ANATOMY AND PHYSIOLOGY OF AVIAN REPRODUCTIVE SYSTEMS

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In the past 10 years, intense interest has developed in determining the sex of birds in avian collections. No sexual dimorphism is evident in many species, especially psittacines, which has lead to the unintentional, but all too frequent pairing of two birds of the same gender. Numerous techniques have been developed to determine the sex in birds. Some of these are highly accurate, others are not. Although there is some degree of risk compared to noninvasive techniques, direct visualization of the gonads offers the highest success rate in accurately determining sex.

The gonads are the sex organs where sperm and ovum are produced. In the male these are called the testes, and in the female, the ovary. As you might expect, the gross appearance of these two organs is morphologically different. It is their location which makes visualization difficult.

In most mammals, including humans, the testes are located in the scrotum which is outside the body cavity. However, in birds, the testes are found within the abdominal cavity, situated on either side of the backbone adjacent to the cranial pole of the left and right kidney. In the female, the ovaries are present within the abdominal cavity of both mammals and birds. There are two ovaries in mammals, but in birds, there is only one functional ovary, which is always located on the left side, positioned similarly as the left testis. To visualize the gonads of birds, one must therefore enter the abdominal cavity surgically.

As you can see already, there are anatomical differences between the gonads of birds and mammals. In fact, there are many unique features and differences between the reproductive systems of the two classes. Nonetheless, in the grand scheme of things, reproduction in birds is not altogether unlike that in mammals. In this paper, anatomical and physiological characteristics of the male and female bird will be presented in order to give the aviculturist a better understanding of what happens when birds breed.

MALE REPRODUCTIVE TRACT

The male bird's reproductive tract consists of the paired testes, epididymis, and ductus deferens. Accessory sex glands (e.g. prostate gland, seminal vesicle, bulbourethral gland) which are present in most mammals, are absent in birds. Also only a few species of birds possess a penile structure (phallus).

TESTES

The testes have two functions, to produce sperm and the male hormone, testosterone.

Grossly, the testes are either oblong or cylindrical in shape, smooth on the surface, and creamy-white in color, although they may be partially or totally pigmented. In cockatoos, for example, the testes are black in color. The testes are very small and usually avascular. In a mature bird, the testes can vary in size and greatly enlarge during the breeding season. In birds with distinct breeding cycles, the testes atrophy after a period of active sexual stimulation. However, the testes never become as small as they were in the prenuptial stage.

Microscopically, the testis consists almost entirely of tubular structures known as seminiferous tubules. Two types of cells line these tubules, spermatogonia cells and Sertoli cells.

The spermatogonia cells proliferate and differentiate through definite stages of development to form sperm. Spermatogonia initially multiply and grow to form considerably enlarged cells called primary spermatocytes. These cells then enter a period of maturation in which the first maturation division forms secondary spermatocytes and the second maturation division forms the spermatids. Each spermatid develops into a spermatozoan. Spermatids are produced by meiotic division, that is, without replication of chromosomes, merely a division of those already present. Therefore, each spermatid has half of the normal complement of chromosomes, none of them paired.

Sertoli cells are large cells interspaced between spermatogonia which extend from the base of the seminiferous epithelium to the interior of the tubules. Spermatids attach themselves to the Sertoli cells and some specific relationship seems to exist between the two cell types which cause the spermatids to change into active sperm.

Seminiferous tubules of immature males are small and lined by a single layer of cells. The mature testis has large irregular-shaped tubules with a multi-layered germinal epithelium consisting of cells representing all stages of spermatogenesis. This is what causes the testis to swell in size during the breeding season.

Testosterone is produced by cells known as interstitial cells of Leydid. These cells are located in the spaces between seminiferous tubules. Testosterone is responsible for a variety of secondary sex characteristics such as male sexual behavior (including song), feather form and color (if different from the female), and the development of a comb and wattles in some species. Testosterone may also help maintain spermatogenesis once it has been established under the influence of the pituitary gland.

In mammals, increasing the temperature of the testes can inhibit spermatogenesis. This is the reason the testicles are located in a dangling scrotum outside of the body cavity.

