

GENERAL CONSIDERATIONS

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Histomorphophysiological, biochemical and experimental studies on skeletal muscles of vertebrates in general and aves in particular have not only provided enough basic information about their metabolic peculiarities and adaptation (George and Berger, 1966) but also proved conclusively the existence of two types of muscle fibres. Based on this scheme of biochemical characterization of muscles, the broad white fibres are reported to be loaded with high concentration of glycogen as fuel and adapted for anaerobic metabolism while the narrow red fibres are loaded with fat as the main fuel and adapted for aerobic metabolism. In comparison to skeletal muscles, studies on smooth muscle in general and of stomach complex in particular have been less attempted and explored, though scanty literature is available. In recent times the avian stomach in general has attracted the attention of many investigators who have conducted studies on embryological, morphological and experimental aspects and as a result of which much is known about its development (Blessing and Müller, 1974; Austin and Ricklefs, 1977; Butler and Jones, 1982; Klem *et al.*, 1982, 1983 and 1984; Kehoe and Ankney, 1985; Garcia *et al.*, 1986; Majumdar *et al.*, 1988; Patak and Baldwin, 1988; Kenney *et al.*, 1990; Nitsan *et al.*, 1991). Interest in the structure and function of the gastric apparatus arose in ^{the} early days of scientific, biological investigation and played a prominent role in the development of a general understanding of nature of digestive process in birds. Usually the gastric apparatus consists of two relatively distinct chambers, an anterior glandular stomach (proventriculus) and a posterior muscular stomach (ventriculus, also known as gizzard). The former functions principally in secretion of the gastric juice and as a passage way from the oesophagus to the muscular stomach; it may also function as a storage organ and as an organ of acid proteolysis. The muscular stomach functions as an organ of mechanical digestion in many species (it is often the functional analog of the teeth). Thus the morphological and functional differentiations of the stomach has the greatest range of variations of all internal organs of birds. The spindle or cone shaped glandular stomach is significantly correlated with the volume of food intake. The muscular stomach of birds is frequently considered as a compensatory organ for the lack of a chewing apparatus. It functions as a storage organ until such time as the gastric juice penetrates sufficiently to effect the acid proteolysis or until it passes into the intestine. The mechanical grinding function of this organ is the most striking; as an accessory device in this function, the muscular stomach of many species contain many stones. It also has a role in propelling food into

the intestine and filtering the undigestible materials which can be formed into pellets and are, from time to time, regurgitated. As a comparison of muscular stomach in various groups of birds, it is generalized that the large variations in size and muscularity of ventriculus are found in birds which are known to differ in diets (Shah and Panicker, 1975). Heavily muscular and large sized ventriculus is seen in those birds which feed on grains and seeds, while that of birds of prey is relatively less muscular. Intermediate form of ventriculus for their degree of muscularity and size are seen in birds which feed on mixed diet and in all frugivores.

The activity of the ventriculus muscle determines its size, in that the walls must contract harder to grind feed in absence of grit than in its presence (King and McLelland, 1979). There are reports that factors other than the presence or absence of grit in the rations affect the development of ventriculus. The size of the proventriculus is determined largely by the mechanical considerations, being increased in size to accommodate the prey or other bulk food swallowed, whereas the size of the ventriculus was related directly to the amount of energetic grinding required to allow penetration of digestive enzymes. The nature of the food as well as the amount of feed passing through the digestive tract has an influence on the thickness and firmness of the ventriculus.

The digestive tract is one of the most readily accessible routes for substances to enter body. Therefore it requires reasonably fail-safe mechanism for the careful selection of the substances that will be allowed entry. This is accomplished by a variety of mechanisms including palatability, vomiting or increased rate of passage and degradation of substance before they are permeable to intestinal tract. As creatures with intense metabolism, birds require rapid, powerful and efficient digestion of food. The spindle shaped glandular stomach is an innovation with birds. Those species of birds with efficient glandular stomach generally have weak, thin-walled muscular stomach. The ventriculus is shaped something like a thick biconvex lens. The mucous epithelial lining of this organ secretes a keratinous fluid that hardens into horny plates or ridges serving as millstones for the mechanical grinding of food. The ventriculus also functions as a trap that prevents sharp bones and indigestible fragments from proceeding down the alimentary canal. In a variety of species, seasonal change in diet parallels a change in stomach structure and function (Spitzer, 1972; Miller, 1975).

