Kurt E. Anderson(1), Frank M. Hilker(2), and Roger M. Nisbet(3)

(1) University of California, Riverside
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Directional dispersal plays a large role in shaping ecological processes in diverse systems such as rivers, coastlines and vegetation communities. We describe an instability driven by directional dispersal in a spatially explicit consumer–producer model where spatial patterns emerge in the absence of external environmental variation. Dispersal of the consumer has both undirected and directed components that are functions of producer biomass. We demonstrate that directional dispersal is required for the instability, while undirected diffusive dispersal sets a lower bound to the spatial scale of emerging patterns. Furthermore, instability requires indirect feedbacks affecting consumer per capita dispersal rates, and not activator–inhibitor dynamics affecting production and mortality as is described in previous theory. This novel and less-restrictive mechanism for generating spatial patterns can arise over realistic parameter values, which we explore using an empirically inspired model and data on stream macroinvertebrates.

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Kate E Buenau, Pacific Northwest National Laboratory
Andrew J Tyre, University of Nebraska, Lincoln

Estimating the value of information for habitat restoration: Using population models to prioritize research for the piping plover (Charadrius melodus) on the Missouri River

Restoration programs operating under high epistemic uncertainty face tradeoffs between spending money directly on restoration or investing in research. We demonstrate a method to prioritize research needs according to the monetary value of information, based on the potential for additional information to change the optimal amount of habitat restoration estimated by a numerical model. As a case study, we use a population model of the threatened piping plover (Charadrius melodus), which nests on emergent sandbar habitat (ESH) on the Missouri River. Plover reproductive success is dependent upon the availability of ESH, which the US Army Corps of Engineers is managing through habitat creation and restoration. To calculate the value of information, we used the model to determine the level of ESH restoration at which population growth rates will exceed a target with a specified level of certainty. We calculated optimal rates of restoration under full uncertainty and then with estimation error removed from individual parameters. We then determined the reduction in the cost of the optimal management action for each perfectly known parameter value compared to the full-uncertainty scenario. We found that information on the average reproductive rate for plovers was roughly twice as valuable as information on first-winter survival, which were the only two parameters for which perfect information led to large predicted savings in restoration costs. While calibrating the method to calculate optimal restoration actions involved some challenges, including limitations on the ability to compare results across different scenarios, we found that the ability to prioritize research needs in terms of potential cost savings increased the utility of the model for resource managers.
William Chen, Harvey Mudd College  
Kerim Aydin, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration

The resilience of an ecosystem determines how robust it is to disturbances. Studying the resilience of a marine ecosystem allows us to evaluate if a sudden increase in fishing in the ecosystem will negatively impact the ecosystem’s sustainability. Our project compared the resilience of the marine ecosystems in the Aleutian Islands (AI), the Eastern Bering Sea (EBS), and the Gulf of Alaska (GOA) using food web models. From each food web model, we generated random scenarios that took into account the uncertainty of the food web data, and we numerically projected them forward in time. By introducing a temporary perturbation to the level of cod fishing in each scenario and looking at how many years it took the scenarios to recover from the perturbation, we could compare how resilient each ecosystem was to changes in cod fishing. Regardless of the magnitude of the perturbation, AI had the lowest proportion of scenarios that recovered (as low as 51%), while EBS and GOA had similar proportions of recovered scenarios (as low as 66.8% and 63.7%, respectively). In the long run, cod populations in all ecosystems were not shifted by the perturbation. However, 24 other species in AI were shifted by the smallest perturbation, while EBS had 13 species shifted and GOA had 8. Current management aggregately sets fishing quotas for AI and EBS. However, our results imply that the Aleutian Islands ecosystem is drastically different from the Eastern Bering Sea ecosystem. Thus, current quotas may not protect AI from overexploitation.

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John P. DeLong, Yale University

The potential connection between exploitation and interference competition was recognized long ago but has not been evaluated. We measured the levels of both forms of competition for the protist Didinium preying upon Paramecium. Across populations, exploitation intensity was tightly coupled with interference intensity. The variation in interference competition was as large across populations of Didinium as has been observed previously across species. The link between exploitation and interference competition alters our understanding of how interference competition influences population dynamics. Instead of simply stabilizing systems as suggested by current theory, variation in interference levels can shift population dynamics through qualitatively different regimes because of its association with exploitation ability. Strong interference competition pushes a system to a regime of deterministic extinction, but intermediate interference generates a system that is stable with a high competitive ability. This may help to explain why intermediate levels of interference are most common.

