

Sexual Selection Discussion in Class Thursday October 25th:

Looking ahead to the week we return from break, there is a very heavy reading list that week on which you may want to get a head start. Recently the classic work of Bateman has been called into question both for technical details and theoretical validity. Importantly, the researchers who oppose the conclusions of Bateman, point to problems with the current assumptions in Biology and caution readers about potential biases that arise. In my opinion, both sets of readings have valid points that should be considered. Therefore, regardless of which you agree with most strongly, you should be able to define the strongest parts of either argument.

In preparation for class discussion.

Everyone will read

Tang-Martinez, Zuleyma (20 January 2017). "Data Should Smash the Biological Myth of Promiscuous Males and Sexually Coy Females". The Conversation. Retrieved 24 Aug 2018.

Half of the class (last name starting with A-L) will carefully read

Gowaty, P.A., Kim, Y.K., and Anderson, W.W (2012) Repetition of Bateman's classic study PNAS 109:11740-11745.

Snyder, B.F., and Gowaty, P.A. (2007) A reappraisal of bateman's classic study of intrasexual selection. Evolution 61:2457-2468

Half of the class (last name starting with M-Z) will carefully read

Janick, T., Haderer, I.K., Lajeunesse, M.H., Anthes N. (2016) Darwinian sex roles confirmed across the animal kingdom. Sci. Adv. 2:e1500983.

Fritzsche, K., Arnqvist, G. (2013) Homage to Bateman: sex roles predict sex differences in sexual selection. Evolution 67:1926-1936.

Each group should also familiarize themselves with the other pair of readings.

For your assigned set readings you should:

- Briefly state the major argument of each assigned paper.
- List a few of the strongest pieces of evidence for that argument.
- What impact does this argument have on current research in animal behavior?
- What impact does this argument have more broadly on society?

(this will not be turned in but you will be called on to address these points)

After briefly reading the other set of readings, consider how you will present and argue in support of your assigned set of readings. Revisit the above points to formulate your thoughts.

Some other papers on the topic include:

Roughgarden, J., and Akcay, E. (2010) Do we need a sexual selection 2.0? Animal Behaviour 79: e1-e4.

Shuker, D.M. (2010) Sexual selection: endless forms or tangled bank? Animal Behaviour 79: e11-e17.

All readings are available on the course syllabus.

LECTURE GOALS:

- Understand Biological definition of sex.
- Understand **intra-** and **inter-sexual selection** as evolutionary processes that affect the two sexes differently to produce sex-role behavior and sexual dimorphism.
- Prepare to read the papers for class discussion Thursday October 25th.

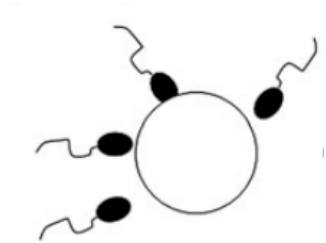
LECTURE OUTLINE:

1. Sexual reproduction is a form of reproduction where two morphologically distinct types of specialized reproductive cells (gametes) fuse.
2. In the biological sense “female” is defined as the individuals that produce larger gametes (eggs) while “male” is defined as the individuals that produce smaller gametes (sperm).
3. In many animal species, sex-determination does not occur according to the XY chromosomal mechanism that we are familiar with from mammals and flies.
 - a. In birds, females are the heterogametic sex
 - b. In many reptiles, sex is determined by temperature
 - c. In many fish species, sex is determined by social interactions.
 - d. In some species, there are only females.
4. Not all animals exhibit a fixed sex throughout their lives.
5. Various forms of hermaphroditism exist in fish (and other organisms).
6. Darwin defined intra- and inter-sexual selection (see notes below).
7. Others have added insight to the definition.
8. Bateman's Principle (a.k.a. the Bateman Gradient) provides empirical evidence to explain the direction of sexual selection.
9. When Bateman's Gradient is reversed, the result is "sex-role reversal" and sexual selection is reversed.
 - a. Sex-role reversal can be typical for the species.
 - b. Sex-role reversal can be variable within a species.
10. Sexual selection can act on primary and secondary sexual characteristics as well as behaviors and “extended phenotypes”.
11. Genetic Theories for mate choice (usually female)
 - a. Direct Benefit Theory
 - b. Good Genes Theory
 - c. Sexy Sons Theory (a.k.a. runaway selection)
12. Multiple genetic models may apply to a single species. (example: birds)
13. Non-genetic (i.e. learned) mate preferences also occur.
 - a. Sexual imprinting
 - b. Mate choice copying.
14. What Darwin didn't know and we are only now beginning to appreciate:
 - a. Male-male competition persists after mating, as sperm compete with each other.
 - b. Females may continue to choose, long after mating by selecting which sperm fertilize her eggs.
 - c. There is more female-female combat and also male choice than previously appreciated.

