Desert Ecology and Ecological Theory

Eleventh 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

3 June, 2010
Evens Auditorium, Blaustein Institutes for Desert Research
Ben-Gurion University, Sede Boqer Campus

Program

09:15	**Reception & refreshments**
09:45	**Ecology Student Award in memory of Merav Ziv**
10:00-11:00	**<u>Keynote</u>: Lauri Oksanen (Univ. of Turku, Finland) – Why do plants defend themselves, when it counts so little for terrestrial trophic dynamics?**
11:00-11:10	**Refreshments**
11:10-11:40	**Bertrand Boeken** (Ben-Gurion Univ.) - New insights in the functioning of water-limited ecosystems – landscape heterogeneity, resource redistribution and the role of organisms as ecosystem engineers.
11:40-12:00	**Hagai Shemesh** (Ben-Gurion Univ.) - Plant adaptations to variable season length.
12:00-12:10	**Break**
12:10-12:30	**Keren Embar** (Ben-Gurion Univ.) - Risk management in gerbils foraging in a structurally complex desert landscape.
12:30-12:50	**Ophir Levy** (Tel Aviv Univ.) - Biophysical modeling of activity times and microhabitat use of golden spiny mice: from basic principals to community structure.
12:50-14:00	**Lunch**
14:00-14:30	**Osnat Gillor** (Ben-Gurion Univ.) – Biogeography of active and dormant soil microbial communities along a steep precipitation gradient.
14:30-14:50	**Orr Spiegel** (Hebrew Univ.) - Incorporating density-dependence into the directed dispersal hypothesis.
14:50-15:00	**Break**
15:00-15:20	**Sharon Renan** (Ben-Gurion Univ.) **-** Foraging mode versus searching movements: distinct behavior categories in a sand-dwelling lizard.
15:20-15:50	**Abraham Haim** (Univ. of Haifa) – Integrative physiology – the transfer of environmental signals to the reproduction system of desert adapted rodents.
15:50-16:15	**<u>Invited</u>: Uriel Safriel (Hebrew Univ.) – Discussion and summing up.**

Why do plants defend themselves, when it counts so little for terrestrial trophic dynamics?

Lauri Oksanen
Department of Biology, University of Turku, Turku, Finland and Department of Natural Sciences, Finnmark University College, Alta, Norway
lauoks@utu.fi

For decades, two opposite views of terrestrial food web dynamics have persisted side by side. One of these, recently championed e.g. by Donald Strong and Gary Polis, emphasizes the importance of plant defenses and their diversity and maintains that these suffice to prevent runaway consumption of plant biomass. The other view claims that plants are vulnerable to food limited herbivores and cascading impacts of predators account for the persistence of biomass-rich plant communities. A corollary of the latter view is that there must also be terrestrial ecosystems, where the potential of herbivores to control community level plant biomass is realized, because in unproductive areas, already sparse herbivore populations, which do not suffice to support predators, can deplete the slowly growing vegetation. Today, there is a compelling body of evidence to the favor of the latter view.

On the other hand, however, plants do defend themselves against herbivores and many plant communities are dominated by plants with low palatability and high concentrations of defensive chemicals. How comes this if plant defenses have no impact? Here I think the question is incorrectly formulated. What promotes the fitness of an individual plant is not regulation of herbivores – the advantages of that are shared by all plants. From the standpoint of an individual plant, defenses work fine if they promote its ratio of expansion rate to loss rate (Holt's r/a). The contribution of carbon based plant defenses to this ratio depend on the availability of mineral nutrients, which determine the marginal value of reduced carbon, and of the intensity of herbivory. The latter relationship is not linear but quadratic: the marginal gains of defensive allocations are at their highest under intermediate grazing pressure, when herbivory is substantial but still selective. Analysis of marginal gains and costs of defenses predict that the herbivory will drive the vegetation to one extreme or another. Depending on the balance between nutrient availability and intensity of herbivory, the vegetation can either develop towards grassland, dominated by palatable plants with high re-growth rates, or towards heathland (garrigue, maquise etc.), dominated by semi-prostrate woody plants with low palatability and low maximum growth rate.

New insights in the functioning of water-limited ecosystems – landscape heterogeneity, resource redistribution and the role of organisms as ecosystem engineers

Bertrand Boeken

Wyler Department of Dryland Agriculture, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Israel

bboeken@bgu.ac.il

Many commonly held ideas about the functioning of desert ecosystems and the role of vegetation have been changed or discarded by empirical and theoretical studies in the central and northern Negev. The assumption that all processes related to productivity and diversity in drylands can be explained by water availability alone has been replaced by a more complex and realistic view, where ecosystems function as a result of interactions between landscape heterogeneity, water and other resources, and organisms (plants, animals and microorganisms).