In addition, the scrotum is well supplied with sweat glands and the testes have a specialized arrangement of blood vessels which aid in keeping the testes cool. The intra-abdominal testes of birds function at a temperature which is no different between that of the body. The threshold at which raised temperatures interfere with spermatogenesis is undoubtedly higher in birds than in mammals.

EPIDIDYMIS

The epididymis is a structure embedded within connective tissue at the attachment of the testis to the dorsal body wall. It consists of a chord-like system of ductules. It is very short by comparison with that present in mammals. The networks of seminiferous tubules (from the testis) unite in the epididymis and the contents flow into and through the ductules, ultimately emptying into the ductus deferens.

In mammals, sperm is stored in the epididymis. Sperm also undergoes a maturation process in these ductules in which they develop mobility.

DUCTUS DEFERENS

In birds, the ductus deferens is the major storage organ for sperm on each side of the abdomen. It is a very extensive, convoluted tube which runs posteriorly, along the midline, parallel with the ureter. In the posterior abdomen, the convolutions of each ductus enlarge greatly; in the pelvis it is straight for a short distance prior to becoming sac-like before ending in the cloaca by an erectile papilla (ejaculatory duct) which projects into the latero-ventral urodeum. The urodeum is the mid-region of the cloaca.

Sperm undergo maturation in the ductus deferens of birds, not in the epididymis. Sperm taken directly from the epididymis lack fertilizing capacity, whereas those taken from the ductus deferens can fertilize. About one-half to two-thirds of the contents of both ducti are expelled during ejaculation. In sexually active birds, it takes one to four days for sperm to be formed and reach the ductus.

PHALLUS

The phallus is analogous to the mammalian penis. There are two main varieties of phallus' in male birds, the truly intromittent organ as seen in ratites (ostrich) and anseriforms (swans, geese) and the non-intromittent type which is present in domestic fowl and some passeriforms. Psittacines lack a phallus.

The phallus is located on the ventral lip of the vent. It is not to be confused with the opening of the ductus deferens in the urodeum on the end of a slender conical projection which is known as papilla.

Psittacines copulate by eversion of the cloacal wall containing the slightly raised papilla which facilitates the transfer of semen to the everted orifice of the oviduct of the female during cloacal contact.

The phallus is different from the mammalian penis in three ways. Its erectile mechanism is lymphatic, not vascular, semen travel via the external surface, as opposed to the internal urethra, and finally the phallus is solely reproductive and urinary.

SEMEN

The volume of semen in one ejaculate averages 0.25 ml in the turkey, 0.50 ml in the chicken, but may be only 0.05-.10 ml in an average size parrot. Volume varies widely among avian species. It is extremely viscous due to the high density of sperm per unit volume. 100 Billion sperm are required for optimal fertility in the domestic fowl.

In mammals, seminal fluid before ejaculation consists of fluid secretions from the testis, epididymis, and ductus deferens. Sperm stored in the epididymis and ductus deferens are infertile, possibly due to a slightly acidic environment and a lack of certain nutrients required to maintain mobility. However, at the time of ejaculation, fluids from the accessory sex glands are added which raises the pH and adds nutrients causing the sperm to become fertile. This process is called capacitation. Although sperm can live for many months in the male genital ducts, once they are ejaculated, they can live for only 24-72 hours at body temperatures.

In birds, no capacitation of sperm is necessary for fertilization to take place (sperm taken directly from the ductus deferens can fertilize). No accessory sex glands are present, so seminal fluids are composed of secretions originating only from the testis, epididymis, and ductus deferens. In addition, a lymph-like fluid generated during erection and causing an engorgement of the phallic structures in the cloaca can be made to pass through the epithelial lining and intermix with the seminal fluid. This fluid is called “transparent fluid” and its significance is debatable. Unlike mammals, avian sperm, once ejaculated and inseminated into the hen’s oviduct can retain their fertilizing power for a period of many days to weeks.

