Sexual & Asexual Reproduction

- Sexual reproduction: Production of haploid gametes (by both sexes) & their union to form a zygote
  - Both genomes involved in meiosis
- Production of genetically variable offspring
- Asexual reproduction: The production of reduced (haploid) or unreduced (diploid) eggs
- Clonal inheritance
  - identical, unmodified genomes transmitted
- 4 general mechanisms involving sexual and asexual reproduction

Hybridogenesis

- Production of reduced gametes by both sexes, but only maternal genome is transmitted to next generation.
- Meiosis occurs, but not until paternal genome is deleted and maternal genome is duplicated.
- Clonal inheritance. Only of one genome!

Bisexual Reproduction (Sexual)

- Most species reproduce via sexual reproduction
  - 2 sexes (male & female)
- Meiosis occurs in this individual during gamete formation
- Both genomes involved during meiosis

Eastern Dwarf Tree Frog, *Litoria fallax*

Hybridogenetic diagram:

\[
\begin{array}{c}
\text{♂} \\
BB \\
\downarrow \\
⊗B \\
\downarrow \\
\text{AB}
\end{array}
\]
Hybridogenesis Occurs in Only a Few Anurans

- *Rana esculenta* complex of Europe
  - Involves 2 species: *R. lessonae* and *R. ridibunda*
  - Both male & female hybrids formed by crossing these species
  - Hybrids originally classified as "*R. esculenta*"

see fig. 4.17

Gynogenesis

- Unisexual species
- Production of unreduced eggs, but development must be initiated by contact with sperm, termed *klepton*
- Meiosis does not occur
  - Individual will produce new unreduced eggs
- Truly clonal inheritance

The *Rana esculenta* Hybridogenesis Case

<table>
<thead>
<tr>
<th>Males</th>
<th>LL (<em>lessonae</em>)</th>
<th>RR (<em>ridibunda</em>)</th>
<th>RL (<em>esculenta</em>)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL</td>
<td>LL</td>
<td>RL</td>
<td>RL, RRL, RLL</td>
</tr>
<tr>
<td>RR</td>
<td>RL</td>
<td>RR</td>
<td>RE (RR)</td>
</tr>
<tr>
<td>RL</td>
<td>RL</td>
<td>RE</td>
<td></td>
</tr>
</tbody>
</table>

L = *R. lessonae*  
R = *R. ridibunda*  
RE = variable exclusion of *R. lessonae* genome  
I = inviable

Gynogenesis

- occurs in some fish
- salamanders of the *Ambystoma jeffersonianum* complex
  - sexual species are *A. jeffersonianum* & *A. laterale*
  - unisexual species are: *A. platineum* and *A. tremblayi*

Types of hybrids known:
- Diploid
  - LJ, LT
- Triploid (gynogenetic)
  - LJ, LJJ, LLL, LJT, LTT, LTTi
- Tetraploid (parthenogenetic)
  - LLJ, LJJJ, LLLT, LTTT, LTTTi, LJJTi, LJTT

Silvery Salamander  
*Ambystoma platineum*  
From Illinois (Redmer)

Tremblay’s Salamander  
*Ambystoma tremblayi*  
From New Jersey
Parthenogenesis

• All female populations (unisexual)
• Meiosis does not occur
  - Individual will produce new unreduced eggs
• Truly clonal inheritance
• No males or sperm required

Parthenogenesis

• Parthenogenesis occurs in several (~30) squamate groups.
  - Most studied in the teiid genus *Cnemidophorus*
  - ~45 *Cnemidophorus* species & ~ 15 are parthenogenetic
    – Unisexual species may be diploid or triploid
    – Pseudocopulation: one individual plays the role of male
    – Females involved in pseudocopulation produce more eggs - behavior enhances gonadal activity
• Other Squamates
  - *Rhamphotyphlops braminus* (snake)
  - Some lacertids
  - Some geckos

