



Committee on Evolutionary Biology
&
Ecology and Evolution
Annual Retreat

April 11th, 2010

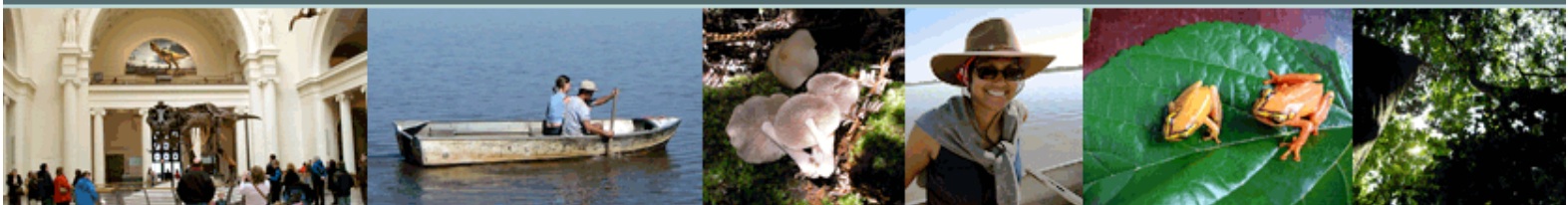
Hosted by the

Chicago Botanical Gardens

<http://www.chicago-botanic.org/>

Glencoe, Illinois USA

Committee on Evolutionary Biology
University of Chicago



Morning Session

Welcome by Greg Mueller

9:00	Libby Eakin	"Using agent-based models to understand how Gypsy moth feeding behavior affects susceptibility to an obligately lethal virus"
9:15	Matt Horton	"Combining metagenomics, metabolomics and genome wide association studies to unravel species interactions."
9:30	Nathan Smith	"Phylogenetic Analysis of "Pelicaniformes" (Aves) Based on Osteological Data: Implications for Waterbird Phylogeny and Fossil Calibration Studies"
9:45	Dave Kennedy	"Using response-time data to fit mechanistic models of within-host pathogen growth"
10:00	Aaron Kandur	"A Mechanistic Investigation of Range Limits Across Scales"

15 Minute Break

10:30	Bin He	" Evolutionary Dynamics of Transcription Factor Binding Sites in <i>Drosophila</i> "
10:45	Cindy Carlson	" Ecology and Social Organization of Wild Pigtail Macaques (<i>Macaca nemestrina leonina</i>)"
11:00	Brandon Kilbourne	"The Scaling of Limb Rotational Inertia in Quadrupedal Mammals"
11:15	Elizabeth Scordato	"Causes of long-term fluctuations in a sexually selected trait"

A Working Lunch (11:30 – 1:30)

Coates on "Job Talks & Postdocs"

Jablonski & Kidwell on "The Strategic Components of Graduate Education"

LaBarbara on "Sources for Small Grants"

Afternoon Session I: Behavior & Evolutionary Ecology

1:30 Paul Grabowski "Population structure and adaptation of switchgrass in sand dune ecosystems"

1:45 Katherine Brooks "The evolution and maintenance of sociality in Belding's ground squirrels (*Urocitellus beldingi*)"

2:00 Natasha Bloch "Differential Opsin expression in New World warblers and its possible impact on color vision"

2:15 Andy Dosman "Examining the relationship between animal personality and behavioral plasticity"

2:30-3:00 BREAK

3:00 Traci Viinanen "The effects of rare, dominant alleles controlling plant morphology and seed yield on resource allocation in wild and elite breeding lines of intermediate wheatgrass (*Thinopyrum intermedium*)"

3:15 Matt Heintz "Play behavior characterized in infant chimpanzees"

3:30 David Wheatcroft "Birds cooperatively attack predators only when immediately beneficial"

3:45 Nate Upham "Evolution of the New World rodent superfamily Octodontoidea: using multiple genes and fossils to understand a Miocene radiation"