The study of avian gastrointestinal tract anatomy as it affects feed utilization is still in its infancy. There have been a number of studies on the anatomy of the avian digestive tract (Bolton, 1971; Ziswiler and Farner, 1972; Hodges, 1974; Barnard and Prosser, 1975; Hill and Strachan, 1975; King and McLelland, 1979; Hill, 1976; Blahos and Care, 1981; Klem *et al.*, 1982, 1983, 1984; Griminger, 1983; Sturkie, 1986; Nitsan *et al.*, 1991). These studies are concerned on the gross and microscopic anatomy of the fowl and have seldom related structure to function. A relatively shorter digestive tract when compared with mammals, is found in avian species and this relative decrease is in the intestinal region and therefore, suggests that the bird has lesser area for digestion and absorption than its mammalian counterparts. Further, the avian digestive system has evolved to a level of performance consistent with the energy requirements.

Of all the higher organisms birds are the most widely distributed species. Through the eons, they have developed certain peculiarities that had led to their survival. This has resulted from a remarkable degree of adaptation. Although, the capacity of flight has to be the foremost adaptation; however, related to that ability to fly are a number of adaptations which in case of our domesticated species may be a bane as much as a boon. The avian gastrointestinal tract has also undergone such adaptive processes. The structural peculiarities exhibited by animals to procure and consume various types of food are innumerable. Not only feeding apparatus and its mechanism undergo modifications according to the type of food, but the entire digestive system also gets geared and committed as per the specific type of ingested food. In some cases these adaptations work to the advantages of domesticated birds; in some instances, however, it puts the bird at a disadvantage. For example, the crop is a great storage organ, nevertheless, it is prone to a host of problems such as impaction and fungal infection. The extremely acidic gizzard, particularly in young birds, is frequently afflicted with erosion and ulcerations. As more high powered, purified type of diets are developed, the greater the tendency of the proventriculus to become atrophied. On the other hand, the high acidity, intense vascularity and rapid motility of the gut and the higher metabolic rate of the bird generally contribute to a remarkable efficient system for conversion of feed stuff to animal protein. However finer may be the mechanism of digestion, absorption and assimilation of food, they follow the predetermined infallible methods tried and improved during the course of evolution. Though the chordate alimentary canal is built on a basic ingenious architectural prototype, the multitude of variations exhibited by individual species are accountable to the type of food they consume. While the variations in the structure

of beak and feet are believed to be due to the influence of the food on them, the alimentary canal also equally demonstrates variations under such influences.

Such variations exhibited by digestive tract should logically reflect on their physiological activities too. With varied force that would be required to treat the food of different consistency, variation in the activities of the stomach complex could, naturally, be expected. In order to understand the histomorphological and physiological features of development and owing to the lack of adequate information regarding the developmental and metabolic aspects and the metabolites and enzymes involved thereof, an investigation on these lines deemed necessary and hence, in accordance, was carried out. The investigation deals with a comparative study on the stomach complex of developing domestic fowl, *Gallus gallus domesticus* and Japanese quail, *Coturnix coturnix japonica*. Study was also extended to the stomach complex of few adult birds showing preferential food habits. The adult birds selected for the study were House swift, *Apus affinis*; House sparrow, *Passer domesticus* and the Blue rock pigeon, *Columba livia*. Since these aspects have been treated as individual topics for discussion in separate chapters in the thesis, it was thought necessary to piece together all these findings and present them in a complete generalized picture. In the present study, both the posthatched birds viz., the domestic fowl and *coturnix* quail of 0, 5, 10, 20 and 30 days of age and adult birds were used. Such grouping would give a better understanding of any significant variations in morphophysiological characteristics such as increase or decrease in body weight, organ weight, different component of the organs, differences in the concentration and distribution of few metabolites and enzymes taking place during this time interval.

