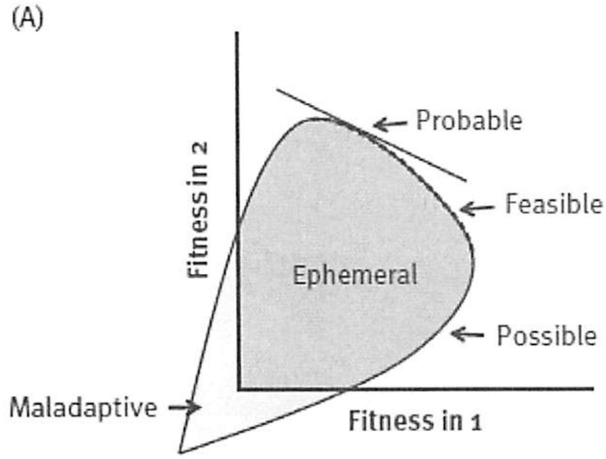
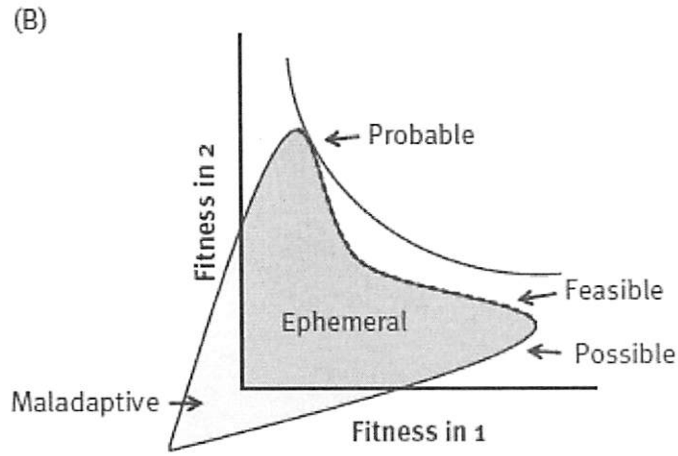
Biology 3671:

EVOLUTIONARY CONCEPTS

Notes and Tutorials 2014



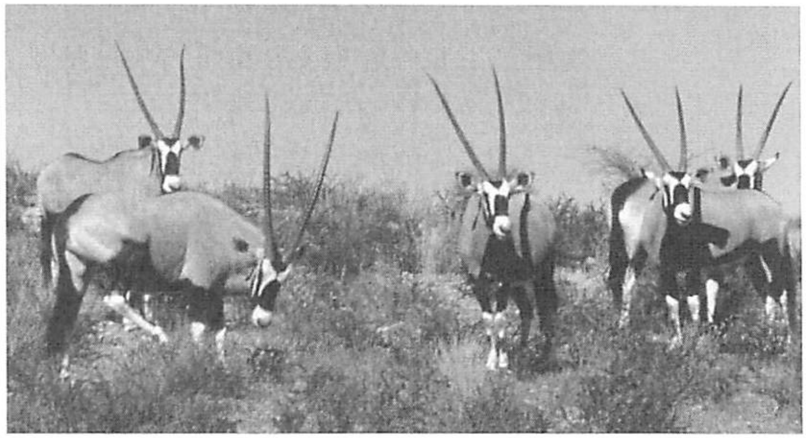


© Douglas Morris
Department of Biology
Lakehead University

COURSE SUMMARY

EVOLUTIONARY CONCEPTS

(0-0;2-2)



Biology 3671 - 2014

Instructor:

Dr. Douglas Morris

Office: CB4017

Lab: CB3019

Text:

- Morris, D. W. and P. Lundberg. 2011. Pillars of Evolution. Oxford University Press, Oxford, UK.
- Morris, D. W. 2014. Biology 3671: Evolutionary concepts. Notes & tutorials 2014.

Office Hours:

Tuesday: 13:00-14:00 & Thursday: 13:00-14:00 (7 January - 3 April 2014 only)

Other Times by Appointment

Lectures: Tuesday & Thursday 14:30-15:50 Room RB 2047.

