

The 16th Sede Boqer Symposium in Memory of Merav Ziv

Species Invasion and Range Expansion

30 April, 2015

George Evens Family Auditorium

The Jacob Blaustein Institutes for Desert Research

Ben-Gurion University of the Negev, Sede Boqer Campus, Midreshet Ben-Gurion

Program

- 09:15 *Reception & refreshments*
- 09:30 *Memories of Merav & Ecology Student Awards*
- 09:45-10:30 **Keynote: Tim Blackburn: Following birds along the invasion pathway**
- 10:30-10:45 *Refreshments*
- Theory & Overviews***
- 10:45-11:00 **Salit Kark:** Determinants of spatial invasion patterns of alien birds in Australia vs. Europe
- 11:00-11:15 **Yuval Zelnik:** Survival mechanisms in the face of predator invasion
- 11:15-11:30 **Jonathan Belmaker:** Predicting alien fish species introduction and spread
- 11:30-11:45 **Itai Granot:** How important are specialization and competitive abilities for becoming invasive?
- 11:45-12:00 **Yoni Vortman:** The nutria's tail – a tale of natural selection?
- 12:00-13:15 *Lunch*
- Mechanisms & Processes***
- 13:15-13:30 **Shirli Bar-David:** Range expansion of the Kuhl's pipistrelle bat in Israel: what can be learnt from population genetics?
- 13:30-13:45 **Shachar Ben Cohen:** Morphological and behavioural variation of house sparrow populations in Israel – is there evidence of invasion from the south?
- 13:45-14:00 **Renanel Pickholtz:** Movement ecology of an invasive fish (*Siganus rivulatus*) in its native and invaded regions
- 14:00-14:15 **Itay Berger:** Conflicting effects of invasive common mynas (*Acridotheres tristis*) on foraging and nesting behaviors of native house sparrows

- 14:15-14:30 **Austin Dixon:** What makes a good invader: A lesson from experimental intercontinental comparisons of two desert rodent communities?
- 14:30-14:45 *Refreshments*
- Pathways & Control***
- 14:45-15:00 **David Ben-Yakir:** *Chilo partellus* a new invasive stalk borer in Israel
- 15:00-15:15 **Mey-Tal Gewing:** All aboard! Marine vessels as a vector for non-indigenous ascidian dispersal in the Mediterranean Sea
- 15:15-15:30 **Idan Shapira:** Conspecific attractiveness in invasive Norway rats can facilitate pest control
- 15:30-15:45 **Tamar Yeger:** Ministry of Environment protection activities in combating invasive species
- 15:45-16:00 **Boaz Yuval:** Who is eating Darwin's finches?
- 16:00 *Coffee and goodbye*

Following birds along the invasion pathway

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Biological invasions by alien species represent one of the primary ways in which human activities are changing global biodiversity. Yet, not all species become invaders, suggesting that there must be variation in factors that determine success or failure. I will discuss how evidence from one particular taxonomic group, birds, helps us to understand what drives the invasion process. I focus on birds because old and new data are giving us new insights into the patterns and processes underlying invasions by species in this taxon.

Determinants of spatial invasion patterns of alien birds in Australia vs. Europe

Salit Kark

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The outcomes of alien species introductions are determined by a wide range of biotic and abiotic factors, as well as human-related factors. In this study, we aimed to test fundamental drivers of invasion success and introduction outcomes, developing a spatially explicit information system of invasive bird introductions across Australia. Using historical information, published books, papers, reports and atlas sources, we generated a spatially explicit, event-based database of introduction records of birds in Australia. This allows us to examine spatial patterns of success and failure of introductions across Australia and across groups, examining spatial and temporal trends, as well as the major factors significantly related to the invasion patterns. We find that human-related factors are the most important determinants of introduction outcomes in Europe, while the best predictors of introduction outcomes of alien species in Australia are natural factors, such as native species richness. We compare results from Australia with an earlier study we led in Europe and the Mediterranean, disentangling the relative role of climatic, biotic and socioeconomic factors shaping invasion at a continental scale. Outcomes can help policy makers to more effectively mitigate biotic invasion threats, prioritize action and to spatially allocate efforts and limited conservation and management funds.

