N Harcourt-Brown
30 Crab Lane Harrogate
North Yorkshire HG1 3BE
United Kingdom

It is nearly correct to say that female birds lay eggs, whether or not a male is present. It is more likely that the female will lay in the right circumstances if a male is present and in all probability the eggs will be fertile. However turkeys are potentially parthenogenetic and will lay infertile eggs that contain an embryo if incubated! The incidence is 32-49% of infertile eggs (Olsen, 1960). The embryo usually dies at an early stage. It has been recorded in poultry far less frequently but the presence in non-domestic species is unrecorded.

FORMATION OF THE EGG

It has become a tradition to refer to the body cavity of the bird as the coelomic cavity, because there is no diaphragm to divide it into thorax and abdomen. To me, this always sounds a laboured terminology. King and McLelland (1984) divide the trunk (the whole body between the neck and the tail) into the thorax, abdomen and pelvis. All authorities use the terms thoracic and abdominal air sacs so I tend to use thorax and abdomen as anatomical terms.

In embryonic birds, two ovaries form but cells from the right ovary migrate to the left. In almost all adult birds only the larger left ovary only is functional and only a left oviduct forms. Sometimes a small right ovary is present. The blood supply to the ovary is large and the vessels are short. The ovary is closely attached to the body wall, next to the adrenal gland and cranial division of the kidney. The ovary has many obvious follicles; these are small in immature and non-breeding birds. In adult sexually active birds the follicles are enlarged dramatically by the presence of yolk. This large follicle develops suspended on a stalk of smooth muscle, blood vessels, and nerves. It contains a large primary oocyte surrounded by a multi-layered wall that is potentially divided by a white meridional band, the stigma. The stigma is devoid of connective tissue and smooth muscle and has fewer nerves. At ovulation the stigma is split; the (secondary) oocyte is ‘grabbed’ by the infundibulum, a task made easier by the discrete size of the left abdominal air sac which almost encloses the ovary directing the oocyte to the funnel-shaped entrance of the infundibulum. If the oocyte is shed but not enveloped by the infundibulum it falls into the peritoneal cavity and is usually reabsorbed.

The oviduct is supported by the muscular cord, the dorsal and ventral ligaments; it has five parts. The first part, the infundibulum, picks up the oocyte after it has been shed by the ovary and surrounds it with a first (chalaziferous) layer of albumen (egg white). Fertilisation of the oocyte by the sperm is limited to a period of about 15 minutes, being the period between release of the oocyte from the ovary and it being covered with albumen. This is possible because sperm are contained in folds in the mucosa of the oviduct. The egg passes through the magnum where the rest of the albumen is added. In the isthmus the two shell membranes are produced which cover the egg and also predict its final shape. The egg then enters the uterus (shell gland) where it spends 80% of its time in the oviduct. Firstly the egg absorbs water and enlarges to a plumped egg-shape. Then the calcium carbonate and protein shell (testa) is produced that is finally covered with a cuticle giving the egg its shiny appearance. The shell contains thousands of tiny pores that run from the shell membranes to the surface, allowing the embryo to respire. In parrots the shell is white but many birds have pigments within the shell. The final part of the oviduct is the muscular vagina that in many species has spermatic fossulae, which are capable of sperm storage. In many species, e.g. budgerigar, viable sperm can be stored and released for several days. After mating, some of the sperm is stored; some is able to reach the infundibulum within a few minutes.

It is traditional to describe the egg moving down the oviduct. In reality, because of the length of the oviduct and size of the egg, the egg is relatively static in the abdominal cavity whilst the oviduct moves over it by peristalsis. Whilst this distinction may sound trivial it is the root cause of some of the problems that veterinarians see in breeding birds.

