

## BI 519 Theoretical Evolutionary Ecology

### CONTACT INFORMATION

Peter Buston, Department of Biology  
Phone: 617-358-5412  
E-mail: [buston@bu.edu](mailto:buston@bu.edu)

Tina Barbasch, Department of Biology  
Phone:  
E-mail: [tbarbasch@bu.edu](mailto:tbarbasch@bu.edu)

### LECTURE

M, W, F, 11:15 – 12:05, Department of Biology, BRB 115.

### COMPUTER LAB

Tu, 15:30 – 18:15, Department of Earth and Environment, CAS 435

### OFFICE HOURS

Buston: M, W, F, 13:25 – 14:15, Department of Biology, BRB 531 (with exceptions)  
Barbasch: Tu, Th, 14:30 – 15:30, Department of Biology, BRB

### PREREQUISITES

One semester of biology (BI107) and one semester of calculus (MA123).

### ENROLLMENT LIMIT

15

### OBJECTIVES

The principal objective of this course is to familiarize students with the theory of population ecology, micro-evolution, behavioral ecology and how these theories are interlinked. Students gain enough background to read theoretical evolutionary ecology literature, do simple modeling, and springboard to more complex theory if desired. Students gain hands on experience through homeworks and computer labs. Students learn MATLAB and use it to program their own models and simulations during lab. This course builds on courses such as Ecology (BI 303) and Evolution (BI 309), and complements courses such as Evolution (BI 504) and Behavioral Ecology (BI 508), within the Department of Biology. This course can provide students in Math, Physics and Engineering an insight into how they might apply their skills in the fields of Ecology, Evolution, and Behavior.

### BOOKS & OTHER MATERIALS

There is no perfect text for this course. I will provide comprehensive written lecture notes and all recommended readings (see weekly syllabus). The readings will provide a different perspective and additional context for the lecture notes. Students will have to pay for printing if they make hard copies of these electronic materials, but there are no books or other materials that have to be purchased. Some students find it useful to buy a student license of MATLAB, which currently costs around \$100.

### INTERESTING BIOLOGY TEXTS – ON RESERVE.

Bulmer, M. 1994. Theoretical Evolutionary Ecology. Sinauer Associates, Sunderland, Massachusetts.  
Case, T.J. 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press, New York.  
Dugatkin L.A., Reeve, H.K. 1998. Game Theory and Animal Behavior. Oxford University Press, New York.  
Edelstein-Keshet, L. 2005. Mathematical Models in Biology. SIAM, Philadelphia.  
Gotelli, N.J. 2001. A Primer of Ecology, 3<sup>rd</sup> Edition. Sinauer Associates, Sunderland, Massachusetts.  
Hastings, A. 1997. Population Biology: Concepts and Models. Springer-Verlag, New York.  
Mangel M., Clark C.W. 1988. Dynamic Modeling in Behavioral Ecology. Princeton University Press, New Jersey.  
Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.  
Murray, J.D. 2002. Mathematical Biology I, 3<sup>rd</sup> Edition. Springer-Verlag, New York.  
Otto SP, Day T. 2007. A Biologist's Guide to Mathematical Modeling. Princeton University Press, New Jersey.

### BACKGROUND BIOLOGY TEXTS – ON RESERVE.

Alcock, J. 2009. Animal Behavior, 9th edition. Sinauer.  
Futuyma, D.J. 2009. Evolution, 2nd edition. Sinauer.  
Molles, M.C., Jr. 2009. Ecology. 5th Edition. McGraw Hill, Boston

### BACKGROUND MATHEMATICS & PROGRAMMING TEXTS – ON RESERVE.

Attaway, S. 2009. MATLAB: A practical Introduction to Programming and Problem Solving. Elsevier.  
Lay, D. C. 2006. Linear Algebra and Its Applications. Pearson, Addison, Wesley.  
Stewart, J. 2010. Calculus: Concepts and Contexts. Brooks / Cole, Cengage Learning.

