Today's lecture

- Reproductive isolation
- Hybrids
- Modes of speciation
- Other topics in speciation

One-minute responses

- Q: Are plants living on a toxic mine likely in the process of forming new species?

- A: I use this exact example in this lecture!

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
- Therefore, whever 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

Ligers

Image from Wikipedia, photographer hkandy

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
  - Hemizygosity 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?)

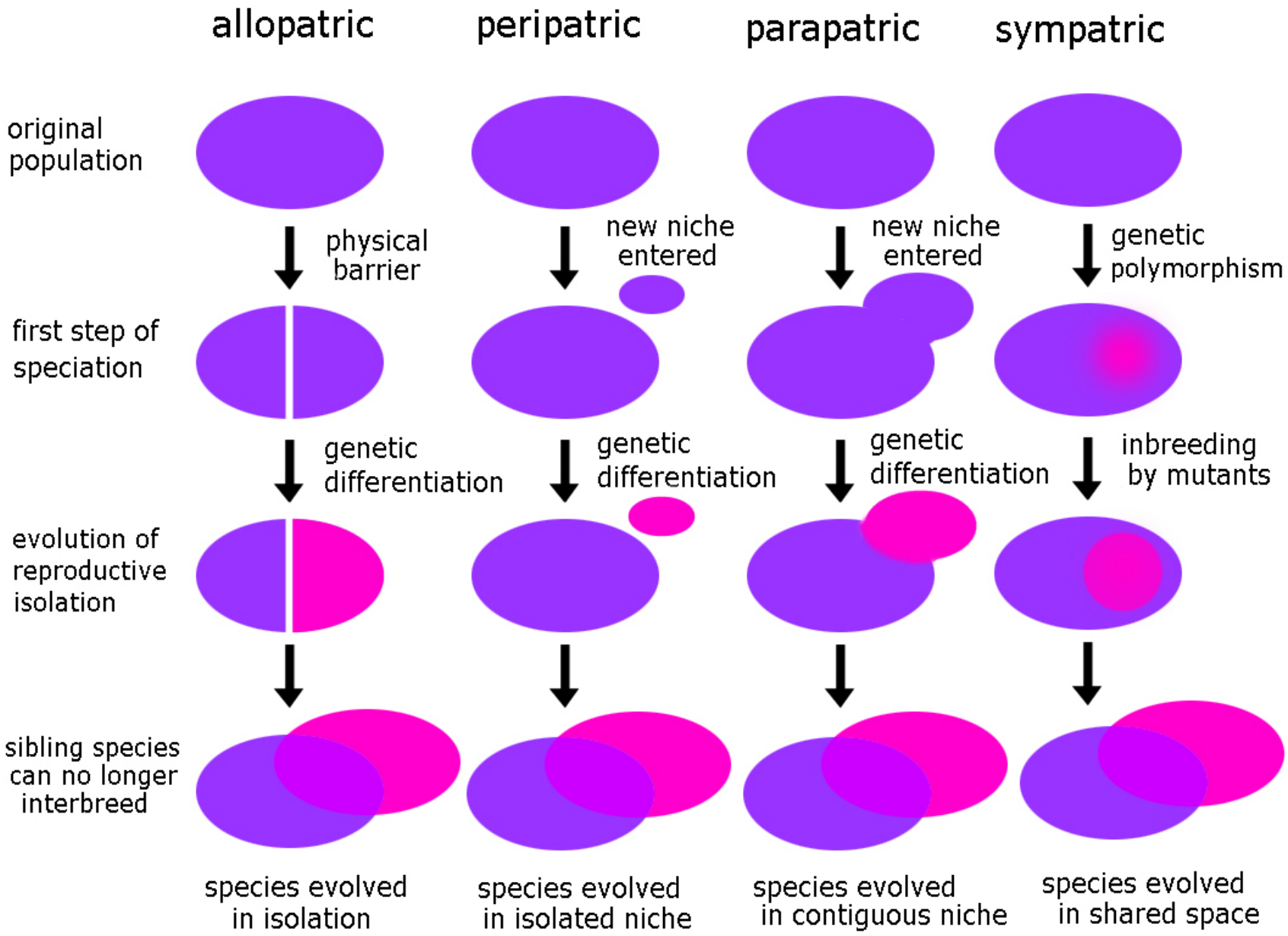
Discussion

- 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

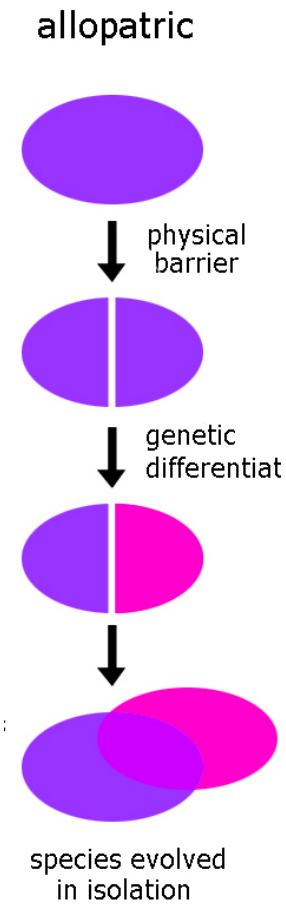
Speciation

- (Gradual) speciation is a process:
  - One well-mixed population
  - Two populations with slight differences
  - Two well-defined populations with clear differences
- Differences could be genomic, morphological, or behavioral
- A given length of separation does not produce a predictable amount of change in genome, morphology, or behavior!


allopatric
peripatric
parapatric
sympatric
original population
physical barrier
new niche entered
new niche entered
genetic polymorphism
first step of speciation
genetic differentiation
genetic differentiation
genetic differentiation
inbreeding by mutants
evolution of reproductive isolation
sibling species can no longer interbreed
species evolved in isolation