Tutorials: As assigned by the registrar:

ALL STUDENTS MUST REGISTER FOR AND ATTEND TUTORIALS

BIOL 3671T W1 Tuesday: 12:30-14:20 CB 3010A; GA Allison Bannister

BIOL 3671T W2 Wednesday: 12:30-14:20 CB 3010A; GA Daniel Brazeau

BIOL 3671T W3 Thursday: 08:30-10:20 CB 3010A; GA Allison Bannister

BIOL 3671T W4 Friday: 09:30-11:20 CB 3010A; GA Daniel Brazeau

ELECTRONIC DEVICES IN LECTURES AND TUTORIAL. Students are not allowed to send or receive phone or text messages, to use E-mail or social networks, or surf the internet. Audio and video recording during lectures and tutorials is strictly prohibited unless permission is granted on an individual basis by the course instructor. All electronic devices other than notepads or laptops used to take notes, and calculators required for assignments and tutorials, must be left out of the room or turned off and located out of sight. No electronic devices other than calculators are allowed during quizzes.

BEHAVIOUR DURING LECTURES AND TUTORIALS. Students must respect the rights of others by conducting themselves at all times in a professional, polite, and civil manner.

There will be at least one guest lecture during the course. GUEST LECTURES ARE AN INTEGRAL COURSE COMPONENT AND STUDENTS WILL BE EXAMINED ACCORDINGLY.

Contents:

Introduction:

This course is designed for the student who wants to understand evolutionary concepts and their application to important questions in biology. The course emphasizes the lock-step connection between evolutionary biology and ecology. Course instruction will include a mixture of lectures, general discussions, tutorials, and investigative assignments. Lectures will emphasize conceptual, empirical, and experimental approaches to the study of evolution. Students are expected to complete supplementary readings and assignments, and to participate fully in tutorials. Lectures and tutorials are integrated to provide a single cohesive body of instruction.

Course Objectives:

1. To help students "think like evolutionary biologists".

2. To introduce students to a broad array of relevant and contemporary issues in the study of evolution.

3. To expose students to the set of essential concepts, theories, and models required to be "literate" in the study of evolution.

4. To inspire students to question and discuss current concepts in evolutionary biology.

5. To assist students in developing the skills, discipline, and study habits necessary for self-instruction in this and other areas of biology.

Evaluation:

Weekly in-class quizzes - 60%. Tutorial assignments, participation, discussion, and reports - 25%. Final term report 15%.

Performance will be evaluated regularly. The evaluation will be based on the student's grasp of important issues, logical reasoning, non-trivial criticisms of the material, and the ability to solve evolutionary problems. Students are encouraged to share their ideas and their questions.

Written or oral reports may be assigned at intervals during the course. Evaluation of these reports will be based on the student's ability to synthesize a field of enquiry, to apply that synthesis to a particular problem, or to develop significant new insights into evolutionary issues. The reports should not, in general, be restatements of review papers. Rather they will require the student to apply what is known (and what is unknown) to an unresolved question. Evaluation will be devoted equally to clarity of presentation, rigour of treatment, and suitability of the report to the assignment.

Report Format:

Read each assignment carefully and include only relevant material. Unless otherwise indicated, maximum length of reports including tables, figures, and references will be six typed pages (double-spaced, 2.5 cm margins, minimum height of lower-case letters 2 mm).

Report Due Date:

All regular reports will be due either at the end of the tutorial, or as announced in lecture. Late submission will be penalized at the rate of 10 % per calendar day unless prior permission is received. The due date for the final report is 15:50 3 April 2014. ***Reports submitted after 3 April 2014 will not be accepted for grading.***

Report Style:

Be concise. Use the active voice. Organize your thoughts before you begin writing. Omit needless or redundant words. Express your thoughts as clearly as possible even if it means re-writing the report. Write in your own words. Use quotations sparingly, and only when you cannot express the idea clearly yourself. Never borrow a phrase without quotations. Never repeat observations, interpretations, or ideas without proper citation. Never cite a reference that you have not read.

FINAL TERM REPORT = TAKE-HOME ASSIGNMENT

Students will be given components of the final take-home report throughout the term. Students are encouraged to answer each component in a timely fashion. Submit the entire assignment as a single submission on or before the 3 April 2014 due date. Where possible, type the answer to each question or assignment (double-spaced, 2.5 cm margins, minimum height of lower-case letters 2 mm). The due date for the final report is 15:50 3 April 2014. *Reports submitted after 3 April 2014 will not be accepted for grading.*

Please note: The take-home term report is a term project and not a final examination. Students will be ineligible to write a special examination as outlined in general regulation VII in the Lakehead University Calendar.

