Lecture 3: Chondrichthyes
Diversity of methods of embryonic nutrition

- **Chondrichthyes**- cartilaginous fish.
  - Have large eggs, low fecundity.
  - Internal fertilization
  - Wide range of viviparity, ovoviviparity, lecithotropic viviparity, yolk dependent viviparity, placental viviparity, etc.
  - Include: Batoid fishes (rays, skates), sharks, chimeras.
- **Claspers**- used by chondrychthes males to deliver sperm into female reproductive tract.
- **Tanning**- oxidative crosslinking of proteins that results in toughening of the egg-cases. These are tough but permeable. Delivery of oxygen to the egg was a predecessor to viviparity.
- **Chimeras (Ratfish)**
  - **Oviparous, some viviparous fossils**

- **Batoid fishes**
  - Skates are oviparous
  - Sawfish, guitarfish, electric rays, rays are viviparous
  - **Rays**- lay 1-2 eggs per day, and number of eggs is determined by length of breeding season.
  - **Guitarfish**-ovovivparity, 6/litter**.**
  - **True rays-** small eggs, uterolactation feeds embryos. Litter of 1-15, gestation of 2-4 months. Less yolk in egg as a result of uterlactation. Incl sting ray, manta ray.
    - **Cownosed ray-** has 3000x weight gain, 11-12 month gestation, can live 30-100 years, don't start reproducing till 20-30.
- **Shell gland-** gland in reproductive system of batoid fishes that secretes shell around egg. Egg then retained or laid.
- **Ovoviviparity-** yolk-based viviparity. Develop within eggs that remain within the mother's body up until they hatch or are about to hatch. This strategy of birth is known as **ovoviviparity**. It is similar to vivipary in that the embryo develops within the mother's body. Unlike the embryos of viviparous species, ovoviviparous embryos are nourished by the egg yolk rather than by the mother's body. However, the mother's body does provide gas exchange.
- **Lecithotrophic viviparity- yolk based viviparity.**
- **Uterolactation-**
- **Trophonemata**- uterine villi that secrete milk for uterolactation

- **Sharks**
  - Multiple origins of viviparity, litters of 1-300
  - **Spiny dogfish**
    - Ovoviviparity=lecithotropic viviparity
    - Highly vascularized uterine mucosa
    - 40% weight loss in utero
    - 23 month gest; 7 pups/litter
- **Lamniform sharks**
  - *All have Oophagy*
  - No uterine compartments
  - Produce eggs all through pregnancy, and fetuses eat unfertilized eggs.

- Litters 2-18, gest 1 year/
- Embryo in pic has large yolkfilled stomach
- **Sandtiger shark** (a lamniform shark)
  - **Intrauterine embryonic cannibalism**—only 1 survives per uterus→ 2 per gest.
  - 9-12 month gest
  - Oophagy and adelphophagy
  - 25,000x weight gain in utero, eat 17,000 eggs

— **Carcharhiniformes**
- Largest order of sharks
- Multiple reproductive models: oviparity +/- egg retention, yolk-dependent viviparity, placental viviparity.
- **Chain dogfish**
  - Oviparous without egg retention
  - Sperm viable for 2 years
  - 2 eggs/15 days, with 256 day development. Total 24 eggs/ season.
  - A lot of sharks have sperm storage. You can estimate how many males a female mates with by looking at testes size.
- **Catsharks**-some of these complete most of development in utero, but lay eggs before hatching
- **Tiger shark**
  - Yolk dependent viviparity
  - 13-16 mo gestation, 10-82 pups.
  - Each pup in own vascularized compartment
  - Yolk sac does not form a placenta

— **Carcharinid (requiem sharks)**
- Each embryo in own uterine compartment
- Most have large yolk-filled eggs
- Yolk sac forms a placenta after yolk is depleted.
- 10x weight gain in utero
- **Atlantic sharpnose shark**
  - These a re placental requiem sharks
  - Placenta includes egg envelope
- **Spadenose shark**
  - Extreme example of placental nutrition
  - Placental barrier lacks egg envelope
  - 50,000x weight gain in utero

— **Evolution of oophagy in sharks**—has evolved independently in lamniforms, carcharhiniformes, and orectoloboforms. Primary determinant of litter size is number of eggs ovulated and filled with yolk.

— **Thorson's rule** –see wikipedia. Its for invertebrates, but I thought I remembered something similar from class?

— *Main point: different methods of embryonic nutrition*

Lecture 4-Teleosts: Bony Fishes
Diversity of degree and type of parental care

- **Rayfinned fishes**
  - Include bowfin, sturgeon, bichirs, paddlefish, and gar, as well as teleosts
  - **All except teleosts are freshwater fish**
- **Reproduction in teleosts**
  - Do not have oviducts- hollow ovaries replace oviduct
  - **Chorion** depositin in follicle. Different from amnionte chorion in structure and origin. Tough around embryo.
  - Meroblastic cleavage of egg
  - Eggs small, up to 25 mm
- **Paternal care in teleosts**
  - Most marine (salt water) ones have pelagic eggs. Only some marine ones guard eggs
  - Freshwater ones have domercile eggs, and egg guarding is common
  - Paternal care is more common than maternal
  - Only 3% of species have internal fertilization
  - Only 2% of species have viviparity
  - Many many independent origins of vivparity, maternal care, and paternal care from ancestral state of external fertilization with no parental care. None with internal fertilization have paternal care. See diagram with numbers in packet.
- **Parental guarding**
  - **Gunnel/butter-fish**-curls around eggs to protect them. Pick out sick ones, but have reduced opportunity to feed
  - **Mouth brooding ciclets**- they hold the developing fry in their mouths. Examples of male, female, and biparental. There are parasitic fish that sneak their eggs in, and there is also risk with male mouth feeders—they need to be well fed, or they might eat the eggs.
  - **Sticklebacks-Oviparous with paternal care**
    - Nest site for ovaposition. Female lays eggs and leaves, then male comes back and fertilizes them.
    - There are some territorial fish who will come and fertilize eggs before other males
    - There are female mimics who will act opportunistically to fertilize the eggs
    - **Paternal care**
      - Nest building and nest guarding
      - Fanning of eggs with pectoral fins to keep water moving across them,
      - Removal of diseased eggs, breeding males lose “condition.
      - Breeding males have reduced survival
      - Males sometime eat eggs in own nest (trade-off—sacrifice some percent of offspring to hopefully be able to care for the rest of them.
    - **Reproduction**