Our studies on annual plant communities in the arid, rocky Halukim Range near Sede Boqer and in semi-arid loessial shrubland in Park Shaked have shown that 1) there are strong source-sink relations between different types of landscape patches for the horizontal flow of water, sediment, organic matter, and plant seeds, 2) many of the landscape patches, both sources and sinks, are created and/or maintained by organisms as ecosystem engineers (crust-forming cyanobacteria, mound-forming shrubs and digging and burrowing animals), and 3) though water availability and distribution drive primary production, herbaceous plant biomass is also strongly constrained by sink limitation, as well as by seed limitation of plant recruitment and density.

These and more detailed insights have fundamentally changed our understanding of the functioning of water-limited ecosystems, the role of plant population and community dynamics, and the way plants are adapted to heterogeneous, unpredictable desert conditions. Furthermore, our insights from open, water-limited systems, besides assisting in prevention and restoration of land degradation, have also contributed to understanding more mesic ecosystems, where landscape heterogeneity and the role of animals and plants in shaping it are less easily recognized, and source-sink relationships are less pronounced.

Plant adaptations to variable season length

Hagai Shemesh[1,2] **& Ariel Novoplansky**[1]
[1]Life Sciences Department, Ben-Gurion University of the Negev, Israel
[2]Miterani Department of Desert Ecology, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel
hagaigg@gmail.com

Environmental uncertainty is one of the most profound selective factors faced by wild organisms and it is particularly critical in annual plants, where the length of the growing season is often highly variable and unpredictable. While underestimating the season length might result in missed-opportunity cost, overestimating it may end in fatal stress during or even prior to reproduction. Plants can cope with this uncertainty via deterministic or plastic bet-hedging in both plant size and architecture. We hypothesized that developmental decisions concerning the size and the number of new organs express a trade-off between risk-avoidance and resource-use efficiency. Predictable environments are expected to promote the development of large and highly-efficient structures that optimally take advantage of available resources and developmental time. In contrast, risk-averting adaptations to unpredictability are expected to include the development of a larger number of relatively small organs. Such development in "small steps" may decrease overall efficiency but also reduce the risk of losing large organs due to early cessation of the growing season. Testing the effect of water availability, competition and ecotypic origin on *Emex spinosa*, *Trifolium purpureum* and *Hippocrepis unisiliquosa* revealed variable developmental strategies. While *Trifolium* displayed architectural plasticity, ecotypic differentiation was more evident in *Emex* and *Hippocrepis*. The results demonstrate that environmental unpredictability selects for architectural bet-hedging, which involves both deterministic and plastic adaptations of plant allometry.

Risk management in gerbils foraging in a structurally complex desert landscape

Keren Embar, Burt P. Kotler and Shomen Mukherjee

Mitrani Department of Desert Ecology, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Midreshet Ben-Gurion 84990, Israel
embarkeren@gmail.com

Research in the Negev Desert has taught us that gerbils and their predators participate in a foraging game. In this game, gerbils manage risk of predation using behavioral tools of time allocation (when, where and for how long to forage) and vigilance, while predators manage fear. Theory inspired by this game predicts that the optimal level of a forager's vigilance should be affected by its encounter rate with predators and the effectiveness of its vigilance. Desert bushes are a common feature of the landscape and are used by both predators and prey. The bushes provide food and shelter for the foragers and a cover for ambush for the predators. We predict that bushes that obstruct the sightlines of the foragers will reduce the effectiveness of their vigilance and alter their risk management. We tested the effect of blocked sightlines along the vertical (vigilance directed against owls) or horizontal axis (vigilance directed against foxes) on vigilance and time allocation by gerbils at risk of predation from barn owls or foxes.

In general, gerbils harvested less seeds and allocated less time to foraging in dangerous patches, and used more vigilance while foraging where and when risks were higher (i.e., in the presence of predators and in bright moonlight). Blocking of vertical and horizontal sightlines reduced gerbil vigilance and interacted synergistically to further alter risk management. Moreover, in the presence of a predator, the gerbils' response to the blocked sightlines was more severe-foraging less food and spending less time and vigilance in the patches with the increased risk. This was especially so in the presence of predator that was expected to most benefit from blocking that particular type of sight line. These results strongly indicate the importance of sightlines and landscape features such as bushes in risk management and the forging decisions of gerbils, demonstrating that bushes provide mixed blessing to gerbils by providing concealment and shelter, but making vigilance ineffective. This work demonstrates how desert rodents continue to provide a crucible in which ecological theory is inspired and tested.

