

INTRODUCTION

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Birds are the most widely distributed species amongst all the higher organisms. Through the eons, they have developed certain peculiarities that have led to their survival. This has resulted from a remarkable degree of adaptations. Although, the capacity of flight has been the foremost adaptation; related to that ability to fly are a number of adaptations which, in case of our domesticated birds, 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 mechanisms undergo modifications according to the types of food, but the entire digestive system also gets geared and committed according to the specific type of food they ingest. In some cases these adaptations work to the advantage of the domesticated species; in some instances, however, these put 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 types of diet are developed, the greater the tendency of the proventriculus to become impacted and 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 the conversion of feed stuffs into animal protein.

Digestive System

The digestive tract is one of the most readily accessible routes for substances to enter the body. The selection of substances that will be allowed entry is accomplished through a variety of mechanisms including food selection (palatability), rapid rejection of irritant by emesis (vomiting), increased rate of passage and degradation of substances before they have access to the more permeable intestinal tract. Many of the processes responsible for the digestion and absorption are common to most species; others have resulted from adaptations to the diet, environment and other physiological characteristics of the animal through divergence from a common or more primitive form or by convergence - the appearance of similar structure in completely unrelated species. The study of avian gastrointestinal tract anatomy as it affects feed utilization is still in its infancy. Though there have been a number of major studies on the

anatomy of avian digestive tract (Bolton, 1971; Hill, 1971; Ziswiler and Farner, 1972; Barnard and Prosser, 1973; Hodges, 1974; Hill and Strachan, 1975; King and McLelland, 1979; Blahos and Care, 1981; Klem *et al.*, 1982, 1983, 1984; Griminger, 1983; Sturkie, 1986; Nitsan *et al.*, 1991), these studies have been concentrated mainly on the gross and microscopic anatomy of fowl and seldom related structure to function. The digestive tract in avian species is relatively shorter than that of mammals and most of the relative decrease is in the intestinal region. This suggests that birds have less area for digestion and absorption than its mammalian counterpart (Browne, 1922). The avian digestive system has evolved to a level of performance consistent with the energy requirements. Interest in the structure and function of the gastric apparatus arose in the early days of scientific biological investigations and played a prominent role in the development of a general understanding of the nature of digestive process in birds.

Avian Stomach: Its Uniqueness

In structure, the stomach of fish, amphibians, reptiles and mammals, is a relatively simple tubular or asymmetric expansion of the digestive tract. With the exception of some fish and the larval toads, all vertebrates have a stomach or analogous organ serving as a site for storage, maceration and some physical breakdown of food. Other major function of the stomach includes the initiation of protein digestion. However, in birds, the gastric apparatus consists of two relatively distinct chambers, an anterior glandular stomach (proventriculus) and a posterior muscular stomach (ventriculus also known as gizzard) (Figures 1 and 2). The division of the stomach into at least these two parts and in many forms, the development of a storage diverticulum in the oesophagus, are the unique characteristics of the general structural plan of the avian digestive system. However, the embryonic origin and differentiation of the digestive tract do not differ qualitatively from that of the other vertebrates (Farner and King, 1972).

Proventriculus

The proventriculus, which externally appears to be no more than an expanded portion of the oesophagus, is conical in shape and lies between the oesophagus and the ventriculus. Its internal lumen is narrow and the walls have anastomosing folds, grooves and evenly distributed proventricular papillae (Hodges, 1974). The mass of proventricular glands makes up the greater

Figure 1. Generalized morphology of avian stomach.

1. Oesophagus 2. Proventriculus 3. Cranio-dorsal thin muscle 4. Caudo-dorsal thick muscle 5. Gizzard 6. Caudo-ventral thick muscle 7. Tendinous centre 8. Cranio-ventral thick muscle 9. Duodenum.

Figure 2. Longitudinal section of avian stomach.

1. Oesophagus 2. Proventriculus 3. Cranio-dorsal thin muscle 4. Cuticle 5. Caudo-dorsal thick muscle 6. Caudo-ventral thin muscle 7. Gizzard 8. Cranio-ventral thick muscle 9. Gland opening on papillae 10. Deep glands.