TUTORIALS:

Students are required to participate in weekly tutorials. Tutorials will consist of a mixture of problem sets, workshops, and assigned readings. Please ensure that you have completed the reading assignment before attending the tutorial.

Depending on length, the total assignment, or a random subset of each assignment, will be evaluated to complete the tutorial grade. When possible, we will use a peer-grading system where

students correct one another's assignments.

Tentative Timetable 2014

Jan. 7 & Jan. 9 Topic 1: The Evolutionary Paradigm

Jan. 14 & Jan. 16 Topic 2: Mechanics I: Chance vs Systematic Change

Jan. 21 & Jan. 23 Topic 3: Mechanics II: Beyond Mendelian Genetics

Jan. 28 & Jan. 30 Topic 4: Function I: Beyond Mechanics

Feb. 3 & Feb. 5 Topic 5: Function II: Mappings

Feb. 11 & Feb. 13 Topic 6: Structure I: Evolutionary Games

Feb. 17 - Feb. 21 Study Week - No Classes

Feb. 25 & Mar. 4 Topic 7: Structure II: The Structure Matrix

Feb. 27 Tentative Special Guest Lecture

"Evolution and Ecology"

Mar. 6 & Mar. 11 Topic 8: Scale I: Grain and Habitat Selection

Mar. 13 Topic 9: Scale II: Softness of Selection

Mar. 18 & Mar. 20 Topic 10: Dynamics I: Evolutionarily Stable Strategies

Mar. 25 & Mar. 27 Topic 11: Dynamics II: Adaptive Dynamics

Apr. 1 & Apr. 3 Topics 12 & 13: Adaptation

Apr. 3 Final Report Due: 15% of grade

How to Study Evolution:

An understanding of evolutionary concepts is essential for all biologists. Some students have difficulty making the transition from rote learning to conceptual thinking. Others are confused on the difference between a clear understanding of concepts, often aided by mathematics, and arm-waving generalities. A vague understanding of evolution will lead, at best, to an even more vague understanding of biology. How, then, can students maximize their ability to learn evolutionary concepts?

Here are a few suggestions.

- **Form, or join, a study group.**
- **Supplement your lecture notes by annotating the figures and equations in your text.**
- **Redraw graphs, rewrite equations, and explain them to your study group.**
- **Review your lecture notes before you attend the next lecture.**
- **Make sure that you understand the mathematics, rather than memorizing equations or graphs.**
- **When confused, get help immediately from your study group, demonstrator or instructor.**
- **Ask yourself, and your study group, questions about the material rather than relying on quizzes to do that for you.**
- **Be an active participant in tutorial and classroom discussions.**
- **Try to imagine specific examples for each concept that you explore.**
- **Ask yourself at frequent intervals "how could I improve on or test this idea"?**
- **Never commit the "fallacy of complexity" by criticizing a model as too simple of a caricature of nature unless you have a clear and parsimonious alternative.**

- **Read Darwin's "On The Origin of Species by Means of Natural Selection" available on the web at**

CORRECTIONS: Pillars of Evolution

Students in Biology 3671: Please make the following corrections directly in your textbook.

Page 25: Replace all upper-case fitness symbols (e.g., W_{11}) with lower-case (e.g., w_{11})

Page 26, line 3: Replace "w" with "$\overline{w}$".

Page 26, line above equation (2.8): Replace "Equation 2.5" with "Equation 2.7".

Page 26, second line from bottom: Insert "in equation 2.8" after "…for q".

Page 28, footnote 20: Replace "var(T)" with "V_T".

Page 33, Table 2.1: "Locus 2" should be moved down to be in line with "*Bb*". "Genotypes" should be moved down to be in line with "AA".

Page 36, legend to Figure 2.4: Replace "…at low and high ends of the environmental gradient" with "in the two environments".

Page 37, lines 1 and 2: Replace "…at the low end of the environmental gradient and negative at the other" with "…in environment 2 and negative in environment 1".

Page 42, legend to Figure 2.7: Replace "Dense stippling" with "Sparse stippling" in sentence 5. Replace "Sparse stippling" with "Dense stippling" in sentence 6.

Pages 44 and 45: Replace "gizard" and "gizards" with "gizzard" and "gizzards" respectively.