FEMALE REPRODUCTIVE TRACT

The female bird’s reproductive tract consists of the left ovary and the left oviduct. The left and right ovary and oviduct develop embryonically as paired structures, but after hatching, the right ovary and oviduct degenerate. If the left ovary is removed from a chick before 30 days of age, the remnants of the right ovary will develop into an ovitestis, which may be capable of producing sperm.

OVARY

The ovary has two functions, to produce the ovum and the female hormones, estrogen and progesterone. In addition, some testosterone is also produced by the ovary.

The left ovary is found in the body cavity cranial to the left kidney adjacent to the adrenal glands. It is attached to the body wall by a thin ligamentous structure called the mesovarian.

The ovary consists of two parts, the medulla and cortex. The medulla contains connective tissue, nerves, smooth muscle, and blood vessels. The cortex covers the medulla and contains oogonia. Oogonia are precursor cells which form oocytes and eventually the ovum (counterpart to sperm). By the time of hatching, oogonia have stopped multiplying and begin to enlarge. They are now called primary oocytes. Within the ovarian cortex of the adult hen, several hundred primary oocytes may be visible to the naked eye. About 12,000 are visible microscopically. Few of these will ever enter the stage of rapid growth. Primary oocytes visible on the ovary are often termed follicles, which pertain to the primary oocyte and its membranous covering.

Grossly, in the ovary of a very young, immature bird, follicles are not evident. The ovary is flattened and may resemble a piece of fat. It may contain smooth grooves or folds which make it seem 'brain like' in appearance. The ovary of an older immature female has a fine granular surface which resembles cobblestone. This is consistent with very early follicular development. The ovary of a mature bird has a grapelike cluster of small, but prominent follicles which are easy to identify. As the breeding season approaches, several of the follicles enter a phase of rapid growth and maturation, becoming yolk-filled just before ovulation. After sexual activity, the ovary goes into a resting phase where it becomes diminutive in size again. However, a large number of follicles will remain larger than as all appeared in the prenuptial phase. Such an ovary is described as mature, but inactive.

In those few follicles which undergo rapid growth during sexual stimulation, yolk material accumulates and the primary oocyte gradually grows to full size. The avian primary oocyte is the largest cell in the animal kingdom. In the domestic fowl, its final weight is about 20 g. After reaching its full growth, the primary oocyte completes two maturation divisions, the first of which form the secondary oocyte and the first polar body. This occurs about two hours before ovulation. This division is a reduction or meiotic division which means the secondary oocyte has only one half the normal numbers of chromosomes. Ovulation occurs next. This is when the follicle splits at one end (this area is called the stigma) and the secondary oocyte is engulfed by the oviduct. The second maturation division, forming the ovum and second polar body occurs in the oviduct. Probably penetration by the spermatozoan is needed before this division can be completed. Penetration occurs about 15 minutes after ovulation. Since it must occur before the secondary oocyte becomes covered by albumen, it presumably happens in the infundibulum. Fertilization is the actual fusion of the male and female pronuclei (chromosomes).

In birds, sex is determined by the female and not by the male as in mammals. Chromosomes in all animals are paired. The sex chromosomes (there are two) are called either X or Y. In mammals, the male has an XY configuration. The female is XX. In birds it is the opposite. Sex is actually determined before ovulation. If the secondary oocyte receives an X chromosome, the chick will be male (XX). All sperm carry an X chromosome. If the secondary oocyte receives the Y chromosome, the chick will be a female (XY).

The large yolk-filled follicles on the ovary of breeding birds occupy a considerable portion of an already crowded abdominal cavity. The number of oocytes that will ultimately ovulate and produce eggs is a characteristic of the species and/or individual. Budgerigars are 'determinate layers', meaning they lay a fixed number of eggs. Many other birds (including most large psittacines) are 'indeterminate layers' and can quickly replace eggs which are lost from their clutch or removed. Aviculturists take advantage of this physiologic trait and pull eggs for incubation knowing the parents will often 'double clutch.' Domestic fowl lay up to 350 eggs a year.

