APPM 4370/5370: Modeling in Mathematical Biology, Spring 2026

Instructor: Prof. Zack Kilpatrick, ECOT 647, zpkilpat@colorado.edu

Lecture Time & Location: Tues/Thurs 9:30-10:45am, ECCR 155

Office hours: Tues 12-1pm, Wed 10-11am, or by appt

Course webpage: Hosted on Canvas

Slack: You should have received an invite for the 'APPM 4390/5390: Modeling in Mathematical Biology' Slackspace, for discussions. Urgent questions to me should be emailed or asked in person.

Course Overview: This course explores how mathematical and computational methods can be used to understand and model biological systems across scales—from molecules and cells to organisms and populations. We will develop and apply techniques from linear algebra, differential equations, dynamical systems, probability, stochastic processes, and statistical inference to problems in the life sciences. Topics include stochastic search and foraging, synchronization of biological oscillators, pattern formation in development and ecology, disease dynamics, and decision-making in organisms and collectives. Students will learn how mechanistic mathematical models can reveal organizing principles in biological behavior, pattern, and function. Programming exercises in Python or MATLAB will accompany most modules, emphasizing numerical simulation, visualization, and data interpretation.

This course is for mature undergraduates (4000 level) and graduate students (5000 level). We will move quickly and cover a broad range of material. Students are expected to supplement lectures with readings and engage deeply with the problem sets. Prior coursework in differential equations, linear algebra, and programming is required; probability is recommended. This intensive learning experience will equip students with a working knowledge of key mathematical biology techniques and the ability to interpret and construct models found in current research literature.

***Tentative* and *Ambitious* Course Outline:**

Week of	Material Covered	Book Reference
Jan 8	overview, modeling frameworks, diffusion, random walks, search times	Berg; Bressloff (Ch. 4–5)
Jan 13	stochastic search, active transport, first-passage problems	Bressloff; Berg
Jan 20	optimal foraging, Marginal Value Theorem, stochastic patch models	SK; CM
Jan 27	dynamic programming, noisy decision rules, extensions of MVT	MH
Feb 3	perceptual and collective decision making, drift–diffusion models	Bogacz; KS
Feb 10	collective search, quorum sensing, social foraging	Couzin et al.; KS
Feb 17	synchronization in biology: oscillators, fireflies, cardiac & β-cells	ET (Ch. 7–8)
Feb 24	Kuramoto model, phase reduction, strong coupling	ET; Strogatz
Mar 3	pattern formation, reaction–diffusion systems, Turing mechanism	Murray Vol. II (Ch. 1–4)
Mar 10	morphogenesis, animal patterns, territorial models	MP (2019); Murray
Mar 17	**Spring Break**	
Mar 24	epidemic modeling: SIR and SEIR systems, equilibria and thresholds	BC; KR
Mar 31	delays, feedback, stochastic and network epidemics	Hethcote (2000); KR
Apr 7	**Project Work Time**	—
Apr 14	**Project Work Time**	—
Apr 21	**Project Presentations**	—

Note: The above course schedule comprises 12 weeks of lectures, 2 weeks of project work time, and a week of project presentations. Lecture material has been scheduled so that every two weeks covers a thematic *module* which you will also explore on the homework. See below for rough names of these modules.

Enforced Prerequisites: Differential Equations (APPM 2360 or equivalent) and Matrix Methods (APPM 3310 or equivalent) with a minimum grade of C-.

Recommended Prerequisite: APPM 3570/STAT 3100 (Applied Probability); STAT 2600 (Intro to Data Science); CSCI 3022 (Intro to Data Science with Probability and Statistics); or equivalent.

