Chapter

Avian Reproduction

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Abstract

There are about 10,400 living avian species belonging to the class Aves, characterized by feathers which no other animal classes possess and are warm-blooded vertebrates with four-chamber heart. They have excellent vision, and their forelimbs are modified into wings for flight or swimming, though not all can fly or swim. They lay hard-shelled eggs which are a secretory product of the reproductive system that vary greatly in colour, shape and size, and the bigger the bird, the bigger the egg. Since domestication, avian species have been basically reared for eggs, meat, pleasure and research. They reproduce sexually with the spermatozoa being homogametic and carry Z-bearing chromosomes, and the blastodisk carries either Z-bearing or W-bearing chromosomes, hence, the female is heterogametic, and thus, determines the sex of the offspring. The paired testes produce spermatozoa, sex hormones and the single ovary (with a few exceptions) produces yolk bearing the blastodisk and sex hormones. Both testis and ovary are the primary sex organs involved in sexual characteristics development in avian. In avian reproduction, there must be mating for fertile egg that must be incubated to produce the young ones. At hatch, hatchling sex is identified and reared to meet the aim of the farmer.

Keywords: avian species, chromosomes, embryogenesis, hatchability, incubation

1. Introduction

1.1 Avian species

Avian species is a group of warm-blooded vertebrates constituting the class Aves, characterized by feathers, toothless beak, laying of hard-shelled eggs, high metabolic rate, four-chambered heart and a strong but lightweight skeleton. They vary in size from about 5.5 cm long (i.e. bee hummingbird) to as long as 2.8 m (i.e. ostrich). There are about 10,400 living avian species spread widely across the world with more than half capable of flying (i.e. passerine or perching birds). They have wings that vary widely depending on the species; however, there existed the Moa and Elephant birds that were the only known groups without wings. The wings normally develop from the forelimbs for flight and the tail feathers for flight control. Meanwhile, further evolvement has led to loss of flight ability in some birds such as ratites, penguins and diverse endemic island species even with well-developed feathers and wings. However, the digestive and respiratory systems of birds are physiologically suited for flight; hence, some avian species have adapted to aquatic environments for survival such as seabirds and water birds; thus, they have the capability to swim and feed in water [1].

Birds are feathered theropod dinosaurs and constitute the only living dinosaurs yet, could be considered as reptiles in the modern cladistics viewpoint, and their closest living relatives are the Crocodilians. They are believed to be descendants of the primitive Avialans (whose members include Archaeopteryx that first appeared about 160 million years ago in China [2]. According to deoxyribonucleic acid evidence, modern birds categorized as Neornithes evolved in the middle to late Cretaceous and diversified tremendously around the time with Paleogene extinction event about 66 million years ago that exterminated the Pterosaurs and all non-avian dinosaurs [3]. Several of the social bird species pass on knowledge from generation to generation because of their ability to communicate with visual signals, calls, sing and participate in such behaviours as cooperative breeding and hunting, flocking and mobbing of predators. These attributes could best explain why birds are sometimes referred to as social and cultural animals. Most bird species are socially monogamous but not necessarily sexually, because this habit may be for a breeding season, sometimes for years but rarely for life. Some other species have breeding systems that are polygamous, i.e. one male with several females and seldom polyandrous, where a female has various males. Birds produce their progenies by sexual reproduction, where the female releases yolk with a blastodisk on the surface that must be fertilized by the spermatozoon released by the male during mating or artificial insemination. The female usually lays fertilized eggs in a nest and incubated for a length of time characterized by the avian species. Although the hatchlings could be altricial or precocial, the dam/dams (i.e. parent/parents) usually have an extended period of parental care after hatching except, a few species such as Australian brush turkeys that do not exhibit this habit [4].

There are more than 10,400 extant bird species in the world. Across North America and South America alone, there are more than 4400 species, approximately 2700 different species in Asia, and about 2300 are found in Africa. In Europe (west of the Ural Mountains), there are more than 500 species, and more than 700 species are found in Russia with Costa having the highest concentrations of roughly 800 bird species.

1.2 Determination of sex in avian species

According to Osinowo [5], the spermatozoa in avian species are homogametic and carry Z-bearing chromosome, whereas the ovum (blastodisk/blastoderm) carries either Z-bearing or W-bearing chromosomes. Therefore, the female is heterogametic and as such determines the sex of the offspring. At fertilization, the union of Z-bearing chromosomes from both the male and female will result in male offspring (ZZ) while the union of a W-bearing chromosome ovum (blastoderm) develops into female offspring (ZW). Consequently, determination of sex mechanisms in avian species differs from that of the mammals where the male is the sex determinant. However, aberrations may occur due to non-disjunction of sex chromosomes, translocation, deletion or mutation of genes forming ZZZ, ZZW or ZZO zygotes with attendant defects as recorded at the Department of Animal Science, University of Ibadan, Nigeria [6].

1.3 Male reproductive system

In all avian species, the paired testes which are the gonads that produce the gametes—spermatozoa are retained in the abdominal cavity towards the cephalic border of the kidneys, where they originated from the mesonephric ducts forming the Wolfian duct. Therefore, the testes have the same temperature (40°C) as the body yet, spermatogenesis occurs, and the spermatozoa remain viable at body temperature. Unlike mammals that require scrotum for thermoregulation before spermatogenesis can occur and be viable. According to Johnson [7], each of the testes is attached to the body wall by the mesorchium and is encapsulated by a fibrous inner coat, the tunica albuginea and a thin outer layer, the tunica vaginalis. One of the two testes may be larger (depending on the species) yet, both will be functional. The weight of the testes in chickens constitutes about 1% of the total body weight, depending on the breed and about 9–30 g per testis at sexual maturity. However, in seasonal breeders, testis size may increase by 300–500 folds during the reproductive active season as compared with the nonbreeding state.