Afternoon Session II: Evolution: History & Genetic Mechanisms

1:30 Chris Meyer "Mapping of Botanical Defense Systems"

1:45 Sophie McCoy "The Influence of Ocean Acidification on Crustose Coralline Algae Dynamics"

2:00 Will Tyburczy "The effects of seasonal breeding and recruitment on predator prey dynamics"

2:15 Rebecca Dikow "Reconstructing genome histories with phylogenetic trees: examples from the Gamma-proteobacteria"

2:30-3:00 BREAK

- | | | |
|------|----------------|---|
| 3:00 | Ben Krinsky | "New genes and male reproductive function in <i>Drosophila</i> " |
| 3:15 | Aaron Savit | "Origin and Maintenance of the Circum-Amazonian Distribution: Insights from Environmental Niche Modeling and Implications for Biogeography" |
| 3:30 | Kacy Gordon | "Does gene function constrain enhancer evolution in <i>C. elegans</i> ?" |
| 3:45 | Matthew Nelsen | "Dating the Origins of Lichen Symbionts" |

Talk Abstracts

Natasha Bloch "Differential Opsin expression in New World warblers and its possible impact on color vision"

Despite having one of the most elaborate photopigment arrays among vertebrates, color vision in birds has been relatively understudied. As a consequence, we do not have a realistic estimate of how much different species of birds vary in their color vision, and the impact that differences in their photopigment (opsin) properties could have on their perception of their environment and plumage ornaments. In this part of my doctoral research, I investigated how much opsin expression levels vary among species of New World warblers, and whether the observed differences are associated with each species' ecology and plumage coloration.

Katherine Brooks "The evolution and maintenance of sociality in Belding's ground squirrels (*Urocitellus beldingi*)"

There are many theories to explain the evolution of sociality, with some focusing on ecological explanations and others on reducing the fitness costs of living alone. Ground squirrels exhibit many forms of social organization and have been the focus of much empirical social evolution research over the past 40 years. Despite all of this work, we are still not sure which factors contribute most to social system evolution. In my dissertation research, I will evaluate multiple hypotheses for the evolution and maintenance of sociality in Belding's ground squirrels, *Urocitellus beldingi*. I will evaluate the physiological and fitness benefits of sociality, how sociality affects predation risk and how resource distribution affects sociality. I will also conduct a comparative phylogenetic analysis of sociality in the Marmotini, the tribe to which *U. beldingi* belongs.

Cindy Carlson "Ecology and Social Organization of Wild Pigtail Macaques (*Macaca nemestrina leonina*)"

Little is known about the ecology and social organization of wild pigtail macaques (*Macaca nemestrina leonina*). In order to better understand this species, census data on groups living in the Mo Sing To – Klong E Tau area of Khao Yai National Park, as well as behavioral data on a single social group were collected. Focal animal follows, instantaneous scans, and ad libitum behavioral measures were taken. Dominance style, group sex ratio, patterns of interaction, general activity budget, and home range use will be discussed.

Edna Davion "Do colugos have genes for colour vision?"

It has long been accepted that mammals were generally small and nocturnal for the first two thirds of their evolution (210 to 65 mya). It has also been widely accepted that ancestral primates remained nocturnal, with some descendant lineages secondarily developing diurnal behaviour. Early terrestrial vertebrates seemingly had tetrachromatic vision: 4 colour opsin genes corresponded to 4 cone types for photopic vision and a rhodopsin gene corresponded to rods for scotopic vision.

Extant placental mammals, including most primates, are typically dichromatic; 2 ancestral colour opsin genes (SWS2 and RH2) and corresponding cone types have been lost. Uniquely among placental mammals, humans, apes and certain diurnal monkeys are truly trichromatic. Nocturnal mammals consistently possess cones, previously thought to serve photopic vision exclusively. Surprisingly, two different cone types (Medium/Long-wave Sensitive M/LWS and Short-wave Sensitive SWS1) are commonly present in the retina of nocturnal mammals. But SWS1 opsins have been suppressed in several lineages, including 3 groups of primates (loris group, dwarf lemurs and owl monkeys). Retention of cone opsins in nocturnal primates led some authors to infer a diurnal ancestry. Here we examine these claims in light of phylogenetic analysis of opsin genes of representative genera of the supraordinal clade Euarchonta.