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Eric Eager, Brigitte Tenhumberg and Richard Rebarber, University of Nebraska-Lincoln

A Stochastic Model for the Plant-Seed Bank Dynamics of a Disturbance Specialist

We derive a stochastic integral projection model for a general disturbance specialist plant and its seed bank, with wild sunflower (Helianthus annuus) in mind. We show through simulation studies how the probability of a disturbance and the mean depth of disturbance affect the quasi-extinction probability and long-term mean and variance of the total seed bank population. Specifically, we show that the mean depth of disturbance has a non-monotone effect on the long-term viability of the seed bank population.
Eric Eager, Brigitte Tenhumberg and Richard Rebarber, University of Nebraska-Lincoln

Global Stability of Plant-Seed Bank Models

We present a general, nonlinear, discrete-time plant population model coupled with an age-structured seed bank, as it is widely observed that germination and survival probabilities of seeds in a population's seed bank can decrease with age. We show that, given ecologically motivated assumptions on the population data, the plant-seed bank model has a globally stable equilibrium population. We also show how this equilibrium population can be calculated via the solution of a system of three equations in three unknowns. We apply our results to a published model for the annual plant Sesbania Vesicaria.

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Martha Ellis, University of Montana
Elizabeth Crone, Harvard Forest

Transient responses in a noisy world

Most populations exist in an environment that is constantly varying on some level. Two distinct sets of methodology have been developed to address this variability. Stochastic dynamics include small disturbances or perturbations in describing population dynamics. Transient dynamics focus on the short-term, deterministic response of a population to a single change in otherwise constant conditions. These two processes are related to one another: transient responses contribute to the variability of stochastic dynamics. However, the relationship between the two and the implications for practical applications, particularly given the increasing focus on transient dynamics in management, is unclear. This study explores the role of transient responses in stochastic dynamics for five perennial plant species that have been the focus of long-term monitoring. Across the species, transient responses contributed more to stochastic growth rate than variability in vital rates. Indicators of transient behavior for the populations varied greatly among years such that populations that had high transient potential in some year had very low transient potential in other years. Transient potential of an average matrix does not appear to be indicative of the total contribution of transient dynamics to stochastic dynamics. However, for populations with high transient potential, transient responses tended to be in the opposite direction as variation in vital rates, suggesting that transient dynamics may have a buffering effect on population dynamics. In sum, transient dynamics may play a large role in stochastic dynamics and more needs to be done to understand how to interpret large transient responses in a stochastic environment.

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José Flores, University of South Dakota  
Eduardo Gonzalez-Olivares, Pontificia Universidad Católica de Valparaíso, Chile

A Gause predator-prey model with double Allee effect on prey and ratio-dependent functional response

We analyze a ratio-dependent predator-prey model incorporating double Allee effect on prey in which the functional response is a function of the ratio of prey to predator. The main mathematical feature of these types of model is that the ratio-dependent functional response is undefined at the origin; hence the origin needs to be studied using blowing up techniques. Recent ecological research suggests the possibility that two or more Allee effects can generate mechanisms acting simultaneously on a single population especially in renewable resources. We show that incorporating Allee effect on prey equation significantly modifies the dynamics of the original model without Allee effect, as the modified model involves other non-topological equivalent behaviors. The modified ratio-dependent model with Allee effect presents two, one or none equilibrium points at the interior of the first quadrant. We prove the existence of parameter subsets for which the system can have a Hopf bifurcation, and also a Bogdanov-Takens bifurcation. We show the existence of separatrix curves in the phase plane determining that the long-term dynamics of the system is high sensitivity to initial conditions. We discuss the biological relevance of the model regarding coexistence and extinction showing simulations of the results.

