BIRS Workshop 13w5151
Current Challenges for Mathematical Modelling of Cyclic Populations

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Nov 10, 2013–Nov 15, 2013

1 Overview and Recent Developments

Population cycling is a ubiquitous phenomenon, applying across a number of animal, insect and bird populations in a wide variety of ecosystems [24, 33]. Furthermore, the dynamics of oscillating populations generate events of significant management and economic concern. For example, important cyclic events include periodic insect outbreaks, (e.g. spruce budworm [4], mountain pine beetle [5]), population lows in economically valuable fish stocks (e.g. salmon [21]), closure of grouse moors during troughs in population cycles [18] and cycles in the observed effectiveness of biocontrol agents [12]. Our ability to manage, anticipate, and mitigate the effects of these cyclic populations rests heavily on our mathematical understanding of the processes that generate or drive the observed cyclicity.

The study of population cycles via mathematical modelling has a long history, dating back to the work of Lotka and Volterra almost 100 years ago. Substantial modeling effort has been expended to explain how population cycles form and persist [8, 33]. Nevertheless definitive explanations for cycling have emerged only recently and only for some species, with mathematical modelling playing an important role in many of the studies. These studies have given ecologists and managers some very useful tools for managing and understanding cyclic populations. The cause of cycles remains unknown in many cases however, and mathematical modelling has an important role to play in this ongoing work.

Part of what makes it so difficult to pin down the cause of cyclicity in individual populations is that there are a myriad of factors that could be implicated. First, there are internal properties of systems that make them prone to cycles. These include density-dependent interactions between and within species, oscillations in reproductive rates, and integration of thermal or daylight inputs. Mathematical studies have clearly demonstrated that such properties can induce population cycles [31, 14, 27]. In addition, a number of important external drivers provide significant dynamic forcing. These include temperature shifts due to climate change [13, 30], spatial shifts due to anthropogenic habitat fragmentation [34], food web shifts due to introduction of invasives [16] as well as diurnal and annual oscillations. When a system that is prone to cycles is coupled to an external forcing, the resulting dynamics can be extremely complex [22, 29, 15, 11]. Population cycles thus present significant mathematical challenges in their temporal, spatial and spatio-temporal aspects.

Many models of cycles have focussed on predator-prey dynamics without regard to spatial patterns, although there are some models of synchrony across broad regions that have considered space [9]. With the advent of increased computing resources and GIS technology, there has been substantial theoretical work with spatially-explicit mathematical models aimed at understanding the interaction of species with each other and with the landscape [6, 25, 10, 17]. In recent years, more work has been done, both in mathematical modelling and in ecology, toward understanding the role of space in population cycles [28, 23]. A number of cycling populations exhibit marked geographic synchrony, although many show geographic variation in the period or amplitude of cycles even if the dynamics are synchronous. Spatial heterogeneity may affect cycles via a number of mechanisms, such as movement and dispersal of individuals over the landscape [7, 26], or contact rates between predators and prey [8, 20].

Three recent developments have raised the profile and importance of research on population cycles. Firstly, it has become clear that climate change is having a major effect on the demographic parameters of many cyclic populations [19]. Recently, it has been shown that season length can affect the onset or stability of cycles in stable populations [35], as can habitat fragmentation and loss [32]. These findings point to potentially large effects of climate change that are, at present, only very superficially understood. Secondly, an increasingly large amount of high quality spatiotemporal data on cyclic populations is becoming available, and in many cases this reveals complicated spatial dynamics, layered on top of the temporal cycles. Thirdly, there is an increasing awareness of the environmental importance of population cycles, due for instance to the risk of extinctions during periods of low density, or damage to economically valuable crops during periods of high density.

This increase in ecological interest and importance coincides with recent mathematical developments that have the potential to confront the ecological challenges in a robust manner. These developments include new methods for studying the dynamics of periodically forced oscillators; the theory of absolute and convective stability and its study via the absolute spectrum; new methods linking invasion dynamics with spatiotemporal behaviour behind invasion; new work on averaging techniques which enable analytic study of seasonally complex models; methods in spatiotemporal statistics that enable newly available spatiotemporal data sets to be used effectively; and new methods in spatial optimal control theory that provide a firm and robust foundation for parameter estimation.

2 Presentation Highlights

The workshop brought together 21 ecologists and mathematicians in the beautiful setting of the Banff International Research Station for Mathematical Innovation and Discovery (BIRS) to share ideas and discuss recent progress and new ideas. The workshop was organized under the umbrella of the pan-Canadian thematic year 'Models and Methods in Ecology, Epidemiology and Public Health' as part of MAP 2013.

Invariably, the classic examples of population cycles, the Canada lynx–snowshoe hare system and the vole system in Fennoscandia, played a prominent role throughout the workshop. Other experimental systems ranged from parasites and diseases to salmon. More theoretical presentations included the effects of stochasticity on cycles and statistical methods for parameter estimation.