Rebecca Dikow "Reconstructing genome histories with phylogenetic trees: examples from the Gamma-proteobacteria"

A phylogenetic systematic study using complete genome data for 22 members (19 species, three additional strains of one particular species) of Shewanellaceae (Bacteria: Gamma-proteobacteria: Alteromonadales) is presented. The initial challenge is to find homologous regions across unannotated complete genome sequences. From those regions that were found common to all 22 taxa, a total of 3,361,015 aligned base-pairs was analyzed and resulted in a tree of 7,875,803 steps. Beyond this initial hypothesis of relationships, analysis of these data allows us, by optimizing characters and consulting genome annotations, to consider genome evolution from a phylogenetic perspective. Comparison of gene content and gene order in those regions of primary homology mentioned above allows one to make hypotheses of gene homology not based solely on annotation, but also on phylogeny. Hypotheses of lateral gene transfer, recombination and other genome-level evolutionary processes can be made using these character optimizations. Rather than representing an approach that ignores the actual character transformations based on the tree topology, the study presented here attempts further exploration of characters and their histories.

Andy Dosman "Examining the relationship between animal personality and behavioral plasticity"

Perhaps the most fascinating aspect of behavior is that it can be subject to such large variation, both within and between individuals. Behavior has long been considered the most labile of traits. This has led to assumptions of optimal plasticity of behavior across environments and contexts. However, data are accumulating from a broad range of taxa showing that behavior does not vary as expected. Individuals often show consistent differences across environments, a concept that has been termed animal personality. These consistencies do not preclude phenotypic plasticity, but imply limited plasticity. Using Belding's ground squirrels (*Urocitellus beldingi*) I will present data experimentally testing mechanisms of plasticity. Manipulations of behavioral contexts will show the relationship between plasticity and animal personality. These findings will be integrated into research measuring selection and quantitative genetic parameters in a free-ranging population of Belding's ground squirrels. This approach aims to understand behavioral variation at both proximate and ultimate levels, and will clarify the factors involved in the evolution of plastic traits.

Libby Eakin "Using agent-based models to understand how Gypsy moth feeding behavior affects susceptibility to an obligately lethal virus"

It is known that individual Gypsy moth caterpillars vary in their risk of infection by the obligately lethal virus, LdNPV. In order to understand how resistance to a disease can evolve, it is important to tease apart risk of infection, a complex trait, into the biological components that determine it. I use field experiments and computer simulations to see how variability in caterpillar feeding behavior can cause variability in risk of LdNPV infection. My goal is to determine if feeding behavior plays a role in shaping long-term Gypsy moth - LdNPV dynamics.

Paul Grabowski "Population structure and adaptation of switchgrass in sand dune ecosystems"

Within coastal sand dune ecosystems, switchgrass (*Panicum virgatum*) survives in very harsh and variable conditions. Ground cover, indicator species, and fine-scale weather monitoring illustrate that plants in close geographic proximity are subject to very different and often extreme environmental stressors. Previous work has shown latitudinal adaptation in switchgrass, but at a finer geographic scale, is there habitat adaptation in dune ecosystems? I am using a reciprocal transplant experiment to test for local adaptation in our field site, Indiana Dunes State Park. To complement the reciprocal transplant, I am using second generation sequencing methods to measure population structure of switchgrass within our field site and at the regional level using samples collected from additional dune systems and other switchgrass populations throughout the Great Lakes region.

