Biol 418 Evolutionary Ecology

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Lectures: Tue, Thu 9:30 – 10:30
Biosciences 1001
Biol 418 Evolutionary Ecology

No book for the course. Weekly readings instead.

Midterm: none

50% Assignments up to 5 short essays on discussion topics

40% Final Exam

10% Tutorial discussions

Tutorials involve reading a research article beforehand and contributing to a discussion of an overarching question.

For example,

"Why manipulate traits in field studies of natural selection?"
Allometric Engineering: A Causal Analysis of Natural Selection on Offspring Size

Barry Sinervo, Paul Doughty, Raymond B. Huey, Kelly Zamudio

Techniques of offspring size manipulation, "allometric engineering," were used in combination with studies of natural selection to elucidate the causal relation between egg size and offspring survival of lizards. The results experimentally validate premises underlying theories of optimal egg size: fecundity selection favoring the production of large clutches of small eggs was balanced by survival selection favoring large offspring. However, large hatchlings did not always have the highest survival, contrary to most theoretical expectations. Optimizing selection on offspring size per se was the most common pattern. Moreover, matches between average and optimal egg size were qualitative, not quantitative, perhaps reflecting known functional constraints on the production of large eggs.
Purpose of discussions:

Opportunity to:

- Read the primary literature
- Develop and articulate views, however preliminary (you talk)
- Recognize and develop improved arguments
- Synthesize a logical argument to answer a basic question

Readings provided at the course web site
What is Evolutionary Ecology?

The study of the ecological causes and consequences of evolutionary change, past and present.

Today’s lecture:

An example of an interesting problem in evolutionary ecology:

   Intracellular symbionts and their consequences

How an ecological interaction affects evolution, and how evolution might have ecological consequences.
An intracellular symbiont *Wolbachia* bacterium in a mosquito cell

*photo: AJ Cann
http://www.flickr.com/photos/ajc1/3003087548/*
Intracellular symbionts and host sex ratio

Important facts:

1) Intracellular symbiont lives inside cells.

2) Many examples in nature: rickettsia bacteria, microsporidia, viruses, Wolbachia (a bacterium).

3) Symbionts may be parasites, commensals, or mutualists (e.g., may be linked to viral resistance in host).

4) The usual mode of inheritance is vertical (mother to offspring via egg or seed) rather than horizontal (via infection)

5) Many of these symbionts alter the sex ratio of host individual.
### Intracellular symbionts and host sex ratio

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<th>Mechanism</th>
<th>Wild type</th>
<th>Selfish</th>
<th>Mitochondria</th>
<th>Plastids</th>
<th>Younger endosymbionts</th>
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<td><strong>Male killing, harming, and sterility</strong></td>
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<td><strong>Cytoplasmic incompatibility</strong></td>
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</tbody>
</table>

**Mitochondria**

- **Across metazoans**
  - Drosophila, Homo, others
  - Across angiosperms
  - CMS in hundreds of species

**Plastids**

- Angiosperms - ?
  - Implicated in peas and evening primrose

**Younger endosymbionts**

- Wolbachia
  - Diverse arthropods [31]
  - Rickettsia
    - Coleoptera [247]
  - Others - (e.g., Spiroplasma, Microsporidia, Arsenophonus)
    - [249–252]

- Wolbachia
  - Diverse arthropods [31]
  - Rickettsia
    - Hymenoptera [247]
  - Others (e.g., Cardinium)
    - [248,252]

- Wolbachia
  - Diverse arthropods [31]
  - Cardinium
    - Acari [248]
  - Microsporidia
    - Crustaceans [252]

- Wolbachia
  - Diverse arthropods [31]
  - Cardinium
    - Diverse arthropods [248,253]

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**Figure 3. Mechanisms of reproductive manipulation in cytoplasmic genomes.**

Four mechanisms of reproductive parasitism of arthropods have been described in younger endosymbionts such as *Wolbachia*: male killing/harm eliminates or reduces male functions, parthenogenesis results in asexual production of exclusively females, feminization causes males to develop as females, and cytoplasmic incompatibility prevents males with the selfish variant from mating with wild-type females [247–253]. However, mitochondrial genomes have only been documented to cause male harm/killing (not the other mechanisms), and evidence for plastids causing reproductive manipulation is scarce.