Frédéric Barraquand (Tromsø) laid out several critical questions about mechanisms of population cycles and thereby set the stage for the entire workshop. He started with a short history on the modeling of cyclic populations, which began in the 1920s when Charles Elton studied the arctic lemming cycles and the snowshoe hare–Canada lynx cycles. Site-specific data are characterized by high-amplitude fluctuations and noise and are used to determine local mechanisms for occurrence – or not – of these cyclic fluctuations. Frédéric reported on the relative importance of specialist and generalist predation in initiating cycles, and then considered the importance of resource depletion (e.g. browsing of mosses, plants). More recently, there has been apparent disappearance of lemming cycles, and in the search for mechanisms a link to climate change emerged. In the end, he advocated new research that considers the interaction of all these different factors.

Gail Wolkowicz (McMaster) presented a simplified model of phytoplankton populations and explored model predictions for algal bloom development. Her model was relatively simple, and yet yielded highly complex patterns, such as a period-doubling cascade likely leading to chaos, and a phenomenon called an "echo bloom" where small changes in one parameter made for large differences in model behaviour. This led her to raise an important philosophical question about modelling: How can we identify the mechanisms behind any complex patterns we observe if already simple models can produce a wealth of complicated behaviour? In particular, how sensitive are model patterns to the underlying assumptions?

Dennis Murray (Trent) presented detailed data on lynx-hare cycles in North America, including stable isotope studies of lynx diet. He found that the percentage of hares in the lynx diet was closely correlated with the likelihood of the population to cycle, as well as lynx juvenile recruitment. There is strong evidence that lynx predation on alternative prey is strongly dependent on hare density. Nevertheless, latitudinal changes in lynx predation on hares seem to be more important in determining the likelihood for population cycles. Frithjof Lutscher (Ottawa) considered predator-prey interactions when predation behaviour changes between seasons. In particular, Frithjof investigated the predator-prey relationship arising from a predator with generalist behaviour in the summer, when alternative prey is abundant, and specialist behaviour in the winter, when alternative prey is scarce. Karen Abbott (Case Western) explored how stochasticity can produce large qualitative changes to ecological dynamics when the underlying deterministic structure has alternative stable states. Variance and autocorrelation of the noise can induce switching between alternative states, or even show some "attraction" to unstable equilibria.

Jeremy Fox (Calgary) talked about his work on spatial synchrony, motivated particularly by cyclic systems (lynx over all of Canada, Gypsy moth over large distances). He began by presenting a theoretical model: A two-patch predator-prey model with environmental and demographic stochasticity. He then reported corresponding empirical results obtained using a microcosm experiment in his laboratory. The major conclusion was that population interactions, driving population cycles, are a crucial amplifier of dispersal-induced synchrony.

Frank Hilker (Bath) asked how one could control chaotic behaviour. While chaos is thought to have many positive effects on ecological communities, it can have detrimental effects for populations whose chaotic solutions regularly exhibit very low densities. Ecosystems can be threatened if these populations skirting extinction are an important food source for other members of the ecosytem. Control of chaotic systems has been studied in physical systems, but the interventions one can use in physical systems are not always ethical or feasible in ecological systems. Frank gave a comprehensive overview of several different control methods and discussed management implications. Don DeAngelis (Miami) added a novel perspective to the hare-lynx cycle by including plant-herbivore interactions. The browsing by hares can be quite intense during peaks in hare cycles. Since plants have developed defenses (toxins) that are initiated with browsing and that take some years to dissipate, cycles can emerge. Bret Elderd (Louisiana State) talked about the importance of pathogens for population cycles in insect populations such as the gypsy moth. Field experiments with the Fall-armyworm and virus system, which is more amenable to small-scale experiments, revealed that induced plant defenses can decrease population heterogeneity in disease transmission, and the decreased variability can cause the system to cycle. In a second experiment, Bret found that increased temperature also decreased population heterogeneity and was thereby another avenue for the development of increased disease transmission.

Jude Kong (Alberta) presented a model for an indirectly transmitted bacterial disease composed of a bacteria-phage system coupled with a human susceptible-infected system. He showed that the bacteria-phage system could cycle in the reservoir and entrain the human susceptible-infected system, causing it to cycle. Alternatively, a joint essentially annual cycle can emerge. Kelsey Vitense (U of Washington) explored the separate and joint effects of habitat fragmentation and generalist predation on population cycles. Specifically, she wanted to understand why the showshoe hare and Canada lynx show strong cycles in the northern parts of their range but much or completely attenuated cycles in the southern ranges.

