

Course business

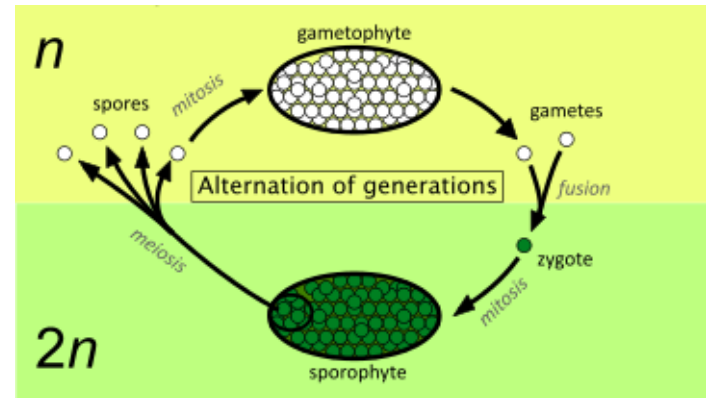
- Final is 2:30-4:20 Wednesday Dec. 13
- Mainly on second half of course but will use the basic concepts and techniques from the first half:
 - Genetic drift
 - Gene flow
 - Natural selection
 - * Directional selection
 - * Overdominance and underdominance
 - Linkage and recombination
- Last session before final will be a review

One-minute responses

- Q: Could creatures with unusual reproductive systems have been influenced by Wolbachia?
 - Haplodiploid ants, bees, wasps
 - Hermaphroditic nematodes
 - Parthenogenic aphids
 - etc.
- A: I don't know! Could be a great research question.

Expression of haploid genotype not always suppressed

- In many plants:
 - Diploid plant makes haploid spores by meiosis
 - Spores grow into haploid plant
 - Haploid plant makes haploid gametes by mitosis
 - Fertilization produces a diploid plant
- How do they avoid evolutionary conflict between haploid and diploid?



Sporophyte (top) and gametophyte (bottom) of a fern

Conflict between levels of organization

- <http://music.bababrinkman.com/track/revenge-of-the-somatic-2>
- Gangsta rap about cancer as a conflict between levels
- (strong language)

Speciation

- Species definitions
- Troublesome species
- Pre-mating and post-mating isolation
- Next lecture: modes of speciation

A personal note

- I will present several answers to “what is a species?”
- I think all of them are broken!
- I will therefore not ask for species definitions in homework or exams.

Species definitions

Ernst Meyer proposed the **biological species concept (BSC)**: A species is an interbreeding population that is reproductively isolated from other such populations.



Wolf, by Jan Nijendijk



Coyote, by Yathin S. Krishnappa

Possible weaknesses of BSC

- Doesn't help with asexuals
- Troublesome in prokaryotes where individuals may have “sex” with drastically unrelated types and gain a few genes from them
- Clumps some populations that seem separate:
 - wolf, dog, coyote
 - plum, apricot

Possible weaknesses of BSC

- Separates some things that don't feel like species:
 - Flies with different strains of Wolbachia
 - Newly arisen tetraploids
- Hard to apply to extinct species
- What if gene flow is all one way? One species or two?

Genic species definition

Due to Chong-I Wu

- Speciation has occurred when:
 1. Gene pools of adaptive loci would not mix even if the barriers to gene flow were removed, and
 2. Advantageous mutations are often (not necessarily always) restricted to the population in which they arise.
- This focuses more on adaptation. It is open to most of the same criticisms as the BSC. Differences:
 - New polyploids
 - “Wolbachia species”
 - Wolves and coyotes?