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Jean Philippe Gibert, University of Nebraska-Lincoln

On spatially structured food webs and the complexity-stability dilemma

A central question in ecology is to understand how networks of interacting species such as food webs shape biodiversity and species persistence in nature. It is known that the stability of food webs decays with diversity, a long-standing problem known as the complexity-stability dilemma. It was shown that food web structure and the spatial structure of interacting populations can stabilize food webs. The challenge now is to understand how food web structure is constrained by the spatial distribution of interacting populations to address how specific spatial distributions will affect food web stability. To address that issue, I first generated theoretical food webs using well–known probabilistic models (e.g. niche model). Then, I generated theoretical spatial distributions such as those found in empirical systems (i.e. nested, mosaic and homogeneous distributions). Finally, I used those distributions to eliminate interactions from the food webs that could not happen because of a lack of co-occurrence between a given pair of species. Preliminary results suggest that the spatial distribution of interacting species affects food web structure when we consider totally connected networks. To address whether different spatial distributions of species affect food web stability I analyzed simple linear-chain consumer-resource models with explicit patch-dynamics that simulated nested, mosaic and homogeneous distributions. Preliminary results suggest that nested distributions are more stable than any other spatial distribution. In sum, these results suggest that particular spatial distributions of interacting populations will have a broad impact in both food web structure and food web stability.
Sarah E. Haas and Ross K. Meentemeyer, University of North Carolina at Charlotte

Spatiotemporal effects of landscape heterogeneity on the spread and persistence of an emerging forest pathogen

Describing the distribution and dynamics of epidemiological invasions is crucial to disease management but is complicated by the spatial heterogeneity and temporal variability inherent to natural ecosystems. Despite advances in theoretical and empirical approaches in disease ecology and epidemiology, we still have little empirical understanding of the factors governing space-time disease dynamics over landscape- to regional-scales. Here, we apply survival analysis to examine the environmental drivers of transition among disease stages (i.e., susceptible, infected, dead) of plants infected with sudden oak death—an emerging forest disease caused by the generalist plant pathogen Phytophthora ramorum—across an oak woodland ecosystem in Sonoma County, California (275-km² study extent). We parameterize the model using a large-scale, observational dataset obtained from monitoring 3,981 host plants across 200 sites from 2005-11. Effects of numerous variables are analyzed, including: forest stand density and structure, competent host density, species richness and evenness, and site- and landscape-level abiotic effects. Preliminary analyses show marked increases in the number of oak (Quercus spp.) hosts exhibiting lethal canker infections, with a multi-year temporal lag from the onset of infection to eventual disease-induced mortality. Spatial patterns of oak mortality across the study area coincide with severity of foliar infection levels in the two most competent, inoculum-producing host species (bay laurel and tanoak). Our analytical approach shows promise for quantifying the impact of variables (including non-linear effects and biotic-abiotic interactions) on host infection and mortality rates across spatiotemporal scales. These results will then subsequently be used to parameterize a stochastic epidemiological model for the next phase of this research.

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Gabriela Hamerlinck, University of Iowa

Predicting the Outcome of Competition on an Ecological Time Scale

Colonization of new hosts and/or habitats can be a precursor to ecological speciation when organisms experience new selection pressures and tradeoffs that lead to the establishment of barriers to gene flow between populations associated with different habitats. Preadaptations to novel hosts may therefore provide a "jump start" to host shifting shifts and ecological speciation. This work provides a mathematical model for morphological preadaptations among races of Diachasma alloeum, parasitic wasps of Rhagoletis flies. Successful parasitism by the wasp eventually kills the fly, making this a typical, if highly specialized, predator-prey dynamic. Our model is based on modifications proposed to the Nicholson-Bailey model of host-parasitoid interactions by Hassell et al. (1994). The evolutionary simulations presented here describe a suite of characteristics that allow one parasitoid race to better utilize a novel resource and colonize the new host.

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Yu Jin, University of Alberta

Seasonal effects on population persistence in streams

We address the critical domain size problem for seasonally fluctuating stream environments and determine how large a reach of suitable stream habitat is needed to ensure population persistence of a stream-dwelling species. The unidirectional nature of stream flow and seasonal fluctuations in the stream environment are two key factors in determining whether population can persist. We characterize the fluctuating environments in terms of seasonal correlations among the flow, transfer rates, diffusion, and settling rates, and we investigate the effect of such correlations on the critical domain size problem.
Lauren Kiser, Bethune-Cookman University

