Amphibians: diversity, life history, and declining populations

1. The move to land: lobe-finned fish

Compared to “ray-finned fish” (salmon, tuna, etc), “lobe-fins” have:
- Reduced skeletal elements in their fore and hind fins,
- Greater flexibility at what would become elbows and knees, and
- More muscularization of proto-limbs (∴ more power and control).
- Most lobe-fins (including us) also have choanae (internal nostrils that open into the oral cavity), which allow breathing through the nose.

Tetrapods:
- Lost anal and dorsal fins
- Fully transformed remaining fins into muscularized limbs.
- Dactyly (evolution of digits)
- Aquatic → terrestrial habitat

Why make the move to land? What problems are caused by a move to land?

2. Some diagnostic characters of “modern amphibians”
- Glandular skin that contains both mucous and poison glands (but no epidermal structures)
- Three-chambered heart (two atria, one ventricle)
- Cutaneous respiration (most species also have lungs, but the three-chambered heart does not provide enough pressure to fully inflate the lungs, so amphibian lungs aren’t that efficient)
- Complex inner ear anatomy: the “papilla amphibiorum,” a membrane that allows amphibians to hear acoustic signals of less than 1,000 Hz (very low “bass” sounds).
- Highly variable chromosome number, genome size, and ploidy.

Where Linneaus got it right and where he got it wrong:

3a. Major groups: caecilians (Gymnophiona): Limbless, burrowing, tropical amphibians
- Circumtropical (except Madagascar)
- Adults are almost entirely subterranean (and therefore mostly blind)
- Internal fertilization, plus some very interesting parental care and reproductive modes.

3b. The salamanders (Caudata): salamanders (and newts, which are just a small group of often aquatic salamanders within the family Salamandridae)
- The only major group of amphibians with both tails and limbs
- Most diverse in SE U.S.—adaptive radiation spread them to most of North America and some of Central America, plus a few in Europe and east Asia (while ancient landmass of Laurasia existed).

Salamander life histories

- Most common life history: aquatic larvae, terrestrial adults, internal fertilization via spermataphore, eggs laid in water. (True amphibious lifestyle)
- Alternate life histories: ***paedomorphosis***. Reproductive adults retain larval characteristics, typically those associated with an aquatic lifestyle (these individuals live their entire lives in water). Adaptations include retention of external gills and dorsal fins. Species may have obligate or facultative paedomorphosis.
- *Notophthalmus viridescens* ("Eastern Newt"). 3 part life history: Aquatic larvae metamorphose into terrestrial, non-reproductive efts, which stay on land for several years before metamorphosing again into aquatic, reproductive adults.

How do salamanders breathe? What are the respiratory organs of salamanders?

Body shape can drive ecology & behavior: Being lungless, plethodontids have evolved long, thin bodies, yielding high surface area: volume ratios for increased efficiency of cutaneous respiration. What is the downside of this body shape?

3c. Diagnostic features of Anura: *What makes a frog a frog?*

- The tailless amphibians: postsacral vertebrae are fused into the "tailbone".
- Various adaptations for jumping, including elongated, fused hindlimbs.
- Most frogs have no ribs.
- More geographically widespread than Gymnophiona or Caudata, but still more prevalent in the tropics than elsewhere.
- Most are nocturnal.
- Almost all anurans have external fertilization, and almost all are oviparous.
- Most anurans mate in a posture called ***amplexus***, in which the male grasps the female in the armpits or at the waist. In some species, amplexus can last for months.
- Length of breeding season is often limited by climate, or seasonal availability of breeding sites (such as ephemeral pools). Temporal patterns of reproduction can be roughly divided into two types: ***explosive breeding*** and ***prolonged breeding***. What generalities are likely to be true regarding which frogs breed explosively, and which have prolonged breeding seasons?

Frog life histories: the common mode, and alternate modes:

4. Amphibian habitat

- Given that many amphibians spend part of their lives on land, and part in the water, those species are likely to live close to the border between land & water.
- Amphibians with "typical" life histories—aquatic larvae and terrestrial adults—can be broadly separated into two types: those that live in lentic, or slow moving water (such as

lakes and ponds), and those that live in lotic, or fast moving water (such as rivers and streams).
- What might some of the differences between these 2 broad types be?