Parthenogenetic *Cnemidophorus*

Examples
• *C. neomexicanus* (2N) < *C. inornatus* (m) x *C. tigris* (f)
• *C. velox* (3N) < *C. inornatus* (m) x *C. burti* (f) <<<
  < intermediate parthenoform x *C. inornatus* (m)
• *C. exsanguis* (3N) < *C. burti* (m) x *C. inornatus* (f) <<<
  < intermediate parthenoform x *C. septemvittatus* (m)

Similarities of Asexual Organisms

• Origins of asexual species usually are the result of hybridization between two bisexual species
• Most populations are unisexual female (“she-male”) individuals
• Reproduction is via clonal inheritance (at least in part)
Gametes, Fertilization, and Development

Eggs of amphibians and reptiles are structurally very different.

**Amphibians**
- Production of jelly-covered eggs.
- Generally laid in water or moist location on land.
- Only one embryonic membrane, the yolk sac.

**Reptiles - Amniotic Egg**
- Outer shell (leathery or calcareous) protects against water loss
- Eggs of squamates and some turtles take up water during development
- Eggs of crocodilians and some turtles don’t take up water during development
- Shell provides mechanical protection
- Three unique embryonic membranes

Embryonic Membranes of Amniotic Eggs

**Amnion**
- Inner most membrane surrounding embryo

**Chorion**
- Outermost membrane

**Allantois**
- Outgrowth from the rear of gut during development, later it lies beneath the chorion
- Eventually, much of allantois fuses with chorion - chorioallantoic membrane
- Provides large surface for gas exchange
- Unfused portion of allantois stores nitrogenous waste products

**Yolk Sac**
- Maintains the integrity of the yolk proteins

Egg Formation

**Amphibian & Reptile Eggs Provided with Yolk**
- Synthesized in liver
- Consists of lipoproteins, phosphorylated proteins & glycogen
- Provides nutrients to developing embryo

Amount of yolk & relative proportions of main components vary across taxa
Egg Formation

- In some species, embryo’s nutrient source comes mostly from yolk (lecithotrophy)
- Egg-laying (oviparous) species and some live-bearing (viviparous) species.
- Some viviparous species provide some or most nutrients to embryo via a placenta (placentotrophy)
  - e.g. Mabuya heathi, Thamnophis ordinoides, T. sirtalis

External fertilization

Eggs fertilized outside of the female reproductive tract.

- Ancestral condition of Amphibia
- Most anurans exhibit external fertilization
- Eggs released into water, nest, onto substrate or on land.
- Sperm released over eggs (milting)

Internal Fertilization

Eggs fertilized within female reproductive tract

- Independently derived in a few lineages of amphibians
  - *Ascaphus* and few *Eleutherodactylus* possess internal fertilization
  - Intromittent organ in *Ascaphus*
  - Cloacal apposition in *Eleutherodactylus*
- Most salamanders: Salamandroidea
  - Males produce a spermatophore
  - A proteinaceous base topped with a package of sperm
  - Female picks up spermatophore with her cloacal lips (cloacal apposition)
Fertilization in Amphibians

• Most anurans exhibit external fertilization
• Basal salamanders Sirenidae & Cryptobranchoidea
  - Eggs released into water
• Internal in all caecilians
  - Phallodeum - male copulatory organ

Fertilization in Reptiles

Internal fertilization

• Ancestral condition for Reptilia
• Possession of shelled egg requires internal fertilization
• Turtles and crocodilians
  - Males have a single penis
• Sphenodon - the male lacks a copulatory organ and fertilization is completed through cloacal apposition as in birds

Fertilization in Reptiles

Squamata

• Males have paired hemipenes (singular: hemipenis)
• Evagination of cloacal wall; everted when engorged with blood
• Surface ornamented with folds, papillae, and/or spines

Parental Care

Providing care to the eggs and offspring

• Protection and increases chances of offspring survival
• Parental care comes at a cost
• Investment of time and energy
• May increase risk of predation of parent(s)
Parental Care: Amphibians