A comparative study of the organ growth showed that the precocial birds are at a more completely developed stage than the altricial species. This initial enlargement in the digestive organs allows nestling to process large amounts of food relative to body size presumably contributing to the high growth rates seen in most altricial and semi-precocial birds (Ricklefs, 1968, 1973). Ricklefs (1973, 1974) reported that the internal and external development differs in precocial chicks as the chicks under this mode of development are more mature at hatching than altricial young. Nevertheless, all the work done on developing stomach complex of birds have utilized either chick of adult fowl and result from many different types of studies yield a general picture of precocial species (Blessing and Müller, 1974; Okuro and Ikeda, 1974;

Nishida, 1976; Nishida and Nishida, 1978, 1985; Akester, 1986). Since the generality of this pattern among other species with the same mode of development has not been established, it was thought desirable to use developing coturnix quail as another model. If a comparison is made between fowl and quail, the latter has more advantages, as listed below, than the former. The advantages are:

1. General care of the species is very easy because of its small body size and hardiness.
2. Low feed requirement.
3. More rapid growth and earlier sexual maturity.
4. Greater laying ability and shorter incubation period.
5. Shorter generation interval.

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When considering the commercial aspects of fowl and quail, the latter proves to be more beneficial than fowl. Since any detail regarding quail is not much known, the following information about this bird is given in brief, so as to know as to why it is considered more beneficial than fowl. Quails, which are seen in wild, are known in Gujarat by different names like 'Limbdī' and 'Bhatakiyu' and in Hindi speaking state by the name 'Butter'. The species which is reared is commonly known as Japanese quail. This species is usually found in Japan, Hong Kong, Korea, France, Italy, Germany and Britain and is used for egg production and table purpose. In 1974, these quails were brought to India by Central Avian Research Institute (CARI), Izzatnagar, U.P. and used as model for research activities. In 1989-1990, along with the programme of poultry development, Intensive Poultry Development Board (IPDB), Dahod, Gujarat, initiated the move to start quail farming in Dahod, due to the conducive atmosphere in that part of the state. Now, as more and more information about quail is becoming available, the demand has also become very high.

Within two weeks after hatching, the quail will adjust themselves to the surrounding environment and therefore, utmost care has to be taken only during the first two weeks (chick stage) with respect to the health and cleanliness, in which case the mortality rate will be normal. Thereafter, the rearing becomes easy as the mortality rate comes down from 5-7% to 1-1.5%. Moreover, the common poultry diseases like fowl pox and *Ascaridia galli* (the common round worm in chicken) are not usually seen in quails and therefore, they are not subjected to any immunization

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and deworming. Ulcerative enteritis, a common disease found in quails can also be controlled by streptomycin. Even aspergillosis can be controlled by maintaining proper humidity in the brooder house. Therefore, it is clear that quail rearing is much more beneficial and profitable than the fowl rearing. The following reasons are provided by the Deputy Director, IPDB, Dahod, Gujarat.

1. Less area is required and less cost incurred to begin with/whereas in case of fowl more area and high cost are required. ✓
2. In one sq.ft. area 6 to 8 quails can be reared/whereas one fowl requires 2 sq.ft. area. ✓
3. Quails are disease free and no immunization is required. Fowl is prone to different kinds of poultry diseases and hence there is need for immunization for 6 to 7 weeks. ?
4. In case of quail daily intake of feed is 20 to 25 gm/whereas each chick eats about 110 to 120 gm of feed daily. ✓
5. In a year quail eats about 8.5 to 9.0 kg of feed and lays 280 to 300 eggs, whereas in fowl feed consumption per annum is of about 42 kg and lays 250 to 280 eggs. Hence in quail low feed requirement than fowl.
6. Quail starts laying eggs between 6 ^{and} 8 weeks of age and hen starts laying eggs from 20 to 22 weeks of age.
7. Meat of quail is tasty, less watery, tender and with low cholesterol content/whereas fowl is more fatty, watery and with high cholesterol content. ✓
8. Because of small size and less amount invested more people buy quail, whereas less people can buy fowl because the amount to be invested to buy such huge bird is always more.

