ECOLOGY AND EVOLUTIONARY BIOLOGY

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The Department of Ecology and Evolutionary Biology (EEB) offers broad education in the biological sciences. The subject matter includes molecules, cells, organs, organisms, and ecosystems and the evolutionary processes that shape them. The department offers a B.A. and a B.S. degree. The B.A. program is intended for students who are interested in ecology, evolution, and organismal diversity as part of a liberal education but do not intend to pursue graduate work in the discipline. The B.S. program is designed for students planning to attend medical or veterinary school or to pursue graduate study in ecology and evolutionary biology, other biological disciplines, or the environmental sciences. The two programs share the same prerequisites and core requirements but differ in their electives and senior requirements.

Students majoring in EEB select one of two tracks. The requirements for track 1 emphasize courses appropriate for careers in ecology, evolutionary biology, and environmental science; track 2 is most appropriate for premedical and pre-veterinary students because it allows them to use as electives many courses required by medical schools. The EEB major offers opportunities for independent research in both laboratory-based and field-based scientific investigations.

COURSES FOR NONMAJORS

Several EEB courses have no college-level prerequisites and are suitable for nonmajors. These include all 100-level offerings as well as 200-level courses that deal with particular organism groups such as plants, fish, mammals, birds, or insects.

PREREQUISITES

The prerequisites for the major are intended to provide core scientific literacy; they include courses in biology, chemistry, physics, and mathematics. The introductory biology sequence BIOL 101, 102, 103, and 104 is required. Also required are a two-term lecture sequence in general chemistry, CHEM 161, 165 or CHEM 163, 167, taken with associated laboratories, CHEM 134L and 136L, and one term of organic chemistry, CHEM 174 or 175, or CHEM 220 or 221, with associated laboratories, CHEM 222L or 223L. Optionally, CHEM 174, 175, taken with CHEM 222L, 223L, satisfies the chemistry requirement. Two terms of physics are required, PHYS 170, 171 or higher, and one term of mathematics, MATH 115 or higher (not MATH 190), or S&DS 101-106. A different statistics course approved by the director of undergraduate studies may be substituted for the mathematics prerequisite.

A new online program, ONEYS, for Physics, will be offered in the summer by the Mathematics and Physics departments and by the Center for Teaching and Learning, to review math skills needed in preparation for introductory physics courses.

Acceleration credit awarded in chemistry, mathematics, and physics, or completion of advanced courses in those departments, may be accepted in place of the corresponding prerequisites for the EEB major. Students who have mathematics preparation equivalent to MATH 115 or higher are encouraged to take a statistics course (most often STAT 101-106) and/or additional mathematics courses such as MATH 120, 121, 222, or 225. Because chemistry courses are prerequisite to several EEB courses, students are strongly urged to take general and organic chemistry in the first and sophomore years. Students who place out of general chemistry should take organic chemistry during their first year. Finishing the prerequisites early allows for a more flexible program in later years.

PLACEMENT PROCEDURES

Students can place out of the introductory biology sequence (BIOL 101, 102, 103, 104) only by means of the biology placement examination administered jointly by the biological science departments, EEB, MB&B, and MCDB.

Potential EEB majors are expected to take the mathematics placement test. Those who place above the level of MATH 112 may proceed to prerequisite courses for the EEB major; those who place into MATH 112 must take calculus before other prerequisites.

For information about placement examinations, refer to the Calendar for the Opening Days of College and the First-Year Website. The Chemistry department arranges placement in chemistry courses.

REQUIREMENTS OF THE MAJOR

B.A. degree program Beyond the prerequisites, the B.A. requires three lecture courses and one laboratory, for three and one-half course credits, and the senior requirement. In track 1, the required courses are E&EB 220, 225, and a lecture course on organismal diversity chosen from E&EB 246–272, along with its associated laboratory. Required courses in track 2 include E&EB 290, E&EB 295 or BENG 350, MCDB 300; and E&EB 291L.

B.S. degree program The B.S. requirements are the same as those for the B.A., with the addition of at least two electives, for two course credits, in either track 1 or track 2. At least one of the electives must be a lecture or a seminar. Most EEB, MCDB, or MB&B courses numbered 200 or above qualify as electives, as do most research courses and laboratories in a biological sciences department or in the Yale School of Medicine. Courses from other departments may qualify with permission of the director of undergraduate studies (DUS).