OVIDUCT

The oviduct is attached to the dorsal body wall by the mesotubarium ligament. In the immature or non-breeding hen, the left oviduct is an inconspicuous, narrow tube, straight and uniform in diameter. In the sexually active bird, the oviduct undergoes tremendous enlargement and occupies a large part of the abdominal cavity. An increase in length causes a folding of the oviduct upon itself. Glandular development results in a thickening of its walls which differentiates it into five functional regions associated with egg formation: the infundibulum, magnum, isthmus, uterus, and vagina.

INFUNDIBULUM

The first section of the oviduct has two components, a thin walled funnel which rapidly tapers into a tubular region. The funnel opening is an elongated slit which faces the ovary. The ovulated secondary oocyte is grasped and literally swallowed by the infundibulum (funnel). This catching process is made easier by the left air sac which tightly encloses the ovary in the 'ovarian pocket' except caudally where the funnel opens. Nonetheless, not all ovulated oocytes are successfully captured. Some are lost into the body cavity where they are either harmlessly absorbed or become involved in egg peritonitis. This is known as internal laying. Penetration by spermatozoan occurs in the funnel. The function of the tubular region is unclear. Formation of the yolk membrane's outer layers, chalaziferous layer of albumen, and chalazae probably begin here.

MAGNUM

The magnum secretes the thick albumen protein around the ovum. It is the longest and most coiled part of the oviduct. It is readily distinguished from the infundibulum by its greater external diameter and markedly thicker wall caused by the presence of numerous glands packed into massive mucosal folds. The stimulus to secrete albumen may be mechanical, arising from the passage of the ovum along the magnum. The yolk membranes are strong and permit considerable squeezing as the ovum is passed along by smooth muscle contractions.

ISTHMUS

This region is short with less prominent mucosal folds. The division between the magnum and isthmus is marked by a thin, translucent line which can be seen on the mucosal surface with the unaided eye (in domestic fowl). The isthmus produces two shell membranes which are loosely secreted around the ovum and albumen.

UTERUS

The segment of the oviduct immediately succeeding the isthmus is of similar diameter but after a short course, expands to form a pouch in which the egg is retained during the entire period of shell formation.

VAGINA

The vagina is the short terminal portion of the oviduct proximal to its opening into the urodeum. Powerful muscles of the vaginal wall and a well-developed, muscular sphincter at the uterine-vaginal junction serve to expel the egg. The lining of the vagina has tubular crypts that act as 'sperm nests' for storing sperm. In domestic fowl and many other species, the capacity for fertilization is retained for several weeks after a single insemination. Within minutes after insemination, sperm reach the infundibulum, but they disappear within 24 hours only to reappear in the lumen in small numbers at the time of each subsequent ovulation. How sperm survive in the vagina or what causes them to be released is unknown.

FORMATION OF THE EGG

In the domestic fowl, the egg traverses the oviduct in about 25 hours.

The raw materials of the yolk (proteins and lipids) are synthesized in the liver, travel through the blood to cells in the ovarian cortex which pass them to the oocyte where they are reorganized into yolk spheres and fluid for the embryo. The germinal disc is a small disc of cytoplasm containing the remnants of the nucleus. It can be seen on the surface of the yolk of a fresh egg as a circular, opaque white spot, 3-4 mm in diameter.

The egg passes through the infundibulum in about 15 minutes during which time tubular glands lay down a thin layer of dense albumen immediately surrounding the yolk known as the chalaziferous layer. Connected to this layer are two chalazae which appear as

twisted strands of dense albumen, the function of which is to suspend the yolk between the two ends of the egg.

The egg takes about 3 hours to traverse the magnum. During this time it acquires albumen. Albumen is much less viscous than yolk, the solid component being composed almost entirely of protein. Albumen contributes to the aqueous environment of the embryo, has antibacterial properties, and is a source of nutrition for the embryo.

Movement through the isthmus is slow, taking about 1 and ½ hours. The inner and outer shell membranes are formed here.

