DOI: 10.1079/WPS20033

Feathering in commercial poultry I. Feather growth and composition

S. LEESON[1]* and T. WALSH[2]

[1]Department of Animal & Poultry Science, University of Guelph, Guelph, Ontario Canada N1G 2W1, and [2]Novus International, 530 Maryville Ctr. Drive, St. Louis, MO 63141 USA

Feather growth, structure and patterns of moulting are important characteristics of poultry in commercial environments. As the market age for broilers continues to decline, the "maturity" of feather cover becomes even more important for protection of the skin and underlying tissue. Feather growth begins at around day 5 of incubation while keratinisation is complete 2 – 3 d prior to hatch. Feathers do not grow randomly over the skin surface, but rather in distinct tracts, which cover at most 75% of the skin surface. Broiler chickens will have about 50 g of feathers by market age, although at this early age some feathers will have already been lost by sequential moulting. Although most modern strains of poultry have white or brown feathers, there are various colour schemes that are again dictated during embryo development. In a subsequent paper, we will detail factors affecting feather growth, moulting and the occurrence of various abnormalities.

Keywords: feathers; broilers; layers; genetics; nutrition; environment

Feather development, structure and anatomy

All birds have feathers, and their structure, distribution and development vary little across species. Most observable are differences in colour, shape and size, although within domestic poultry today, we have greatly reduced such variability and are left usually with white or brown feathers of fairly consistent size and shape within the major domesticated species. Growing feathers are living structures, at least in the follicle area attached to the skin, and as with any organ, development starts during the incubation process. There has been virtually no work conducted on feather embryology in the last 30 years, and much of our knowledge about feather development comes from research observations taken 50-70 years ago. It is unlikely that processes such as cell differentiation have changed over this time, although it is, perhaps, timely to initiate studies in embryonic feather development for modern strains of poultry.

*Corresponding author: e-mail: sleeson@uoguelph.ca

Received for publication July 31, 2003
Accepted for publication October 21, 2003

Embryonic feather development

Feather growth begins at about day 5 of incubation where dermal cells start to form into "lines" that will eventually become feather tracts. Feathers are first visible as clusters of epidermal cells (Lucas and Stettenheim, 1972) that occur at 6-7 days of incubation. Virtually all feather follicles will appear at this time and these will represent most of the feather follicles present even in the adult plumage. Problems with feathering due to inadequacy of follicles therefore relate to problems with development of the young embryo.

The feather germs appear in a fairly set order starting with the femoral, humoral, pectoral and sternal tracts on day 5, the spinal tracts on day 6, and lastly on day 7, the capital and cranial tracts. The pattern of development of follicles within each tract is greatest at the edges of the tract, and this sequential development is repeated when the bird goes through its juvenile moults. The developing feather follicles (germs) will give rise to contour feathers, semiplumes or down feathers as detailed in subsequent sections. The developing feather germ grows into distinct raised areas that are visible to the naked eye at around day 9. The germ bends posteriorly as it grows, due to more active growth on the anterior side, so ensuring that the feather will be contoured to the body. The characteristic barb ridges on the feather are evident in the follicle at day 10. It is at this time that cells differentiate to become characteristic components of the adult feather. By day 12, not only is the feather growing upwards, but also downwards to the deep feather follicle.

As suggested by Lucas and Stettenheim (1972) embryonic feathers do not grow as does a tree with activity at the periphery. Rather, cell division occurs at the base of the feather germ and differentiation occurs as cells move away from the germ. Therefore, the periphery of the feather (tips, barbs, etc) is formed before the rachis. Such differential "age" of separate parts of a feather must be borne in mind when diagnosing feathering abnormalities. For example unsheathed barbules at the base of a feather represent some cessation of prior normal development. Abnormal positioning of feathers (*e.g.* helicopter wings) may relate to earlier problems when follicles orient themselves at around day 8 of incubation.

Keratinisation starts at around day 13 of incubation and the sheath emerging from the skin is fully keratinised by day 16. The length of the rachis (vane) is related to some extent to the size of the chick at hatch. This relationship is most easily observed across species where chick size is more variable. Keratinisation in all feathers is complete by day 19 of incubation. Shortly after hatch, the sheath of each feather dries and flakes away, then the barbs and barbules spread out. Fragments of the sheath and remains of interstitial cells contribute to hatching debris.

