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The 22nd Sede Boqer Symposium in Memory of Merav Ziv

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

1 June 2022

09:15 Reception & refreshments

09:30 Welcome: Merav Seifan, Director, Albert Katz International School for Desert Studies
Memories of Merav & Ecology Student Awards

Session I
Decisions in different contexts
Moderator: Ofer Ovadia

10:00 Guest lecture: Natalie Hempel de Ibarra, *How vision guides foraging bees*

10:45 Refreshments

11:00 Yossi Yovel, *Foraging decision-making in the real world – the bat's point of view*

11:20 Ron Efrat, *Decision-making under relaxed environmental constraints*

11:40 Aviad Heifetz, *Actual versus counterfactual fitness consequences of dispersal decisions in a cooperative breeder*

12:00 Break

12:20 Saskya van Nouhuys, *Variation of host resource availability does not seem to change individual restraint by parasitoid wasps foraging in a natural habitat*

12:40 Benjamen Izbicki, *Social learning and option valuation in the archerfish*

13:00 Keren Klass, *Should I stay or should I go now? Black howler monkey dispersal, demography, and population genetics in a fragmented landscape*

13:20 Lunch break

Session II
Models and mechanisms
Moderator: Michal Segoli

14:15 Guest lecture: Marc Mangel, *Modeling the organism in its world*

15:00 Refreshments

15:20 Edouard Jurkevitch, *Should I go, or should I stay: Prey depletion induces a shift from hunting to resting in bacterial predators, affecting survival*

15:40 Tabea Heckenthaler, *Connecting cooperative transport by ants with the physics of active swimmers*

16:00 Danny Minahan, *High omega-6:3 ratio in the diet of young honeybees impairs nursing performance and may affect the timing of transitions among tasks*

16:20 Liran Sagi, *How do chameleons choose their nesting sites? A decision-making model*

16:40 Ally Harari, *Rational decision-making in moths*

17:00 Coffee and goodbyes

Contact for information: Prof. Ofer Ovadia oferovad@bgu.ac.il

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Session I: Decisions in different contexts

Guest lecture: How vision guides foraging bees

Natalie Hempel de Ibarra

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Bees depend on flowers for nutrition, development, and reproduction like no other group of insect pollinators. For finding and exploiting them bees rely on a visual sense that is well developed but inherently unintuitive for the human observer. The understanding of the mechanistic interactions between movement and visual learning provides useful insights into the cognitive mechanisms that underpin decision-making in foraging bees in different spatial contexts, for example when departing from a nest or a flower. During flight, viewing directions are closely coupled with body movement and determine what bees see, unless flight manoeuvres are actively adjusted to seek relevant visual cues. This has consequences for the behavioural task at hand, and the incurring costs determine when active vision strategies are employed. Conversely, the efficient execution of action sequences can sometimes take a high priority, such as approaching and landing on a flower, and therefore influence which floral cues are learned. Bees may cut corners when deciding where to land and find food, and flowers are likely to exploit the tight connection between vision and movement throughout the different phases of the approach flight and landing sequence.

Foraging decision-making in the real world – the bat's point of view

Yossi Yovel

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Bats are extreme aviators and amazing navigators. Many bat species nightly commute dozens of kilometres in search of food, and some bat species annually migrate over thousands of kilometres. Studying bats in their natural environment has always been extremely challenging because of their small size (mostly <50 gr) and agile nature. We have recently developed novel miniature technology allowing us to GPS-tag small bats, thus opening a new window to document their behaviour in the wild. We have used this technology to track bat pups over 5 months from birth to adulthood. Following the bats' full movement history allowed us to show that they use novel short-cuts which are typical for cognitive-map based navigation. Using miniature microphones placed on the, we can also infer their foraging success and social behaviour. This novel technology thus allows us to document and model foraging decision making in real-life large scale and over long time periods.