The egg occupies the uterus for about 20 hours during which the shell is formed. During the first eight hours, 'pumping' occurs which is the addition of watery solutions from selective uterine glands into the egg. The weight of the albumen is doubled and the albumen becomes multi-layered. During pumping calcification is slow, but during the last 15 hours it is rapid. Every 15 minutes the uterus withdraws from the blood a weight of calcium equal to the total amount circulating at any one moment. Within the femur and tibia of female birds is specialized medullary bone. This bone formation is stimulated by the synergistic action of estrogen and testosterone. Much of the mobilized calcium for shell formation comes from these sites.

The shell consists of the shell membranes, the testa, and the cuticle. At the blunt end of the egg, the outer and inner membranes separate from each other as the egg cools immediately after hatching forming the air sac. The head of the embryo will come to lie close beneath this space.

The major part of the shell is known as the testa. It consists of an organized matrix of fine fibers and a far more bulky (98%) solid inorganic component consisting mainly of calcite (a crystalline form of calcium carbonate). In most birds, thousands of pores open on the surface of the shell and extend between crystals right through to the shell membranes. The pores are covered by the cuticle but are permeable to gases.

Overlying the testa and pores is an extremely thin organic layer called the cuticle. It is water repellent, reduces water loss, and acts as a barrier to bacteria.

Shell thickness varies greatly between species but in general, larger birds have proportionately thicker shells. The thickest shell is that of an ostrich which is only 2 mm. Egg color is due to the secretion of porphyrins by uterine epithelium.

In some species the egg turns 180 degrees just before being layed so that the blunt end comes out first. The significance of this is not known. The egg travels through the vagina in a matter of seconds.

CONTROL OF REPRODUCTION

Stimulation of reproductive activity in birds is under the influence of external stimuli and internal control mechanisms that have developed over the course of evolution to maximize the probability of survival of the young. Despite the wide variety of reproductive patterns among birds, it is clear that all control systems have certain elements in common.

The hypothalamus occupies a central position in the mechanism that controls reproduction. This small structure located within the brain controls the autonomic nervous system (those activities over which an animal has no conscious control). The hypothalamus is either stimulated or inhibited by external or internal factors which affect the release of neurohormones which in turn control the pituitary gland, a tiny organ located on the underside of the brain. The anterior portion of the pituitary gland is an endocrine gland. Hormones are released from here which affect other endocrine glands throughout the body, including the testes and ovary. Hormones which affect the gonads are known as gonadatrophins. The two major ones are Follicle Stimulating Hormone (FSH) and Luteinizing Hormone (LH).

There are at least two patterns of hypothalamic activity that have been identified in birds with respect to gonadatrophic function of the anterior pituitary.

1. **Constant stimulation of the anterior pituitary by neurohormones from the hypothalamus except when inhibited by unfavorable external (environmental) conditions. Examples include the budgerigar and zebra finch. These species are reproductively active year round as long as environmental conditions (e.g. rainfall, temperature, food) are adequate. Superimposed on this are requirements with respect to nesting sites, availability of mates, and behavioral interactions between prospective mates and/or other individuals in the flock.**
2. **Constant inhibition of the anterior pituitary. The hypothalamus is inactive gonadatrophically except when the system receives specific environmental cues which are stimulatory in nature. The most common examples are photoperiodic species from mid to high latitudes. The reproductive cycle of these species is rigidly controlled by day length (photoperiodism). Additional environmental conditions (e.g. singing male, certain types of foods, nest sites) may be needed to achieve complete reproductive activity. Many periodically breeding species are not highly photoperiodic, but rather use other sources of environmental information. This clearly is the case for periodic breeders of the equatorial regions.**

In some species, reproductive activity is based on an endogenous circennial (yearly) cycle that is entrained into an annual cycle by some reoccurring event, be it the annual photo cycle or some other environmental factor.

GONADATROPHINS

In review, hypothalamic stimulation of the anterior pituitary gland produces FSH and LH which in turn stimulate either the testes or ovary.

In the male FSH initiates the growth of seminiferous tubules (spermatogenesis) while LH promotes the development of Leydid cells which in turn produce testosterone. Testosterone initiates male sexual behavior. Testosterone also inhibits the hypothalamus which then inhibits gonadatrophic secretion by the anterior pituitary which then decreases testosterone production. This inhibitory effect of testosterone provides a feedback control system for maintaining testosterone secretions at a constant level.

