

# LevinFest

June 15, 2019  
Bob Wright Centre A104  
University of Victoria

- 9:00 **Welcome**
- 9:05 Simon Levin. **Keynote.** Public Goods, from Biofilms to Societies.
- 10:00 **Break**
- 10:20 Steve Perlman. X Chromosomes That Break the Rules of Mendelian Inheritance.
- 10:40 Daniel Cooney. PDE Models for Multilevel Selection: The Ghost of Lower-Level Selection and Transitions in Biological Complexity.
- 11:00 Rhonda Reidy. Application of Acoustic Methods to Characterize Humpback Whale Prey in British Columbia.
- 11:20 Benjamin Liu. Accelerating Invasions and the Asymptotics of Fat-Tailed Dispersal.
- 11:40 Ismail Belgacem. Reduction and Stability Analysis of a Transcription-Translation Model of RNA Polymerase.
- 12:00 Chai Molina. Universal Evolutionary Stability and Instability in Finite Populations.
- 12:20 **Lunch and Forest Walk**
- 1:40 Mark Lewis. **Plenary.** Understanding Animal Movement Patterns with a Mathematical Eye.
- 2:15 Chadi Saad-Roy. Eco-Evolutionary Consequences of Dynamics of Molecular Characteristics in Influenza A Viruses.
- 2:35 Jingjing Xu. Modelling Chronic Wasting Disease in Mule Deer.
- 2:55 Michael Li. Use Mathematics to Assess the Burden of HIV/AIDS in China.
- 3:15 **Break**
- 3:35 Carla Staver. **Plenary.** Resilience and Stability of Tropical Biome Distributions.
- 4:10 Laura Cowen. Estimating Population Abundance Using Counts from an Auxiliary Population and N-Mixture Models.
- 4:30 Christopher Heggerud. Multiple-Scale Analysis of a Stoichiometric Cyanobacteria Model with Phosphorus Impulses.
- 4:50 David Holloway. Leaf Vein Patterning: Growth Regulator Dynamics of Normal and Transport-Disrupted Development.
- 5:10 David Smith. The Spatial Dynamics of Malaria.
- 5:30 **Closing Remarks**

## **Public Goods, from Biofilms to Societies**

Simon Levin (Princeton University), at 9:05

Ecological and economic systems are alike in that individual agents compete for limited resources, evolve their behaviors in response to interactions with others, and form exploitative as well as cooperative interactions as a result. In these complex adaptive systems, macroscopic properties like the flow patterns of resources like nutrients and capital emerge from large numbers of microscopic interactions, and feed back to affect individual behaviors. In this talk, I will explore some common features of these systems, especially as they involve the evolution of cooperation in dealing with public goods, common pool resources and collective movement. I will describe examples from bacteria and slime molds to vertebrate groups to insurance arrangements in human societies and international agreements on environmental issues.

## **X Chromosomes That Break the Rules of Mendelian Inheritance**

Steve Perlman (University of Victoria), at 10:20

Selfish genetic elements violate the rules of Mendelian inheritance in order to increase their transmission, often at the expense of the organism. They are pervasive and important players in organismal ecology and evolution, but have traditionally been difficult to study because they are often cryptic. Among the most striking examples of selfish genetic elements are selfish X chromosomes that interfere with meiosis; these have been documented so far in insects, plants, and rodents. In insects, males that carry a selfish 'distorting' X chromosome produce a gene product that destroys Y-bearing sperm, so that they produce only (or mostly) daughters. A major outstanding question is to understand the ecological and evolutionary consequences of this extreme sex ratio distortion. What prevents a selfish X chromosome from driving its host to extinction? How does the rest of the genome respond to distortion? We recently discovered a selfish X chromosome in a common woodland fly, *Drosophila testacea*, and I will present research aiming to understand its ecology, genetics, and evolution, including a collaboration with Pauline van den Driessche and Chadi Saad-Roy, on modelling its persistence.