HELPFUL FIGURES & NOTES:

(All PowerPoint files will be available on the Moodle after lecture. This subset of unlabeled and incomplete figures and notes is meant to assist, not replace note taking.)

Anisogamy



Darwin distinguished sexual selection from natural selection:

"Sexual selection depends on the success of certain individuals over others of the same sex ... while natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. "

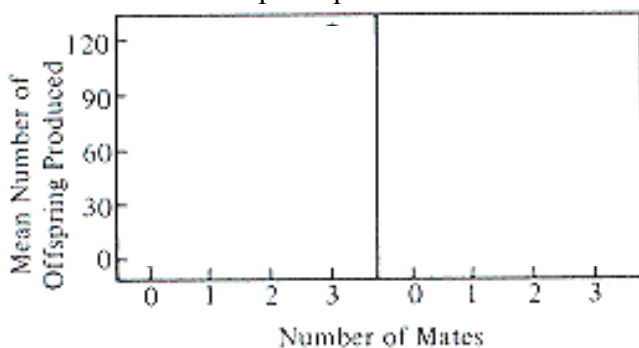
Darwin defined two types of sexual selection.

"The sexual struggle is of two kinds:

-- in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive;

-- while in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners."

Bateman's principle



1)

2)

3)

VOCABULARY:

(Practice writing interesting, informative sentences that include, and capture the meaning of, 4-5 words from this list. To simply memorize a definition, is not sufficient).

Gamete	Intra-sexual Selection
Anisogamy	Competition
Sexual Selection	Choice
Inter-sexual Selection	Sex-Role
Bateman's Principle (a.k.a. Bateman's Gradient)	

PRACTICE EXAM QUESTIONS:

(Answer these questions on your own. If you are unsure of your answer, raise the question at the beginning of the following lecture for clarification.)

1. What defines male and female sexes?
2. Define intra-sexual selection and inter-sexual selection.
3. Why is it wrong to think of sexual selection as opposing natural selection?
4. Explain the results bateman would have obtained if he had worked with a species that showed strong "sex-role reversal"?

READING FOR NEXT LECTURE:

R&W Chapter 6 & 7

Crews D. (1994) Animal Sexuality. Scientific American 94:108-114.

Bachtrog et al (2014) Sex Determination: Why So Many Ways of Doing It? PLoS Biology 12:e1001899.

Anderson M. and Simons L.W. (2006) Sexual selection and mate choice. Trends in Ecology and Evolution 21:296-302.

Clutton-Brock (2007) Sexual selection in males and females. Science 318:1882-1885.

Eens and Pinxton (2000) Sex-role reversal in vertebrates: behavioural and endocrinological accounts. Behavioural Processes 51: 135–147.

Data should smash the biological myth of promiscuous males and sexually coy females

January 20, 2017 5.59am EST

<https://theconversation.com/data-should-smash-the-biological-myth-of-promiscuous-males-and-sexually-coy-females-59665>

Tang-Martinez, Zuleyma (20 January 2017). "Data Should Smash the Biological Myth of Promiscuous Males and Sexually Coy Females". *The Conversation*. Retrieved 24 Aug 2018.

That males are naturally promiscuous while females are coy and choosy is [a widely held belief](#). Even many scientists – including some biologists, psychologists and anthropologists – tout this notion when [interviewed](#) by the media about almost any aspect of male-female [differences, including in human beings](#). In fact, certain human behaviors such as rape, marital infidelity and some forms of domestic abuse have been portrayed as [adaptive traits that evolved](#) because males are promiscuous while females are sexually reluctant.

