Behavioral Modeling in Ecology & Evolution

Eighth Sede Boqer Symposium in Memory of Merav Ziv

10 May, 2007

Evans Auditorium, Blaustein Institutes for Desert Research

Ben Gurion University, Sede Boqer Campus

Mitrani Department of Desert Ecology & Blaustein Center for Scientific Cooperation, Blaustein Institutes for Desert Research, Ben-Gurion University, Sede Boqer Campus
The Zoological Society of Israel
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09:15 Reception & refreshments

09:45 Ecology Student Award in memory of Merav Ziv

Scientific Program

10:00-10:40 **Plenary: Amos Bouskila (Ben-Gurion Univ.) -** Different approaches to modeling foraging games between rodents and their predators

10:40-11:00 **Refreshments**

11:00-11:20 **Shirli Bar-David (Haifa Univ.) -** Recursions in movement patterns of large herbivores: the African buffalo as a case study

11:20-11:40 **Efrat Gavish (Ben-Gurion Univ.)** – Modeling spider movement in agroecosystems

11:40-12:00 **Luba Broitman (Hebrew Univ.)** – Spatially-explicit individual-based model of animal movement in heterogeneous environment

12:00-12:10 **Break**

12:10-12:30 **Dafna Gottlieb (Ben-Gurion Univ.) –** The effect of outbreeding opportunities on the breeding strategy of the palm stone borer beetle

12:30-12:50 **Yael Artzy-Randrup (Tel Aviv Univ.) -** Sympatric speciation under incompatibility selection

12:50-14:10 **Lunch**

14:10-14:30 **Jay Rosenheim (Univ. California, Davis) -** Evolutionary balancing of multiple fitness limiting factors

14:30-14:50 **Tal Avgar (Hebrew Univ.)** – Linking animal behavior and plant ecology: The role of information sharing among seed predators in determining plant recruitment patterns

14:50-15:00 **Break**

15:00-15:20 **Burt Kotler (Ben-Gurion Univ.) -** Foraging games between predators and prey: the role of apprehension in risk management

15:20-15:40 **Michal Segoli (Ben-Gurion Univ.) -** Joint parent-offspring control of brood size in a polyembryonic wasp

15:40-16:00 **Refreshments**

16:00-16:20 **Uri Grodzinski (Tel Aviv Univ.) -** Parents and offspring in an evolutionary game: the effect of supply on demand when parental care becomes more costly

16:20-16:40 **Michal Arbilly (Tel Aviv Univ.) -** Modeling the evolution of self learning in a population of social foragers: Should searchers be “smarter” than followers?

16:40-17:00 **Yoav Perlman (Ben-Gurion Univ.) -** Daring, risk assessment and body condition interactions in steppe buzzards

Modeling the evolution of self learning in a population of social foragers: Should searchers be “smarter” then followers?

Michal Arbilly[1], Uzi Motro[2], Marc Feldman[3], and Arnon Lotem[1]

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Social foragers can search for food independently or follow other group members and scrounge on their food findings. This leads to the "producer-scrounger" game in which the relative payoff of each strategy depends on the frequency each strategy is played by other individuals. This game can result in a mixed ESS of two pure genotypes or in a mixed ESS where each individual has a certain probability to act as a searcher or as a follower (i.e. producer or scrounger respectively). We used a computer simulation to study the evolution of such mixed strategies, and their possible effect on the evolution of self learning strategies. We modeled the evolution of self learning (i.e. learning to associate cues in the environment with the probability of finding food) in the context of this game. We tested whether individuals with a greater tendency to search independently should use different self-learning rules than individuals who use follower strategy more often. Our results suggest a possible linkage between high tendency for searching and learning rules that are more demanding but profitable in the long run. Thus, the adaptive value of cognitive mechanisms may be influenced by social context.

Sympatric speciation under incompatibility selection

Yael Artzy-Randrup and Alexey S. Kondrashov

The existing theory of sympatric speciation assumes that a local population splits into two species under one-dimensional disruptive selection, which favors both of the opposite extreme values of a quantitative trait. Here we model sympatric speciation under selection that favors high values of either of the two independently inherited traits, each required to efficiently consume one of the two available resources, but acts, because of a tradeoff, against those possessing high values of both traits. Such two-dimensional incompatibility selection is similar to that involved in allopatric speciation. Using a hypergeometric phenotypic model, we show that incompatibility selection readily leads to sympatric speciation. In contrast to disruptive selection, two distinct modes of sympatric speciation exist under incompatibility selection: under strong tradeoffs both of the new species are specialists, each consuming its own resource, but under moderate tradeoffs speciation may be asymmetric and involve the origin of a specialist and a generalist species.Also, incompatibility selection may lead to irreversible specialization: under strong tradeoffs, the population speciates if it consists mostly of unspecialized individuals, but remains undivided if most of the individuals are specialized to consume one of the resources. Incompatibility selection appears to be more realistic than disruptive selection, implying that incompatibility between individually adaptive alleles or trait states drives both allopatric and sympatric speciation.