Feather distribution (Pterylosis)

Contrary to popular belief, the feathers of most birds do not grow randomly or uniformly over the skin surface of birds. For most domesticated poultry, feathers grow in distinct tracts. This non-uniform pattern is usually referred to as pterylosis. Only in some ratites, such as ostrich and emus, is there fairly even distribution of feather follicles across the skin, as seen quite clearly in leather products made from these birds. The fact that most birds appear to have a uniform feather cover is due to the discrete angles and layering of feathers, which is designed to give the bird all-over protection for the skin. Nitzsch (1840) was the first to systematically describe pterylosis in birds. The most modern and extensive documentation of pterylosis, feather growth and development in general, is the comprehensive two-volume publication by Lucas and Stettenheim (1972).

In studying feather "problems", knowledge of the naturally featherless areas is perhaps of greater importance than knowing where the feathers should be growing. About 25% of the bird's skin surface is devoid of feather tracts, and these apparently naked areas are referred to as "apteria". The most notable apteria are the areas normally covered by the folded wing, the keel and the parallel central portion of the breast. There are virtually no feathers growing dorsally where the wings join the body or in the two distinct bands that run dorsally from the vent and delineate the boundary between the body and thigh as well as the thigh and drumstick. The inside of the drumsticks and the underside of the wings are also naturally devoid of feather follicles. All birds undergo feather loss or moulting during growth and as adults. For growing birds, the pattern of moulting is fairly predictable. As various generations of feathers grow and shed, they are eventually replaced by adult feathers. Adult birds also lose feathers unnaturally within modern confinement housing, where feathers either break off or are physically removed through contact with other birds and equipment. Under natural light cycles, adult birds will lose most of their feathers in the fall, and this phenomenon can be simulated by so called "force-moulting" procedures as are sometimes used with laying hens. During natural feather growth in juvenile birds, and in moulting of adults, the loss pattern of the primary wing feathers provides a useful indicator of the birds' physiological status. Knowledge of feather tracts on the wing, therefore, provides useful information to farm managers. There are 10 primary wing feathers that, from an evolutionary standpoint, are important in flight. Clipping some of these primaries effectively inhibits flight in many birds.

Feather plumage (Ptilosis)

Plumage usually refers to the shape, size and appearance of the feathers on a bird at any specific time. Plumage, therefore, continually changes in juvenile birds, and becomes fairly consistent in adults. The neck feathers are usually referred to as the "hackles". The hackle feathers of the adult male are very distinctive and can alone be used to differentiate sex of the bird. The male hackles are long, pointed and usually reach down to the wings, while in the female the hackles are less distinctive, rounded in shape and usually blend in with the other body feathers. The hackle feathers of many-coloured males are greatly prized for producing "flies" for fishermen. The plumage of most adult males and females also differ in the pelvic region, where again, the males have much longer and more pointed tail coverts. Abnormalities in growth of these feathers, or physical damage, can cause disruption of this normal arrangement of the primaries, often leading to a characteristic ruffling or "sticking-out" of one or two feathers. In broiler chickens, this latter condition is sometimes referred to as "helicopter wing", where one or two primaries on each side of the body stick out at a 25-45° angle compared to their normal plane, which is parallel to the body.

Feather number, weight and size

Estimates of feather number and weight vary considerably even when data are expressed per unit of body mass, or per unit of metabolic body mass. Counting the number of feathers on a bird is obviously a tedious undertaking, and most of us can appreciate the reasons for lack of accurate data. For adult birds, most estimates of feather number range between seven and nine thousand with feather weight at 3-6% of body weight. Hutt and Ball (1938) provide some formulas for predicting feather numbers based on body weight and surface area. *Table 1* shows estimates of feather weight in more modern strains of broiler chickens.

Table 1 Feather weight of feather-sexed male and female broilers.

