Lecture 18. Reproductive physiology and eggs

Class Business

Reading for this lecture

Required. Gill: Chapter 14

1. Reproductive physiology

In lecture I will only have time to go over reproductive physiology briefly, so you should pay extra attention to this topic in the textbook readings. Here I summarize the main points.

A) REPRODUCTIVE HORMONES

- i) **Follicle-stimulating hormone** regulates gamete formation.
- ii) **Luteinizing hormone** plays a key role in controlling breeding because it regulates the secretion of reproductive hormones in the testes and the development of mature ova in the ovaries.
- iii) **Testosterone** and **estrogen** are produced by the gonads of both males and females, but the relative concentrations of these two hormones differ between the sexes and determine their effects. In many birds, increased testosterone levels in the blood cause the development of secondary sexual characteristics, such as breeding plumage, bright bill and foot colors, growth of skin ornaments, etc.

B) MALE REPRODUCTIVE SYSTEM

- i) Male birds have paired testes, which become greatly enlarged during the breeding season.
- ii) Sperm are produced at night, when body temperatures are slightly lower, and then stored in seminal vesicles which cause a distinct **cloacal protuberance** in breeding males.

C) FEMALE REPRODUCTIVE SYSTEM

- i) Most female birds have only one ovary.
- ii) In birds, females are the **heterogametic** sex. This means that their sex chromosomes differ as do those of male (but not female) mammals. In birds, females are said to have ZW sex chromosomes, while males are **homogametic** (ZZ).
- iii) Female birds can store sperm for later use in special tubules in their reproductive tracts.

D) BENEFITS OF OVIPARITY

- i) Can produce a larger number of large offspring.
- ii) Viviparity may be impossible due to the high body temperature of birds.

2. Egg production

A) COPULATION

- i) Birds do not have external genitalia and copulation usually is very brief and simply involves touching their **cloacas** together.
- ii) As usual, there are some exceptions. Some birds have prolonged copulations; others have penis-like structures that are used to transfer sperm into the female.
- iii) Many birds have elaborate stereotyped post-copulation displays.

B) FERTILIZATION

- i) Fertilization (creating an embryo) occurs after ovulation when the **ovum** is in the **oviduct**.
- ii) In some cases, sperm that has been stored for several weeks is used to fertilize eggs. Hence, extra-pair fertilizations can occur without extra-pair copulations!

C) EGG DEVELOPMENT

- i) The yolk is added while the ovum is still in the ovary (prior to fertilization). Other parts of the egg are added as it passes down the oviduct. The time it takes to form the yolk varies depending on the size of the species.

ii) As the egg travels down the oviduct the egg white (**albumen**), shell membranes, and the pigments that give the egg its external patterning, are sequentially added.

iii) Calcium is an important nutrient in egg development and many female birds will seek out environmental calcium prior to egg production. Experiments have shown that putting snail or egg shell fragments out on bird feeders will attract female birds and that this effect is greatest early in the breeding season.

iv) When birds lay more than one egg in a clutch, they do not produce them all simultaneously. Instead, a female may have several embryos at different stages of development in her oviduct. Each will be laid once it has had all its various layers added. Most birds are able to produce an egg every 1-2 days.

3. Characteristics of bird eggs

A) BASIC STRUCTURE

i) Birds have **amniotic** eggs, which mean that they have more than one extra-embryonic membrane. In addition to a membrane around the **yolk sac**, birds have three other membranes. The **amnion** surrounds the embryo, the **chorion** surrounds all embryonic structures, and the **allantoic** membrane creates a space within the egg that is used during gas exchange and as a place to store waste products. After the embryo leaves the egg, the allantois (including the waste materials) is left behind in the shell.

ii) Amniotic eggs appear to have evolved at lest in part because they allow larger eggs to be formed. This increase in size is possible because the extra membranes allow for improved gas exchange (not just simple diffusion) and structural support. One advantage of increased size, is better thermal stability within the egg.

iii) Bird eggs also are **cleidoic**, which means that they have a rigid (calcareous) shell. The shell provides advantages in that it protects the embryo (e.g., from parasites, invertebrate predators) and that it helps prevent the egg from desiccation. But it also has disadvantages in that it does not allow for the uptake of water through the shell. Consequently, cleidoic eggs need to have all the water that they will need during development on the inside from the time they form.

iv) In addition to the embryo, a bird's egg consists of the yolk (the source of nutrition for the embryo), the albumen (a source of water for the embryo, and also a protective layer that cushions the embryo and buffers against temperature fluctuations), and the shell.

v) Egg shells are made primarily from calcite and the calcium in the shell has a dual function as it is redirected for bone growth as the embryo develops. Although the egg shell is hard it is also filled with tiny pores that allow gases (oxygen and carbon dioxide) and water vapor to pass through.