- 100-300 eggs/clutch, female produces multiple
- Nests may contain multiple
- Males “steal” fertilization
- Males “steal” eggs from other nests—b/c additional food, and because females prefer nests with eggs.
- Females prefer nests with more eggs because that means the male did not eat them, and that another female chose him, so he must be worth something.

— **Viviparity in teleosts: Scorpaenidae (scorpion fish)**
  - Internal fertilization common
  - Viviparity present in sebastes (3 species)

— **Comparison of oviparous species and viviparous species**
  - **Helicolenus dactylopterus (oviparous + internal fertilization)**
    - 10,00-100,000 eggs per season, sperm viable for 10 months
    - Internal fertilization—eggs with early embryos found in ovaries, eggs with late embryos in ocean
  - **Sebastes (viviparous)**
    - Rockfish
    - Long lived, 30-100 years
    - High fecundity, up to 5,000,000 eggs
    - Gestation in ovarian lumen-cavity of ovary
    - Primary lecithotropic development
    - 1-2 month gestation, then pelagic larvae
    - Oviparous species reach same stage of development in 5-10% of the time—these have pelagic eggs. The advantage of viviparity is reduced predation. In oviparous fish they are prone to predation, so there is strong selection for rapid development after release
  - **Zoarcidae** (oviparous except for 3 Zoarces species, who have independent origin of viviparity)—eel pouts
    - Macrozoarces (oviparous)
    - Zoarces (viviparous)
  - **Embiotocidae** (surfperch)
    - Micrometrus minimus

— **Domercile-** sink to bottom of ocean
— **Peleagic-** float around in ocean
— **Meroblastic cleavage-** cell division without cytokenesis?
— **Ovaposition**
— **Ovarian lumen-** hollow ovary which takes the place of uterus?—**Intraluminal gestation**
— **Teleost-** one class of the Actinopterygii (ray-finned fishes)
— **Sebastes**-genus of scorpionfish that are viviparous, widely radiated in the Pacific, over 100 species.
— **Trophotaenia- feeding threads**
— **Main point: different forms of parental care**

Lecture 5- Atherinimorphs:
Diversity of methods of fertilization

- **Atherinimorph**- type of fish
- **Synaphomorphies**- traits that show monophyleticness of group. Shared derived character. Does not provide proof of closeness of relationship, but it demonstrates the relationship
- **Demersal eggs**- sink to bottom of ocean
- **Intramittent organ**

- **Atherinomorph synaphomorphies**
  - Demersal eggs with chorionic filaments and oil droplets
  - Spermatogonie restricted to distal end of testis tubules
  - **Spawing clasp**- make hold on to female with fins
  - Various skeletal structures
- **The testis of the atherinomorphs** are very organized, and more like a conveyer belt than those of other teleosts.

- **Various methods of fertilization**
  - **Fundus heteroclitus**—has a **spawning clasp**. External fertilization Holds onto female, they both release egg and sperm at same time, depositing egg in mollusk shells in low tide zone.
  - **Zenarchopterus robertsi**- internal fertilization and viviparity. They have a **gonopodium** (modified anal fin)
  - **Phallostethid males**-oviparous. Have **priapium** (modified pelvic girdle) for delivery of sperm.
  - **Horaaichthys setnai**- oviparous. Gonopodoium.
  - **Gambusia**- have painful looking spawining clasps
  - **Tomerus gracilis**- oviparous, one egg per day. Internal fertilization. Ovaries contain eggs with embryos. Males have modified anal fin that can be swung forward. The gravid female carries eggs in her ovaries. The modified anal fin has complex terminal modifications.
- **Importance of the spawing clasp:**
  - Predecessor of internal fertilization
  - Internal fertilization is good because females can release large eggs, but few of them. Males don't have to hang around as long
- **Sneak copulation**
  - In Tomerus gracilis, there are many accounts of sneak copulation, male coming up behind female and thrusting his gonapodium in her. Also in Gambusia holbrooki
  - **Poecilia reticulate**
    - Have two types of mating displays:
      - **Sigmoidal display**- Male display, then female allows mating
      - **Sneak copulation**
    - Sigmoidal display is much more common when there is no predator, sneak copulation is more common when predator is there
    - Why?
      - Male can avoid predator
      - Decrease cost to male and female