According to Brody (1945) most organisms undergo change of form due to differential growth rates of different organs and tissues and these changes in growth rates are reflected in the

anatomy and physiology of the animals. The data presented in the morphophysiological studies (Chapter II) showed that the body weight of fowl and quail increased from 30 gm and 4.35 gm on the day of hatching to 1850 gm and 99.16 gm in the adult, an increase of about 6000% and 2200% respectively. The stomach complex of these two birds also showed increase in their growth. The linear development of the digestive organs in both fowl and quail is in an order in accord with that expected in the light of their function. Growth of such organs in relation to their function has been previously advanced by Ricklefs (1967) and Romanoff (1967) in the digestive organs of Redwinged blackbird nestlings and in the liver and ventriculus of Gallus domesticus respectively. Observations made on the development of the component parts of stomach complex of these two species of birds have revealed an increase in size of all the parts. These observations are in conformity with the observation of Ricklefs (1969) that the relative sizes of body components during growth were apparently determined largely by the functional priority of each tissue. Further, Brody (1945), Impekoven (1962), Laird (1965) and Ricklefs (1967) have all indicated that the growth and development involved changes not only in the gross weight but also the relative sizes of component parts.

The adult birds presently under investigations have altricial mode of development and varied feeding habits and even their basic growth data showed phenomenal differences. Yet they do not fall into any linearly accountable categories. It is conclusively believed that the work load of stomach varies according to the size and consistency of food and irrespective of such differences, the relative weight of proventriculus and ventriculus remained little affected (chapter II). Information on the problem of regulation of growth was echoed by Goss (1972). According to him the structural peculiarities of the stomach were under the influence of genes and the birds with inherent habits of preferring specific type of food cannot change their diet of feeding habits.

The present quantitative investigation on the amount of metabolites such as glucose, lipid and enzyme viz. phosphorylase revealed a metabolic flux with regard to the preferential choice and utilization of metabolite in the developing and adult bird. The metabolic machinery, apart from providing energy for cell division, growth and differentiation, should also deal with the carbohydrate, lipid and protein metabolism. Glycogen metabolism in the tissues of most animals is regulated by the balance between its synthesis and degradation. Further the role of fat as a major fuel reserve for energy during long and sustained muscular activity has been well

established and this metabolite, being of high caloric value, serves as an important source for various energy linked reactions in animal tissue (George and Berger, 1966). Large lipid reserves, however, are considered both advantageous and disadvantageous to the animals (Meier and Burns, 1976). The dramatic changes in the concentration of metabolites and activities of enzyme involved in carbohydrate, lipid and protein metabolism taking place from foetal to neonatal stages in mammals and at about the same time of hatching in the chick are established facts (Raheja *et al.*, 1971). Apparently the posthatched phases of avian species are marked by adaptive metabolic shifts preparatory to the establishment of adult pattern of metabolic homeostasis. A predominant carbohydrate metabolism was evident in the stomach complex of developing fowl and quail during the initial days. Shah and Panicker (1974) and Panicker and Shah (1980a), based on their studies on the gizzard of developing pigeon, reported a continuous process of glycolytic metabolism in that organ. From the present investigation it is surmised that the metabolic necessities during the initial days of development of these organs are of low order; nevertheless, the proventriculus is in a higher metabolic status compared to ventriculus and therefore shows an enhanced capacity for the utilization of glucose for the production of energy. Contrary to the above observation, lipid catabolism appear to be significant only during the later part of development in these birds. The glycogen content continued to decline through day 10 with low concentration of phosphorylase in proventriculus and ventriculus of fowl and quail. This decline in glycogen with minimal level of phosphorylase with apparently no lipid catabolism could be related to concomitant spurt in the morphometric development of these organs (chapter II). This observation is in good agreement with observation made by Shah and Panicker (1974 and 1976) and Panicker and Shah (1980a) indicating the possibility of complete oxidation of glycogen for the liberation of energy. When the carbohydrate metabolism fails to satisfy the energy necessities of the fast developing stomach complex, the energy demand is supplemented by the active participation of lipid as noted between days 10 and 30. The transitional period from 30th day to adult is the one where the proventriculus and ventriculus have attained full structural and functional maturity. There was a significant low demand for metabolic necessities at this period as could be evidenced by the increase in glycogen content and decrease in phosphorylase level. When the developmental process is completed with the attainment of adulthood, the lipid level in the proventriculus and ventriculus is reduced to settle down towards the characteristic adult pattern. In this connection, the observation of White *et al.* (1964), that the energy for slow and sustained contractions of smooth muscle is derived from the oxidation of fatty acid is

noteworthy as the ventriculus is chiefly constituted of smooth muscle. It could be noted that though all types of ventriculus are capable of lipid catabolism, the extent of its utilization appears to show a gradation as per the specific type of food ingested by the various groups of birds. The concentration of phosphorylase, when related to the observed value of glycogen, clearly indicates that these birds are differently adapted to utilize glycogen for energy purpose. Perhaps those similarities and differences may be due to the preferential utilization of diet.

