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

The Many Facets of Dispersal

14th 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

23 May, 2013

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

אוניברסיטת בן-גוריון בנגב
Ben-Gurion University of the Negev

The Jacob Blaustein Institutes for Desert Research

The 14th Symposium in Memory of Merav Ziv

The Many Facets of Dispersal

23 May, 2013

George Evens Family Auditorium
The Jacob Blaustein Institutes for Desert Research
Ben-Gurion University in the Negev, Sede Boqer Campus, Midreshet Ben-Gurion

Program

09:15	*Reception & refreshments*
09:30	Memories of Merav & Ecology Student Awards
09:45-10:35	Keynote: Eloy Revilla (Estación Biológica Doñana, Spain) - Dispersal ecology for conservation: where shall we go next?
10:35-10:45	*Refreshments*
10:45-11:35	Keynote: Ran Nathan (Hebrew Univ.) - Dispersal of animals and plants: Unification via the movement ecology approach
11:35-11:45	*Refreshments*
11:45-12:05	Ariel Gueijman (Tel Aviv Univ.) - The evolution of fitness associated dispersal in homogeneous environments
12:05- 12:25	David Shohami (Hebrew Univ.) - Fire-induced population reduction and landscape opening increases gene flow via pollen dispersal in *Pinus halepensis*
12:25-12:45	Itamar Giladi (Ben-Gurion Univ.) - Recent shifts in research focus in the study of the ecology and evolution of myrmecochory, seed dispersal by ants
12:45-12:55	Discussion
12:55-14:10	*Lunch*
14:10 -14:30	Eric Yip (Ben-Gurion Univ.) - When to leave home: a modeling approach
14:30-14:50	Assaf Zvuloni (INPA, Tel Aviv Univ.) - Modeling the dispersal of white-plague coral disease in climate change scenarios
14:50-15:10	Ori Segev (Haifa Univ.) - Influence of stream velocity and predation risk on fire salamander (*Salamandra infraimmaculata*) larval drift
15:10-15:15	Discussion
15:15-15:25	*Refreshments*
15:25-15:45	Tomer Gueta (Ben-Gurion Univ.) - The effect of dispersal patterns on genetic structure: the reintroduced Asiatic wild ass in Israel
15:45-16:05	Yitzchak Ben-Mocha (Tel Aviv Univ.) - Sentinel behavior: Between anti-predator mechanism and social information gathering
16:05-16:25	Orr Spiegel (Hebrew Univ.) - Long-range forays of griffon vultures (*Gyps fulvus*) – optimal foraging or dispersal failure?
16:25	Discussion & summing up

Keynote

Dispersal ecology for conservation: where shall we go next?

Eloy Revilla

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In the last decades the amount of research on dispersal ecology has increased substantially, allowing for the inclusion of dispersal as an inherent ecological process to be considered in the spatial dynamics of populations. Nevertheless, many challenges still remain. In this talk I will go through what I consider some relevant findings and also open questions, as well as their consequences for conservation biology. Many definitions of dispersal are available in the literature, definitions that shifted in time, making newcomers confused about what we are talking about. I will try to use a simple overview that integrates most of the concepts available across different taxa and that should allow for easier generalization. Initially, dispersal was assumed to be a random process and hence there was not much pressure on making predictive models further that diffusion or random walk descriptions of dispersal probabilities. It was clear very soon that those theoretical models were not good enough for making real-world predictions. Nowadays many condition and context dependent factors are recognized as critical in determining the fate of a dispersing individual: age, stage, sex and condition, maternal and genetic factors, abiotic factors, landscape composition, the demographic and social context of the donor and receiving populations, etc. The current race to hunt down the mechanisms affecting dispersal is critical if we aim at modeling dispersal probabilities with some forecasting capacity. Nevertheless, many open questions remain, such as the role of the interactions between the factors controlling dispersal and their covariation with other demographic and life history traits, or how the molecular pathways regulating dispersal are affected by the very strong selection pressure imposed by the high mortality inherent to dispersal under the current global change scenarios. All in all and despite of the recent improvements, we are still far from understanding the spatial dynamics of populations in a comprehensive way, i.e., from considering dispersal as crucial as survival or reproduction processes.