- Saves time
- Female attention on predator is taken advantage of by male

— **Cypriodont phylogeny—origins of internal fertilization and viivparity**
  - Cypriodonts are subgroup of atherinomorphs
  - Have 4 independent origins of internal fertilization
  - 3 independent origins of viviparity.
  - **Kryptoblebias**
    - Self fertilizing—hermaphroditic in Florida
      - Multiple highly inbred genotypes in florida
      - Isolated hermaphrodites lay fertile eggs
      - Genetic evidence for outcrossing
    - Hermaphrodites and males in the Caribbean
      - Genetic evidence for outcrossing
      - Males make only sperm, hermaphrodites have ovatestis.
    - Own eggs and sperm fertilize. Fish can become nearly clonal lineages
    - (aside: Used in toxicology, but should you use genetically diverse or homogenous lineages?)
    - Oviparous with a functional ovitestis
  - **Goodeidae**
    - Restricted to Mexican plateau
    - Internal fertilization and viviparity
    - Anal fin of male is little modified
    - Gestation takes place in ovarian lumen
    - Some species have **trophotaenia**—feeding threads which are embryonic extensions of the hindgut. These vary among species in ability to take up large molecules
    - Some reports of adelphophagy
  - **Anablepidae**
    - Internal fertilization
    - Tubular gonopodium
    - Sperm are free rather than bundled
    - Couple different locations of gestation
      - Within follicle
      - Within ovarian lumen
    - Follicular and ovarian fluids are ingested via mouth and absorbed in gut.
    - They are the 4 eyed fish…dunno why
  - **Poecilidae**
    - Guppies and mosquitofish
    - Internal fertilization
    - Nontubular gonopodium
    - Sperm transferred in bundles
    - Gestation within follicle
    - Overlapping broods (**superfetation**—care more than 1 litter at a time with different rate of development)
    - Variation in degree of **matrotrophy**—different ways of post ovulatory provisioning of offspring

        - *Important concept: An increase in the number of broods is accompanied by a decrease in the number of eggs per brood, so ultimately they end up producing the same number of eggs in a given time (*
        - *Important concept: Increase in egg weight to birth weight implies a high degree of matrotrophy, but a decrease implies not a lot of matrotrophy*

— **Superfetation**
    - Possible that superfetation arises from competiton by sperm to fertilize eggs first. Fertilization of multiple broods at time before eggs fully yolked
    - Next batch of eggs is fertilixed before previous brood has compelted gestation.
    - Once you have early fertilization, you get selection refucing the number of embryos. Decrease in clutch size as the female produces more clutches a t a time

— **Matrotrophy index**
    - The ratio of the dry weight at birth to dry weight at fertilization

LECTURE 6:

For both Gynogenesis and Hybridogenesis:

-species co-exist with related sexual species

-orginated in groups where males were not choosy and mated by surprise

Gynogenesis: sperm do not contribute genes to offspring. Offspring are clones of mother.

-Females are parasitic on sperm of sexual males.

-evolutionary constraint—requires sperm to activate eggs

-EX: Poecilia Formosa (Guppies): all females, sexual parasite on males of Poecilia mexicana and Poecilia latipinna

MECHANISM (P.2monacha-lucida)

-Triploid→MML undergoes mitosis without division creates MMMMLL

-pairing of sister chromosomes

-normal meiosis: MMMMLL→ MML

-activation of egg by sperm but doesn't contribute to genome of egg

EX: Ambystoma spp. (mole salamander)

-2n, 3n, 4n, 5n gynogenetic linages

-gynogenesis at low temperatures, male genomes eliminated

-**karyogamy** (genetic fusion eggs, not eliminating male, so then ploidy increases by one chromosome) at high temperatures

-gynogenetic mtDNAs are all closely related regardless of nuclear genotype suggesting that mtDNA lineage is over 5 million years old.

Hybridogenesis: All offspring are hybrids and female, paternal chromosomes are not transmitted to eggs, so eggs contain only maternal genes.

-This is considered a **hemiclonal lineage**—half genes are cloned and passed on.

-EX. P.monacha-lucida. (found in Puerto Rico)

-hybridogenetic—all female (see above), P.lucida chromosomes are eliminated from eggs during early oogenesis (sexual parasite of P.lucida)

-This hybridogenesis was found to be only a result of having P.monacha and P.lucida together---when P.monacha and P.monacha then there is recombination between maternal chromosomes.

-MECHANISM (specifically explained with P.monacha (f) and P.lucida (m)→P.monacha-lucida offspring

-unipolar spindle (instead of 2 poles) attaches M chromosomes

-L chromosomes scattered in cytoplasm (not attached to spindle)

-separation of M chromatids at meiosis II

-egg nucleus receives only M chromosomes

-fertilization of egg by P.lucida sperm→recreates hybrid offspring.

P.monacha-lucida

-not just a single clonal orgin→mtDNAs of hybrids are diverse

WHO (genes) is more fit?

-female of hybrid since maternal genes are in all offspring and paternal genes in none

Why do P.lucida males continue to mate with P.monacha and hybrids?

-female respond differently or perhaps result of males not being choosy.

Same patterns observed in cases of P. monacha and P.occidentalis with hybrid—P.m-occidentalis

When look in different regions there are different patterns of mtDNA. In the northern most area, single P. monacha mtDNA clone. In the middle area there is a single mtDNA clone older than 100,000 generations. In the south, there are many mtDNA clones.

-assumed that P.monacha used to found in all rivers but became extinct in North

-Hybrids also became extinct until just one lineage left

-Or: female onacha(founder effect) took genes to new are a allowing for new clone.