Weeks of age		Feather weight (g)	Weekly feather loss (g)
Male	1	1.6 ± 0.4	
	2	3.4 ± 1.0	
	3	9.3 ± 3.0	
	4	20.7 ± 2.3	
	5	28.9 ± 4.6	0.1 ± 0.0
	6	42.8 ± 5.3	0.3 ± 0.1
	7	61.8 ± 7.2	1.2 ± 0.2
Female	1	1.3 ± 0.4	
	2	4.5 ± 0.6	
	3	11.7 ± 2.2	
	4	22.6 ± 2.5	
	5	32.7 ± 4.9	0.3 ± 0.2
	6	43.4 ± 10.7	1.3 ± 0.3
	7	51.8 ± 6.1	5.0 ± 0.4

Adapted from Fisher *et al.* (1981)

Table 2 Feather mass of breeder pullets and roosters at sexual maturity.

	Feather weight (g)	(% body weight)
Fast-feather hens	165	6.1
Slow-feather hens	179	6.0
Roosters	235	6.0
Hens	169	5.8

Adapted from Dunnington and Siegel (1986)

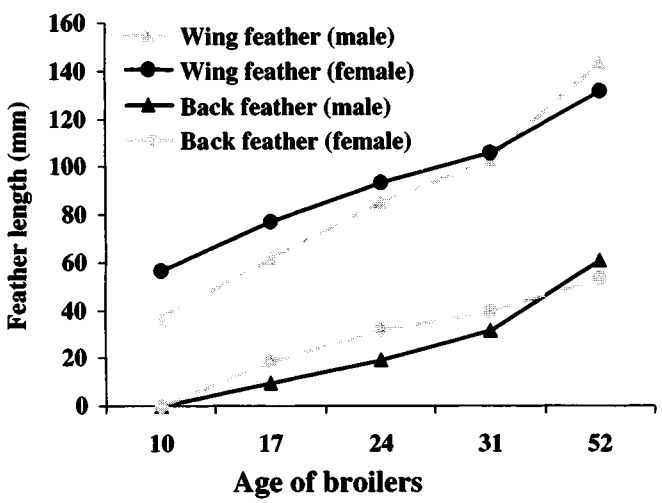

Figure 1 Wing and back feather growth in male and female broilers (adapted from McDougald and Keshavarz, 1984).

Smith and Bath (1995) suggest that individual feathers reach maximum weight at the time they reach 50% dry matter. Most adult feathers are therefore about 50% dry matter although the feather pulp is only 13-15% dry matter. In modern strains of broiler chickens, fast *vs.* slow feathering is commonly used to sex birds, and so genetics can influence early feather weight and size. There do not seem to be any reliable data on feather size and weight of male and female feather-sexed chicks up to 2 weeks of age, which is the period when greatest sexual dimorphism is seen. Certainly by the time of sexual maturity, genetics of slow *vs.* fast feathering seems to have little effect on feather mass (Dunnington and Siegelr, 1986; *Table 2*). As shown in *Table 2*, roosters have more mass of feathers at maturity, although there is little difference when data are expressed per unit of body mass.

The season of the year may also influence feather mass and development. Yalcin *et al.* (1997) showed 4-7 week old broilers to have more feathers in the summer (mean temperature 27°C) than the winter (mean temperature 20°C). The difference was about 0.5% of body weight in favour of summer grown male and female broilers. The exact reason for this difference is unclear but may relate to feather growth being less influenced than is growth rate *per se* during hot weather. Alternately, it is possible that during hot weather, the bird attempts to pump more blood to peripheral regions as a cooling mechanism so that feather follicles receive a greater supply of nutrients. The length of feathers naturally increases as the bird gets older. McDougald and Keshavarz (1984) show an almost linear increase in length of both contour and primary feathers as broilers progress through to market age (*Figure 1*).

Feather structure

Feather structure and size can be very diverse. In some birds the difference in size between the largest and smallest feather within a single plumage can be a factor of x 1000. The major parts of feathers are the central shaft, the vanes on either side and in most cases, an after feather at the base. The base of the shaft that embeds in the follicle is solid epithelial tissue and is never pigmented regardless of plumage colour. A vascularized pulp fills the shaft in the immature feather, but this is resorbed from the tip down as the feather matures. The resorption of the pulp is discontinuous where each phase of activity terminates in a pulp cap. In the adult feather, these can be viewed through the non-pigmented shaft.