Linking animal behavior and plant ecology: The role of information sharing among seed predators in determining plant recruitment patterns

Tal Avgar, Itamar Giladi, Yael Serry, Luba Broitman and Ran Nathan
Department of Evolution, Systematics and Ecology, The Hebrew University

Plant dispersal pattern is the template for its establishment pattern, progressively reshaped by both abiotic (e.g., nutrients, water and light) and biotic (e.g., seed predation, seedling herbivory and competition) factors. Most lifetime mortality in plants occurs mostly between dispersal and germination and is frequently distance- and/or density-dependent; thus distance/density - responsive seed predators often play the dominant role in shaping plant recruitment patterns.

Focusing on ants as model granivores, we introduce a spatially-explicit, individual-based, stochastic model of the foraging activities of colonial, central-place, foragers. The model predicts, for a given set of parameters (characterizing the seed predators and seed dispersal patterns) the spatiotemporal distribution of surviving seeds; hence, it can be used to assess how social interactions among seed predators affect plant recruitment patterns. We test the model predictions against data obtained from manipulated seed predation experiments, in which quarantined colonies preyed on artificially-generated seed shadows. We investigate the sensitivity of the predictions to different levels of information sharing among the foragers, particularly in relation to different characteristics of seed dispersal by the plant.

Overall, our study shows that, on one hand, a single granivorous species may generate different plant recruitment patterns, depending on the dispersal characteristics of the plant; on the other hand, a single plant species may have several different recruitment patterns, depending on the foraging characteristics of its major seed predator.

Recursions in movement patterns of large herbivores: the African buffalo as a case study

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It is expected that large herbivores feed on resources in a profitable patch, moving as it becomes depleted. We hypothesize that large herbivores in a herd-like structure return to "profitable patches" (here referred to as *recursions*) as a function of the resource recovery rate. We illustrate this hypothesis using a simple spatial model that simulates movements of large herbivores in a herd-like structure based on minimal parameters: resource availability, and resource recovery at a specific rate after a local depletion. The model outputs demonstrate that under relatively simple rules return patterns emerge: the resource recovery rates govern the incidences of recursion to previous locations. In cases of high recovery rates the recursion in movement patterns lead to convergence into a repeated closed route, while in cases of low resource recovery rate the movement patterns broadened and the herd moved in a larger route which led to a decrease in the recursion events.

Empirical data on buffalo herd movement collected in Klaserie Private Nature Reserve (1997-1999) and in Kruger National Park, South Africa (2005-2006), as well as the model outputs, are analyzed using several techniques that we have developed and applied to examine both general patterns and finer scale patterns of movement. Recursions to previous locations occur in the studied herds in both wet and dry seasons. Also, convergence to closed routes was recognized as part of the herd's movement patterns during different time scales (i.e. within hours, days and weeks). Future studies are needed to examine the relative role of resource recovery rate as opposed to other factors that might affect recursion patterns of large herbivores.

Spatially-explicit individual-based model of animal movement in heterogeneous environment

Luba Broitman, Guy Sella and Ran Nathan, Department of Evolution, Systematics and Ecology, The Hebrew University

Although environmental heterogeneity is known to greatly impact animal movement patterns, the large number of factors affecting movement decisions, and their complex interdependence, still hinder the efficient use of models to better understand animal movement in heterogeneous environments. We developed a new simulation model to explore how animal's movement path in a heterogeneous environment is affected by its physiological characteristics, food supply, internal state, predation risk and the interaction between these factors. The core of this stochastic spatially-explicit individual-based model is an optimization routine that discerns the fitness-maximizing behavior for the assumed combination of parameters describing key features of the animal and its environment. We parameterized the model using general characteristics (mean speed, body weight etc.) of frugivorous birds available from field observations and literature. The model depicts the movement of several individuals through heterogeneous environment, represented by regular grid, where cells can contain attractors (a food source with variable number of fruits) and differs in the probability of survival (habitat quality). We assume the effects of habitats and attractors on movement decrease with distance, and that movement is further affected by the tendency to continue in a chosen direction. Relative importance of these factors and parameters of corresponding functions were estimated by maximizing the average fitness of individuals that followed different movement decision rules. In this talk, we shall introduce the model and illustrate some preliminary results. The proposed modeling approach can be used to link the factors driving animal movement and the resulting spatial patterns (the movement paths), and can be applied to simulate foraging of diverse arrays of animals (differing in important behavioral and physiological characteristics) and environments (differing in distribution and characteristics of habitats and food resources). Thus, this modeling approach provides ample opportunities to investigate the mechanisms and consequences of animal movements in heterogeneous environments.