- Seen in all 3 major amphibian groups
- Egg attendance: Most common form of parental care among amphibians
  - One parent (or both) remains (or attends) with clutch of eggs during development
  - Only form of parental care seen in salamanders and oviparous caecilians
  - ~20% of salamanders (e.g., many terrestrial plethodontids)

Parental Care: Anurans

- ~10% of anurans exhibit parental care - wide diversity of forms
- Egg attendance most common; usually performed by male
- *Eleutherodactylus*, centrolenid frogs, *Alytes* (Discoglossidae), many hylids

Parental Care: Anurans

Some species also attend offspring

- Dendrobatid frogs: Parents guard terrestrial eggs & transport tadpoles from the nest to water
- Some *Dendrobates*, some hylids, and *Chirixalus*: Females attend tadpoles & periodically provide unfertilized eggs as source of nutrients for tadpoles
- Some large aquatic and semi-aquatic frogs attend tadpoles.
  
  *Pyxicephalus*, some *Leptodactylus*

Parental Care: Anurans

Many species carry the eggs on their back

- terrestrial: *Gastrotheca*, *Hemiphractus*, *Flectonotus*, *Fritziana*
  - Aquatic tadpoles or direct development
- aquatic: *Pipa pipa*
- Rhinoderma darwini: Males carry eggs in the vocal sac; eggs undergo direct development
- Rheobatrachus: Gastric brooding frogs
  - Females swallow fertilized eggs; undergo development in stomach; emerge as froglets
Parental Care: Reptiles
Less common

- Essentially non-existent in turtles
- Exhibited by all crocodilians
- Females guard the nests
- At time of hatching, females open nest may assist young to escape from nest
- Some species carry young to the water
  - e.g., American Alligator
- Parents and young often remain together for several months

Viviparity

- Retention of embryos within the oviducts until development is complete (live birth)
- Common in some groups: caecilians and squamates
- Uncommon in others: batrachians
- Absent in others: turtles & crocodilians
- During evolution, viviparity has been accomplished by gradual increases in the amount of time eggs are retained in oviducts
  - *Liochlorophis vernalis* – Latitudinal crossover

Parental Care

- ~100 squamate species exhibit parental care
- Egg brooding in some pythons
- Egg attendance: *Eumeces*, other taxa??
- Some “advanced” snakes
  - i.e., some colubrids, viperids, and elapids

Viviparity

- Main challenge for evolution of viviparity is gas exchange
- Two main changes have occurred to facilitate/increase gas exchange:
  1) Reduction in the thickness of jelly or shell layers in the egg
  2) Increase amount of vascularization in oviduct and respiratory structures of embryo

Rattlesnake giving live birth
Viviparity

Embryonic respiratory structures
• Amphibians: Greatly modified and vascularized gills or tails
• Reptiles: Increased vascularization and development of the chorioallantoic membrane (placenta)

Embryo nutrition
• Lecithotrophy: all nutrients from egg yolk
• Matrotrophy: in amphibians, larvae receive nutrition from oviductal secretions
• Placentotrophy: in squamates, nutrients exchanged via placenta.

The Pros and Cons of Viviparity

Advantages
• Egg protection
• Increased rate of embryonic development
• Advanced development: increased offspring survival

Disadvantages
• Reproductive output is reduced
• Number of clutches and eggs
• Reduced agility of female: increased risk of predation

Viviparity: Amphibians

~25% of caecilians are viviparous.
• Larvae feed on lipid-rich oviductal secretions or unfertilized eggs

4 species of salamanders
• *Mertensiella* and a few *Salamandra*

6 species of frogs
• *Eleutherodactylus jasperi* and some African bufonids

Viviparity: Reptiles

• Viviparity only evolved in squamates, but independently numerous times (>100X)
• Entirely viviparous: *Xenosauridae, Xantusiidae, Aniliidae, Uropeltidae, Acrochordidae, Tropidophiidae*
• At least 34 derivations in *Scincidae*; at least 14 derivations in *Colubridae*
• Rare in many other ‘families’

Viviparity thought to arise with cool environments
• More rapid development: thermoregulating female