Survival mechanisms in the face of predator invasion

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The Lotka-Volterra equations have been studied for over a century, in order to better understand predator-prey interactions. This has been mostly done using continuous representation of both species numbers and the spatial structure of the ecosystem. In the context of predator invasion, a previously stable system can turn into to an unstable one, leading to either population oscillations or extinction of the invading predators. These results however, typically assume large populations and homogeneous spatial structure. Using a simple model based on the Lotka-Volterra equations, we look at how the discreteness of species can lead to both survival and extinction in different parameter regimes. We find that individuals of both the local prey and the invading predator can have a long- lasting effect on the overall population, via different survival mechanisms. We also look at how these mechanisms depend on the spatial structure of the ecosystem, allowing us to investigate the effects of habitat fragmentation.

Predicting alien fish species introduction and spread

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We use fish invasion via the Suez Canal into the Mediterranean Sea, the world's most invaded marine basin, to examine the environmental and trait constraints on invasion success and range expansion. We show that while climatic affinity can explain introduction success, tropical invaders may spread far beyond their native climatic niches. Thus, our results suggest that climatic models may underestimate the potential spread of invasive species. Ecological traits confer only a limited ability to predict introduction success. However, trait similarity with indigenous species shows distinct patterns of change through time and suggests a role for competition in shaping introduction success. Using both environmental affinity and traits we provide a quantitative ranking of the potential of Red Sea species to become established in the Mediterranean.

How important are specialization and competitive abilities for becoming invasive?

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Invasive species are one of the most acute environmental problems worldwide. Here we wish to understand what makes a species a successful invasive. We experimentally examine two key hypotheses: (1) invasive species are generalists compared to the other species in their native range, meaning they are able to thrive in a wider range of environment conditions. (2) invasive species are less likely to be influenced by competition in the introduced region. We focus on the Mediterranean coast of Israel, which is a major entry route of tropical Red Sea fauna through Suez Canal. We used Israel's unique position between the Red Sea (tropic environment) and the Mediterranean (temperate environment) to test these hypotheses using fouling communities. We designed a unique settlement plate composed of three types of substrate, and two lighting conditions which create six different niches. This heterogeneity is used to assess the degree of niche specialization of species. Initial analyses in the Red Sea indicate that, in contrary to our hypothesis, there are no significant differences in the specialization level of invasive species compared to other species in the invasive's native range. In order to test the second hypothesis we estimated the ratio between the realized and the fundamental niche of native and invasive species in the Mediterranean. This was done by removal experiments where species abundance and specialization were compared between complete fouling communities and plates where all species excluding the focal species were removed. The results again run contrary to our hypothesis, as initial analyses of the results indicates that invasive species are actually more sensitive to competition compared to other species in the invaded region. These findings suggest that invasive do not seem to have an inherent ecological advantage over other species, in their native and invasive ranges alike, that can explain their success.

The nutria's tail - a tale of natural selection?

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Invasive species are known to cause significant ecological and economic damage and require expensive control programs. However, well-documented invasive species introductions may serve as a large-scale spatial (worldwide) and temporal experiment in evolutionary ecology. During the last century, nutria (*Myocastor coypus*) were moved from their native range in Argentina and Chile to every continent except Australia and Antarctica. Today, they occupy a wide latitudinal range in extremely different ecosystems and climates from cold temperate Portland OR, USA to the warmer climate of the Hula Valley in Israel. The occurrence of isolated nutria populations in such distinct climates provides an opportunity to examine whether thermoregulatory adaptations have evolved during the last century in these two populations. Here we show that in accordance with the climatic differences and Allen's rule, nutria tail length (a thermoregulatory organ) significantly differ between the two populations. Further, using X-ray we found a significant difference in the number of vertebrae in the tail itself, while no difference in the total number of caudal and sacral vertebrae. By comparing morphological and skeletal data between these two populations, and other invasive populations and museum specimens we examine whether these significant differences have evolved through rapid natural selection or, alternatively, are a result of phenotypic plasticity or a founder effect. This research emphasizes the potential of the worldwide nutria populations to serve as a model system to study climatic adaptations and sets the ground for examining how environmental differences guide genetic and epi-genetic processes role in vertebrates' skeletal growth.