EGGS

Parrot eggs are white, relatively small and have little difference between the blunt and narrow ends. Most parrots lay their eggs on alternate days. The eggs are incubated from the time that they are laid, usually by the female. Parrots brood their eggs continually. Like nearly all other birds, they turn the eggs regularly. Diurnal raptors have coloured eggs, and there is a more obvious blunt end. They lay every two or three days and incubation may be shared or is mainly by the female. Owls tend to lay round white eggs asynchronously; the female carries out the incubation. As a rule birds that nest in holes lay white eggs; birds that nest in the open have coloured eggs. Many small passerine birds lay their eggs daily; eagles lay eggs up to 5 days apart. The hard outer shell is shaped to resist external forces but is easily broken by force from within. The outer layer of the shell is the cuticle: a thin, hard, continuous outer covering of lipid and protein that gives the egg its smooth sheen. It is responsible for repelling water and bacteria. The testa is the calcified portion (98% $CaCO_3$ and 2% protein matrix) and has a complicated structure. This part of the shell provides most of the calcium required by the embryo. The surface of the testa has pores that open onto the surface (under the cuticle) and also connect with canaliculi that run right though the shell to the membrane. The pores allow gaseous exchange; they are most numerous at the blunt end of the egg. There are two shell membranes. The inner membrane rests on the albumen; the outer membrane is thicker and is attached to the shell. As soon as the egg is laid, cooling allows separation of the membranes at the blunt end to form the air cell.

It has been recognised that the initial composition of the egg reflects the degree of hatchling maturity. Eggs from species with altricial young have higher albumen content (water rich, energy poor) than those producing precocial young (water poor, energy rich). The lipid fraction of the yolks also varies: precocial yolks contain more energy-rich triglycerides. For a given mass altricial bird’s eggs require shorter incubation times.

In parrots, the clear proteinaceous albumen forms about 75% of the egg. It is divided into compartments. The yolk is surrounded by a thick viscous albumen layer, as parent turns the egg it becomes twisted and condensed and forms chalazae. The chalazae resist the tendency of the yolk to float to the most dorsal aspect of the egg. The thick albumen also tends to be a shock-absorber. There are two compartments of more liquid albumen that contain more water and less ovomucin; they prevent the embryo from drying out and allow more rapid mixing and diffusion of nutrients and gases to supply the early embryo. In chickens the composition of the whole albumen is 88.5% water with 11.5% solids that are mostly protein with small amounts of glucose, inorganic ions, and a tiny amount of fat. The albumen is a source of water and mineral ions for the growing embryo and additional nourishment. It is completely used during incubation. Lysozymes and similar proteins in the albumen help to prevent bacterial infection of the egg.

The yolk is orange and on its surface is a visible germinal disc - radiating from this area is the more watery white yolk that is less dense. During turning, the yolk's structure makes the part containing the germinal disc stay most dorsal: closest to the incubating bird. The yolk is covered by two membranes. The yolk is 47.5% solids, 33% lipid, and 17.4% protein and is the main nutrient source for the embryo. In the latter stages of growth the yolk is connected directly to the embryo's intestine. The lipids in yolk are in the form of lipoproteins rather than free lipids.

Calcium for the egg shell is obtained from the duodenum and upper jejunum or from reabsorption of bone. If there is sufficient calcium in the diet (3.5 to 4% for poultry) the intestine is the main source. 60 to 75% of the calcium in the shell is supplied by dietary sources, 25 to 40% from the skeleton. In cases where the diet does not contain sufficient calcium, further calcium is obtained from medullary bone and failing this, from cortical bone. Medullary bone is a labile buffer for calcium demand and even in diets with adequate calcium it is used while demands for calcium are at their highest. It is quickly replaced by calcium absorbed from the gut.

In birds with normal calcium levels in their diet there is little intracortical bone remodeling. However in low calcium diets with or without low vitamin D, bone is removed from the endosteal surfaces and if the diet is very deficient in calcium and vitamin D there is intracortical resorption. As cortical bone is removed, medullary bone is formed but it is only partially calcified.