## **COURSE POLICIES: grading, absences, make-ups, workload**

### **Grading**

#### **Lecture series (40 lectures)**

Homeworks from lecture (10)	30%	(2 lowest can be dropped)
Mid-term exams (2)	30%	
Final exam	20%	

The homeworks and exams are graded on a point or percentage basis. The course isn't curved, i.e., your final grade depends solely on your performance, rather than the performance of everybody else.

#### **Lab series (13 labs)**

Lab write ups, including figures and text (11)	15%	(2 lowest can be dropped)
Matlab code included in weekly write-ups (8)	5%	

The lab write-ups and code are graded check, check + or check -. If you receive all checks, you will get all of the points. Check plus is given for doing something additional in terms of coding or exploration of the problem.

#### **Graduate component**

Work associated with Lecture series and Lab series (described above) becomes	80%
Thesis or dissertation modules (literature review or modeling project) an additional	20%

Note that 8 labs have a question for graduate students. You are expected to tackle at least 5 of these questions in the lab write-ups. As you might imagine, the questions get harder as the semester proceeds.

### **Absences**

Non-attendance is not penalized directly. However, in the past, students that did not attend found it hard to keep up with the course material. Attendance and catching up on missed material is your responsibility.

### **Make-ups & Late work**

There will be no opportunities for make-ups that are not well justified. Similarly, late work will not be accepted if it is not well justified. If you have questions regarding the grading of problem sets or tests, you must resolve the issue within two weeks. For tests, please provide written justification for why you believe your answer was correct. Some "extra credit" questions will be asked on exams, but otherwise extra credit is not available.

### **Workload**

This is a 4 credit course, so you should anticipate spending 8-12 hours per week outside of class time on this course. Students report averaging 4-5 hours per homework (range 2-10 hours depending on student and which homework), 1-2 hours on lab write ups (range 1-4 hours), and 0-2 hours on reading and reviewing lecture material. Students who spent more time reviewing spent less time on homeworks. Students report the workload as heavy, but manageable. More importantly, students also report that they are satisfied with the amount that they learn in the course given the workload. We will work hard, cover a lot of material, and most students learn A LOT!

### **Conduct**

All undergraduate students are expected to know and understand the provisions of the CAS Academic Conduct Code (<http://www.bu.edu/cas/students/undergrad-resources/code/>). All graduate students are expected to know and understand the provisions of the Academic Discipline Procedures (<http://www.bu.edu/cas/students/grad-resources/forms/discipline/>). Cases of suspected academic misconduct will be referred to the Dean's Office.

**LECTURE, READING, ASSIGNMENT & EXAM SCHEDULE (subject to change)**

Date	Lecture	Topic	Reading	Assignment
Friday, January 18	1: <i>Introduction to modeling</i>	Why use quantitative approaches?	Stewart Chapter 1	
<b>Ecological properties of populations I: single, unstructured populations</b>				
Monday, January 22	2: <i>Density-independent growth in continuous time I: forced, non-autonomous systems.</i>	Dynamical systems, forced changes, main theorem of calculus, integration, rescaling.	Stewart Chapter 2	
Wednesday, January 24	3: <i>Density-independent growth in continuous time II: autonomous systems (exponential growth).</i>		Otto and Day 3.2.1, 5.3.1; Hastings 2.1. Stewart Chapter 3	
Friday, January 26	4: <i>Density-independent growth in continuous time II: autonomous systems (exponential growth).</i>		Otto and Day 3.2.1, 5.3.1; Hastings 2.1. Stewart Chapter 4	
Monday, January 29	5: <i>Density-dependent growth in continuous time I (logistic growth).</i>	Explicit solutions of autonomous equations, equilibria, linearization, and stability.	Otto and Day 3.2.2; Hastings sections 4.1, 4.2. Stewart Chapter 5	
Wednesday, January 31	6: <i>Density-dependent growth in continuous time II (logistic growth continued).</i>			
Friday, February 2	7: <i>Density-dependent growth in continuous time III (Allee effects).</i>	Bifurcation		
Monday, February 5	8: <i>Density-dependent growth in continuous time IV.</i>	In-class activity: harvesting problem.	Murray 1.6 on harvesting.	
Wednesday, February 7	9: <i>Density-independent growth in discrete time (geometric growth).</i>	Rescaling, equilibria, and stability in discrete time.	Murray 2.1 and 2.2.	Homework 1 due
Friday, February 9	10: <i>Density-dependent growth in discrete time I (discrete logistic model).</i>	Period-doubling and chaos.	Murray 2.2 and 2.3.	
Monday, February 12 (Guest Lecturer: Tina Barbasch)	11: <i>Density-dependent growth in discrete time II.</i>		Strogatz 10.2-10.7	
<b>Ecological properties of populations II: single, structured populations</b>				
Wednesday, February 14	12: <i>Single structured populations: two state populations I.</i>	Multiple, non-interacting variables, linear homogeneous systems, vectors, matrices	Strogatz 5.1-5.2	Homework 2 due