Range expansion of the Kuhl's pipistrelle bat in Israel: what can be learnt from the population's genetics?

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An understanding of the process of a population's range expansion can be applied to the conservation of recovering species and species that are shifting their range due to climate change and human activity. The insectivore bat Kuhl's pipistrelle, *Pipistrellus kuhlii*, is a common, Mediterranean species that is highly associated with anthropogenic habitats. During the last decades, the species has expanded its range in Israel from the Mediterranean zone south to the desert region. We aimed to explore whether genetic structuring occurred during range expansion, and if so, what can be learnt from the genetic structuring about the expansion process itself. 160 individuals were sampled in 18 foraging and roosting sites, here defined as "subpopulations", throughout Israel and DNA samples were amplified by seven microsatellite loci. Significant genetic differences were found among subpopulations (AMOVA, $\phi_{PT} = 0.03$, $P = 0.001$). STRUCTURE analyses indicated a composition of three main groups ($k=3$): the Mediterranean zone, the Negev Desert and Eilat (the most southern range of distribution). The Negev Desert subpopulations were genetically closer to each other than the other subpopulations (PCA). The Eilat subpopulation was characterized by the lowest genetic diversity: the lowest heterozygosity, the lowest number of alleles and no private alleles, indicating a recent founding event at the wave front of the population's expansion. These findings support theoretical models and agree with some empirical studies that have shown that genetic structure can arise during range expansion, within a few generations and a limited range. Founding events at the range expansion's wave front can lead to a decline in genetic diversity along the expansion front. Such a genetic structure, though it might diminish over time due to gene flow and additional range expansion, has the potential to facilitate adaptive evolution, thereby affecting the population's long-term persistence.

Morphological & behavioral variation of house sparrow populations in Israel – is there evidence of invasion from the south?

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Found on every continent but Antarctica, the house sparrow (*Passer domesticus*) is one of the most common and widely-distributed bird species, particularly due to human mediated introductions in vast parts of the world. Such broad distribution highlights an exceptional ability to adjust to varying conditions. Invading populations of sparrows and other avian species have been studied in order to identify traits which may be related to invasiveness. Among these traits, behavioral flexibility and increased exploratory behavior can be advantageous when invading novel habitats. House sparrows are native to Israel, however, in the southern part of the Arava valley, reside populations that morphologically resemble an oriental subspecies (*P. d. indicus*) which is both smaller in size and has brighter coloration than the local subspecies (*P. d. biblicus*). These populations have been suggested to originate from ship-borne introductions. Interestingly, a similar morphological trend is expected according to known biogeographic rules (Bergmann & Gloger), due to a steep climatic gradient in Israel, from north to south. In this study, we sampled populations of sparrows across rural habitats in Israel. We collected morphological data and blood samples from males and females, while color data was acquired from males only. Selected males at each site were submitted to a behavioral test in the field, where individuals were released and recorded in a closed arena which simulates a novel environment setting. Our results show significant differences between populations in some morphological measures, in correlation with the latitudinal gradient. Additionally, differentiation in some traits between the southern populations and rest of the localities supports the invasive origin hypothesis. Variation was also found in the behavioral assays; however, we cannot yet infer whether it is related to an invasion. Analysis of the genetic data will determine whether the phenotypic variation found is reflected in the genetic structure of the populations.