Bin He "Evolutionary Dynamics of Transcription Factor Binding Sites in *Drosophila*"

Transcriptional enhancers in *Drosophila* are often functionally conserved despite extensive sequence divergence, presenting a challenge to our understanding of how enhancers and specifically transcription factor binding sites (TFBS) evolve. Here we present a population genetics study of ~700 experimentally identified TFBS across 119 *Drosophila* enhancers within and between *D. melanogaster* (mel) and *D. simulans* (sim). In this exclusively mel ascertained TFBS set, we found a general trend of affinity decrease in sim that entails multiple TF and enhancers. We suggested a compensatory gain and loss of TFBS model and supported the model with computationally predicted novel sites. To further investigate the direction and strength of selection acting on TFBS mutations, we classified polymorphic and fixed nucleotide changes into either affinity-increasing or affinity-decreasing. Comparison of polymorphism and divergence pattern in sim between the two classes strongly suggest non-neutral evolution in at least one of the two. Surprisingly, by comparing to a putatively neutral class of sites (McDonald Kreitman test), we found evidence for positive selection on the affinity-decreasing mutations fixed in sim, with an average scaled selection coefficient ($2Nes$) between 2 and 5. We discuss possible explanations for why weak positive selection may be driving loss of functional TFBS. This work proposed a novel aspect of TFBS

evolution that will help understand the complex dynamics of enhancer sequence evolution under functional constraints.

Matt Heintz "Play behavior characterized in infant chimpanzees"

Play behavior is widespread among mammals but the benefits of play are poorly understood. Chimpanzees are an excellent species due to their high rates of play behavior and extended period of development. My research objectives are to determine 1) the relationship between play and development, stress, and health (immediate benefits), and 2) how levels of play during infancy correlate with stress later in life, dominance rank and mating success during adulthood (delayed benefits). I have observed infant chimpanzees in Gombe National Park and collected fecal samples from infant individuals during my first field season (May-November 2009). Play behavior patterns and cortisol levels in infant chimpanzees will be characterized.

Matt Horton "Combining metagenomics, metabolomics and genome wide association studies to unravel species interactions."

The goal of metagenomics is to characterize the features of intact microbial communities; metabolomics offers the opportunity to survey the metabolites produced by an organism or environment in a particular physiological or environmental context. Here we report on our efforts to leverage metagenomics and metabolomics to find the factors in *Arabidopsis thaliana* responsible for the composition of its microbial community.

Aaron Kandur "A Mechanistic Investigation of Range Limits Across Scales"

Distributional limits are poorly understood in most species but are extremely important to development of explanations for how species adapt and how they are likely to react to environmental change. In an attempt to improve understanding in this area I am investigating distributional limits in a tractable and manipulable species *Mytilus californianus* in the Pacific Northwest. By monitoring demographic parameters of populations at multiple scales I am developing a model explaining patterns of *Mytilus* distribution.

Dave Kennedy "Using response-time data to fit mechanistic models of within-host pathogen growth"

Although questions about virulence evolution have been approached from both theoretical and empirical perspectives, incorporation of these two perspectives requires fitting within-host disease models to data. However, fitting these models has proved challenging due to limitations in computing power. Here I show a highly parallel method to find parameter estimates of a mechanistic within-host disease model, using host response-time as input data. The method is initialized by parameter line-searches started at a large number of randomly chosen initial values. A subset (4\%) of parameter sets with the highest likelihood are then subjected to principal component analysis (PCA), transforming the mechanism-based, but correlated parameters into phenomenological, but uncorrelated parameters. Next, multiple simultaneous Metropolis-Hastings MCMC chains are run, with the mean and variance of each proposal distribution determined by the

PCA. Finally, the original parameter posterior density is obtained by back-transforming the output of the MCMC. By using this method, it is possible to fit mechanistic within-host disease models to data, thus allowing future studies to bridge the gap between the theories and observations of virulence evolution.

