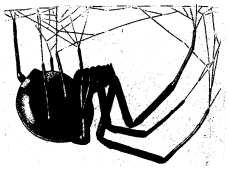

# Recent Developments in Arthropod Ecology and Evolution

## Fourth Symposium in Memory of Merav Ziv

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

**1 May, 2003**

**Seminar room, Blaustein Institute for Desert Research, Sede Boqer Campus, Midreshet Ben-Gurion**

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**09:45 Introduction and opening remarks**

**10:00 Ecology prize in memory of Merav Ziv**

### Scientific Program

**10:15-10:45 Prof. Rachel Galun** (Dept. of Parasitology, Hebrew University) – Evolution of hematophagy

**10:45-11:15 Dr. Einat Zchori-Fein** (Genetics Lab, Newe Ya'ar Research Center, ARO) – Curing mutations with antibiotics

**11:15-11:30 Refreshments**

**11:30-12:00 Dr. Moshe Coll** (Dept. of Entomology, Hebrew University) – Effect of elevated atmospheric $CO_2$ on inter-trophic interactions

**12:00-12:20 Yael Mandelik** (Dept. of Zoology, Tel Aviv University) - Arthropods as biodiversity indicators

**12:20-12:50 Prof. Avraham Korol** (Institute of Evolution, Haifa University) - Population genetics and mate choice in *Drosophila*

**12:50-14:00 Lunch**

**14:00-14:20 Yael Lubin** (Blaustein Institute for Desert Research, Ben Gurion University) –Trial by fire: Social spider survival in periodically burned savanna.

**14:20- 14:40 Dr. Ada Rafaeli** (Dept. of Entomology, Volcani Center) – Regulation of moth sex-pheromone production

**14:40-15:00 Refreshments**

**15:00-15:20 Dr. Tamar Katzav** (Dept. of Zoology, Tel Aviv University) - Queen-worker arms race in the honeybee and the evolution of multiple queen signals

**15:20-15:40 Prof. Boaz Yuval** (Dept. of Entomology, Hebrew University)– Sexual receptivity in the Mediterranean fruit fly

**15:40- 16:00 Yuval Sapir** (Dept. of Evolution, Systematics & Ecology, Hebrew University) - The night habits of male bees: does size matter?

**16:00-16:05 Closing remarks**

# Elevated atmospheric $CO_2$ effects on inter-trophic interactions

**Moshe Coll**[1] and **Lesley Hughes**[2]

[1] Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12 Rehovot 76100, Israel

[2] Department of Biological Sciences, Macquarie University, Sydney, NSW, 2109 Australia

According to predictions, atmospheric $CO_2$ level is expected to double by 2100. Numerous studies have showed that plants have accelerated growth, larger leaf area, and changed defensive and N/C ratios under elevated $CO_2$ conditions. Fewer studies have shown that, generally, these changes in plant properties negatively affect the survival and development of insect herbivores. Studies however, are yet to include the predators in these systems. In a recent investigation, we examined the effect of elevated atmospheric $CO_2$ level on a tri-trophic system that included bean plants, moth larvae (*Helicoverpa armigera*), and a pentatomid predator (*Oechalia schellenbergiii*). This predator, like many other predatory bugs, derive moisture and nutrients also directly from plants; it has been shown that this omnivorous feeding habit is obligatory at the first nymphal stage of *O. schellenbergiii* and it turns to be facultative later in its development. This configuration of a food chain that includes a closed-loop omnivory result in complex direct and indirect (through the prey) effects of elevated $CO_2$ levels on the predator in the system.

# Evolution of hematophagy

**Rachel Galun**

Hebrew University, Jerusalem

Hematophagy, the habit of blood feeding has evolved 17 times in disparate arthropod taxa. In Diptera alone it has evolved independently in 9 families. Most likely hematophagy was exploited by parasites both as a means to find and occupy novel vertebrate host, as well as means for increased motility. In every case, the pre-hematophagous ancestral lineage faced a common set of problems. Mouthparts had to be modified to enable pool or capillary feeding. Yet, it is clear that mouthpart evolution has followed very different paths to derive a common set of phlebotomist tools. Biochemical adaptation took place in the saliva, to overcome problems of hemostasis, vasoconstriction, pain sensation & inflammation. Yet, every blood feeder has enlisted a different biochemical solution, for each of these problems. Adaptation for host location has evolved according to the parasite behavior, special receptors for visual or chemical clues indicating host presence were developed. These clues include light, movement, $CO_2$, a variety of sweat components and other volatiles emitted by the vertebrate host.