Decision-making under relaxed environmental constraints

*Ron Efrat, Anne G. Hertel, Korin Reznikov, Nir Sapir, Oded Berger-Tal, Thomas Mueller

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The acquisition of new behaviors is important for young animals and can affect their fitness. However, behavior acquisition is often limited in time by environmental constraints, also known as Zeitgeber, which prevent the animal from deciding the timing and duration of behavior acquisition. An example of such Zeitgeber is migration, which occurs at specific timing and thus limits the time that young migratory animals must acquire the required behavioral skills. In our study, we removed this natural Zeitgeber by manipulating the timing of first migration for Egyptian vultures (*Neophron percnopterus*). We used data obtained via GPS transmitters to measure the change in daily movement of young vultures prior to their first migration. We then compared this change between a "natural" group (wild-hatched vultures) that migrated a few weeks after gaining independence, and a manipulated group which had 3-8 months of independence before their first migration. The manipulated group consisted of captive-bred vultures that were released after the timing of their first migration, thus "skipping" it and instead migrating after a longer period. We found that although the two groups reached the same movement range prior to migration, the time it took to reach this range and the shape of the increase were different. Under strict time-constraints, wild bird increased movement rapidly and exponentially, while under relaxed time-constraints captive birds delayed this increase and showed great among-individual differences in the timing and shape of this improvement. Our results suggest that when external constraints are removed, animals' decision making can lead to individual differences in the timing and duration of behavior acquisition, differences which might later affect the animals' fitness.

Actual versus counterfactual fitness consequences of dispersal decisions in a cooperative breeder

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In territorial cooperative breeders, dispersing and joining another group may be an important path to breeding. Moreover, an individual's prospects of future reproduction upon dispersal or upon remaining in the natal group might crucially depend on other group members' concurrent decisions to disperse or to stay. We developed a methodology for evaluating how the actual decision of a potential disperser to join or not to join a dispersing individual or coalition affects its fitness in comparison with the fitness consequences it would have had if it had taken the reverse decision – to disperse instead of staying, or to stay instead of dispersing. We then examined with this methodology 64 dispersal events by unisex coalitions of Arabian babblers who could not breed in their group of origin, and aimed to acquire breeding opportunities by joining another group. Fitness consequences were assessed based on breeding success in the ensuing year as the leading criterion, and on social rank as a secondary criterion. We found that 69% of the dispersers and 38% of the individuals who stayed made fitness-enhancing decisions relative to the alternative they faced, and for an additional 10% of dispersers and 21% of those who stayed, their choice yielded fitness consequences on par with those of the alternative choice. These findings suggest that despite the risky and uncertain circumstances in which dispersal decisions are taken, most individuals make informed, fitness-enhancing dispersal choices, taking into account the concurrent choices of their groupmates.

Variation of host resource availability does not seem to change individual restraint by parasitoid wasps foraging in a natural habitat

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When there is conspicuous underexploitation of a limited resource we wonder what mechanisms allow it to remain partially unused. The parasitoid wasp *Hyposoter horticola* finds virtually all host egg clusters in a landscape. There is strong intraspecific competition for hosts, but in the end only about a third of the eggs in each host egg cluster is parasitized. Afterward a deterrent mark is left around the host cluster, which is mostly respected by foraging wasps. Previously we tested and rejected a series of simple constraints that might limit host exploitation, such as asynchronous maturation of host eggs, or individual benefits to the parasitoid of developing in a sparsely parasitized gregarious host nest. We also considered classical hypotheses for the evolution of restraint. Prudent predation and bet-hedging are not explanations because the wasp lives as a large, well-mixed population. An optimal foraging model, including empirically measured costs of superparasitism and hyperparasitism, could explain through individual selection, both the low rate of parasitism and deterrent marking. If the wasps were foraging optimally, we might expect them to parasitize more of each host egg cluster as competition increases because the chance of access to hosts in the future declines. We will present a new empirical test of this potential response to competition. Using field collected data on rate of parasitism and parasitoid sibship within host nests, we found that increased landscape scale host scarcity does not lead to decreased restraint by the wasps.

