Cooperation versus Conflict in Ecological Systems

Sixth Symposium in Memory of Merav Ziv

Mitrani Department of Desert Ecology, Blaustein Institute for Desert Research
Ben-Gurion University, Sede Boqer Campus
The Zoological Society of Israel & The Israel Entomological Society

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09:45 Introduction and opening remarks

10:00 Ecology student award in memory of Merav Ziv

Scientific Program

10:15-11:00 **Prof. Amotz Zahavi (Tel Aviv Univ) - Cooperation in biological systems.**

11:00-11:20 **Refreshments**

11:20-11:40 **Prof. Uzi Motro (Hebrew Univ, Jerusalem) – Models of parental investment conflict**

11:40-12:00 **Noam Werner (Tel Aviv Univ & Jerusalem Zoo) - Competition among helpers in cooperatively breeding cichlids**

12:00-12:20 **Dr. Trine Bilde (Univ of Aarhus, Denmark) - Costs and benefits of group living in spiders**

12:20-12:40 **Michal Gruntman (Ben-Gurion Univ) - Physiologically mediated self/non-self discrimination in plant roots**

12:40-14:00 **Lunch**

14:00-14:20 **Dr. Yuval Gottlieb (Volcani Center) – Secondary symbionts of insects: lesson from Homoptera**

14:20-14:40 **Adi Behar (Hebrew Univ, Rehovoth) - Bacteria in the medfly gut: hitchhikers or collaborators?**

14:40- 15:00 **Dr. Jutta Schneider (Hamburg Univ, Germany) – Sexual cannibalism and conflict between the sexes in orb-web spiders**

15:00-15:20 **Refreshments**

15:20-15:40 **Dr. Alexei Maklakov (Uppsala Univ., Sweden) - Sexual coevolution and female ageing**

15:40-16:00 **Haim Berger (Ben-Gurion Univ) – Novel explanation for the formation and maintenance of dominance hierarchies**

16:00- 16:20 **Amir Perelberg (Haifa Univ & Intl Lab for Dolphin Behaviour Research): Cooperation in dolphins and other animals: insights from human-dolphin interactions.**

16:20-16:40 **Dr. Reuven Yosef (Intl Birding & Research Center, Eilat): Assessment of costs of bee-eater damage to farmers in the Arava region, and solutions to resolving the conflict.**

Cooperation and conflict in social systems

Amotz Zahavi

Department of Zoology, Tel Aviv University & Hazeva Field Study Center

There exists the potential for conflict of interests between cooperating individuals even in the most cooperative systems, such as parents and offspring, a breeding pair, or isogenic unicellular organisms. Many decisions within the cooperative system are taken as a consequence of information passed among individuals. Therefore, it is important to ensure the reliability of the information. The reliability of these signals is maintained by the handicap principle.

Cooperation succeeds because the cooperating individuals invest in the welfare of the cooperation. An individual that contributes to the cooperation rather than exploiting it displays altruism. The handicap principle proposes that the altruist gains by increasing its social prestige within the cooperation.

This interpretation of the altruistic phenomena is a consequence of our long-term research of a cooperative breeding bird, the Arabian babbler, at Hazeva. The social prestige gained by the altruistic activities, is similar to a peacock's tail: It attracts collaborators and deters its rivals within the cooperative group.

I believe that even among social insects it will be possible to find the same principle. Social prestige is an important advantage to a cooperating individual. It may explain phenomena such as the adoption of social parasites and much of the motivation of members of a sexual pair to invest in their offspring.

The Parental Investment Conflict

Uzi Motro
The Hebrew University of Jerusalem

How much should each sex invest in its own brood? While the conflict between the sexes over parental efforts can only be observed in biparental caring species, it nevertheless influences the evolution of the different caring patterns. A possible way of explaining the various parental care patterns (female only, male only or biparental care) is by using game theory approach.

We present a continuous-time, two-stage asymmetric game (with two types of players, the male and the female) to help and characterize the conditions under which different parental care patterns are likely to evolve in certain species. In the first stage each parent has to decide whether he will be the first to undertake parental care, and to what extent, and in the second stage the other parent has to decide whether or not to participate in the parental efforts.

The presentation is based on the paper by Yaniv and Motro (2004).

Yaniv, O., and Motro, U. (2004). The parental investment conflict in continuous time: St. Peter's fish as an example. *Journal of Theoretical Biology* 228:377-388.