Paleontological species definition

Two forms are separate species if they have visible, consistent differences and hybrid forms are not found

- Some species have a lot more “hard” morphology than others
- “Cryptic species” with no morphological differences:
 - Incompatible behavior (e.g. mating dance or song)
 - Incompatible biochemistry (e.g. egg/sperm recognition)
 - Incompatible genetics (e.g. chromosome rearrangements, underdominance)
- Failure to find a fossil is weak evidence that it wasn't there

Asexual species

- Interbreeding can't be used as a criterion for asexuals
- Need to measure “distance” in some way:
 - Genetic similarity
 - Morphology
 - Behavior (e.g. host they can infect or food they can eat)

Asexual species

- Bacterial “species” can contain grossly genetically dissimilar forms
 - Laboratory *E. coli* more different from pathogenic *E. coli* (percentage DNA sequence divergence) than humans from monkeys
- If asexuals occasionally have sex, maybe BSC could be relevant, but...
- *E. coli* apparently got its pencillin-resistance straight from the fungus *Penicillium*

Phylogenetic species definition

- Species are defined by degree of genetic distance
- Requires an arbitrary cutoff
 - Some genera have much higher genetic distances than others
 - Either we have classified a lot of stuff wrong, or the species line is different in different groups
- Can sexual critters that CANNOT interbreed really be the same species?
- Works for asexuals!

A different phylogenetic species definition

- A species is a group of organisms with a common ancestor and unique shared traits among the group
- Example: dogs
 - Probable common ancestor
 - Shared adaptations (sociability, different developmental timing, multiple estrus periods per year, etc.)

Common ancestor is a difficult concept

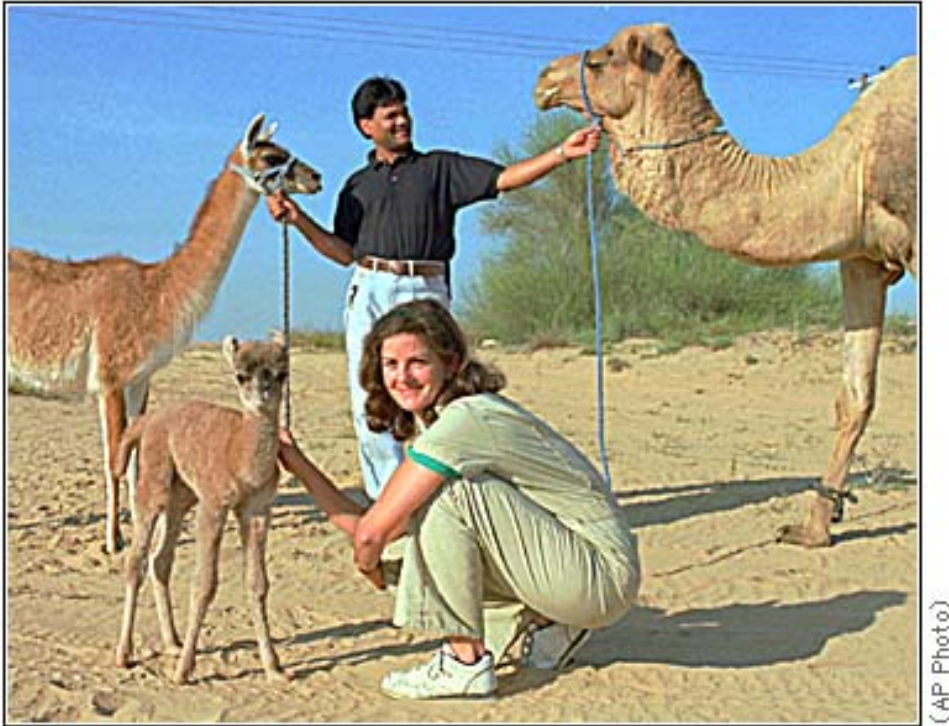
- Consider humans, where some genes:
 - Have a common ancestor for a specific ethnic group (e.g. Duffy)
 - Have a single common ancestor for all humans (e.g. mtDNA) not shared with other hominids
 - Have a common ancestor in the population that gave rise to Neanderthals, Denisovans, and modern humans
 - Have a common ancestor in the common ancestor of the great apes (HLA loci)!
- Even though sub-Saharan Africans apparently share a common ancestor and a unique shared trait (DuffyO) they don't seem to be a species....

Interfertility as a criterion

Degrees of interfertility:

- Freely interbreeds in the wild
- Rarely interbreeds in the wild
- Will interbreed if brought together (as in a zoo)
- Rarely interbreeds even if together
- Can be crossed by human intervention
- Completely uncrossable

With enough effort....