Page 72, upper panel: Change "Habitat 1" on the right-hand-side to "Habitat 2".

Page 76, legend to Figure 3.13: Insert "the" in front of "environmental" (line 3).

Page 82, Box 3.2: All mean fitness terms ($\overline{W}$) should be lower case ($\overline{w}$).

Page 85, equation (3.13): The asterisk should be a superscript.

Page 102, final sentence before the footnotes. Replace "…game," with "…game."

Page 103, last line of paragraph 3: Change "…map can" to "…map".

Page 120, middle of the page: Replace "W" with "w" (lower case).

Page 134, Figure 4.16: Label the three panels. Upper left should be "(A)", upper right should be "(B)", and lower should be "(C)".

Page 135, Figure 1.17: The label "(c)" should be upper case "(C)".

Page 147, 2nd full paragraph, line 4: Replace "…yield convex" with "…yield concave".

Page 168: Easier to understand if "p_i" is replaced with "p_i*" where p_i* is defined as "the probability that another randomly drawn individual is also an altruist"

Page 190, legend to Figure 6.3: Replace "solid" in line 2 with "dashed" and replace "dashed" in line 3 with "solid".

Page 191, top half of page: Replace "zero fitness" and "zero-fitness" with "fitness = 1" (two cases).

Page 232, Figure B7.2.1: Change the values on the ordinate (Y axis) from top to bottom to be 15, 10, 5, 0, -5, -10, and -15.

2014 **Dr. Douglas Morris**

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS

Topic 1: THE EVOLUTIONARY PARADIGM

The Value of a World View
Variation in Mice
Variation in Galapagos Finches
Heritability in Galapagos Finches
Struggle for Existence (= density dependence)
Heritable Variation Influences the Struggle
Adaptation Through Time

Tutorial 1: Learning to think like an evolutionary biologist.

Problems: **Interpreting graphics:** Using only the graphics and their legends, interpret and criticize each of the following figures in your course text (2.1, 3.10, 3.15, 4.3, 4.6, 4.7, 5.5, 6.7, 7.2).

Assignment: Display, in an appropriate figure, the frequency distribution of male and female students in your tutorial group. Write a short and appropriate figure legend. Write an additional sentence describing the pattern revealed by the distribution.

Complete your assignment during the tutorial and submit your report at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 1.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS

Topic 2: MECHANICS I

Chance

Mutation
Drift
Migration

Systematic Change

Hardy-Weinberg Equilibrium
Non-random Mating
Adaptive Evolution
Fitness
Absolute vs Relative Fitness
Adaptive (selection) Coefficient

Tutorial 2: Natural Selection.

Problem: One way to calculate heritability is to plot a so-called mid-offspring mid-parent regression. The mean value of the trait in full sibs is plotted against the mean value of the trait from the parents. The slope of the resulting least-squares linear regression is the estimate of narrow-sense heritability. Today we will evaluate the heritability of human body height. The trait is sexually dimorphic, but can be corrected by multiplying each female's height by 1.08. Using this correction factor, calculate your own body height, the height of your adult siblings, and that of both of your parents. Calculate the arithmetic mean for all offspring (called the "mid-offspring" value) and both parents (mid-parent), and record the data in your instructor's computer. Your instructor will make the anonymous class data available to you. Plot the mid-offspring by mid-parent data and the regression (your instructor will calculate the slope for you).

One can gain an intuitive understanding of heritability from Mendelian genetics. On average, each sexually-produced offspring should share ½ of its genetic composition with each parent. All of the genetic similarity in a trait is included in a contrast between the value of the trait in offspring and the mid-parent value. If one were to use the value for a single parent (usually the male to eliminate maternal effects), the degree of genetic relatedness would be reduced by ½. In this case, heritability would be equal to twice the value of the regression coefficient. Using data from your father only (this corrects for possible maternal effects), re-plot and re-calculate heritability for human body height.

1. In one clear and concise paragraph, evaluate the heritability of human body height with reference to your heritability graphs.