Competition among helpers in cooperatively breeding cichlids

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Studies of cooperative breeding have largely ignored the role of conflict among helpers and how it shapes group dynamics and helping behavior. In this study, performing laboratory experiments with cooperatively breeding cichlids from Lake Tanganyika, we show that secondary group members (potential helpers) occupy home ranges within the group territory and may be aggressive to one another. Experimental removal of secondary group members allowed the individual next in rank to move closer to the removed individual's home range. In the field, dominant secondary group members stayed closer to the brood chamber than subordinate group members of similar size, and proximity to the brood chamber was related to the length of time spent inside. We suggest that space segregation and competition among secondary group members is common in these cichlids, and may limit the opportunities to provide help.

Costs and benefits of group living in spiders

Trine Bilde

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In social animals, the benefits of cooperation are often associated with nest foundation, foraging, or predator defence. Group living, however, increases opportunity for conflict over individual reproduction. For social systems to evolve, the benefits of group living should outweigh the costs. Multiple levels of selection may result in opposing selective forces, i.e. traits can be favoured at one level and selected against at another level. Interdemic selection may override individual selection when groups are founded by single lineages, migration between groups is low, and turnover rate is high. The social spiders fulfil these criteria and provide a unique system to study the factors underlying the evolution of group living. I present results from a field study aimed at quantifying costs and benefits of group living in the social spider *Stegodyphus dumicola* in Namibia. I show that colony survival increases with group size whereas individual reproduction decreases with increasing colony size. Life time reproductive success (LRS) is maximized in groups of intermediate size. Hence, group living appears to be favoured by survival benefits through interdemic selection despite the reproductive costs.

Physiologically mediated self/non-self discrimination in plant roots

Michal Gruntman and Ariel Novoplansky

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Recent evidence suggests that self/non-self discrimination exists among roots. The mechanisms enabling this discrimination, however, are still unclear. In this research we examined the hypothesis that recognition of self-roots is mediated via physiological coordination among roots that are part of the same plant, and that this discrimination is correlated with the amount of physiological background shared by plant parts. This hypothesis was examined in the clonal grass *Buchloe dactyloides*. We compared root growth in cuttings that were grown in the presence of neighbors that belonged to the same physiological individual, were separated from each other for variable periods or originated from adjacent or remote tillers on the same clone.

The results demonstrate that *B. dactyloides* plants developed fewer and shorter roots in the presence of self-roots, which belonged to ramets of the same clone. Furthermore, root development in cuttings that were separated for 60 days prior to the experiment or that originated from remote nodes on the same clone, was greater than that of intact cuttings or cuttings that originated from the same node. These results suggest that self/non-self discrimination in the roots of *B. dactyloides* is mediated by physiological coordination among roots that developed on the same plant rather than allogenetic recognition. The results present a so far unrecognized consequence of clonal integration, which allows avoidance of self competition within clones of the same ramet.

Secondary symbionts of insects: A lesson from Homoptera

Yuval Gottlieb

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Sternorrhyncha are sap-sucking Homoptera that harbor obligatory symbiotic bacteria to fulfill their dietary needs, as well as a facultative microbial community with a diversity of bacterial species. One well-studied system is the symbiotic complex of aphids where one bacterium, the primary symbiont *Buchnera aphidicola*, is essential for survival and fecundity (1), and others, termed secondary symbionts, cause various behavioral and physiological changes in their host. Studies exploring the influence of secondary symbionts in aphids revealed quite a number of roles these tenants play in their host's biology, including conferring resistance to parasitoids (2); influencing host plant preferences (3) and conferring heat resistance (4). On the other hand, other studies indicate negative effects on the aphid hosts. The intensity of these effects, as well as their consequences, depend on environmental factors (5, 6).

The sweetpotato whitefly *Bemisia tabaci* (Gennadius) is known as a severe plant pest, both as a feeder and a vector of viral diseases. Comprehensive characterization of the bacterial community in different *B. tabaci* lines is crucial for understanding various aspects of that pest's biology such as the emergence of more aggressive biotypes and variability in virus-transmission capabilities. Preliminary results showed that some lines of *B. tabaci* contain, among other bacteria, a bacterium in the genus *Rickettsia*. To address the relationship between the host and its symbiont a study on the localization of *Rickettsia* within *B. tabaci* is conducted. Whole-mount fluorescence *in situ* hybridizations of *B. tabaci* in various developmental stages show a general random and uneven localization of *Rickettsia* in the whitefly egg and body. In some cases the bacteria are abundantly distributed around the midgut, a distribution that is unique compared with previously published data. Although the role *Rickettsia* plays in the biology of the whitefly is currently unknown, the close association exhibited by the well-established vertical transmission suggests a beneficial interaction.

A complex of various genomes has been also found in psyllids and mealybugs, and was actually discovered wherever it was looked for. Although the phenotypes of the various bacteria is yet to be unveiled, the already available data suggest that it may have substantial influence on the host, and therefore, arthropods biology should be studied with the consideration of genome conflicts and cooperation.