Riparian zone
- **Definition**: terrestrial zone adjacent to the channel (river, stream) which strongly influences, and is strongly influenced by, the channel. A river and its riparian zone exchange material both on the surface and below the surface (in the hyporheic zone and water table). The riparian zone usually includes the floodplain plus some upslope / terrace land.
- In Western WA, torrent salamanders, (*Rhyacotriton*) giant salamanders (*Dicamptodon*), & tailed frogs (*Ascaphus*) live in the riparian zone of semi-seasonal fast-moving streams.

Effects of forests on rivers
- Shading from solar radiation (temperature and light). A forested riverbank is cooler and darker than an unforested bank. Remove the buffer, ⇑T & rate of evapotranspiration.
- Input of nutrients and sediments from upslope and from uptree (leaves, large woody debris). Remove the buffer, ⇑ erosion and siltation.
- Riparian (buffer) zones also serve to intercept (excess) N from cropland and pasture.
- Habitat creation for aquatic communities along banks (roots, treefalls)

Effects of rivers on forests
- Streams, and therefore riparian forests, are quite different depending on what stream order they belong to.
- Amphibians move frequently between rivers and forests, thus keeping nutrients moving between them as well.
- Nutrients in riparian forests come, in part, from streams, some of which ultimately comes from the marine environment.

Amphibians and nutrient cycling
- Accepted dogma has long been that while amphibians do have effects on populations of their prey species, that's about the extent of their impact on ecosystems.
- New data brings this conclusion into question. One set of researchers (Beard *et al*., 2002) hypothesized that top-down effects of vertebrate predators (specifically frogs) will, in turn, affect nutrient cycling rates in terrestrial systems.
- ***How might you test this hypothesis in the field?***

Why do *ratios* of available nutrients matter for ecosystem function?

Forest management and amphibians

- Through the world, but particularly in the PNW, forests are being managed in ways that impact amphibian (and other) inhabitants, but little research has been done to measure those impacts.
- Since the 1950s, application of N-based fertilizers to managed forest lands, in order to accelerate tree growth and thus increase timber production, has been standard practice.
- In 2001, three forest-dwelling 'phib species were studied with respect to their response to Nitrogen addition in their habitat (Marco *et al.*, 2001): *Rhyacotriton variegatus* (Southern torrent salamander), and *Taricha granulosa* (rough-skinned newt).
- Methods: Two experiments: toxicity and avoidance.
- Results: All species avoided Nitrogen treatments when they had the option. Two of three species suffered an increase in mortality when exposed to Nitrogen fertilizer in the lab. Newts did not.
- Interpretation: Nitrogen fertilization is bad for amphibians. But these results beg a question: Why are two of these species more susceptible than the other?

5. Phenotypic plasticity: the capacity for marked variation in the phenotype as a result of environmental influences on the genotype during development.

A few things that are subject to phenotypic plasticity:

- growth rate
- juvenile and/or adult morphology
- form at reproductive age (facultative paedomorphosis)

Phenotypic plasticity: response to predators & competitors. In wood frog tadpoles (*Rana sylvatica*):

- The presence of competitors induced tadpoles to increase their activity and generally develop larger bodies and smaller tails.
- But while competitor-induced traits provide individuals with increased competitive ability, those individuals have decreased predator resistance as a result.
- Conversely, predator-induced traits provide individuals with increased predator resistance, but decreased competitive ability.
- This suggests that predator- and competitor-induced plasticity have evolved a tradeoff between competitive ability and ability to resist predators. (Relyea, 2002)

Phenotypic plasticity in caudates: case study (Michimae and Wakahara, 2002)

- Larval *Hynobius retardatus,* which breed in early Spring in Japan, have
- two distinct morphs: "normal," and broad-headed, "cannibal" morphs.
- The cannibal morph is induced when density of other larval 'phibs (conspecifics and heterospecifics) is high. Three hypotheses have been proposed to explain this observation, as follows:
- The broad-headed morph is induced to facilitate:
    1. feeding on nutritious conspecifics
    2. exclusion of competitors for food or space; or
    3. feeding on large, tough prey when smaller prey items are unavailable.
    Predictions…?

6a . Declining amphibian populations: Evidence

6b. Amphibian declines: hot spots
Amphibian declines primarily occurring in higher altitude zones: Western US, Costa Rica, Panama, Venezuela, Australia. In general: species with entirely aquatic life histories are most affected; "typical" amphibious life histories are intermediate; and those without aquatic phases the least affected. (Lips, 1998).)