Keynote

Dispersal of animals and plants: unification via the movement ecology approach

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Recent advances in mechanistic modeling, tracking technology and various molecular and analytical tools have enriched our capacity to accurately quantify movement patterns and to disentangle the key parameters affecting dispersal and other movement processes. In lieu of this favorable background, movement ecology has recently emerged to facilitate the unification of movement research. Movement ecology aims at investigating the explicit links between the internal state, the motion and the navigation capacities of the individual and the external environmental factors affecting its movement. Therefore, it provides a natural platform for examining the proximate and ultimate mechanisms underlying dispersal and other movement processes and patterns and their consequences in changing environments. In this talk I will present the basic principles of the movement ecology approach, highlighting the fundamental building blocks that should be considered for understanding why, how, when and where organisms move or disperse, as well as the transdisciplinary links required for developing a general theory of organism movement. More specifically, I will illustrate the application of this approach for unifying the study of apparently distinct dispersal processes of self-propelled sentient animals versus passively-transported organisms such as plants that lack a central nervous system.

The evolution of fitness associated dispersal in homogeneous environments

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Dispersal is a major factor in ecological and evolutionary dynamics, but the evolution of dispersal strategies is still puzzling, in particular when the cost of dispersal is high. Empirical evidence show that the tendency to disperse varies among individuals in many organisms. Which individuals, therefore, should disperse and which should stay? We suggest that dispersal can be viewed as a means to genetically diversify offspring when individual fitness is low, even in a homogeneous and stable environment. Using stochastic simulations we show that selection is likely to favor plasticity in dispersal, where fit individuals are less likely to disperse (Fitness Associated Dispersal or FAD), over uniform dispersal, where everyone disperse with the same probability, throughout the parameter range. Moreover, FAD can evolve under a much wider parameter range than uniform dispersal, even when the cost of dispersal is high, and such dispersal strategy has significant long term effects. We thus predict that individuals of low quality would have an increased tendency for dispersal, even when dispersal brings significant costs.

Fire-induced population reduction and landscape opening increases gene flow via pollen dispersal in *Pinus halepensis*

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Dispersal of pollen and seeds maintains gene flow within and between plant populations. Disturbances that reduce and fragment populations may alter patterns of dispersal and gene flow: theory predicts reduced genetic variation within small population fragments and increased genetic differentiation between them. Here, for the first time, gene flow via pollen dispersal was studied on *the same* plant individuals in *the same* population before and after a fire-induced population drop, in a natural stand of *Pinus halepensis* in Mt. Carmel, Israel. In 1998 a fire killed 96% of the trees in the stand, drastically reduced its density and cleared the vegetation in the area. Thirteen adult trees survived the fire in two highly genetically distinct groups, a northern and a southern, and seven of these trees had serotinous (closed) cones that did not open despite the fire. We collected closed pre-fire and post-fire cones and genetically analyzed the pollen that fertilized the seeds within them using microsatellite markers. The pre-fire pollen showed a strong and significant spatial genetic structure between the northern and southern groups (F_{ST}=0.092) and very high genetic relatedness (F_S=0.146), indicating limited pollen dispersal mainly within, rather than between, the two groups, and limited gene flow from outside. Immediately after the fire the pollen lost all differentiation and became spatially homogeneous (F_{ST}=0) and randomly related (F_S=0), and exhibited the arrival of new unique alleles with no loss of pre-fire alleles. We suggest that the fire caused an increase in gene flow via pollen dispersal by wind in two mechanisms: 1) a drastic reduction in local pollen production due to population thinning, effectively increasing the chances of pollen arriving from outside; 2) an increase in wind speeds in the open vegetation-free post-fire landscape. This research shows that dispersal can alleviate the negative genetic effects of population size reduction; however, unique local genetic variation may be lost in the process.

Recent shifts in research focus in the study of the ecology and evolution of myrmecochory, seed dispersal by ants.

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Myrmecochory (dispersal of seeds by ants) is a common mutualism that is geographically and phylogenetically widespread. This interaction is characterized by a specialized lipid-rich seed appendage called elaiosome, which elicits seed carrying behavior in ants. Upon arrival to the nest, ants remove the elaiosome, feed it to the larvae and leave the seed intact. The consumption of the elaiosome by ant larvae contributes to the colony's reproductive output. Traditionally, myrmecochory has been viewed as a diffuse mutualism where a guild of plants interacts non-specifically with a guild of ants. Research mainly focused on testing various hypotheses concerning the benefits that plants may gain from that interaction. Synthesis of existing knowledge and the accumulation of new evidence over the past decade revealed that myrmecochory is often an asymmetrical mutualistic interaction that is obligatory for the plant and facultative for the ant. Furthermore, the payoffs to the plants are often context-, ecosystem- and partner-specific. The realization that a few species of ants (keystone dispersers) play a disproportional role in efficient seed dispersal lead to a shift in research trends with a new emphasis on the dispersal ecology and behavior of these keystone dispersers. In addition, a whole set of recent studies conducted in various ecosystems tested the hypothesis that plants evolved specific adaptations that increase the probability and intensity of interactions with keystone dispersers (the 'partner choice' hypothesis). In this talk I will review these changes in research focus and will point to some exciting future research directions.