Substitutions permitted Two upper-level courses in Geology and Geophysics (excluding paleobiology courses), Mathematics, Computer Science, or Engineering and Applied Science can be substituted for the required term of organic chemistry and laboratory. A second term of organic chemistry and laboratory and up to two terms of physics laboratories are allowed as electives. Courses from other departments
may also be suitable as electives. All substitutions require the permission of the DUS. College seminars may not be counted toward the requirements of the major.

**Limit on research courses** While independent research courses may be taken multiple times for credit, there are restrictions on the number of such courses that can be included in a student's curriculum. See Course Credits and Course Loads in the Academic Regulations. Interested sophomores and juniors can take E&EB 469 and E&EB 474.

**Credit/D/Fail** No course taken Credit/D/Fail may be counted toward the EEB major, including prerequisites.

**Roadmap** See visual roadmap of the requirements.

### SENIOR REQUIREMENT

**B.A. degree program** Students in the B.A. degree program fulfill the senior requirement either by completing one term of independent study in E&EB 470 or by writing a senior essay. The senior essay may be related to the subject matter of a course, but the senior essay is a separate departmental requirement in addition to any work done in a course and does not count toward the grade in any course. Students intending to write a senior essay must obtain an approval form from the office of the director of undergraduate studies and have it signed by the senior essay adviser before the end of the course selection period. Senior essays must be submitted to the DUS by the last day of classes.

**B.S. degree program** Students in the B.S. degree program fulfill the senior requirement by completing one term of original research in E&EB 475, 476, 495, or 496.

### ADVISING

First-year students considering a major in Ecology and Evolutionary Biology are invited to consult with the DUS. After the first year, students should choose an adviser from the department faculty who has interests comparable to their own and/or is a fellow of their residential college. For additional information, visit the EEB Website. Students in EEB should consult one of the advisers assigned to their class (see below). The course schedules of all EEB majors (including sophomores intending to major in EEB) must be signed by a faculty member in EEB; the signature of the DUS is not required. Students whose regular adviser is on leave can consult the DUS to arrange for an alternate.

Class of 2019: Casey Dunn, OML 326 (432-3109); Erika Edwards, OML 326 (432-3869)

Class of 2020: Carla Staver, OML 404 (436-9200); Alavaro Sanchez, OML 327C (432-6778)

Class of 2021: Adalgisa Caccone, ESC 140 (432-5259); Marta Wells, OML 103 (432-6294)

Class of 2022: Marta Wells, OML 103 (432-6294)

**Graduate courses of interest to undergraduates** Graduate courses in the biological and biomedical sciences that may be of interest to undergraduates are listed in the Graduate School's online bulletin, and many are posted on the Biological and Biomedical Sciences Website. Additional information is available from the DUS and the director of graduate studies. Undergraduates with an appropriate background may enroll with the permission of the director of graduate studies and the instructor.

### STUDY ABROAD

Participation in study abroad field programs is encouraged. Credit for such programs may apply toward the major; interested students should consult the DUS prior to going abroad.

### REQUIREMENTS OF THE MAJOR

**Prerequisites** Introductory biology sequence (BIOL 101, 102, 103, 104); 2-term general chemistry lecture sequence (CHEM 161, 165 or CHEM 163, 167) with labs (CHEM 134L, 136L); 1 term of organic chemistry (CHEM 174 or 175, or CHEM 220 or 221) with labs (CHEM 222L or 223L); CHEM 174, 175 taken with CHEM 222L, 223L satisfies both chemistry requirements; 2 terms of physics (PHYS 170, 171 or higher); 1 term of MATH 115 or higher (not MATH 190) or S&DS 101–106

**Number of courses**

- **B.A.** — 3½ course credits beyond prereqs (not incl senior req)
- **B.S.** — 5½ course credits beyond prereqs (not incl senior req)

**Specific courses required**

- **Track 1** — E&EB 220, 225; 1 from E&EB 246–272, with lab; **Track 2** — E&EB 290, E&EB 295 or BENG 350, MCB 300; and E&EB 291L

**Distribution of courses**

- B.S. — 2 electives as specified

**Substitutions permitted** With DUS permission: other stat course for math or stat prereq; two upper-level courses in G&G, MATH, CPSC, or ENAS for organic chemistry and lab; the second term of organic chemistry and lab and two physics labs for electives