Social learning and option valuation in the archerfish

Benjamin Izbicki

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The behavior of humans and non-human animals is often modified by observing others – i.e., via "social learning." The use of social information to make better decisions and enhance fitness is well documented in many species, and various mechanisms have been suggested for the transfer of skills and knowledge between conspecifics. In this study we first established whether the archerfish (*Toxotes blythii*) is capable of social learning, when facing a binary choice task in which the two options carry a different reward probability. We then tested whether the fish learn by imitating the choices of the demonstrator or by using its reward history to valuate the options. Naïve fish ('students') exposed to experienced demonstrators learned to choose the reward-maximizing option quicker than did the demonstrators, when first exposed to the task. However, they failed to learn the value of each of the two options, when these were presented separately (i.e., not in the context of the task). The demonstrators, on the other hand, were able to associate a value to the options and use the information to choose correctly when, subsequently, the options were presented simultaneously – a feat that the students were unable to replicate. Our results are consistent with behavioral modification through social-learning and suggest that, in the context of binary choice tasks, archerfish learn by imitating the demonstrator's preference (i.e., differential option choice).

Should I stay or should I go now? Black howler monkey dispersal, demography, and population genetics in a fragmented landscape

Keren Klass*, Sarie Van Belle, Alejandro Estrada, Julie Teichroeb, Eva Wikberg, Gwen Duytschaever, Amanda Melin, Gili Greenbaum

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The timing and characteristics of dispersal from the natal region or group is a key decision for primates. Forest loss and fragmentation are an urgent threat to arboreal primates worldwide, with important consequences for dispersal, as the cost-benefit decision-making calculation for dispersal can be very different in a fragmented landscape vs. continuous forest. Both the costs of staying in the natal fragment and of dispersing across the matrix may be higher, in terms of reduced reproductive opportunities for the former and increased energy costs and mortality risks for the latter. These costs can affect male and female decision-making differently, altering sex-specific dispersal patterns, with subsequent demographic (e.g., sex ratios) and population genetic (e.g., inbreeding) consequences. We surveyed endangered black howler monkeys (*Alouatta pigra*) in 32 small (0.2-36 ha) forest fragments located near Palenque National Park (PNP) in Chiapas, Mexico (N=407 individuals). Using genetic and demographic population structure analyses, we aimed to evaluate fragmentation-induced changes to dispersal behavior. We extracted DNA from 56 individually identified and geo-referenced fecal samples, and we used ddRAD sequencing to generate a dataset of 12,942 SNPs. Our genomic analyses revealed fine-scale population structure, with some genetic clusters corresponding to single forest fragments or to small groups of geographically-proximate fragments. We identified several potentially dispersed individuals and genetically assigned them to their clusters of origin. Our demographic analyses showed that the population in forest fragments had significantly fewer adult males than the adjacent population in PNP, suggesting a specific way in which habitat fragmentation may be restricting gene flow: increased adult male mortality during dispersal. Our results suggest that increased costs of crossing the matrix, including mortality risk, may have sex-specific effects on dispersal decision-making and outcomes, with females preferring to remain in their natal group or fragment when possible, while males continue to seek reproductive opportunities outside of their natal location despite higher costs. These changing dispersal patterns may subsequently shape both the demographic and genetic structure of the fragmented population, with implications for its ability to persist long-term in small, isolated forest fragments.