Different approaches to modeling foraging games between rodents and their predators

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Understanding principles and processes in ecology and evolution is not easy. Generating hypotheses and predictions in these disciplines is often not intuitive due, in part, to the many factors that may affect the outcomes of processes. In addition to experimentation, the approach of modeling has gained in recent decades an important role in addressing complex problems in ecology and evolution. Models simplify the real world in a similar way that experiments do. Theoretical models may not provide proofs that we reached full understanding of the system, but they can generate testable hypotheses and predictions and they can assist in the understanding of experimental results. This approach is exemplified with two models of the same system – desert rodents foraging under the risk of predation from visually oriented predators. This system begs for a game theoretic model, and two approaches will be exemplified. A static game has the advantage of simplicity. It can often be solved analytically and its results are relatively easy to interpret. Nevertheless, the simplicity has its costs in terms of realism. Some simplifications embedded in the static approach can be relaxed in a dynamic game, which provides more refined insights and more specific predictions.

Modeling spider movement in agroecosystems

Efrat Gavish

Ben-Gurion University, Dept. of Life Sciences and Mitrani Dept. of Desert Ecology, Blaustein Institute for Desert Research

Spiders are abundant generalist predators in agroecosystems and are considered potential natural enemies of insect pests. Their abundance in crop fields is influenced by reproduction in the fields and migration from the surrounding habitats. Given that spiders in annual crop fields suffer high mortality rate caused by modern agricultural practices, migration is likely an important factor determining spider occurrence and abundance in fields. Spiders can use both aerial and cursorial migration. While aerial migration is species-specific and dependent mostly on climatic conditions, cursorial migration is influenced by various habitat characteristics. We were interested in testing the effect of the migration mode and habitat preference on spider abundance in cultivated fields over the cropping season. We compare population dynamics in wheat from a field study with population dynamics obtained in a spatially explicit individual-based model. The model was developed in Matlab and includes two components: the spatial template (landscape) and the spider type. The landscape template comprises the matrix (natural habitat) and a crop field in the middle of it. Four spider types (functional groups) were used, where migration mode and habitat preference are the specific parameters that differ between them. We modeled the spatial and temporal dynamics of the spiders in a one-crop cycle. For each functional group the population size and distribution across the crop in the end of the season were calculated. We found that the migration mode has a major role in determining spider abundance in fields. The output of the model can be used as a basis for developing an agroecosystem management tool.

The dynamics of a mixed breeding strategy in a haplo- diploid beetle

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Theoretical studies focusing on the role of the reproductive assurance strategy in determining the mating system predict that when the probability of finding a mate is low, an inbreeding strategy may be advantageous over the alternative of producing no offspring due to lack of outbreeding possibilities. This should promote a mixed breeding strategy at the individual and population levels. However, the evolutionary significance of the reproductive assurance strategy has been recently questioned, due to the advantage of inbreeding possibly being outweighed by inbreeding depression.

In the date-stone borer beetle, *Coccotrypes dactyliperda* (Fabricus) the haplo-diploid beetles are subject to extreme inbreeding when a virgin female mates with her son and to outbreeding when females disperse and their offspring breed with non-relatives. This system can serve as an exciting model for evaluating the effects of male availability on the mixed breeding system.

Our goals were to examine the effect of male availability on females' decisions, and to compare the results with the predictions of the reproductive assurance strategy. We studied the effect of male availability on C. *dactyliperda* breeding strategy by mathematical modeling. The model investigates the trade-offs between factors affecting decisions of female *C. dactyliperda* regarding optimal waiting time. The model includes a game situation between several females and gives each female the option of inbreeding or waiting for outbreeding opportunities under various male densities.

We found that females sharing a date stone reproduce according to their life history (e.g. age and number of offspring) and male availability. These results support the reproductive assurance hypothesis. We discuss how the model and data collected from the natural habitat support the reproductive assurance hypothesis and emphasize the importance of both male availability and relatedness.