Brandon Kilbourne "The Scaling of Limb Rotational Inertia in Quadrupedal Mammals"

Recent biomechanical studies have revealed that the metabolic cost of swinging the limbs is a significant portion of the total metabolic cost of locomotion. Such studies suggest that the rotational inertia of limbs is relevant to understanding the mechanics and energetics of terrestrial locomotion. However, scant data on limb inertial properties currently exist. Data on limb inertial properties – limb mass, moment of inertia, center of mass position, and natural frequency – were collected from the fore- and hindlimbs of 17 species of quadrupedal mammals (representing nine families) in order to understand how limb rotational inertia varies with body size. Muscles were left in situ on limb bones in order to measure limb inertial properties for the entire appendicular musculoskeletal system. To standardize comparisons, inertial properties were measured only for limbs in the extended position. As a function of body mass, limb mass scales according to geometric similarity, with limb mass being a constant fraction of body mass across mammals. Fore- and hindlimb center of mass position both scale isometrically with body mass. As a percentage of limb length, fore- and hindlimb center of mass position are independent of body size. Fore- and hindlimb moment of inertia also both scale isometrically with body mass. In both the fore- and hindlimbs, the scaling of limb natural frequency is also not significantly different from the predictions of geometric similarity. The relationship between limb natural frequency and body mass is negative, paralleling the scaling of stride frequency between small and large mammals.

Ben Krinsky "New genes and male reproductive function in *Drosophila*"

The study of newly arisen loci ("new genes") provides interesting insights into numerous biological processes and the origins of phenotypic novelties. In particular, certain new genes in the genus *Drosophila* are thought to have evolved rapidly under positive selection for male reproductive functions. Herein, I will describe ongoing work to characterize the specific reproductive function of a recently duplicated gene called Zeus. This work is beginning to shed light not only on how evolution has shaped the reproductive system in flies, but also elucidate broader concepts, such as the evolution of gene-gene interaction networks.

Sophie McCoy "The Influence of Ocean Acidification on Crustose Coralline Algae Dynamics"

Ocean acidification has the potential to dramatically alter the nearshore environment in decades to come. Many important intertidal species such as coralline algae may experience conflicting responses to this new stressor. Through manipulations in the laboratory and in the field, their responses to ocean acidification and potential implications for the coastal community can be assessed.

Chris Meyer

"Mapping of Botanical Defense Systems"

Plants have a system of physical, chemical, and indirect defense strategies that make up their immune system. These defensive traits are measured in a large mapping panel of *Arabidopsis thaliana* collected from around the world. Single nucleotide polymorphisms associated with various defense traits will be mapped via genome-wide association mapping.

Aaron Savit

"Origin and Maintenance of the Circum-Amazonian Distribution:
Insights from Environmental Niche Modeling and Implications for
Biogeography"

The circum-Amazonian distribution occurs in a variety of avian and nonavian taxa and begs inquiry into the origin and maintenance of this unique distributional phenomenon. This distribution extends across, through, or on the edge of major biomes that are highly differentiated floristically. I use environmental niche modeling to evaluate the hypothesis that climatic conditions during the last glacial maximum provided more suitable habitat and greater interconnectivity among several circum-Amazonian groups relative to present distributions. I also review the evolutionary backgrounds of taxa that have this distribution, and consider the implications of their varying geographical and temporal origins. My results indicate that periodic expansions and contractions of non-Amazonian forest with which circum-Amazonian taxa are often associated have been instrumental in establishing and maintaining this distributional trend and that taxa with this pattern have diverse historical backgrounds.

