The Jacob Blaustein Center for Scientific Cooperation
The Jacob Blaustein Institutes for Desert Research
Ben-Gurion University of the Negev

The Ecology of Sex

13th Sede Boqer Symposium in Memory of Merav Ziv

Photo: Trine Bilde

Mitrani Department of Desert Ecology & Blaustein Center for Scientific Cooperation

The Zoological Society of Israel

17 May, 2012

Evens Auditorium, Blaustein Institutes for Desert Research
Ben-Gurion University, Sede Boqer Campus

Program

09:15 **Reception & refreshments**

09:30 **Memories of Merav & Ecology Student Awards**

09:45-10:30 **<u>Keynote</u>: Juan Carranza (University of Cordoba, Spain) – Red deer in a dry environment: consequences of sexual selection in males and females**

10:30-10:50 **Yoni Vortman** (Tel Aviv Univ.) - Reproductive isolation through multiple sexual signals in a diverging barn swallow population

10:50- 11:10 **Boaz Yuval** (Hebrew University) - Sexual and natural selection shape the mating system of the Medfly

11:10-11:30 ***Refreshments***

11:30-11:50 **Ally Harari** (Volcani Center) - The role of female sex pheromone in mate choice of male moths

11:50-12:10 **Iara Sandomirsky** (Ben-Gurion Univ.) – Lolita's web: Juvenile female mating in the brown widow spider

12:10-12:30 **Amiyaal Ilany** (Tel Aviv Univ.) - Do loud sounds save energy? Singing and energy expenditure in wild rock hyrax males

12:30-12:50 **Amotz Zahavi** (Tel Aviv Univ.) – Sexual selection and signal selection

12:50-13:00 **Discussion**

13:00-14:15 ***Lunch***

14:15-14:45 **Yossi Loya** (Tel Aviv Univ.) **-** Repetitive sex change in mushroom stony corals

14:45-15:05 **Maya Kleiman** (Ben-Gurion Univ.) - Evolution of obligate sex in finite population: the roles of sexual selection and recombination

15:05-15:25 **Yael Dagan** (Tel Aviv Univ.) - The significance of sexual and asexual reproduction in the freshwater snail *Melanoides tuberculata*

15:25-15:40 ***Refreshments***

15:40-16:00 **Gad Degani** (Tel Hai College) – Environment sex determination and hormone variations of male and females in eels *Anguilla anguilla*

16:00-16:20 **Tamar Keasar** (Univ. of Haifa) - Sex allocation in a polyembryonic parasitoid with cannibalistic females

16:20-16:45 **Arnon Lotem** (Tel Aviv Univ.) **- Discussion & summing up**

Keynote

Red deer in a dry environment: consequences of sexual selection in males and females

Juan Carranza

Ungulate Research Unit, CRCP Game and Fish Research Centre,
University of Cordoba, Cordoba, Spain
email: jcarranza@uco.es

I will start by introducing the Mediterranean environment of Southern Iberia, and the conditions prevailing during the red deer rutting season. Then I will show how these conditions influence the mating strategies of males and females. Red deer populations are managed for hunting in these areas. Management usually involves supplementary feeding during the summer and early autumn including the rut, and the high hunting pressure on adult males in some populations may produce altered population structures, i.e. female biased sex-ratio and younger mean age of males. These management conditions may have effects on female aggregation, on the degree of polygyny, on the transmission of genetic variability to the next generation and on the dispersal behaviour of males and females. Finally I will focus on how selection acting differently on males and females may produce consequences in life history and reproductive parameters.

Reproductive isolation through multiple sexual signals in a diverging barn swallow population

Yoni Vortman[1], Arnon Lotem[1], Roi Dor[2,3], Irby Lovette[3,4], and Rebecca, J. Safran[2]

[1]*Department of Zoology, Faculty of Life Sciences, Tel-Aviv University, Israel*
[2]*Department of Ecology and Evolutionary Biology, Univ. of Colorado at Boulder, USA*
[3]*Fuller Evolutionary Biology Program, Cornell Lab of Ornithology, 159 Sapsucker Woods Rd, Ithaca, NY, 14850, USA*
[4]*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY, 14853, USA*