Ambystoma spp. (mole salamander)

-2n, 3n, 4n, 5n gynogenetic linages

LECTURE 7

Amphibians: caecilians, frogs and salamanders

-characteristically have large yolky egg

Caecilians:

CHARACTERISTICS

-legless, all have internal fertilization, oviparous females guard eggs, many species are viviparous (multiple orgins)

Oviparous species:

-Ichthyophis (fish snake)

-eggs laid underground. Female looses weight during brooding, large clutch (22-58). Larger females produce bigger clutch and larger larvae

-Boulengera taitanus

-brooding females develop special thick skin and hatchlings feed on mothers' skin

Vivaporous

-oral ingesting of uterine fluids (nutrious)

-fetal teeth rasp oviduct wall

tryplonectids

-larval gills form a placenta

-also observed **oophagy** (egg eating) and **adelphophagy** (brother eating)

Salamanders:

CHARACTERISTICS:

-external fertilization: males guard eggs

-internal fertilization: females guard eggs

-single origin of vivaparity

-Salamandroidea: spermatophores with internal fertilization

-paved way for prolonged egg retention (vivaparity) in S. luschani, S. salamandra, and S. atra

Mertiensiella caucasia: oviparous; internal fertilization

S.luschani: viviparous; preliminary evidence of oophagy, two offspring fully metaphorphed

S. salamandra: (fire salamander): variable reproductive modes, sometimes adelphophagy, oophagy, most development occurs in uterus (3-9 mos), dev. from yolk reserves

S. atra: 50 eggs per oviduct, only one fertilized egg in each oviduct. 2-4yrs gestation, older fetuses eat oviduct epithelium

Frogs:

-most have external fertilization (**amplexis**: female releases eggs and male fertilizes them)

-Vivaparity in Eleutherodactylus (largest genus of vertebrates) jasperi and Nectophrynoides (genus)

Eleutherodactylus

-direct development from eggs, no tadpole stage, gills reduces/absent, membranous, vascualrized tail forms respiratory membrane in egg (acts as extra membrane for gas exchange)

-E.coqui

-oviparous frog, amplexus for 7-10hrs, large eggs, dev. in less than month

-Male tends 1-3 clutches and delivers water to eggs, increase in embryo wet mass, parental care is essential! If no care, then they dehydrate and die

-E. jasperi

-probably extinct

-**lecithotrophic vivaparity** (yolk source of nutrients, not mother)

Nectophyrnoides

Includes both vivparous and oviparous forms.

-Viviparous form:

-N. occidentalis

-embyos free in uterine lumen, ingest uterine milk, no placental structures, gestation 9ms, yolok poor eggs.

LECTURE 8

-Frogs continued:

Demonstrates how parental behavior affects survival.

-Osteocephalus oophagus—Pair returns every 5-7 days to spawn, and older tadpoles eat fertilized eggs. Unprovisioned tadpoles starve

-Osteophilus brunneeus: early clutches are fertilized and later clutches are used as food for larvae, unprovisioned tadpoles starve

-not all have post zygotic parental care: Kurixalus idiootocus

-Kurixalus eiffingeri:

-male hydrates eggs, female lays trophic eggs to feed off of, tadpoles have beak, large gut for egg eating

-Dendobatidae (poison arrow frogs)

-toxins from diet of ants and mites

-sm. Clutches of terrestrial eggs (tended by paretnst)

-tadpoles carried to water on back of male

-egg and larval cannibalism is common

-Dendrobates auratus

-males defend territories, possibly with multiple clutches

-males tend eggs, moisten them, and carries them to pool after hatching

-females try to exclude other females from territory and eat other females' eggs

-Dendrobates pumilio

-males defend territory, female carries tadpole individually to leaf axil and feeds with trophic eggs

-Dendrobates vanzolinii

-each frog has unique color pattern

-territorial monogamous pair

-tree hollow contains single tadpole

-second tadpole to new hollow, fed by mum with eggs

-Rhheobactrachus silus

-extinct

-mother swallows eggs and young develop in mother's stomach

-Assa darlingtoni

-female remain until hatching, larvae enter male inguinal pouches

-no well developed mouth or color in tadpoles since not feeding and protected

-Rhinoderma rufum (Darwin's frog)

-terrestrial eggs, taken into vocal sac after 8 days, partial development

-male releases eggs into water, where finish dev.

-Rhinoderma dawinii

-large terrestrial eggs, eggs taken into vocal sacs

-gestation in vocal sac

-monogamous in a breeding season.

-**Non-oviductal gestation**

Alytes	Male	Hind legs
Rheobatrachus	Female	Stomach
Assa	Male	Groin
Rhinoderma	Male	Vocal sacs
Pipa	Female	Back
Hemiphractinae	Female	Back
Dendrobatidae	Either sex	back

Amniotes: Terms and Examples

- Amniotes: any of a group (Amniota) of vertebrates that undergo embryonic or fetal development within an amnion and include the birds, reptiles, and mammals
- Meroblastic cleavage: the yolk does not divide (solving problem w/large egg)
    - Examples: hagfish, cartilaginous fishes, caecilians, amniotes
- Extraembryonic Membranes:
    - Chorion: ectoderm +mesoderm; highly vascularized outer membrane that in placental mammals helps make the placenta
    - Yolk sac: endoderm+ mesoderm; sac attached through stalk to intestinal cavity.
    - Amnion: ectoderm+ mesoderm surrounds embryo and contains amniotic fluid
    - Allantois: endoderm +mesoderm formed as a pouch from the hindgut; in placental mammals associated with chorion in formation of placenta.