Elizabeth Scordato

"Causes of long-term fluctuations in a sexually selected trait"

Socially selected traits are assumed to have costs and benefits. If these costs and benefits fluctuate over time, it is reasonable to expect trait values to fluctuate as well. We used a 25-year dataset spanning 3 populations of wild *Phylloscopus humei* (Hume's warbler) to investigate causes of annual variation in the size of a socially selected plumage trait. The wing bar, a carotenoid-based stripe on the greater cover feathers, is a condition dependent trait used in male competition and territoriality. It can vary up to 15% in average size from year to year with no overall change in the population mean over time. Variation in wing bar size is related to breeding date the previous year: years in which population mean fledge date is earlier resulted in birds returning the following year with large wing bars ($r = -0.745$, $p < 0.05$). Fledging date is correlated with spring temperature and rainfall, suggesting that birds that fledge earlier returning in higher condition (eg, with larger wing bars). Moreover, trait means for chicks and adults are correlated within and across years, indicating a degree of heritability in wing bar size. We evaluate two possible explanations for these patterns: selection and condition-dependent maternal effects. We use a pedigree-based animal model to differentiate between these alternatives.

Nathan Smith

"Phylogenetic Analysis of "Pelecaniformes" (Aves) Based on
Osteological Data: Implications for Waterbird Phylogeny and Fossil
Calibration Studies"

Debate regarding the monophyly and relationships of the avian order Pelecaniformes (tropicbirds, pelicans, frigatebirds, sulids, anhingas, and cormorants) has been a classic example of discordance between morphological and molecular estimates of phylogeny. This lack of consensus seriously hampers interpretation of the peleciform fossil record, which is quite extensive and has major implications for understanding patterns of character evolution (e.g., possible multiple origins of wing-propelled diving), and for dating deep splits in higher-level avian phylogeny (e.g., the origin of modern orders and families). The monophyly and phylogenetic relationships of the avian order Pelecaniformes was assessed through the analysis of a morphological phylogenetic dataset of waterbirds encompassing 59 taxa and 464 characters. Parsimony analyses reject the monophyly of Pelecaniformes, recovering tropicbirds as distantly related to the remaining members of the order, which are supported as a monophyletic Steganopodes (pelicans, frigatebirds, sulids, anhingas, cormorants). ILD tests suggest that some major anatomical partitions of the dataset may possess different phylogenetic signals, and partitioned phylogenetic analyses reveal that this discrepancy is localized outside of Steganopodes, and can primarily be attributed to a few problematic taxa (e.g., flamingos, tropicbirds). The Plotopteridae, an extinct family of wing-propelled divers, are recovered as the monophyletic sister taxon to a cormorant–anhinga clade, suggesting numerous convergent adaptations in the pectoral limbs of plotopterids and penguins. The relationships of several fossil peleciforms representing key calibration points for studies of higher-level avian diversification are also well resolved. These include *Limnofregata* (sister taxon to Fregatidae), *Prophaethon* and *Lithoptila* (successive sister taxa to Phaethontidae), and ?*Borvocarbo stoeffelensis* (sister taxon to Phalacrocoracidae). The sister taxon relationships of these fossil taxa are robust to alternate phylogenetic hypotheses, and do not change when ‘backbone’ phylogenetic constraints based on recent morphological and molecular studies of higher-level avian phylogeny are imposed. However, the successive outgroup relationships of several “stem fossil + crown family” clades (e.g., *Limnofregata*/Fregatidae; *Lithoptila*/Phaethontidae) remain highly variable and poorly supported across recent studies of avian phylogeny. Thus, the impact these fossil calibrations have on future studies of higher-level avian temporal diversification will depend heavily on the extant sister taxon relationships of both Phaethontidae and Fregatidae.

Will Tyburczy

"The effects of seasonal breeding and recruitment on predator prey
dynamics"

A large variety of organisms have discrete breeding seasons during a year, and organisms with much longer intervals between reproductive episodes (e.g. periodic cicadas) have been shown to experience significant reductions in their predator populations between breeding seasons.

However, most models of predator-prey relationships treat reproduction as a continuous phenomenon, so it is unknown how the annual reproduction of organisms may affect predator-prey dynamics. I am currently performing a set of manipulative experiments using the classic whelk-

barnacle predator-prey system, at sites that differ in their temporal patterns of prey recruitment. By fitting the data from these experiments to two sets of models that either include or exclude seasonally varying parameters, I can determine the effects of seasonal breeding on the system, and subsequently predict the trajectories of predator and prey populations at these sites.