Although many environmental factors impact on reproductive activity, the seasonal breeder responds most strongly to long day length. Testicular interstitial cells produce testosterone that influences reproductive behaviour such as territorial aggression and song. Other changes observed in seasonal breeders include testicular hypertrophy and enlargement of the ductus deferens and seminal glomus. The testis is elliptical, yellowish and consists of a large number of slender and convoluted ducts called seminiferous tubule where spermatozoa are produced. These ducts connect to the paired vas deferens terminating in the small papilla that serves as an intromittent or a copulatory organ. Although birds are one of the groups which reproduce through internal fertilization, they have repeatedly lost the intromittent organ; thus, most avian species do not have penis. However, larger birds such as duck, ostrich and emu have penis. Ostrich has a conical-shaped penis that is wider at the base as given by Brennan and Prum [8]. Even if birds reproduce through internal fertilization, 97% of the males absolutely lack a functional intromittent organ. While the other 3% have intromittent organ, copulation occurs through brief insertion of the male organ into the vagina before ejaculation. On the other hand, vast majority of the birds comprising nearly 10,000 species transfer spermatozoa via cloacal contact between the male and female in a manoeuvre described as ‘cloacal kiss’ [9]. Nevertheless, a functional intromittent organ is known to be present in most species of Palaeognathae (ostriches, rheas, kiwis, tinamous, cassowaries and emu) and Anseriformes (waterfowl, ducks, geese and swans) with high variability in the intromittent organ morphology.

In waterfowl, for example, the intromittent organ varies greatly in length, characterized by surface elaborations (both spines and grooves) and spiral counterclockwise [10]. This variation is most likely due to an intersexual arms race resulting from a mating system in which forced extra-pair copulations are frequent. While drake has a penis that is coiled along the ventral wall of the cloaca when flaccid, it has an elaborate spiral shape when erect. The drakes often force sex on the ducks to scatter their genes, and the ducks have evolved complex anatomical defenses against these unwanted attentions. But the lymphatic erection in the male offers a way around these, because it allows a rapid on/off means of extending the penis to enable deep insemination [11].

1.3.1 Spermatogenesis

The sequence of events in the development of avian spermatozoa from spermatogonia is known as spermatogenesis. It occurs in the seminiferous tubules in the testes and involves several physiological processes such as spermatocytogenesis, meiosis and spermeogenesis [12]. The germ/stem/primitive/primordial cells or the spermatogonia develop into primary and secondary spermatocytes. During the meiotic phase, maturation division of the spermatocytes results in spermatids with a reduced number of chromosomes and gradually transforms into spermatozoa. In some avian species such as guinea fowl and domestic fowl, spermeogenesis involves 10 different morphological sequences but about 12 in Japanese quails [13–15]. During spermeogenesis, biochemical processes involving acrosome and axoneme formation, loss of cytoplasm and replacement of nucleohistones with nucleoprotamine accompanied with nuclei condensation and transformation of spermatids into spermatozoa without further cell division occur [16].

Consequently, spermatogenesis sequences could be simplified as Spermatogonia → primary spermatocytes → secondary spermatocytes → spermatids → spermatozoa. The produced spermatozoa are stored in the epididymis and vas deferens until ejaculation, when they will be released through the intromittent organ. The semen volume in avian species is probably the lowest among livestock species but has the highest spermatozoa concentration per semen volume. Adeoye et al. [17] and Almahdi et al. [18] attributed this to lack of accessory glands in avian species which are well developed in other livestock species particularly mammals.

1.4 Female reproductive system

Essentially, avian species do not have cervix in their reproductive system, thus the lower end of the oviduct opens into the cloaca. The cloaca contains openings for the reproductive, digestive and urinary tracts. The paired ovaries are only present in most avian species at few days old (about 5–10 days of post-hatch). Thereafter, the right ovary and the right fallopian tube regress, leaving only the left ovary and the left fallopian tube near the kidneys, where they first differentiated from the paramesonephric duct forming the Müllerian duct. However, Fitzpatrick [19] reported that red-tailed hawk (*Buteo b. borealis*) has clearly a definite vestige of a right ovary consisting of 23 follicles at adult stage. If with a single ovary, some poultry species have the capability to lay several eggs per annum (200–350 eggs in chicken), what if both ovaries were intact and functional? The physiological explanation to this phenomenon seems not to be available, because some avian species such as hawks and owls have both ovaries intact [20] yet, they can only lay a few eggs per annum (about 2–5 eggs per clutch in a reproduction cycle). At hatch, avian female hatchling's ovary has about 4000 follicles and will never have new ova produced in life. Out of this, only some are fully developed and ovulated in a life span of a mature poultry female bird. The large follicles are round, yellow and loosely connected or attached to the ovary by the follicular stalk, and the yolk sac is richly supplied with blood and nutritional materials. The largest follicle containing the blastodisk ovulates when the yolk sac ruptures. Only one large follicle is ovulated at a time but two or more may be ovulated resulting in double yolk egg or seldom double eggs with a shelled egg inside another shelled egg. **Figure 1** shows a typical female avian reproductive tract as culled from Suyatma and Hermanianto [21].

Avian oviduct is a complex organ with different segments that converts nutrients from the feed consumed into the various components of a well-formed egg. Early changes associated with rising oestrogen levels in female, include osteomyelosclerosis and hypercalcemia. Ovulation is then induced by leutinizing hormone, which is followed by eggshell calcification under the control of progesterone. Sources of calcium for shell production include intestinal absorption from the diet, renal control of calcium levels and mobilization of bone calcium deposits. During oviposition,

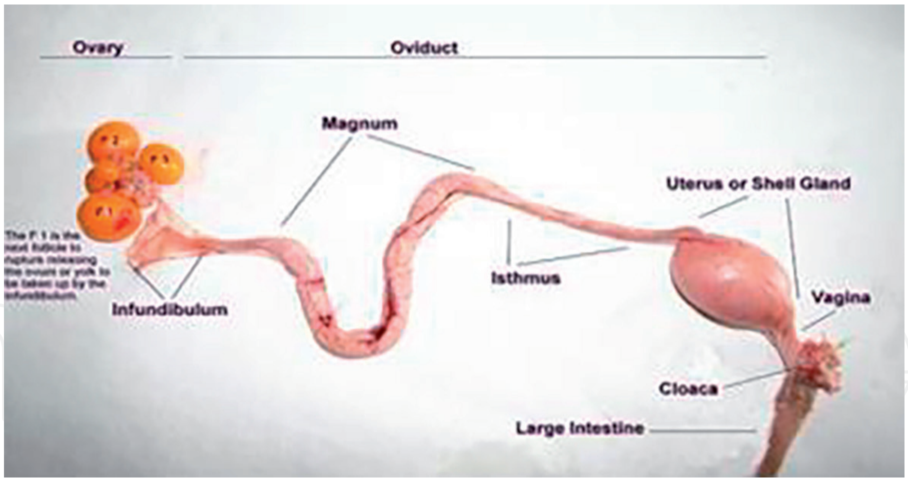

Figure 1.
Female avian reproductive tract. Source: Suyatma and Hermanianto [21].