Mounting evidence suggests that multiple sexual signals evolved to provide comprehensive information about mate qualities but it is unclear whether they also evolve to signal population identity. This type of multiple signaling may be adaptive when a diverging population cannot be distinguished from its neighboring populations by one signal alone but can be uniquely characterized through a mixture of sexual signals. Here we demonstrate that conditioning mate choice on the expression of such a mixture of signals can facilitate pre-zygotic reproductive isolation in a diverging barn swallow population (*Hirundo rustica transitiva*). By testing changes in female preferences before and after male sexual ornament manipulation, we demonstrate that females respond positively only to enhancement of both signals (tail elongation and color darkening), neutrally to the control group or to any manipulation of a single trait (tail elongation, color darkening, or tail shortening), and negatively to males manipulated to resemble males of the nearby Egyptian (*H.r. savignii*) population (tail shortening and color darkening). These preferences cause local females to be strongly attracted to high-quality males from the local population, which express both signals, but not to high-quality males from neighboring European (*H.r. rustica*) or Egyptian populations, which express only one of these signals (long tail streamers or dark ventral coloration, respectively). Conditioning mate choice on multiple sexual signals may thus facilitate pre-zygotic reproductive isolation between diverging populations, suggesting a novel explanation for the evolution of multiple sexual signaling.

Sexual and natural selection shape the mating system of the Medfly

Boaz Yuval

Department of Entomology, Faculty of Agriculture, Food and Environment, Hebrew University of Jerusalem, Rehovot 76100, Israel
email: yuval@agri.huji.ac.il

I will review a number of studies that have examined the effects of copulation and insemination on female fruit flies (Diptera: Tephritidae). I will examine the hypothesis that the functional anatomy of the female reproductive tract, patterns of sperm transfer and storage, and post-copulatory changes in female behavior result from sexual selection. Furthermore I will suggest that independent of the forces and conflicts that drove their evolution, the presence of two functional types of sperm storage organs and the sperm husbandry they promote, may currently be maintained through natural selection, by optimizing sperm economy and allowing females to postpone their next copulation. As this mechanism benefits both males and females, it may be perpetuated without invoking conflict between the sexes.

The role of female sex pheromone in mate choice of male moths

Ally R. Harari[1] **and Tirtza Zahavi**[2]

[1]*Department of Entomology, the Volcani Center, Bet Dagan, 50250, Israel*
aharari@agri.gov.il
[2]*Extension Service, Ministry of Agriculture, Kiryat Shmona, 11016, Israel.*
tirtzaz@yahoo.com

The role of female sex pheromones in natural selection as a means for species recognition and avoiding hybrid offspring has been widely accepted, but their significance in shaping sexual selection through mate choice has been largely ignored. As a result of natural selection, variation in sex pheromone characteristics among females is expected to be low and males are not expected to choose mates. Sexual selection, however, may result in variation in pheromone traits among females and males are expected to choose females based on this variation. Here we show that significant variation in pheromone amounts exists in females within a population, that pheromone amounts in glands of large females is greater than in glands of small females, and that males choose their mates based on their pheromone characteristics. These results are puzzling in light of the widely accepted low cost to female moths in producing sex pheromone. We demonstrate possible costs of pheromone production for females and discuss the likely reasons for males to be choosy.

Lolita's web: juvenile female matings in the brown widow spider

Iara Sandomirsky[1], Ally Harari[2], Yael Lubin[1], Maydianne Andrade[3]

[1] *Mitrani Department of Desert Ecology, Blaustein Institutes for Desert Research,Ben-Gurion University, Israel, email: iarasand@bgu.ac.il*
[2] *Department of Entomology, Agricultural Research Organization, Beit Dagan, Israel*
[3] *Integrative Behaviour and Neuroscience Group, University of Toronto at Scarborough, Canada*

Juvenile female matings are proposed as an alternative mating tactic for the brown widow spider *Latrodectus geometricus* and the new tactic is analyzed in the context of the known life history of the species. Anecdotal observations suggested that males of the brown widow spider sometimes mate with sub-adult (final instar) females in nature, opening a hole in the female's exoskeleton to inseminate their newly-developed spermathecae. Here we document the occurrence of sub-adult matings, and examine whether this behavior develops as a male or a female tactic by analyzing how the reproductive success of each sex is affected. In laboratory trials we compared the outcome of pairings between adult males and adult or sub-adult females. Males paired with sub-adults mated with reduced investment in courtship, had higher initial mating success, and were more likely to be polygynous in comparison with males mating with adult females. Our data suggest that sub-adult female matings can evolve as an alternative male mating tactic. Sub-adult matings might also serve females as a mating insurance tactic under variable and unpredictable male densities.