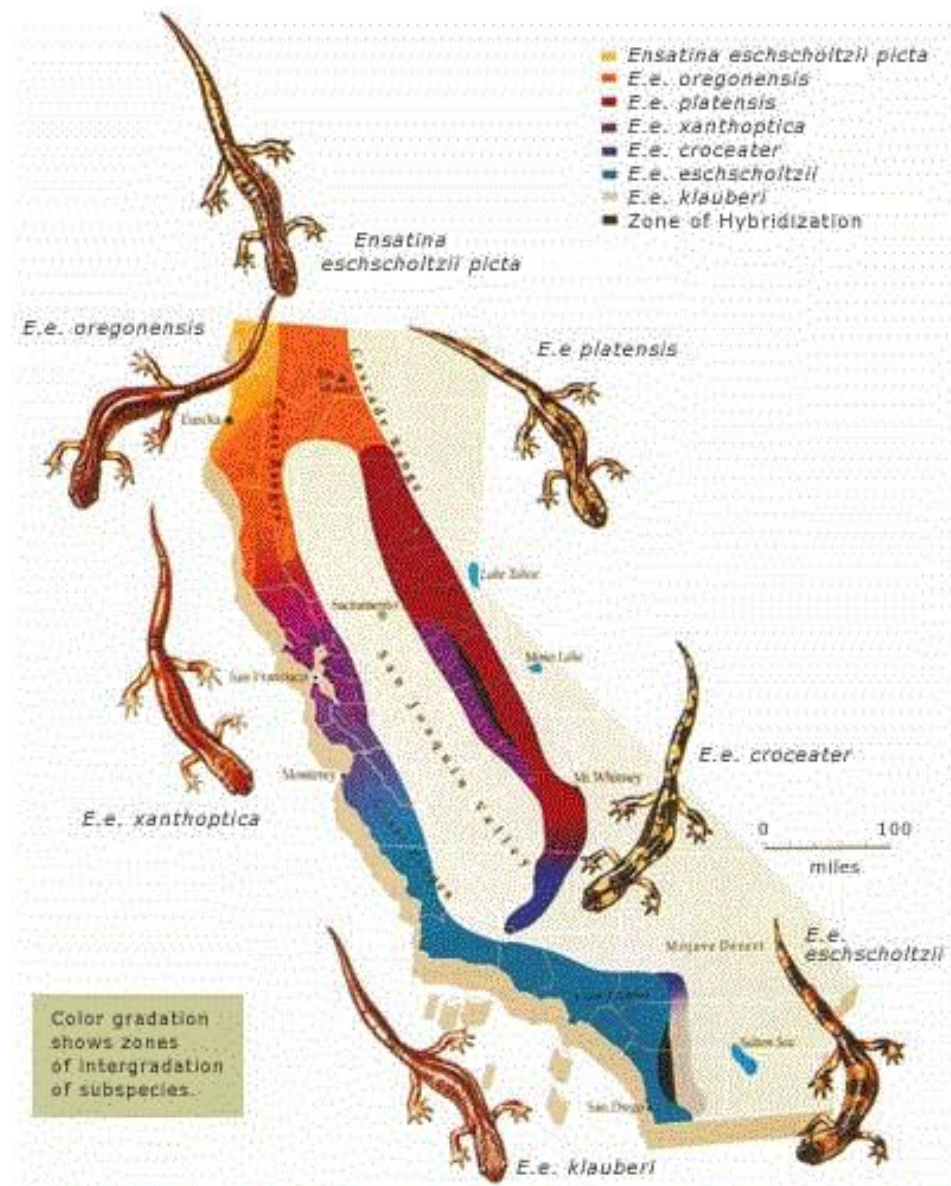
Cross, by artificial insemination, between camel and llama, species thought to have diverged 30 million years ago

Isolation by infection

- Male *Drosophila* infected with *Wolbachia* can no longer reproduce with uninfected females
- *Wolbachia* infection causes instant one-directional reproductive isolation
- Two *Wolbachia* strains can cause bi-directional isolation—by the BSC, speciation
- It is odd to think of an infection as changing a fly's species!

