# Roadmap

- Sex-linked traits
- Sex ratio selection
- Sex determination

# Selection on an X-linked trait: hemophilia

(These fitnesses are guesses as I could not find a solid estimate. Prior to 1960 the mean life expectancy of a male hemophiliac was 11 years.)

| Genotype | H-W | observed fitness |
|---|---|---|
| $X^H X^H$ female | $p^2$ | 1.0 |
| $X^H X^h$ female | $2pq$ | 1.0 |
| $X^h X^h$ female | $q^2$ | 0.2 |
| $X^H Y$ male | $p$ | 1.0 |
| $X^h Y$ male | $q$ | 0.2 |

- If $q$ is low, most selection acts on males
- Next-generation allele frequencies different in males and females

# Selection on an X-linked trait: hemophilia

Assume starting $p(X^H)$=0.8 (among X chromosomes!)

| Genotype | fitness | before selection | after selection | renormalized |
|---|---|---|---|---|
| $X^H X^H$ | 1.0 | 0.32 | 0.32 | 0.331 |
| $X^H X^h$ | 1.0 | 0.16 | 0.16 | 0.165 |
| $X^h X^h$ | 0.2 | 0.02 | 0.004 | 0.004 |
| $X^H Y$ | 1.0 | 0.40 | 0.40 | 0.476 |
| $X^h Y$ | 0.2 | 0.10 | 0.02 | 0.024 |

- We could get $p(X^H)$ from this, but it would be misleading as it differs in males and females
- To do the next generation, draw a Punnet square
- $p(X^H)$ in females $= 0.827$
- $p(X^H)$ in males $= 0.952$

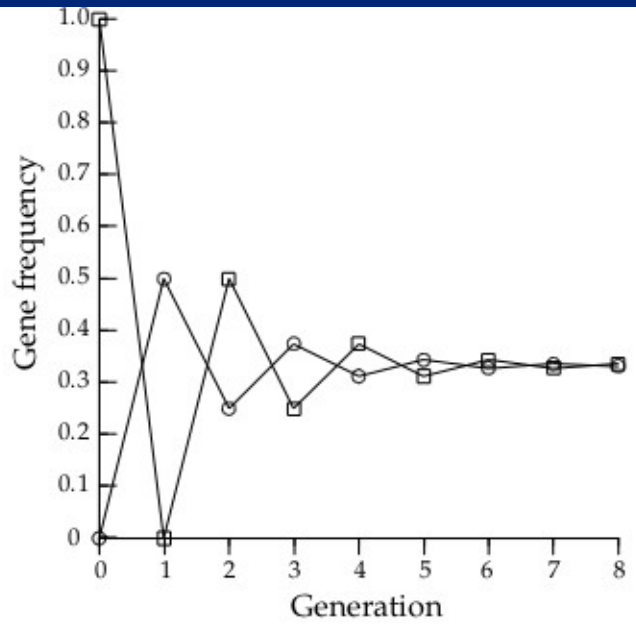



Figure 1.3: Gene frequency changes resulting from initial sex differences of gene frequencies in the two sexes (circles are for females, squares for males) at a sex-linked locus (with initial gene frequencies $p_m = 1$, $p_f = 0$).

# A puzzle

- Most sex-related traits are autosomal
- Most sex-linked traits have nothing to do with sex:
  - Color vision
  - Clotting factor
  - G6PD
- Very few traits are Y-linked

## Thoughts about lack of X-linked sexual traits

- One switch may be more robust than multiple ones
- X inactivation (in mammals) could interfere with X-linked sex traits
- X arose from autosome and retains random genes from that autosome

## Lack of Y traits

- Y chromosome has potential issues:
  - No recombination (except in pseudo-autosomal region)
  - Intense hitchhiking
  - Reduced $N_e$
  - Fewer options for repair of damage (no pairing partner)

- If gene present on both Y and autosome, Y version more likely to turn into a pseudogene and be lost

## Sex ratio is a selected trait

- In a obligately sexual, gendered organism:
  - Males and females contribute equally to next generation's gene pool
  - If one sex is rarer, each individual of that sex contributes more
- An allele that preferentially creates one sex:
  - Will tend to be in that sex
  - Will tend to make that sex more common
  - Will therefore decrease in frequency

## Practice problem

- Suppose:
  - Every 100 individuals consists of 90 females and 10 males
  - Population size is constant
- How many offspring does the average female have?
- How many offspring does the average male have?
- For getting your genes into grandchildren, should you have a son or a daughter?