## **PDE Models for Multilevel Selection: The Ghost of Lower-Level Selection and Transitions in Biological Complexity**

Daniel Cooney (Princeton University), at 10:40

In this presentation, we will discuss PDE models for multilevel selection, with an emphasis on studying the evolution of cooperation when there is reproductive competition both between individuals and between groups. We focus on the derivation and analysis of the long-time behavior of the replicator dynamics for multilevel selection in the Prisoner's Dilemma, showing that how whether the individual advantage of defectors or the group advantage for groups with cooperations wins out in the long run depends on the relative selection strength at the two levels. A notable finding is the ghost of lower-level selection: if groups are best off with a mix of cooperators and defectors, then there will always be fewer cooperators than optimal at steady state, even in the limit of infinitely strong selection strength at the group level. While this ghost phenomenon can be an impediment to achieving optimal group outcomes, we discuss assortative and reciprocity-based mechanisms for game-theoretic interactions which can help overcome the ghost and potentially allow for the eventual transition to the construction of a cooperative unit capable of operating at a higher level of selection.

## **Application of Acoustic Methods to Characterize Humpback Whale Prey in British Columbia**

Rhonda Reidy (University of Victoria), at 11:00

Removal and subsequent recovery of large whales in the North Pacific could drive potentially large changes in prey biomass consumption with unknown impacts to fisheries management. Developing a cost-effective sampling framework for obtaining time-series data on prey composition and spatiotemporal dynamics of baleen whale feeding remains a major challenge. We investigate a sampling method that measures a variety of surface and deep-water prey characteristics in North Pacific Humpback Whale feeding areas near northern

and southern Vancouver Island, British Columbia (B.C.). The vertical distribution of prey is continuously recorded near feeding Humpback Whales from a small vessel using an Acoustic Zooplankton and Fish Profiler (AZFP), following fine-scale transects to map three-dimensional prey fields. The surveys are conducted in daylight hours in regions with and without foraging Humpback Whales to describe prey in the areas used by the whales. Regional mid-water prey sampling informs the species composition of acoustic signal data, while humpback fecal sampling provides information about which prey species are actually consumed. Results show consistent differences between feeding regions, with Humpback Whales targeting shallow Pacific Herring aggregations off northern Vancouver Island but deep layers of Walleye Pollock and euphausiids in southern Vancouver Island waters. Fecal samples from surveyed whales in southern waters comprise mainly bones from juvenile Walleye Pollock or Pacific Cod, while surface observations document juvenile herring as the dominant humpback prey in northern waters, thus linking Humpback Whale foraging to concurrent measures of prey from the AZFP. Given the current lack of knowledge about Humpback Whale diet and the whales impact on forage fish in B.C., this combined approach provides a quantitative framework for intensive baseline sampling that is needed in B.C. for accurately estimating diet and regional prey requirements of Humpback Whales at the level required for making important fisheries decisions.

### **Accelerating Invasions and the Asymptotics of Fat-Tailed Dispersal**

Benjamin Liu (University of Washington), at 11:20

Integrodifference equations (IDEs) are used in ecology to model the growth and spatial spread of populations. With IDEs, dispersal is specified with a probability density function, called the dispersal kernel, and the shape of the kernel influences how rapidly invasions progress. Invasions where the dispersal kernel is fat-tailed have long been known to display exotic behavior, such as acceleration without bound, but analysis of these invasions has proven difficult. In this talk, we apply tail additivity, a property of regularly varying probability densities, to model invasions with fat-tailed dispersal in one dimension. We analyze point-release and front-release invasions, corresponding to newly established and well-established populations, and we find that front-release invasions gain a permanent speed-up over point-release invasions, invading at a faster geometric rate that persists for all time. Since accelerating invasions are qualitatively different than constant-speed invasions, we also discuss how measures of invasion must be modified and reconsidered when invasions accelerate.

### **Reduction and Stability Analysis of a Transcription-Translation Model of RNA Polymerase**

Ismail Belgacem (University of Victoria), at 11:40

We investigate two different ways of modelling biological networks with differential equations: a classical way using Hill functions and a detailed way following classical mass-action kinetics. Taking the second approach, we study the reduction and stability analysis of a transcription-translation model of RNA polymerase where we have a closed loop from the RNA polymerase produced by gene expression to the transcription step (RNA polymerase is needed to transcribe its own gene). Using model parameters given by biologists, we separate the full system into fast and slow subsystems and we reduce it using singular perturbations to a system of two ordinary differential equations and two algebraic equations. In addition to the trivial (zero) equilibrium, this system has a unique positive equilibrium that is globally stable when the amount of the ribosome ( $R_0$ ) is large. The proof uses monotone systems theory. If  $R_0$  is small, the origin is the unique equilibrium and is globally stable and we compute a threshold value of  $R_0$ . These results are consistent with several biological experiments dealing with adaptation of living organisms to their environment, which show that if the amount of ribosomes is large then the cell will continue to live and if the amount of ribosomes is small then the cell will die.