Cindy Greenwood (UBC) gave a brief primer on the Ornstein-Uhlenbeck (O-U) process and stochastic differential equations, and showed how adding stochastic components to an ODE system with damped oscillations can result in sustained oscillations. She also showed that the two-dimensional stochastic process is approximated by a matrix times a rotation process times a two-dimensional standard O-U process with independent components. This approximation makes it possible to see how the phase and amplitude of the oscillation interact. Stilianos Louca (UBC) pointed out that observed limit cycles could arise from intrinsic limit cycles (e.g. arising from a Hopf bifurcation in a deterministic ODE) or extrinsic periodic forcing (e.g. annual variation or El Nino effects) of an otherwise stable system. He developed a method that could be used to determine which of these two mechanisms is operating in a given timeseries. Chris Stieha (Cornell) presented models to explore the effects of constitutive or induced plant defenses on plant-herbivore cycles, particularly in agricultural systems involving pest herbivory. He found that many plant responses lead to stable pest populations that were higher than the original cyclic populations.

David Campbell (SFU) began his presentation with an overview of statistical methods for parameter estimation in differential equations models with a discussion and recommendation for each. In the second part of his talk, he introduced a method for probabilistically solving a differential equation in the presence of chaos and outlined the advantages of using these ideas in parameter estimation.

Rachel Taylor (Heriot-Watt) included seasonal forcing in a vole-weasel model to explore changes in cycle period as a result of seasonal variations in breeding season length. She found that cycle length decreased with decreasing latitude, suggesting an alternative explanation to the commonly accepted generalist hypothesis. She also found that multiannual cycles had larger amplitude than annual cycles. Flora Cordoleani (UC Santa Cruz) presented a stochastic age-structured model for cyclic salmon dynamics and their relation to the Pacific Decadal Oscillation (PDO). She found that decreased survival in salmon populations led to increased susceptibility to environmental flucturations, resulting in the emergence of cyclic dynamics that could then be synchronized through PDO forcing. Christina Cobbold (Glasgow) asked: What information is necessary to predict the effects of changing landscape configuration on forest insect population dynamics? To answer this question, she ran simulations of two model systems using integrodifference equations on a series of theoretical landscapes that varied in amount and aggregation of suitable habitat. She also extended the dispersal success idea to her models, developing mathematical approximations to the full equations that were extremely helpful in predicting and understanding the dynamics. She found that the effects of habitat arrangement are largest when habitat is somewhat scarce.

Huaiping Zhu (York) gave an overview of mechanisms that lead to periodic solutions in two-species predator-prey models, including global bifurcations and relaxation oscillations. Then he extended the models to include seasonally forced parameters. Rebecca Tyson (UBC Okanagan) presented several classic predator-prey models with diffusion, and compared and contrasted their behaviour under habitat fragmentation. She also showed that much of the numerically observed behaviour could be predicted using a first-order ODE approximation to the full PDE systems.

3 Scientific Progress Made

The schedule of the workshop gave ample time for unstructured discussion, and participants made good use of all the opportunities to network and learn from one another. There was an ideal mix of ecologists and mathematicians, resulting in a fertile flow of ideas across all of the disciplines represented. In addition, during several carefully organized break-out sessions, participants identified and compiled a list of current challenges in cyclic population modeling.

All of the breakout sessions were organised around a common goal: To produce a paper that would present a compendium of open problems in the research area of the workshop. The discussions that arose around this goal fostered a veritable wellspring of ideas. While everyone at the workshop was interested in modelling cyclic populations and understanding their behaviour, the variety of approaches taken to the topic were almost as numerous as the participants. The breakout session discussions were thus extremely productive, both for the sharing of ideas and the discovery of new approaches. Furthermore, the exercise of formulating open problems in the field encouraged everyone to organise their thoughts in a focussed and productive way, thus maximizing the effectiveness of the learning that occurred. A number of themes emerged, and we briefly discuss these below.

Through the talks and associated discussions, the workshop participants became widely aware of the role of stochasticity and its potential effects in cyclic populations. Through the talks, we carefully explored the dynamical systems aspects of several models, particularly the bifurcation structure relevant to population cycles. From the stochastic point of view it is also interesting where the limit points are and the bifurcations from limit points to bistability. Such highly detailed information from deterministic systems puts us in an ideal position to begin formulating and investigating stochastic versions of these models.

Several talks highlighted the paucity of high quality timseries data for a broad range of cyclic species. Some researchers address this problem by creating microcosm experiments in which most of the variables can be carefully controlled. These experiments have indeed shown that commonly-used population models are appropriate descriptors of at least some systems that exhibit population cycles. Furthermore, they yield useful information that is helpful in the interpretation of the existing ecological data. The phenomena of synchrony, phase-locking and the paradox of enrichment can all be observed, quantified and manipulated in these microcosm experiments.

During the workshop, it became clear that many researchers have different concepts of chaos. Contrasting definitions were used during the talks, and the juxtaposition of these was very informative. It also allowed for fruitful discussions of the several working definitions of chaos and the different frameworks in which the behaviour can be interpreted.