Friday, February 16	13: <i>Single structured populations: two state populations II.</i>	Eigenvalues, and eigenvectors.		
Monday, February 19	<i>Presidents' Day Holiday</i>			
Tuesday, February 20	14: <i>Single structured population in discrete time: Migration and multistate populations.</i>	Multiple, non-interacting variables, linear systems in discrete time.		
Wednesday, February 21	15: <i>Single structured populations: Age structure I.</i>	Life tables, Leslie matrices, estimating population growth rate, sensitivity analysis	Gotelli chapt. 3.	Homework 3 due
Friday, February 23	16: <i>Single structured populations: Age structure II</i>			
<b>Ecological properties of populations III: interacting populations</b>				
Monday, February 26	17: <i>Introduction to interacting populations I.</i>	Isoclines, equilibria, linearization, stability in 2 dimensions	Otto and Day 8.2.1, 8.2.2; Hastings chapt. 6.	
Wednesday, February 28	18: <i>Introduction to interacting populations II.</i>			Homework 4 due
Friday, March 2	19: <i>Lotka-Volterra competition I.</i>		Otto and Day 3.4.1, 4.2.4; Hastings sections 7.1-7.3.	
March 5 – March 9	<i>Spring Recess</i>			
Monday, March 12	20: <i>Lotka-Volterra competition II.</i>			
Wednesday, March 14	21: <i>Lotka-Volterra predator-prey.</i>	Structural instability. In-class activity: analyzing predator-prey models.	Otto and Day 3.4.2, pp. 307-308.	<b>Mid-term exam 1 due</b>
Friday, March 16	22: <i>Predator-prey models with stability: one factor modifications</i>		Hastings 8.3-8.6.	
Monday, March 19	23: <i>Predator-prey models: two factor modifications</i>	Classification of stabilizing and destabilizing factors, limit cycles, Andronov-Hopf bifurcations.	Bazykin 3.3.	
Wednesday, March 21	24: <i>Predator-prey models: two factor modifications (continued)</i>			Homework 5 due

<b>Evolution: change in allele frequencies</b>				
Friday, March 23	25: <i>Factors of microevolution.</i>	Space of genotypes, mutation, selection, sex, migration, and drift: history as initial conditions.	Hastings sections 3.1 and 3.2.	
Monday, March 26	26: <i>Selection and genetic load.</i>	Changes in allele frequencies, haploid selection model, relation to logistic model, multiplicative and additive fitness, Lyapunov function, fitness and stability surfaces.		
Wednesday, March 28	27: <i>Selection and segregation.</i>	Panmixia of zygotes and gametes, diploid selection model.	Otto and Day section 3.3. 4.2.3, 4.4.1; Hastings chapt. 3.4 pp. 48-64.	Homework 6 due
Friday, March 30	28: <i>Mutation and mutation-selection balance.</i>		Otto and Day pp. 181-183; Hastings 3.4 pp. 64-68.	
Monday, April 2	29: <i>Fisher's Fundamental Theorem and Wright's gradient equation.</i>		Hastings chapt. 3.5.	
Wednesday, April 4	30: <i>Evolution of quantitative traits.</i>	The gradient equation, Malthusian fitness.	Lande 1976 pp. 314-317 only.	Homework 7 due
<b>Behavior: evolution of phenotypes</b>				
Friday, April 6	31: <i>Hawk-dove game</i>	Evolutionary game theory: pairwise contests. ESS models, optimization, invasion theory.	Maynard Smith chapt. 2.	
Monday, April 9	32: <i>Mixed strategies and generalized two-player games</i>	Evolutionary game theory: games against the field		
Wednesday, April 11	33: <i>Evolutionary conflicts: foraging theory I</i>	Dynamic programming	Mangel and Clark chapt. 2.	Homework 8 due
Friday, April 13	34: <i>Evolutionary conflicts: foraging theory II</i>			
Monday, April 16	<i>Patriots' Day Holiday</i>			