Birds: Terms and Examples

- Archosaurs: monophyletic group of reptiles including crocodiles and dinosaurs
- Intromittent organ: external organ of a male organism that is specialized to deliver sperm.
    - Birds typically lack one.
- Precocial: can move around at birth and maintain a stable body temperature. Ex**.** Ratites/tinamous and crocodiles
- Altricial: can't move around at birth, fed w/in the nest. Ex. Duck, chicken
- Cooperative breeding: parents +helpers
    - Malarus cyaneus: male kids become helpers, hoping to inherit nest. 66% of offspring sired from outside social group, with females visiting those males before dawn.
    - Dacelo novaeguineae (kookaburra): breeding male most care, helper female least care. Male helpers reduce offspring death due to siblicide and starvation. Oftentimes, youngest chick gets killed.
- Homogametic: same type of sex chromosome. Mammals=female, birds=male. Heterogametic is the opposite!
    - Some birds are able to control the sex of their offspring:
        - Eclectus roratus produce lots of males, followed by lots of females.
        - Acrocephalus sechellensis: poor territory leads to more males, rich territory leads to more daughters, and having helpers reduces the number of offspring and makes the numbers male biased.
    - An important result of this skewing of birth ratios is that the minority population will leave more genes so that sex gene dispersal is a 1:1 ratio.

Squamates: Terms and Examples

- Squamates: largest order of reptiles, including lizards and snakes. 45 of origins of viviparity in lizards, and 35 in snakes. 20% of squamates are viviparous. Very little parental post partum care.
- Cold-climate hypothesis: Cold climates favor egg retention because mothers are able to maintain higher average egg temperatures and avoid extremes of cold.
    - Lacerta vivipara: most northernly range of any squamate (48% of body fluid freezes!);

        - oviparous populations in the south have parchement eggs, 1 to 2 month egg retention, and 1 to 2 months of incubation. 2 to 3 clutches per year
        - viviparous populations further north (slide 22 for diagram) have thin eggs, 3 month gestation and one clutch/year.
    - Mating balls: in Thamnophis sirtalis parietalis, females courted by dozens of males
        - Males force anoxic air onto female's respiratory surface, causing cloacal gaping, allowing intromission with male hemipenis.

Possible Short Essays

- Why are there no viviparous birds?
    - Egg retention isn't adaptive
    - You have to maintain high temps in the oviduct
    - Constraints on flight
- Why are there so many origins of viviparity in squamates:
    - Important to realize that the origins aren't all in one branch of the evolutionary tree. Rather, they pop up due to differential extinction/speciation, and recent environmental changes.
    - The cold climate hypothesis (see above) provides one explanation.
    - The tradeoff is you have less clutches, which might be why evolution keeps returning to oviparity.

Lecture 13: Lactation

- Hair, milk, and dentary forming the lower jaw are traits shared by monotremes, marsupials, and eutherians
- Mammary glands produces milk
- Purposes of proto-milk: nutrients, waster, pheromones, antimicrobials
- Milk secretion in non-mammals: uterine milk in sharks, ovarian milk in teleosts, mucus -prolactin promotes mucus production in some fish, crop milk in pigeons
- Male and female pigeons make crop milk, lipid and protein rich promoted by prolactin
- More dilute milk = feeding more often
- Milk components: lactose, protein, lipids (fats)
- Lactose (disaccharide): glucose and galactose (osmotic component of milk)
- Lactose synthetase contains lactalbumin only expressed in epithelial cells of females, it is related to lysozyme an antimicrobial, and is secreted in milk
- Lactase: catalyzes breakdown of lactose, not expressed by most adults, yet its persistence is in dairying population with independent origins i.e. Europe, Africa,
- Lipids: principle energy source, plasma membrane bound globules most are 1-4 micrometers.
- Proteins: caseins, lactalbumin, immunoglobulins (primarily imunoglob. A in humans but doesn't pass through the gut), growth factor
- Caseins: micelles or colloidal aggregate carry calcium (milky appearance), source of phosphorous, has active peptides which may affect opioid receptors in brain, k casein clots milk reducing surface areas and slowing digestion, it

undergoes rapid molecular evolution to various forms i.e. alpha or beta casein, and is related to proteins responsible for calcium deposition on enamel
- Red Kangaroo: females simultaneously suckle young of varying ages, teats will grow with young, very sophisticated system.
- Hooded Seal: lactates for 4 days, neonate grows from 22-43kg which is 80% fat, mother loses 16% of her fat
- Tree Shrew: twins which mother feeds for 5 mins. every 48 hrs, infants drink 1/3 of body weight in 1 minute, weaned at 4 weeks
- Chimp: lactate for 4 years, give birth every 5 years, gestation for 225 days
- Humans delayed maturation is adaptation to extract more parental care, maternal response is early weaning to increase fecundity
- Communal suckling is reported in communal breeding animals i.e. lions, while non-reproductive meerkats will feed pups

Lecture 14: Monotremes

- 31 living species of these egg laying mammals
- males essentially have 5 X c'somes and 5 Y c'somes, while females have a pair of 5 X c'somes they merely inactive paternal set of X c'somes
- in reproduction shell membrane is deposited in oviduct, embryo hatches after 2/3 gestation, a chorio-vitellin placenta forms from the yolksac
- Birth canal opens and closes, only open at time of birth doesn't exist before 1st birth has lateral vaginas
- Sperm structure varies some American (Ameridelphia) species have paired sperm attached at head, which swims better in higher viscosity
- Didelphis Virginiana: carry young on teat for 70 days, releases 60 ova at ovulation, litter size 6-9, first litter weaned in may is male biased, second litter weaned in August or September is female biased.
- Macropus rufus (kangaroo): post-partum estrus and conception followed by diapause – development is arrested suckling of older sibling in pouch, teats produce different milk for young at different stages, possible to have joey at foot joey in pouch and an arrested embryo
- Antechinus stuartii: males disperse after weaning, females stay in maternal territory, males die in first year after 2 week mating session, 7% of females survive to next year, litters have multiple fathers which enhances female fitness, with 6-10 teats 13% of mother wean entire litters others often eat their own offspring in order to achieve a number they can support, older mothers produce almost all daughters and almost all liters have daughters, for males either they all survive weaning or none survive weaning