Movement ecology of an invasive fish (*Siganus rivulatus*) in its native and invaded regions

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The marbled rabbitfish (*Siganus rivulatus*) is an herbivorous fish native to the Indo-Pacific region, which has been remarkably successful in establishing large populations in the Eastern Mediterranean. In the Gulf of Eilat (Red Sea), rabbitfishes comprise less than 3% of relative fish-abundance, whereas in the Mediterranean they are found in much greater numbers, and constitute up to 80% of coastal fish biomass. Accordingly, school sizes of *S. rivulatus* in the Red Sea are commonly small with up to ten individuals, while in the Mediterranean- they are frequently found in groups of hundreds and thousands. Along the Mediterranean coast, intensive grazing by rabbitfishes is shown to have a devastating impact on biodiversity, resilience of ecosystems, and community structures. Given the negative impact of rabbitfishes in their invasive but not native ranges, we ask whether invasion is associated with shifts in behavior. For example, low interspecific competition and low predation risk may result in larger range sizes in the invasive range. Using acoustic telemetry, rabbitfish movements were recorded in real-time through implanted tags, within their native and invaded ranges (Eilat in the Red Sea and Sdot-Yam in the Mediterranean, respectively). Surprisingly, we find that rabbitfish display little variation in behavior between regions. Thus, tagged fish in both regions have a very restricted home-range, with a total area (mean \pm S.D.) of $13,000\text{m}^2$ ($\pm 6,000\text{ m}^2$) and core area (50%) of $3,000\text{m}^2$ ($\pm 2,000\text{ m}^2$). In both regions movements were found to be confined to hard substrates with movement trajectories within core areas characteristically tortuous with slow swimming over short distances. Movements beyond core areas, on the other hand, are faster, for long distances and often with a consistent swimming direction. All tagged rabbitfish displayed very high affiliation to specific sleeping sites and used areas situated within the areas utilized by day for sleeping grounds at night. The similarity in fish behavior between regions is surprising in light of the supposedly lower levels of predation and interspecific competition, and high resource availability in the Mediterranean. This suggests that in this case, high impact by invasives can be found even in the absence of behavioral plasticity.

Conflicting effects of invasive common mynas (*Acridotheres tristis*) on foraging and nesting behaviors of native house sparrows

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Although the Common myna is an aggressive species that was introduced to many parts of the world, relatively little is known about its influence on the behavior and breeding success of native species. This study examines the influence of the presence of mynas on the foraging and nesting behaviors of house sparrows in the field and in captivity. Using a video camera the vigilance of foraging sparrows was quantified in the presence and absence of mynas. Additionally, an experiment in aviaries which examined the sparrow's preference to forage alongside mynas, doves (as a control) or other sparrows was conducted. The influence of mynas on the nesting behavior of sparrows was also examined by placing Myna or dove decoys near sparrows nests while the nestlings were being fed. Surprisingly, in the field, sparrows that foraged alongside mynas were less vigilant and spent more time foraging than sparrows that foraged without mynas. Furthermore, in aviary experiments, the sparrows preferred to forage alongside mynas. On the other hand, when presented near the sparrow nest, the myna's decoy decreased nestlings feeding rate by the female, and male ceased feeding altogether. Thus, our results suggest that sparrows perceive their environment as safer when foraging alongside mynas, but treat mynas as potential nest predators when encountering them at the vicinity of the nest. Consequently, invasive mynas may improve the foraging success of native sparrows but reduce their breeding success.

What makes a good invader: A lesson from experimental intercontinental comparisons of two desert rodent communities?

