial decisions; a number of consecutive bad choices—where a group are led to poor foraging areas, or risky habitats—can be fatal. Such social decisions are made even more difficult where animals face unexpected dangers or an environment which is constantly changing, something all animals are increasingly encountering in our rapidly changing world. In this talk I will discuss coordination and decision-making in animal groups with some examples from sheep, baboons, and humans. I will highlight the simple rules-of-thumb (or heuristics) that individuals use, and how individual heterogeneity, and the costs and benefits related to decision outcomes, can determine individual contributions to collective patterns of behaviour.

Monday 11.50
The Handicap Principle and Illicit Markets
Andrew Mell

There are at least two empirical puzzles regarding criminals. First, despite the efforts of police forces to eliminate them, they act in a brazen or ostentatious manner. Second is the question of how illicit trade can take place at all given that criminals do not have access to the government's contract enforcement services. We build a model explaining how brazen behavior can help solve the enforcement problem. If criminals differ in their ability to evade the police, then less able criminals, foreseeing less future surplus, will be less disciplined by reputational concerns. In order to avoid being cheated by such incompetent criminals, more competent criminals can act in a brazen way and only trade with others who do likewise. This signalling and screening sorts the competent and incompetent criminals as the latter cannot afford to mimic the brazen behavior and trade and is similar to the selection for a handicap in evolutionary biology.

Monday 12.10
Ontogenetic effects on cooperative behaviour in marine cleaning mutualism
Redouan Bshary, Sharon Wismer & Ana Pinto

Evolutionary game theory typically assumes that behavioural strategies have a strong genetic component. In some cases, however, ample opportunity for learning exists. Learning could be particularly useful if conditions and hence associated optimal strategies differ unpredictably on very small scales. We will present data that suggest that these conditions apply to the cleaner wrasse *Labroides dimidiatus*. These fish occupy small territories where other reef fishes visit to have ectoparasites removed. Conflict arises because cleaners prefer protective client mucus over ectoparasites. Cleaners are open water spawners, with pelagic egg and larval stages. This destroys any local genetic structure. When young cleaner return to reefs they may settle in different habitats, which may be just meters apart from each other. Habitats are linked to client density, diversity, and composition. This may in turn affect the relative importance of learning for the development of optimal strategies. We compared cleaners from two habitats: patch reefs ('simple environment') and continuous reefs ('complex environment'). We found that cleaners from continuous reefs were more willing to eat cooperatively against their preference, and more able to solve cognitive tasks linked to cleaning interactions. Models need to incorporate mechanisms to account for such differences.

Contributed Talks Session 2

Monday 14.00
The Role of Passionate Individuals in Economic Development
Roman Zakharenko

In this paper, I merge two theories – theory of "passionate individuals" by Gumilev [2009(1989)] and Memetics by Dawkins [1976] – to develop a formal growth theory that states that societies become more developed when their members have more intrinsic motivation to solve problems of social importance (i.e. make "cultural contributions").

Individuals derive utility from genetic fitness (i.e. the number of surviving children) as well as from cultural fitness, defined as the amount of appreciation ("honor") of one's cultural contribution by future generations. To make a cultural contribution, one must study/honor cultural contributions of the past, which leads to multiple steady states. In the survival steady state, individuals expect that no one in the future will be interested in their cultural contribution, which makes them allocate all energy onto maximization of genetic fitness and care little about cultural contributions of the past. In the passionate steady state, individuals expect high appreciation of their cultural contribution and thus spend a lot of energy onto making such a contribution, which makes them highly appreciate cultural contributions of the past. Empirical implications of theory are also discussed.

Monday 14.20
Network architecture, learning, and the spread of (mis)information
Sam Yeaman

How does misinformation spread through a population and persist? To what extent do differences in the architecture of social networks affect the spread of misinformation, relative to the ways that individuals transmit, evaluate, and retain pieces of information (traits)? Here we assume that traits vary in their transmissibility, and that each trait also has an intrinsic value that is positive or negative, which could represent its effect on fitness or welfare or the accuracy of its information content (or some other abstract value). We use individual-based simulations to study how the accumulation of traits with different values is affected by different social network architectures and by different rules governing the ways that individuals transmit, evaluate, and retain or discard traits according to their value. While considerable research has explored how network architecture affects percolation processes, we find that the relative rates and modes by which individuals transmit and evaluate traits can have much more profound impacts on the average value of accumulated traits (i.e. the level of (mis)information) than differences in network architecture. In particular, any variance among individuals in the rate they evaluate and discard traits reduces the average value of culturally accumulated information, irrespective of whether highly connected individuals are also common evaluators. This suggests that changes in communications technology may have influenced cultural evolution more strongly through changes in the amount of information flow, rather than the details of who is connected to whom.