Lecture 15: Eutherians

- Four groups: Afrotheria- insectivores with African specific radiations includes elephants, manatee, and golden mole Xenarthra- 3 living groups anteaters, armadillos, sloths Laurasiatheria- whales, bats, true mole Euarchontoglires- rodents, treeshrew, primates
- Placental arrangement: implanting embryo burrows into uterine tissue
- Chorioallantois contacts uterus to make vasculature
- Invasive trophoblasts concentrate on spiral artery to create maternal blood space for chorionic villi to exchange resources, trophoblasts cause the artery to dilate providing more blood flow

- Not all eutherian mammals have invasive embryos, some primates have noninvasive embryo
- 3 different placentas: epitheliochorial (non-invasive b/c tissues in contact with one another) - uterine epithelium contacts chorion in lemurs/bushbaby and in horses cows, pigs and whales, endotheliochorial- endothelium of capillaries touches chorion in tree shrew, hemochorial placenta- maternal blood contacts chorion in apes and monkeys
- Such that all eutherians have some degree of invasion of maternal tissue by trophoblasts

Lectures 16 and 17 – Genomic Imprinting

Generally speaking, what is good for a gene in an individual is good for all genes in the individual. There is equality and "symmetry" among genes because each has 50% chance of being transmitted to future offspring.

Pronuclear substitution in mice (IVF)

Androgenetic embryo = all genes from father (hypergrowth of placenta, poor fetal growth)
Gynogenetic embryo = all genes from mother (underdeveloped placenta and yolk sac, "starved" embryo)
Neither type of embryo developed properly → paternal genes play a role in growth of placental/nutrient obtaining tissues

Asymmetry of genes occur when fitness of non-descendant relatives is taken into account (full siblings and half-siblings)

Hypothesis: gene expression depends on whether an allele is paternally or maternally derived
In non-monogamous species, paternally derived alleles tend to promote selfishness in the fetus while maternally derived alleles tend to suppress selfish behavior. Why?

- → All maternally derived alleles in the fetus are present in the mother and have a 50% chance of being present in future offspring. Paternally derived alleles are not present at all in the mother and have, at best, only 50% chance of being present in future offspring (full siblings). Therefore, paternally derived alleles will benefit if fetus is selfish at a cost to the mother and her future offspring.
- → Paternally derived genes will be particularly intensified in "sibling rivalry"
- → Paternally derived genes will favor extraction of benefits and resources from the mother
- →

Example:

IGF2 promotes growth (paternally imprinted)	vs.	CDKN1C inhibits growth (maternally imprinted)

So normally, there is a balance between growth promotion and inhibition.
When things go wrong…

Beckwith-Wiedemann Syndrome (fetal overgrowth)

Either 2 copies of IGF2 are activated or there are no activated copies of CDKN1C

Silver-Russell Syndrome (fetal growth retardation)

Either 2 activated copies of CDKN1C or no paternally activated IGF2

Genomic imprinting conflicts at a larger level:

- Extended juvenile/growth period is an example of offspring attempt to extract more care and resources
- Early weaning and overlapping juvenile care (multiple offspring) is the maternal counter-adaptation to offspring selfishness
- Prader-Willi Syndrome (paternally derived genes silent)
    - Exaggerated reduction on maternal demands (sleepiness, poor suck, poor growth)
    - But after weaning, child exhibits non-discrimination of food choices, eats obsessively, becomes obese
    - Conjecture: paternally derived genes favor suckling (more nutritious food, more demanding on mother) but do not favor supplemental foods (longer suckling, later weaning)
- Angleman Syndrome (maternally derived genes silent)
    - Exaggerated increase on maternal demands (hyperactivity, uncoordinated suck and swallow, premature puberty)

Genomic Imprinting in huddling

- Heat costs energy; huddling saves energy by allowing for (partial) "free-riding" on the heat contributions of other members
- How much should a member "contribute" to the communal heating bill?
- Paternally derived genes should favor less heat contribution and more free-riding (cold pup in a warm huddle), especially if there is a high probability that not all or none of the littermates share the same father
- Maternally derived genes should favor group cooperation (all littermates share the same mother)

Dispersal according to genes

Heterogametic gender (in mammals, XY = males; in birds, ZW = females) should tend to disperse

In mammals:

- All daughters are clones for paternally derived genes on X chromosomes (100% relatedness on X chromosome from father)
- Sons are not related at all; female-based kinship groups
- Genes for cooperative female behavior should be enriched on X-chromosome

In birds:

- Sons are clones and 100% related
- Hence, male helpers at nest, females disperse

Conflicts involved in pregnancy:

- Maternal investment is associated with an opportunity cost:
  - Investment in the current fetus means cost to future offspring.
  - Maximum maternal investment is different depending on the genes under observation:
    - Non-inherited maternal haplotype:
      - Has no interest in the survival of the offspring.
      - Benefits from the early demise of the offspring.
    - Inherited maternal haplotype:
      - Cost is ½
    - Paternally-derived genes:
      - Favors greater demands on the mother
      - Cost is increased by the probability of shared paternity.
- How does pregnancy occur when there are genes that benefit from no pregnancy:
  - The concept that explains this is called the parliament of genes:
    - Suppression of individual genes that threaten the welfare of the whole.
- Conflict occurs over:
  - Whether to miscarry or not
  - Nutrient quality of maternal blood
  - The amount of blood reaching the placenta.