Does extended singing conserve energy? Vocalization and energy expenditure in wild rock hyrax males

Amiyaal Ilany[1], Adi Barocas[1,2], Michael Kam[3], Tchia Ilany, Eli Geffen[1]

[1]*Department of Zoology, Tel Aviv University, Tel Aviv 69978. Israel.*
[2]*Department of Zoology and Physiology and Program in Ecology, University of Wyoming, 1000 East University Avenue, Laramie, WY, 82071, USA*
[3]*Desert Animal Adaptations and Husbandry, Wyler Department of Dryland Agriculture, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Beer Sheva 84105, Israel.*

In many species individuals advertise their quality via vocal communication. Although sound production requires energy, it is still unclear as to the extent to which vocalizing increases metabolic rates. A substantial energetic cost of vocalization may suggest that it serves as a handicap. In the rock hyrax (*Procavia capensis*), males produce loud complex songs that convey multiple types of information about the singer, including social rank, hormone levels and body size. In this study, we measured the length and the acoustic power of singing and indirectly evaluated the cost of singing, estimated the total energy expenditure (field metabolic rate; FMR), and measured the length of other sounds and activities in the field. We used the doubly-labeled water method in parallel to recording males' sounds and activities by attaching miniaturized recorders to their necks. As hypothesized, both average daily singing duration and singing acoustic power were positively correlated with social ranking (David's score) of the signaler. However, contrary to our predictions, the duration of singing had a negative effect on FMR. In addition, the duration of other social sounds, such as twitters and grunts indicating close-range encounters, had a positive effect on FMR. Higher-ranked males sang more, suggesting that singing is not advantageous to low-ranking individuals. We suggest that males that advertise their qualities by singing may conserve energy by reducing social activities, while those that sing less often must engage in costly social encounters. Thus, while emitting loud sounds may impose an immediate energetic cost, the overall energy expenditure of the signaler is reduced. Singing may, therefore, serve as a handicap to the signaler, not for its energetic cost but in exposing it to potential predators.

The theory of signal selection

Amotz Zahavi

Department of Zoology, Tel Aviv University, Ramat Aviv, 69978 Israel

Darwin defined sexual selection as the selection operating among members of the same sex. Sexual selection included signals that deter sexual rivals and attract mates as well as weapons for fighting rivals and as well as other traits that serve in the competition among members of the same sex. However, although the term sexual selection is still widely used, traits that help in fighting sex rivals are also of help to fight over food or territory, and signals that attract mates or deter sexual rivals are not different from signals that attract collaborators for other reasons or deter rivals.

But signals unlike all other traits lose their function when all signalers can signal alike. Hence I proposed that signal selection is a distinct mechanism within natural selection. The investment in the signal (handicap) tests the reliability of the information encoded in the signal. The special mechanism of signal selection provides the option to explain many unsolved evolutionary phenomena that stimulated Darwin to propose the term sexual selection but define more clearly what is special in signals including signals used for sexual activities. Phenomena like the evolution of extravagance, altruism, and suicidal tendencies can be interpreted as traits that benefit their owners. The interaction between signal selection and the selection of all other traits can explain how individuals can gradually change from one peak of adaptation to another without invoking environmental change. The properties of the signal may also be of help to understand the message encoded in the signal. We use this simple relationship to interpret the information encoded in signals within the multicellular organism.

Repetitive sex change in mushroom stony corals

Yossi Loya

Department of Zoology, Tel Aviv University, Ramat Aviv, 69978 Israel
Email: yosiloya@tauex.tau.ac.il

Observations of stony coral reproduction have seen a progression in perspective, from the classic presumption of internal fertilisation followed by release of planulae larvae, through a renaissance during the 1990s in which broadcast spawning of gametes became the most common pattern observed, to the present, in which diversity of reproductive modes, including sex reversal and various methods of asexual propagation, have all been observes as part of the modern reproductive vista in many coral communities. To date, the reproductive mode of 450 coral species is known, nevertheless, the reproductive modes of corals in the family Fungiidae are relatively poorly studied. Here I review the findings over five years of observations of various reproductive traits and seasonal reproductive patterns of mushroom corals from northern Okinawa. I indicate, for the first time in stony corals, four species that change sex (*Ctenactis crassa*, *Fungia scruposa and F. repanda*) and one species (*C. echinata*) that exhibits multiple sex reversals, reported here for the first time.