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Examples of exotic species are increasingly abundant across most parts of the world. While many of these species may invade successfully, most (~90%) will fail to establish, naturalize, and invade into the target region. This produces a difficulty for managers to determine where to focus their efforts and resources to combat the damaging invasions that cost billions of dollars annually, degradation of ecological integrity, and extinctions of species. Before accurately assessing species invasibility, it is important to understand the role of constraint breaking adaptations on the community scale. Constraint breaking adaptations are defined as a physiological, morphological, or behavioral trait that produces a shift in fitness function by producing a relaxation or elimination of tradeoffs. In the desert rodent communities of the Mojave Desert, such constraint breaking adaptations may include external cheek pouches and bipedal locomotion. These anti-predatory adaptations may be in response to constraint breaking adaptations of their sensory-pit bearing predator, the sidewinder rattlesnake (*Crotalus cerates*). Using 'common garden' experiments, we created "invaded communities" by combining the Merriam's kangaroo rat (*Dipodomys merriami*) and desert pocket mouse (*Cheotodipus penicillatus*) from the Mojave with the Allenby's gerbil (*Gerbillus andersoni allenbyi*) and the greater Egyptian gerbil (*Gerbillus pyramidum*) from the Negev together in the presence of natural and novel predators. These allowed us to examine the effects of constraint breaking adaptations on the community structure, and thus invasibility. Preliminary results support that *D. merriami* would be invasive to the Negev due to its ability to deplete resource in all tested conditions. Alternatively, the desert pocket mouse appears to be less invasive due to its inefficient foraging in the presence of predators and its small size that allows for other species to win in interference competition. While analysis and experiments are still in progress to better understand these complex interactions, understanding constraint breaking adaptations on the community level should be an advantage in better understanding 1) which species pose the greatest threats, 2) the vulnerability of a community to invasion, and 3) the resultant community structure following a successful invasion.

***Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) a new invasive stalk borer in Israel**

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The spotted stalk borer (SSB) was found for the first time in Israel on July 2010, about 10 km southwest of the Haifa port. It is likely SSB arrived to Israel with plants imported from Africa for feeding farm animals. SSB spread rapidly and by 2013 it was found throughout Israel from the Hula valley to the Northern Negev. From 2011 to 2014, SSB became the major pest of both sorghum and corn. SSB almost displaced completely the other two stalk borers, that were major pests of corn since the 1980's, *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae) and *Sesamia nonagrioides* Lefebvre (Lepidoptera: Noctuidae). Although SSB is of a tropical origin, it is capable of entering diapause during cold or dry periods. In Israel, SSB enters diapause from September to November. Post diapause emergence of SSB occurs from March to early April. About 70% of the diapausing larvae emerged successfully in the spring. SSB develops 5-6 generations from May to October. SSB attacks both sorghum and corn plants at all growing stages. SSB larvae feed mainly on growing tips of young plants and in the stems. The main damage that SSB causes is death of young plants and incomplete development of infested plants. So far, no natural enemies of SSB were found in Israel. SSB continue to spread northward and it reached Cyprus by 2012 and Turkey by 2014.

All aboard! Marine vessels as a vector for non-indigenous ascidians dispersal in the Mediterranean Sea

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Ascidians (Phylum: *Chordata*, Sub-phylum: *Tunicata*) are considered to be very successful invaders, exploiting marine vessels as their main path of introduction. Non-indigenous ascidians are now commonplace in both tropical and temperate waters, thus creating severe damage both to natural fauna and to aquaculture by overgrowth. The Mediterranean Sea is also part of the global ascidian invasion. However, ship-mediated introductions have been only incidentally documented in the Mediterranean. The main goal of our work is to acquire better understanding of marine vessels role in alien ascidians' dispersal in the Mediterranean. We have conducted surveys in five Israeli shipyards in which recreational, commercial and military vessels are docked. To date thirty two marine vessels have been examined. Crafts usage, size, home port, sailing trails, and last shipping date were recorded, along with ascidians detected and their location on the craft (hull, propeller, rudder, seachest and thruster). Samples were taken to the laboratory for morphologic and molecular identification. Alien ascidians were detected on 47% of the vessels, two of them for the first time in the Israeli coast. Two thirds of the ascidians were found on large commercial crafts. In many cases, despite the fact that the vessel was in constant movement and well maintained, ascidians were located in the protected area of the seachest. The results of our research verify that marine vessels are a vector for non-indigenous ascidians. In addition, it provides an early detection tool which will enable a rapid response once alien ascidians are observed. More importantly, the current research emphasizes the need to prevent ascidians' fouling on specific areas of the vessel, e. g. the sea-chest. In this manner both ship owners and marine local fauna will benefit from more efficient, environmental and economic treatments against ascidians fouling.