**Senior requirement**

- **B.A.** — E&EB 470 or senior essay
- **B.S.** — at least one term of E&EB 475, 476, 495, or 496

### FACULTY OF THE DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

**Professors**

†Richard Bribiescas, †Nicholas Christakis, Michael Donoghue, Casey Dunn, Erika Edwards, †Alison Galvani, †Vivian Irish, Walter Jetz, Thomas Near, David Post, Jeffrey Powell, Richard Prum, †Eric Sargis, †Oswald Schmitz, †David Skelly, Stephen Stearns, Paul Turner, †J. Rimas Vaišnys, Günter Wagner (Interim Chair)
Associate Professors †Forrest Crawford, †James Noonan, †Jeffrey Townsend, David Vasseur
Assistant Professors †Craig Brodersen, †Liza Comita, Alvaro Sanchez, Carla Staver
Senior Lecturer Marta Martínez Wells
Lecturers Adalgisa Caccone, Linda Puth
†A joint appointment with primary affiliation in another department or school.

Introductory Courses

[ E&EB 050, The Evolution of Beauty ]

* E&EB 106a / HLTH 155a / MCDB 106a, Biology of Malaria, Lyme, and Other Vector-Borne Diseases Alexia Belperron
Introduction to the biology of pathogen transmission from one organism to another by insects; special focus on malaria, dengue, and Lyme disease. Biology of the pathogens including modes of transmission, establishment of infection, and immune responses; the challenges associated with vector control, prevention, development of vaccines, and treatments. Intended for non–science majors; preference to freshmen and sophomores. Prerequisite: high school biology. sc

E&EB 115a / F&ES 315a, Conservation Biology Linda Puth
An introduction to ecological and evolutionary principles underpinning efforts to conserve Earth’s biodiversity. Efforts to halt the rapid increase in disappearance of both plants and animals. Discussion of sociological and economic issues. sc

* E&EB 126b / G&G 126b, History of Life Derek Briggs, Pincelli Hull, and Bhart-Anjan Bhullar
Examination of fossil and geologic evidence pertaining to the origin, evolution, and history of life on Earth. Emphasis on major events in the history of life, on what the fossil record reveals about the evolutionary process, on the diversity of ancient and living organisms, and on the evolutionary impact of Earth’s changing environment. sc

* E&EB 145b, Plants and People Linda Puth
The interaction of plants and people throughout history explored from biological, historical, anthropological, and artistic perspectives. Basic botany; plants in the context of agriculture; plants as instruments of trade and societal change; plants as inspiration; plants in the environment. Includes field trips to the greenhouses at Yale Marsh Botanical Garden, the Yale Peabody Museum and Herbarium, the Yale Farm, and the Yale Art Gallery. sc

* E&EB 175Lb, Virus Discovery and Evolution Alita Burmeister
An inquiry-based, hands-on introduction to sampling bacteriophages (bacteria-specific viruses) from natural environments. Emphasis on lab methods to characterize viruses via growth assays and genome sequencing, and to experimentally evolve viruses on bacteria. Readings and discussion on virus biodiversity, role of viruses in the environment, and virus applications to solve human problems. sc ½ Course cr

[ E&EB 190, The Evolution of Beauty ]

E&EB 210a / S&DS 101a, Introduction to Statistics: Life Sciences Jonathan Reuning-Scherer and Walter Jetz
Statistical and probabilistic analysis of biological problems, presented with a unified foundation in basic statistical theory. Problems are drawn from genetics, ecology, epidemiology, and bioinformatics. qr

E&EB 246a, Plant Diversity and Evolution Michael Donoghue
Introduction to the major plant groups and their evolutionary relationships, with an emphasis on the diversification and global importance of flowering plants. To be taken concurrently with E&EB 247L. Prerequisite: a general understanding of biology and evolution. sc

E&EB 247La, Laboratory for Plant Diversity and Evolution Michael Donoghue
Hands-on experience with the plant groups examined in the accompanying lectures. Local field trips. To be taken concurrently with E&EB 246. sc ½ Course cr