Reference Key

- **Berg:** Berg, H. C. Random Walks in Biology, Princeton University Press (1993).
- **Bressloff:** Bressloff, P. C. Stochastic Processes in Cell Biology, Springer (2nd ed., 2021).
- **Stephens & Krebs (SK):** Stephens, D. W., and Krebs, J. R. Foraging Theory, Princeton University Press (1986).
- **Clark & Mangel (CM):** Clark, C. W., and Mangel, M. Dynamic State Variable Models in Ecology, Oxford University Press (2000).
- **McNamara & Houston (MH):** McNamara, J. M., and Houston, A. I. Models of Animal Behavior: Ecology, Evolution, and Cognition, Cambridge University Press (2009).
- **Bogacz:** Bogacz, R. "Optimal decision-making theories: linking neurobiology with behavior." Trends in Cognitive Sciences 11 (2007).
- **Keener & Sneyd (KS):** Keener, J., and Sneyd, J. Mathematical Physiology, Springer (3rd ed., 2021).
- **Ermentrout & Terman (ET):** Ermentrout, G. B., and Terman, D. Mathematical Foundations of Neuroscience, Springer (2010).
- **Strogatz:** Strogatz, S. H. Nonlinear Dynamics and Chaos, Westview Press (2nd ed., 2015).
- **Murray:** Murray, J. D. Mathematical Biology II: Spatial Models and Biomedical Applications, Springer (3rd ed., 2003).
- **Maini & Painter (MP):** Maini, P. K., and Painter, K. J. "Turing's model for biological pattern formation and the robustness problem." Interface Focus 9 (2019).
- **Brauer & Castillo-Chavez (BC):** Brauer, F., and Castillo-Chavez, C. Mathematical Models in Population Biology and Epidemiology, Springer (2nd ed., 2012).
- **Keeling & Rohani (KR):** Keeling, M. J., and Rohani, P. Modeling Infectious Diseases in Humans and Animals, Princeton University Press (2008).
- **Hethcote:** Hethcote, H. W. "The mathematics of infectious diseases." SIAM Review 42 (2000).

Programming: You are welcome to program in python (with or without jupyter notebooks), MATLAB, julia, or any other language you find most straightforward for model implementation. Extensive MATLAB documentation and help can be found here: https://www.mathworks.com/help/matlab/
Anaconda provides python and juypter notebook installations: https://docs.anaconda.com/anaconda/install/
Jupyter notebooks examples are on the Canvas page; otherwise here's a few tutorials:
https://www.learnpython.org/
http://cs231n.github.io/python-numpy-tutorial/
https://docs.scipy.org/doc/numpy/user/numpy-for-matlab-users.html

Grading: 72% for six problem sets (12% each); 28% for final project.
Final grades determined on a 10-point scale, subject to possible *down*shifting of thresholds.

Problem Sets: Assigned roughly every two weeks, aligned to modules. Collaborate on ideas, but submit your own clear write-ups. Graded 0–100. **Unclear work (messy derivations, unreadable figures/code output) will be marked incorrect.** Each assignment integrates math, programming, and biological interpretation within the problems. In addition, *every student must complete one extension track per assignment*: either a **technical** (deeper analysis/derivation) or a **conceptual** (synthesis/interpretation/literature) extension. You may switch tracks across assignments. Python/MATLAB code files may be submitted but are not required if plots and results are clearly presented. ***Upload to Gradescope by 11:59pm on the due date.*** Late work not accepted.

Assignment Schedule	Date Assigned	Due Date	Module Topic
Problem Set 1	Thu Jan 8	Thu Jan 22	Search, Diffusion, & Transport
Problem Set 2	Thu Jan 22	Thu Feb 5	Foraging
Problem Set 3	Thu Feb 5	Thu Feb 19	Decision Making & Collective Behavior
Problem Set 4	Thu Feb 19	Thu Mar 5	Synchronization
Problem Set 5	Thu Mar 5	Thu Mar 26	Pattern Formation
Problem Set 6	Thu Mar 26	Thu Apr 9	Disease Dynamics
Project Proposal	Thu Jan 8	Thu Apr 2	
Final Project Report & Slides	Thu Jan 8	Tue Apr 21	

Projects: Mathematical biology spans systems from molecules to ecosystems, and our modules can only touch a fraction of these. The final project gives you the chance to explore a topic in greater depth—linking modeling, simulation, and biological interpretation around a question that genuinely interests you.

By **Thu Feb 27**, I will post a list of papers and project ideas, any of which can serve as the core reference for your work. You are also welcome to propose your own topic—please discuss it with me well before the proposal deadline if so. **You may work in groups of two or three.** Email me once your team and topic are confirmed.

By **9 am on Thu Apr 2**, upload a one-page PDF project proposal outlining: (1) the biological question to be addressed, (2) the mathematical and computational methods to be used, (3) references that will guide your analysis, (4) preliminary hypotheses or expected results, and (5) a plan for addressing foreseeable difficulties. Each group submits one proposal listing all members.

By **9 am on Tue Apr 21**, submit a **7–10 page written report** including: an introduction motivating the problem; a methods section describing the model and simulations; results with plots and interpretation; and a discussion with extensions or open questions. The report must specify each member's contributions.