Bacteria in the medfly gut: hitchhikers or collaborators?

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Insect microbiology is a developing discipline that has already shown that microbes play essential roles in the life of their hosts. The objectives of our research are to characterize the medfly's gut microbial community, and to discover and study functions performed by the populations forming this community.

We found that members of the *Enterobacteriaceae* constituted the dominant bacterial populations of the medfly gut. *Klebsiella* spp. were present in all medfly individuals and were found in different combinations with *Citrobacter freundii*, *Enterobacter* spp. or *Pectobacterium* spp. We discovered that these diazotrophic bacteria actively fix nitrogen within the fly's gut, potentially supplying a significant proportion of the nitrogen used by the adult fly.

Moreover, populations of pectinolytic bacteria identified as *Pectobacterium* spp. and *Klebsiella* spp. were found in every individual and were also shown to fix nitrogen. This pectinolytic community was larger in larvae and pupae than in adult flies. Accordingly, we suspect that maceration of fruit tissues induced by pectinolytic activity provides ample carbohydrates that fuel the dinitrogen fixation function within the rotting fruit, thereby providing nitrogenous compounds to the growing larva in this nitrogen-deficient environment.

Since the only other instance of proven biological nitrogen fixation in an animal is in termites, our findings suggest that this phenomenon maybe widespread within different orders of the Insecta. If, as we suspect, this relationship extends beyond the few species studied to date, it would provide massive amounts of fixed nitrogen ready to travel up the food chain by predation, down the food chain by decomposition, and to successive generations of the insect hosts.

Sexual cannibalism and conflict between the sexes in orb-web spiders

Jutta M. Schneider
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Sexual cannibalism may have evolved as a mating strategy that maximizes a male's reproductive success. However, there is strong intra- and interspecific variation in the degree of male complicity suggesting that sexual conflict plays a role as well. A conflict of interests is obvious in sexually cannibalistic spiders when the male attempts to escape a potentially deadly attack of the female. Spider males possess paired mating organs, the pedipalps, that they insert into the equally paired female genital openings. However, in many sexually cannibalistic species, only one pedipalp can be used at a time and insertions are generally interrupted by a new courtship sequence. The female can attack the male at any time during the sequence. Males should have an interest to survive a first insertion in order to empty their entire sperm supply. Females, however, may benefit from limiting a male to a single insertion, thereby retaining sperm storage capacities for future males. In the orb-web spider *Argiope bruennichi*, females stereotypically attack every male immediately after copulation starts and 80% of the males will not survive their first copulation. I will illustrate costs and benefits of sexual cannibalism for males and females using *A. bruennichi* as an example.

Sexual coevolution and female ageing

Alexei A. Maklakov

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Selection can favour the evolution of a high reproductive rate early in life even when this results in a subsequent increase in the rate of mortality, because selection is relatively weak late in life. However, the optimal reproductive schedule of a female may be suboptimal to any one of her mates, and males may thus be selected to modulate female reproductive rate. Because of such sexual conflict, coevolution between males and females may contribute to the evolution of senescence. By using replicated beetle populations selected for reproduction at an early or late age, we show that males evolve to affect senescence in females in a manner consistent with the genetic interests of males. 'Late' males evolved to decelerate senescence and increase the lifespan of control females, relative to 'early' males. Our findings demonstrate that adaptive evolution in one sex may involve its effects on senescence in the other, showing that the evolution of optimal life histories in one sex may be either facilitated or constrained by genes expressed in the other. We further show that 'early' and 'late' females evolved different age-specific rates of remating. 'Early' females were more likely to remate with control males as they aged, while 'late' females were more resistant to remating later in life. Thus, female remating rate decreases with age when direct selection on late-life fitness is operating and increases when such selection is relaxed. Our findings not only demonstrate that female resistance to remating can evolve rapidly, but also that such evolution is in accordance with the genetic interests of females.

Keywords: male-female coevolution, senescence, remating rates, sexually antagonistic coevolution, *Acanthoscelides obtectus*, life history

Quantitative balance between cooperation and conflict involved in maintaining dominance hierarchies

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Key words: Group-stability, dominance hierarchy, subordinate, cooperation.