Havrid et al. (2019) *Current Biology*
Sex ratio theory

Most organisms have a 50:50 sex ratio at conception. This makes sense for three reasons.

1. Genes residing on chromosomes are transmitted to future generations through both sons and daughters.

2. In each generation, every female must pair with a male to produce offspring.

3. Therefore, if the sex ratio is not 50:50, the rarer sex will on average obtain more matings, and leave more offspring, than the more common sex.

4. Any mutation that causes its bearer to produce more of the rarer sex, and fewer of the commoner sex, will have an evolutionary advantage.

5. This advantage persists until the sex ratio evolves to 50:50.

This is the accepted explanation for why so many organisms have a sex ratio close to 50:50.

Not convinced? Need to see the math to be convinced? See link to “Further notes on the evolution of sex ratio” on the main page course web site.
Intracellular symbionts and host sex ratio

But what happens if genes residing on chromosomes are NOT transmitted to future generations through both sons and daughters?

How is *Wolbachia* transmitted?

Answer: via daughters of the host species, not via sons.

Cytoplasm is passed from mother to offspring (egg) but not from father to offspring (sperm).
Intracellular symbionts and host sex ratio

Therefore, a mutation in the symbiont (living in the cytoplasm) that interferes with sex ratio of hosts, causing it to produce more daughters than sons, would have an evolutionary advantage.

It doesn’t stop there.

If a female-bised sex ratio should result, then a mutation in the host that counteracts interference by the intracellular symbiont, and restore a 50:50 sex ratio, would have an evolutionary advantage.
**Intracellular symbionts and host sex ratio**

Example:  
_Armadillidium vulgare_  
the pill-bug or woodlouse

In some populations (Wolbachia-free), Males are ZZ, females are ZW.

In most populations (having Wolbachia), most infected ZZ individuals are female. The Wolbachia causes feminization.

In some populations, the W chromosome has been lost, so that ZZ are male and ZZ+Wolbachia are female.

It doesn’t stop there, because additional genetic factors can occur that affect these dynamics. A genetic factor M counteracts the feminizing effects of Wolbachia. A second feminizing factor f may be present.
Intracellular symbionts and host sex ratio

This could ultimately lead to the evolution of a new mechanism of chromosomal sex determination. Here is a schematic of a proposed evolutionary sequence. Seemingly in accord with this hypothesis, Beckign et al (2017) showed that terrestrial isopods have a high rates of evolution of sex determination across the clade.

Intracellular symbionts and host sex ratio

Might this evolutionary dynamic have ecological consequences, say on population size?

Perhaps population growth in *Armadillidium vulgare* is faster in those periods or locations where the sex ratio is strongly female-biased.

Nobody has investigated this, to my knowledge.
Lessons for Evolutionary Ecology

1) Evolution is a contemporary process. The dichotomy between “ecological time” and “evolutionary time” is blurred. For example, sex ratio can evolve rapidly from year to year.

2) This dynamic evolution is happening under the flower pots in your back yard.

3) Many phenomena in nature that we take for granted, such as the 50:50 sex ratio, have been moulded by ecological selection pressures.

4) Ecological interactions between a symbiont and its hosts can have unexpected evolutionary consequences. These consequences may affect ecological dynamics in turn.
Lessons for Evolutionary Ecology

5) The “level” at which natural selection acts can become blurred. In the example of symbionts and sex ratio evolution, natural selection is acting on individuals of two distinct species that have conflicting evolutionary “interests”.

But what if cytoplasmic genes causing sex ratio manipulation occur not in a bacterium but instead in the host’s own mitochondria (as is the case in gynodioecy in many species of plants - the pollen sterility factor is in the mitochondria).

At what level is selection acting in this case? Dawkins has argued that the best way to view this is that selection acts on genes not individuals.

6) Genes don’t evolve in a direction that is good for the species.

7) These are interesting hypotheses, but how can we test them?

In this course we will investigate such ideas in evolutionary ecology using a combination of theory (models of the process, which generate predictions for testing) and tests based on experiments and comparative studies.