In addition to those studies examining the behaviour of particular models, other speakers compared and contrasted the dynamics of a number of apparently similar cyclic predator-prey models. The population cycles were challenged with perturbations due to habitat fragmentation and heterogeneity. Sometimes the models responded in similar ways, while at other times the models responded very differently. It is thus clear that the choice of model is important when it comes to including spatial effects. A number of important open questions arose from this work.

During the discussions and question periods it became clear that there are a number of aspects to climate change not simply restricted to changes in temperature or variability thereof. In addition, the response of a given species to climate change is likely strongly affected by the longevity of individuals and the recruitment rate. The corresponding effect on the ecosystem hinges on the role vulnerable species play in the food chain (e.g. keystone species in any position in the food chain).

Finally, there was much discussion concerning the wide variety of possible causes behind any observed cyclic behaviour, as well as the ways in which cycles can disappear. Both phenomena are important, and it was illuminating to see, through numerics, dynamical systems analysis and careful analysis of empirical data, how these different causes can be distinguished and modeled. Everyone expressed active interest in incorporating the new ideas into their work, and were excited to see how the different approaches informed each other.

4 Open Problems

The workshop participants are all engaged in writing a review paper that will be a compendium of open problems in the modelling of cyclic populations. Here we present a selection of some of the emerging themes under which questions were organised, as well as a sampling of problems under each theme.

1. **Forcing and Noise**
    - Can we, given some cyclic data, determine whether a given observed cycle is caused by internal mechanisms or forced from the outside?
    - What are the limits of the "weak noise" assumption typically made in analytical treatments? Can we develop tools for dealing with "strong noise"?
    - More philosophically, is there a difference between forcing and noise?
2. **Eco-Evolutionary Dynamics**
    - How should individual dynamics be incorporated into mathematical models? When do we need to think about individual variation and when can we use the mean?
    - Are the observed effects of population cycles in a model due to individual variation, maternal effects or evolution?
    - Do cycles in the host population make it harder or easier for a disease to emerge?
3. **Interfacing with Data**
    - How can we explain more clearly to empiricists what is the role of models?
    - What new microcosm experiments can we design to help pinpoint the weaknesses in models or theory?
4. **Novel Mathematics**
    - Can we develop new multiscale methods for cyclic populations, particularly when stochasticity is present?

- Can we develop new mathematical methods and/or models for partitioning the influence of epigenetic plasticity, genetic plasticity and phenotypic plasticity?
- Can we develop new methods to predict limit cycle amplitude and period from the mathematical equations of the model?

Many more questions were formulated within each of the topics above, and across several other themes identified before and during the meeting. After the initial identification of themes, and open problems within each topic, two full breakout sessions were reserved for writing in pairs. The format of working in pairs to write up the material generated during the first two breakout sessions went extremely well.

5 Outcome of the Meeting

The meeting played an important role in bringing together researchers who study population dynamics. It was the first meeting of its kind, and the enthusiasm among the participants was gratifying. The workshop topic was ideal in that it was focussed enough so that everyone was deeply interested in everyone else's work, but generated such a wide variety of approaches, observations and problems that participants were continually being surprised and intrigued by the work of others.

The meeting has already resulted in several new active collaborations, mostly between researchers who had never before met. Over 20% of the participants were young researchers (e.g. graduate students and postdocs), and they were keen to embark on new research projects and incorporate new ideas into their current work. In addition, many fruitful contacts were established between the faculty at the workshop, with active collaborations initiated among some, and the strong likelihood of future active collaborations also established.

The most tangible outcome of the workshop is the list of open problems written up during the group discussions, and the plans for a paper to be published in 2014. The writing of the paper is being spearheaded by Frédéric Barraquand, and the workshop participants have already engaged in writing significant portions of the manuscript. We anticipate that a first complete draft will be ready by the end of January.

6 Abstracts of Talks

Speaker: **Karen Abbott** (Case Western Reserve University - USA)
Title: *Stochasticity and bistability in insect outbreak dynamics*
Abstract: Ecologists have long recognized the possibility that some outbreaks could be explained by the presence of alternative stable states in insect dynamics, where a low-density attractor maintained by predation coexists with a high-density attractor maintained by food limitation. Under a deterministic world-view, outbreaks represent rapid switches between these two equilibria. In a stochastic world, however, the story can be more complicated, We study a stochastic version of a classic outbreak model to explore the influence of stochasticity on outbreak dynamics caused by attractor switching. Interestingly, we find that the dynamics switch not only between the two stable equilibria, but also to an unstable equilibrium in the model. We further find that the relationships between the number of stable and unstable equilibria visited changes in a non-monotonic way with several attributes of the stochasticity (intensity and color). Our work highlights the strong and often non-intuitive effects that stochasticity can have on a system relative to its deterministic counterpart, and provides a novel perspective on insect outbreaks in a stochastic world.