PGF2 alpha and vasotocin stimulate powerful uterine contractions in the presence of calcium. Incubation is associated with falling leutinizing hormone levels and rising prolactin levels. If the hen actually enters reproductive quiescence at this time, then molt will follow. Molt is associated with the total regression of the reproductive tract [22].

1.5 Avian egg formation

Avian egg formation is independent of mating because once mature yolk with the ovum (blastodisk) is released, it is swept into the fallopian tube and stays for a short time in the ampulla region where fertilization occurs. With fertilization or no fertilization, chalaza is secreted on the yolk within 15 min in the infundibulum and then moves to the magnum which is the longest portion of the oviduct and albumen is secreted within 3 h. Then, it moves to the isthmus where shell membrane is secreted within 1 h 15 min. The whole combinations move to the shell gland portion of the oviduct where calciferous shell is secreted to encapsulate the yolk, chalaza and albumen forming a shelled egg. It takes about 18–22 h in the shell gland before moving to the vagina where cuticle is secreted to cover the shell pores, and it stays for a few minutes in the vagina for mucous secretion that will aid lay. It takes about 26 h for an egg to be fully formed in the avian oviduct before lay; hence, the hen will skip a day after laying for six days (6/7 days). The large follicles, usually about five, are in graded sizes with the largest ovulating first. A mature ovary weighs 40–60 g. All avian species lay eggs but only the poultry birds such as fowl, turkey, duck and quail eggs are commonly available for human consumption. According to Campbell et al. [23], egg lay in birds results from a complex natural endowment whose prime aim is to procreate. Many other animal species including insects, worms, fishes, reptiles and mammals produce eggs, but the avian eggs are much larger than others due to the food reserve for embryonic development. Avian egg is a secretory product of the reproductive system that varies greatly in colour, shape and size, and the bigger the bird, the bigger the egg. Also, the laying capacity of avian birds varies greatly as seen in **Table 1** culled from Campbell et al. [23]. Meanwhile, regular removal of eggs from the nest may increase the rate of egg production among avian species; however, some birds may abandon the nest, if the eggs are removed, and others may continue to lay in order to establish a clutch for incubation.

S/N	Avian species	Number of eggs laid per annum
1	Hornbills	1
2	Pigeons	2–4
3	Gulls	4
4	Graylag geese	5–6
5	Mallard ducks	9–11
6	Ostriches	12–15
7	Partridges	12–20
8	Fowl	350 and above

Table 1.
Avian birds laying capacity.

1.5.1 Hormonal regulation of avian egg formation

Egg production process is dependent on hormone synchronization and balance. Otherwise, hormone secretion without awaiting the proper signal may result in yolkless, thin-shelled and shell-less eggs as well as formation of shelled egg inside another shelled egg. Essentially, the physical appearance and functioning of avian species could be affected by endocrine secretions. Therefore, some endocrine effects may result from direct action of a single hormone. Hence, the physiological activities of avian species, particularly the female, are dependent on a complex interrelationship of glandular effects as found in the complex hormonal control of ovulation and egg formation [23]. The avian oviduct is usually under control and is stimulated at the most appropriate time to receive the released yolk containing the blastodisk. Ovarian follicle secretions are responsible for the enlargement of the oviduct, vent, spread of the pubic bones, female plumage pattern, mobilization of fat deposit in the yolk and calcium for shell formation. Also, the secretion of albumen is apparently under the control of androgen synthesized by the ovarian interstitial tissue. While eggshell formation is partially controlled by parathyroid glands, the thyroid gland partially controls the seasonal changes in egg laying, feather colouration and feathering during molting.

1.6 Mating

The males mount the females during mating, and the spermatozoa are introduced into the cloaca using intromittent organ. In avian species, mating does not play any role in egg production; however, time of mating determines the rate of egg fertility because it is believed that the eggs may obstruct migration of the spermatozoa to the fallopian tube where fertilization occurs. Spermatozoa are capable of staying up to 3 weeks or 3 months (depending on the avian species) in the uterovaginal portion of the genital organ called 'spermatozoa storage tubule'. Thus, even after withdrawal of the males from the flock or cage or cessation of artificial insemination, the females can still lay fertilized eggs for up to 10–21 days [24]. The uterovaginal junction in the female reproductive part functions as spermatozoa storage tubules. Thus, after a single mating or insemination, the spermatozoa migrate through the vaginal to the spermatozoa storage tubules for subsequent release to fertilize the ovum on the yolk at the ampulla section of the fallopian tube region of the oviduct.

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Before now, it was believed that subsequent release of the spermatozoa from the spermatozoa storage tubule was not regulated but occurs in response to the mechanical pressures of a passing ovum, because no contractile elements associated with the spermatozoa storage tubule were found [25, 26]. Recently, several studies reported that spermatozoa maintenance and release from the spermatozoa storage tubules are events regulated during the ovulatory cycle. This was demonstrated by Matsuzaki et al. [27] when progesterone stimulated the release of resident spermatozoa from the spermatozoa storage tubules in Japanese quail with a contraction-like morphological change of the spermatozoa storage tubules. Also, it was shown that the release process was somewhat supported by the lubricant effect of cuticle materials secreted from the ciliated cells of the uterovaginal junction as well as unknown materials supplied from the spermatozoa storage tubules epithelial cells, in events coincidently triggered under progesterone control. Furthermore, Ito et al. [28] found secretory granules in spermatozoa storage tubules epithelial cells and the number of the secretory granules fluctuated during the ovulatory cycle, indicating that spermatozoa storage tubules epithelial cells and unknown materials in the lumen of the spermatozoa storage tubules possibly influenced spermatozoa motility, respiration and metabolism.