6c-1. Observing amphibian declines: The sad tale of Karen Lips and her montane frogs in Costa Rica.

- The chytridiomycete fungus appears to be the proximate cause of many recent declines.
- This fungus has now been found in sick and dead adult anurans collected during mass mortality events in Central America, Australia, and Europe (Berger *et al.*, 1998); and most recently, the Sierra Nevada in California (Fellers *et al.*, 2001).

6c-2. Global warming & infectious disease

- Climate change may raise the transmission rate of many diseases—effects not only on humans, but amphibians, too.
- At least one recent mass extinction associated with pathogen outbreaks is tied to global warming: Seventeen years ago, in the mountains of Costa Rica, the Monteverde harlequin frog (*Atelopus* sp.) vanished along with the golden toad (*Bufo periglenes*). An estimated 67% of the 110 or so species of *Atelopus*, which are endemic to the American tropics, have met the same fate, and the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) is now implicated.
- Analysing the timing of losses in relation to changes in sea surface and air temperatures, the authors conclude with 'very high confidence' (> 99%) that large-scale warming is a key factor in the disappearances.
- Temperatures at many highland localities are shifting towards the growth optimum of *Batrachochytrium*, thus encouraging outbreaks. Two, coincident changes are observed:
  - night-time temperatures in these areas are shifting closer to the thermal optimum of *Batrachochytrium*, and
  - increased daytime cloudiness prevents frogs from finding 'thermal refuges' from the pathogen.
- Climate change is thus promoting infectious disease and eroding biodiversity (Pounds *et al*., 2006)

6c-3. Responses to pollution

- Both *Rana lessonae* and *R. esculenta* (hybrid between *R. lessonae* and *R. ridibunda*) display some phenotypic plasticity in response to environmental changes.
- Triphenyltin (TPT) compounds are used worldwide as agricultural fungicides.
- TPT is known to kill fish (e.g. some *Oncorhynchus* spp—salmon and trout) and arthropods, including mosquito larvae, odonate (dragonfly and damselfly) larvae, and snails.

- Fioramonti *et al* (1997) performed an experiment to test effects of TPT, pH, and genotype on tadpoles. (Why pH? Accumulation of TPT is known to be pH dependent.)

Affects of TPT, pH, and genotype on survival to metamorphosis

- TPT slows growth rate / lengthens time to metamorphosis in both parental species and hybrids.
- Lower pH better for parental species (*R. lessonae*); hybrids do better at high pH.
- Survival of parental species much lower in polluted habitats; hybrids are better generalists, and are not as affected.

However: Recent USGS (U.S. Geological Survey) research suggests that rural areas and farms may be friendlier to frogs and toads than urban areas. In two Midwestern states, both frog and toad abundance and species richness were low in urban areas but near normal in agricultural areas. The majority of the land in the Midwest is cultivated, monocropped agricultural land. Amphibian populations in these agricultural lands actually do okay, if…***what?***

6c-4. Amphibian declines: the role of "indirect effects"

6c-5. Overexploitation

6c-6. Amphibian declines: additional hypotheses

- Life histories put them at greater risk (amphibious w/absorptive surfaces; carnivorous (bioaccumulation); both metamorphosis & emergence from aestivation may release toxins all at once)
- Climate change not related to disease (increased UV, holes in ozone, and temperature change put ectotherms at particular risk)
- Acid rain (low pH decreases fertilization rate, as sperm decay)
- Habitat loss and degradation from deforestation, mining, dams, grazing, urbanization
- Pesticides, fertilizers, and pollutants (which are often endocrine disrupters)
- Introduced predators & competitors

6d. Small group workshop

1. You are a new researcher in an ecosystem once thought to be teeming with several species of amphibians, but you aren't finding many. How do you go about assessing whether or not you're seeing a real, and permanent, decline in amphibian populations? What questions do you ask, and how do you answer them?
2. Now that you have concluded that several species in this region are indeed declining, how do you go about figuring out what's causing the decline? Using some of the possible hypotheses (from readings (especially Collins & Storfer, 2003) and lecture), devise tests that will allow you to distinguish between some of these hypotheses.