Speaker: **Frédéric Barraquand** (University of Tromsø- Norway)
Title: *Mechanistic models for lemming cycles: Recent progresses and challenges ahead*
Abstract: The literature on population cycles now considers often site-specific models, designed to explain the variation in densities observed at a particular location (as opposed to general models). Two important site-based mechanistic models for population cycles in lemmings have been developed, using nonlinear ordinary differential equations. One explains the fluctuations of the collared lemming at Traill island, Greenland (Gilg et al. Science 302(5646)), suggesting a strong role of predators, while another tackles cycles of the brown lemming at Point Barrow, Alaska (Turchin & Batzli Ecology, 82(6)), suggesting plant depletion can drive

lemming oscillations. In light of empirical studies and new model simulations, I discuss these results, and point to important challenges that remain, in particular concerning the connection to the data collected.

Speaker: **David Campbell** (Simon Fraser University - Canada)
Title: *Probabilistically solving differential equation models*
Abstract: Chaotic differential equation models are characterized by the divergence of solutions with respect to very small changes in initial system states. When a numerical solver is used, finite solver precision and the discretization grid influence the long term solution behaviour. Changes in the solver, the grid or the tolerance will produce divergent solutions even for a fixed initial state. This talk presents an alternative to deterministic numerical integration; probabilistically solving a system of differential equations. Using a gaussian process regression model on the system states and derivatives thereof, realizations from a functional distribution of solutions can be produced. The methodology is applied not only to quantifying the functional uncertainty induced by solving differential equation models, but also highlights how that uncertainty propagates through to parameter estimation with particular attention to chaotic systems, ill-conditioned models, and systems containing unmodelled functional uncertainty. Examples used in this talk include the chaotic Lorenz attractor ODE and Kuramoto-Sivashinsky PDE system, and the Jak-Stat delay differential equation model.

Speaker: **Christina Cobbold** (University of Glasgow - Scotland)
Title: *The effects of spatial structure on population cycles: Insights from host-parasitoid models*
Abstract: Understanding cycles of forest-defoliating insects is of major importance for forest management. Forest destruction may have complicated effects on population cycles, and the nonlinear interactions are difficult to understand from data alone. We therefore constructed 2D-spatial models to understand the effects of forest patchiness on defoliator cycles, focusing on defoliator cycles driven by parasitoids. Our models show that removing habitat can increase defoliator density when parasitoids disperse much farther than defoliators, because the benefits of release from parasitoids exceed the costs of dispersal mortality. This novel result helps explain the empirical observation that forest fragmentation increases the duration of forest tent caterpillar outbreaks. Our models also show that arranging habitat in larger patches can mitigate the effects of habitat loss, with clear implications for forest management. To better understand our results, we developed a 'local' dispersal success approximation to our model, which shows that defoliator spatial dynamics can be predicted from the proportion of dispersing animals that land in suitable habitat. This approximate model is practically useful because its parameters can be estimated from widely available data.

Speaker: **Flora Cordoleani** (UC Santa Cruz - USA)
Title: *The cohort resonance phenomenon, a possible explanation for cyclicity in salmon populations*
Abstract: The cohort resonance phenomenon is a recent notion described by [1, 2] as a way that age structured populations show greater sensitivity to environmental variability on time scales that are very long (i.e., slowly varying) and time scales near the generation time of the population. In this presentation I will show how this phenomenon could explain the cyclic dynamics observed in some salmon populations. Based on the work done by [3] on Pacific salmon I will provide an example of the link between cohort resonance and the dynamics of spring-run chinook salmon populations in the Columbia River, Oregon, and will give some insights on the conditions necessary for these populations to exhibit a cyclic behavior.

Speaker: **Don DeAngelis** (University of Miami - USA)
Title: *Modeling the dynamics of the woody plant-snowshoe hare interaction with age-dependent toxicity of twig segments*
Abstract: Modeling is used to study the effects that woody plant chemical defenses may have on population dynamics of boreal hares that feed almost entirely on twigs during the winter. The model takes into account that toxin concentration often varies with the age of twig segments. In particular, it incorporates the fact that the woody internodes of the youngest segments of the twigs of the deciduous angiosperm species that these hares prefer to eat are more defended by toxins than the woody internodes of the older segments that subtend and support the younger segments. Thus, the per capita daily intake of the biomass of the older segments of twigs by hares is much higher than their intake of the biomass of the younger segments of twigs. This age-dependent toxicity of twig segments is modeled using age-structured model equations, which are reduced to a system of delay differential equations involving multiple delays in the woody planthare dynamics. A

novel aspect of the modeling was that it had to account for mortality of non-consumed younger twig segment biomass when older twig biomass was bitten off and consumed. Basic mathematical properties of the model are established together with upper and lower bounds on the solutions. Necessary and sufficient conditions are found for the linear stability of the equilibrium in which the hare is extinct, and sufficient conditions are found for the global stability of this equilibrium. Numerical simulations confirmed the analytical results and demonstrated the existence of limit cycles over ranges of parameters reasonable for hares browsing on woody vegetation in boreal ecosystems. This showed that age dependence in plant chemical defenses has the capacity to cause hareplant population cycles, a new result. (Joint work with Rongsong Liu, Stephen A. Gourley and John P. Bryant)