Once on the host, the parasite penetrates or lacerates the host's skin, it salivates and tastes whatever is available. In many cases purine nucleotides provide a positive stimulus for blood gorging. This aspect will be discussed in details, as my own research dealt with it, in a variety of blood sucking invertebrates.

The overriding message in considering all of these adaptations is that no general consistent, morphological, physiological, or biochemical adaptations have been detected among all hematophagous lineages. However, the arthropods when faced with a common set of problems associated with gaining access to vertebrate blood, have taken up many independent but ultimately convergent paths.

# Queen-worker arms race in the honeybee and the evolution of multiple queen signals

**Tamar Katzav**

Department of Zoology, Tel Aviv University

Social insects are typified by a reproductive division of labor, in which more or less sterile individuals rear the offspring of fecund individuals. However, due to genetic asymmetry in relatedness between offspring, queen-worker conflict over reproduction is still a common feature. In honeybees the queen seems to have almost absolute dominance over male egg production. This successful domination can be explained by kin selection theory, since the queen is multiply-mated creating a new genetic asymmetry between workers and male in the colony. The question is whether this reflects a resolved queen-worker conflict or is it only a stage in an ongoing arms race between the queen and workers over male production? The queen social dominance is mediated by pheromones. In the honeybees queen specific signals include the queen mandibular gland, Dufour's gland, a tergite gland and a fecal pheromones. This complex pheromonal system provides a tool for assessing the evolutionary forces implicated in this battle.

The focus of this talk is Dufour's gland secretion. Both its caste specific secretion and its biosynthetic plasticity raised questions regarding its function, and the social mechanisms regulating its activity. Bioassays using glandular extract revealed that it constitute a part of the signal attracting workers to the queen. As a queen signal, Dufour's gland secretion may also play a role in the maintenance of reproductive dominance by the single queen, a system that is more complex than a one-pheromone one-signal system.

Supersession of an old, less fecund queen is common in honeybees, as in other eusocial insects. In honeybee colonies, queen quality was suggested to be monitored using a complex of several signals, although the nature of these signals is still elusive. Dufour's gland secretion may inform the workers about the queen quality/queen fecundity. The retention of the queen-like biosynthetic abilities in worker Dufour's gland raises an interesting evolutionary question. Does it reflect an incomplete process of caste differentiation or did it specifically evolved later?

# Population genetics and mate choice in *Drosophila*

**Avraham B. Korol**
Institute of Evolution, University of Haifa, Haifa 31905, korol@esti.haifa.ac.il

The last decade can be characterized by a growing interest to a detailed revision of relationships between geographical or chronological isolation, random drift, and natural and sexual selection at the initial steps of speciation. Two main scenarios of evolving sexual isolation are considered in the theory of evolution, *allopatric* and *sympatric* (with and without geographical separation, respectively). Several models were proposed for evolution of premating isolation, including divergent ecological selection and sexual selection. However, the relevance of theory to reality remains unclear, especially with respect to sympatry. In particular, next to nothing is known about the genetic basis of differentiation contributing to speciation process. It is not obvious how many and what types of genes are involved in incipient isolation. Although some progress was made toward molecular elucidation of *Drosophila* "speciation genes" in the last years, no study appears to have successfully identified genes participating in isolation between natural populations.

Substantial genetic differentiation was discovered between subpopulations of *D. melanogaster* inhabiting opposite slopes of "Evolution canyon" (Lower Nahal Oren, Mt Carmel) that display notable physical and biotic contrasts. It was manifested in a complex of life history traits, tolerance to heat and desiccation stress, habitat choice, slope-specific courtship behavior (including females' and males' reaction to the origin of the sexual partner) and courtship songs, and mate choice (positive assortative mating) exhibited by both sexes and confirmed in preliminary tests with *simulans*. Genetic differentiation of microsatellite markers and divergence in the regulatory region of heat-shock protein gene *hsp70B* was also found. Preliminary Northern blot analysis points to some interslope differentiation in the expression of several genes from the heat-shock protein family, especially *hsp*83 and heat-shock transcription factor (*hsf*). Sequence polymorphism analysis of a few candidate genes, presumably involved in speciation process (participating in mate choice [*per*, *desat2*, and *nonA*]) is underway.