In some other animal species such as bat, Holt [29] reported that the spermatozoa in the oviduct could be stored for up to 5 months, and Holt and Lloyd [30] stated that reptiles such as turtles, snakes and lizards have obvious potential for spermatozoa storage in the oviduct for an extremely long period of up to 7 years. This phenomenon appears to guarantee and insure against not finding mating partners in some breeding seasons as well as optimizes the timing of the birth of their offspring until a suitable season for nursing arrives. Perhaps, the most remarkable duration of spermatozoa storage was observed in bees [31] and ants [32] that can store spermatozoa for nearly their entire lives. In domestic birds including chickens, turkeys, quails and ducks, Bakst [33] and Bakst et al. [34] stated that once ejaculated spermatozoa enter the female reproductive tract, they can survive for up to 2–15 weeks depending on the species. Spermatozoa storage duration of some avian species is presented in **Table 2**. The disparities may be related to the varying number of spermatozoa storage tubules present in the uterovaginal junction of the avian species (see **Table 3**).

S/N	Avian species	Spermatozoa storage duration (weeks)	References
1	Fowl	2–3	Brillard [35]
2	Turkey	10–15	Brillard [35]
3	Quail	1–2	Adeyina et al. [36]

Table 2.
Spermatozoa storage duration of some avian species.

S/N	Avian spp	No. of spermatozoa storage tubules	References
1	Fowl	5–13,000	[37, 38]
2	Turkey	20–30,000	[37, 38]
3	Quail	3467	[39]

Table 3.
Number of spermatozoa storage tubules found in some avian species.

The number of spermatozoa storage tubules in the uterovaginal junction may determine the rate of egg fertility in avian species.

1.7 Fertilization in avian species

If an egg is carefully windowed and the content emptied into a dish, an opaque circular white spot could be seen on the yolk's surface (see **Figure 2**). That spot is called blastodisk in unfertilized or table eggs and blastoderm in fertilized or hatchable eggs. The blastodisk or blastoderm measures about 3–4 mm in diameter in most avian species, and it contains the chromosomes.

The most important part of an egg is the nucleus or germ that develops into the embryo if there where fusion of the pronuclei of the spermatozoon cell and the germinal disk. Other components of the egg provide food and protection for the embryo. An avian egg has shell, shell membrane, albumen, yolk and germinal disk. The eggshell is composed of about 8000 pores for water and gaseous exchange between the egg and the environment. However, a thin film of protein material called cuticle tends to seal the pores in order to reduce loss of water, gases and prevent microbial invasion. Fertilization is the union of the male and female gametes to produce single-celled zygote. When the yolk is fully mature, it is released from the ovary into the peritoneal cavity where it is swept into the infundibulum and stays in the ampulla region awaiting union with the spermatozoon. It is only in avian species that the ovary releases large yolk with the ovum (also called blastodisk) on the surface.

Following deposition of semen in the uterovaginal region of the oviduct, the spermatozoa migrate to the ampulla section of the fallopian tube to fertilize the egg (blastodisk) on the yolk. Meanwhile, the eggs usually become fertile about four days after the rooster was introduced to the female. However, without mating, insemination and fertilization, avian species still produce shelled eggs. Such eggs are referred to as table eggs or unfertilized eggs or unhatchable eggs; thus, they are purely for human consumption and will never hatch if incubated. But if there was mating, insemination or fertilization, the eggs that will be produced may be fertilized. Such eggs are referred to as fertile or hatchable eggs and could be incubated to produce hatchlings. Avian egg fertility could be influenced by age, nutritional plane, genetic inconsistency, mating or insemination failure and environmental factors. This eventually affects the flock fertility depending on the egg production capability of the female or semen production capability of the male or both sexes. For instance, if the spermatozoa are promptly released from the spermatozoa storage tubules, there might be decrease in egg fertility, and if the male is too old, there might be decrease

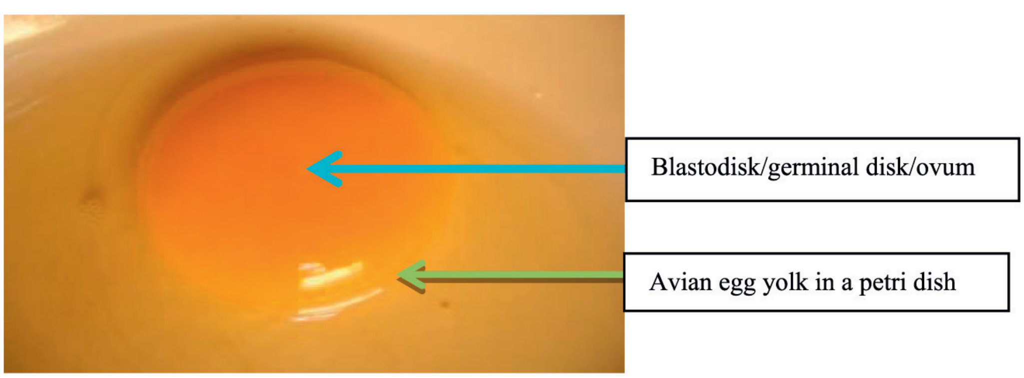

Figure 2.
Avian yolk with blastodisk on the surface.

in spermatozoa quantity and quality resulting in fertility failure. Also, if the male is not interested in mating, there may be irregular mating activity resulting in mating failure. The process of fertilization in avian species involves the release of ovum (blastodisk) that must be swept into the infundibulum and migration of the deposited spermatozoa to meet the ovum at the ampulla region of the fallopian tube where capacitation and syngamy occur.

1.7.1 Capacitation

After ejaculation, the spermatozoa migrate through the uterine body to the ampulla region of the infundibulum. Immediately the spermatozoon comes in contact with the blastodisk on the yolk surface, a physiological mechanism involving enzymatic activity (hyaluronidase) is initiated to remove antigenic seminal factors from the surface of the spermatozoon. This process is referred to as capacitation.