Ring species

- *Ensatina* salamanders
- Each adjacent pair of populations in this ring can interbreed
- Populations from the far ends of the ring cannot

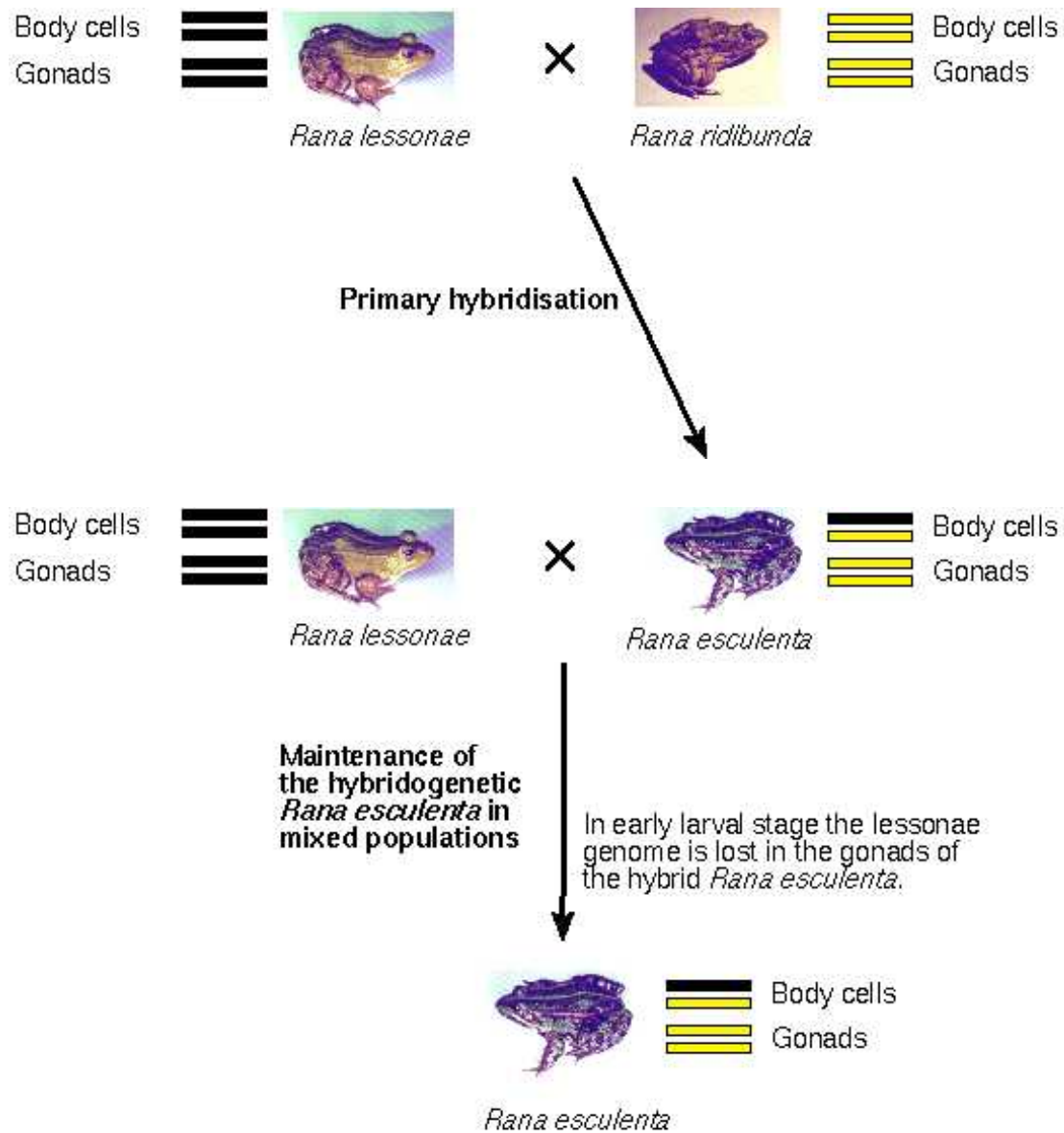


Ring species

- How many species?
 - BSC: just one (gene flow)
 - Genic: more than one? (differential adaptation)
 - Phylogenetic:
 - * Depends on cutoff
 - * May vary from gene to gene
 - * Poorly defined if differences are not fixed (i.e. polymorphism within populations)
- This may be speciation in mid-process
- Another species like this: black-headed gulls (around the world)