When to leave home: a modeling approach

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While some animals widely distribute their offspring in space and time, others group their offspring together. These grouped offspring may then choose both whether to disperse and when to disperse away from the natal group. I used a 'game against the field' approach to model when animals should disperse away from the natal site, given that there is a trade-off between competition among relatives at the natal site and an increasing probability of surviving dispersal with age. I begin with a three strategy model, in which offspring may disperse immediately, partway through development, or at maturity, and show that each strategy may be an ESS, with the possibility of stable mixed strategies when relatedness is less than one. I expand this model to include an arbitrarily large number of discreet time intervals to expand its applicability to biological systems. I use the expanded model to examine how the relationship between the age of dispersal and dispersal survivorship affects the possibility of intermediate dispersal times. When the relationship between dispersal age and dispersal survivorship is concave (i.e. the second derivate is positive), terminal dispersal times are favored over intermediate dispersal times, and the reverse is true if the relationship is convex. This suggests that patterns of natal dispersal should correspond to modes of juvenile development.

Modeling the dispersal of white-plague coral disease in climate change scenarios

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Coral reefs are in global decline, with coral diseases increasing in prevalence and spatial extent, and expected to worsen with increased future thermal stress. Here, based on real data, we develop and test a spatiotemporal index and a novel epidemiological model combined with a maximum-likelihood fitting procedure to assess the transmission patterns and mechanism of white-plague coral disease (WPD). We link the model to seawater temperatures and test the potential effect of increasing sea-surface temperature. Our results suggest that the likelihood of a susceptible coral to become infected is governed both by seawater temperatures and by its spatial location relative to nearby infected corals. Under a scenario of raising temperatures, results show that the spatial nature of the system has a protective effect, restricting the sizes of annual epidemics. We believe that this is because the decrease in the density of susceptible corals discount for the increase in the transmission strength of the disease caused by raising temperatures (i.e., each of these parameters work in a different direction). However, under an extreme demographic scenario, when recruitment is free-space regulated and the coral community density remains relatively constant, even an increase of only 0.5°C can cause epidemics to double their intensity. In contrast to other generic models in the literature, our model captures the dynamics of WPD both in space and time, and takes into account the highly seasonal nature of annual WPD outbreaks. Our study puts forward novel modeling approaches for investigating coral disease dynamics in space and time, and provides new insights on the spreading mechanism of WPD, which are likely to be relevant to other coral diseases as well.

Influence of stream velocity and predation risk on fire salamander (*Salamandra infraimmaculata*) larval drift

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Floods in ephemeral streams due to rains can temporarily connect isolated pools and provide otherwise spatially restricted organisms with the option to stay or leave. Fire salamander (*Salamandra infraimmaculata*) larvae, commonly deposited into rock pools along dry riverbeds, are often exposed to such flooding. To determine if larvae alter drift in response to different velocities and perceived risk of predation we conducted indoor artificial flow experiments, manipulating water flow within the range of flow in natural intermittent streams. Anesthetized larvae ('passive drifters') drifted out of a central pool faster than conscious larvae at low velocities but not at high velocity rates, suggesting that conscious larvae actively resisted hydraulic pressures. Drift of small larvae in the presence of a caged, larger cannibalistic conspecific was faster, indicating that the larvae perceived and attempted to avoid the predator. A field survey, where *Salamandra* larvae were individually identified along eight adjacent rock pools in a temporary stream, confirmed that during a discharge event, a small fraction of a larval population successfully colonizes down-stream pools. Specifically, mark-recapture (total 165 individuals) indicated that 61.2% were found in the same pool, 18.2% disappeared from all eight pools, 19.4% were new recruits, and 1.2% were recaptured in a lower-elevation pool. Our findings confirm that larval drift occurs in ephemeral streams, that it is in part behaviorally controlled and that it can be mediated by predation risk. Larval drift can serve as a dispersal pathway for amphibians and may be of particular importance on local scales when the terrestrial habitat surrounding breeding sites is fragmented thus restricting the movement of terrestrial stages.