Waterfowl are fundamental to any coastal system—economic, ecological or social. Development, overharvesting and other environmental issues are negatively impacting their populations. In order to sustainably manage waterfowl, an adaptive approach employing risk assessment modelling is necessary. The “Combined Ecological-Societal Systems Model” was utilized to map out Mission-Aransas National Estuarine Research Reserve (MANERR); using Oracle Crystal Ball software, Monte Carlo simulations compute potential management decisions to determine outcome probabilities. The objectives are to: 1) use integrated modelling to improve management practices at MANERR; 2) reinforce the efficacy of CESSM methodology; 3) provide evidence for continued conservation and preservation of waterfowl and their habitat. Expected results show a strong inverse relationship between increasing development and exponentially decreasing duck populations. This model is more precise due to the inclusion of all stakeholders’ preferences, which garners greater public support and increases the potential for future enjoyment and existence of waterfowl.

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Glenn Ledder, University of Nebraska-Lincoln

An Optimization Model that Links Masting to Seed Herbivory

Masting is a life history strategy whereby perennial plants have one or more years of little or no reproduction, punctuated by years with massive reproduction events. The literature on masting focuses on description of this behavior, particularly the common observation that individuals in a population act in synchrony. To date, there is no published work that connects masting to characteristics of the ecological niche of the plant species, such as the overall growing capacity or the extent of seed herbivory. In this study, we develop a resource-based optimization model with seed herbivory risk as a key parameter, and we show that the optimal strategy for such a scenario can be periodic masting, with the masting interval an increasing function of seed herbivory risk. In particular, this model suggests one possible reason why a species of conifer in Norway exhibits a masting cycle of two years in part of the country and a cycle of three years in another part.

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J. David Logan, John Janovy, Jr. and Brittany E. Bunker, University of Nebraska-Lincoln

The Life Cycle and Fitness Domain of Gregarine (Apicomplexa) Parasites

We examine the fitness characteristics of gregarine parasites (Ph. Apicomplexa) and how these evolutionarily long-lived parasites are shaped by their life cycle stages inside and outside a definitive insect host. Their fitness and population characteristics have not been subject to modeling efforts that help understand their species longevity or ecological interactions with their hosts. We develop a dynamic, mechanistic population model represented by a system of differential equations for two of the parasite stages: the mature parasite, or trophont, inside a definitive insect host, and the infectious oocyst stage in the water environment of the host. In contrast to many classical macroparasite models, the force of infection between oocysts and hosts is of sigmoid type. Inside the host, production of the water borne infectious state is a linear, differing from the classical ‘May-pairing’ model for negative binomially distributed adults. We examine equilibria for different parameter values, which leads to the definition of a fitness parameter that acts as a bifurcation parameter. The saddle—node transition shows good cause for the establishment and long-time persistence of this common, widespread parasite. It is parameterized by extensive data gathered at Cedar Point Biological Station. Applications include parasite control in fish aquacultures. [The research was supported by a UBM grant from NSF.]
Maeve Lewis McCarthy  
Murray State University

*Modeling Facultative Paedomorphosis in Arizona Tiger Salamanders*

The Arizona Tiger Salamanders at the Mexican Cut Nature Preserve in Colorado form a closed population due to the elevation of their habitat. They exhibit facultative paedomorphosis in which salamander larvae either metamorphose into terrestrial adults or become sexually mature while still in their larval form. Although many salamanders exhibit cannibalism of larvae, the Arizona Tiger Salamander also exhibits cannibalism of young by the aquatic adults. We formulate ODE models of this system. We discuss the analysis and interpretation of the models.

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Holly V. Moeller, Stanford University  
Michael G. Neubert, Woods Hole Oceanographic Institution

*Accounting for Habitat Damage Increases the Economic Optimality of Marine Reserves*

Marine reserves -- areas closed to fishing -- are often touted for their conservation benefits (e.g. protection of essential fish habitat, increases in fish population and biomass). However, reserves are frequently viewed as economically costly because closures deny fishermen access to potentially valuable fishing grounds. To address this issue, we explore a spatially-explicit bioeconomic model that accounts for habitat damage from fishing gear. We solve the model for the profit-maximizing distribution and intensity of fishing effort without designating reserves a priori, and show the emergence of reserve networks. These results suggest that reserves may in fact be economically beneficial, especially when fishing gear damages habitat. We also explore alternative management schemes in which the regulatory body has varying degrees of spatial knowledge about fishing activities, and find an explicit value for spatial knowledge.