An opinion

- “Species” is a human construct
- Gene pools in nature do all sorts of things
- Some are much more separate than others, but...
- there is no hard line between connected and separated gene pools



Hybridogenic species

- An adaptation in *P. lessonae* will be present in *P. esculenta* but not transmitted from there
- An adaptation in *P. esculenta* will be inherited only by *P. esculenta*
- Not "biological species" as they interbreed
- *P. esculenta* may be a "genic species" because it has its own pool of adaptations
- *P. esculenta* has distinctive morphology and behavior

Ambystoma platineum

- All-female species; sperm needed only to activate the egg
- Usually triploid ($3N$) but sometimes $4N$, $5N$
- In preparation for meiosis they double their chromosomes one time more than usual
- Is this self-fertilization or cloning?



Amazon salamanders

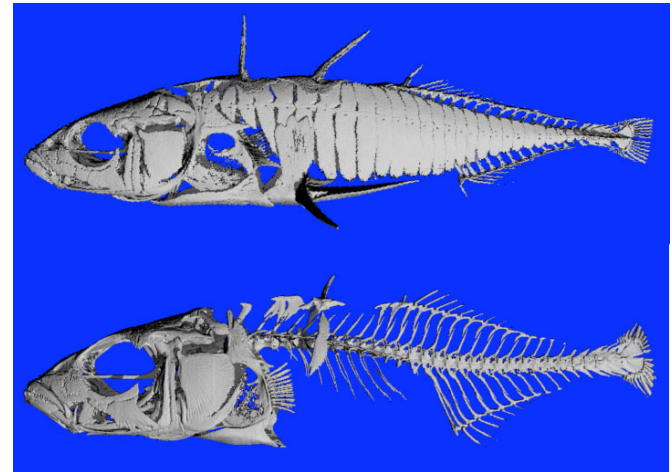
- They may carry chromosomes from the sexual species *A. jeffersonianum*, *A. laterale*, *A. tigrinum* or *A. texanum*
- Many have chromosomes from multiple sexual species
- Often the mtDNA is from a different species than the nuclear chromosomes
- Probably a few sperm sneak through to increase ploidy—they are not 100% asexual

Amazon salamanders

- Genome-wide, *A. platineum* animals are not particularly related to each other
- The only thing they share is (hypothetically) a group of genes which lead to the all-female phenotype
- Does the existence of *A. platineum* cast doubt on the validity of the sexual species?
- Can *A. platineum* itself be considered a species at all?

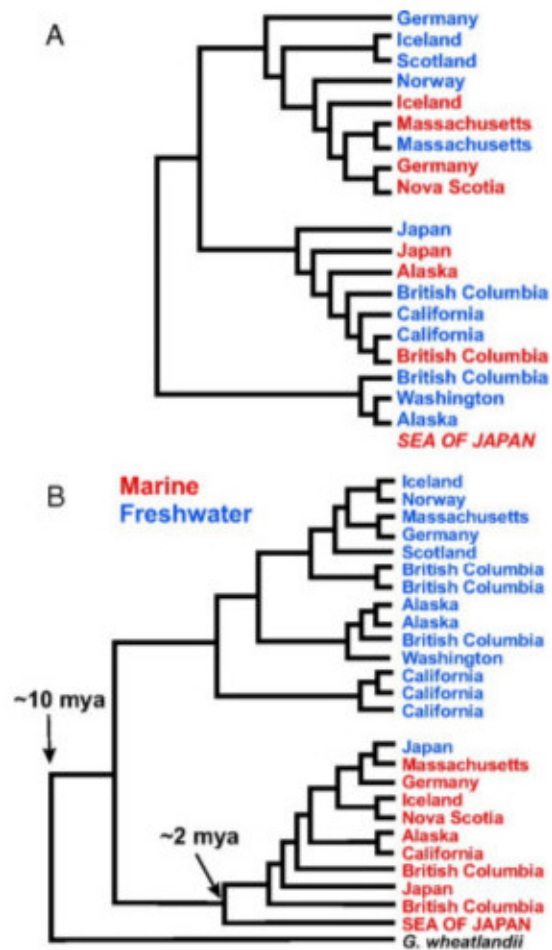
The species boundary is not where you think

- Three-spined sticklebacks live in both fresh and salt water
- Salt-water populations have heavy bony plates, fresh-water do not
- This difference is purely genetic (it doesn't matter where you raise the fish)
- Are these two species of sticklebacks?