species evolved in isolated niche
species evolved in contiguous niche
species evolved in shared space

Allopatric speciation

- "Separate homelands"
- A population is divided by a physical barrier, and the two parts evolve separately
- No selection for reproductive isolation
- Isolation can develop as a side effect of drift and adaptation
- If the species later come into contact, selection favors pre-mating isolation



Allopatric speciation

Forces that can lead to reproductive isolation in allopatric species:

- Adaptations to different environments
- Changes in major developmental pathways
- Changes in gene order
- Changes in chromosome number or structure
- Genetic drift in key traits such as mating behavior, egg/sperm recognition

Allopatric speciation–examples

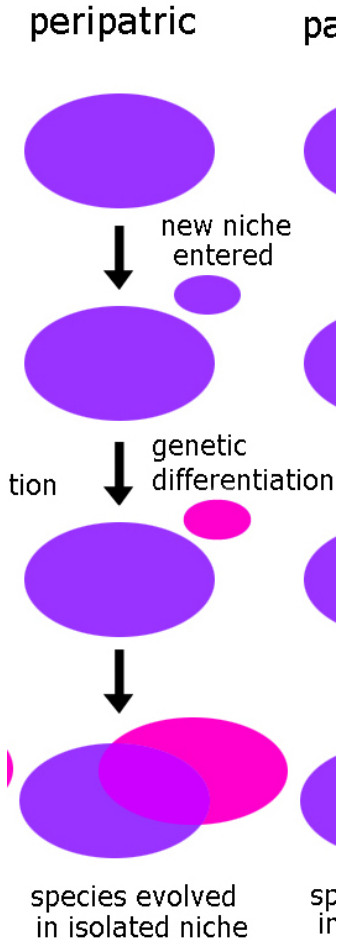
- Separation of continents (camel versus llama)
- Ice Age separation of populations (salamanders)
- Isolation of a lake from river system (kokanee)

Allopatric speciation sometimes fails to happen

- Mangosteen populations in Africa and South America:
  - interfertile
  - appear similar
  - considered the same species
- How did they cross the Atlantic? Or have they been isolated since Africa split from South America (Cretaceous)?
- In Madagascar (40 km from Africa) are 19 distinct indigenous species of mangosteens
- Without a force actively promoting reproductive isolation, it does not always arise