Each group will also deliver a **10–15 minute in-class presentation** during the week of **Apr 21**.

Projects will be graded based on both the written report and the oral presentation. You should demonstrate mastery of the reference material, meaningful modeling progress toward your scientific question, and a clear, well-organized presentation complete with visuals and biological interpretation.

Class Policies:

- Come to class as some of the material to be presented in lecture will not be contained in the required text.
- Classroom discussion and questions are encouraged and supported.
- I will make arrangements for classes I miss due to travel or illness.
- Arrive on time (5 minutes early if possible) as important announcements are presented at the beginning of class.
- Late homework and projects are not accepted.
- Violations of the honor code will be handled according to university policy (see below)

Students with disabilities (official CU policy): If you qualify for accommodations because of a disability, please submit your accommodation letter from Disability Services to me in a timely manner so that your needs can be addressed. Disability Services determines accommodations based on documented disabilities in the academic environment. Information on requesting accommodations is located on the Disability Services website.

Contact Disability Services at 303-492-8671 or dsinfo@colorado.edu for further assistance. If you have a temporary medical condition or injury, see Temporary Medical Conditions under the Students tab on the Disability Services website.

Classroom Environment: Students and faculty each have responsibility for maintaining an appropriate learning environment. Those who fail to adhere to such behavioral standards may be subject to discipline. Professional courtesy and sensitivity are especially important with respect to individuals and topics dealing with race, color, national origin, sex, pregnancy, age, disability, creed, religion, sexual orientation, gender identity, gender expression, veteran status, political affiliation or political philosophy. Class rosters are provided to the instructor with

the student's legal name. I will gladly honor your request to address you by an alternate name or gender pronoun. Please advise me of this preference early in the semester so that I may make appropriate changes to my records. For more information, see the policies on classroom behavior and the Student Code of Conduct.

Honor Code: All students enrolled in a University of Colorado Boulder course are responsible for knowing and adhering to the Honor Code. Violations of the policy may include: plagiarism, cheating, fabrication, lying, bribery, threat, unauthorized access to academic materials, clicker fraud, submitting the same or similar work in more than one course without permission from all course instructors involved, and aiding academic dishonesty. All incidents of academic misconduct will be reported to the Honor Code (honor@colorado.edu); 303-492-5550). Students who are found responsible for violating the academic integrity policy will be subject to nonacademic sanctions from the Honor Code as well as academic sanctions from the faculty member.

I assume submitted work is generated by students themselves, working individually or in groups. Students should not have another person/entity do the writing or solving of any portion of an assignment, which includes hiring a person or a company to complete assignments or using artificial intelligence tools like ChatGPT.

Additional information regarding the Honor Code academic integrity policy can be found at the Honor Code Office website.

Sexual Misconduct, Harassment, Discrimination, and/or Related Retaliation: The University of Colorado Boulder (CU Boulder) is committed to fostering a positive and welcoming learning, working, and living environment. CU Boulder will not tolerate acts of sexual misconduct intimate partner abuse (including dating or domestic violence), stalking, protected-class discrimination or harassment by members of our community. Individuals who believe they have been subject to misconduct or retaliatory actions for reporting a concern should contact the Office of Institutional Equity and Compliance (OIEC) at 303-492-2127 or cureport@colorado.edu. Information about the OIEC, university policies, anonymous reporting, and the campus resources can be found on the OIEC website.

Please know that faculty and instructors have a responsibility to inform OIEC when made aware of incidents of sexual misconduct, discrimination, harassment and/or related retaliation, to ensure that individuals impacted receive information about options for reporting and support resources.

Religious Observances: Campus policy regarding religious observances requires that faculty make every effort to deal reasonably and fairly with all students who, because of religious obligations, have conflicts with scheduled exams, assignments, or required attendance. If you have any such obligations on assignment due dates or exam days, let me know by the end of the first week of class, and we can work together to accommodate your schedule.

See the campus policy regarding religious observances for full details.

Preferred Student Names and Pronouns: I will gladly honor your request to address you using your preferred name and gender pronoun. Please advise me of this preference early in the semester if it conflicts with information provided by the registrar, so that I may make appropriate changes to my records. You should be able to update your preferred names and pronouns via the student portal; that preferred name and/or pronoun will then be listed on my roster. In the absence of such information, the name that appears on my roster will be the one I check and refer to in my gradebook.