Sticklebacks

- Loberg Lake in Alaska lost its fresh-water population
- Plated fish invaded from the ocean
 - In 13 generations the population was plateless
 - Too fast for mutation
 - Ocean population must contain genes for plateless condition (recessive?)
- In a phylogenetic tree, fresh-water sticklebacks are related to local salt-water sticklebacks
- Maybe they could become a new species, but they haven't yet



(A) whole genome, (B) fresh-water adaptation gene

Pre-mating reproductive isolation

- Reproduction fails before fertilization happens:
 - Different breeding season
 - Different mating grounds
 - Different mating behavior
 - Males and females not attractive to each other
 - Incompatible genitals
- *Presence of the other species does not reduce fitness*

Post-mating reproductive isolation

- Reproduction fails around or after fertilization:
 - Mating is sterile
 - Hybrid offspring are inviable or sickly
 - Hybrid offspring are sterile
- *Presence of the other species can reduce fitness*

Cost of post-mating isolation

- If there is no pre-mating isolation, contact between species reduces the fitness of individuals in the contact zone
- They will mate but produce few or no viable offspring
- Therefore, wherever there is:
 - Post-mating isolation
 - Contact between the species
- ...then there is selection for pre-mating isolation
- Species pairs that have only post-mating isolation probably never interact

Practice problem



Image from Wikipedia, photographer hkandy

Practice problem: Ligers

- Hybrids of a male lion and a female tiger
- Lion and tiger ranges do not overlap today but did in the past; legends suggest wild-born ligers may have existed then
- Sometimes happen by accident in zoos/circuses
- Male ligers do not produce viable sperm, but females can be fertile
- What can we say about reproductive isolation of lions and tigers?

Haldane's Rule

- “In hybrids, when one sex is absent, defective, or sterile, it is the heterogametic sex” (two unlike sex chromosomes)
 - Male mammals, flies (XY)
 - (60 documented cases of fertile female mules; none of fertile males)
 - Female birds, butterflies, campion flowers (ZW)
- Few exceptions, mostly in *Drosophila*

Haldane's Rule – why?

Various theories:

- Hypotheses that explain both XY and ZW
 - Hemizygoty of sex chromosome is a vulnerability
 - Haploid parts of the genome diverge faster so become incompatible sooner
- Hypotheses for heterogametic males only:
 - Males evolve faster (sexual selection, smaller effective population size)
 - Meiotic drive in sperm easier than in eggs
- More than one of these may be true

Ligers and tigons

- Liger (male lion x female tiger):
 - Huge animals
 - Male sterile, female sometimes fertile
- Tigon (male tiger x female lion):
 - Lion-sized animals
 - Male sterile, female sometimes fertile
- Differences likely due to epigenetic imprinting (male and female leave different “marks” on the genomes they transmit)
- Does follow Haldane’s Rule

Hybrids vs. species

- Old view:
 - Species should be protected
 - Hybrids need not be protected, and perhaps should be eliminated
- New view:
 - Populations with unique genetic traits are valuable even if hybrid
 - Many ecologically important species originated as hybrids
 - Hybridization bad if it displaces original species (Northwest Crows?)

Discussion

- Red wolves are currently a protected species
 - If they turn out to be an ancient gray wolf/coyote hybrid, would that matter?
 - If they turn out to be a recent hybrid, would that matter?
 - Should we try to prevent wolf/coyote hybridization? (Usually done by sterilizing coyotes in overlap areas)



Image by LaggedOnUser



One-minute responses

- Tear off a half-sheet of paper
- Write one line about the lecture:
 - Was anything unclear?
 - Did anything work particularly well?
 - What could be better?
- Leave at the back on your way out