E&EB 250a, Biology of Terrestrial Arthropods Marta Wells
Evolutionary history and diversity of terrestrial arthropods (body plan, phylogenetic relationships, fossil record); physiology and functional morphology (water relations, thermoregulation, energetics of flying and singing); reproduction (biology of reproduction, life cycles, metamorphosis, parental care); behavior (migration, communication, mating systems, evolution of sociality); ecology (parasitism, mutualism, predator-prey interactions, competition, plant-insect interactions). To be taken concurrently with E&EB 251L. sc

E&EB 251La, Laboratory for Biology of Terrestrial Arthropods Marta Wells
Comparative anatomy, dissections, identification, and classification of terrestrial arthropods; specimen collection; field trips. Concurrently with or after E&EB 250. sc ½ Course cr

E&EB 264a, Ichthyology Richard Harrington
A survey of fish diversity, including jawless vertebrates, chimaeras and sharks, lungfishes, and ray-finned fishes. Topics include the evolutionary origin of vertebrates, the fossil record of fishes, evolutionary diversification of major extant fish lineages, biogeography, ecology, and reproductive strategies of fishes. sc
E&EB 265La, Laboratory for Ichthyology  Richard Harrington
Laboratory and field studies of fish diversity, form, function, behavior, and classification. The course primarily involves study of museum specimens and of living and fossil fishes. Concurrently with E&EB 264. sc ½ Course cr

* E&EB 272b, Ornithology  Richard Prum
An overview of avian biology and evolution, including the structure, function, behavior, and diversity of birds. The evolutionary origin of birds, avian phylogeny, anatomy, physiology, neurobiology, breeding systems, and biogeography. Enrollment limited to 50. sc

* E&EB 273Lb, Laboratory for Ornithology  Richard Prum
Laboratory and field studies of avian morphology, diversity, phylogeny, classification, identification, and behavior. Enrollment limited to 12. sc ½ Course cr

Intermediate and Advanced Courses
Prerequisites for all intermediate and advanced E&EB courses are BIOL 101, 102, 103, and 104, or permission of the instructor.

E&EB 220a / EVST 223a, General Ecology  David Vasseur and Ann Staver
The theory and practice of ecology, including the ecology of individuals, population dynamics and regulation, community structure, ecosystem function, and ecological interactions at broad spatial and temporal scales. Topics such as climate change, fisheries management, and infectious diseases are placed in an ecological context. Prerequisite: MATH 112 or equivalent. sc

E&EB 223Lb, Evolution, Functional Traits, and the Tree of Life  Marta Wells
Study of evolutionary novelties, their functional morphology, and their role in the diversity of life. Introduction to techniques used for studying the diversity of animal body plans. Evolutionary innovations that have allowed groups of organisms to increase their diversity. sc ½ Course cr

E&EB 226b, Evolutionary Biology  Alvaro Sanchez De Andres and Jeffrey Powell
An overview of evolutionary biology as the discipline uniting all of the life sciences. Reading and discussion of scientific papers to explore the dynamic aspects of evolutionary biology. Principles of population genetics, paleontology, and systematics; application of evolutionary thinking in disciplines such as developmental biology, ecology, microbiology, molecular biology, and human medicine. sc

* E&EB 230a / EVST 221a / F&ES 221a, Field Ecology  Linda Puth
A field-based introduction to ecological research, using experimental and descriptive approaches, comparative analysis, and modeling for field and small-group projects. Weekly field trips explore local lake, salt marsh, rocky intertidal, traprock ridge, and upland forest ecosystems. Includes one Saturday field trip and a three-day trip during the October recess. Concurrently with or after E&EB 220 or with permission of instructor. sc

* E&EB 235a / HLTH 250a, Evolution and Medicine  Stephen Stearns
Introduction to the ways in which evolutionary science informs medical research and clinical practice. Diseases of civilization and their relation to humans’ evolutionary past; the evolution of human defense mechanisms; antibiotic resistance and virulence in pathogens; cancer as an evolutionary process. Students view course lectures on line; class time focuses on discussion of lecture topics and research papers. Prerequisite: BIOL 101–104. wr, sc

E&EB 255a / G&G 316, Invertebrates  Casey Dunn
An overview of animal diversity that explores themes including animal phylogenetics (evolutionary relationships), comparative studies of evolutionary patterns across species, organism structure and function, and the interaction of organisms with their environments. Most animal lineages are marine invertebrates, so marine invertebrates are the focus of most of the course. This lecture must be taken concurrently with the lab E&EB 256L. sc