Biophysical modeling of activity times and microhabitat use of golden spiny mice: from basic principals to community structure

Ofir Levy, Tamar Dayan, Warren P. Porter, and Noga Kronfeld-Schor

Department of Zoology, Tel Aviv University, Ramat Aviv, Israel
levyofi@gmail.com

The effect of climate on activity patterns of desert animals and consequently on the structure of desert ecological communities has rarely been studied. We studied field foraging behavior of diurnal rocky desert golden spiny mice (*Acomys russatus*) and developed a two-stage statistical model to describe how biotic and a-biotic conditions affect this behavior. We found that energy expenditure and evaporative water loss, as predicted by a biophysical model, constrain spiny mouse foraging behavior. During summer ambient temperatures (T_a) increased to a range where mice needed to evaporate water in order to prevent hyperthermia; foraging behavior declined sharply when the necessary evaporation rate increased to 0.2 [mg $H_2 0$/sec*gram], when T_a was higher than 41°C during summer in the exposed between-boulder (BB) microhabitat. After accounting for the effect of climate, we found that foraging time was shorter in the BB microhabitat than in the protected UB microhabitat, probably because of risk of predation. Moreover, foraging sessions were fewer during summer than winter, probably due to high arthropod availability in summer, which offer higher caloric content than the sunflower seeds in our artificial food patches. Under RegCM future climate scenarios for 2100, maximum T_a in the study area will increase by 5.2°C and 3.6°C in A2 and B2 scenarios respectively; our biophysical model shows a reduction in the number of hours available for foraging in the BB microhabitat from 10 in current climate to 7 and 9 in A2 and B2 scenarios respectively. Consequently, mice may be forced to concentrate their summer foraging in more sheltered microhabitats, under boulders, where summer active vipers are a serious predation risk. Moreover, mice may shift their activity towards morning and evening. This reduction in spatial and temporal niche may increase intraspecific competition.

Biogeography of active and dormant soil microbial communities along a steep precipitation gradient

Angel R.[1], Conrad R.[1], Sklarz M.Y.[2], Soares M.I.M.[2] and Gillor O.[2]

[1]Max-Planck-Institute for Terrestrial Microbiology, Karl-von-Frisch-Strasse 8, Marburg, D-35043, Germany; [2]Zuckerberg Institute for Water Research, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 84990, Israel
gilloro@bgu.ac.il

Biodiversity of soil microorganisms captivated ecologists for over a century, yet only in the recent decades could their curiosity be gratified, spurred by advances in molecular biology. In this study we extracted DNA and RNA from soils to survey biogeographical patterns in the diversity of archaea and bacteria along a steep precipitation gradient. Thirty soil samples were retrieved from 5 long-term ecological research stations, collected from open patches and from underneath the canopy of the predominant perennial at each site. The molecular fingerprint of the soils was taken using terminal restriction length polymorphism (TRFLP) of 16S rRNA amplified from DNA and reverse-transcribed RNA.

The TRFLP patterns of active (RNA) and total (DNA) microbial community significantly differed. DNA-based patterns indicate that diversity within sites is not statistically significant ($P>0.3$) unlike the diversity among the sites. Conversely, the RNA fingerprints suggest that diversity in arid and semi-arid soils and of open patches at the southern Mediterranean site differ significantly ($P<0.001$) from the 2 northern sites and from the southern Mediterranean soils retrieved from under plant canopy. These differences could largely be explained by a combination of precipitation and vegetation cover. Although both approaches linked patch type with different microbial populations, the DNA-based patterns pointed to significant differences ($P<0.0001$) in the community composition of arid, semi-arid and the 3 Mediterranean sites, while the RNA-based fingerprints were found to tightly correlate to soil's water content. The active microbial communities harbored in dry soils (<6%) significantly differed from those detected in more moist soils (>10%). Our results suggest that in dry climates biogeographical patterns could not be elucidated by the active microbial communities, but by DNA-based analyses that capture both the dormant and active populations linking them to their ecosystem of origin.