Nate Upham "Evolution of the New World rodent superfamily Octodontoidea: using multiple genes and fossils to understand a Miocene radiation"

The New World hystricognath rodent clade Caviomorpha is comprised of 13 extant families grouped into four superfamilies. Of these, the most diverse is the superfamily Octodontoidea, which is currently known from 38 living genera and 183 species across six families. Representative taxa from the Octodontoidea occupy nearly every major habitat type across South America, from lowland arid deserts and tropical forests to isolated highland habitats, as well as habitats in Central America and the Antilles. These rodents also exploit most rodent macroniches, from strictly fossorial to scansorial, to arboreal and even semi-aquatic forms. The earliest fossil members of the Octodontoidea are known from the Late Oligocene in Argentina (24.5-29 Mya), and caviomorphs likely arrived in South America by the Early Eocene (~50 Mya), thus providing ample time for the New World diversification of this rodent lineage. Yet are evolutionary time and history sufficient to explain the regional and local patterns of species richness within octodontoid rodents (i.e., a “time-for-speciation effect”)? Or has competition for ecological niches, particularly from the northern rodent “invaders” at the time of the Great American Biotic Interchange, had a greater influence on patterns of octodontoid species richness? Understanding the relative contributions of historical and ecological processes on this rodent diversification should be aided by gathering information on the patterns, timing, and rates of evolutionary divergence within the superfamily. However, the dearth of genetic data for many octodontoid rodent groups is currently constraining these analyses; only 65.8% of genera (25 of 38) and 25.7% of species (47 of 183) have genetic data available for four targeted genes (12 rRNA, GHR, vWF, and TTH). Today, preliminary efforts to enhance the temporal and phylogenetic resolution of this radiation are discussed, including results using 836 bp of mitochondrial DNA and two fossil calibration points.

Traci Viinanen “The effects of rare, dominant alleles controlling plant morphology and seed yield on resource allocation in wild and elite breeding lines of intermediate wheatgrass (*Thinopyrum intermedium*)”

Resource allocation, one of the most successful theories in modern ecology, states that energy allocated to one function is not available to other functions. Empirical work on clonal species suggests there is a bivariate trade-off between allocation to sexual (seeds) and asexual (rhizomes and stolons) reproduction. However, not all studies have found evidence for this trade-off, suggesting that the negative relationship between seed production and vegetative reproduction is integrated with other factors. It is likely that a combination of genetic, physiological, and ecological mechanisms maintain the relationship between sexual and asexual reproduction, and I predict that the most important factor will be that which limits seed production. Intermediate wheatgrass (*Thinopyrum intermedium*) is an ideal model organism for studying resource allocation trade-offs

because of the strong evidence for rare, dominant alleles that constrain plant height, tillering, rhizome production, fertility, seed size, head size, and leaf length in elite breeding lines. I will test for linkage and pleiotropy as potential genetic mechanisms maintaining the trade-off and pollen quality as a specific mechanism for limiting seed production. Through crosses and establishment of mapping populations, I will also determine if these alleles elicit resource trade-offs in wild accessions of Intermediate wheatgrass.

David Wheatcroft "Birds cooperatively attack predators only when immediately beneficial"

The evolution of cooperation remains difficult to explain, because, by definition, animals engaging in a cooperative behavior benefit others, but might themselves incur costs. One solution to this problem—reciprocity—is that individuals only cooperate with others that are likely to “return the favor” in the future, while another solution is that individuals only cooperate when they can derive immediate benefits. Using a game theoretic analysis of a classic cooperative behavior—avian mobbing of predators—and a series of field experiments, I show that birds only attack predators when immediately beneficial. This result contrasts with earlier studies and has implications for how we understand the evolution of similar cooperative behaviors.