Monday 14.40
What if everybody else thought like me?
Joanna Masel

Models of learning, reciprocity and altruism cannot explain all aspects of observed human contributions in the public good game. I will present an alternative model, based on and extending an existing model of animal foraging. Human players recognize a correlation between their own contribution and the likely contributions of other players. The correlation is calculated by treating a player's own conjectured contribution just like any other data point within a Bayesian learning model. Although players recognize that this correlation is not causal, by using quasi-magical thinking they nevertheless choose to maximize expected utility conditional on their own action rather than standard expected utility. Results from the model explain previously puzzling quantitative trends in the data.

Monday 15.00
Evolution of social learning when high expected payoffs are associated with high risk of failure.
Michal Arbilly, Uzi Motro, Marcus W. Feldman and Arnon Lotem

In an environment where the availability of resources sought by a forager varies greatly, individual foraging is likely to be associated with a high risk of failure. Foragers that learn where the best sources of food are located are likely to develop risk aversion, causing them to avoid the patches that are in fact the best; the result is sub-optimal behavior. Yet, foragers living in a group may not only learn by themselves, but also by observing others. Using evolutionary agent-based computer simulations of a social foraging game, we show that in an environment where the most productive resources occur with the lowest probability, socially acquired information is strongly favoured over individual experience. While social learning is usually regarded as beneficial because it filters out maladaptive behaviours, the advantage of social learning in a risky environment stems from the fact that it allows these learners to circumvent risk aversion and revisit the best food source despite repeated failures. These results demonstrate that the consequences of individual risk aversion may be better understood within a social context and suggest one possible explanation for the strong preference for social information over individual experience often observed in both humans and animals.

Monday 15.20
The evolution of social brain in an agent-based model of group-level cooperation
Tamas David-Barrett and Robin Dunbar

In this paper we present an agent-based network model of behavioural synchronisation: we show how the evolution of language, gossip, and strategic lying affected the maximum size of a human group that faced the problem of group-level cooperation. We show that (1) memory and calculation capacity limits group size; (2) the ability to pass on third party information (a) is evolutionarily adaptive for the individual agent, and (b) increases the maximum group size; (3) in socially stratified groups, low status agents are best off passing on third party information originating from high status nodes, while high status agents are best off passing on the latest information irrespective of the status of the source; (4) in socially stratified groups, it is advantageous for agents to pass on incorrect information (lie) up the ranking, but not down; and (5) such strategic lying by the individual and its detection by others, puts a high calculation burden on the agents, while at the same time decreasing group efficiency and thus limiting group size. In summary, we show that memory, language, and gossip assumes larger brain and allows larger group size, while language-facilitated strategic lying assumes further increase in brain size, but limits group size. As a consequence, language-using agents should have 'too large' calculation capacities compared non-linguist benchmarks.

<u>Contributed Talks Session 3</u>

Monday 16.20
Effects of reliability on whether to follow social or floral signals in foraging bumblebees
Aimee Dunlap, Anna Dornhaus, and Dan Papaj

How do animals weigh the relative value of social and individual sources of information? One link between theory of individual learning and theory of social information use is the importance of reliability of acquired information. Information, whether personal or social in origin, must be reliable for learning to be of benefit. Nectar-foraging bumble bees provide a good system for evaluating the relative role of reliability in individual versus social learning. Bees show robust individual trial and error learning of floral attributes of many types. Bees also use a variety of social cues to inform their floral choices. Using a factorial design, we varied the reliability of floral versus social information in predicting the presence of a nectar reward. If following basic economic predictions, bees should rely primarily on the more reliable source of information. Deviations from this prediction can give us a window into the evolutionary importance of each information type. And indeed, bees do deviate from our economic predictions, with unreliability having stronger effects on use of social information than use of personal information. Moreover, both types of information interact across levels of reliability. The interacting effects of reliability in personal versus social information in particular suggest that the role of reliability in one source of information must be considered in the context of reliability in the other source.

Monday 16.40
Demography and ecology drive variation in cooperation across human populations
Shakti Lamba & Ruth Mace

Large-scale cooperation between unrelated humans is a major evolutionary puzzle. Current theory posits that such cooperation evolved via group-level selection acting on populations amongst which variation is maintained by cultural transmission. Critically, selection can occur at the group-level only if stable behavioural variation is maintained between populations in the face of migration. Cross-cultural variation in cooperation is taken as evidence supporting these cultural group selection models. However, the observed variation may reflect adaptive responses to different ecologies. We test the hypothesis that variation between populations is driven by differences in demography and local ecology rather than culture. We use one-shot, anonymous ultimatum games, public goods games, and a new 'real-world' measure of behaviour to demonstrate significant variation in cooperation across 21 villages of the same endogamous small-scale forager society. This within-culture variation is comparable to that found previously across 15 different small-scale societies. We identify individual and population descriptors that explain some of this variation. Finally, we find that behaviour in an economic game correlates with a 'real-world' measure of cooperation. Our findings challenge cultural group selection models of large-scale cooperation as behavioural variation driven by demographic and ecological factors is unlikely to maintain stable differences essential for selection at the population-level. We recommend re-interpretation of cross-cultural data on cooperation predominantly sampled from one (or few) populations per society; behavioural variation currently attributed to cultural 'norms' may be explained by local evolutionary dynamics.