Whilst laying, poultry will preferentially consume a diet supplemented with oyster shell grit. Preference for calcium rich food during this time has been shown in other species of birds as well. Great Tits (*Parus major*) use snail shells as a source of calcium. Consumption of shells increases significantly a few days before, during and after laying a clutch of eggs. Females in areas with few snail shells lay fewer eggs and these eggs have shells that are thinner or even missing. Females that have been deprived of calcium and then allowed to eat snails shells start to lay eggs with 1-2 days. (Gravelands and Bereland,1996)

Other species have been shown to consume extra calcium. Sandpipers (*Calidris* spp.) breeding in the arctic have lemming (*Lemmus trimucronatus*) bones in their stomach during follicular development. Other birds, such as Red-billed Queleas (*Quelea quelea*) eat calcareous grit. This has been reviewed by Tordoff (2001).

ALLANTOIC MEMBRANE

The choriallantoic membrane grows in the extra embryonic coelom, in the space between the yolk sac, amnion, and chorion. It moves the chorion aside from the amnion and yolk sac and presses it tightly to the shell membrane as well as the albumen in the small end of the egg. It has a number of roles: It is the bladder - it isolates the end products of nitrogen metabolism that are produced from the kidneys, reabsorbs the water and leaves the urates, from day 5 of incubation. 90% of the urates are formed in the last week of incubation. This accumulation of fluid expands the allantois until it reaches the shell membrane. As it is pressed up against the wall of the egg it acts as a respiratory membrane. The walls of the allantois secrete fluid that dilute the albumen allowing it to be more easily absorbed by the embryo. Finally the membrane has a fringed margin, whose fibres enter the shell membrane. It has grown to cover the entire shell membrane and secretes carbon dioxide and water (HCO_3^-), which converts the CaCO3 into a soluble form. During the incubation period the shell loses 6.4% of its calcium in this way, so that the skeleton has a ready supply of calcium. Poor quality shells give poor quality bone!

Egg-related information based on Scaly-headed Parrot (*Pionus maximiliani*):

- Parent bird weighs 230 grms
- Skeleton (non-breeding) weighs 14.5 grms (6.3% of bodyweight)
- A clutch of 5 eggs weighed 72.5 grms (31.5% of bodyweight)
- Total weight of their shells was 6.2 grms (42.7% of skeleton)
- Time from laying first to last = 9 days

REFERENCES

Avian incubation: behaviour, environment, and evolution (2002) Ed D.C. Deeming Oxford University Press, Oxford UK.
A very interesting book packed full of information that would be difficult or expensive to find elsewhere.

Graveland JR, Van der Wal R, Van Balen JH, Van Noodwjk AJ. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature*. **368**: 446-448

Gravelands, J. and Berends, J.E. 1997. Timing of calcium uptake and effect of calcium deficiency on behaviour and egg-laying in captive great tits. *Physiological Zoology*. **70**: 74-84

Olsen, M.W. 1960. Performance record of a parthenogenetic turkey male. *Science*. **132**: 1661-1662.

FEMALE REPRODUCTIVE DISEASE

Because obstetrical problems have many causes the prognosis varies. Start by obtaining a general and reproductive history followed by a physical examination. Obviously egg binding etc are not problems that affect males but in sexually monomorphic birds a careful history and general scepticism is important.

Ask the owners:

- How long have they owned the bird?
- Age of bird, rearing etc.
- Sex – how do they assess this?
- How long has it been unwell, signs etc.
- Is there a previous history of egg-laying.

Egg Binding and Dystocia: Egg binding is the failure of an egg to pass through the oviduct at a normal rate (delayed oviposition). Dystocia is the mechanical obstruction of an egg in the caudal reproductive tract. This obstruction can result in cloacal impaction and/or prolapse. It can be caused by:

- hypocalcaemia and other nutritional deficiencies (most common);
- illness due to infection or disease; and
- problems with the oviduct, uterus, or vagina which can be caused by tumours, torsion, hernias etc, old age and/or obesity.

In many texts some lists of causes are valid but some are speculative as there is no evidence base for the claims.