## Two refinements

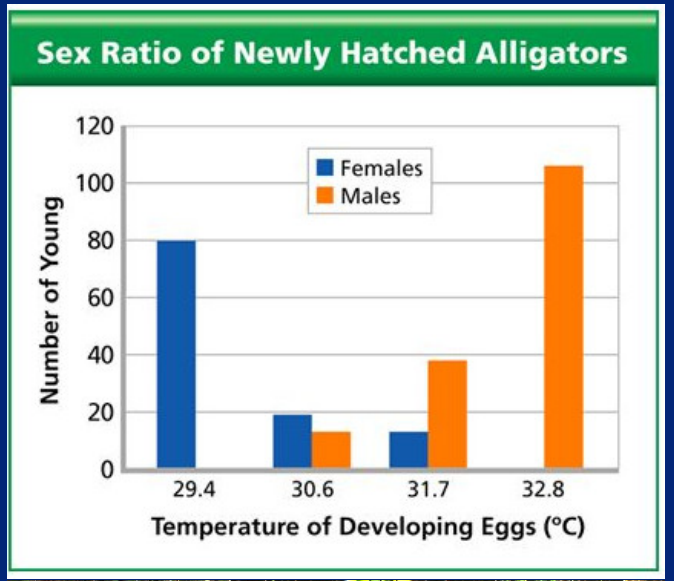
- What if one sex is cheaper to produce?
  - Equilibrium at equal $investment$
  - Cheaper sex will be more common
- Equalizes sex ratio at breeding age, not at birth
  - Human sex ratio 105-107 males per 100 females at birth
  - True worldwide and does not rely on technology
  - Male mortality prior to reproduction is higher

## This principle does not hold when–

- Not all individuals have both male and female parents
  - *C. elegans* – hermaphrodites and males
  - Haplodiploids – males have no male parent
- Individuals change sex during their lifetimes

## American alligators

- 72% female (1995-1999 in Louisiana)
- Males are high-temperature sex (i.e. this is not global warming)
- Is this stable? If so, why?
- Are cold female babies cheaper to raise than hot male ones?
- Different mortality of sexes?



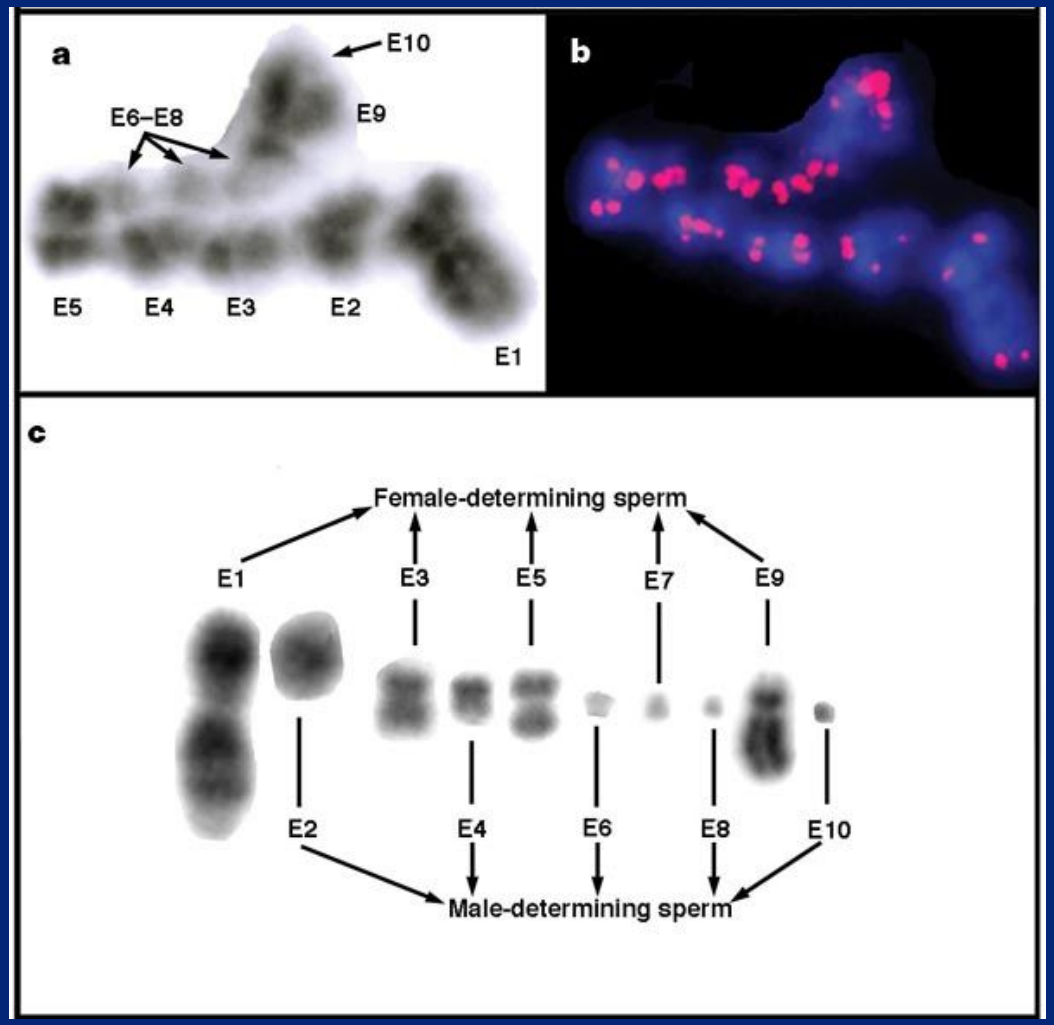

# Deer fine-tune their sex ratio

- Big males are more likely to reproduce
- Big sons are expensive for mother
- Mothers tend to have more sons when the mother is:
  - Large
  - Well-fed
  - Socially dominant
- Probably due to sex-specific miscarriage

