Biology of Symbiosis (BIOL 256), Fall 2005
SYLLABUS

Instructor: David Hibbett
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Office hours: By appointment
Optional text: Surindar Paracer and Vernon Ahmadjian. 2000. *Symbiosis, An Introduction to Biological Associations. Second Edition.* Oxford University Press. ISBN 0-19-511807-3. One copy is on reserve in the Science Library, another is in the Goddard Library Special Collections: Faculty Area.
Meetings: Mon./Thurs., Room 355, Lasry Biological Science Center, 1:25-2:40.

Please read this entire document carefully

What is this course all about?
Symbioses are intimate associations involving two or more species. Symbioses are incredibly diverse. Familiar examples include corals (associations between cnidarians [animals] and dinoflagellates [unicellular algae]), lichens (fungi and green algae or cyanobacteria), and malaria (involving the apicomplexan, *Plasmodium*, and its mosquito and human hosts). The establishment of symbioses has shaped the evolution of individual clades and entire ecosystems. For example, it has been suggested that the evolution of mycorrhizal symbioses (involving plants and fungi) was a key innovation that allowed plants to colonize the land and establish terrestrial ecosystems.

Symbiosis is a major source of evolutionary and ecological novelty. It is therefore of general interest to understand the processes that establish, maintain, and disrupt symbioses. Symbioses are mentioned in many biology courses, but one rarely encounters a course that takes symbiosis as its central focus. This course will survey the diversity, evolution, and natural history of symbioses through articles in the primary literature. These research articles will focus on specific questions concerning individual symbioses. By the end of the semester, I hope that we will be able to address the following general questions concerning the natural history and evolution of symbioses: 1) Are symbioses stable endpoints in evolution? 2) Do symbioses begin as antagonistic interactions and tend to evolve toward mutualism? 3) Does symbiosis promote or retard speciation? 4) Do some groups of organisms enter into symbioses more easily than others?

This course is also about the process of communicating in science. Scientific communication takes many forms, but principally it includes writing, presentation, discussion, and reviewing the work of others. This course will provide practical experience in all of these activities and is intended to help you learn how to function as independent scientists.

How is this course organized?

Overview: At our first meeting I will give an overview of general issues relating to symbioses and describe the structure of the course. On August 29, the library staff will lead a workshop on strategies for locating papers using the internet and other resources of the Clark University Libraries. We will also take time to discuss the anatomy of a scientific research paper, the process of publishing in science, and the difference between reviewed and non-reviewed publications. On September 1, I will lead a discussion of a research article, acting as both the "Presenter" and "Discussion

Leader" (explained below). Beginning on September 8 the class format will shift to student-led discussions. We will interrupt the discussions for two sets of "writing workshops", which will be coordinated with due dates for two assigned essays. Guidelines for the essays are attached.

Student-led discussion sessions: There will be approximately 20 student-led discussion sessions this semester. In each session, one student will be assigned as the "presenter" and another student will be assigned as the "discussion leader".

The job of the presenter is to choose a symbiotic system and locate a peer-reviewed primary research article about that system for discussion. You may not choose a paper that was assigned to you in another class, or any paper that was used in prior editions of this course. A folder with copies of the articles that students selected in earlier versions of the course will be placed on reserve in the Science Library—these could be very useful as you search for your own papers to present. In class, the presenter will provide a brief introduction to the general topic. Afterwards, the discussion leader will facilitate a discussion on the research paper. The discussion leader will be chosen in class by random sampling with replacement. Some suggestions for running discussions are attached.

Papers for the first set of discussions must be submitted by September 1. You must provide me with a copy of the paper and a brief synopsis of the paper, with an explanation of why you think the paper is appropriate to this course. If I do not feel the paper is appropriate, I will ask you to choose another paper. Papers for the second set of discussions must be chosen by October 17, with a synopsis as above. Please note that the Goddard Library workshop on August 29 will provide a great opportunity to locate papers for discussion.

Web-based discussion tool: To facilitate discussion, we will use a web-based tool (developed specifically for this course by the staff of the ITS) that allows you to post comments on individual readings and reply to other student's comments. Your posting must consist of:

1. A *brief* summary of the main points of the paper. State the main question addressed in the study, the methods used, and the major conclusion. Please keep your summary between 150 and 300 words (that's short!).
2. A set of three comments or questions about the paper.
3. A set of three numerical ratings of the paper according to the following criteria: Scientific content, writing quality, graphics.

