

Syllabus for  
BIOL 4203/5501 – Evolution of Sex – Fall 2014

Root Gorelick

University Centre 280

Monday/Wednesday 1:05 – 2:25 pm

Contact Information and Office Hours

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E-mail – Use CULearn e-mail (your e-mails may get lost in my other e-mail accounts)

Office Hours – Monday and Wednesday 10:10 – 11:00 am (or by appointment)

Office – 4625 CTTC (just south of the gym and child care)

TA: Mary Daniel

Preamble

This course addresses many areas of evolution of sex, including evolution of meiosis and sex determination. Genetics clearly underlies meiosis, sex determination, and other aspects of sex. However, sex is clearly also an organismal phenomenon that is idiosyncratic enough that an evolutionary perspective is needed to truly understand what sex is and does.

We all have a notion of what sex is. Some of us study it. Many of us engage in it. Yet the distinction between what is and what is not sex can be a slippery slope. Remember Bill Clinton and Monica Lewinsky? Remember the legal case surrounding Little Sister's Bookstore? These two questions go to the legal definitions of sex. By contrast, in this course, we will examine the equally elusive evolutionary definitions of eukaryotic sex, which also appears in evolutionary sociology. Many interesting and inextricably-related questions arise:

- What is sex? Why is it so pervasive?
- Why is the two-fold cost of sex a Trojan horse?
- What was/is the original and current functions of sex?
- Does sex with oneself count as sex? Why does automixis not refer to a hybrid SUV?
- What determines sex? Who can change sex? Do sex chromosomes inhibit sex change?
- What's the difference between sex and gender? Why is it possible being transgendered?
- Does sex rejuvenate? What is the relationship between sex, death, and development?
- Why does sex still persist after roughly 1-2 billion years?
- Why are haploids usually male in haplo-diploid insects and mites?
- Are there differences between females and males? Are they sociological constructs?
- Does sex have anything to do with chromosomes or hormones?
- Who has sex? What is an individual? Which individuals are sexual?

Being that sex is so pervasive, we need to better understand what it is, how it functions, and how it evolved. This course will supply you with a fundamental evolutionary understanding of sex. We will try to answer the above questions, as well as understand what the current open problems are in the field.

“The *way* we approach the challenge of learning will shape us as much as *what* we seek to learn.”  
(Taiaiake Alfred 2005; italics in original)

## Details

This will be a seminar course on the evolution of eukaryotic sex (prokaryotic sex is completely different beast with two backs). You will be expected to thoroughly read and understand the papers each week. You will be expected to participate enthusiastically and insightfully in our weekly class discussions. You will get chalk on your hands. We will cover material for which nobody yet knows the answers, so don't be shy. Despite the fact that some papers are old, these are all still active research areas.

We will cover two broad, yet very distinct topics in evolution of sex (1) meiosis and karyogamy and (2) the distinction between females and males, followed by (3) a trio of miscellaneous sexual topics. While the first third may seem more in keeping with a traditional biology course, the second two-thirds will undoubtedly be more memorable and will almost certainly forever change your views of sex.

During the first third of the term we will tackle the cellular/subcellular aspects of sex, namely meiosis and karyogamy. We will begin with an historical overview (last 175 years), followed by evolutionary history of putative early forms of meiosis. This will devolve into discussion of what exactly is sex, what are the functions of sex, why is sex maintained and so ubiquitous.

During the second third of the term we will tackle a very different topic, namely how the differences between females and males evolved. We will start by asking whether or why there are more than two sexes. Next, we will discuss the female-male dichotomy, which I ultimately argue is a false dichotomy. There is a continuum between females and males in virtually all species, including humans!

During the final third of the course we will cover a suite of topics that do not necessarily fit in with the rest of the course, but are nonetheless interesting active areas of current research: orgasm, sexual selection, and individuality.

### 1. Meiosis & Karyogamy

08 Sept	Intro & History	Meirmans (2009)
15 Sept	Early evolution	Cleveland (1947), Boyden (1950)
22 Sept	Automixis	Gorelick & Carpinone (2009)
29 Sept	Multicellularity	Niklas <i>et al</i> (2014)
06 Oct	Functions of sex	Gorelick & Heng (2011)

### 2. Female-Male Difference

15 Oct	Phalluses	Fausto-Sterling (2000)
20 Oct	Trans-sex	Hird (2006)
03 Nov	Gyno/Andro-genesis	Normark (2009)
10 Nov	Female vs male	Gorelick (2012 <i>BioScience</i> ) Gorelick, Carpinone, Derraugh (2013)

### 3. *Ménage à trois*

17 Nov	Orgasm	Symons (1979), Darling (1937)
24 Nov	Sex & individuality	Gorelick (2012 <i>Biology &amp; Philosophy</i> )
01 Dec	Sexual selection	Gorelick, Derraugh, Carpinone, Bertram (2011)

### 4. Graduate student presentations

08 December

10 September

Meirmans S. (2009) The evolution of the problem of sex. In *Lost sex: the evolutionary biology of parthenogenesis* (editors: Schön, Martens, van Dijk) Springer. Pages 21-46.