1.7.2 Syngamy

This is a process in which the capacitated spermatozoon crosses the ovum barriers (i.e. cumulus oophorus, zona pellucida, perivitelline and plasma membrane) before final fusion of the pronuclei, resulting in a single-celled zygote. This will subsequently undergo series of mitotic and meiotic division, during cleavage and differentiation into the various parts of the embryo. The embryo derives nutrients from the yolk and albumen, grows rapidly within the eggshell and emerges as hatchling following incubation.

1.8 Avian eggs incubation

Incubation is the process of providing optimum temperature, air circulation and relative humidity suitable for embryo development, growth and emergence as hatchlings. This process could be natural, where the broody hen sits on the eggs and covers them with the feathers in order to provide suitable environmental conditions for hatching. Since some avian species do not naturally incubate and hatch their eggs, artificial incubators are used to simulate environmental conditions required to stimulate embryonic development and growth until the emergence of hatchlings.

1.8.1 Natural incubation

In some avian species, the female birds lay eggs every day or every other day and after laying some eggs that the feathers can cover fully, it stops instinctively and begins to sit on the eggs for incubation. In fowl, for example, once a hen lays a clutch of eggs normally between 3 and 12 eggs, instincts take over.

Thus, it constantly fusses over them, adjusting them just so throughout the day and rarely leaving the nest for more than a few minutes. The broody hen rotates the eggs during incubation for about 96 times in 24 h and keeps the eggs at the correct humidity by splashing water on them from its beak. Motherhood is a big responsibility for a female bird because if it is neglectful, the incubated eggs will never hatch and, if hatched, the hatchlings may be deformed [40]. However, in some other avian species, both male and female are involved in the incubation process. In few occasions, two hens may mutually incubate the eggs that were either laid by one of the hens or both of them (see **Figure 3a–d**).

Figure 3.
(a and b) Two-hen mutual broody excerpted from a final year project at NSUK Teaching and Research Farm, Nasarawa State, Nigeria and (c and d) Single-hen broody excerpted from a final year project at NSUK Teaching and Research Farm, Nasarawa State, Nigeria.

In these cases, when either of the couple or the two hens is on bouting, the other sits on the eggs. Generally, at the beginning of the incubation, the female sits on the eggs for a longer time before taking a bout. Meanwhile, when ambient temperature is high, the hens spend less time sitting on the eggs, and some hens deliberately cool-off their eggs by sprinkling water or standing in front of the eggs just to provide shadow over the eggs. Whereas in penguin, the female lays an egg and dives into the sea to feed, leaving the male to warm up and incubate the egg by placing it in-between the web toes, brood patch and a warm fold of feathers, where it is cushioned and protected for 9 weeks. The egg remains in that location until it hatches during the coldest months of the Antarctic winter. During this period, the male penguin does not eat and may lose up to half of the body weight; hence, the male penguin must be fat and healthy prior to the breeding season.

In some cases, foster broody hens could be used to incubate eggs from other hens, breeds or species. This is common in local settings where there are no artificial incubation facilities. In Nigeria, for instance, local broody hens are used in incubating guinea fowl, turkey and partridge eggs. In this case, the foster broody hen should be big, in order to cover more eggs during the period, and should have a good brooding and mothering records. Characteristics of such broodiness are that the hen stops laying after a sizeable number of eggs have been laid, remains sitting on the eggs for a longer time and should have enough feathers with a broad broody patch and be able to spread its wings and makes a distinctive clucking sound. In some instances, these brooding characteristics may be induced or tested using dummy eggs or even stones. A maximum of 14–16 eggs may be brooded by a foster broody hen, but hatchability often declines with more than 10 eggs, depending on the size of the hen.

Feed and water should be provided in close proximity to the broody hen, in order to keep it in better condition and reduce embryo damage due to the cooling of the eggs, if it has to leave the nest to scavenge for feed and water far away. The hen keeps the eggs at the correct humidity by splashing water on them from her beak. This is a further reason for providing it with easy access to water. In very dry regions, slightly damp soil can be placed under the nesting material to assist the hen in maintaining the correct humidity between 60 and 80%. Fertile eggs from other birds are best added under the brooding hen between one and four days after the start of brooding. In Bangladesh, Sutcliffe [41] reported that local broody hens will even sit on and hatch a second clutch of eggs. However, it often loses considerable weight in the process especially, if sufficient attention was not paid to the provision of food and water. Eggs initially need a very controlled heat input to maintain the optimum temperature, because the embryo is microscopic in size. As the embryo grows in size, it produces more heat than it requires and may even need cooling. Therefore, moisture levels (relative humidity) of 60–80% are important to stop excess moisture loss from the egg contents through the porous eggshell and membranes. According to Sutcliffe [41], there are some factors to consider for a successful natural incubation. These include the following:

- Provision of feed and water close to the broody hen.
- The broody hen should be examined to ensure that it has no external parasites.
- Any eggs stored for incubation should be kept at a temperature between 12 and 14°C at a high humidity of between 75 and 85% and stored for no longer than seven days.
- Extra fertile eggs introduced under the hen from elsewhere should be introduced at dusk.
- The eggs should be tested for fertility after one week by holding them up to a bright light (a candling box works best). If there is a dark shape inside the egg (i.e. the developing embryo), then it is fertile. But if completely clear (translucent), it means the egg is infertile.
- Setting of eggs should be timed so that the hatchlings are two months of age at the onset of major weather changes such as either the rainy or dry season and winter or summer.
- A plentiful natural feed supply over the growing period of the hatchlings should be targeted in order to ensure a better chance for higher survival rate.

Successful avian species instinctively lay and incubate their eggs at a time of the year when the hatchlings will have a better supply of high protein and energy feed sources in the environment. For example, guinea fowl and some species of water fowl (ducks and geese) will only lay and incubate the eggs in the rainy season. However, seasonal changes in weather patterns are also times of greater disease risk. Generally in avian species, a hatchability of 80% of eggs set from natural incubation is normal, but a range of 60–70% is considered satisfactory. The major hindrance in natural incubation is predation especially by hawks, cats, dogs and snakes and environmental hazards particularly uncovered ditches and soil erosion.