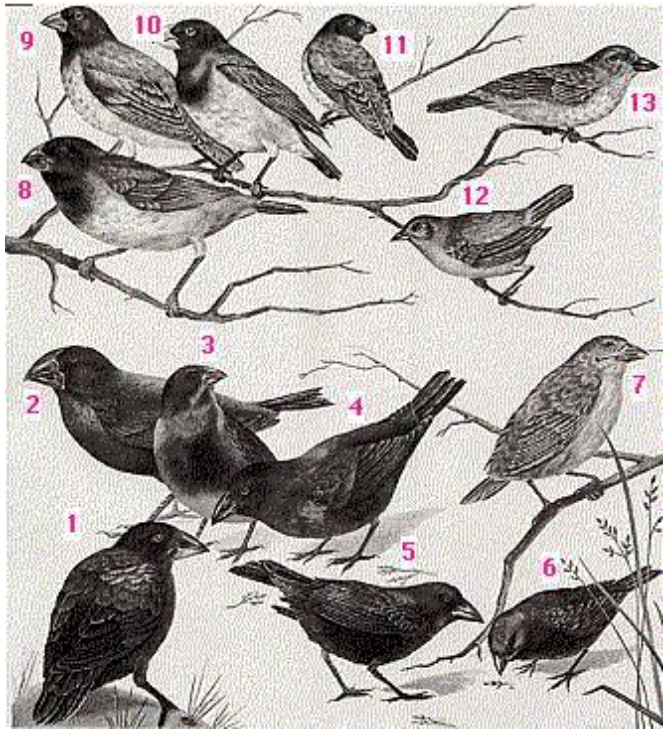
Peripatric speciation

- A variant of allopatric speciation
- A *small* group is isolated from the main population
- Genetic drift causes rapid genetic divergence
- Newborn peripatric species have low genetic diversity (bottleneck)
- After a long time, may be hard to tell



Peripatric speciation–examples

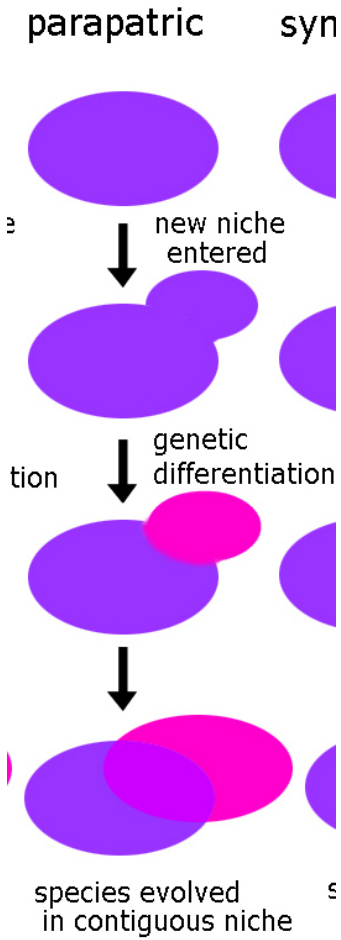
- Colonization of an island (Hawaiian Drosophila, Darwin's finches, Malagasy mangosteens)
- Habitat fragmentation (grasshoppers)
- Colonization of a new host (SIV virus becomes HIV)



1-7 are ground finches, 8-13 are tree finches.

Parapatric speciation

- "Adjacent homelands"
- Two populations are partially separated, but there is still significant gene flow
- Migration will prevent populations from evolving independently if $4Nm >> 1$ unless opposed by strong selection
- How can populations becomes species in the face of strong gene flow?



Parapatric speciation in action

- The grass *Anthoxanthum odoratum* can live on metal-contaminated soil
- Initially gene flow was probably high, but hybrids are unfit
- Modern populations on toxic soil have a different flowering season
- Other plants in the same situation become asexual instead