15 September

- a. Cleveland L (1947) The origin and evolution of meiosis. *Science* 105: 287-289.
- b. Boyden A (1950) Is parthenogenesis sexual or asexual reproduction? *Nature* 166: 820.

22 September

Gorelick R, Carpinone J (2009) Origin of sex: the evolutionary joys of self sex. *Biological Journal of the Linnean Society* 98: 707-728.

29 September

Niklas KJ, Cobb ED, Kutschera U (2014) Did meiosis evolve before sex and the evolution of eukaryotic lifecycles? *BioEssays* 36: in press. DOI 10.1002/bies.201400045.

6 October

Gorelick R, Heng H (2011) Sex reduces genetic variation: a multidisciplinary review. *Evolution* 65: 1088-1098.

13 October

Fausto-Sterling A (2000) Of gender and genitals: the use and abuse of the modern intersexual. In *Sexing the body: gender politics and the construction of sexuality*. Fausto-Sterling. Basic Books. Pages. 45-77.

20 October

Hird M (2006) Animal transex. *Australian Feminist Studies* 21: 35-50.

3 November

Normark B (2009) Unusual gametic and genetic systems. In *Sperm biology: an evolutionary perspective* (editors: Birkhead, Hosken, Pitnick). Academic Press. Pages 507-538.

10 November

- a. Gorelick R (2012) Meiosis is not gender neutral. *BioScience* 62: 623-624.
- b. Gorelick R, Carpinone J, Derraugh L (2013) Fundamental differences between females and males? In *Challenging popular myths, of sex, gender, and biology* (editor: Ah-King). Springer. Pages 9-22.

17 November

- a. Darling F (1937) *A herd of red deer: A study in animal behavior*. Oxford University Press. [we will only read pp. 168-173, 182-183]
- b. Symons D (1979) The female orgasm: Adaptation or artifact? In *The evolution of sexuality*. Don Symons. Oxford University Press. Pages 75-95.

24 November

Gorelick R (2012) Mitosis circumscribes individuals; sex creates new individuals. *Biology & Philosophy* 27: 871-890.

1 December

Gorelick R, Derraugh L, Carpinone J, Bertram S. Post-plasmogamic pre-karyogamic sexual selection: mate choice inside an egg cell. *Ideas in Ecology & Evolution* 4: 14-23.

Grades (undergraduate only)

- 40% Participation
- 40% Quizzes/Assignments
- 20% Final Paper/Outline

Except for the first day, you will be marked on your participation. Your four lowest of two-dozen participation marks (which could be zero, in case of absence) will be dropped and the twenty highest participation marks retained. Each day's maximum participation mark will be 2 points. ( $20 \times 2\% = 40\%$ )

During all but the first and last week, you will either have an in-class quiz at the beginning of class or have a short writing assignment to hand in. There will be no make-up quizzes. All assignments must be handed in no later than the start of the class on which it is due. Half credit will be deducted if the paper is between 1 and 24 hours late. No credit will be given after that first day. Your two lowest quiz/assignment scores will be dropped and the eight highest scores retained. Each week's maximum quiz/assignment mark will be 5 points. ( $8 \times 5\% = 40\%$ )

On or before 26 November 2014, you are required to hand in a review paper or research paper about evolution of sex. On or before 15 October 2014, you are required to hand me a title and abstract/outline of your planned paper. I will provide you approval and/or feedback the next week, including whether the topic is reasonable and feasible. Start thinking about this now. At no penalty, you are welcome to hand in polished versions early for further feedback. The title/abstract/outline will be worth a maximum of 5 points, while the final paper will be worth a maximum of 15 points. ( $5\% + 15\% = 20\%$ ).

Assignments may be different for undergraduates and graduates. Expectations will be higher for graduate students on assignments and especially the final paper.

For Graduate Students only

Each graduate student will be assigned one week when they are responsible for leading the discussion. You should not only be ready to answer all questions, but be ready to facilitate the discussion with leading questions.

Grades (grad students only)

- 30% Participation (I will pro-rate your scores from 40 to 30 for the term)
- 30% Quizzes/Assignments
- 20% Final Paper/Outline
- 10% Leading discussions
- 10% Presentation of final paper

On the last day of class, 8 December 2014, graduate students will be required to present the findings from their final paper to the class. This could be in the form of a powerpoint presentation, debate, etc.

Deadlines and rules for the final paper, outline, quizzes and assignments will be the same for graduate students as for undergraduates. See the previous page for details.