Monday 17.00
Male cleaner fish, Labroides dimidiatus, adjust punishment of female partners according to the stakes
Nichola Raihani

Punishment can operate as an important deterrent to would-be cheats in cooperative interactions (Clutton-Brock & Parker 1995; Fehr & Gächter 2000, 2002). In humans, the severity of cheating affects the strength of punishment which, in turn, affects the punished individual's behaviour in subsequent rounds (Egas & Riedl 2008; Nikiforakis & Norman 2007). Here, we show such flexible adjustments for the first time in a non-human species, the cleaner wrasse, Labroides dimidiatus. We exposed pairs of cleaners to a single model client offering two types of food, preferred and non-preferred. Analogous to real cleaner-client reef fish interactions, one of the pair eating a preferred food item led to model client removal and was treated as cheating by the other cleaner. Male cleaners punished their female partners more severely in two experimental situations where female cheating caused a greater payoff reduction to the male. First, larger, dominant males punished females more severely when females cheated during interactions with high value, rather than low value, model clients. Second, manipulation of the size asymmetries within pairs resulted in cheating females receiving more punishment from similar-sized males. This pattern may arise because, in this protogynous hermaphrodite, cheating by similar-sized females may reduce size differences within the pair to the extent that females change sex and become reproductive competitors (Nakashima et al. 2000). In response to more severe punishment from males, females refrained from eating preferred food and thus behaved more cooperatively. Our results highlight the need for future studies to explore punishment as a quantitative trait when aiming to explain its evolution and persistence.

Tuesday 17.20
Variation in growth strategies in cooperative meerkats
Sinéad English & Tim Clutton-Brock

In stable social groups where body size is a predictor of success at attaining the dominant position, individuals may strategically modify their growth rate according to their position in the hierarchy. Such strategic growth could be achieved if individuals adjust their food intake according to the relative costs and benefits of increased body mass. Growing too fast may be costly, for example, if dominant individuals monitor subordinate growth and direct aggression to minimise any threat to their position. Evidence for strategic growth and its consequences in wild populations of cooperative species is lacking, requiring both detailed behavioural observation and repeated measures of body mass over an individual's lifespan. Here, I examine variation in growth strategies in groups of cooperative meerkats in which there is intense intrasexual competition for the dominant breeding position. Using long-term data from a wild population of habituated individuals, I investigate whether subordinate individuals adaptively increase their growth rate according to the relative benefits of being larger than their competitors; and if dominant individuals target aggression to faster growing individuals to minimise the threat posed to their valued position.

Monday 17.40
Comparing chimpanzee and human strategy in the game of Matching Pennies
Rahul Bhui

Comparing the actions of multiple species in interactive settings suggests what mental abilities and neural mechanisms are responsible for strategic behaviour. We contribute to the sparse experimental literature on this topic by analyzing data from chimpanzees and humans playing the game of Matching Pennies. Players each choose one of two actions, with one player (the "Matcher") wanting to match the other's choice and the second (the "Mismatcher") wanting to play the opposite of the first's choice. We find that chimpanzees play close to the predicted game theoretic solutions, whereas humans play further away from the predictions but attain higher payoffs, supporting the long-standing view that humans have a prodigious capacity for cooperation. We also see that Mismatchers have consistently longer reaction times than Matchers even when payoffs are symmetric, indicating a role-based cognitive disparity which could be predicted based on past neuroeconomic studies but not classical game theory.

Tuesday 19th April 2011

Contributed Talks Session 4

Tuesday 11.30
Understanding human cooperation in Public Good Games
Max Burton-Chellew

The results of numerous public goods experiments have revealed a consistent result of intermediate cooperation that declines rather steadily over repeated rounds of the experiment. Whilst much has been made of these above zero (and therefore 'irrational') levels of voluntary contributions to public goods, there is still no agreed upon explanation. Participant learning would arguably appear to be the most parsimonious explanation but has often been rejected or simply ignored in favour of explanations that rely on pro-social preferences and /or strong reciprocity. Participants are argued to be responding to the contributions of other participants, and the relative difference between their own contributions and the average level of the group. Whilst the data fit these post-hoc explanations, learning cannot be ruled out because the scope for reinforcement learning correlates with the relative difference in participant contributions. We directly test the role of reinforcement learning in public good experiments and argue that the overall pattern of results from numerous public good experiments can largely be explained by such a mechanism. Whilst we cannot yet rule out strong reciprocity or pro-social preferences, we can perhaps provide a more parsimonious explanation for the typical result, and also one that, in contrast to the leading theories, is consistent with the effects of changes in group size and Marginal Per Capita Return (MPCR).