Session II: Models and mechanisms

Guest lecture: Modeling the Organism in Its World

Marc Mangel

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Organisms in the natural world need to make all sorts of decisions (choosing one behavior from a repertoire of many behaviors) in the face of limited information and a wide range of brain sizes. I will summarize a program of research conducted with colleagues at the University of Bergen and describe two of our key results. Our assumption is that rather than making perfect decisions, animals use rules (heuristics) that arise from different levels of biological organization (genes, physiology, individual experience, social experience). These heuristics perform well across a range of situations, including those not previously encountered by the organism and lead to characteristics such as homeostatic drive, instinct, and emotion. Although cognitive abilities vary among animals, all but the very simplest have a brain that can take information from several sensory systems. We assume that the animal holds a representation (the Subjective Internal Model (SIM)) of itself and its surroundings in its brain. We also assume a common architecture in which an array of sensory cues is monitored to help prioritize behaviors such as feeding, escape, or migration. These sensory systems feed into Survival Circuits (SCs) that link sensing to behavioral response. If the animal is relaxed and nothing important happens, it can maintain many types of information in its SIM and relate to all of it without evoking survival circuits. However, if an internal or external cue indicates some level of urgency, this cue becomes dominant and determines the Global State of the organism, which then restricts the SIM so the brain attends only the urgent task. If several cues evoke different survival circuits simultaneously, the strongest of them will take control. The combination of current Global State and response of the SC, determines the behavioral option through a projection of the SIM forward. The parameters of SCs, GSs, and the SIM evolve in response to natural selection. Two of the results that emerge from our work are these. First the amount of variation in populations declines as the level of biological organization increases. That is, there may be only a few ways to solve the life history problem, but many different physiologies and genomes that can underlie this solution. Second, animal personalities emerge. For example, from a homogeneous initial gene pool, individuals who are competition sensitive/tolerant or risk taking/averse may evolve according to individual experience.

Should I go or should I stay: Prey depletion induces a shift from hunting to resting in bacterial predators, affecting survival

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The small size of bacterial cells necessitates rapid adaption to sudden environmental changes. *Bdellovibrio bacteriovorus* is an obligate predator of bacteria that invades a prey cell to replicate. It is common in oligotrophic environments. At the prey-searching, non-replicative, attack phase (AP), predator cells are highly motile, respire at high rates, and rapidly consume their own contents. We show that under starvation for prey, individual cells whether prolong normal swimming, alter swimming pattern, or stop swimming, with increasing frequency for that sequence, over hours, concomitant with changes in energy metabolism. Upon introduction of prey or nutrients to swim-arrested cells, motility is rapidly reinitiated, along with sweeping changes in gene expression and gene regulation. These changes largely differ from those of the paradigmatic stationary phase. Through gene expression analysis, gene inactivation, growth assays, and *in-situ* localization, we show that the secondary signal cyclic-di-GMP (CdG) regulates the swim arrest-reactivation response to prey availability. We demonstrate the essential role of two CdG-regulated motility brake proteins in it, and the control over its strength by a CdG riboswitch, all located at the cell poles, and their survival-promoting effect. Yet, swim-arrest is costly as it imposes a fitness penalty in the form of delayed growth. Thus, obligate predators evolved a CdG-controlled response to prey depletion, possibly providing populations a time-dependent "choice" between "long term" survival through energy conservation and "short term" fitness by acquiring prey.

Connecting cooperative transport by ants with the physics of active swimmers

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Ants are known for their ability to efficiently transport large food items towards their nest. Previous studies of this cooperative transport behavior focused on the microscopic mechanisms by which ants decide on the travel direction and coordinate their efforts towards it. Here, we investigate the trajectories of carried objects of varying sizes by statistical means. We find that trajectories emerging from single ant's decision-making processes are described excellently by a Brownian motion of the velocity vector, thereby connecting the motion of the load to that of active swimmers, like e.g. self-propelled cells. The model allows the prediction of various system properties like the group size threshold at which ants lose the ability to turn around its travel direction. Most strikingly, the model parameters fulfill simple scaling relations in terms of the number of load-carrying ants, which connects this statistical model to the established microscopic descriptions.