Life threatening circulatory disorders, shock, and nerve paralysis can occur during dystocia. It has been suggested that these occur secondary to compression of pelvic and renal vasculature and nerves. However, cessation of defaecation and urination will lead to severe metabolic disturbances. Pressure necrosis of the oviduct results in rupture.

Egg-laying lethargy is normal but seeing it in a bird on the perch is unusual; they are usually in their nest box.

The egg bound bird is depressed, lethargic, quiet, and tachypnoeic. It has a wide non-perching stance and can have uni- or bi-lateral paresis/paralysis. The abdomen and cloaca are usually doughy and swollen; an egg may be palpable. BEWARE it is depressingly easy to fail to palpate a shelled egg! Always take a radiograph.

Tail wagging, dyspnoea, straining, decreased frequency of defaecation are abnormal whereas an increased volume of faeces, as well as nesting behavior is more likely to be normal.

It is suggested that in cases of severe dystocia, the bird’s feet may become "blue-white", indicating vasculature compromise and warranting immediate intervention.

Clinical examination: is the bird ill while laying an egg or is it egg bound?

- If it is ill – treat it!

- Abdominal palpation
- Radiography – in a box if very ill, otherwise under GA

If the bird is unwell, patient stabilization is critical. Ideally fluids (saline or LRS) should be given subcutaneously, but initially supplementation with an IV bolus may be needed. Placement of a jugular or metatarsal vein IV catheter, or an interosseous catheter, should be reserved for cases of severe dehydration. Subcutaneous 10% calcium borogluconate should be given in all situations. The patient should be placed in a warm, humid, (oxygenated) incubator. The incubator should be covered and the bird should be kept quiet.

In the UK it is unusual to see very ill, dehydrated patients. Usually a radiograph followed by a blood sample for ionised calcium level is all that is needed. If the bird is unwell and has medullary bone present a CBC + biochemistry is necessary.

Hypocalcaemia is the most frequent cause of egg binding, usually secondary to low calcium diets.

In birds with a prolapse, the tissues should be cleaned with warm sterile saline and coated with sterile lubricant whilst the bird is given fluids, food, and general support before surgery is carried out. It is professionally negligent to stuff prolapses back into the cloaca and place a purse string suture.

In laying parrots and birds of prey radiography should show medullary bone in most long bones. Well-developed medullary bone suggests adequate calcium reserves for egg production. Ultrasonography is useful for the diagnosis of impacted soft-shelled eggs, ectopic soft shelled or shell-less eggs, and salpingitis, as well as to differentiate oviduct masses from other caudal abdominal masses.

The hormonal treatments are available, but the author prefers to use supportive care described above and minimal (or major) surgical intervention described below. Prostaglandin E2 and E1 (PGE2 and PGE1) are known to relax the uterovaginal sphincter and increase uterine contraction. PGE2 gel (Prepidil) or PGE1 liquid (Caverject) are recommended topically, applied to the uterovaginal sphincter. The dose for PGE2 is 0.1 mL per 100 gram bird. If the uterus is intact, free of disease or neoplasia, and the egg is not adhered to the oviduct, then the contractions produced by PGE2 gel are forceful enough to expel an egg safely within 15 minutes of application. Prostaglandin F2a is dangerous when compared to PGE2. It is not the prostaglandin of choice in birds as it elicits generalized smooth muscle contractions and does not specifically relax the uterovaginal sphincter.

Similarly, oxytocin has been recommended to stimulate the oviduct. Oxytocin it is not produced in birds, given parentally it produces profound cardiovascular effects as well as painful and potentially ineffective smooth muscle contractions.