Monday 11.50
The need of cooperation partners induces wild vervet monkeys to act according to supply and demand
Riccardo Pansini

A number of theoretical papers have investigated the mechanisms by which cooperation may evolve but very few studies have examined the social setting in which cooperation naturally occurs. In this study we experimentally test the law of supply and demand in three groups of vervet monkeys engaged in a cooperation experiment. In these experiments, individuals belonging to two classes of different sizes have to cooperate in order to obtain a food reward. I intentionally assigned the individuals to two fictitious classes, one comprised of two individuals and the other comprised of the remaining members of the group. Criteria to administer rewards were subsequently linked to the assignment of class: a reward was only administered if cooperation partners were of a different class. I predicted that the value of the contribution to the cooperation of a member of the small class is relatively higher than the value of the contribution of a member of the large class. This should lead to an asymmetrical division of the reward and/or a shift in the exchange rates for 'social commodities', such as grooming or tolerance. The experiment induced the monkeys to cooperate first at the feeders, and to exchange social behaviours differently after, as a result of having cooperated. To test market theory models, I analysed whether the distribution of exchange of beneficial behaviours had changed due to the reward criteria based on assigned class. Because one class was less numerous than the other, its members acquired a privileged status and became in demand as cooperation partners. After cooperating the monkeys adjusted social

behaviours' exchanges in favour to the smaller class of cooperators. They therefore adapted to the law of supply and demand as predicted by biological market theories.

Tuesday 12.10
Between-group competition and human social behaviour
Mikael Puurtinen

A distinctive feature of human behaviour is the widespread occurrence of cooperation among unrelated individuals. Explaining the maintenance of costly within-group cooperation is a challenge because the incentive to free-ride on the efforts of other group members is expected to lead to decay of cooperation. However, the costs of cooperation can be diminished or overcome when there is competition at a higher level of organizational hierarchy. I will describe the results from experiments where we have studied the role of between-group competition on within-group cooperation, and on the use and effects of costly punishment. Further, I will describe results from an experiment designed to test if between-group competition emerges spontaneously as a consequence of individual decision making in groups. All experimental results underscore the importance of between-group competition in motivating human cooperative behavior, and the psychological inclinations of humans to perceive ingroup and outgroup social interactions differently.

Contributed Talks Session 5

Tuesday 14.00
Evolving information in living systems, a pathway for the understanding of cooperation and major transitions
Livio Riboli-Sasco

We define information in living systems as a reproducible and versatile catalyst. We argue that a key dimension for the evolution of information and the understanding of life is informactivity, a measure of the contribution to fitness of information. We then move to a clarification of information processing characteristics. We organise these characteristics into three sets related to content-holding processes, interfacing and transferring processes. We argue that evolution can play with mobility and interoperability of information which are aggregates of first order characteristics. We also argue that a better understanding of how these processes evolve will lead to a better and more exhaustive perception of major transitions in evolution. We then exemplify how in certain "pro-cooperative" environments interoperability co-evolves with cooperative behaviours. We argue that a Red Queen process affecting the way informations about public good production are interoperated may allow for cooperation to be maintained.

Tuesday 14.20
Group formation and the evolution of sociality
Silvia de Monte

The formation of sizable groups is a fist key step in the emergence of sociality. Within the realm of microorganisms, 'evolutionary players' with primitive communication and processing skills, social behaviour is associated to peculiar aggregation processes, as for instance in *Dictyostelium discoideum*. We adopt here a game-theoretical approach to elucidate the role of group formation in the evolution of sociality. Players are endowed with a binary social strategy, underpinning the group size distribution faced by an individual. Within groups, individuals play a public goods game, where the cost of cooperation corresponds to the cost of enhanced aggregation proneness. In this setting, the coupling of the evolutionary dynamics with the that of group size distribution leads to the establishment of social behaviour. Sociality is shown to evolve under weaker hypothesis than in cases where group size is held constant by neglecting the process of group formation. The general results will be illustrated by means of a toy model for microbial aggregation, where group formation stems from differential adhesiveness.

Tuesday 14.40
Social Identities in Evolutionary Equilibrium
Eric Dickson

The role that social identities play in influencing behaviour is of increasing interest to game theorists and experimentalists in economics and political science. This paper presents a model in which social identity commitments emerge endogenously in evolutionary equilibrium, discusses comparative statics of the model suggesting when identity commitments are likely to be more or less intense and relates the findings to empirically-observed cases.