The revealed remarkable divergence has evolved despite a very small interslope distance (a few hundred meters only), which is much smaller than the spreading capability of *Drosophila*. The geographical conditions of the canyon permit the mixing of flies by migration, hence these circumstances can be considered as sympatric. Therefore, we hypothesized that adaptation to the contrasting microclimates in the canyon overwhelms migration and leads to genetic divergence between the sympatric populations, partial sexual isolation, and, perhaps, to speciation. The obtained results call for critical further experiments that will include systematic testing of sequence polymorphism of DNA markers (micrtosatellites and SNPs) and candidate genes presumably involved in adaptation (to contrasting temperature-humidity conditions) and speciation (participating in mate choice), expression analysis of candidate genes, study of parallel ecological microsite differentiation in similar canyons and adjacent areas using *melanogaster*, *simulans*, and other drosophilids, and monitoring seasonal and between-year variation in population genetic structure for DNA markers and candidate genes. The objective is to validate the obtained pattern and compare competitive explanatory scenarios, especially the hypothesis of re-colonizations followed by habitat choice. Once sympatric explanation is verified, the obtained evidence should allow discriminating between alternative models of sympatric isolation.

# Trial by fire: Social spider colony demographics in periodically burned grassland

**Yael Lubin**

Mitrani Department for Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University, Sede Boker, 84990, Israel (lubin@bgumail.bgu.ac.il)

Nature conservation authorities in southern Africa burn the grassland in nature reserves to reduce the incursion of woody plants and to encourage the growth of new grass for grazing. Studies have shown significant negative effects of burning on the abundance, species diversity and community composition of smaller vertebrates and invertebrates. Social arthropods are likely to suffer from repeated burning, as destruction of the colony means a permanent loss of the entire reproductive unit. Nests of social spiders of the genus *Stegodyphus* (Eresidae) are a prominent feature of African savannas and their size and visibility make them potentially good indicators of ecological consequences of fire. The colonies are sedentary and their nests may persist for several years, although individuals have an annual life cycle. We explored the mortality patterns and the effects of burning on survival of colonies of two species of social spider, *Stegodyphus mimosarum* and *S. dumicola* that live sympatrically. We compared colony mortality in burned and unburned areas to determine if colony mortality was due to burning or, alternatively, to natural senescence. Analysis of five years of nest mortality data together with information on the burning regime in Spioenkop Nature Reserve, KwaZulu-Natal Province (South Africa), indicate that colony extinction in *S. mimosarum* is independent of the burning regime, while burning is a significant cause of colony mortality in *S. dumicola*. The different responses of the two species are likely a result of different colony dynamics and nesting sites.

# Arthropods as biodiversity indicators: The effect of sampling effort on species diversity measurements

**Yael Mandelik**

Department of Zoology, Tel-Aviv University

Arthropods are commonly used as biodiversity indicators. One of the fundamental issues raised is the appropriate sampling effort needed to represent species diversity in these species-rich taxa. We investigated the effect of sampling effort on measurements of species richness and diversity of beetles (Coleoptera), moths (Lepidoptera), and vascular plants, in the Sansan Nature Reserve, Jerusalem Mountains. We placed 60 pitfall traps in a 6000 $m^2$ plot in order to sample ground beetles, and 5 light traps to sample moths. Two 1000 $m^2$ plots were used for vegetation sampling. Bootstrap procedure was used to estimate the relationship between sampling effort (number of traps) and species richness and diversity of beetles and moths. Both beetles and moths showed a two-phased diversity curve, with a very steep phase followed by gradual moderation. However, slopes of the moths curve were much more moderate. These differences correspond to lower evenness and higher richness found in the beetle community. A vegetation species-area curve showed a steep phase until 100 $m^2$, and a significant moderation afterwards. Sampling beyond 1000 $m^2$ had no significant effect on richness and diversity. In sum, sampling effort is a highly influential factor in the quantification of species diversity and should be carefully determined prior to any detailed biodiversity study.

# Regulation of Moth Sex-Pheromone Production

**Ada Rafaeli**

ARO, The Volcani Center, Institute of Technology and Storage of Agricultural Products, P.O. Box 6, Bet-Dagan 50250, Israel.