## Structure of Classes

1. Each week will begin with a quiz or handing in of an assignment, immediately followed by a short conversation about the quiz or assignment.
2. The majority of each class will be an open discussion of the assigned paper(s). At first, I will lead the discussion. However, after the first three weeks, I expect that I will facilitate, but not lead, the discussion. Thus it is incumbent on you to not only understand the papers, but to also have a list of comments and questions prepared. In fact, I encourage you to write down this list and read from it if you want.

Depending upon enrolment, we may split up into smaller groups for discussion. **If weather is decent, we may move to the outdoors.** Thus, if you arrive late, you will have to find us. If you are someone who tends to be late, it may help to get the cellphone number of a colleague whose is punctual, so that you can find our location.

## Final Paper

The final paper can be on any subject of your choosing so long as it relates to the evolution of eukaryotic sex. The most important aspect of the paper is couching an interesting and tractable causal question. The paper should be an original synthesis of existing literature, with the goal that you could submit the paper for possible publication. Admittedly, I hope, but do not necessarily expect, that many of you will achieve this goal of publishing the final paper. At a minimum, I will be looking for the following items in your paper:

- Are causal questions and hypotheses clearly stated?
- Are the hypotheses your own or someone else's?
- Have the hypotheses been tested or are they testable? How?
- Attention to detail in scouring and citing the literature
- Ability to put your ideas on top of what you read (synthesis)
- Coherent writing, plus use of spelling and grammar checking

Half of the way through the term on 15 October 2014, you be will required to submit a proposal or outline and/or abstract for your final paper. This gives me the opportunity to provide you with one or more rounds of feedback before you proceed. Remember, the more details you provide, the more feedback you will get from me. This should translate into a better paper.

If the final paper is handed in late (i.e. after 26 November 2014), I shall deduct 20% per day. The same applies to the outline/abstract due on 15 October 2014. For the final paper, you will be required to hand in both a paper copy and an electronic version as an e-mail attachment.

Course e-mail – CULearn has an e-mail account specific to each course that is accessible only to students registered in the course. I will send individual messages and course notices using the CULearn e-mail, so check your account frequently. Use this method for course-related e-mails and not my other e-mail accounts. Also contact the TA via CULearn e-mail.

### Written work

All written work that you submit must be in your own words. If two or more people have effectively the same answers, I reserve the right to give each person a score of half what they ordinarily would have received. If the same people have effectively identical answers in subsequent assignments, I will assign grades of zero to each of these people.

Transcription of somebody else's written or spoken words without quotation marks or without citation to the original source constitutes plagiarism. Failure to include quotation marks (or other distinguishing marks) and a full citation constitutes a *prima facie* violation of the university's academic integrity policy, which will be immediately referred to the dean for adjudication. If you copy someone else's work and then substitute roughly half the words therein, this also constitutes a *prima facie* case of plagiarism.

Copying someone else's words but then substituting half of the words therein also constitutes a *prima facie* case of plagiarism. See the *Guardian's* hilarious article regarding "sinister buttocks" ([here](#)) for what this might entail, and note that this still would be sent to the dean as a presumptive case of plagiarism.

Unless otherwise specified, all written assignments should conform to the following standards:

1. Be typed in 12-point font with 1-inch margins
2. Be spelling and grammar checked, as well as proofread
3. Begin with your name; please do NOT include student ID numbers

### Academic Integrity Policy

The University is committed to ensuring fairness and consistency in the completion of examinations, including quizzes. As part of this commitment, students are required to follow proper examinations procedures. A student who commits a violation of this policy on an examination, test, or take-home examination, or obtains or produces an answer or unfair advantage by deceit, fraud, or trickery, or by an act contrary to the rules of the examination are subject to the sanction under this Policy.

**CAVEAT:** I reserve the right to alter this syllabus at any time, but promise to only do so for good cause, such as a flu pandemic or huge earthquake. If I get hit by a bus or something akin to that, whoever takes over teaching the course also reserves the right to alter the syllabus when they step in. In the past, the only time I have altered a syllabus during middle of the term was due to a labour strike.

CHECK YOUR GRADES on CULearn:

Marks will be posted on CULearn. Please check your marks frequently and file any appeals as soon as possible. For participation marks, it is incumbent upon you to appeal before the subsequent class. For quiz and assignment grades, appeals must be filed in writing via CULearn e-mail within one week (7 calendar days) of the grades being posted on CULearn.

Grades on your final paper will NOT be posted on CULearn because approval of final course grades by the department chair and dean are required per university rules. Once the registrar releases final course grades, you are free to ask me about your final paper.

REGARDING E-MAIL: Your e-mails must be formal, polite, and proofread in order to guarantee a response from me. I reserve the right to ignore e-mails that are chocked with spelling and grammar errors. Use the automatic spelling and grammar checker. I reserve the right to ignore e-mails that address me only by my first name or otherwise appear overly colloquial. You are here to learn, which includes learning how to effectively communicate with those who evaluate your performance.