### **Universal Evolutionary Stability and Instability in Finite Populations**

Chai Molina (International Institute for Applied Systems Analysis & Princeton University), at 12:00

Analyses of biological and cultural evolution in explicitly finite populations typically consider one of the two canonical, but unrealistic, population-genetic schemes for translating differences in *fitness* to changes in the frequencies of genotypes over time: the Moran and Wright-Fisher processes. Because the mechanistic

details of how traits spread influence the probability that either trait takes over, uncertainty about these details casts doubt on analyses that predict outcomes of evolutionary processes. Here, we characterize the circumstances under which selection favours or opposes fixation of mutants, for any of a very wide class of biologically feasible models of selection (including, in particular, the Moran and Wright-Fisher processes), and derive conditions for universal evolutionary stability, that is, evolutionarily stability that is independent of the selection process. Because current models of evolution often involve the simplifying—but unrealistic—assumption that the population is infinite, we also use this framework to identify situations in which evolutionary outcomes in finite populations align with, or differ from, the predictions of infinite-population models.

### **Understanding Animal Movement Patterns with a Mathematical Eye**

Mark Lewis (University of Alberta), at 1:40

Animal movement patterns have long been the subject of mathematical and ecological interest. How do individual behavioral decision rules translate into macroscale patterns of space use such as foraging, patrolling or territories? A mixture of tools including mechanistic models, random walks and other mathematical tools can be used to connect underlying processes to the observed patterns. Here interactions are complex and may involve memory of past events, as well as a cognitive map. I will connect the models closely to detailed biological data, and make applications to a spectrum of different emerging patterns, ranging from territories in Amazonian birds to patrolling in wolves

### **Eco-Evolutionary Consequences of Dynamics of Molecular Characteristics in Influenza A Viruses**

Chadi Saad-Roy (Princeton University), at 2:15

Influenza A viruses (IAVs) are negative sense RNA viruses that cause seasonal human infections. These viruses are under strong immune selection, and, as RNA polymerases are error-prone, are thus able to evolve rapidly to successfully evade host immunity due to previous infection. As host immune responses to IAV infection focus on the hemagglutinin (HA) surface protein of IAVs, unravelling HA evolution is crucial to elucidate IAV disease dynamics. While the HA protein is continually under strong immune selection, this protein also has underlying biophysical and functional constraints that additionally shape its fitness landscape. Furthermore, significant efforts have been undertaken to develop Universal Influenza Vaccines that confer broad protection for multiple IAVs. Thus, it is key to understand how these molecular features that impose constraints interplay with evolutionary and transmission dynamics across scales. In this talk, I will present results of recent work to show that signatures of molecular characteristics can be detected at population scales and will discuss downstream implications.

### **Modelling Chronic Wasting Disease in Mule Deer**

Jingjing Xu (University of Alberta), at 2:35

Chronic Wasting Disease (CWD) is a 100% fatal, untreatable, infectious prion disease in cervids, e.g., mule deer, white-tailed deer, elk, causing problems to cervid population size, the hunting tradition, and the ecological system. It is transmitted via direct deer-to-deer interactions as well as by environmental contamination. In turn, the direct interactions depend upon the social structure and movement behaviours of the cervid hosts. Our model considers both the direct contact (deer to deer) and the indirect contact (contaminated soil or vegetation to deer), and the difference in dispersal distance and group size between males and females. We build a differential equation model tracking the change of susceptible and infected deer of both sexes and the environmental hazard (prions), based on the deer movement around their home ranges. This model brings insight into the spread of CWD, and our main object is to assess the effect of environmental heterogeneity on the contact rate of CWD. (Co-authors: Mark Lewis and Evelyn Merrill, University of Alberta)

### **Use Mathematics to Assess the Burden of HIV/AIDS in China**

Michael Li (University of Alberta), at 2:55

I will show how mathematical models can be used to analyze surveillance data of HIV infections in China and produce estimations of the disease burden in terms of HIV incidence, HIV deaths, undiagnosed HIV+ populations, and people living with HIV. This is a collaborative work with Dr. Yiming Shaos research group at China CDC.