Fax: 972-3-9604428 Email: vtada@volcani.agri.gov.il

In several Lepidopteran species, PBAN (Pheromone Biosynthesis Activating Neuropeptide) has been implicated in the stimulation of species-specific pheromones, which are synchronously produced and released for mate finding. On the other hand, the involvement of juvenile hormone (JH) in reproductive behavior of moth species has not been clearly defined. PBAN shares a common C-terminal (FXPRL-$NH_2$) with a functional diverse peptide family (PBAN/pyrokinin/myotropin). It has been isolated and its sequence determined from six different species of Lepidoptera although its regulatory role in pheromone biosynthesis has been demonstrated in over 20 different lepidopteran species. Much evidence has accumulated indicating its direct role on the pheromone producing cells associated with the intersegmental membrane situated between the $8^{th}$ and $9^{th}$ abdominal segments of the ovipositor tips of female moths. Normal activation of pheromone production may involve several interdependent mechanisms including both neural and humoral modulators. These modulators may be differentially activated, but closely coupled, depending on both physiological and environmental factors. I present herein evidence from recent studies concerning the role of JH in up-regulating the expression of a putative PBAN membrane receptor. In addition I discuss the modulatory roles of octopamine and male accessory gland factors on PBAN's mode of action. Future understanding of the modulatory mechanisms for hormonal control, their interaction and their gene regulation will be important in understanding insect reproductory behaviour, speciation and ultimately in designing ways to control the fertility of unwanted insect pests.

# The night habits of male bees: does size matter?

**Yuval Sapir**

Dept. of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem.

E-mail: sapir@vms.huji.ac.il

It has been observed that the large nectarless flowers of *Oncocyclus* irises serve as night shelter for males of solitary bees, mainly of the *Eucerinii* sub-family. Night sheltering within flowers may play a role in floral evolution, if bees select their night shelter according to preferred floral traits. In this work, the role of colour and size of the flowers were studied. As flowers of the *Oncocyclus* irises are at least partially dark, the solar energy absorbed by the dark parts of the flower during early morning hours can be an optional reward for the overnight-sleeping insects. Temperature measured within the Iris flowers was equal to ambient air during the night. However, the temperature was rising faster than the ambient air and was up to 6°c higher in the flower shortly after sunrise. The main benefit for the sleeping insects might be the possibility of earlier morning activity. Earlier activity commence might be advantageous in locating flower patches with higher nectar production that will later attract females. Indeed, in emergence experiment, where male bees were placed in black and white cones, within dark-coloured Iris flower and on the ground, the first to emerge in the morning were those in the black cone and in the flowers. In those shelters, the temperature was higher than the ground surface and the white cone in 3ºc to 5ºc in the time of emergence.

To study the role of floral traits in attracting male bees, artificial cone-shaped models mounted on stalks were used in binary choice experiments of colour and size. Significantly more male bees were found in black cones than in white ones, which usually hosted no males, but similar numbers of males were found in both small and big cones. This suggests a high preference for dark-colour night-shelters, regardless of size. These results may explain the evolution of dark colours in the *Oncocyclus* irises, but do not resolve the question of flower size.

# Sexual Receptivity in the Mediterranean Fruit Fly

**Boaz Yuval**

Department of Entomology, Faculty of Agriculture, The Hebrew University

Sexual receptivity in female insects is a multi-faceted phenomenon. Focusing on sexual receptivity in medfly (*Ceratitis capitata*, Diptera: Tephritidae) females, I toy with the idea that receptivity is related to complexity of the mating system. I will offer a review of the literature on remating in the medfly and present results of a recent study. The objective of this study was to examine the relative contributions of copula duration and sperm transfer to the inhibition of sexual receptivity of female Mediterranean fruit flies. Females choosing to remate had significantly fewer sperm in their spermathecae than females who chose not to remate. Duration of a female's first copulation did not affect her subsequent receptivity. Furthermore, on the first day following copulation significantly more females whose first mate was sterile and from a laboratory strain (sterile males transfer fewer sperm than wild males) chose to copulate than did females whose mate was fertile and recently derived from wild stock. Finally, I will offer a synthesis of the available information on remating in this species, and suggest that while females are facultatively polyandrous, copula duration, sperm transfer and male accessory gland secretions act in succession to inhibit female receptivity.

## Curing mutations with antibiotics

**Einat Zchori-Fein**

Genetics Laboratory, Newe Ya'ar, ARO

The importance of symbiotic microorganisms in every aspect of insect biology has been demonstrated in several systems. Symbionts have been shown to influence aspects such as the mode of reproduction, host-parasitoid interactions, performance under extreme environmental conditions and nutrition of their insect hosts. Although this field of research is growing rapidly, many entomologists are still unaware of the influence symbionts may have on insects, and the possibility processes involving symbionts will affect the outcome of their studies. Several case studies in which biological phenomena have been erroneously attributed to the insect's genetics will be presented and discussed