Conspecific attractiveness in invasive Norway rats can facilitate pest control

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Invasive rodents pose major issues for conservation, human health and agriculture. Eradication of invasive rodents is feasible, but detection of individuals at low densities using traditional methods is difficult. We tested the hypothesis that in social species, conspecific attraction might be more appealing than food in the invasive Norway rat *Rattus norvegicus*. We compared trapping devices containing male and female laboratory rats at four conservation sites and three zoological parks infested with wild Norway rats, and in two manipulated rat incursions into a rat free island. We predicted that live conspecific would be more attractive to wild Norway rats, and that males will be more attracted than females to the live lures. Live lures were significantly more attractive to wild Norway rats compared with food baits at all conservation sites. Slightly more (but not significantly) males were caught than females. Live lures were more efficient attractants in two out of the three zoos. In the two incursion scenarios where single male rats were released on a rodent free island, invading animals were caught within one to five nights from trap activation and only with female lures. Animal behaviour can be a strong tool in conservation practices. In the current study we show that laboratory rats are highly efficient as lures for their wild conspecifics in situations where food baits might fail. We suggest that live lures should be considered as additional method in future management plans for the control of invasive Norway rats.

Ministry of Environmental Protection activities in combating invasive species

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Invasive species have major environmental implications, with which the Ministry of Environmental Protection (MoEP) deals daily. While there is wide consensus within the ministry's Natural Resources Department on the need to treat invasive species, professional differences occasionally arise regarding optimal treatment methods, since the MoEP is responsible for various environmental aspects affected by invasive species, such as agriculture and public health. There are three methods of dealing with invasive species: prevention of introduction, prevention of further distribution of species, and eradication. A recent study conducted by the MoEP found that the most effective way, both environmentally and economically, to deal with invasive species in Israel, is to prevent their introduction.

There are two types of introduction: intentional introduction, such as import of potentially-invasive non-native species (i.e gardening), and unintentional introduction (i.e stowaways). The unintentional introduction is the more challenging one. Thus the MoEP works with the Israel Tax Authority and with the Ministries of Agriculture and Health, which supervise the gateways to Israel – seaports, airports, and land borders. Still, invasive species have managed to enter Israel as “stowaways” within the past few years. Once an invasive species has been detected, the MoEP works to prevent its spread to other areas in the country. Prevention of the spread and establishment of invasive species is a long and difficult battle. Sometimes, the harm that an invasive species does to public health (*Aedes albopictus*) or agriculture (*ambrosia confertiflora*) requires measures such as the use of pesticides that might temporarily harm nature and the environment in affected areas. The MoEP performs a number of activities including: promoting invasive species legislation, with an emphasis on preventing introduction; publishing a book listing invasive plants and a booklet for gardeners on dealing with unwanted species; preparing and implementing a national program to eliminate invading plant species in moist habitats; and organizing meetings of local and international experts.

Who Is Eating Darwin's Finches?

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There are 13 extant species of finches in the Galapagos archipelago. The role of these species in the history of evolutionary theory, from its inception to its current state, is immeasurable. About 25 years ago a dipteran nest parasite (*Philornis downsi*), invaded the Galapagos and rapidly became established throughout the archipelago. The effect of this parasite, whose larval stages feed on the blood and tissues of nestlings, has been devastating. Currently 2 of the 13 finch species are on the verge of extinction, and the populations of many others are in decline. In my talk I will review biological aspects of this invasion and discuss the available approaches for its control. Finally, I will describe in detail the recent work of my colleagues and I on developing symbiont based approaches to control the fly.