Two opposing forces, cooperation and conflict, must exist in social systems with dominance hierarchies. If cooperation is absolute, i.e. there is no conflict, subordinates do not challenge their superiors and, therefore, will never advance in rank and would benefit little by remaining in the group. On the other hand, if subordinates constantly challenge their superiors, the group becomes too unstable to exist. Thus, for social hierarchies to exist, the stability of groups must lie between these two extremes, but is expected to vary over time and between groups. Rank order, the commonly used numerical description of dominance hierarchies, does not account for this variance. Here we present a method to quantify group-stability by adding a second dimension to the rank order scale, which we term potential social power (PSP). PSP includes measurable attributes that may change over time and contribute to the individual's domination abilities such as: physical characteristics (e.g. size, age, etc.), behavioral characteristics (e.g. tendencies towards aggressiveness, tolerance, or avoidance), and previous experience (winner/loser effect). We hypothesize that the deltas between PSP values of consecutively ranked individuals will influence the balance of cooperation versus conflict between them, and predict the time until a change in rank occurs. The relationship between the mean and variance of these deltas is an index to the stability of the group, thus enabling the prediction of future group social-dynamics and inter-group comparisons. This model quantitatively describes the mechanism that stabilizes the group albeit the de-stabilization brought about by the subordinates' striving to advance in rank. Specifically, destabilization brings about a directional changes in rank order towards increased stability.

Cooperation in dolphins and other animals: insights from human-dolphin interactions

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Cooperation, like altruism, has long posed theoretical problems in the social and natural sciences because of the implication that individuals are behaving for the benefit of others. Current theory emphasizes how individuals are selfishly motivated by their own immediate gains to maximize "expected utility". Moreover, by treating immediate outcomes as surrogates of fitness, psychological motivation is also assumed to parallel the evolution of cooperation by natural selection. Data supporting these positions, however, have been based mainly on models that oversimplify the expression of cooperation by reducing it to behaviors and outcomes that are experienced individually. In the laboratory, subjects are anonymous and physically isolated. In nature, where cooperation is inherently a social act, there can be a bias to cooperate, expressed as more cooperation than expected from immediate material gains. Individuals sometimes prefer to cooperate when non-cooperation is materially more beneficial. When learning the complex strategies of joint actions, individuals may receive few material rewards. And individuals may work together even when outcomes are not shared equally and some receive little or nothing. These kinds of phenomena were generated with a laboratory model based on rats in which pairs were rewarded for coordinating shuttling within a shared chamber. In particular, individuals preferred cooperation over non-cooperation by a ratio of 3:1 when material rewards were equalized. We also found a similar cooperation bias within a group of Bottlenose dolphins (*Tursiops truncatus*) when coordinating breathing and when petted by human trainers in a swim-with-dolphins facility in Eilat, Israel. To explain how a behavioral bias can be adaptive, we adopt an explanatory perspective that combines both psychological and evolutionary processes and the complex linkages between them. Two main hypotheses guide our research: 1) The learning and motivation to cooperate are determined by proximate psychological processes that include two kinds of immediate outcomes: from material gains (if any) and from affective states associated with engaging in joint actions for shared outcomes. The latter can reward cooperation even when immediate material gains are lower or absent. 2) An "irrational" cooperation bias can be adaptive if social relationships develop and are strengthened by cooperating together, with eventual probabilistic long-term consequences for individual fitness during a latter stage of life, and sometimes in a different "evolutionary currency", based on those relationships.

ASSESSMENT OF COSTS OF BEE-EATER DAMAGE TO FARMERS IN THE ARAVA REGION, AND SOLUTIONS TO RESOLVING THE CONFLICT

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Eilat is situated at the northern edge of over 2000 km of continuous desert and is an important staging area for millions of migratory birds of over 230 species. Establishment of agricultural communities in the Arava valley over the past 5 decades has resulted in a conflict between local farmers and migratory populations of European (*Merops apiaster*) and Blue-cheeked (*M. persicus*) bee-eaters. The peak flowering and pollination period of sunflower, melon and watermelons coincides with the peak migration period of the bee-eaters during both spring and autumn. During this period, apiarists are hired to put bee hives out near the flowering crops for pollination purposes. The bee eaters, unfortunately, take many bees, thus reducing pollination and the coincident honey crop. For the past 6 years the IBRCE has been hired to reduce the problem which is done by mist netting bee eaters and transporting them north or south, depending on the season, away from the conflict zones. Until 2004 no empirical data was collected and the efficacy of bee eater removal was not clear. However, in autumn 2004 an "experiment" was forced upon us that clearly demonstrated the effectiveness of bee eater capture and transport and its financial ramifications. For six autumn seasons (1998-2003) we have captured bee eaters in the watermelon fields of a local farm where an average of 8.5 tons of melons were picked; 6 tons being of export quality. In autumn 2004 the owners chose not to have the bee eaters removed. The net result was a 4 ton crop, with only 1 ton of export quality fruit. This translated into a financial loss of NIS 800,000 for the season. We do not have data concerning the apiarist's losses in bees and honey. I conclude that although our sample size is one season only, this is a case in which it mightn't be wise to increase the sample size.