Parents and offspring in an evolutionary game: the effect of supply on demand when parental care becomes more costly

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Young of many species solicit food from their parents using extravagant begging displays. Prominent ESS (Evolutionarily Stable Strategy) models view begging as a costly, 'honest' signal of offspring need; and their common interpretation that supply should reduce demand has been usually supported. However, some studies identified cases where poor supply did not increase demand (needy nestlings begged less then nestlings in better condition). To understand whether such findings can nevertheless be consistent with honest-signaling theory we further explore Godfray's seminal honest signaling model (Godfray 1991, *Nature* 352:328-330) to find out what it predicts regarding the effect of supply on demand. Comparing the stable strategies for different values of parental care costs (in terms of future reproductive success) we found that while an increase in parental cost always lowers parental supply, the effect of this diminished supply on offspring begging (demand) is not monotonous. At elevated costs of parental care, despite a reduction in parental supply, offspring may paradoxically reduce their level of begging. Although signaling models assume that the marginal value of receiving extra food is higher when supply is low, at high cost levels a further increase in cost also causes parents to be less responsive to begging, making begging less effective in obtaining the extra food. Thus, even within honest signaling theory, positive as well as negative relations between supply and demand are possible predictions when different ranges of the cost of parental care are taken into consideration.

Foraging games between predators and prey: the role of apprehension in risk management

Burt Kotler, MDDE, Blaustein Institute for Desert Research, Ben-Gurion University, Sede Boqer Campus

Foraging animals have numerous tools for managing risk of predation. Foremost among these are time allocation and vigilance. Together, their use determines a forager's giving-up density (GUD) in a depletable resource patch. We examined Allenby's gerbils (*Gerbillus andersoni allenbyi*) exploiting depletable seed resource patches in a large vivarium. The gerbils foraged under varying microhabitats and moon phases while subjected to the presence of a red fox. We measured time allocation electronically and GUDs from the amount of seeds left behind in resource patches. From these, we estimated handling times, attack rates, and quitting harvest rates (QHRs) of the gerbils. Gerbils displayed greater vigilance (lower attack rates) at bright moon phases (full<wane<wax<new). Interestingly, gerbils were more vigilant in the bush than the open microhabitat, suggesting that vigilance is less effective in the open. At the same time, gerbils displayed higher GUDs in the open than the bush and in brighter moon phases (wax>full>new>wane). Finally, gerbils displayed higher QHRs in the open than the bush and at new and waxing moon phases than at waning and full moon phases. Differences in foraging behavior between microhabitats heavily reflect time allocation, while differences across moon phases reflect changing time allocation and vigilance, as well as changes in the marginal value of energy to the foragers. In this manner, gerbils apply multiple tools to manage risk in an environment of constantly changing opportunities.

Daring, risk assessment and body condition interactions in steppe buzzards

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Trading-off food and safety is considered a predominant component of foraging behavior. We suggest that predators' response to risks inflicted by their prey follows similar rules to those of prey under predation risk. We studied how predators' behavior is affected by the marginal value of the prey to the predator, by examining how the daring of Steppe Buzzards (*Buteo buteo vulpinus*) facing novel prey is affected by their body condition. We measured the time it took juvenile buzzards to attack a mouse placed in a Bal-Chatri cage trap and related it to their body condition. We found that buzzards in poorer body condition tended to hesitate less before approaching novel prey than did buzzards in better body condition. We suggest that behavioral decisions of predators are affected by the risks that may be inflicted by the prey, especially if unfamiliar or potentially harmful.

Offspring control of brood size in a polyembryonic parasitoid wasp

Michal Segoli, Department of Life Sciences, Ben-Gurion University

Brood size has important implications for the fitness of both parents and offspring. While parents may control brood size via production and care of offspring, offspring may further alter brood size via competition and aggression. In polyembryonic parasitoid wasps, each wasp egg proliferates into many genetically identical embryos inside the host. Thus, offspring may affect brood size by adjusting the degree of clonal proliferation. In the genus *Copidosoma*, some of the female embryos develop into soldier larvae, which attack and kill competitors inside the host and never mature and reproduce. Thus, soldier aggression may be another mechanism for offspring to affect final brood size. I investigated how relatedness between competing clones inside a host affects clonal proliferation and soldier aggression, which may, in turn, affect final brood size. Using a static game model I examined situations in which two clones, of different sex and relatedness combinations, compete inside the host. For two competing male clones, the model predicted that brood size should decrease as relatedness increases. For two competing female clones, brood size was predicted to increase as relatedness increases. The model predicted no effect of relatedness on brood size when one male and one female clone were competing. To test these predictions experimentally, I allowed two eggs (laid either by the same female, or by different females) to develop in hosts, and recorded brood size at adult emergence. The results suggest that brood size is affected by relatedness, but only when females are present in the host. Thus, offspring control over brood size in response to relatedness is probably mediated by soldier aggression and not by clonal proliferation.