2. Provide a one-sentence explanation why human males tend to be taller than females.

Submit your report, including your graphs, one-paragraph response, and one-sentence explanation, at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 2: 13-24.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 3: MECHANICS II

Polygenic Inheritance
Genotype × Environment Interaction
Additive Genetic Variance
The Breeder's Equation
Response to Selection
Selection Differential
Epistasis and Pleiotropy
Genotypic Plasticity
Reaction Norms
Role of Development
BIDE

Tutorial 3: Chance in Evolution

Today you will work with your tutorial leader to assess the role of different types of chance in evolution. In order to do this, imagine that the population of interest is composed of two equally-size clones (genotypes 1 and 2) that reproduce asexually. Your task is to use Excel to simulate how different types of chance events alter the frequencies of the two clones through time.

The first simulation will evaluate the effect of chance on survival to reproduction. Each individual has an equal probability of survival. Those which survive all produce the same number of offspring that enter the next generation. Work with your tutorial leader to determine the size of the population, the size of the subset that will reproduce, and the number of offspring from each successfully reproducing individual. Simulate those choices in Excel. Use the frequencies from each generation to generate a graph of the change in the frequency of genotype 1 through time. Repeat the simulation enough times to demonstrate the effect of genetic drift on evolution.

The second simulation will impose an additional form of demographic stochasticity. This simulation will be identical to the first except that it will also impose chance on offspring number. Each reproducing individual will have an equal probability of producing few or many offspring. Again, work with your tutorial leader to develop a simple and convincing simulation of this process. Repeat the same number of simulations as above and graph the change in the frequency of genotype 1 through time.

In one concise paragraph, compare the results of the different simulations. Explain the patterns that you observe. What message do they convey about the evolution of disjunct populations? Submit your full report, including graphs, at, or before, the end of the tutorial session.

Required Reading: Morris and Lundberg 2011: Chapter 2: 25-52.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 4: <u>FUNCTION I</u>

Failure of the Breeder's Equation
Cooke's Equation
Unidirectional Adaptation
Fitness-mapping Functions
Fitness sets
The Adaptive Function
Fine vs Coarse Grain
Specialists, Generalists, and Polymorphisms
Possible Adaptive Strategies
Optimum Reaction Norms

Tutorial 4: Systematic Adaptation and Chance in Evolution

Today you will work with your tutorial leader to assess evolutionary change caused by adaptation against a stochastic background. You will use the same population and stochastic approach as in tutorial 3, but with an overlay of adaptation. Your task is to use Excel to simulate how different contributions to fitness alter the expected frequencies of the two clones through time.

The first simulation will evaluate the effect of differences in survival between the two clones. Those which survive all produce the same number of offspring that enter the next generation. Work with your tutorial leader to determine the expected difference in survival between clones, and how to incorporate that into the Excel model of drift that you built last tutorial (simulation 2 in tutorial 3). Simulate those choices in Excel. Use the frequencies from each generation to generate a graph of the change in the frequency of genotype 1 through time. Repeat the simulation enough times to demonstrate the joint effects of variation in survival and genetic drift on evolution.

The second simulation will impose an additional form of adaptation associated with differential reproduction between clones. Again, work with your tutorial leader to develop a simple and convincing simulation of this process. Repeat the same number of simulations as above and graph the change in the frequency of genotype 1 through time.

Compare the results of the different simulations in one concise paragraph. Explain the patterns that you observe. How does this message differ from the one that you submitted in tutorial 3 (be sure to restate that message)? Submit your full report, including graphs, at, or before, the end of the tutorial session.

Required Reading: Morris and Lundberg 2011: Chapter 3: 53-71.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 5: FUNCTION II

Habitat and Density
Mapping
The Nested Mapping of Fitness
The Demographic Framework
Fitness Maps Including Environment
Canalized Traits
Neutral Traits and Characters
Demographic Rates Vary with Environment
Covariance Between Functions
Selection Gradients
Standardized Trait Values
The G-Matrix

Tutorial 5: Using Fitness Sets and the Adaptive Function to Model Evolution

Work with your tutorial leader to explore the adaptive evolution of specialist versus generalist phenotypes. Assume that the phenotypic variation of the species of interest can be summarized by 20 'discrete' phenotypic classes. Imagine that the species is fine-grained in habitat use and occupies two habitats (1 and 2) that differ in expectations of survival and reproduction. The distribution of clutch sizes is symmetrically distributed (mode of 10) about a different phenotype in each habitat (phenotype 5 in habitat 2, phenotype 15 in habitat 1). Clutch size declines by 1 with every phenotype class less than, or greater than, the mode. Mortality of offspring is the same in each habitat and increases at a constant rate (0.06) with clutch size.