There are three main types of feather that vary in structure, size and appearance. Visible to the naked eye are the contour feathers that protect the bird against physical injury. The wing and tail feathers of modern commercial strains of poultry are less well-developed than in wild birds, since there is no need for flight. These contour feathers consist of a shaft onto which two series of parallel barbs, collectively called the feather vane, are attached. The barbs themselves have rows of interlocking barbules that give the feather its shape and rigidity (Bradley, 1972). The down feathers, or plumules, are quite evident on the day-old chick, but can also be seen sparsely dispersed under the contour feathers in the adult bird (Ede, 1964). Plumules have a shorter shaft and the barbules do not interlock—the more "fluffy" structure provides a greater level of insulation. The third type of feather is the plumule where barbs are confined to the tip. The main part of the feather shaft is termed the rachis, which is almost solid and four-sided in cross-section, being slightly wider than it is thick. The vanes provide the bulk of the feather, radiating out on each side of the central shaft. Although the vanes are not exactly opposite each other on each side of the rachis, there is usually an equal number on each side of the feather. The vanes lock together with hooklets or barbules, and effectively maintain the characteristic shape of the feather. Abnormalities in barbule development can lead to a frizzled or ruffled appearance. Adult and juvenile birds also have down feathers comparable to those seen on the young

chick. In most poultry species, the down feathers are confined to areas that will be "featherless" (apteria), such as on the body beneath the wing. The down feathers are sparsely distributed, and should not be confused with an area of new feather development following a natural or induced moult for whatever reason. The hair-like feathers easily seen on the bird following conventional plucking are known as filoplumes. Most filoplumes consist of a fine elongated shaft with a few vanes at the tip. It is thought that the filoplumes act as a sensory system to inform the bird of the general positioning of the body feathers. Preening may, therefore, be initiated from signals produced by the filoplumes.

Feather generations and moulting

As the bird grows from a chick to an adult bird, it undergoes a series of moults during which successive generations of feathers develop. Four generations of feathers grow out of the same follicle, each successive feather pushing out the previous juvenile generation. Although feathers are continually being shed, even during non-moult periods, all follicles are formed during embryo development and once hatched the follicle number is fixed. Both the feather follicle and the emerging feathers are derived from the epidermis of the skin. Incubation conditions and especially feathering, can affect feather development. Merat and Coquerelle (1991) indicated retarded growth of feathers if the embryo is subjected to temperatures of 38.6°C *vs.* a control temperature of 37°C in the mid-period of incubation.

All chicks are covered with a dense coat of down when they hatch, although, even at this time the second-generation feathers are starting to appear. The earliest juvenile feathers to appear are usually the wing feathers and a sex-linked recessive gene influences their development. Incorporation of this gene into the genome allows for simple sex differentiation of chicks at hatch, although the ability to distinguish sex by length of the primaries becomes much less reliable once chicks are 2-4 d of age.

The second moult usually begins at around 4-5 weeks, and for the modern broiler chicken, this is the only moult of significance. Even at this time, there will still be natal down in the head region and perhaps some around the abdomen. With the notable exception of the quail and pheasant, the head and neck regions are usually the last to receive each successive generation of feathers. In most birds therefore, a "poorly" feathered head and neck region, relative to most other body parts, is quite normal. There is also variability and confusion regarding the moulting of the primary feathers. In turkey and broiler breeders, for example, the status of the moulting pattern of the primaries is often used as a management tool to help assess the stage of approaching maturity. In many birds the two or three outermost primaries may not be moulted regardless of feeding or environmental conditions. They can be retained for the full breeding cycle, and only be replaced after the first natural or induced moult. During a moult, the old feather is simply pushed out by the new feather. The emerging feather is physically attached to the older feather, and as it emerges from the outer sheath, the bond is broken and the older feather is shed. Feather follicles can be induced to produce a new feather at almost any time, if a feather is plucked from the follicle. The sequence of moult is orderly, probably under the action of hormones released by adjacent follicles (Voitkevich, 1966). In most poultry, the wing feathers moult in sequence starting with the proximal primaries. The wing feathers are first to moult, followed by the body feathers and lastly the head and neck feathers. Under natural conditions, males moult before females (Spearman, 1971). In force-moulted laying hens, the new primary wing feathers will achieve maximum length in about 10 weeks following initiation of the programme (Andrews *et al.*, 1987).