B) EGG SIZE AND NUMBER

i) Egg sizes vary among species, with larger species generally having larger eggs. When egg size is compared to the size of the female, however, many small species lay eggs that are relatively larger those of big birds. Birds such as the Brown Kiwi lay eggs that are relatively massive – up to 25% the size of an adult female (check out Fig 17-1 in Gill). Other birds invest even more resources in their young when they lay multiple eggs. For example, a clutch of shorebird eggs can weigh over 60% of the female's mass.

ii) Egg size also varies within species, and within a clutch – larger eggs usually lead to larger young, which are more likely to survive.

iii) A group of eggs laid together at the same time is referred to as a **clutch**. Clutch size is fixed in some species (i.e., all have the same number of eggs), but can be very variable in others. Even species with fixed clutch size often replace eggs that are lost – sometimes almost indefinitely. In some species, however, clutch size is **determinate** – birds lay a fixed number of eggs and no more.

C) COLORS AND SHAPE

i) Egg colors also vary hugely among species, with a range of different base colors and all sorts of different markings. Usually these patterns help to camouflage the eggs. Often, egg markings are somewhat predictable within individuals, and it is sometimes possible to spot an egg that has been "dumped" in a nest by another female by its distinct pattern.

ii) The eggs of many hole-nesting species lack pigments or patterns, presumably because an egg in a dark hole does not need camouflage. That patterning has been lost in several different lineages of birds suggests that birds incur some cost in creating patterned eggs.

iii) Although you might think that all eggs are "egg-shaped" there is actually a lot of variation on the basic theme, from almost round to extremely pointed ("pyriform") eggs. In some cases, shape seems to be adaptive. The pyriform eggs of many shorebirds seem to be well suited for efficient "packing" within the nest. A similar shape in murres seems to have evolved to cause the eggs to roll in a circle when knocked, which prevents them from rolling off the edge of the narrow cliff ledges where their parents nest.

4. Incubation

For an egg to develop and survive it needs to be kept at an appropriate temperature. This means that birds need to keep it warm when the air is cold and that they also need to prevent it from getting too hot. The constant attention that goes with incubation can also help to protect eggs from getting rained on, prevent them from being found and eaten by predators, etc.

A) KEEPING EGGS WARM

i) Birds typically prevent their eggs from getting too cold by sitting on them, with the eggs up against their belly skin. During the breeding season incubating birds develop a **brood patch**. This involves a loss of feathers on their belly, skin thickening, development of fluid below the surface, and increased vascularization. These things all help increase the transfer of heat to the eggs.

ii) Some birds incubate in other ways – by filling their nests with down, by putting eggs on or under their feet, etc.

iii) The development of incubation behavior is regulated by the hormone **prolactin**, sometimes through interactions with testosterone (which inhibits parental care behavior) or estrogen.

iv) Incubation usually does not start until all of the eggs in a clutch have been laid. Consequently, the development of all of the embryos starts at the same time and the eggs hatch synchronously. But, some species begin incubation right after the first egg is laid. In this case, the first eggs get a head start and hatch earlier than the last laid eggs. In species with **asynchronous hatching** (e.g., owls, hawks, rails), this can lead to big size differences within a brood of chicks.

B) PREVENTING EGGS FROM GETTING COLD

In hot, dry, places birds also need to worry about their eggs overheating and desiccating. In these species, sitting over the eggs functions largely to shade them from the sun. In some cases, birds will periodically leave the nest and go to get their belly feathers wet. When they return, the wet feathers help to cool the eggs down as well as maintaining a humid microclimate in the nest.

C) TURNING EGGS

Another key job that incubating birds must perform, is to periodically turn their eggs over. This behavior helps move eggs around within the clutch to make sure that all are warmed adequately and also prevents the chorioallantois from getting stuck to the shell membranes which prevents normal development.