In the female, FSH is the primary hormone responsible for follicle growth. However, small amounts of LH are also required for this process. As the follicles increase in size, they begin to produce estrogen and progesterone. These hormones in turn affect the secretion of gonadatrophins which regulate ovarian function.

Progesterone is the most important ovarian hormone regulating pituitary activity and it seems that its concentration in the blood determines whether it is stimulatory or inhibitory. Its action is mainly on LH. LH is clearly involved in hormonal control of ovulation of the mature follicle. The maximal amount of LH released into the blood occurs 6-8 hours before ovulation. An increased amount of circulating LH apparently increases progesterone secretion from the follicle before ovulation. The higher progesterone levels then surpass the critical concentration level required to change from positive to negative feedback. Therefore progesterone is now inhibitory to additional LH secretion which helps prevent more than one follicle from ovulating at the same time.

The postovulatory follicle shrinks to a thin-walled sac which undergoes rapid regression. In mammals, a corpus luteum develops on this site which continues to produce progesterone which helps prepare the uterus for the recently released ovum and inhibits additional follicles from ovulating. However in birds, progesterone secretion decreases rapidly in the postovulatory follicle and is negligible after 24 hours. This helps decrease progesterone to a low level again which is stimulatory for additional LH secretion which promotes ovulation of the next mature follicle.

Estrogen is involved in the induction of numerous female sex characteristics such as the development of an incubation patch, plumage color, the development of the oviduct, nest-building behavior, and the mobilization of calcium for egg-shell production. Estrogen probably works synergistically with other hormones (e.g. progesterone, prolactin) to initiate these activities.

Aside from its role in the ovulatory cycle, progesterone acts with estrogen in the development of the oviduct and probably promotes incubation behavior.

The role of testosterone in the blood of female birds of certain species is poorly understood. It is produced by interstitial cells within the ovarian cortex.

ONSET OF MATURITY

The onset of maturity in birds is probably genetically controlled but it may be influenced by external factors. Sexual maturity is defined as the summation of morphological and physiological changes which culminate in the normal reproductive ability of the animal. In the female, oviposition or passage of the first egg is taken as the onset of sexual maturity. It cannot be so accurately determined in the male.

The most important factor regulating the development of reproductive capacity in most species is light (photoperiodism). The normal pathway for photoperiodic stimulation is through the pupil to the retina and from hence by way of the optic nerve to the hypothalamus. Light can also penetrate the soft spongy bone of the head and stimulate the hypothalamus via the pineal body.

Normally lengthening the photoperiodism to 12-14 hours is stimulatory but this obviously varies among species. A continuing change in day length (increasing daily illumination), especially at the shorter photoperiodism is very stimulatory in initiating reproductive activity. Also certain wavelengths of light (e.g. red) are more stimulatory than the blue or violet portions of the spectrum.

Nutrition also plays an important role in reproduction. Any nutritional deficiency, particularly of vitamins and certain minerals can retard both growth and sexual maturity. Calcium deficiency leads to a reduction in FSH secretion which inhibits or decreases the number of maturing follicles. It is also required for egg shell formation. Diets high in fat (e.g. sunflower seeds, safflower seeds, peanuts) increase the likelihood of calcium deficiency. Aside from being low in calcium to start with, the fats of oil seed diets combine with available calcium ions in the gut to form insoluble soaps which are not absorbed.

As a general rule, sexual maturity occurs at six months in budgerigars, lovebirds, and cockatiels. Most conures are capable of breeding at 1 to 2 years, lories and lorikeets around 2 years. Pionus species, small cockatoos, and miniature macaws vary between 2 and 3 years. Amazons, Greys, large Cockatoos, and Macaws begin breeding between 4 and 6 years. Domestic-raised psittacines appear to go to nest and produce fertile eggs at a younger age than their wild counterparts do. Decreased stress in captive-raised birds may be a contributing factor.