### **Resilience and Stability of Tropical Biome Distributions**

Carla Staver (Yale University), at 3:35

A mechanistic understanding of biome distributions is a critical issue in modern ecology, especially in the context of predictive models of past and future climate change. While we can explain the current distribution of many biomes accurately, our predictions are less successful in dynamic systems where vegetation-environment feedbacks are significant. The challenge is to integrate feedbacks more fundamentally into a coherent theory of ecological process that determines biome distributions currently, and that will shape them into the future. Savannas and grasslands cover 40% of the Earth's land surface and forests cover another 30%. Understanding the dynamics among these biomes will help explain biosphere dynamics, past, present and into the future. I will combine empirical and theoretical work for insights into the mechanisms that give rise to the emergent stability of savanna, despite variability in vegetation structure within the biome.

### **Estimating Population Abundance Using Counts from an Auxiliary Population and N-Mixture Models**

Laura Cowen (University of Victoria), at 4:10

We develop a method for estimating population abundance for difficult to count populations. This is made possible using an easy to count auxiliary population with a known link to the target population. The method uses the N-mixture model framework with the addition of a layered hidden Markov model component. We apply the new methods to estimate the population of an Ancient Murrelet seabird colony, estimating the adult population size using Ancient Murrelet chicks as an auxiliary population. Clutch size is used as the link to convert from auxiliary estimates to target population estimates. The population is seen to decrease over the period 1995 to 2006, from 901 to 761 breeding pairs. We compare our estimates to the Canadian Wildlife Service (CWS) survey estimates of 1995 and 2006. Our estimates indicate a smaller abundance than the CWS estimates for 1995, and larger for 2006. Our method can be used to estimate the adult population size between CWS survey years. These methods improve upon the CWS survey methods, and can be applied to many other populations having known or parametric links to auxiliary populations.

### **Multiple-Scale Analysis of a Stoichiometric Cyanobacteria Model with Phosphorus Impulses**

Christopher Heggerud (University of Alberta), at 4:30

Cyanobacterial blooms are becoming a global concern due to the increasing prevalence of eutrophication. The dependence of cyanobacteria dynamics on phosphorus and light inputs is modeled via stoichiometric approach. The dynamics occur in distinct phases that allow us to make use of multiple time-scale analysis to uncover the driving mechanisms of each phase. As a result, we are able to approximate the length of time a bloom persists after an impulse of phosphorus. This framework helps to establish the use of multi-scale methods in stoichiometric models, and provides deeper understanding of cyanobacteria dynamics.

### **Leaf Vein Patterning: Growth Regulator Dynamics of Normal and Transport-Disrupted Development**

David Holloway (British Columbia Institute of Technology), at 4:50

The growth regulator auxin plays a central role in development across plants. Auxin spatial patterning is critical in the phyllotactic arrangement of leaves along a stem, the shapes of the leaves themselves, and venation within leaves. These patterns depend on polar auxin transport (PAT) at the cellular level, particularly the preferential allocation of PIN efflux proteins to certain areas of the plasma membrane. Two

general mechanisms have been studied: an up-the-gradient (UTG) allocation dependent on neighbouring-cell auxin concentrations, and a with-the-flux (WTF) allocation dependent on the flow of auxin across walls. We developed a combined UTG+WTF model for leaf venation. The model simulates intracellular and membrane kinetics and intercellular transport, and is solved for a 2D leaf of several hundred cells. We find that vein initiation in the leaf margin and cell polarization towards new veins is UTG-driven, while WTF is critical for vein extension. UTG is important for joining veins to form a network structure. The model produces the experimentally observed succession of effects when PAT is increasingly inhibited by NPA treatment. Venation patterns are highly correlated with leaf shape; this model enables the investigation of how PAT dynamics contribute to the diversity of leaf shapes across plants.

### **The Spatial Dynamics of Malaria**

David Smith (University of Washington), at 5:10

Human malaria is a disease caused by infection with a parasite that is transmitted by mosquitoes. Using historical and contemporary examples, I will discuss the pivotal role mathematical models have played developing metrics to measure malaria transmission, framing complex problems, and advancing the quantitative study of malaria epidemiology. In particular, I will trace the concept of  $R_0$  in defining a threshold condition for malaria elimination with a focus on models of mosquito movement, human movement, and heterogeneous malaria spatial dynamics. Here, I will argue that local spatial heterogeneity combined with changes in human societies and behaviors offer the best explanation for global changes in the distribution of malaria over the past century.