Tuesday 15.00
Evolutionary game theory of public goods, from microbes to terrorists
Marco Archetti

I will show that in generalised public goods games (not restricted to the N-person prisoner's dilemma), in which the public good is a non-linear function of the individual contributions (which is the case in most social species ranging from bacteria to humans) intermediate levels of cooperation can be stable in one-shot interactions without assortment, spatial structure, relatedness, punishment, fairness or other forces that are commonly believed to be necessary to maintain cooperation in evolutionary biology. This helps explain (i) some apparently puzzling observations about cooperation in microbes, (ii) the frequency of suicide terrorist attacks in recent conflicts and (iii) the paradox of voting in political economy. It also allows a prescriptive approach to the study of cooperation: we can devise practical ways to improve the production of public goods in social dilemmas without invoking assortment, relatedness, punishment or repeated interactions.

Contributed Talks Session 6

Tuesday 16.20
Behavioural attainability of evolutionary stable strategies in repeated interactions
Ralph Dobler

Theory for the evolution of social interactions based on continuous strategies often assumes for simplicity that expressed behaviours are independent from previous encounters. In reality, however, such dependencies are likely to be widespread and often strong, generating complex behavioural dynamics. To model this process and illustrate potential consequences for the evolution of behavioural interactions, I consider the behavioural dynamics of the interaction between caring parents and their demanding offspring, a prime example for long series of interdependent and highly dynamic interactions. These dynamics can be modelled using functions describing mechanisms (reaction norms) for how parents and their offspring respond to each other in the interaction. This way the general conditions under which the behavioural dynamics converge towards a proximate equilibrium can be established and I refer to such converging interactions as behaviourally stable strategies (BSSs). I further demonstrate that there is scope for behavioural instability under realistic conditions; that is, whenever parents and/or offspring 'overreact' beyond some threshold. By applying the derived condition for behavioural stability to evolutionary models of parent-offspring conflict resolution, numerical simulations show that evolutionarily stable strategies (ESSs) of current models are not necessarily behaviourally stable. Because behavioural instability implies that expressed levels of behaviours deviate from the ESS, behavioural stability is required for strict evolutionary stability in repeated behavioural interactions.

Tuesday 16.40
Cooperation and communication: How much can cheap talk do?
John Lazarus and Jonathan Sayers

Can cheap talk enhance cooperation, or does the risk of deception render costless communication worthless? We describe an infinite population evolutionary model of one-shot dyadic encounters employing the Assurance, or Stag Hunt, Game to examine this question. To the 'basic' cooperation and defect (C and D) strategies we add agents with two additional traits: a signal (honest or dishonest concerning their 'default' action, C or D) and a belief system (each signal is either believed or disbelieved [i.e. the action opposite to that signalled is believed]). Signals have no cost, emulating cheap talk scenarios. Agents choose the best response to the action they believe the other party will select (C against C, and D against D). When signalling agents meet a basic C or D agent, from whom they receive no information, they play their default action. The ESS zones CC and DD fill the two-dimensional space defined by the starting frequency of C play and the pattern of payoffs. Our results show that: (a) the addition of signalling agents to the basic (non-signalling) game increases the size of the CC zone; (b) in the area of the space in which the increase in payoff for choosing the best response is greater when that response is D (call it 'payoff advantage is to D'), signalling agents are extinct at the ESS (and are therefore 'catalysts' for cooperation since they increase the CC zone); (c) when the payoff advantage is to C, signallers go to fixation and basic strategists go extinct; (d) in the latter case the ESS signallers are default D players that believe C signals and disbelieve D signals (and half signal honestly, and half dishonestly). Therefore when these signallers meet they always play CC and gain the benefit of joint cooperation. These ESS agents are 'cautious optimists' in the sense that they play D in the absence of information (so never suffer the sucker's payoff) but believe C signals and disbelieve D signals. Cheap talk therefore either acts as a catalyst for non-signalling

cooperation, or results in cautiously optimistic signalling, depending on the payoff structure of the game.

Tuesday 17.00
Social opportunities and the evolution of fairness
Jean-Baptiste André and Nicolas Baumard

I will present a model on the evolution of the division of a resource between two individuals. Individuals are paired randomly and split the resource according to a strategically asymmetric bargaining mechanism akin to the ultimatum game, in which a dominant individual (so-called the "proposer") makes an offer that the subordinate (the "responder") can only entirely accept or refuse. In this interaction, evolution does not lead to a fair division of the resource but rather tends to favor the dominant side. We show that the possibility for subordinate individuals to play a different role in a future interaction, would they refuse the current interaction, is the key lever to overcome this difficulty. When the role individuals play in each interaction is chosen at chance, our analysis shows that each individual receives at least a fraction $1/2 - c$ of the resource at evolutionary equilibrium, where c represents the cost of postponing the interaction. When postponing the interaction has a very small cost, the resource division is quasi-fair. As compared to our first analysis on the subject (André and Baumard, in press), this novel analysis helps highlighting the fact that fairness is not a consequence of the possibility for individuals to change (or choose) partner per se; it is fundamentally a consequence of the possibility for dominated individuals to change role. Fairness evolves when individuals are "socially totipotent", and partner switching thus leads to the evolution of less injustice only to the extent that it gives dominated individuals a fresh chance of being dominant. This might offer a tentative way to help explain why fairness has evolved in humans, but not in other social species.