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Jeffrey Musgrave and Frithjof Lutscher, University of Ottawa

*How individual movement behaviour in fragmented landscapes affects persistence*

Formulating mathematical models for population dynamics and spread of invasive insects, in heterogeneous landscapes, has garnered much attention in recent years. In particular, these models have been developed on fragmented landscapes, since fragmentation may lead to extinction and poor conditions between habitats may slow the spread of a population. Inherent to this problem is the assumption of how a population disperses across an interface. It was widely accepted that the density and flux of a population density must be continuous across an interface. Ovaskinanen and Cornell recently showed that, under certain conditions, the density may not be continuous. To study these phenomena, we formulate an integrodifference equation (IDE) on a periodic landscape, consisting of good and bad patches. To investigate the effect of different movement assumptions on persistence and spread, we first derive several dispersal kernels to implement into the IDE. We then derive explicit formulae for the critical size of a good patch necessary for persistence, and compare how the different assumptions about behaviour at an interface affect persistence. The effect of these assumptions on the spread of the population is briefly discussed.
Angie Peace, Arizona State University

There has been important progress in understanding ecological modeling through the development of the theory of ecological stoichiometry. Modeling under this framework allows food quality to affect consumer dynamics. The effects of nutrient deficiency on consumer growth is well understood. However recent discoveries in ecological stoichiometry suggest that consumer dynamics are not only affected by insufficient food nutrient content (low P:C) but also by excess food nutrient content (high P:C). Boersma and Elser (2006) and Elser et al. (2006) reported empirical data demonstrating a "stoichiometric knife edge" in which animal growth is reduced not only by food with low P content but also for food with high P content. Here we investigate the growth response of daphnia to varying food 'qualities' of algae. We performed empirical work in the lab to observe and capture the shape of the "knife edge". We present a Lotka-Volterra type model that captures the dynamics of the observed "knife edge".

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Joseph S. Phillips and Jean Philippe Gibert, University of Nebraska-Lincoln

Energy flux as a determinant of food web stability

Characterizing the factors that determine the stability of biological communities is a long standing issue in ecology. A recently proposed approach seeks to understand how food web stability is altered by increased energy flux through trophic levels (Rip and MacCann 2011). The approach is centered on a reinterpretation of classical pairwise consumer-resource models (e.g. Lotka-Volterra, Rosenzweig-MacArthur) to link key parameters, such as mortality and carrying capacity, to energy flux. Results from two species models suggest that increasing consumer mortality decreases energy flux, which in turns reduces stability. Moreover, increasing carrying capacity of the resource decreases flux, which decreases stability. However, it is critical to analyze multispecific assemblages as well as the effects of energy flux for the stability of multispecies systems to assess the generality of these results. To evaluate these results in a multispecific context, we explored the effects of mortality and carrying capacity in simple food web motifs (e.g. apparent competition, intraguild predation) with more than two species. We found that an increase in consumer mortality or in resource carrying capacity does not always lead to increased or decreased stability, respectively. One shortcoming of this approach is that parameters such as mortality and carrying capacity may have complex relationships with energy flux, making them poor indicators of how flux affects stability. Future work will address this issue through the use of generalized models, allowing a more direct analysis of how flux affects stability of broad classes of general food web models.
Linear differential equations in a one dimensional domain are often used to study the relationship between persistence and domain size in river system populations. However, scaling an interval can ignore that, at larger scales, a river system's geometry resembles a tree rather than an interval and that habitable cross sectional areas may vary throughout the system. Our question is how and when scaling up a tree structure affects persistence differently than scaling up an interval. We use a diffusion-advection equation in a metric tree graph, with linearized growth rate around the zero steady state, to identify when a single population will grow at low density, by doing a principal eigenvalue analysis in terms of domain scaling parameters and advection speeds. The metric graph represents a continuous tree system where edges represent actual domain; this mathematical framework is commonly referred to as a quantum graph. We primarily assume a lethal downstream boundary condition and interior junction and upstream boundary conditions which do not allow organisms in or out of the domain. We scale the tree domain by adding branching levels, with various assumptions on cross section and branch length decay going upstream in the system. Our results indicate that only under a special cross section assumption does the tree system scale the same as the one dimensional domain. In other cases, scaling the one dimensional domain can either underestimate or overestimate persistence depending on how the one dimensional domain is considered to scale. In a specific example, assuming diffusion only, a constant cross section, bounded edge lengths, and lethal conditions at all boundary points, the principal eigenvalue is bounded below uniformly over increases in tree size. This is in contrast to the corresponding one dimensional problem whose principal eigenvalue can be driven to zero with increasing interval size. In addition, using numerical methods we quantify the decay of the principal eigenvalue with increases in domain size in the different systems, comparing over various parameter assumptions.