E&EB 256La, Laboratory for Invertebrates  Casey Dunn
The study of invertebrate anatomy and diversity in a laboratory and field setting. Activities will include will examine live animals and museum specimens, as well as local field trips. Some field trips will fall on weekends. This lab must be taken concurrently with the lecture E&EB 255. sc ½ Course cr

[ E&EB 275, Biological Oceanography ]
[ E&EB 280, Mammalogy ]

E&EB 290b, Comparative Developmental Anatomy of Vertebrates  Günter Wagner
A survey of the development, structure, and evolution of major vertebrate groups. Topics include the micro-anatomy of major organ systems, the developmental underpinnings of the vertebrate body plan, and the development, structure, and evolution of the major organ systems such as the locomotory system, sensory organs, digestive tract, reproductive tract, and nervous system. sc

* E&EB 291Lb, Comparative Anatomy of Vertebrates Laboratory  Staff
Microscopic examination of histological and embryological preparations. Dissection of selected vertebrate species including shark, bony fish, frog, lizard, and rat. To be taken with E&EB 290. sc ½ Course cr

E&EB 300a / ANTH 300a / EVST 182a, Primate Behavior and Ecology  Eduardo Fernandez-Duque
Socioculture of primates compared with that of other mammals, emphasizing both general principles and unique primate characteristics. Topics include life-history strategies, feeding ecology, mating systems, and ecological influences on social organization. sc, so
[ E&EB 310, Evolutionary Systems Biology ]

[ E&EB 320, Advanced Ecology ]

E&EB 326b, Plant Structure and Function  Erika Edwards
The primary aim of this course is to examine the relationship between the structure of plants and their physiological systems, and the role of the environment in shaping the evolution and diversity of vascular plants. Lectures focus on exploring the basics of plant morphology, and the anatomical and physiological adaptations of leaves, stems, and roots to different habitats. A comparative, phylogenetic approach is emphasized. Students work on a set of group projects that are designed to test long-standing assumptions about the evolution and adaptive nature of certain plant traits. Projects differ from year to year, and although the general theme is chosen by the professor, students are expected to play a large role in experimental design and focus. Students leave the class with a solid foundation both in plant anatomy and eco-physiology and in applying a phylogenetic comparative approach to studies of organismal biology. Furthermore, they gather first hand experience in data collection, experimental design, data analysis, and the collaborative presentation of a scientific study. Students must also enroll in E&EB 327L as a co-requisite. Prerequisite: E&EB 246 and BIOL 104, or permission of the instructor.

* E&EB 342b / ANTH 335b, Primate Diversity and Evolution  Eric Sargis
The diversity and evolutionary history of living and extinct primates. Focus on major controversies in primate systematics and evolution, including the origins and relationships of several groups. Consideration of both morphological and molecular studies. Morphological diversity and adaptations explored through museum specimens and fossil casts. Recommended preparation: ANTH 116 or BIOL 104.

* E&EB 336b / HSHM 453b / HUMS 336b, Culture and Human Evolution  Gary Tomlinson
Examination of the origins of human modernity in the light of evolutionary and archaeological evidence. Understanding, through a merger of evolutionary reasoning with humanistic theory, the impact of human culture on natural selection across the last 250,000 years.

E&EB 380b, Life History Evolution  Stephen Stearns
Life history evolution studies how the phenotypic traits directly involved in reproductive success are shaped by evolution to solve ecological problems. The intimate interplay between evolution and ecology. After E&EB 220 and 225, or with permission of instructor.

E&EB 428a / AMTH 428a / G&G 428a / PHYS 428a, Science of Complex Systems  Jun Korenaga
Introduction to the quantitative analysis of systems with many degrees of freedom. Fundamental components in the science of complex systems, including how to simulate complex systems, how to analyze model behaviors, and how to validate models using observations. Topics include cellular automata, bifurcation theory, deterministic chaos, self-organized criticality, renormalization, and inverse theory. Prerequisite: PHYS 301, MATH 247, or equivalent.