Tuesday 17.20
Evolutionary conflict and its resolution: help from economics?
Michael Cant

Evolutionary conflict arises when the fitness optima of two or more individuals (or individual units of selection) cannot be satisfied simultaneously. Conflict arises between loci within the genome over phenotypic expression; between cell lineages in multicellular organisms; and between the members of family groups and cooperative societies over food and reproduction. Game theoretical models have been widely employed to study the outcome of these biological conflicts. These models are strikingly similar to models of economic conflict, although these parallels are little appreciated. Here I suggest examples where economic models are useful to understand patterns of social evolution; and discuss the role of information in conflict resolution at different levels of organization.

Poster Abstracts

Tuesday 19th April 2011
15:20-16:20

Sex roles in parental care: specialisation and cooperation
Zoltán Barta, Tamás Székely Andás Liker and Freya Harrison

Biparental care usually occurs if one parent cannot raise the young alone, and its stability is maintained if parents only partially compensate for decreases in their partner's care effort. Behavioural and evolutionary models of biparental care generally assume that "care" is a unidimensional variable. In reality, care often comprises several qualitatively different behaviours and investment in one care behaviour (e.g. provisioning) may be incompatible with investment in another (e.g. defence). In many species with biparental care, males and females specialise in providing different types of care. We hypothesised that sex-specific costs of care behaviours and ensuing role specialisation could stabilise cooperation between parents, as it would result in compensation becoming more costly or even impossible. We used an individual-based simulation to test this hypothesis. Our results may be applicable to behaviours other than parental care, as individuals can exhibit role specialisation in various social contexts.

An expert system for the global environmental crisis
Fredrik Dalerum

Human populations are threatened with dramatic changes to their living environment. We are facing species extinction rates far exceeding historical baselines, a climate change that we still have not been able to quantify the extent, rate and consequences of, and a rapid depletion of much of natural capital such as old growth forest, clean water and fossil fuels. However, many areas of the earth are still experiencing exponential human population growth, which coupled with a continued increase in economic growth projects to increased destructive human footprint on the environment. Promoting change into a more sustainable relationship with our environment is therefore of extreme urgency. In this presentation, I suggest a simple decision tree aimed at identify the highest priority areas to facilitate such a transition. These include developing novel economic theory that includes a sustainable utilization of physical resources, finding political solutions for implementing such theory in governmental policy, and, perhaps most importantly, developing ways to increase in human awareness of environmental and sustainability issues. Such awareness will likely be necessary for a global transition in human values from being centred around material possessions towards being centred around non-material values. Such a fundamental change in human value norms is likely to be necessary for the success of any political implementation of novel sustainable economic theory.

Dynamic evolution of a cloud seeding project
Federica Farolfi and Daniele Cassese

Water is fundamental in any society, involved in every productive process and indispensable for civic use. Water supply is subject to uncertainty, because weather variability has a pivotal impact on the hydrological cycle, substantially affecting production costs and output levels. Weather modification techniques allow to reduce the negative impact of weather variability on the economy. Among the existing techniques, clouds-seeding showed to be an effective and sustainable tool to increase precipitation (Shivaji Rao, 2005), and to reduce the cost of a negative shock in case of drought. Although the single operations of seeding have an affordable costs, the initial investment in order to create the necessary infrastructures can be very high (Dennis, 1980; Griffith, 2010). It involves buying aircraft and generators, hiring meteorologists and statisticians to study the design of the operations and control their results (Keyes, 2006). For the single agent alone, it would not turn to be profitable to undertake the initial investment, but if a meaningful number of agents interested in cloud seeding join their efforts, they may be able to create a centralized structure, with all the means and competencies necessary to cloud seeding operations.

This centralized structures act on a regional basis, so that, once the investment is realized, all the agent in a certain region can have access to cloud seeding operations at an affordable cost. The investment decision problem can be analyzed as a public good game with voluntary contribution. Following Hauert et. al. (2002) we consider a large population of players, randomly chosen for playing the game. There are three possible strategies in the population: The Good, who contribute to the investment; The Bad (free rider), who does not contribute to the investment but, once realized, enjoys the advantages of cloud seeding; The Dry, who is against weather modification and does not participate to the game. The amount of resources necessary for creating the structure in a certain region can be considered as given, so the investment would be profitable only when the number of cooperators is such that the single share of the total cost is less than the individual benefit. In order to discourage defection, assume that there is an agreement establishing that at the end of each game the goods punish the bads, imposing them a fine proportional to the aggregate loss for the cooperators deriving from not having realized the project. The amount of the fine is increasing in the number of cooperators, so that punishment can be considered as a collective strategy (Bowles, 2004) and is increasing with weather variability. At the end of each stage a certain amount of individuals is matched with a "model" changing its strategy in that of its model if this induces a higher payoff. The evolution of the three strategies is studied by means of replicator dynamics. Results show that if the cost of the fine is high enough, cooperation emerges as a stable strategy and the project is realized. On the other hand, a sequence of positive weather conditions, making the cost of punishment low, may discourage cooperation.