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Katherine Scranton, UC Berkeley

Time-to-event data are common in ecology but are rarely analyzed with sophisticated tools common in other fields. Obstacles in applying survival time models to ecological data include the variation of natural systems and interval-censored data. We develop a mixed-effects Weibull model for interval-censored data on time-to-maturation of individuals in a cohort. We incorporate a fixed difference between types of cohorts, and two levels of random effects. There is no available software for mixed-effects survival analysis for interval-censored data, so likelihood calculations with numerical integration of random effects were programmed in R. A simulation study was conducted under different magnitudes of variation to evaluate the power of the likelihood ratio tests and the precision of parameter estimates. Differences in the mean scale as small as 5% can be detected with high power under low variation. Under higher variation, larger differences of 18% can be detected with 80% power. Omitting random-effects produces biased estimates of the Weibull parameters and highly inflated type I error rates in likelihood ratio tests. The methods developed in this paper for fitting hierarchical frailty models to interval censored data would be applicable to a wide range of ecological processes such as survival, oviposition, or onset of disease.
Meredith V. Trotter, Shripad D. Tuljapurkar and Siddharth Krishna-Kumar, Stanford University

Sensitivities of the variance in population growth rate: Applications to conservation

Population dynamics in variable environments are affected by both the mean and the variance of the stochastic growth rate. However, traditional sensitivity analyses of stochastic matrix models only consider the sensitivity of the mean growth rate. We have derived an exact method for calculating the sensitivity of the variance in population growth rate to changes in demographic parameters. We apply this new analysis tool to an example population of at-risk Polar bears (Ursus maritimus). Increasing the variance of population growth necessarily increases the width of confidence bounds around estimates of population size, growth, probability of and time to quasi-extinction. We demonstrate how demographic changes, due to either environmental change or management intervention, affect the mean and variance of stochastic growth in our at-risk population. In many cases we find that the same changes in parameters lead to increases in both the mean and variance of growth, which complicate predictions about overall population impacts. Our results suggest it is unwise to treat the mean of a stochastic process as giving a full description of the dynamics. The inclusion of variance sensitivities allows a more complete understanding of population dynamics.

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Shane Wilson, Andrea Russell, Katie Diebel, (advised by Kyle Fey), Luther College

Two-Sex Deer Population Dynamics with Effects from Seasonal Harvesting

Fluctuations in a county’s deer population throughout a year are dependent not only on the carrying capacity of the environment and the proximity to fawn birthing season, but also on the number and variety of hunting licenses issued. In the formulation of our model, we assume that there are three types of licenses issued: archery, general firearm, and doe-only firearm. We further assume that the length of the archery season is significantly longer than the firearm season and the ratio of general to doe-only firearm licenses is predetermined; these assumptions allow us to segment the year into the deer’s natural breeding season and the hunting seasons. The model is sex-specific, allowing us to track both doe and buck populations. By employing numerical methods to approximate the system of ordinary differential equations, we will determine how many hunting licenses should be issued in order to establish a stable population of bucks and does.

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Joy Zhou, University of Washington

Life on the Move: Modeling Climate-Driven Range Shifts with Integrodifference Equations

Many species are responding to climate change by shifting their ranges poleward in latitude or upward in elevation. For species with limited dispersal abilities, we naturally ask: can they keep up with climate change? In our attempt to assess the impact of climate change on population persistence, we analyze an integrodifference equation that combines growth, dispersal, and a constant-speed shift in habitat. We find that, for our model, the population goes extinct if its range shifts faster than a critical speed. This critical speed for extinction depends on both growth parameters and the dispersal kernel.