If the bird does not lay the egg within the expected time (definitely within 24 hours) it should be anaesthetised and the egg manipulated towards the vent. This is done by palpation and slowly pushing the egg caudally. Constant gentle pressure usually forces the egg to become visible through the opening vent. Once the end of the egg is visible lubricated cotton bud can be used to push the oviduct over the egg. With care and firm caudally directed pressure it is usually possible to expel the egg. Sometimes the egg shell adheres to the oviduct and it proves impossible to deliver the egg without the risk of a prolapse. The longer the shelled egg has been present, especially if there has been no cuticle formation, the more likely the oviduct is to have adhered. In these cases it is possible to deliver the egg by making a small hole, aspirating the contents and if the egg is soft shelled it will collapse. If the shell is hard it must be broken up and removed piece meal. With care and common sense this is a safe procedure. Sometimes it is necessary to aspirate with a needle placed through the abdominal wall. It is useful with soft-shelled eggs as they are easily passed after having being collapsed.

On rare occasions the egg is laid into the cloaca where it can cause acute obstruction to urination and defaecation. It can be difficult to remove from the oviduct, but can either be broken up or delivered by an episiotomy. I prefer the former.

In some cases where it is impossible to deliver the egg from the oviduct through the vent, delivery requires surgery. My personal preference is for a ventral midline laparotomy. In some cases a hysterectomy is indicated.

SURGICAL TECHNIQUE FOR DELIVERING AN EGG

- Pluck the bird midline from the caudal edge of the sternum to the vent. This space is often devoid of feathers just before and during incubation as it is the brood patch. Sterilise the skin and drape with a plastic drape.

- Midline incision through the skin. Tent up the muscle layer and carefully make a midline incision from the edge of the sternum to the space between the pubic bones

- Enter the cavity below being careful not to cut the intestines that are close to the surface.

- Enter the left side of the abdominal peritoneal cavity and find the egg and oviduct (they may be separate).

- In most cases the oviduct needs to be incised longitudinally to expose the egg. The egg needs removing either as a whole or piecemeal. If the egg is to be cut up, make a small hole in the most dorsal (to the incision) part of the egg and aspirate the contents. The cut up and remove the egg shell.

- It is usually possible to close the oviduct with a continuous suture pattern with 4/0 or 5/0 absorbable suture material.

- Once closed, inspect the oviduct for more eggs.

- Inspect the ligaments for tears and if these are present they must be repaired.

- If the oviduct (or suspensory ligaments) is irreparable it must be removed completely. It is not possible to remove the ovary from an actively breeding bird. Whilst haemostat clips are useful it is quite possible to carry out this procedure without them. Large blood vessels may require ligating but can often be prevented from bleeding by tearing them between two pairs of artery forceps.

- It appears to be unusual for a bird to ovulate when the oviduct has been removed.

- Repair the peritoneal structures as you leave the abdomen, again with fine absorbable suture material. Repair the abdominal musculature with 4/0 PDS. I use 3/0 or 4/0 Vicryl Rapide for the skin layer.

SUGGESTED READING

Anatomy

Handbook of avian anatomy: Nomina Anatomica Avium, (2nd Edition J. J. Baumel Ed.) Nuttall Ornithological Club, Harvard University, Massachusetts.
Extremely useful: the fundamental anatomical text. It standardises and defines the names of anatomical structures.

Birds their Structure and Function. A S King and J McLelland, (1984) Baillière Tindall, London.
A 'cheap', good, anatomical overview.

Form and Function in Birds. Editors A S King and J McLelland Academic Press London. Volumes I-IV.
Expensive but the most comprehensive text available.

A Colour Atlas of Avian Anatomy. J McLelland (1990) Wolfe Publishing Ltd Aylesbury, UK.
A very useful book using high quality photographs to give an excellent guide to general avian anatomy.

Physiology

Sturkie's Avian Physiology. 5th Edition. Editor G C Whittow (2000) Academic Press, Harcourt Science and Technology Company, California.
Much useful information including a chapter on flight

Radiology

Atlas of Avian Radiographic Anatomy. Smith, S. A. and Smith, B. J. (1992). Saunders and Co., Philadelphia.
There are some very clear illustrations in the book

Atlas of Diagnostic Radiology of Exotic Pets. Rübel G, Isenbügel E and Wolvekamp P. (1991).Wolfe Publishing Limited, London.
A useful set of normal and pathological radiographs illustrating birds from many genera