The structure of the human placenta:

- Spiral artery delivers the maternal blood into the placental cavity.
- Chorionic villi:
  - Absorb:
    - Nutrients
    - Oxygen
  - Release:
    - Hormones
    - Waste
    - Fetal cells, that circulate maternal blood
- Umbilical cord conducts the blood from the fetus to the chorionic villi and vice a versa.
- Uterine vein takes the blood from the cavity back into maternal blood stream.

Control of pregnancy in mammals:

- Mother produces:
  - Luteinizing hormone is produced by the anterior pituitary and stimulates Corpus luteum.
  - Progesterone is produces by corpus luteum and affects the uterus.
- Placenta:
  - Chorionic gonadotrophin: affects the corpus luteum and shuts it off. It is present only in the species with invasive placenta (monkeys, apes, horses)
  - Progesterone: substitutes the corpus luteum entirely after 7 weeks.

Maternal carbohydrate metabolism:

- Mothers keep the glucose level lower during the first trimester
- Maternal sensitivity to insulin decreases as pregnancy progresses, as a result of fetal effects in order to increase the amount of food available to it.
- Maternal response is to increase insulin production (which stores carbohydrates) as the pregnancy progresses, even though this is in contrast to what normally happens.

Maternal blood pressure in pregnancy:

- Fetus favors higher blood pressure going through the placenta.
- As pregnancy starts, mother has lower than usual blood pressure, but as the pregnancy progresses the blood pressure increases as a result of fetal hormones.
- Blood circulation during pregnancy:
    - Blood goes between:
        - Placenta and the lungs
        - Maternal tissues and the lungs
        - Placenta and maternal tissues
    - Both the uteroplacental circulation and the non-placental circulation can have independently modified blood resistances, which affect the blood pressure.
        - Fetal's share of the blood supply increases when maternal resistance is increased and when uteroplacental resistance is decreased.
        - It is in fetal interest to:
            - Increase maternal resistance
            - Decrease uteroplacental resistance
        - It is in maternal interest to
            - Decrease maternal resistance
            - Increase uteroplacental resistance
    - Poiseuille's Law:
        - Laminar flow in a rigid tube.
        - The law shows that laminar flow depends on the pressure difference between the two tubes
        - Applying this law to conflicts in pregnancy, we understand that it is in fetus' interest to both increase maternal resistance and decrease uteroplacental.
- Pregnancy-induced hypertension:
    - 10% of pregnant females develop it.
    - It is a result of fetus exerting too much pressure to increase blood pressure.
- Preeclampsia:
    - 3% of pregnant females develop it.
    - It is the pregnancy-induced hypertension plus proteinuria (pissing proteins).
    - Preeclampsia results from offspring trying to increase blood pressure in the placenta. It does this first by affecting uteroplacental and non-placental resistances. Occasionally, the fetus starts damaging maternal blood vessels in order to decrease pressure in them.
- How is it possible that offspring can kill its mother?

- There is no communication between mother and the fetus, because these pathways are not evolutionarily credible – they just can't evolve.

Hormone overproduction during pregnancy:

- Pregnancy hormones:
  - Luteinizing hormone – produced by the pituitary and affect corpus luteum
  - Chorionic gonadotrophin – produced in the placenta and affects corpus luteum
  - Growth hormone – produced by the pituitary and increases the usage of lipids as energy sources
  - Placental lactogen – produced by the pituitary with a similar function to the growth hormone.
  - Progesterone – produced by corpus luteum and supports pregnancy.
  - Estradiol
- The concentration of these hormones increases enormously during pregnancy, because the placenta produces them, as the fetus is trying to take more resources from the mother.

Growth hormone:

- Promotes lypolisis and blood lipid content.
- It is most expressed in anorexia nervosa and during starvation, but its effect on growth is switched off.
- Comparative genetics of GH:
  - It is identical between most mammalian groups.
  - It has undergone substantial changes in apes, cows and mice.
    - This is because Placental lactogens have evolved independently in these three lineages. They have evolved by duplications of lactogen gene. Therefore, the gene was less constrained and free to mutate.

Hormone production:

- Because the offspring optimum is higher than the maternal optimum for the production of all pregnancy hormones, the theory predicts that the placenta will produce all the hormones.
- Growth hormone confirms this prediction.
- Both the placenta and the maternal pituitary produce the prolactin receptor protein (PRLR). Therefore, placental lactogen acts as an antagonist to pituitary prolactin.

Lecture 20: Spotted Hyenas

Multiple species of hyenas –

Aardworlf
Striped Hyena
Brown Hyena
Spotted Hyena

The Brown Hyena seems to have social patterns closest to that of the spotted hyena

Brown Hyena – male-based dispersion, female-based clans
- 1-4 cubs born in a birthing den, which are then brought to a communal den
- communal suckling

LIKEWISE

Spotted Hyena – female-based clans, with male-based dispersal
- 1-3 cubs born in a birthing den – HOWEVER
- Spotted hyena has unusually long gestation length compared to other animals, cubs are born with fully erupted teeth and fight within minutes of birth – one cub usually emerges as dominant and prevents the other from nursing, making it starve to death

Spotted hyenas have distinct social stratification:
- all adult females are higher ranked than males
- higher ranked females are able to eat more – and their offspring can eat more, and thus higher-ranked females have many more surviving offspring
- offspring share mothers rank – daughters inherit mother's rank, males lose all rank when disperse, the rank of an immigrant male is determined on arrival sequence