Speaker: **Bret Elderd** (Louisiana State University)
Title: *Understanding disease transmission in a changing environment: Biotic and abiotic effects*
Abstract: The boom and bust cycles of insect pests are often driven by a host-pathogen interaction between the pest and a virus that causes a fatal infection. However, the intensity of the viral outbreak changes depending upon biotic and abiotic conditions. To examine how changing conditions affect disease transmission, field and laboratory experiments were conducted on and transmission models were constructed for two insect pests, the forest-defoliating gypsy moth and the crop-defoliating fall armyworm. For the gypsy moth, changes in the chemistry of the leaf tissue on which the gypsy moth feeds affects disease transmission rates and, in turn, the cyclic dynamics of the pest. For the fall armyworm, increasing temperatures increase disease transmission, which can also alter long-term cyclic dynamics. Together, these results demonstrate that both biotic and abiotic factors that change the intensity of the host-pathogen interaction are important for determining disease transmission over the short term and population dynamics over the long term.

Speaker: **Jeremy Fox** (University of Calgary - Canada)
Title: *Spatial synchrony of predator-prey cycles: models, experiments, and consequences*
Abstract: Spatially-separated populations of the same species often exhibit synchronous fluctuations in abundance, with many of the most dramatic examples coming from species exhibiting cyclic dynamics. Both dispersal and spatially-synchronous environmental forcing (the Moran effect) can generate synchrony, but their effects are difficult to tease apart in nature because experimental manipulations are impossible at the relevant spatial and temporal scales. I have developed laboratory microcosms of protist predators and prey into a model system for studying spatial synchrony of predator-prey cycles. Using a combination of mathematical models and experiments, I will show how low rates of short-distance dispersal can synchronize even widely-separated populations by forcing them to cycle in phase, a phenomenon known as phase locking. I will also illustrate the effects of environmental and demographic stochasticity on spatial synchrony. I will conclude by using stochastic metapopulation models to explore how local extinctions and spatial synchrony affect metapopulation persistence. I show that under certain conditions, local extinctions actually promote metapopulation persistence, by interfering with spatial synchrony.

Speaker: **Priscilla Greenwood** (University of British Columbia (Vancouver) - Canada)
Title: *Population Cycles Sustained by Noise*
Abstract: Many deterministic population models produce oscillations which damp to a fixed point. In nature we often observe sustained, not damped, oscillations with a narrow-band of frequencies, and also of unaccountable oscillating amplitude. It is generally understood that damped oscillations, which are intrinsic to many deterministic systems, will be sustained in the presence of, even small, system or environmental noise. Here we use stochastic process tools to derive a simple explicit approximation to such a stochastic process of sustained oscillations. Considerable understanding of the dynamics of a cycling population can be obtained from the explicit approximation.

Speaker: **Frank Hilker** (University of Bath - England)
Title: *Stabilizing fluctuating populations: Chaos control methods in ecology*
Abstract: Many populations exhibit regular or irregular oscillations which we may wish to ”control” as troughs correspond to potentially undesirable outbreaks (e.g., of pest species) and troughs may lead to extinction (e.g., of endangered species). In this talk, I will present and review a number of control strategies that perturb the population size (via culling or re-stocking) to (i) avoid undesirable dynamics or (ii) achieve certain desirable dynamics such as population stabilisation.

Speaker: **Jude Kong** (University of Alberta - Canada)
Title: *Indirectly Transmitted Infectious Diseases: From Microscopic Cycles to Macroscopic Cycles*
Abstract: Many infectious diseases that spread indirectly via reservoir remain endemic and epidemic in the world, causing thousands of deaths annually in locations lack of adequate sanitation and water infrastructures. Yet, their dynamics are still not fully understood. We present two models with a Minimum Infection Dose (MID) for such an infectious disease: iSIR and iSIBP models. We perform global and sensitivity analysis on the iSIR model and our findings indicate that to control the period and the intensity of disease outbreaks, it is better to focus on the environmental factor (represented by the bacterial carrying capacity) rather than on the sanitation (represented by the shedding rate). We extend the iSIR model by incorporating bacteriophage to obtain the iSIBP model. When the endemic equilibrium is unstable, only microscopic limit cycles exist in the case that the bacterial carrying capacity is less than MID; otherwise, both microscopic and macroscopic limit cycles exist. Our theoretical study suggests that Increasing pathogen shed rate increases the amplitude and the period of limit cycles.