Sex change occurs when an individual changes from one functional sex to another. The direction of sex change occurs mainly from male to female (protandry) or vice versa (protogyny) but sometimes may be bidirectional. Compared with *C. echinata*, *F. repanda* exhibits relatively earlier sex change, significantly slower growth and higher mortality rates, in accordance with sex-allocation theory. Sex ratio in both species is biased towards the first sex. The multiple sex reversal displayed by *C. echinata* greatly resembles that of dioecious plants that display labile sexuality in response to energetic and/or environmental constraints. I posit that, similar to these plants, sex change in corals increases their overall fitness reinforcing the important role of reproductive plasticity in the Phylum Cnidaria in determining their evolutionary success.

Evolution of obligate sex in finite population - the roles of sexual selection and recombination

Maya Kleiman[1] and Lilach Hadany[2]

[1]*Department of Chemistry, Ben-Gurion University of the Negev, Be'er-Sheva, Israel*
[2]*Department of Molecular Biology and Ecology of Plants, Faculty of Life Sciences. Tel Aviv University, Ramat Aviv, 69978, Israel*

The evolution of sex is one of the major open questions in evolutionary biology. Sexual reproduction carries high costs. Yet most higher eukaryotes engage in sexual reproduction, at least part of the time. Many models explaining the advantage of sexual reproduction over asexuality have been proposed. Most of these models find an advantage for low frequency of sexual reproduction over complete asexuality [1], almost no models exist explaining the evolution and maintenance of obligate sex, in comparison with facultative sex. In fact, it seems that organisms that engage in sexual reproduction only part of the time make the best of both worlds. Another possible advantage for sexual reproduction may lie in sexual selection. Sexual selection can have the form of males competing over females or territory or females selecting the most attractive male e.g. the one with the longest tail. However, a genetic flow between a facultative and an obligate population, makes it harder to see the advantage for obligate sex. Recently it has been shown that sexual selection can even explain the advantage of obligate sex invading into a facultative population [2], but under extreme conditions. Also it was found that very high rates of sexual reproduction are favored as long as sexual selection and natural selection act in the same direction [3].

Here we develop a stochastic simulation for the invasion of an obligate allele into a facultative population when sexual selection is used. Unlike the previous models, we consider a diploid and finite population, different recombination rates and the takeover of obligate sex rather than partial sexuality.

We find that there is a range of parameters for which the obligate allele is able to take over. We also find a range of parameters for which polymorphism occurs - the allele for obligate sex remains in a constant percentage within the population. This phenomenon was never discussed before although it exists in plants. An additional new discovery regards a counter intuitive short term advantage for obligately sexual reproduction, especially when in contact with a facultative population. This allows the takeover of an obligate allele despite the long term disadvantage. This short term advantage was never shown in the literature previously.

The significance of sexual and asexual reproduction in the freshwater snail *Melanoides tuberculata*

Yael Dagan* **and Frida Ben-Ami**

*Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, *E-mail: yaeldaga@post.tau.ac.il*

Sexual reproduction is ubiquitous among multicellular eukaryotes despite the many disadvantages of sexual reproduction compared to asexual reproduction. One of the most prominent hypotheses to explain the ubiquity of sex is the Red Queen hypothesis, which postulates that parasites track common host genotypes, giving rare host genotypes an advantage. This creates time-lagged negative frequency-dependent selection against common genotypes on the hosts. Under this model there is an advantage to sexual reproduction because it results in the production of genetically variable progeny, some of which may have rare genotypes and thus evade infection. We examined whether the frequency of sexual reproduction is correlated with the prevalence of infection by trematodes in 27 populations of the freshwater snail *Melanoides tuberculata*. We also explored the effects of snail density on sexuality and parasitism. Furthermore, we investigated the genetic structure and genetic variability among 14 *M. tuberculata* populations using allozyme electrophoresis analysis. We found that males were absent from all but one uninfected population. Moreover, in infected populations males comprised up to 23% of the population. We found no correlation between male frequencies and infection prevalence, and between snail density and infection prevalence. From a total of 215 snails collected from 14 sites, 142 different clones were found. A sufficiently common clone within a given site was only found in four sites (i.e., among the four sites the common clones differed from one another). In addition, only five clones were present in at most two different sites, and none of these clones were considered common. These results suggest that the genetic variability of asexuals in natural populations is very high.