The effect of dispersal patterns on genetic structure: the reintroduced Asiatic wild ass in Israel

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Understanding the role of landscape features in shaping a population's genetic structure can provide valuable insights into processes such as gene flow and dispersal. Of particular interest is the effect of landscape features on the development of genetic structure in reintroduced populations which are of conservation concern. Specifically, landscape features may affect dispersal from release site and home range establishment at the individual level and range expansion and differentiation into sub-populations at the population level. These processes should be reflected in the population's genetic structure. We explored the development of genetic structure in the reintroduced Asiatic wild ass (*Equus hemionus*) and evaluated the effect of landscape features on this process. The Asiatic wild ass was reintroduced into the Negev, between 1982-1993. Currently the population is estimated at about 250 individuals, distributed throughout the region. We combined genetic data and landscape analyses: Three hundred ninety-three fecal samples, collected throughout the Negev, were analyzed using mitochondrial DNA (mtDNA) genetic markers. The samples were delimitated to subpopulations according to their geographical locations. The genetic structure of the population was tested using Pairwise *Fst* tests, Spatial AMOVA and a Barrier analysis. The analyses revealed a significant genetic difference between the "East" subpopulation (the Arava), and the rest of the population (*Fst*=0.13, P= 0.04). Landscape analyses, conducted using FRAGSTATS and ArcGIS, indicated that the "East" area was characterized by high quality habitat patches (high vegetation cover), and low landscape connectivity to the rest of the region. We suggest that the "East" subpopulation was initiated following a founder-effect of individuals who dispersed from the release site area and remained in the 'new area', due to the high quality of the habitat and limited landscape connectivity to other areas. The development of genetic structure, within the wild ass's range of distribution, after a few generations since reintroduction onset, supports the view that range expansion of populations in heterogeneous environment can lead to significant genetic differences between sub-populations. Moreover, it illustrates the considerable effect that landscape features, and specifically landscape connectivity, may have on dispersal patterns and, hence, on gene flow.

Sentinel behavior: Between anti-predator mechanism and social information gathering

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Sentinel behavior is an important element in the daily activities of many cooperative species. A broad agreement, based on theoretical and empirical research, exists concerning the function of this behavior as an anti-predator mechanism. Nonetheless, the question for the role of sentinel behavior is still in dispute. The presented study is based on eight consecutive months of field work, during which six social groups of Arabian babblers (*Turdoides squamiceps*), each including at least two competing males, were intensively observed. It was found that, in accordance with empirical evidence and theoretically grounded predictions, predator presence has a significant positive effect on the duration of sentinel behavior. However, in contrast to the above predictions, this effect was short-lived. On the other hand, social factors such as the presence of foreigner conspecifics have a much stronger effect. Moreover, competing males were found to differ in their sentinel effort in relation to the group's location within the territory: Alpha males show decreased sentinel effort at the territory's border as compared to their efforts in the center; whereas Beta males show the opposite pattern: They increase their sentinel effort at the border as compared to their efforts in the center. These differences, within the same individual and among the two social ranks, were observed when there were no foreigner conspecifics near the focal group. The fact that Beta males - whose reproductive options within the group are restricted and who therefore face the dilemma whether to stay in their group or whether to disperse - increase their sentinel effort at the border of the territory - where the social information that is needed for the above described decision is available - suggests that they seize the sentinel position to collect and/or to convey important social information. This finding indicates that there are other functions, of social nature, which explain an additional portion of the phenomena of sentinel behavior.

Long-range forays of griffon vultures (*Gyps fulvus*) – optimal foraging or dispersal failure?

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Dispersal events occur when individuals are established in a new breeding area, differing from their origin. Long-range forays (LRFs), during which animals perform roundtrip journeys away from their origin, are often too short for breeding at a distant site along the track. Such movements are still poorly described and understood. They might represent failed dispersal events, exploratory journeys to obtain information about various resources and even optimal foraging bouts. We studied the movements of griffon vultures (*Gyps fulvus*) in general, and LRFs events in particular. Using GPS-transmitters we obtained high-resolution (10 min interval) long movement tracks (339 ± 36 days; Mean ± S.E.) from 47 adults. Data from an independent 3D accelerometer provided complementary information about behavior and energy expenditure. Vultures were very loyal to their main roost and foraged mostly within a confined activity region (HR50% kernel: 867 ± 124 km^2) with occasional excursions to adjacent regions in Israel and Jordan (displacement of <250 km). Nevertheless, six females and one male performed eight LRFs to Egypt and Saudi-Arabia (displacement of 300-1700 km from the HR; 48 ± 12 days long), despite higher energy expenditure and low food intake rate during these journeys. While most non-LRF excursions occurred during summer, LRF events occurred during autumn, prior to the breeding season. We found no evidence to support simple optimal foraging principles as possible explanation for LRF behavior. We also found no significant genetic structure between LRF and non-LRF individuals. The destinations (a diverse set of vulture colonies), the seasonality (timed to vultures' courting period) and the female sex-bias all suggest that these LRFs are motivated by social and/or reproductive drivers, presumably reflecting non-fruitful breeding dispersal attempts. Our results highlight a unique phenomenon and emphasize the need to further investigate dispersal costs in free-ranging wild animals.