Speaker: **Stilianos Louca** (University of British Columbia (Vancouver) - Canada)
Title: *Discerning externally forced oscillations and autonomous limit cycles using noisy ecological time series*
Abstract: Population cycles are ubiquitous in nature and have triggered ecologists interests for decades. Given a noisy time series exhibiting a spectral peak, how can one decide wether the observed cycles are driven by an external periodic force, or are part of an autonomously emerging limit cycle? Using a set of generic mathematical models, I show that random perturbations of the focal system leave characteristic signatures on its power spectrum and autocovariance, that differ between limit cycles and forced oscillations. Our work shows that random perturbations of ecological cycles can give valuable insight into their underlying dynamics.

Speaker: **Frithjof Lutscher** (University of Ottawa - Canada)
Title: *Prey and generalist predator through the seasons*
Abstract: Behavior of prey and predator can change with the seasons. A typical modeling approach for this situation is to make model parameters periodic functions of time. This approach changes the intensity of a certain process, but not the functional dependencies of the process itself. Inspired by data from the Kluane project, we present a model where the functional dependencies change, specifically from a generalist predator in the summer to a specialist (due to lack of alternative resources) in the winter. We use averaging techniques and numerical simulations to uncover the dynamics of the resulting system. This is joint work with Rebecca Tyson.

Speaker: **Dennis Murray** (Trent University - Canada)
Title: *Anatomy of a population cycle: Canada lynx as a case study*
Abstract: Canada lynx and their primary prey, snowshoe hare, are well known for their 10-year population cycles across much of the boreal forest of North America. Notwithstanding the longstanding interest and extensive past research into lynx patterns of cyclicity, there remain several unknown aspects of lynx cycles, including the extent of spatio-temporal variability in cyclicity, whether such variability relates to predator-prey relationships, and whether lynx cycles are becoming increasingly attenuated as is the case for natural fluctuations in several birds, insects and mammals. We analyzed lynx fur harvest time series and found that populations that cycled exhibited consistent 8-10 year cyclic periods with higher amplitude being observed among northern populations. The amplitude of lynx cycles was correlated with the proportion of snowshoe hare in the lynx diet, as determined by stable isotope analysis of lynx hair from each region. Seeking further detail into the lynx-hare relationship and its role on observed cyclic patterns, we dissected the role of demography on lynx cycles by developing matrix models identifying lynx demographic attributes potentially driving observed cyclic patterns. Our analysis revealed that changes in lynx reproductive potential, such as those typically observed during a snowshoe hare cycle, were the greatest contributor to variability in cyclic amplitude. In a related modeling effort, we showed that trapping harvest pressure could exert a significant stabilizing effect on lynx population cycles, and that harvest closures when trapping is an additive source of mortality will help maintain cyclic propensity. Finally, we show that a major challenge in understanding the drivers of population cyclicity in natural systems remains the statistical analysis of such cycles using standard

approaches, and that differentiating between populations that experience natural variability in cyclic propensity versus those undergoing actual cyclic attenuation will remain difficult given the quality of numerical data typically available for such investigation.

Speaker: **Chris Stieha** (Cornell University - USA)
Title: *Effects of plant defense on herbivore population cycles*
Abstract: Insect herbivores can be devastating to natural and agricultural plant populations. To control these pests, plant defenses, such as resistance and tolerance, have been employed, but the long term implications of these defenses on herbivore population dynamics have not been exhaustively studied. Plant resistance, a well-studied defense, decreases herbivore survival or fecundity and is predicted to stabilize herbivore populations. Plant tolerance, an under-studied defense, reduces the negative effect of herbivory on the plant's fitness, which potentially increases the amount of consumable biomass available for the herbivore. In an extreme case of tolerance known as overcompensation, plants that experience low levels of herbivory have a higher fitness than undamaged plants. Tolerance and overcompensation have been shown to initially increase plant fitness/yield, but the increase in consumable biomass could increase the herbivore density and subsequently cause a decline in plant fitness/yield. To determine the long term implications of tolerance and overcompensation on herbivore population dynamics, we have added tolerance and overcompensation to mathematical models that quantified the effects of resistance and food limitation on herbivore population dynamics. Our analyses of the new models reveal complex effects of tolerance, food limitation, and plant resistance on herbivore population dynamics. Resistance or food limitation with or without plant tolerance lead to stable herbivore densities. The combination of resistance and food limitation leads to either stable densities or cycles. The addition of tolerance or overcompensation eliminated these cycles, but the stable herbivore density within these systems can be larger than the herbivore density at the peak of the cycle in a system without tolerance or overcompensation. Our work stresses the importance of tolerance and overcompensation in the bottom-up framework of herbivore population dynamics and suggests that tolerance and overcompensation in crop systems may increase pests populations and may not necessarily result in a greater yield. (Joint work with Karen Abbott and Katja Poveda)