The concentration of myoglobin in a muscle is generally regarded as an index of capacity of the muscle for aerobic metabolism and sustained activity. Myoglobin containing muscle is physiologically slow or tonic muscles and the myoglobin lacking muscle is fast or phasic (George and Berger, 1966). The stomach muscle contracts continuously and rhythmically when the birds take food but more heavier contractions should be maintained during prolonged repetitive digestion of food. Therefore, the proventriculus and ventriculus contain large amount of myoglobin to reserve adequate oxygen for aerobic energy phosphate synthesis and to facilitate the oxygen diffusion into the muscle (Baldwin and Patak, 1988). In the present study, an increased myoglobin concentration was the feature during different days of development. Among the adult birds, the myoglobin concentration was highest in proventriculus and ventriculus of quail, followed by fowl, pigeon, sparrow and swift. As inferred, an elevated level reflects limitation in oxygen delivery as the ventriculus receives a relatively slow amount of blood flow in comparison to the absorptive area of the gut. SL

Activity of adenosine triphosphatase (ATPase) is an indication of energy consuming activities of the cells engaged in the synthesis and active transport of metabolites across the cell membrane. In metabolically active tissues or organs such as stomach, the synthesis and hydrolysis of ATP are characteristic features. Skeletal and cardiac muscles of vertebrates have been the focus of physiological, biochemical and histochemical studies, but the smooth muscles of vertebrates in general and avian stomach in particular attracted little attention in the past. So a series of studies on the amount and distribution of ATPase in the stomach complex of developing fowl and quail and of adult birds were undertaken to understand the metabolic aspects underlying the development of that part of avian alimentary canal. The activity of ATPase in the proventriculus and ventriculus of these developing birds is related not only to the need of energy for secretory function but also to the laying down of connective tissue around the smooth muscle

fasciculi. In case of adult birds, the food habits are taken into consideration while ascribing any particular role for the enzyme. Perhaps the adult birds under investigation here are primarily adapted to grains and seeds (except swift) but have secondarily taken to insects or mixed type of food. Hence variation in the concentration of ATPase in the stomach complex of adult birds are justifiable.

Among the various enzymes, phosphatases have drawn considerable attention in recent times due to their purported importance in different aspects of cell metabolism. Voluminous literature is available on the role of phosphatases in various vertebrate tissues, but only scanty literature is available on the role of these enzymes in the stomach complex of developing and adult avian species. Observations on acid and alkaline phosphatases indicated fluctuations in their concentration in the stomach complex of fowl and quail during the posthatched development. In the adult birds, the acid phosphatase was maximum in swift proventriculus followed by that of sparrow, quail, pigeon and fowl. Nevertheless, compared to acid phosphatase, the alkaline phosphatase activity was very low in the stomach complex of the birds studied. The distribution and concentration of these enzymes are discussed in relation to the functional development of the organ and to the extent of dietary influence on these enzymes.

From the present investigations, the interesting aspects that are brought about are as follows:

1. The morphometric observations revealed that the digestive organs of fowl and quail developed linearly in an order broadly in accord with that expected in the light of their function.
2. The adult birds do not fall into any linearly accountable categories; however, they differ from each other in the size and thickness of their component parts which are undoubtedly based on the type and consistency of the food.
3. Variations in the type and consistency of food consumed are reflected on the rate and time of attainment of functional status by the metabolic and enzymatic machinery of the stomach complex.

4. The elevated concentration of myoglobin in the proventriculus and ventriculus of developing and adult birds was related to the high capacity to deliver oxygen to the tissue and with the sustained contractility of the organ and also to the synthesis of energy rich phosphate for their effective functioning.
5. The active participation of phosphatases (both specific and non-specific) in the functional differentiation of the stomach complex; their activities are related not only to the need of energy to the secretory functions but also for the formation of the connective tissue around the smooth muscle fasciculi. In the adult birds, the variations observed in the activity of the phosphatases are due to the preferential diet with varied consistency consumed by them.