Parapatric speciation

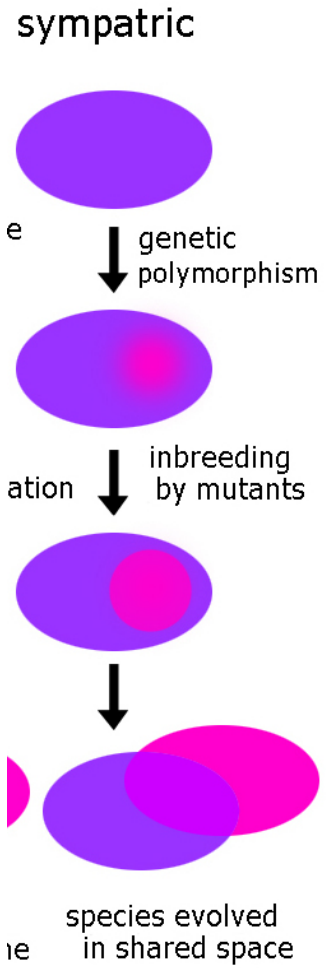
- I studied 5 groups of ducks in South America
- Mountain populations have unusual hemoglobins which help them fly at high altitude
- In 4 of the groups, mountain and lowland are considered the same species, and genetics suggests considerable gene flow
- In 1 case, mountain and lowland are considered separate species, though there is apparently still a little gene flow
- Gene flow lowers fitness, so reproductive isolation may eventually arise

Puna Teal (*Anas puna*), photo courtesy of Dick Daniels

Silver Teal (*Anas versicolor*), photo courtesy of Claudio Dias Timm

Sympatric speciation

- "Same homeland"
- Speciation with no physical separation at all
- How could this happen? Possibilities:
  - Polyploidization
  - Wolbachia
  - Self-fertilization or cloning innovations
  - Intense inbreeding
  - Non-physical barriers



Non-physical barriers: host plant

- Maggot flies in North America lived on native hawthorn
- Settlers introduced apple about 200 years ago
- Populations are differentiating because:
  - Female flies tend to lay eggs on plants of their natal type
  - Male flies tend to look for mates on plants of their natal type
- This situation could lead to sympatric speciation

Non-physical barriers: time

- Some Pacific salmon take exactly two years to breed
- Population A spawns 2014, 2016, 2018...
- Population B spawns 2013, 2015, 2017...
- Could these speciate?
  - Pro: gene pools appear separate
  - Con: no environmental differences to adapt to
  - Con: even one renegade breeder per year could keep gene pools connected

Periodic cicadas

- The periodic cicada has reproductive isolation by time
- Some species have 17-year cycles, others 13
- 13-year cicadas may originate from "mistakes" made by 17-year cicadas
- 13-year populations are more closely related to nearby 17-year populations than to each other

Speciation discussion problems

- Each Greek island has its own species of water frogs
- Physically and behaviorally similiar, but not interfertile
- During the Ice Age, lower sea levels allowed frogs to move among islands
- Today salt water is a near-complete barrier to frog movement

- What is plausible mode of speciation?
- What additional evidence would we like to have?

Speciation discussion problems

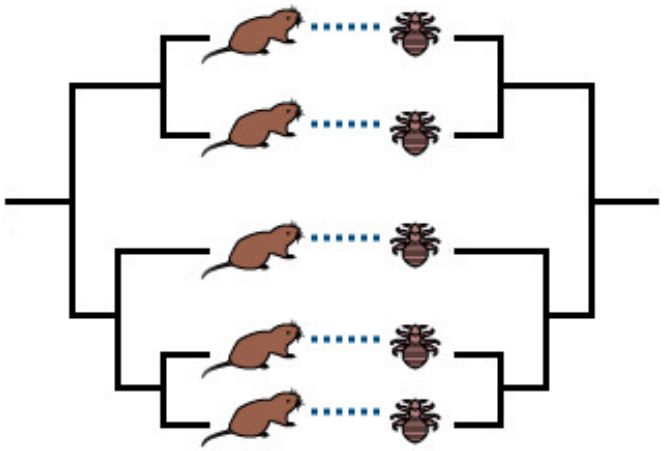
- Fossils considered potentially a hominid species $Homo$ $floresiensis$ found in Indonesia
  - Human-like creatures around 3'6" tall and 55 lbs
  - Otherwise somewhat similiar to $Homo\ erectus$
  - Small stone tools present in strata
  - Brain of type specimen smaller than that of a chimpanzee
  - Last dates around 13,000 years ago
- Species or anomaly? How could we find out?