1.8.2 Artificial incubation

In artificial incubation, many eggs of similar age (clutch) could be incubated at the same time depending on the capacity of the incubator. The artificial incubator could be homemade or commercial but should typically have heating source, air circulator (fan), temperature regulator (thermostat) as well as water trough and egg trays. Artificial incubator is designed to simulate and mimic the mother hen's role in natural incubation of providing fertile eggs with optimum environmental conditions (temperature, egg turning and humidity) to stimulate embryonic development until hatching [42]. Fertile eggs stored for as long as 7–10 days at room temperature (10–15°C) could be set for incubation. According to ISA [43], eggs should not be incubated the same day it was laid, in order to avoid hatching failure. Woodard et al. [44] stated that on incubation days 0–12, the temperature should be adjusted to 37.5°C, 13–15 days (37.2°C), and on day 16, the temperature should be 37°C and increased to 37.6°C on day 17 when the chicks are expected to emerge. On the other hand, Musa et al. [45] recommended 39.4°C in the tropics, whereas Ferguson [46] gave a range of 37.5–38°C as optimum incubation temperature in poultry production.

It has been shown that environmental temperature is the most important factor in incubation efficiency; therefore a constant incubation temperature of 37.8°C is the thermal homeostasis in avian embryos and gives the best embryo development and hatchability. Thus, incubator temperature should be maintained between 37.2 and 37.7°C [47–49]. Although the acceptable range of incubation temperature varies between 36 and 37°C, Idahor [50] stated that Japanese quail embryo's mortality may be recorded if the temperature drops below 36°C or rises above 40°C for several hours. It was demonstrated that if temperature is at either extreme for several hours, Japanese quail eggs may not hatch. Also, it was observed that overheating was more critical than underheating during the study; hence, running incubator at 40°C for 5 h seriously affected the Japanese quail embryo, whereas running it at 36°C for 5 h only resulted in late hatching. Similarly, Lourens et al. [51] reported significant embryo mortality and lower hatchability in fowl eggs subjected to 38.9°C incubation temperature. Consequently, several researchers have investigated the factors affecting fertility and hatchability in avian species with the sole aim of combating them. For example, it has been shown that age of the breeders, plane of nutrition, mating ratio as well as poor level of management affected fertility in poultry production [52]. Others reported that egg storage conditions, strain of birds, shell quality, season of the year, incubation condition and turning frequency affected hatchability of fertile eggs in poultry birds [53–55]. Recommended optimum incubation temperatures in some avian species are presented in **Table 4** as adapted from Sartell [56].

1.9 Avian embryogenesis

At fertilization, the avian egg is only fertile, and zygote will only develop outside the body during incubation with appropriate temperature and relative humidity. Fertile eggs begin to develop to embryo when the temperature exceeds physiological zero temperature given as 26–36°C. Below or within this range of temperature, embryonic growth is believed to be halted and at above it (i.e. 36–40.5°C) which is described as the lower limit of optimal development growth is resumed. At above 40.5°C which is the upper lethal temperature, malformation of embryo or embryonic death could occur [57, 58]. According to Boerjan [59], avian embryonic growth could be halted or slowed down and eventually arrested, if the temperature falls below

Avian species	Range of temperature		Typical incubation period (days)
	Celsius (°C)	Fahrenheit (°F)	
Fowl	37.4–37.6	99.3–99.6	21
Guinea Fowl	37.5	99.5	28
Turkey	37.2–37.5	99–99.5	28
Pheasant	37.6–37.8	99.6–100	23–27
Chukar Partridge	37.5	99.5	23
Japanese Quail	37.6–37.8	99.6–100	16–18
Bobwhite Quail	37.5	99.5	22–23
Ducks	37.4–37.6	99.3–99.6	28
Indian Runner Duck	37.5	99.5	28–30
Mallard	37.5	99.5	28–30
Muscovy Duck	37.5	99.5	35–37
Swan	37.5	99.5	30–37
Geese	37.4–37.6	99.3–99.6	28–30
Ostrich	35.8–36.4	96.5–97.5	42
Canada Goose	37.5	99.5	28–30
Egyptian Goose	37.5	99.5	28–30
Emu	35.8–36.1	96.5–97	50–56
Grouse	37.5	99.5	25
Amazons	36.8–37.0	98.3–98.6	24–29
Macaws	36.8–37.0	98.3–98.6	26–28
Love Birds	36.8–37.0	98.3–98.6	22–24
Peafowl	37.5	99.5	26–29
Pigeon	37.5–38.2	99.5–100.5	17
Rheas	35.8–36.4	96.5–97.5	35–40

Sources: [56].

Table 4.
Recommended optimum incubation temperature in some avian species.

'physiological zero'. That is the level at which incubation temperature is low enough to keep embryonic cell activity at a greatly reduced rate but reversible level. Essentially, the embryo still has the potential to continue its development again if normal temperature is restored. That is why the term 'arrested development' should be preferred to 'stop development' that is commonly used. As a result, 'physiological zero' should not be restricted to a specific or particular set point temperature, instead to a range of temperature from 12 to 20°C, depending on the milieu of egg handling and storage duration. Hence, the reasons why different set points temperature for 'physiological zero' is defined in different ways depending on the situation being described. The definition of 'physiological zero' was first presented by Edwards [60] as the set point temperature of about 21.0°C, and below this value, there was no embryonic growth. The terms of reference for 'physiological zero' were reviewed by Proudfoot [61] to include a storage temperature range of 11.5–21°C. Fasenko [62] introduced the term 'embryonic diapause' as an alternative to the traditional 'physiological zero' temperature regime. This updated definition recognized that some cellular metabolic processes still continue, but gross morphological changes such as shape and structure are arrested. 'Embryonic diapause' has been described in many vertebrate species such as turtles, marsupials and even mammals such as Roe deer. 'Embryonic diapause' or 'embryonic dormancy' describes a stage at which metabolic activity and cell division are downregulated or arrested and can be regarded as a strategy for coping with temporarily unfavourable environmental conditions. In avian species, embryonic development could be arrested after laying and cooling the eggs down to room temperature of between 22 and 25°C. During this cooling period under optimal conditions, the embryo develops from gastrula stage IX–X as described by Eyal-Giladi and Kochav [63] to stage XII–XIII reported by Gilbert et al. [64].