Interesting sex-ratios of newborn cubs that are brought to the communal dens:
- in one instance, about half/half ratio of single cubs/ twin cubs brought to the communal den
- in that instance, among the twins there was a strong bias of having mixed-gender twins (male-female pairs)
- BEFORE CLAN FISSION (Before males disperse)
- 28 male cubs, 20 females total – but in twins, still bias of male-female pairs
- AFTER CLAN FISSION (After males disperse)
- 14 males total, 26 females total – bias of male-female pairs doesn't exist anymore in twins

The most notable aspect of the female spotted hyena is her masculinized genitalia:
- occurs before the fetal ovary emerges as a sexual structure, so influenced by maternal androgens (male-like hormones)
- but not completely dependent on androgens
- Possible sexual mimicry, because female hyenas face aggression from higher ranked females – maybe mimic the genital structures of males to avoid this aggression
- This mimicry can also happen to protect against neonatal sibling aggression, infanticide by other females, and interclan territory
- High costs, however – 10-20% of mothers die at first birth because essentially have to give birth through a penis
- 60% of first offspring die at birth, asphyxiating in the penile structure
- Mothers who have been treated with anti-androgens experience NO DEATHS of first-born cubs

Spotted Hyenas have greeting ceremonies in which they sniff each other's "penises," a ceremony that reestablishes social bonds and puts reproductive organs in close proximity to powerful jaws

Females are dominant over males and are larger – perhaps the masculinized penis is a by-product of natural selection selecting for higher androgen levels (i.e. more aggressive and therefore more dominant females)

Mating with a peni-form clitoris is difficult as-is for the male – forced copulation is basically impossible – so females can choose male mating on relationships with males

Lecture 22: Huddling

Key example species – Emperor Penguin:

Adult males fast four months and care for eggs in Antarctic winter, 5000 males huddle to reduce weight loss by 25-50%, have a rotating system to make sure males in the warm center of the group have to rotate out and be on the cold fringes for a time too

Isolated males prevented from huddling have a higher body temperature than males that huddle

These kind of cooperative behaviors exhibit themselves throughout the animal kingdom – many primates who are "solitary" will sleep in groups

The Mouse Lemur –

Solitary foraging at night, but group sleeping of 3+ female relatives and infants during the day

Adult males sleep alone

Offspring huddles

Generating heat in a huddle reduces one's own resources and benefits others – ideally, one could "cheat" by being a "cool" pup in the middle of a warm huddle (free-riding)

Within precocial offspring (large size and fairly independent at birth, able to maintain stable body temp) - need to consume more oxygen as it gets colder

On the other hand, altricial offspring (like mammals born hairless and with eyes not open yet, don't maintain stable body temperatures on their own) – consume more oxygen as ambient temp gets warmer

Lecture 21 Marmosets

- Trouble with twins
  - Pronghorn-
    - 2 uteruses
    - Long blastocyst
    - One surviving embryo per side (the ones closest to the cervix)

        - Necrotic tip extends up to kill embryo nearer to the fallopian tube
        - Obligate siblicide
        - Intrauterine competition between embryos
        - May help with balanced running by the mom
    - Cows
        - Single uterine cavity
        - Usually one, but sometimes dizygotic twins that share placenta
        - In cattle, XX individuals that share the uterus with an XY twin develop into sterile intersexes known as freemartins
        - Anastimosis between blood vessels
        - Sex-specific hormones circulate to female side, causing a masculinizing effect
    - Armadillo phylogeny
        - Sloths
            - Single uterine cavity (no internal divisions)
        - Dasypus novemcinctus
            - simplex uterus with litter abilities
            - single implantation site
            - same-sexed quadruplets
            - single corpus luteum in ovary
            - quadruplets are monozygotic
            - implantation delayed > three months
            - invasive hemochorial placentation
            - human like
            - common extraembryonic membrane
            - no evidence of in utero competition
            - There is no evidence that armadillo littermates are particularly cooperative
    - Cebidae
        - Cooperative breeders among primates
        - Helpers (usually previous offspring) take some of the load off the parents
        - Marmosets and Tamarins
            - Twinning
            - Chimerism (they're all bone marrow chimeras of their co-twins, so there are XX and XY cells circulating)
                - Females have lymphosites with Y chromosome
                - **Possible essay question:** Why not intersex externally?
            - Cooperative breeding
                - fathers and helpers do most of the carrying of infants
                - helpers reduce carrying by father
                - parents and helpers share food with infants
                - some species have postpartum estrus
            - conventional simplex uterus
                - 2 placental discs with anastimosis (share blood supply)

        - Twin-twin transfusion syndrome (happens more with fewer connections; probability of unequal blood sharing is increases)
        - If you cut a fallopian tube, you can get non-chimeric singletons
            - **Possible essay question:** How does this affect behavior?
- Hypothesis
    - a full-sib's offspring are nieces/nephews
    - a parent's offspring are brothers/sisters
    - relatedness to nieces/nephews = 1/4
    - relatedness to brothers/sisters = 1/2
    - relatedness to own offspring = 1/2
    - sibs would prefer each other to help parents produce extra brothers and sisters
    - sibs' cells in chimeric somas may favor reproductive suppression
    - bias in the system favors cooperative breeding
- Marmosets have low levels of MHC class I diversity and are particularly vulnerable to viral disease
    - Response to chimerism?
    - Not vulnerable to each others' T cells
    - Fitness costs in terms of immunity
- Why did it evolve?
    - Expression of competition in uterus
    - Both twins sending T cells into each other
    - Sharing of blood cells facilitates some peace between genotypes