Speciation discussion problems

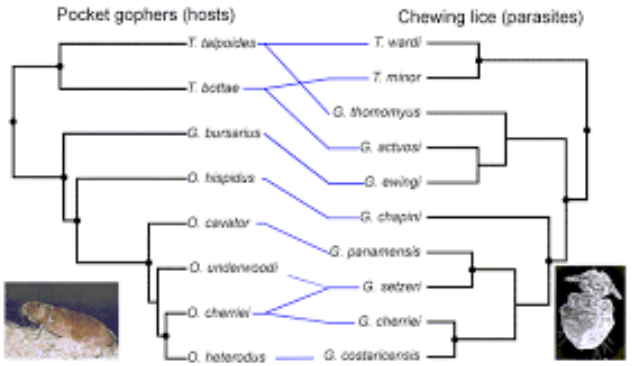
- Hypothesis 1: dwarf island species
  - Other Indonesian island taxa also smaller than average (mammoths, etc)
- Hypothesis 2: pathology such as Laron syndrome
- Unfortunately no DNA has been recovered from fossils (tropical climates are not good for DNA survival)
- Interesting recent approach: look for divergent ancient sequences in modern inhabitants of the area

Cospeciation

- Host species and parasite species often speciate together
- Species trees of the two groups will look very similar
- Example: gophers and gopher lice
- Reproductive isolation of hosts may isolate parasites
- Adaptation of hosts may spur adaptation of parasites (or vice versa)



Idealized schematic



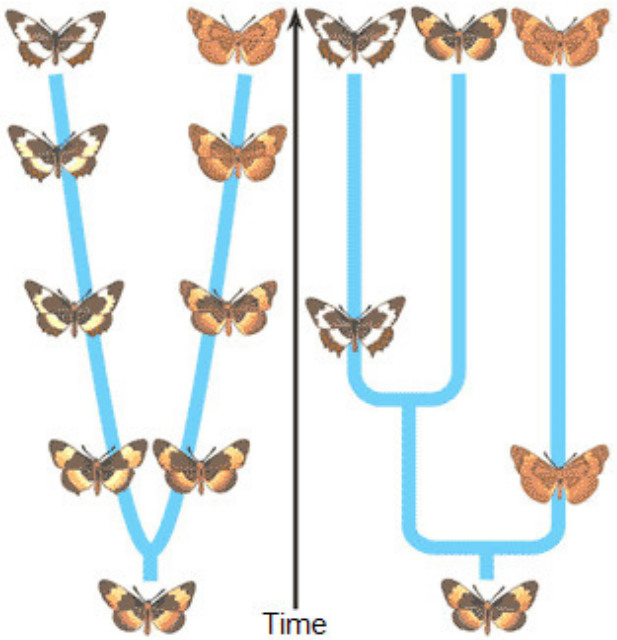
Real data

Gradual versus punctuated

- Classical model: species slowly accumulate differences

- Punctuated equilibrium model (Stephen Gould and colleagues)
  - Burst of change at speciation
  - Relative stasis elsewhere

- Favored by paleontologists, who find bursts of change in the fossil record



(a) Gradualism model. Species descended from a common ancestor gradually diverge more and more in their morphology as they acquire unique adaptations.

(b) Punctuated equilibrium model. A new species changes most as it buds from a parent species and then changes little for the rest of its existence.

Some thoughts on punctuated evolution

- Paleontological species definition encourages this view because "gradual" species can't be recognized as such
- Not all species evolve the same way
- Major changes in body or lifestyle probably require a burst of changes

Domesticated foxes

- Long-term breeding project started by Belyaev in Siberia, 1959
- Fox kits selected for sociability with humans
- Results not only sociable but oddly dog-like

Wild silver fox: image by Zefram

Russian domesticated foxes

Domesticated foxes

- Complex differences from wild foxes:
  - Very tame even when raised in cages
  - Domestic-like color patterns
  - Wagging tails, whining, barking
  - Can follow pointing finger or gaze
  - A few try to reproduce more than once/year
  - Differences in hormone levels, developmental timing
  - Differences in skull and body plan

- Major change in developmental pathway?

Stasis

- Some organisms appear to change very little over time:
  - ginkgo
  - coelacanth
  - horseshoe crab
- Other organisms change much more rapidly and diversify into multiple species
- Ideas:
  - Change-resistant developmental "program"
  - Broad ecological niche
  - No improvements in easy reach
  - Cryptic species?

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