The definition of physiological zero temperature was restricted specifically to stages XII–XIII of development. If the embryo has developed beyond this stage and primitive streak development has started, reduced temperatures will slow down development and finally result in early mortality of the embryo. This may explain the higher rates of early mortality often recorded, when eggs are kept too long in the nests and when egg cooling is too slow [65, 66]. Therefore, optimum incubation temperature could be given as 37.5–37.6°C but should be reduced to 36.9°C during the last 3 days of the incubation period [44, 67, 68]. Ainsworth et al. [69] stated that in developmental biology experimentations, avian species have been used as models in morphogenesis studies. For example, some staging of Japanese quail embryo development has been attempted but incomplete due to variations in descriptions, staging and incubation processes which were always difficult. It appeared to be a general agreement that at early stages of embryogenesis, there were some developmental differences between fowl embryo [70] and quail embryo [69]. Yet, the basis for these differences has not been established experimentally; hence, Ainsworth [69] constructed a 46-stage series, irrespective of the enhanced ontogeny observed in the Japanese quail in order to make the staging series comparable. At the early stages of development (Stage 4–28), Japanese quail stage series was identical to the Hamburger and Hamilton (HH) stage in fowl chick series as the rate of development of both species was indistinguishable. At the mid stages (Stage 29–35), the descriptions of morphological changes of each stage were still comparable between fowl chick and Japanese quail chick series. At later stages of development (Stage 36–46), the HH stage fowl chick series was no longer comparable to the quail series with regard to incubation periods and morphological descriptions.

It has been reported that biological engineering in avian species has advanced, for example, artificial *in ovo* culture of one-celled zygote of blastoderm stage, made the production of adult bird possible [71]. Similarly, some trials to produce transgenic of chimeric birds have been conducted [72], and the use of avian embryo in teratological test has been anticipated [73]. Nakane and Tsudzuki [74] established that series of normal stages in the development of Japanese quail embryo skeleton composed of 15 stages. In that study, the time of chondrification and calcification of the skeleton were recorded every 24 h from incubation day 3–17 at 37.7°C. It was reported that the knowledge of skeletogenesis stages in Japanese quail embryo will be useful as a normal control not only in experimental embryology, teratology and developmental engineering but also in identifying mutant embryos with skeletal abnormalities. Japanese quail embryo developmental growth was expressed on daily bases by Idahor et al. [75] as culled from NSAP 2018 Proceedings. See **Figure 4a** and **b** as given by Hamburger and Hamilton [70] and Idahor et al. [75].

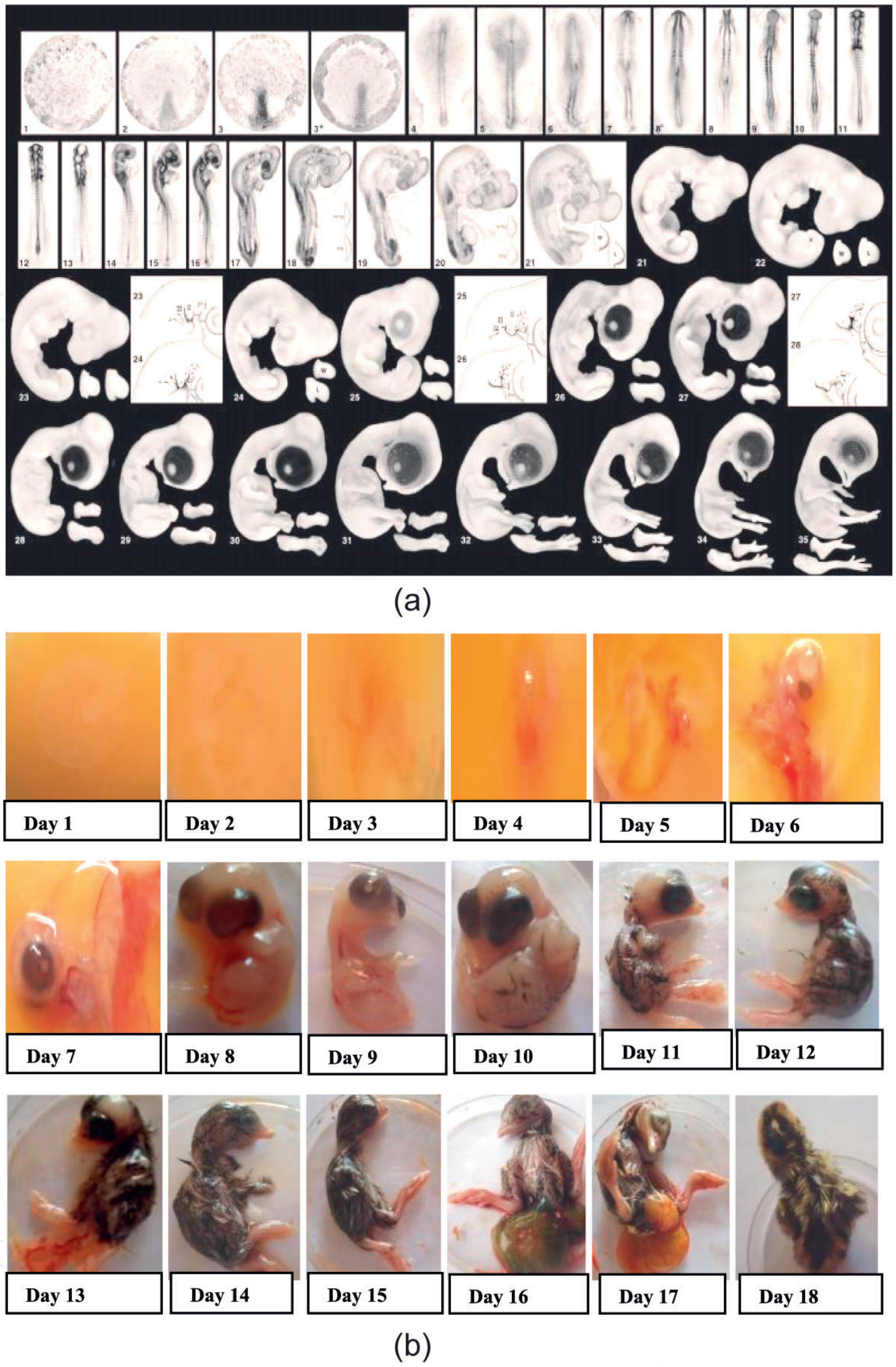

Figure 4.
(a) Stages of chick embryonic development adapted from Hamburger and Hamilton [70] and (b) Japanese quail embryo developmental stages culled from NSAP 2018 Proc. as given by Idahor et al. [75].