Wednesday, April 18	<i>35: Evolutionary conflicts: parental allocation</i>		Mangel and Clark chapt. 6.	<b>Mid-term exam 2 due</b>
Friday, April 20 (Guest Lecturer: Tina Barbasch)	<i>36. Evolutionary conflicts: parental negotiations</i>			
Monday, April 23	<i>37: Age structure dynamics</i>	Iteroparity and semelparity and return to the Leslie matrix.		
Wednesday, April 25	<i>38: Selection in variable environments</i>	Arithmetic and geometric means.	Bulmer chapt. 5 pp. 89-93.	Homework 9 due
Friday, April 27	<i>39. Grad student presentations</i>			
Monday, April 30	<i>39: Evolution of dispersal</i>	In-class Activity: paper discussion.	Hamilton and May 1977.	
Wednesday, May 2	<i>40. Wrap-up and Review</i>			Homework 10 due
Friday, May 4	<i>Study Period</i>			
Monday, May 7	<i>Final Exams</i>			Final Exam due (12:30 – 14:30)
Wednesday, May 9	<i>Final Exam Due</i>			Final Project due (15:00 – 17:00)
Friday, May 11	<i>Final Project Due</i>			Grades due

## COMPUTER LAB SCHEDULE

The goal of these labs is for you to explore the models and to learn how to program in MATLAB. In the past, most students were able to finish the entire lab and some of the write up in the time provided. As much as I want all of you to learn MATLAB programming, I also do not want it to get in the way of exploring the models. So, I will release a working version of the MATLAB code for the week in the last half hour of the lab. Part of your lab write-up grade is based on having a working code of your own, but students who use my code will receive credit for the rest of the write-up. If you need extra lab time to finish or for homeworks, MATLAB is available in certain computer labs on campus. You should bring a memory stick to lab in order to save your programs for write-ups and use in later labs or you can e-mail them to yourself.

Tuesday, January 23, Lab 1: *Introduction to MATLAB*

Attaway: Chapter 1, Intro to Matlab, pp 3-15 and pp 21-31; Chapter 2, Intro to Programming pp 45-57

No Assignment

Tuesday, January 30, Lab 2: *Exploring growth in single populations with continuous time*

Attaway: Chapter 2, Simple Plots, pp 58 - 63; Chapter 2, User-defined functions, pp 68 - 75

Code and Write up Assignment (Grad component available)

Tuesday, February 6, Lab 3: *Exploring the Allee effect and harvesting models*

Code and Write up Assignment (Grad component available)

Attaway: Chapter 3, Relational operators, Logical operators & Selection statements.

Tuesday, February 13, Lab 4: *Chaos in the discrete time logistic model*

Control statements and subroutines in Matlab

Code and Write up Assignment

Attaway: Chapter 4, For loops, nested for loops and while loops.

Tuesday, February 20: Monday Schedule

Tuesday, February 27, Lab 5: *Review of Matlab and special projects*

More on matrices in Matlab

No Assignment

Attaway: Chapter 5, Vectorization of code.