Environment sex determination and hormone variations of male and females in eels *Anguilla anguilla*

Gad Degani

MIGAL–Galilee Technology Center, P.O. Box 831, Kiryat Shmona 11016, Israel and School of Science and Technology, Tel-Hai Academic College, Upper Galilee, Israel
Gad@migal.org.il

The European eel (*Anguilla anguilla*) is a catadromic teleost species with a complex life cycle, which takes place both in sea and freshwater environments. A high variation in growth was discovered in eels grown under aquacultural conditions. Significant differences between growth rate and size were found between the two sexes, with females growing faster and larger than males. High density increased the percentage of males that developed during the period of sex determination, and shelters increased the number of females in the populations, as caused by 17β – estradiol (E2) and other phytoestrogens. When E2 was provided in the diet, there was an increase in the growth rate of the eels. The cloned cDNA of aromatase (P450) from the European eel contains an open reading frame of 1539bp, encoding a deduced protein of 513 residues. Its expression during sex determination, as measured by mRNA, was significantly higher in females than in males. Treatment of the eels with a P450 inhibitor reduced the female percentage during sex determination. Their growth was affected not only by eel density in the water, but also by growth hormone (GH). GH has an effect on vitellogenesis brought about by E2, and insulin-like growth factor 1 (IGF1) stimulates luteinizing hormone (LH) production from the pituitary. According to the mRNA expression of the cloned and sequenced cDNA of European eel GH, females showed a significantly higher GH transcription than males. Follicle stimulation hormone (FSH-β subunit) cDNA, which consisted of 1068bp, encoded a 108 amino acid peptide. mRNA FSH and LH expression, which were examined in males and females after sex determination, were significantly higher in females than in males. Both GH and gonadotrophins affect gonadal function, and gonadal steroids (particularly estrogen) modulate the production of the hypothalamic GH-releasing factors. Suggested model are implies that the environment, GH, gonadotrophins and steroids on the growth of the European eel.

Sex allocation in a polyembryonic parasitoid with cannibalistic females

Tamar Keasar[1], Max Buegler[2], Chronis Remboulakis[1], Roei Shacham[1], Frank Thuijsman[2]

[1]*Dept. of Biology & Environment, University of Haifa – Oranim, Tivon, Israel*
[2]*Dept. of Knowledge Engineering, Maastricht University, the Netherlands*

Parasitoid wasps are convenient subjects for testing sex allocation hypotheses. However, the intricate life histories of many parasitoids are often insufficiently captured in simple analytical models. In the encyrtid polyembryonic wasp *Copidosoma koehleri*, a clone of genetically identical offspring develops from each egg, with fewer individuals in male clones than in female clones. Furthermore, some female larvae develop into cannibalistic soldiers that attack competitors within the host's body, while males do not form soldiers. These features complicate the prediction of sex allocation patterns in *Copidosoma*. We developed an individual-based simulation model, where numerous random starting strategies compete and recombine for many generations, until a single stable sex allocation evolves. Life-history parameter values (e.g., lifetime fecundity, clone-sizes and larval survival rates) were obtained from empirical studies. The model predicts the evolution of a male-biased sex allocation, which becomes more extreme when hosts are parasitized more than once (super-parasitized). To test this prediction, we reared freshly emerged adult parasitoids at either low or high density for 48 hours under laboratory conditions, allowed them to mate, and presented them with hosts in excess. As predicted, females from all treatments produced more male offspring clones than female clones. Female wasps reared at high density produced a higher proportion of super-parasitized hosts, and a more extreme male bias in their broods, than females reared at low density. These results demonstrate the potential of evolutionary dynamic models to generate realistic and testable predictions for complex behavioral decisions.