1.10 Hatchability

The fully grown embryo uses the egg tooth to carefully window the eggshell and emerges as day-old hatchling. At hatch, some avian species could walk and scavenge on their own; hence, they are referred to as precocial birds. Examples are ostriches, geese, turkeys, ducks, fowls, pheasants and partridges. Whereas, others such as golden eagles, doves, pigeons, starlings, robins, wrens and hummingbirds cannot walk or fend for themselves; hence, they are regarded to as altricial birds; thus, they depend on the dam and/or sire for survival. Some factors such as age of breeders, mating system, eggs set and storage conditions, incubation temperature, ventilation, relative humidity and egg turning angle may affect hatchability [47, 51, 76]. Since incubation temperature has been described as the most critical environmental concern during hatchery operations.

Table 5 shows the most appropriate time to transfer incubated eggs to the hatcher compartment in the incubator, in order to achieve the recommended 60–70% hatchability. Hatchability could be determined using:

$$\text{Hatchability} = \frac{\text{Total number of hatchlings}}{\text{Total number of fertile eggs}} \times \frac{100}{1} \quad (1)$$

Common name	Incubation period (days)	Incubation conditions		Hatcher conditions		
		Temp (°F)	R/H (%)	Transfer day	Temp (°F)	R/H (%)
Canary	13–14	100.5	56–58	11	99	66–74
Chicken	21	99.5	58	18	98.5	66–75
Cockatiel	18–20	99.5	58–62	15–18	99	66–74
Cockatoo	22–30	99.5	58–62	20–27	99	66–74
Conure (sun)	28	99.5	58–62	25	99	66–74
Conure (various)	21–30	99.5	58–62	18–27	99	66–74
Dove	14	99.5	58	12	98.5	66–75
Duck	28	99.5	58–62	25	98.5	66–75
Muscovy duck	35–37	99.5	58–62	31–33	98.5	66–75
Finch	14	99.5	58–62	12	99	66–74
Domestic goose	30	99.5	62	27	98.5	66–75
Geese (various)	22–30	99.5	62	20–27	98.5	66–75
Grouse	24–25	99.5	54–58	22	99	66–74
Guinea	28	99.5	54–58	22	99	66–74
Lovebird	22–25	99.5	58–62	20–22	99	66–74
Macaw	26–28	99.5	58–62	23–25	99	66–74
Mynah	14	100.5	56–58	12	99	66–74
Parakeet	18–26	99.5	58–62	15–23	99	66–74
Budgerigar	18	99.5	58–62	15	99	66–74
Parrot (various)	18–28	99.5	58–62	15–25	99	66–74
Parrot (African grey)	28	99.5	58–62	25	99	66–74
Chukar partridge	23–24	99.5	62	20	99	66–74
Peafowl	28–29	99.5	58–62	25–26	98.5	66–75
Ptarmigan	21–23	99.5	58–62	18–20	99	66–74
Raven	20–21	99.5	58–62	17–18	99	66–74
Ring-neck pheasant	24–24	99.5	58–62	21	99	66–74
Pheasant	22–28	99.5	58–62	20–25	99	66–74
Pigeon	17–19	100.5	58	14	99	66–74
Bobwhite quail	23	99.5	54–58	21	99	66–74
Japanese quail	17–18	99.5	58–62	15	99	66–74

Common name	Incubation period (days)	Incubation conditions		Hatcher conditions		
		Temp (°F)	R/H (%)	Transfer day	Temp (°F)	R/H (%)
Swan	33–37	99.5	58–62	30–33	99	66–74
Turkey	28	99.5	54–58	25	98.5	66–75
Emu	49–50	97.5	32–40	47	97.5	69
Ostrich	42	97.5	32–40	39	97.5	69
Rhea	36–42	97.5	50	34–37	97.5	69

Source: [77].

Table 5.
Incubation period and when to transfer to hatcher in some avian species.

1.11 Chick sex identification

In avian species, sex identification is critical because in egg-laying operations, the male hatchlings are irrelevant, thus should be discarded. At hatch, all the identified males are supposed to be destroyed but could be reared as poussins for meat. However, the time and resources required to rear them are apparently a waste except in a free-range system. Nevertheless, at hatch, the sex of the hatchling may be identified in some species, whereas it may be impossible until several days of post-hatch in some other species. With hi-tech facilities, hatchling sexing could be done in various ways but sex-linked genes where plumage pattern or wing feathering is used to identify hatchling sexes at a day old is commoner. Even with the hi-tech facilities, hatchling sex identification in Japanese quail is impossible until about 3 weeks of age. According to Campbell et al. [23], some other sexing techniques in avian species include cloacal examination to view the rudimentary papillae and proctoscope to locate the testes. The sexed avian species should be reared as hatchlings, growers, finishers and breeders to meet the aim of the farmer.

1.12 Conclusion

Most avian species have brilliant senses and flight capability though few flightless species exist. They possess wings, beaks and lightweight hollow skeleton. Some of the avian species have been domesticated while others are still in the wild. In any case, both wild and domesticated are relevant to human existence as they complement the ecosystem for enhanced ecological sustainability. They are essentially classified as egg-type, meat-type or dual-purpose type. They have varied chromosome numbers, and the sex is determined by the female because it is heterogametic. All the males possess paired testes that are retained within the abdominal region, and some of them have intromittent organ while few others have penis. The female has a single ovary capable of producing so many eggs in a breeding season. While many reproduce all year round, a few are seasonal breeders. Egg production is not dependent on mating but infertile eggs will be laid purely for human consumption, whereas mating is required for fertile eggs that must be incubated for procreation. The egg is very rich in nutrients, and its biological value is approximately 100%. Avian species can live for several years except a few that can live for less than 5 years. Consequently, knowledge of avian reproduction is sacrosanct to protect avian species all over the world through intensive domestication process, deliberate breeding strategies among other measures to enhance their sustainability.

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