BIRS Workshop 13w5151: Current Challenges for Mathematical Modelling of Cyclic Populations
Nov 10 - 15, 2013

MEALS

*Breakfast (Buffet): 7:00–9:30 am, Sally Borden Building, Monday–Friday
*Lunch (Buffet): 11:30 am–1:30 pm, Sally Borden Building, Monday–Friday
*Dinner (Buffet): 5:30–7:30 pm, Sally Borden Building, Sunday–Thursday
Coffee Breaks: As per daily schedule, in the foyer of the TransCanada Pipeline Pavilion (TCPL)
***Please remember to scan your meal card at the host/hostess station in the dining room for each meal.**

MEETING ROOMS

All lectures will be held in the lecture theater in the TransCanada Pipelines Pavilion (TCPL 202). An LCD projector, a laptop, a document camera, and blackboards are available for presentations.

SCHEDULE

Sunday

16:00	Check-in begins (Front Desk - Professional Development Centre - open 24 hours)
17:30–19:30	Buffet Dinner, Sally Borden Building
20:00	Informal gathering in 2nd floor lounge, Corbett Hall Beverages and a small assortment of snacks are available on a cash honor system.

Monday

7:00–8:45	Breakfast
8:45–9:00	Introduction and Welcome by BIRS Station Manager, TCPL
9:00–9:30	30-minute Lecture (Frédéric Barraquand)
9:30–10:00	30-minute Lecture (Gail Wolkowicz)
10:00–10:30	Coffee Break, TCPL
10:30–11:00	30-minute Lecture (Frithjof Lutscher)
11:00–11:30	30-minute Lecture (Dennis Murray)
11:30–12:00	30-minute Lecture (Karen Abbott)
12:00–13:00	Lunch
13:00–14:15	free time
14:15	Group Photo; meet in foyer of TCPL (photograph will be taken outdoors so a jacket might be required).
14:30–15:00	Current challenges: Group Brainstorming Session
15:00–15:30	Coffee Break, TCPL
15:30–16:30	Breakout sessions (should we split this into two half-hours?)
16:30–17:30	free time
17:30–19:00	Dinner
19:00–19:15	reporting back from breakout sessions
19:15–20:15	60-minute Lecture (Jeremy Fox)

Tuesday

7:00–9:00	Breakfast
9:00–10:00	60-minute Lecture (Hao Wang)
10:00–10:30	Coffee Break, TCPL
10:30–11:00	30-minute Lecture (Don DeAngelis)
11:00–12:00	30-minute Lecture (Bret Elderd)
12:00–13:00	Lunch
13:00–14:00	Guided Tour of The Banff Centre; meet in the 2nd floor lounge, Corbett Hall
14:00–15:00	free time
15:00–15:30	Coffee Break, TCPL
15:30–16:30	Breakout sessions
16:30–16:45	Reporting back from breakout sessions
16:45–17:45	60-minute Lecture (Frank Hilker)
17:45–19:30	Dinner
19:30–20:30	Opportunity to go to the Banff Hot Springs

Wednesday

7:00–9:00	Breakfast
9:00–10:00	60-minute Lecture (Priscilla Greenwood)
10:00–10:30	Coffee Break, TCPL
10:30–11:00	30-minute Lecture (Stilianos Louca)
11:00–11:30	30-minute Lecture (Chris Stieha)
11:30–13:00	Lunch
13:00–17:30	Group Hike (destination depending on weather and snow conditions)
17:30–19:30	Dinner
19:30–20:30	Public Lecture: Leading Ideas Series: Megadisaster - The Science of Predicting the Next Catastrophe, Florin Diacu (website: http://www.banffcentre.ca/event/6288/leading-ideas-series-megadisaster-the-science-of-predicting-the-next-catastrophe/?d=2013-11-13+19:30)

Thursday

7:00–9:00	Breakfast
9:00–10:00	60-minute Lecture (David Campbell)
10:00–10:30	Coffee Break, TCPL
10:30–11:00	30-minute Lecture (Rachel Taylor)
11:00–11:30	30-minute Lecture (Flora Cordoleani)
11:30–13:00	Lunch
13:00–15:00	free time
15:00–15:30	Coffee Break, TCPL
15:30–16:30	Breakout sessions
16:30–16:45	Reporting back from breakout sessions
16:45–17:15	30-minute Lecture (Christina Cobbold)
17:15–17:45	30-minute Lecture (Huaiping Zhu)
17:45–19:30	Dinner
19:30–20:30	Opportunity to go to the Banff Hot Springs

Friday

7:00–9:00	Breakfast
9:00–9:30	30-minute Lecture (Jude Kong)
9:30–10:00	30-minute Lecture (Kelsey Vitense)
10:00–10:30	Coffee Break, TCPL
10:30–11:00	30-minute Lecture (Rebecca Tyson)
11:00–11:30	wrap-up discussion (led by Frédéric Barraquand and Rebecca Tyson)
11:30–13:30	Lunch

Checkout by 12 noon.

** 5-day workshop participants are welcome to use BIRS facilities (BIRS Coffee Lounge, TCPL and Reading Room) until 3 pm on Friday, although participants are still required to checkout of the guest rooms by 12 noon. **

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ABSTRACTS
(in alphabetic order by speaker surname)

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 Tromso - 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 Davis - 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 cyclesusing noisy ecological time series*
Abstract: (not provided)

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.

References

[1] Bjornstad, O. N., Fromentin, J.-M., Stenseth, N. C. and Gjosater, J. (1999) **Cycles and trends in cod population.** *Proceedings of the National Academy of Science USA*, 96, 5066-5071.

[2] Bjornstad, O. N., Nisbet, R. M. and Fromentin, J-M (2004). **Trends and cohort resonant effects in age-structured populations.** *Journal of animal ecology*, 73, 1157-1167.

[3] Worden, L., Botsford, L. W., Hastings, A. and Holland, M. D. (2010). **Frequency responses of age-structured populations: Pacific salmon as an example.** *J. Theor. Pop. Biol.*, 78, 239-249.