These ideas, which are pervasive in Western culture, also have served as the cornerstone for the evolutionary study of sexual selection, sex differences and sex roles among animals. Only recently have some scientists – fortified with modern data – begun to question their underlying assumptions and the resulting paradigm.

It all comes down to sperm and eggs?

These simple assumptions are based, in part, on the differences in size and presumed energy cost of producing sperm versus eggs – a contrast that we [biologists call anisogamy](#). [Charles Darwin was the first to allude](#) to anisogamy as a possible explanation for male-female differences in sexual behavior.

His brief mention was ultimately expanded by others into the idea that because males produce millions of cheap sperm, they can mate with many different females without incurring a biological cost. Conversely, females produce relatively few “expensive,” nutrient-containing eggs; they should be highly selective and mate only with one “best male.” He, of course, would provide more than enough sperm to fertilize all a female’s eggs.

In 1948, Angus Bateman – a botanist who never again published in this area – was the first to test Darwin’s predictions about sexual selection and male-female sexual behavior. He set up a series of breeding experiments using several inbred strains of fruit flies with different mutations as markers. He placed equal numbers of males and females in laboratory flasks and allowed them to mate for several days. Then he counted

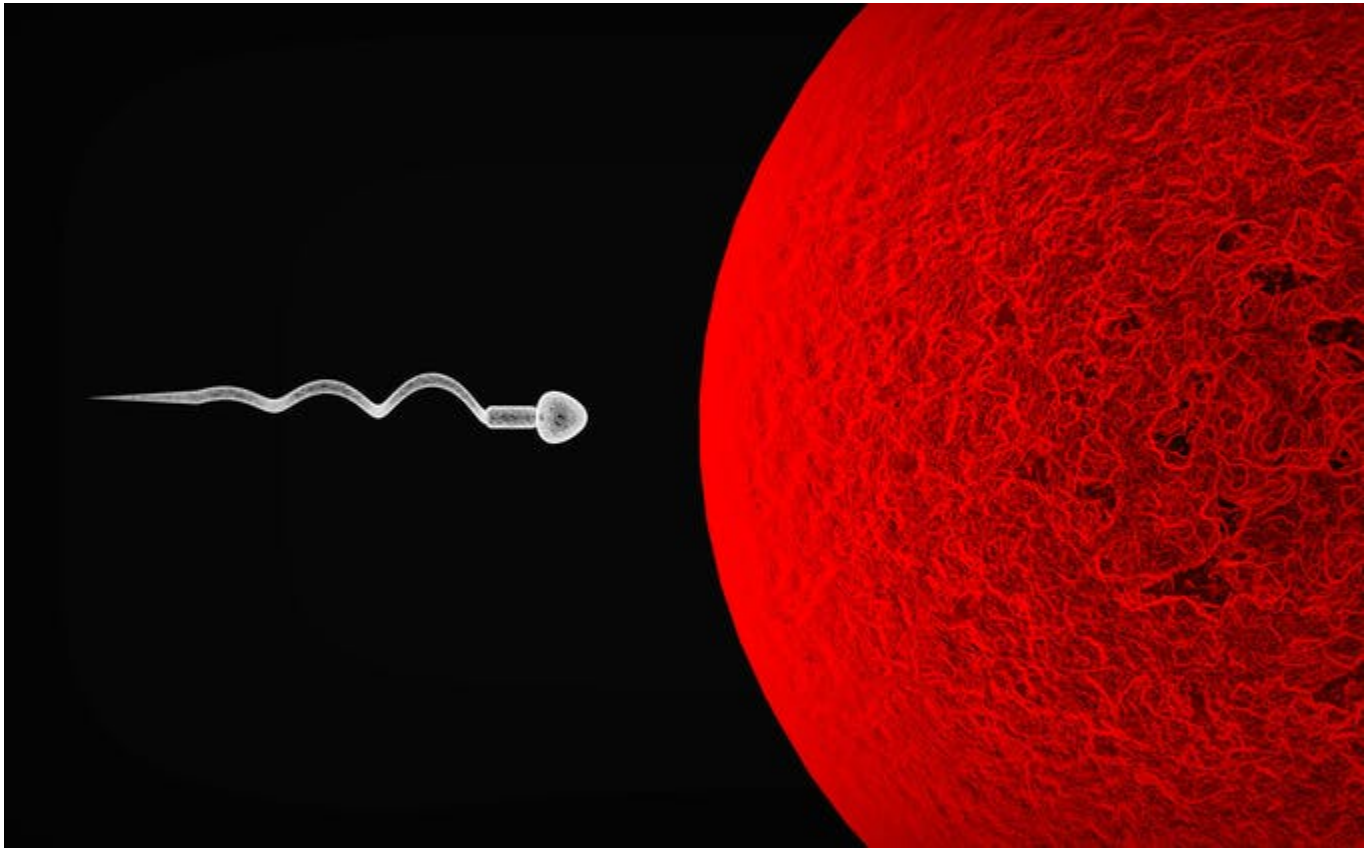
their adult offspring, using inherited mutation markers to infer how many individuals each fly had mated with and how much variation there was in mating success.