Assortment and repetition: a recipe for cooperation.
Julian Garcia

Economists have often devoted attention to repetition as a means to explain cooperation. Biologists, on the other hand, seem to have stressed the role of population structure. Here we combine these two mechanisms in order to understand how they interact and complement each other. We propose a model with two main parameters: continuation probability in a repeated game and level of assortment of the population structure. By analysing pair-wise stability in a restricted strategy set we were able to classify the parameter space of the model into four regions. Each corresponds to a different predicted level of cooperation. Using computer simulations we show that this result also holds for an infinitely large unbounded strategy set. We show that in the presence of repetition, a marginal change in assortment goes a long way in promoting cooperative behavior.

Echolocation as a source of information for eavesdropping conspecific bats
Klemen Koselj, Björn M. Siemers

Echolocating bats produce high frequency calls, which reflect from surrounding objects. The resulting echoes are used by the callers for orientation in darkness. The echolocation signals are emitted in a pattern that is adapted to the current task (e.g. prey capture). Con- and hetero-specific bats can potentially eavesdrop on this pattern to glean information on the echolocating bat. The aim of our research is to determine whether eavesdropping bats interpret and use information in the echolocation signals emitted by other individuals and whether they use information in the resulting echoes. Here we show that a horseshoe bat's decision whether to attack a prey or not is encoded in its echolocation pattern. Thus, not only current actions of the echolocating bat, but also its intentions can be overheard by nearby conspecifics. This raises further questions about the role of echolocation signals in the social lifestyle of these mammals.

Cooperation and cheating can lead to the evolution of diversity in siderophore-producing bacteria
William Lee

Diversity in siderophore producing bacteria is high, but how such diversity has arisen and how it is maintained remains enigmatic. Siderophores are secreted into the extracellular environments to bind iron; then, they can be taken up by any organism that has the suitable receptor. In other words, organisms (strains, or clones) share their siderophores as a common good. Assuming that the production of siderophores is costly, this common good system may favour non producing siderophore users (cheaters). We suggest that diversity arises from the interplay between siderophore producing (cooperators) and non-producing (cheaters) individuals: when there are many cheaters exploiting a siderophore type it would be beneficial for a mutant to produce a siderophore that is incompatible with the dominant population. Here we analyse a mathematical model of metapopulations to investigate the potential for the emergence of diversity. We found that diversity indeed collapses in the metapopulation when cheaters are absent. When present, cheaters prevent any strains of cooperators from becoming dominant over the others: they counteract genetic drift by regulating the populations of cooperators. However, they are rare most of the time and only appear when one of the siderophore types becomes common.

Do Food-associated Calls Affect the Patch Departure Decisions of Social Foragers?
Lisa O'Bryan

Animals foraging within cohesive social groups benefit by not only maximizing their foraging success, but also maintaining cohesion with groupmates. Group members can collectively achieve these goals by attending to public information about each other's foraging success within a food patch. Doing so will bring each individual's patch quality estimate closer to the true value of the patch, both improving and synchronizing the patch departure decisions of all group members. Thus, individuals within cohesive foraging groups may not only benefit from obtaining public information, but also by facilitating its acquisition by others, a circumstance that can promote signal evolution. My dissertation research aims to test the hypothesis proposed by Valone (1996) that intragroup food-associated calls function by broadcasting information about the caller's foraging success to its groupmates. This challenges standard hypothesis that food-associated calls attract extragroup individuals to a food patch. I am using chimpanzees (Pan troglodytes) as my study system, as they both forage socially and produce an intragroup food-associated call whose function remains unclear. I am conducting playback experiments with captive chimpanzees to determine how broadcasting these calls affects the patch departure decisions of unsuccessful foragers. I expect these studies to clarify the role food-associated calls play in coordinating the foraging decisions of animals within cohesive social groups.