READINGS can be found in 3 separate places:

1. Papers that I personally authored, can be found on CULearn.
2. Papers that can be downloaded from the library website, you should download.
3. All other papers can be found in the **Course Pack**, which is on sale at the Carleton University Bookstore (ground floor of the University Centre) for about \$20.

NOT required, but this is amazing reading that is freely available for download:

Weismann, A. (1891 [1892]) Amphimixis or the essential meaning of conjugation and sexual reproduction [translators: E. B. Poulton, A. E. Shipley, L. J. Gould, E.R. Lankester, S. H. Vines, F. Gotch, and D. G. Ritchie]. In: *Essays upon heredity and kindered biological problems - Volume 2*. pp. 100-222. Clarendon Press, Oxford.

PLEASE READ Mike Dorf's brilliant 23 August 2010 *FindLaw* column ([here](#)) about how to be successful in any university course. This will be well worth the few minutes it takes to read.

Possible paper topics for final paper  
(these are only a subset of *ad hoc* ideas)

Evolution of Meiosis

Is any aspect of sex (meiosis, outcrossing, fertilisation) adaptive?  
Is parthenogenesis sex? Are *Giardia*, bdelloids, dewberries, and dandelions really asexual?  
Does complete automixis fundamentally differ from more pedestrian obligate self-fertilisation?  
Should restitutional meiosis and premeiotic doubling count as sex?  
Why are meiosis, recombination, fertilisation, and outcrossing (sometimes) maintained?  
Are individuals or species with higher recombination rates more sexual than ones with lower rates?  
Is geographical parthenogenesis real? What establishes and maintains it?

Females versus Males

Environmental versus genetic sex determination  
How does an individual change sex and why is this so difficult in humans?  
Multiple origins of hermaphrodites: complementary males, polyploidy, and environmental shocks  
How did Y chromosomes get so short in mammals, but X chromosomes get so long in mosses?  
Why do males exist? The so-called two-fold cost of sex (cost of males? cost of meiosis?)  
What is sexual selection and does it really exist?  
Why recreational sex? See bi bonobos and masturbating dogs & red deer  
Why do detachable penises seem to evolve so often? Are they advantageous?  
Do mating types of fungi and slime molds count as separate sexes?

Philosophy & Miscellany

Sex and individuality (“the beast with two backs”): multi-level selection and social cohesion  
Can populations be individuals, say in eusocial insects?  
Why populations (not individuals) are the central unit in the modern synthesis  
Is there a relationship between sex, aging, and death (and maybe the Hayflick limit)?  
Sexually, why are humans so boring?  
Create a liberal feminist, queer, or trans evolution of sex

## Requests for Academic Accommodations

You may need special arrangements to meet your academic obligations during the term because of disability, pregnancy or religious obligations. Please review the course outline promptly and write to me with any requests for academic accommodation during the first two weeks of class, or as soon as possible after the need for accommodation is known to exist. See the Equity Services website to view the policies and to obtain more detailed information on academic accommodation at <http://carleton.ca/equity/accommodation>.

### **For Students with Disabilities:**

Students with disabilities requiring academic accommodations in this course must register with the Paul Menton Centre for Students with Disabilities (PMC) for a formal evaluation of disability-related needs. Documented disabilities could include but are not limited to mobility/physical impairments, specific Learning Disabilities (LD), psychiatric/psychological disabilities, sensory disabilities, Attention Deficit Hyperactivity Disorder (ADHD), and chronic medical conditions. Registered PMC students are required to contact the PMC, 613-520-6608, every term to ensure that I receive your Letter of Accommodation, no later than two weeks before the first assignment is due or the first in-class test/midterm requiring accommodations. If you only require accommodations for your formally scheduled exam(s) in this course, please submit your request for accommodations to PMC by the deadlines published on the PMC website.

### **For Religious Obligations:**

Students requesting academic accommodation on the basis of religious obligation should make a formal, written request to me for alternate dates and/or means of satisfying academic requirements. Such requests should be made during the first two weeks of class, or as soon as possible after the need for accommodation is known to exist, but no later than two weeks before the compulsory event. Accommodation is to be worked out directly and on an individual basis. I will make accommodations in a way that avoids academic disadvantage to the student. For more details, see Carleton Equity Services "Student Guide".

Students who have questions or want to confirm accommodation eligibility of a religious event or practice may refer to the Equity Services website for a list of holy days and Carleton's Academic Accommodation policies, or may contact an Equity Services Advisor in the Equity Services Department for assistance.

### **For Pregnancy:**

Pregnant students requiring academic accommodations are encouraged to contact an Equity Advisor in Equity Services to complete a *letter of accommodation*. During the first two weeks of class or as soon as possible after the need for accommodation is known to exist, the student must write to me with any requests for academic accommodation.