Tuesday, March 6, Spring Recess

Tuesday, March 13, Lab 6: *Manipulation of Leslie matrices*

Code and Write up Assignment (Grad component available)

Tuesday, March 20, Lab 7: *Dynamics of a competition model*

Code and Write up Assignment (Grad component available)

Tuesday, March 27, Lab 8: *Analysis of the Lotka-Volterra predator-prey model and modifications*

The symbolic toolbox in Matlab

Write up Assignment Only (Grad component available)

Tuesday, April 3, Lab 9: *Simulation of allele frequency changes and genetic load*

Code and Write up Assignment

Tuesday, April 10, Lab 10: *Evolution of a quantitative trait*

Code and Write up Assignment

Tuesday, April 17, Lab 11: *Simulation of 2 and 3 player games*

Code and Write up Assignment (Grad component available)

Tuesday, April 24, Lab 12: *Investigation of a dynamic state-variable model, patch selection*

Write up Assignment Only (Grad component available)

Tuesday, May 1, Lab 13: *Investigation of the Hamilton and May model*

Required reading: Hamilton and May 1977

Write up Assignment Only (Grad component available)

## BI519 Thesis or Dissertation Module (GRADUATE STUDENTS ONLY)

There are two choices of modules listed below. The goal of either module is to help you incorporate theory into your thesis or dissertation. **This project is 20% of your grade** and, as you can imagine, it will require effort.

**Requirements:** The completed module should be presented as a 6-10 page (single space) write up with appropriate references (minimum 8) and formatting for a scientific paper. A one page prospectus of your ideas will be due **Friday, April 6**. This will allow me time to give you feedback on your proposal before it is due. Students who have not turned in a prospectus have occasionally had problems at the end of the semester with the appropriateness of their project, so I encourage you to put some effort into the prospectus. The more you give me, the better feedback I can give you. You will present your model to the class in a 10 minute talk, on **Friday, April 27**. The final write up will be due **Wednesday, May 9**.

**Workload:** In the past, students have spent 8-10 hours per week on the project during the last four weeks of classes. I usually meet with students regularly during this period to answer questions and discuss the direction of the project. Most students usually wish they had started their projects sooner, so I encourage you to start as early as possible. Please consider handing in your prospectus earlier than April 6. Some students have been caught unprepared in the final weeks of class when the presentation and write-up are due because there are also homeworks, in-class discussions, and labs due in those final weeks. Since students have the entire semester to work on the project and can drop 2 homeworks and 2 labs, I am not very sympathetic to this situation. Although, I hope overall that you will find me flexible and willing to meet with students and work with them on their projects.

**Expectations:** The best projects are ones that provide the seed for a portion of your thesis or dissertation or are something that eventually will be publishable. I do not expect you to complete a dissertation chapter for this course, but if you can outline an appropriate idea and do some work that shows it is feasible, you will receive an A for this module. I also want to make clear that if you are doing something completely theoretical for your dissertation/thesis work, it is NOT appropriate to turn in a summary of your overall project. I am looking for you to do something specific for this class.

### Option 1: Literature review of models relevant to your area of research

Review, in detail, at least three different models that provide predictions or describe systems related to your area of research. This review should minimally include a description of the models and their biological interpretation, your critique of the models themselves and their assumptions (e.g., are they “good” models), and a discussion of how the models as a group can inform your research. I hope that this will help you develop the theory section of the literature review for your thesis or dissertation. In grading this option, I am looking for your ability to accurately and succinctly summarize other theory papers, synthesize the body of work, and explain the implications in the context of your work. The format will be flexible since review papers often use different formats. **Grading:** Summary of theory (40%), critique of theory (15%), synthesis of theory (15%), implications and links to your own work (20%), quality and clarity of writing (10%).

### Option 2: Modeling project relevant to your area of research

Use what we have learned in class and your Matlab skills to construct a simple model that you are interested in investigating for your research. Your write up should include the biological justification and interpretation of the model, a complete mathematical investigation of the model, and a discussion of how the model results can inform your research. I hope that you might use this option to begin developing a “modeling” chapter for your thesis or dissertation. In grading this option, I am looking for your ability to represent the biology of your system mathematically, clearly state assumptions and if they are realistic, analysis, and interpretation of results in the context of your work. The format should follow the usual scientific paper format (e.g., Introduction, Methods, Results, Discussion). **Grading:** Biological justification of model (20%), clarity of assumptions (15%), model formulation (i.e., does your model represent what you mean for it to, 15%), model analysis (20%), implications and links to your own work (20%), quality and clarity of writing (10%).

Please feel free to discuss your ideas with me ahead of time. I am happy to meet with you and/or give you feedback at any point during the semester.