Group-size diversity in multiplayer social dilemmas
Jorge Pena

Social dilemmas and the theoretical puzzle of the evolution of cooperation in sizable groups are studied from a game theoretical perspective using models such as the public goods game and the N-person snowdrift game. In the traditional setup of evolutionary dynamics in infinite and well-mixed populations, the average fitness of cooperators and defectors is calculated from the interactions of groups of N individuals formed at random according to binomial sampling. Despite the fact that group-size diversity is a common feature of both natural and social systems, most of the relevant literature has focused on the simple case where all groups are of the same size, i.e. when N is constant. Here, I study the effects of group-size diversity in three different models: (i) the classic public goods game (i.e. the N-person prisoner's dilemma), (ii) the public goods game with discounting and (iii) the N-person snowdrift game without threshold. Instead of assuming a fixed group-size, N is now a discrete random variable distributed according to different probability functions, such as the Poisson, Geometric and Waring distributions. The results show that, by Jensen's inequality, group-size diversity is effective in promoting cooperation when the difference in the average payoff between cooperators and defectors times the group size is a convex function. As a result, having varying group sizes does not affect the evolutionary dynamics of classic public goods games, but systematically enhances cooperation in the public goods game with discounting. For the N-person snowdrift game without threshold, cooperation is greatly enhanced for low cost-to-benefit ratios while it is slightly hampered for high cost-to-benefit ratios.

Coexistence of cooperators and defectors in well mixed populations beyond Snowdrift games: An escape from the Prisoner's Dilemma in the competition for one limiting resource
Rubén Requejo Martínez

The origin and maintenance of cooperation in biological systems is one of the main issues in evolution. The extensive study of the prisoner's dilemma by evolutionary game theorists has provided a number of mechanisms that promote the evolution of cooperation; however, the implications of resources use and limitation have not been widely studied within this framework. May the limitation of resources available for a population foster cooperation? Here we present a simple model of a well-mixed population of cooperative and non-cooperative individuals where the limitation of resources is considered explicitly. In the absence of resources limitation, the situation equals a well-mixed non-iterated prisoner's dilemma; however resource limitation drastically alters the game structure allowing for stable coexistence between cooperative and selfish individuals. Surprisingly, the generated game structure is different from a Snowdrift game, until now the only case yielding coexistence in well-mixed populations of cooperators and defectors. The origin of this unexpected behaviour roots in a self-organizing process which modifies the interaction payoffs – which are not constant– so that the payoff matrix is tuned to zero. A simplified analytical treatment describing this unexpected outcome is also presented. This result may provide new insights into the origin of cooperation as well as on the maintenance of biodiversity.

Evolution of familial interactions by antagonistic co-adaptation
Dimitri Stucki and Mathias Kölliker

Differences in the optimal amount of resources allocated to depending young by parental care generate an evolutionary conflict. Because parents are equally related to all offspring, but each individual offspring is closest related to itself there is an evolutionary conflict favouring mechanisms in offspring (e.g. begging) which increase their share of obtained investment. To date, the resolution of this conflict was modeled as either purely within-brood or purely between-brood competition. This study is the first to model both forms of competition simultaneously. We use individual based simulations where parents produced a number of clutches, contingent on whether the previous clutches demanded more or less than the maximal resources available. Parental investment is determined by the interplay of parental sensitivity to begging, a baseline amount of investment, clutch size and offspring begging. These traits determine together how much resources are allocated to each clutch and how they are distributed within the clutches. Simulations are currently running. The study shall show how the future reproductive success forces offspring to co-adapt their begging level to parental provisioning traits, and that stable co-adaptation outcomes are possible even in the absence of direct begging costs. Further we plan treatments to investigate the effect of within-brood and between-brood competition on the evolution of parent-offspring communication.

Strategic deception undermines the stability of cooperation in games of indirect reciprocity
Számadó, Sz., Szalai, F. & Scheuring, I.

Indirect reciprocity is often claimed as one of the key mechanisms of human cooperation. Indirect reciprocity works only if there is a reputational score keeping and these scores are homogeneous within the population. That is, each individual can tell with a high probability which other individuals were good and bad in the previous round. Gossip is often purported as a mechanism that can maintain such coherence of reputations in the face of errors of transmission. Random errors, however, are not the only source of uncertainty in such situations. The possibility of deceptive communication, where the signaller aims to misinform the receiver cannot be excluded. Here we show that if deceptive strategies are allowed in the population, then the coherence of reputations collapses and in turn this results the collapse of cooperation. This collapse is independent of the norms, cost and benefit values.

Evolutionary dynamics of social dilemmas in small heterogeneous populations
Bernhard Voelkl

Real world social dilemmas frequently occur in small groups with clear structuring. Here I am studying the evolutionary dynamics of dyadic interaction games on small, heterogeneous graphs. Considering a classical payoff matrix for a dyadic game with payoff S for cooperating with a defector, T for defecting a cooperator, and normalizing the payoff for mutual cooperation to 1 and mutual defection to 0, the S-T parameter space was sampled systematically. I show how population size and heterogeneity alter the parameter range under which cooperation is favored by studying star graphs and multi edge graphs with heterogeneous degree distributions. Finally, I simulate social dilemmas on a sample of real-world social networks. Results of the latter simulations are surprisingly rich, showing that heterogeneity can increase the fixation probability for cooperation for certain parameter combinations while it can decrease it for others.