You will be able to view other student's postings, but only after you have made your own posting. Each assignment will have a deadline of 7:00 pm the night before class, beyond which you will be unable to make a posting. The site is: https://www.clarku.edu/departments/biology/biol254/index.cfm.

Writing workshops and essays: You will write two short (approx. 10 page) review essays, which should be related to the topics that you assign for class discussion. We will divide the class into two groups and conduct a pair of "writing workshops" associated with each set of essays, using the on-line writing tool *Comment*. Essays will be handled much like articles being submitted for consideration for publication in a scientific journal. You will submit your essay at least one week before the writing workshop. This first submission will be graded on a 100-point scale.

Members of each writing workshop will provide comments on-line for each essay in their workshop group. At the workshop, we will discuss each essay in turn, focusing on writing issues as well as scientific content. After the writing workshop, you will revise your essay and resubmit it to me as hard copy, along with a concise

statement describing changes that you have made in response to the comments received via *Comment*. The revised essay will be graded on a 100-point scale, and the scores for the first submission and the revision will be summed. Participation in the workshop and submission of comments on-line will also be scored for points (see below).

How will grades be calculated?
Points will be awarded as follows:

Task/due date:	Points available:
First paper for discussion selected by Sept. 1, with synopsis	30 (15 points for selection that I deem inappropriate; no points for late selections or selections without a synopsis)
Second paper for discussion selected by Oct. 17, with synopsis	30 (as above)
Essay 1 first submission by Oct. 13	100 (late submissions marked down by 20 points per day)
Essay 1 revision by Oct. 31, with explanation of changes in resp. to comments	100 (as above)
Participation in writing workshop 1	20 (must submit comments on all papers and participate in the discussion to receive any points)
Essay 2 first submission by Nov. 28	100 (as above)
Essay 2 revision by Dec. 15, with explanation of changes in resp. to comments	100 (as above)
Participation in writing workshop 2	20 (as above)
Participation in student-led discussions	500 To get credit for each day's discussion you must 1) submit comments on-line, 2) show up for class, and 3) participate in the discussion. You are allowed to miss one discussion with no questions asked. After that, you will lose 50 points for each missed discussion.
TOTAL	1000 points (A=900-1000, B=800-899, C=700-799, etc.)

Expectations and general advice:
I am offering this course because I want to learn more about symbioses and share what I have learned with you. This is the same attitude that I expect you to bring to the course. In the early part of the semester, I will provide a general framework for thinking about symbioses, but the direction that the course takes later on, and the general tone of the course, will be up to you. With that in mind, I have the following advice: As presenter, try to choose subjects that will be of interest to other students in the class. Realize that we all have different backgrounds, and enter discussions with the goals of understanding the material that is being presented and helping others to understand. Do not be shy about posing questions or making speculations—speak up if you are uncertain about anything. Never ridicule your colleagues or make derisive remarks

(this also goes for the authors of the papers we read—just because they are not in the room does not give us license to trash them). If your colleagues make errors, point them out or ask them to clarify their remarks. Do not take such critical comments personally. Be grateful for constructive criticism. Point out the strengths as well as weaknesses of published articles and student essays. Relax—you are among friends.

Course schedule (tentative):