Incorporating density-dependence into the directed dispersal hypothesis

Orr Spiegel & **Ran Nathan**

Department of Evolution, Systematics & Ecology, The Hebrew University of Jerusalem, Jerusalem, Israel

orr.spiegel@mail.huji.ac.il

The directed dispersal (DrD) hypothesis, one of the main explanations for the adaptive value of seed dispersal, asserts that enhanced (non-random) arrival to favorable establishment sites is advantageous for plant fitness. However, as anticipated by the ideal free distribution theory, enhanced seed deposition may impair site suitability by increasing density-dependent mortality, thus negating the advantage postulated by the DrD hypothesis. This conflict may be particularly pronounced in animal-mediated dispersal systems, in which DrD is relatively common, because animals tend to generate local seed aggregations, and in arid ecosystems, where suitable habitat for many plants is limited and patchily distributed. To investigate possible solutions to this conflict, we combine a simple analytical model and a simulation model. The models predict intermediate optimal DrD levels (that maximize fitness gain in comparison to a null model of random arrival), which depend on attributes of the plants, the dispersers, and the habitat. Additionally, the simulation model predicts the optimal DrD levels to be an evolutionary stable strategy.

We highlight the need to revise the DrD hypothesis to include the countering effects of density-dependent mortality inherently imposed by enhanced arrival of seeds to specific sites and to incorporate the revised hypothesis in designing empirical studies of plant recruitment and in management practices. We demonstrate the relevance of the revised hypothesis to a system of bird-mediated dispersal of a fleshy-fruited shrub in the Judean Desert and elucidate previous results from empirical studies reporting little or no support for the DrD hypothesis.

Foraging mode versus searching movements: Distinct behavior categories in a sand-dwelling lizard

Sharon Renan and **Amos Bouskila**

Department of Life Sciences, Ben-Gurion University of the Negev, Be'er Sheva 84105
pazsh@bgu.ac.il

Lizards are both predators and potential prey. Because many of the behavioral options that increase foraging efficiency often increase the risk of predation too, a tradeoff can form between food and safety. Therefore, during foraging, lizards need to continuously assess their environment in order to make anti-predator behavioral decisions. Differences in food resources and in predation risk are likely to influence time allocation, foraging mode (FM) and microhabitat preferences of lizards.

We examined whether searching movement, FM and microhabitat use of the lacertid *Acanthodactylus schreiberi* differ among habitats and with age. We conducted the study at Caesarea and Nizzanim in stabilized, semi-stabilized and active sand dunes. The lizards' behavior was determined by direct individual observation. On top of most commonly used indices for foraging movement, we employed the newly suggested index, percent of attacks while moving, arguing that this is the most direct measure for FM. Lizards moved more and spent more time in the open microhabitat in active dunes than in semi-stabilized and stabilized dunes. Interestingly, the FM showed an opposite direction: lizards in active dunes captured more prey from ambush whereas lizards in the stabilized dunes captured more prey while moving. Juveniles moved more and spent more time in the open microhabitat than adults, but did not differ in their FM. We suggest that different factors influence different aspects of foraging behavior: search movement and microhabitat use are primarily affected by food abundance and the risk of predation, while FM is mainly influenced by prey type or visual field in the habitat.

Integrative physiology - the transfer of environmental signals to the reproduction system in desert adapted rodents

Abraham Haim

The Israeli Center for Interdisciplinary Research in Chronobiology, Department of Evolutionary and Environmental Biology, University of Haifa, Mount Carmel, Haifa 31905
ahaim@research.haifa.ac.il

The desert as an unpredictable ecosystem in regards to resources, challenges the rodents inhabiting it. Reproduction is a highly energy-consuming process and therefore must be carefully synchronized to occur with sufficient availability of environmental resources as water and food in order to be successful. While rodents inhabiting predictable ecosystems out of the tropics would benefit by timing their reproduction to an ultimate predictable cue as photoperiod, in the unpredictable ecosystem as the desert, such a cue can be misleading and therefore desert adapted species, will need to use a more proximate signal. In our laboratory, we have been studying such signals among others by comparing between desert and non desert adapted rodents using different populations of the genus *Acomys* as well as the social vole, *Mycrotus socialis*, a mesic adapted species. As in deserts salinity increases with time since the last pulls of water into the ecosystem, we tested increasing salinity treatment and a treatment with anti diuretic hormone (ADH known also as vasopressin -VP). ADH is released during an osmotic stress due to dehydration for instance. Our results show that both treatments affect the reproductive system of the *Acomys* desert adapted populations but not that of *A. cahirinus* from Mount Carmel, a mesic adapted population. Furthermore, VP receptors were identified on the testis and white adipose tissue of desert adapted *Acomys* populations. As mice were acclimated to short and long photoperiod our results show that photoperiod may be an initial signal for reproduction, but in order to promote the process, an ultimate signal on water availability is essential. Our results show an integrative endocrine response, as the same signal used under osmotic stress to improve water balance, can suppress the reproductive system in desert adapted rodents.