Imagine that habitat 2 is twice as common in the landscape as is habitat 1. Derive the adaptive function and calculate which phenotype has the greatest fitness. Repeat with habitat 1 and 2 equally common. Repeat for equally common habitats assuming that mortality is twice as great in habitat 1 as it is in habitat 2.

Draw the fitness sets and adaptive functions for the three scenarios that you have modelled. Illustrate which phenotype has maximum fitness. Write a single concise paragraph explaining the difference among the scenarios, and interpret the evolutionary significance. Submit your labelled illustrations and paragraph at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 3: 72-87.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 6: <u>STRUCTURE I</u>

Trait vs Function
State
Strategy
The Mating Game
Evolutionary Game Theory
Fitness Payoffs
Pure vs Mixed Strategies
Rock-Paper-Scissors
Evolutionary Structure
Tradeoffs

Tutorial 6: Investigating Evolutionary Tradeoffs

Download and read the article by L. W. Simmons and D. J. Emlen (2006) entitled "Evolutionary trade-off between weapons and testes" (PNAS 103: 16346-16351) available from the e-journals at the LU Library or directly from http://www.pnas.org/content/103/44/16346.full.pdf+html, as well as Douglas Emlen's publication webpage http://dbs.umt.edu/research_labs/emlenlab/publications.htm.

Use your reading of Simmons and Emlen to help answer the following questions. Use no more than three sentences for each answer.

1. List two assumptions underlying the conditions that should lead to a tradeoff between weaponry and testes size?

2. If one cauterizes the thoracic horns of male *Onthophagus* beetles, what other traits might be expected to increase in size during development? Was there any evidence that Simmons and Emlen controlled for this potential effect?

3. Would you expect a similar tradeoff between testes size and other traits in any sexually dimorphic species? Why or why not?

4. Horn and testes sizes are phenotypically plastic traits in Onthophagine beetles, and respond to nutritional differences during development. Which of the two traits (horns versus testes) would be expected to be least plastic to variation in nutrients? Briefly explain your reasoning.

5. Does the increased body-size of cauterized beetles reveal an evolutionary trade-off. If so, how can we be certain?

6. An underlying principle responsible for tradeoffs is that resources (or time) spent on one trait (or activity) cannot be simultaneously allocated to another. Using this principle, speculate on whether tradeoffs come into play in mate selection by humans. Justify your answer.

Submit your answers at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 4: 88-111.

2014 **Dr. Douglas Morris**

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 7: STRUCTURE II

Optimization
Polymorphic Traits
Constraints
Allometry
Heterochrony
Genetic vs Proximity Structure
The Structure Matrix
Evolution in Multiple Environments
Feasible vs Possible Trait Values
Traits with Multiple Functions
Traits with no Effect on Function

Tutorial 7: Phenotypic Plasticity in Evolution

Download and read the article by C. K. Ghalambor et al. (2007) entitled "Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments" (Funct. Ecol. 21: 394-407) available from the e-journals at the LU Library or directly from http://www.mckaylab.colostate.edu/reprints/Ghalambor_etal_2007.pdf.

Use your reading of Ghalambor et al. to help answer the following questions. Use no more than three sentences for each answer.

1. Will global warming be more, or less, likely to reveal adaptive vs non-adaptive phenotypic plasticity? Will this depend on the types of traits considered? Justify your answer.

2. Why should 'hopeful monsters' be more likely in a stressful environment?

3. What type of selection would you expect to emerge if mosaic reaction norms are antagonistic to one another? Explain your answer.

4. What is an all-purpose reaction norm?

5. Is an all-purpose 'generalized' or specialized adaptive reaction norm more likely to be associated with reduced gene flow between populations? Justify your answer.

Submit your answers at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 4: 112-136.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 8: SCALE I

Match Scale with Interest
Allometry Revisited
Grain-size Revisited
Density Dependence in Fitness Sets
Rigid vs Flexible Adaptive Landscapes
Stable Landscapes
Habitat Selection
The Habitat Isodar
Case Studies with Small Mammals
A Case Study with a Large Mammal
Habitat-Selecting Algae

Tutorial 8: Density Dependence and Adaptation

Recall your earlier Excel simulations where you determined the optimum phenotype arising through a fitness-sets analysis. In this tutorial, you will add more realism to the simulations by explicitly assessing the influence of density on fitness. Work with your tutorial leader to develop a reasonable model that incorporates density dependence, and modify the Excel 'program' to assess its effect. Vary the parameters in the model (one at a time) to assess how each one influences the optimum phenotype.