Date	Topic/Presenter
Aug. 25 R	Course introduction; Definitions and evolutionary dynamics of symbioses
29 M	How to find, read, evaluate, and explain a scientific paper. *Meet in Goddard Library*
Sept. 1 R	Instructor-led Discussion: TBA **First reading selections due**
8 R	Justin Golub: Agrawal, A. A., and J. A. Fordyce. 2000. Induced indirect defence in a lycaeid-ant association: the regulation of a resource in a mutualism. Proc. Roy. Soc. London B. 267: 1857-1861.
12 M	Sarah Assefa: Huntzinger, M., R. Karban, T. P. Young, and T. M. Palmer. 2004. Relaxation of induced indirect defenses of Acacias following exclusion of mammalian herbivores. Ecology 85: 609-614.
15 R	Lauren Jorgensen: Buck, K. R., and W. N. Bentham. 1998. A novel symbiosis between a cyanobacterium, *Synechococcus* sp., an aplastidic protist, *Solenicoloa setigera*, and a diatom, *Leptocylindrus mediterraneus*, in the open ocean. Marine Biology 132:349-355.
19 M	Daniel Kousathanas: Silliman, B. R., and S. Y. Newell. 2003. Fungal farming in a snail. Proc. Nat. Acad. Sci. USA. 100: 15643-15648.
22 R	Mika Kuwahara: Harrison, R. D. 2000. Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. Proc. R. Soc. Lond. B 267:911-915.
26 M	Emily Lescak: Lewis, C. L., and M. A. Coffroth. 2004. The acquisition of exogenous algal symbionts by an octocoral after bleaching. Science 304: 1490-1492. Also read on-line supporting material.
29 R	Kathy Nguyen: Moreau, J., and T. Rigaud. 2003. Variable male potential rate of reproduction: high male mating capacity as an adaptation to parasite-induced excess of females? Proc. R. Soc. Lond. B 270:1535-1540.
Oct. 3 M	Katie O'Brien: Freckleton, R. P., and I. M. Côté. 2003. Honesty and cheating in cleaning symbioses: evolutionarily stable strategies defined by variable pay-offs. Proc. R. Soc. Lond. B 270:299-305.
6 R	*DH away—No class*
10 M	*Fall Break—No class*
13 R	Danielle Stehlik: Johnson, P. T. J., K. B. Lunde, D. A. Zelmer, and J. K. Werner. 2003. Limb deformities as an emerging parasitic disease in amphibians: evidence from museum specimens and resurvey

	data. Conservation Biology 17:1724-1737. **Essay 1 first submission due**
17 M	Instructor-led Discussion: Bidartondo et al. 2002, Hibbett 2002. **Second reading selections due**
20 R	**Writing workshop 1a** Lauren, Daniel, Mika, Emily
24 M	**Writing workshop 1b** Kathy, Katy, Danielle, Sarah
27 R	Justin Golub: Gegear, R. J., M. C. Otterstatter, and J. D. Thomson. 2005. Does parasitic infection impair the ability of bumblebees to learn flower-handling techniques? Animal Behavior 70: 209-215.
31 M	Sarah Assefa: Heckman, D. S., D. M. Geiser, B. R. Eidell, R. L. Staufer, N. L. Kardos, and S. B. Hedges. 2001. Molecular evidence for early colonization of land by fungi and plants. Science 293: 1129-1133. **Essay 1 revision due**
Nov. 3 R	Lauren Jorgensen: Medel, R. 2001. Assessment of correlational selection on tolerance and resistance traits in a host plant-parasitic plant interaction. Evolutionary Ecology 15: 37-52.
7 M	Daniel Kousathanas:
10 R	Mika Kuwahara: Goffredi, S. K., V. J. Orphan, G. W. Rouse, L. Jahnke, T. Embaye, K. Turk, R. Lee, and R. C. Vrijenhoek. 2005. Evolutionary innovation: a bone-eating marine symbiosis. Environmental Microbiology 7: 1369-1378.
14 M	Emily Lescak: Pereira, E.S., Ferreira, R.L.M., Hamada, N., and Lichtwardt, R.W. 2005. Trichomycete fungi (Zygomycota) associated with mosquito larvae (Diptera: Culicidae) in natural and artificial habitats in Manaus, AM Brazil. Neotropical Entomology. 34: 325-329
17 R	Kathy Nguyen:Matsuura, K. 2005. Distribution of termite egg-mimicking fungi ("termite balls") in Reticulitermes spp. (Isotptera:Rhinotermitidae) nests in Japan and the United States. Appl. Entomol. Zool. 40: 53-61.
21 M	Katherine O'Brien: Zanette, L., E. Macdougal-Shackleton, M. Clinchy, and J. N. M. Smith. 2004. Brown-headed cowbirds skew host offspring sex ratios. Ecology 86: 815-820.
24 R	*Thanksgiving—No class*
28 M	Danielle Stehlik: Zanette, L., E. MacDougall-Shakleton, M. Clinchy, J. M. N. Smith. 2005. Brown-Headed Cowbirds Skew Host Offspring Sex Ratios. Ecology 86: 815-820. **Essay 2 first submission due**
Dec. 1 R	TBA
5 M	**Writing workshop 2a** Daniel, Mika, Kathy, Danielle
8 R	**Writing workshop 2b** (last day of classes) Lauren, Emily, Katy, Sarah

15 R	**Essay 2 revision due** (finals week)

Notes on Student-led Discussions

In each class period there will be one student who serves as the "Presenter" and another student who serves as the "Discussion Leader" (the latter selected by random sampling with replacement).