E&EB 464b / ANTH 464b / ARCG 464b, Human Osteology  Eric Sargis
A lecture and laboratory course focusing on the characteristics of the human skeleton and its use in studies of functional morphology, paleodemography, and paleopathology. Laboratories familiarize students with skeletal parts; lectures focus on the nature of bone tissue, its biomechanical modification, sexing, aging, and interpretation of lesions.

E&EB 469a or b, Tutorial  Marta Wells
Individual or small-group study for qualified students who wish to investigate an area of ecology or evolutionary biology not presently covered by regular courses. A student must be sponsored by a faculty member who sets requirements and meets weekly with the student. One or more written examinations and/or a term paper are required. To register, the student must submit a written plan of study approved by the faculty instructor to the director of undergraduate studies. Students are encouraged to apply during the term preceding the tutorial. Proposals must be submitted no later than the first day of the second week of the term in which the student enrolls in the tutorial. The final paper is due in the hands of the director of undergraduate studies by the last day of reading period in the term of enrollment. In special cases, with approval of the director of undergraduate studies, this course may be elected for more than one term, but only one term may be counted as an elective toward the requirements of the major. Normally, faculty sponsors must be members of the EEB department.

E&EB 470a or b, Senior Tutorial  Marta Wells
Tutorial for seniors in the B.A. degree program who elect a term of independent study to complete the senior requirement. A thesis, fifteen to twenty pages in length, is required. A student must be sponsored by a faculty member who sets requirements and meets weekly with the student. To register, the student must submit a written plan of study approved by the faculty instructor to the director of undergraduate studies. Students are encouraged to apply during the term preceding the tutorial. Proposals must be submitted no later than the first day of the second week of the term in which the student enrolls in the tutorial. The final paper is due in the hands of the director of undergraduate studies by the last day of reading period in the term of enrollment. Normally, faculty sponsors must be members of the EEB department. Enrollment limited to seniors. Fulfills the senior requirement for the B.A. degree.

E&EB 474a or b, Research  Marta Wells
One term of original research in an area relevant to ecology or evolutionary biology. This may involve, for example, laboratory work, fieldwork, or mathematical or computer modeling. Students may also work in areas related to environmental biology such as policy, economics, or ethics. The research project may not be a review of relevant literature but must be original. In all cases students must have a faculty sponsor who oversees the research and is responsible for the rigor of the project. Students are expected to spend ten hours per
week on their research projects. Using the form available from the office of undergraduate studies or from the Canvas, students must submit a research proposal that has been approved by the faculty sponsor to the director of undergraduate studies, preferably during the term preceding the research. Proposals are due no later than the first day of the second week of the term in which the student enrolls in the course. The final research paper is due in the hands of the director of undergraduate studies by the last day of reading period in the term of enrollment.

* E&EB 475a and E&EB 476b, Senior Research  
Marta Wells
One term of original research in an area relevant to ecology or evolutionary biology. This may involve, for example, laboratory work, fieldwork, or mathematical or computer modeling. Students may also work in areas related to environmental biology such as policy, economics, or ethics. The research project may not be a review of relevant literature but must be original. In all cases students must have a faculty sponsor who oversees the research and is responsible for the rigor of the project. Students are expected to spend ten hours per week on their research projects. Using the form available from the office of undergraduate studies or from the Canvas, students must submit a research proposal that has been approved by the faculty sponsor to the director of undergraduate studies, preferably during the term preceding the research. Proposals are due no later than the first day of the second week of the term in which the student enrolls in the course. The final research paper is due in the hands of the director of undergraduate studies by the last day of classes in the term of enrollment. Fulfills the senior requirement for the B.S. degree. Enrollment limited to seniors.

* E&EB 495a and E&EB 496b, Intensive Senior Research  
Marta Wells
One term of intensive original research during the senior year under the sponsorship of a Yale faculty member. Similar to other research courses except that a more substantial portion of a student's time and effort should be spent on the research project (a minimum average of twenty hours per week). A research proposal approved by the sponsoring faculty member must be submitted to the director of undergraduate studies; forms are available from the office of undergraduate studies. For research in the fall term, approval is encouraged during the spring term of the junior year. Proposals are due no later than the first day of the second week of the term in which the student enrolls in the course. The final research paper is due in the hands of the director of undergraduate studies by the last day of reading period in the term of enrollment. One term of intensive research fulfills a portion of the senior requirement for the B.S. degree. 2 Course cr per term.