Lecture 13 – Reproduction II: Morphology & Cyclicity

I. Morphology – Reproductive morphology varies considerably among mammals.

A. Male *internal* reproductive morphology is only somewhat variable.

1– Gametes are produced in testes, specifically in the seminiferous tubules.

2 – Sperm is collected in the epididymis, where it's sometimes stored.

3 – The gametes travel through the vas deferens to the urethra, and mammals all engage in internal fertilization. There are lots of glands that contribute to seminal fluid (including the prostate, which is very susceptible to malignant tumors).

4 – The position of the testes varies.

Testes may remain in the abdominal cavity permanently (e.g., Monotremes, xenarthrans, most marine mammals).

They may reside in abdominal cavity and, during breeding season, descend into the scrotum via the inguinal canal (e.g., bats and rodents).

They may be permanently housed in the scrotum (e.g., most primates, carnivores).

Male *external* reproductive morphology is more variable.

5. Marsupials have a bifurcate penis, which mirrors the female morphology.

6. Many mammals have a baculum, a bone that forms at different points in the penis (Primates, Rodents, Insectivorans, Chiropterans, & Carnivorans).

In some groups, bacular morphology evolves really quickly. This is especially the case in some sciurids.

1 - It's an important taxonomic character, like in chipmunks.

2 - It's almost certainly under sexual selection. In some forms (especially chipmunks and ground squirrels), it appears suited to a sperm removal function, so it may play a role in sperm competition.

Because its presence of is common in lots of eutherian mammals, it was long thought to be homologous across eutherians. However, the phylogenies suggest that it has evolved independently several times (Schultz et al. 2016. - pdf on website). This makes sense, as it's a heterotopic sesamoid bone.

Therefore, it probably serves different functions in different groups.

B. Female internal morphology is much more variable.

For example, female marsupials have two lateral vaginas and a medial birth canal.

Variability in Eutherians:

1 - Gametes form in the ovaries.

2 – Fertilization typically takes place in the oviduct.

3 – Fertilized egg moves into the uterus, where it implants.

4 – The uterus is connected to the vagina by the cervix.

5 – There is variation in the degree of fusion.

Shown here is a **duplex** uterus of rodents & rabbits, where there's a right & left uterus, each with a separate cervix opening into the vagina.

In a **bipartite** uterus (carnivores), the distal ends are fused and there's a single cervix.

In a **bicornate** uterus (e.g., cetartiodactyls & perissodactyls), there's more fusion of the two uteri, and a distal body of the uterus.

In a **simplex** uterus (e.g., primates, xenarthrans), the uteri are fused into a single body.

II. Cyclicity -

A. By far, most mammals are iteroparous, and have more than one cycle per lifetime.

B. In a few insectivorous metatherian mammals, males are semelparous. There is a single reproductive cycle during the life of an individual: *Antechinus*, a genus of Dasyurid marsupials.

Males all die after a single frantic bout of reproduction. This is driven by extreme sperm competition (Fisher et al. 2013. Sperm competition drives the evolution of suicidal reproduction in mammals. PNAS 110:17910-1791.) and is termed "suicidal reproduction." Death is caused by very elevated levels of stress (as indicated by the high concentrations of stress hormones).

C. Cycles - Overview

Estrous Cycle

Ovarian Cycle – production of ova

Uterine Cycle – preparation of uterus for pregnancy

Monestrous (one per year) versus Polyestrous (>1 per year).

Spermatogenic Cycle – production of sperm

In general, male cycle tends to track the female cycle in species with infrequent estrus, but there are interesting exceptions.

D. Control of Cyclicity. Primarily, all cycles are under control of the pituitary hormones.

Very often this cyclicity is regular, as is the case in humans.

Or cycles actually may be induced, & there are many cues (behavioral, visual, or environmental) that can induce the pituitary to initiate reproductive cycles.

Perhaps most importantly, environmental cues perceived by any of a variety of senses act on the pituitary, and thereby **confer seasonality**.

Examples. *Microtus montanus* Montane vole, both males and females become reproductively active in response to a substance, 6-MBOA, that is present in high concentrations in young actively growing plants. Young are produced only when adequate food is available.