Responsibilities of the Presenter:

- Choose a topic for discussion, referring to the reserve text or other general materials at your disposal (other text books, accessible review articles, etc).
- Select one primary research paper for in-depth discussion. Please note that this may not be a paper that was assigned in another class, or any paper that was selected in a previous running of this course.
- Optionally, you may select some general background readings that will provide an introduction to the system that is the focus of the primary research paper.
- In class, provide a *brief* overview of the basic biology of the symbiosis. Talk about what organisms are involved and the nature of their interaction. You may wish to consider highlighting some of the parameters of symbioses that we discussed in the first lecture (i.e., number of partners, specificity of association, genetic diversity/sexuality of symbionts, obligate vs. facultative nature of association, mode of transmission of symbionts, etc). Use overheads and the board to make your points. *Do not review the primary research paper*. The goal of this presentation is to bring everyone up to speed on the basic biology of the chosen system, and prepare the class to discuss the paper(s).
- Scan the figures in the paper and paste them into a presentation (e.g., PowerPoint) or make overheads and bring them to class. Let me know well in advance if you will need a computer (I can bring my laptop).
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Responsibilities of the Discussion Leader:

- Give a *brief* summary of the objectives of the paper. What questions are being addressed? You may wish to state the title of the paper, and then decode it—what does the title mean? Did the paper actually do what the title implies?
- Resist the temptation to analyze the paper in detail—you are supposed to provide a platform for discussion, not give a monologue. However, you may wish to have some questions prepared or critical comments on specific aspects of the paper, which you could use to prod discussion.
- Talk about what aspects of the paper were confusing to you. If you disagree with the conclusions, or just aren't completely convinced, say so.

How to find candidate papers for discussion:

You should aim to identify a set of candidate papers on a specific topic, and then choose from among those papers the one paper that is best for an in-class discussion (the rest may be useful for your essays). So, how do you identify a general topic?

- Read in the reserve text or other general sources to find a subject (which could be based on a specific symbiosis, organism, or ecosystem) that interests you.
- Look for and read *review articles*, which summarize research in broad or narrow areas. Review papers are rich sources of literature citations.
- Once you have found a paper or topic of interest, use HighWire or Ingenta (or Science Citation Index at WPI or Holy Cross) to pick up the thread and find additional literature, including recent literature. You may find it useful to search by subject, author, or journal title. Remember, the Librarians are available to help you in these endeavors.
- After collecting a set of papers on a topic (for some subjects, there may be very few papers available), select the best one for class discussion (see below).

How to select an appropriate paper for discussion:
To determine if a paper is appropriate for our course, you need to consider whether the subject of the study is consistent with our course, and also whether the paper is going to be accessible to your classmates.

To determine if the subject of a paper is appropriate for our class, you must identify the central question that motivates the study (you should be able to do that by reading the Introduction). The following paragraphs describe some of the kinds of questions addressed in ecological and evolutionary studies of symbioses:

Ecological studies address questions about the interactions of organisms with each other and the abiotic environment. Ecological studies often address the biotic and abiotic factors that limit the ranges or habitats of individual species, or the factors that regulate the biological diversity of ecological communities. The field of molecular ecology uses molecular techniques to detect and identify symbiotic organisms, and characterize symbiotic communities.

Evolutionary studies address the origins of symbioses, as well as the history and mechanisms of changes in symbioses (including cospeciation, diversification, and shifts between parasitism and mutualism). Phylogenetic studies use evolutionary trees (most often derived from molecular characters) as tools to study the pathways of evolution leading to symbioses. "Microevolutionary" studies address processes of evolutionary change that occur within species or populations—intergrading with population genetics, and with applications in conservation biology.

To determine if a paper is going to be accessible to your classmates you simply have to read it yourself and decide if you can follow it. If so, it will be OK for your classmates. Realize that in almost every paper we read there will be sections that are challenging. It is fine to assign papers that use unfamiliar methods (e.g., phylogenetic methods or statistical analyses), as long as the purpose of the methods is clear. It is also reasonable to expect that we will have to do some background reading in textbooks to understand some papers fully.

Guidelines for Essays

The essays are an important part of this course and collectively are worth 40% of your grade. This document provides some suggestions for organizing your essays.