One of Bateman's most important conclusions was that male reproductive success – as measured by offspring produced – increases linearly with his number of mates. But female reproductive success peaks after she mates with only one male. Moreover, Bateman alleged this was a near-universal characteristic of all sexually reproducing species.

In 1972, theoretical biologist Robert Trivers highlighted Bateman's work when he formulated the theory of "parental investment." He argued that sperm are so cheap (low investment) that males evolved to abandon their mate and indiscriminately seek other females for mating. Female investment is so much greater (expensive eggs) that females guardedly mate monogamously and stay behind to take care of the young.

In other words, females evolved to choose males prudently and mate with only one superior male; males evolved to mate indiscriminately with as many females as possible. Trivers believed that this pattern is true for the great majority of sexual species.

The problem is, modern data simply don't support most of Bateman's and Trivers' predictions and assumptions. But that didn't stop "Bateman's Principle" from influencing evolutionary thought for decades.



A single sperm versus a single egg isn't an apt comparison. [Gametes image via www.shutterstock.com](http://www.shutterstock.com).

Examining the assumptions about males

In reality, it makes little sense to compare the cost of one egg to one sperm. As comparative psychologist [Don Dewsbury pointed out](#), a male produces millions of sperm to fertilize even one egg. The relevant comparison is the cost of millions of sperm versus that of one egg.

In addition, males produce semen which, in most species, contains critical bioactive compounds that presumably are [very expensive to produce](#). As is now also well-documented, sperm production is limited and males can run out of sperm – what researchers term “sperm depletion.”

Consequently, we now know [males may allocate more or less sperm to any given female](#), depending on her age, health or previous mated status. Such differential treatment among preferred and nonpreferred females is a form of male mate choice. In some species, males may even [refuse to copulate with certain females](#). Indeed, [male mate choice](#) is now a particularly active field of study.

If sperm were as inexpensive and unlimited as Bateman and Trivers proposed, one would not expect sperm depletion, sperm allocation or male mate choice.

Assumptions about females don't match reality

[Birds have played a critical role](#) in dispelling the myth that females evolved to mate with a single male. In the 1980s, approximately 90 percent of all songbird species were believed to be “monogamous” – that is, one male and one female mated exclusively with one another and raised their young together. At present, only about 7 percent are classified as monogamous.

Modern molecular techniques that allow for paternity analysis revealed [both males and females](#) often [mate and produce offspring with multiple partners](#). That is, they engage in what researchers call “extra-pair copulations” (EPCs) and “extra pair fertilizations” (EPFs).

Because of the assumption that reluctant females mate with only one male, many scientists initially assumed promiscuous males coerced reluctant females into engaging in sexual activity outside their home territory. But behavioral observations quickly determined that [females play an active role in searching for nonpair males and soliciting](#) extra-pair copulations.

Rates of EPCs and EPFs vary greatly from species to species, but the superb fairy wren is one socially monogamous bird that [provides an extreme example](#): 95 percent of clutches contain young sired by extra-pair males and 75 percent of young have extra-pair fathers.