Dipodomys (Kangaroo rats) are desert rodents that live for several years. In particularly dry years there is no seed crop; 0% of females become reproductively active.

Again, these environmental cues operate **external to cycles** to confer seasonality.

This seasonality is important for two reasons. It allows:

1) Breeding when there is sufficient food to fuel postnatal growth of young.
2) Sufficient food to fuel lactation for mother. This is particularly important because (as we discussed earlier this semester) lactation is around twice as expensive as gestation.

On top of this cyclicity, several mechanisms have evolved that **operate within a cycle** for optimizing the timing of birth.

1) **Delayed Fertilization** (Sperm Storage) - occurs in both males and females.

Vespertilionid bats – In *Myotis*, spermatogenesis ends by late August and males store sperm in the epididymis (a sperm-storage organ associated with testicles) until breeding in late October as the bats congregate at hybernacula. Females then store sperm in the uterus for up to three months prior to fertilization in February.

Allows for parturition (birth) in spring after about 3 – 4 months, when aquatic insects are starting to emerge and become abundant.

2) **Delayed Development** - Occurs in a few bats

Blastocyst implants but then becomes dormant *after* implantation.

In *Artibeus* (a phyllostomid), the embryo implants in the endometrium in mid-summer, development halts until early winter. Parturition occurs at the end of the dry season, when fruits are most plentiful.

3) **Delayed Implantation** - Common - Chiroptera, Carnivora, Xanarthra, Cetartiodactyla, Rodentia, Insectivora

After copulation, the fertilized zygote reaches the blastocyst stage and then becomes dormant.

It remains floating either in the oviduct or uterus and is encased in its protective coat, the **zona pellucida**. Development halts and the embryo becomes dormant.

After a period of dormancy, which may last up to nine months, the blastocyst implants and gestation continues.

May be **obligate,** and always occur (e.g., *Ursus americanus*).

May be **facultative**, and occur only when conditions are bad, as in many rodents.

It's been well studied in carnivores, and until ~17 years ago, it was thought that delayed implantation evolved several times.

Both Lindenfors et al. (2003. Evolution, 57:1952) and Thom et al. (2004. Evolution, 58:175 - pdf on course website) examined delayed implantation in the context of (incorrect) carnivore phylogeny and there appears to have been a single origin in the Carnivora.

It's just the family Mustelidae in which it has been lost repeatedly.

Further, within mustelids, it appears that the taxa that experience greatest seasonality are most likely to retain delayed implantation. There is also an association with longevity; short-lived taxa can less afford to delay reproduction.

4) **Macropodid Embryonic Diapause** - Some biologists lump this with delayed implantation, but since macropodid embryos only attach loosely to the endometrium, many folks treat this as a separate mechanism.

This is facultative; it only occurs if there is already a joey in the marsupium.

A joey is born and, as mentioned, there's no interruption in the estrous cycle in marsupials.

A post-partum estrus occurs. Typically, another ovum is fertilized while the first offspring is still very poorly developed and attached to the nipple.

The suckling of the 1st neonate triggers hormonal suppression of the second blastocyst, preventing further cell division and preventing attachment to the endometrium. This **embryonic diapause** can last **up to 235 days (the shell membrane protects embryo).**

When the 1st joey leaves the pouch, hormonal suppression of the second embryo ceases and normal attachment and gestation of the blastocyct occurs.

Since gestation is so short, **30 days**, the 1st joey is still suckling when the younger sib is born.

Thus, adjacent mammae provide milk of different composition.

The older joey suckles from a nipple that is producing milk of little or no carbohydrates, whereas the younger joey is suckling from a nipple that is producing milk with very high carbohydrates content.

Again, a post-partum estrus occurs, and a third embryo is fertilized.

Female kangaroos usually have three offspring going at a time - An old joey
- A very young joey
- An embryo in diapause

We often hear the marsupial mode of reproduction characterized as vastly inferior and primitive relative to that of eutherians. This is referring to the efficiency of transport of maternal nutrients across the placenta. The situation just described this is actually a very highly derived system that allows essentially a back-up embryo to be perpetually available.