I expect these essays to be written as "mini-reviews", similar to articles in *Trends in Ecology and Evolution*, but shorter (see below). Rather than focusing on a single study, as we have been doing in class, you should pick an active area of research (i.e., one where there are multiple studies by different authors) and write a critical summary of its major issues. Below, I have some suggestions about how I might choose to structure this kind of paper, but this is not a formula that you must follow. There is no one "correct" way to write a mini-review. You should write this as you see fit.

The Introduction: If I were writing an essay for this class, I would begin with one or at most two introductory paragraphs that describe the system and the problems that it presents. If it is appropriate, I would explain the significance of this system to general issues in the study of symbioses (e.g., stability of mutualisms, specificity of parasitisms, etc.). I would tell the reader what kinds of organisms are involved, without relying solely on their scientific names (e.g., I would not assume that everyone knows that the Pterulaceae is a group of coral fungi), where they live, and what they do. If the organisms are economically or culturally important I might briefly mention that also. After reading my introduction, I would hope that the reader understands the major questions that the paper will address, and is convinced that the system is interesting and worthy of study.

The main body of the text: In the body of the paper, I would briefly recap the major research initiatives in the area, reviewing their successes and failures. Often, I would organize this section chronologically (i.e., citing the oldest studies first), but if I am reviewing a large number of different kinds of studies I might choose to organize this section according to the methods that were used. For example, I would divide my discussion into sections treating research in molecular phylogenetics, common garden experiments, anatomical studies, etc. I would talk in general terms about the methods that people have used to study the organisms, but I would not try to describe experimental procedures or data in detail—that is what the primary literature is for. Instead, I would emphasize general questions and major conclusions of prior studies. If possible, I would indicate connections between the studies, and I would certainly point out conflicting results. Nothing engages a reader like controversy.

Conclusions: In the concluding section of the paper I would aim to present a synthesis with a novel perspective regarding the state of the field. If appropriate, I might suggest new experimental approaches that could resolve remaining questions. Since this is a review, I might feel free to include some speculative comments that could suggest hypotheses to be addressed later, but I would be sure to label my speculations as such. If I had mentioned the relevance of the system to general questions regarding symbioses in my introduction, I might return to that topic here, addressing whether the work to date has succeeded in answering any of those general questions.

Title and headings: Choose your title carefully. It should be engaging and descriptive without being too long. Headings and subheadings are not required, but they can be very helpful to readers, and I recommend that you use them. Typical research papers have the major headings **Introduction, Materials and Methods, Results, Discussion**, and **Literature Cited**, but those would not be appropriate for your essays. Be creative in your use of headings and subheadings—for example, some could take the form of questions. Here is a possible title and set of headings and subheadings for an essay on evolution of mycorrhizal symbioses that also considers ecological and physiological observations:

Title: Host-Switching in Mycorrhizal Fungi: A Challenge to the Stability of Mutualisms?
Introduction—Patterns of Diversity in Mycorrhizal Symbioses
Prior Studies on Host-Fungus Associations in Mycorrhizae
Host Specificity in Mycorrhizal Basidiomycetes—Field Observations
Plant-Specific Responses to Mycorrhizal Symbionts
Molecular Phylogenetic Studies—How Common is Host Switching?
Conclusions and Future Directions

This is a cooked-up example, but I hope it shows that you can imply the logical structure and flow of your paper from the title and headings alone. A reader who skims the title and headings before reading your text would already have a framework in mind for organizing the information that you will present.

References: A high quality bibliography is expected, but you should not attempt to cite every article on your chosen topic. Instead, you should cite the landmark papers that stake out major points of view. Your reference list should contain mostly peer-reviewed primary research papers, but may also include review articles, books, and chapters in edited volumes. Do not cite internet sources unless they are peer-reviewed and archived. Cite works in the text in the format Author (date) and list references alphabetically by author in a Literature Cited section following the text. Do not use footnotes. Direct quotations of more than a few words are not permitted.

Illustrations and tables: These are not required and in most cases should be avoided.

Length: Up to ten pages, excluding references. I expect that most essays will be eight to ten pages long.

Target audience (very important!): You should write your paper with your classmates in mind—after all, they will be reading (but not grading!) your essay. Therefore, you should think about what makes a paper enjoyable to you. What kinds of information do you look for when you read a paper? What kinds of topics interest you? If you write a paper that you would enjoy reading, then your peers will probably enjoy it also. You should avoid unnecessary technical jargon, define essential scientific terms, and clearly describe experimental methods. However, you don't need to define terms like "natural selection", "ribosome", or "phylogeny".