High omega-6:3 ratio in the honey bee diet affects decision-making and impairs performance of nursing and foraging behaviors

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Decision making is a cognitive process of information acquisition and processing that leads to actions being performed by individuals, and if within a social system, by groups. Individual honey bees (*Apis mellifera*) exist as part of highly structured societies with complex individual and group level decision making. Thus, when the decision-making process of individuals is impaired, this can have negative consequences for the group. There exist a variety of environmental stressors that can result in impaired cognition and decision making, notably imbalanced nutrition. For example, the balance of the essential fatty acids (EFAs) omega 6 and omega 3, which must be consumed through the diet of honey bees, affects cognitive performance and behavior. In our research we find that an overabundance of omega-6 relative to omega-3 fatty acids (high Ω6:3 ratio) in the diet of honey bees impairs the ability of individuals to associate stimuli to a sugar reward, while also resulting in earlier foraging onset, shortened lifespan, and impaired nursing behavior. We discuss these findings from honey bees in the context of individual and social decision making, and how the resource environment may affect the decision-making process.

How do chameleons choose their nesting sites?
A decision-making model

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Reproduction is the most important stage in an animal's life, and it is greatly affected by environmental conditions. In reptiles, reproduction is possible only above a certain body size. Several reptiles survive only one reproductive season (semelparity) due to the intense energetic cost of reproduction and nesting. Many studies discuss effects of incubation conditions on reptile eggs and hatchlings, but the studies were done in the lab and did not consider the intricate variation in natural conditions. Studying natural nests excavated in the soil is extremely difficult, due to the inability to find the nests. Consequently, it is not known where most reptiles lay eggs or how they choose nesting sites. The desert chameleon (*Chamaeleo chamaeleon musae)* is an exception – despite its very deep nests, we developed methods for finding the females and their nests. It turns out that the females abandon several nesting attempts before choosing the location in which they excavate the deep nests and deposit the eggs. How do the chameleons choose the nesting sites? Why do they dig such deep nests, compared to other reptiles? The answers to these questions are crucial to predict the effects of climate change on the decisions of chameleons. If conditions while excavating the nest will not indicate conditions during incubation, nests will become an ecological trap. During the last few years, we have been characterizing the desert chameleons' nests. The nests are 1.5 m long and reach almost one meter in depth. Female chameleons usually abandon a new nest after digging to a depth of 30 cm. We built a dynamic state variable model to understand the decision process of females and to predict the effects of climate change on the decisions. The model suggests that chameleons with a high energetic state will take more risks in choosing the best nesting sites while chameleons in medium energetic state will dig in the first possible nest they will find, possibly leading to death before laying the eggs. The decision is mostly influenced by the costs of walking and digging, and by the probability of finding a proper nest. Mistakes in the decisions will have greater impact on individuals with a high energetic state that take higher risks.

Rational decision-making in moths

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In most sexual breeding species, females are polyandrous, thus, most females mate more than once, whereas, in the minority of species, females are monandrous, whereby most females in the species mate once only. Males in both mating systems typically mate more than once. The benefit for females in polyandry is generally taken as increasing genetic variation in offspring, while males pay the cost of sharing fertilization with other males. On the other hand, monandrous females benefit from decreased male harassment and reduced costs of sexual conflict with males. Males benefit from siring all offspring of their mates. Most females *of Lobesia botrana (the European berry moth)* are monandrous (90%). Polyandry in this species is recessive and autosomally inherited. Our hypothesis in this study was that monandry is driven in this species through the mating decision of males: males benefit from mating with monandrous females; thus, discrimination of monandrous from polyandrous females should evolve. Moreover, reproductive costs and benefits may also affect monandrous and polyandrous females differently, further influencing male mate preference.

To test for costs and benefits of monandry and polyandry mating systems in *Lobesia botrana*, we applied strong selection for polyandry, producing 70% of remating females vs. 90% of monandrous females in the wild type. Searching for a cost imposed on males and females in the two mating systems, we compared fitness parameters of females and males in the selected lines and tested males' preference for pheromones of monandrous and polyandrous females.

As predicted, we found (a) higher reproductive cost of polyandrous females, (b) male preference for mated polyandrous females over mated monandrous females, and (c) virgin monandrous over mated polyandrous females. But surprisingly, males chose virgin polyandrous over virgin monandrous females. I will discuss possible explanations for this allegedly irrational decision-making.