Speaker: **Rachel Taylor** (Heriot-Watt University - Scotland)
Title: *The impact of variations in seasonal forcing in the Fennoscandian vole system*
Abstract: Seasonality is an important component in many population systems and factors such as latitude, altitude and proximity to the coastline affect the extent of the seasonal fluctuations. But how do these changes in seasonal fluctuations impact on the population cycles? I employ the Fennoscandian vole system as a case study, focussing on variations in the length of the breeding season. Using a combination of bifurcation analysis and direct simulations, I consider the effects of varying both the level of generalist predation and the length of the breeding season; these are the main changes that occur over a latitudinal gradient in Fennoscandia. The main effect of varying the breeding season length is changes in the period of the multi-year cycles, with higher period for shorter breeding season lengths. This concurs with the gradient of periodicity found in Fennoscandia.

Speaker: **Rebecca Tyson** (University of British Columbia (Okanagan) - Canada)
Title: *The Effect of Habitat Fragmentation on Cyclic Populations*
Abstract: Habitat fragmentation is an important area of concern in species conservation. Habitat fragmentation can affect population distributions through reductions in suitable habitat, and through organism responses to different habitat types and the transitions between them. I explore the effect of habitat fragmentation on cyclic predator-prey dynamics as modeled through several different predator-prey equations. Our results show generally that habitat loss decreases the amplitude and the average density of the prey and predator populations, but that many of the reponses observed in the various models exhibit marked differences. This work highlights the complexity of the interplay between population cycles, habitat fragmentation, and edge-mediated behaviour, and the need to study such systems in greater detail.

Speaker: **Kelsey Vitense** (University of Washington - USA)
Title: *Theoretical impacts of habitat fragmentation and generalist predation on population cycles*
Abstract: Many cyclic species undergo dramatic fluctuations in abundance in northern latitudes but exhibit

damped oscillatory dynamics in their respective southern ranges. Proposed explanations for the observed reductions in population density and cycle amplitude include increased habitat patchiness and higher densities of generalist predators. Using the snowshoe hare and Canada lynx as a case study, I use advection-diffusion-reaction models with one-dimensional movement to explore the relative and combined impacts of habitat fragmentation and generalist predation on predator-prey population cycles. The results of this theoretical study will provide insight into which data types should be collected in future fieldwork to evaluate hypotheses related to the suppression of population cycles and to assess threats to population persistence.

Speaker: **Hao Wang** (University of Alberta - Canada)
Title: *Study the "Strict Homeostasis" assumption in ecological stoichiometry via bifurcations* (needs to speak early in the week)
Abstract: Not only carbon (C) but also nutrient elements such as nitrogen (N) and phosphorous (P) ar e pivotal for organismal growth, reproduction, and maintenance. Newly emerging mathematical models linking population dynamics with these key elements greatly improve historic trophic interaction models and resolve many existing paradoxes. Most of these models assume strict homeostasis in heterotroph and non-homeostasis in autotroph due to the fact that the stoichiometric variability of heterotroph is much less than that of autotroph. Via bifurcations we study when the strict homeostasis assumption is sound and when not. Incorporating light dependence on the growth of autotrophs, the resulting dynamics reveal a series of homoclinic and heteroclinic bifurcations in low light conditions giving the explanation for why microcosm experiments have had unreliable results in low light conditions. (Joint work with R.W. Sterner, J.J. Elser and A. Raghavan)

Speaker: **Gail S. Wolkowicz** (McMaster University - Canada)
Title: *Oscillations in phytoplankton growth due to limitation by light and nitrogen*
Abstract: A mathematical model of growth of two types of phytoplankton: Non-nitrogen-fixing and nitrogen-fixing phytoplankton that compete for light and nutrients is modelled and analyzed. We consider stability and persistence of the different populations and discuss the qualitative behavior of the system under different environmental conditions. In particular, we compare the predictions of the model when the assumption of constant water depth is relaxed to allow the water depth to vary in an annual cycle due to natural seasonal forcing.

Speaker: **Huaiping Zhu** (York University - Canada)
Title: *Dynamical modeling of mosquito population with temperature*
Abstract: The development of mosquitoes is highly dependent on environmental conditions, especially temperature. Even though there have been extensive modeling studies for the abundance of mosquitoes, seldom incorporate the accummulative effect of daily temperature. In this talk, I will present a matrix population model to address the accumulative impact of daily temperature on the development of mosquito population. I will also introduce the refine model with impact of over-wintering, and application of modeling mosquito-borne diseases.

7 Acknowledgements

Due to unfortunate circumstances, Rebecca Tyson was the only organiser able to attend the workshop, leaving the production of the report largely up to her. She would thus like to express her sincere thanks and appreciation to Frithjof Lutscher and Cindy Greenwood who both helped enormously with the preparation of this report.

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