Create a simple table illustrating the main results from your simulations, then write a single paragraph that explores the significance of your results to our understanding of evolution. In one additional sentence, state how an increase in the effect of density in the most productive (largest clutch size) habitat is likely to influence the results.

Submit your full report (table and paragraph) at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 5: 137-153.

2014 **Dr. Douglas Morris**

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 9: <u>SCALE II</u>

Adaptive Landscapes of Habitat Selection
The Ideal Free Distribution
Negative Frequency-Dependent Adaptation
Behaviour and the Adaptive Function
Can Habitat Selection Purge Mutation Load?
Selection Gradients Depend on Density
Soft vs Hard Selection
Habitat Constrains Adaptation
Cooperation
Multi-Level Selection

Tutorial 9: Workshop on Multilevel Adaptation

Download and read the article by D. S. Wilson and E. O. Wilson (2009) entitled "Evolution for 'the good of the group'" (Am. Sci. 96: 380-389) available from the e-journals at the LU Library or directly from http://evolution.binghamton.edu/dswilson/wp-content/uploads/2010/12/American-Scientist.pdf.

Divide the tutorial, randomly, into pairs of two-player 'teams'. Team 1 will work only as individuals. Team 2 will have the option of working together. Listen carefully as your tutorial leader explains the task each 'team' is to perform, and how the 'winner' is to be chosen.

Answer the following questions:

1. Explain, in a single paragraph, how traits and strategies with public benefits, but incurring individual costs, can be adaptive.

2. Explain, in a single paragraph, the likely consequence for group-living organisms, of traits or strategies which benefit individuals but create public costs.

3. Write a single paragraph assessing whether single 'player' awards (such as most outstanding, highest scoring, etc.) are beneficial or harmful in cooperative games.

4. Do study groups make sense in the context of multi-level selection? Why, or why not?

5. Science is supposed to be a cooperative (or at least collaborative) unselfish pursuit where public investment is rewarded through improved knowledge. Using your understanding of multi-level selection, assess whether the penchant for national and international awards is likely to enhance or reduce cooperation.

Submit your answers at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 5: 153-178.

2014 **Dr. Douglas Morris**

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 10: DYNAMICS I

Density dependence
Equilibria
The Meaning of Carrying Capacity
Fitness-Generating Functions (G-functions)
Invasibility
Evolutionarily Stable Strategies (ESS)
Fitness Maxima
Fitness Minima
Ecological Opportunity
Branching Points

Tutorial 10: Workshop on Speciation

Download and read the article by Dolph Schluter (2009) entitled "Evidence for ecological speciation and its alternative" (Science 323: 737-741 available from the e-journals at the LU Library or directly from http://www.sciencemag.org/content/323/5915/737.full.pdf. Interested in alternatives to ecological speciation? Read S. R. McDermott and M. A. F. Noor (2010) "The role of meiotic drive in hybrid male sterility" (Phil. Trans. Roy. Soc. 365: 1265-1273) http://www.ncbi.nlm.nih.gov/pmc/articles/PMC2871811/pdf/rstb20090264.pdf.

Use your reading of Schluter's speciation perspective to work with your tutorial leaders and other students on designing a definitive test to differentiate between 'ecological' and 'mutation-order" speciation. Work together to develop appropriate hypotheses to distinguish, clearly, each form from the other.

Answer the following questions:

1. List three reasons why ecological speciation should be 'easier' to achieve in allopatry than in sympatry.

2. Why does Schluter consider speciation associated with sexual selection as potentially being either ecological or mutation-order speciation?

3. Write a short paragraph illustrating how mutation-order speciation might complement ecological processes of speciation?

Submit your answers at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 6: 179-198.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 11: DYNAMICS II

Adaptive Extinction
Evolutionary Branching
Stable Polymorphisms
Sympatric Speciation
Evolutionary Feedback Environment
Arms Races
Red Queen Dynamics
Spatial Dynamics
Bet Hedging
Partial Migration

Tutorial 11: Adaptive Radiation

Download and read the article by S. Gavrilets and J. Losos (2009) entitled "Adaptive radiation: contrasting theory with data" (Science 323: 732-737) available from the e-journals at the LU Library or directly from http://www.oeb.harvard.edu/faculty/losos/jblosos/pdfs/Gavrilets_and_Losos_2009.Science.pdf. Interested in learning more? Check out Losos and Mahler (2010) http://www.oeb.harvard.edu/faculty/losos/jblosos/pdfs/Losos%20and%20Mahler.%202010.pdf.