Feather colour

Most domesticated poultry have feathers that are white or brown or a mixture of these two colours. A number of breeds of chicken, turkey and duck obviously have much more colourful feathering, but few of these are important commercially. Most poultry are white feathered, a situation that arose in the late 1960's due to problems with processing coloured feathered birds due to residual pin feathers, etc. Most meat birds are, therefore, white feathered. About 50% of the laying hens are white, the remainder are brown feathered, which is a correlated trait for production of brown eggshells.

Feather colour results from an interaction between the epidermal cells that form the feather and a source of pigment, which is usually melanin. Deposition of pigment can be continuous or discontinuous, leading to solid colours or various colour patterns. In birds that have patterned feathers, and especially barred feathering, disruption of the pattern due to nutritional imbalance for example, is easily seen in the developing feathers. The pigmenting cells at the base of the feather follicle are in place prior to initial feather growth, since feather down in the day-old chick can be coloured. Different feather colours occur in different regions of the body and at different regions within a single feather, suggesting a very complex genetic control mechanism that influences cellular differentiation.

Melanin is the most common feather pigment, although combinations with carotenoids and porphyrins lead to a vast range of colour potential. Melanin is most often derived from the amino acid tyrosine which is usually in abundance in most diets. The copper-containing enzyme tyrosinase is critical in melanin formation, which is why copper deficiency often influences plummage colour or pattern. For example, the barring pattern in bronze turkeys is disrupted when birds are fed copper deficient diets. The melanoproteins produce specific patterns and colours as categorized by Bohren *et al.* (1943). The more intense colours involve greater quantities of pigment and it has been suggested that this adds to the strength of the feather (Carr, 1957). Even feathers from the White Leghorn contain melanins, although their low content and scant distribution result in what is apparently a white feather. Similarly, in barred feathers, the non-barred portion of the feather simply contains fewer melanin depots. The melanin pigments are deposited at the time that feather keratinisation occurs, which is within 1-2 mm of the feather follicle. Once the feather is completely keratinised, then no further pigmentation can occur. Attempts to enhance feather colour in adult birds by nutritional modification is a futile exercise. Feather colour in adults can only be influenced following a moult. Feather colour can be influenced by hormonal balance, with thyroid status having perhaps the greatest influence. A deficiency of thyroid hormone leads to more red/brown colouration, while an overly active thyroid leads to much darker black/brown colour due to extra melanin deposition. The sex hormones also influence feather colour. For example, in Brown Leghorn birds' sexual dimorphism of feather colour is under the control of oestrogen although the effect is influenced by thyroid status (Trinkaus, 1953; Voitkevich, 1966). Sex hormones can (but do not always) influence melanoblast differentiation. Genetics rather than hormone balance essentially control the different feather down colours of day-old chicks. However, if oestrogen or testosterone levels are altered in the developing embryo, down colour can be affected. Merat (1990) suggests that selection for genes that suppress feather colour results in improved feed efficiency in layers, possibly due to better retention of feather cover as birds age.

Feather attachment

Feathers are attached to the body through the follicle. However, it is not clearly understood why feathers are so difficult to remove from the live bird since there is little evidence of direct muscular contraction around the base of the feather. Without some means of enhancing feather release, such as hot-water scald, or electrical stimulation, the force required to remove individual feathers can be equivalent to 1 and 4 kg for body contour and wing primaries, respectively.

Feather retention is under the control of the autonomic nervous system (Ostmann *et al.*, 1963). When birds are stressed, they may shed some of their feathers. This is sometimes referred to as "fright-moult" and occurs very quickly suggesting a nervous reaction rather than one influenced by a hormonal change such as would occur with natural moult. The "fright-moult" may be an evolutionary response to escape from predators. Using scanning electron microscopy, Angel *et al.* (1982) showed that immature feathers are held in place by indentations of the follicle wall cells into the feather shaft. As the feather matures, there are keratinised bridges holding the feather in place. Levinger (1975) studied numerous factors that could be used during processing to aid release of feathers from the follicle.