This situation is not limited to birds – across the animal kingdom, females frequently mate with multiple males and produce broods with multiple fathers. In fact, Tim Birkhead, a well-known behavioral ecologist, concluded in his 2000 book [“Promiscuity: An Evolutionary History of Sperm Competition,”](#) “Generations of reproductive biologists assumed females to be sexually monogamous but it is now clear that this is wrong.”

Ironically, Bateman's own study demonstrated the idea that female reproductive success peaks after mating with only one male is not correct. When Bateman presented his data, he did so in two different graphs; only one graph (which represented fewer experiments) led to the conclusion that female reproductive success peaks after one mating. The other graph – largely ignored in subsequent treatises – showed that the number of offspring produced by a female increases with the number of males she mates with. That finding runs directly counter to the theory there is no benefit for a “promiscuous” female.

Modern studies have demonstrated this is true in a broad range of species – females that mate with more than one male produce more young.



What's happening in society outside the lab can influence what you see inside it. [National Library of Ireland on The Commons](#)

Seeing what society leads you to expect

So if closer observation would have disproved this promiscuous male/sexually coy female myth, in the animal world at least, why didn't scientists see what was in front of their eyes?

Bateman's and Trivers' ideas had their origins in Darwin's writings, which were greatly [influenced by the cultural beliefs of the Victorian era](#). Victorian social attitudes and science were closely intertwined. The common belief was that males and females were radically different. Moreover, attitudes about Victorian women influenced beliefs about nonhuman females. Males were considered to be active, combative, more variable, and more evolved and complex. Females were deemed to be passive, nurturing; less variable, with [arrested development equivalent to that of a child](#). "True women" were expected to be pure, submissive to men, [sexually restrained and uninterested in sex](#) – and this representation was also seamlessly applied to female animals.

Although [these ideas may now seem quaint](#), most scholars of the time embraced them as scientific truths. These stereotypes of men and women survived through the 20th century and influenced research on male-female sexual differences in animal behavior.

Unconscious biases and expectations can influence the [questions scientists ask and also their interpretations of data](#). Behavioral biologist Marcy Lawton and colleagues [describe a fascinating example](#). In 1992, eminent male scientists studying a species of bird wrote an excellent book on the species – but were mystified by the lack of aggression in males. They did report violent and frequent clashes among females, but dismissed their importance. These scientists [expected males to be combative and females to be passive](#) – when observations failed to meet their expectations, they were unable to envision alternative possibilities, or realize the potential significance of what they were seeing.

The same likely happened with regard to sexual behavior: Many scientists saw promiscuity in males and coyness in females because [that is what they expected to see](#) and what theory – and societal attitudes – told them they should see.

In fairness, prior to the advent of molecular paternity analysis, it was extremely difficult to accurately ascertain how many mates an individual actually had. Likewise, only in modern times has it been possible to accurately measure sperm counts, which led to the realization that sperm competition, sperm allocation and sperm depletion are important phenomena in nature. Thus, these [modern techniques also contributed to overturning stereotypes](#) of male and female sexual behavior that had been accepted for more than a century.



What looks like monogamy at first glance very often isn't. [Waved Albatross image via www.shutterstock.com.](https://www.shutterstock.com)

Bateman's research has not been replicated

Besides the data summarized above, there is the question of whether Bateman's experiments are replicable. Given that [replication is an essential criterion of science](#), and that Bateman's ideas became an unquestioned tenet of behavioral and evolutionary science, it is shocking that more than 50 years passed before an attempt to replicate the study was published.

Behavioral ecologist Patricia Gowaty and collaborators had found numerous methodological and statistical problems with Bateman's experiments; when they [reanalyzed his data, they were unable to support his conclusions](#). Subsequently, they reran Bateman's critical experiments, using the exact same fly strains and methodology – and [couldn't replicate his results or conclusions](#).

Counterevidence, evolving social attitudes, recognitions of flaws in the studies that started it all – Bateman's Principle, with its widely accepted preconception about male-female sexual behavior, is currently undergoing serious scientific debate. The scientific study of sexual behavior may be experiencing a paradigm shift. Facile explanations and assertions about male-female sexual behaviors and roles just don't hold up.