Use your reading of Gavrilets and Losos to help answer the following questions. Use no more than three sentences for each answer.

1. What, exactly, is an adaptive radiation?

2. Invasive species typically encounter great ecological opportunities. Would you expect them to radiate into numerous species or remain as a single taxon? Justify your answer.

3. Evolutionary biologists typically place huge emphasis on adaptive radiations, but not radiating extinctions. What might account for this? Explain your answer.

4. Is a non-adaptive radiation possible? Justify your answer.

5. How would you test for differences between adaptive and non-adaptive radiations?

6. Is the continued fragmentation of natural habitats by human activities likely to induce or stall adaptive radiations of species? Explain your answer.

Submit your answers at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 6: 199-215.

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 12: Adaptation I

Adaptive Radiation
Convergent Evolution
Fit Between Form and Function
Condition Dependent Characters
Biogeography and Niche Evolution
Case Study: Damselflies
Incumbent Replacement

Tutorial 12: Convergent Evolution

Download and read the article by Jonathon Losos (2009) entitled "Convergence, adaptation, and constraint" (Evolution 65: 1827-1840) available from the e-journals at the LU Library or directly from http://www.oeb.harvard.edu/faculty/losos/jblosos/pdfs/Losos.%20Evolution.%202011.pdf.

Use your reading of Losos (2009) to help address the following statements and questions. Write short paragraphs to address each point.

1. Distinguish, clearly, between convergent and parallel evolution.

2. Explain how convergent phenotypes can emerge through phylogenetic constraints.

3. Distinguish, clearly, between adaptations and exaptations. Do exaptations represent convergence? Why or why not?

4. Which of the following is a more reliable indicator of convergent evolution: different combinations of trait values performing a constant function, or different functions produced by the same trait? Explain your answer.

5. Explain how "parallel phenotypic evolution can result from nonconvergent molecular evolution".

6. Why is it necessary to distinguish convergent evolution from constrained evolution?

Submit your answers at, or before, the end of the tutorial.

Required Reading: Morris and Lundberg 2011: Chapter 7: 217-237.

2014 **Dr. Douglas Morris**

BIOLOGY 3671 - EVOLUTIONARY CONCEPTS - TUTORIAL GUIDE

Topic 13: Adaptation II

The Possible, Ephemeral, and Feasible
Epiphenomena
Maladaptation
Invasion vs Extinction

Tutorial 13: Workshop: The Future of Biodiversity

Download and read the articles by B. Sinervo et al. (2010) entitled "Erosion of lizard diversity by climate change and altered thermal niches" (Science 328: 894-899) and by R. Huey et al. entitled "Are lizards toast" (Science 328: 832-833)available from the e-journals at the LU Library or directly from http://www.biolsci.monash.edu.au/research/acb/docs/erosion-lizard-diversity.pdf and http://www.oeb.harvard.edu/faculty/losos/jblosos/pdfs/Huey%20et%20al%202010%20Science.pdf respectively.

Contemplate and discuss the following questions.

1. Why might other vertebrate taxa be more, or less, vulnerable to extinction through climate change?

2. What are the likely evolutionary consequences of diminished lizard diversity? Will there be more, or less, ecological opportunity. Justify your answer.

3. If lizards are threatened by elimination of thermal niches, might the same be true of many invertebrate taxa? How would you investigate this possibility?

4. Many biologists imagine that species will be able to survive global warming through geographic range expansions. Why is this solution unlikely for many reptilian taxa?

5. Why are many invertebrate species more likely to adapt to warmer thermal regimes than are reptiles?

6. Are government policies on endangered species effective at averting extinctions? Why, or why not?

7. Where, in your list of personal priorities, does the global extinction crisis rank?

8. Why are societal concerns in general, and government actions in particular, indifferent to the global loss of biodiversity? What are the likely future consequences?

Required Reading: Morris and Lundberg 2011: Chapter 7: 238-248.