Keratinisation and feather composition

Keratinisation occurs as feathers mature, when tissue turns into a hardened lignin-like material. Keratin is a scleroprotein that is virtually resistant to degradation by most proteolytic enzymes. During processing of feathers, it is necessary to apply conditions of high temperature and pressure in order to realize hydrolysis of the protein. Keratin represents about 85% of feather protein and is characterized by a high sulphfur content, much of which is in the form of the amino acid cystine. Consequently, feather growth necessitates a high dietary requirement for this amino acid. During incubation, keratinisation of feathers starts between 12-19 days of incubation. At the end of this period some feathers have the characteristic scaly tissue that is composed of numerous keratin layers (Beckingham-Smith, 1973). Keratin synthesis is coordinated with cell differentiation beginning at the tip of the developing feather sheath (Matulionis, 1970).

Several polypeptide chains in a coiled arrangement constitute a filament known as a feather myofibril (Spearman, 1966). As fibrils are produced, they become aligned and form the vane, barbs or barbules etc. These fibrils themselves become attached to form even thicker and denser fibrils (Lucas and Stettenheim, 1972). The cell contents then dehydrate and become replaced with other keratinous fibrils. The rigidity of the structure is due to the hydrogen bonding of the helix proteins that became even larger by coiling much like the production of wire cable. Cystine, by virtue of its disulphide bonds, stabilizes the cylindrical units into very strong cables (Moran *et al.*, 1966).

Keratinisation occurs while cells are developing, unlike the situation with hair in mammals. This means that disruption of keratinisation at different times during feather development (*e.g.* nutrient deficiency) will have a differing effect on the visual appearance of the growing feather. Feathers can take on unusual shapes because of this disruption to development of keratin.

There is considerable variation in the amino acid composition reported for feathers (Graham *et al.*, 1949; Block and Weiss, 1956; McCaslaud and Richardson, 1967; Fisher *et al.*, 1981; Stilborn *et al.*, 1997). To some extent such variance is attributable to the fact that feathers are not always harvested and handled under similar conditions and in some instances values relate to "feather meal" which is a feed ingredient produced by variable systems of processing. Fisher *et al.*, (1981) showed that amino acid content was quite

Table 3 Feather amino acids for mixed sex broilers.

	Age (days)				
	14	**28**	**42**	**56**	**84**
Protein %	93.9^{b}	91.2^{c}	95.7^{a}	93.4^{b}	94.6^{ab}
Amino acid (%):					
Arg	6.8^{ab}	6.4^{c}	6.8^{ab}	6.4^{c}	7.0^{a}
Cys	7.5^{bc}	7.9^{a}	7.2^{cd}	6.8^{d}	7.7^{ab}
Hist	1.4^{a}	0.7^{b}	0.6^{c}	0.6^{cd}	0.5^{d}
Iso	4.3^{d}	4.5^{c}	4.6^{b}	4.6^{bc}	4.8^{a}
Leuc	7.8^{b}	7.7^{b}	7.9^{b}	7.8^{b}	8.3^{a}
Lys	3.0^{a}	1.9^{b}	1.9^{b}	1.7^{c}	1.6^{c}
Meth	1.1^{a}	0.6^{bc}	0.7^{b}	0.6^{bc}	0.6^{bc}
Phenyl	4.6^{cd}	$4.7b^{cd}$	4.8^{ab}	4.7^{abc}	4.8^{a}
Threo	4.7^{b}	4.8^{ab}	4.9^{a}	4.8^{b}	4.9^{a}
Trypto	1.0^{a}	0.8^{b}	0.7^{bc}	0.7^{cd}	0.7^{d}
Tyrosine	3.1^{a}	2.8^{b}	2.6^{c}	2.6^{c}	2.3^{d}
Valine	5.9^{bc}	6.5^{a}	6.5^{a}	6.0^{b}	5.7^{c}
Total EAA	51.2^{a}	49.2^{b}	49.1^{bc}	47.7^{d}	48.8^{bcd}

Means with no common superscript within each row differ significantly ($P<0.05$).
Adapted from Stilborn *et al.* (1997)

consistent over time with minor decreases in methionine and increases in the threonine, valine and leucine contents. Nitsan *et al.* (1981) in fact suggested that amino acid content of feathers is quite consistent across most domesticated species. Stilborn *et al.* (1997) published data relevant to more modern strains of broiler (*Table 3*).

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