# XX/XY sex determination

- Most mammals
  - Sex determined by a master gene on the Y
  - XO are sterile females
- Flies
  - Sex determined by ratio of X to autosomes
  - X0 are low-fertility males
- I suspect these arose independently

# Platypus sex chromosomes



# ZZ/ZW system and haplodiploidy

- Birds, butterflies, some amphibians:
  - ZW female, ZZ male
  - Platypus has been suggested to represent an intermediate as it has both Y-like and W-like material
- Ants, bees, wasps, thrips, some other arthropods
  - Males are haploid (from unfertilized eggs)
  - Females are diploid (from fertilized eggs)
  - Decision to fertilize is up to the mother

# Temperature dependent sex determination

- Some reptiles and fish:
  - Sex is determined by temperature
  - Low temperature is male in some species and female in others
  - Parents may influence gender of offspring during egg-rearing
  - May be advantageous if optimal survival temperature varies between sexes

## Evolutionarily unstable?

- Normally ZW/ZZ
- Some ZZ females at extreme temperatures
- Selective breeding at high temperatures lost the W completely leading to a temperature-dependent system with no sex chromosomes
- FAST evolutionary change!
- One paper: Deveson et al. (2017) Science Advances.

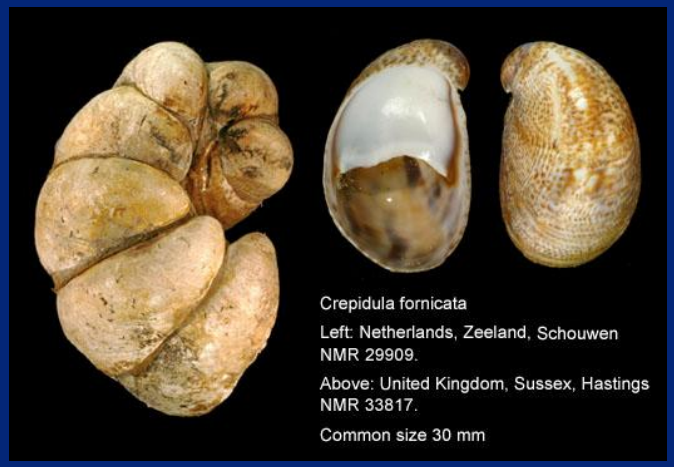
Bearded Dragon

## Sex Determination

- Some fish and molluscs
  - Sex changes during an individual's life
  - Usually male when small and female when large
  - Females invest more in their offspring (large egg, small sperm) so better to be male if you are small and can't invest much
  - Opposite case can happen if there is male/male competition and size matters

# Sex Determination

- The mollusc *Crepidula fornicata* lives in stacks
- The bottom animal becomes female; all others become male
- Lowest, largest male fathers 86% of offspring
- I don't know why the others become males...



## What about plants?

- Males XY, females XX (campion)
- Males and females are haploid: males have Y, females have X (liverwort)
- Choice of male vs. hermaphrodite made based on neighbors' pheromones (fern)
- One gene system: different alleles are male, female, or hermaphrodite (papaya)
- Two gene system: different allele combos are male, female, hermaphrodite or have separate male and female flowers on the same plant (cucumber)

# "Amazon" species

In some lizard and fish species:

- Only females exist
- They must mate so that a sperm can trigger egg development
- They discard the male genome and clone their own
- Reliant on related "normal" species to provide males

Amazon Molly, *Poecilia formosa*, a species which lacks males.

## Lonely Amazons

- Males of the sexual species have an incentive not to mate with Amazons:
  - Wastes time and energy
  - Exposed to STDs
- Amazons can go extinct if:
  - Males refuse to breed with them
  - They outcompete species that have males
- This has been observed in artificial ponds
- Species like this arise fairly often, but don't last long

## Why are these traits so diverse?

- In humans, sex chromosome abnormalities common
- Across the Tree of Life, huge diversity of sex determination systems
- Drastic changes between closely related species (i.e. Amazons)
- Why is an essential capability so volatile?
  - Male/female competition?
  - Involvement in speciation?

# Male/female conflict of interest

- If you are a sperm:
  - Fertilizing an egg gives you a chance to pass on your genes
  - Failing to fertilize gives you nothing
  - No penalty for polyspermy
- If you are an egg:
  - Need to be fertilized exactly once
  - Polyspermy is a disaster
- This leads to an arms race between sperm and eggs
- There may be no stable solution

## Wednesday

- Inversions
- Translocations
- Changes in chromosome number
- Meiotic drive

## One-minute responses

- Please:
  - Tear off a slip of paper
  - Give me one comment or question on something that worked, didn't work, needs elaboration, etc.