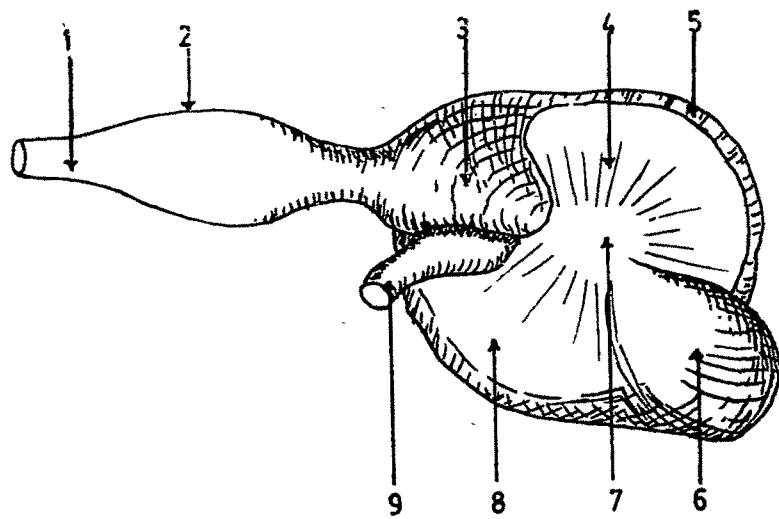


FIG. 1

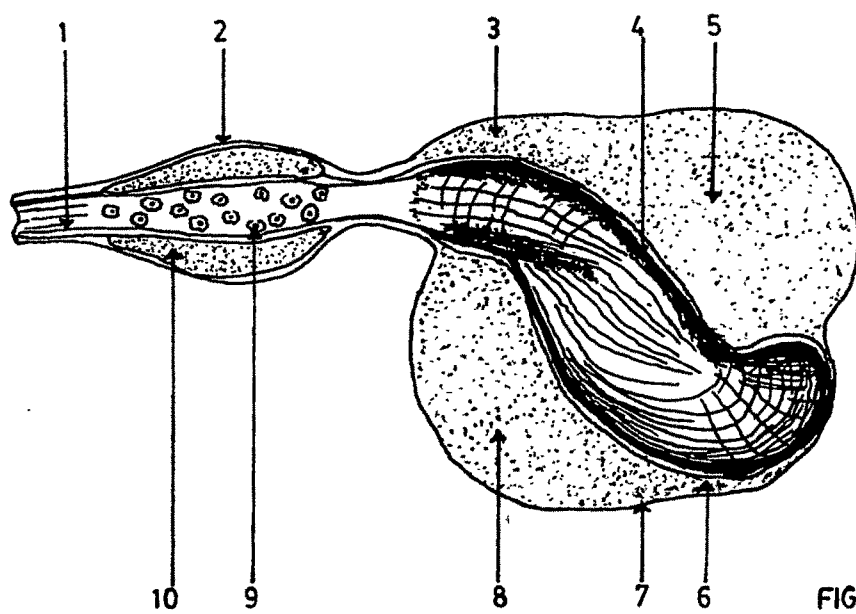


FIG. 2

part of the thickness of the proventricular wall. Radiating from the central cavity of the gland (lumina) are a number of tertiary ducts, which in turn go on to form the secondary duct. Several such ducts form short primary ducts which open into the lumen (Menzie's and Fisk, 1963). Surrounding each lobule is a connective tissue septum consisting of collagen and elastic fibres together with a few muscle fibers (Calhoun, 1954; Hodges, 1974).

Ventriculus

Externally, the ventriculus is a biconvex mass of muscle and tendon. The cone shaped proventriculus opens into the ventriculus anteriorly and from its lateral side originates the small intestine. The bulk of the ventriculus can be separated into four semi-autonomous muscles radiating from the central tendon. Internally the ventriculus is covered by a hard cuticle. Numerous ridges and grooves are also evident and openings to the proventriculus and small intestine are also prominent. Ventriculus secretes a tough abrasive membrane which is chemically a polysaccharide protein complex (Eglitis and Knouff, 1962; Luppá, 1962; Tonoer, 1964; Webb and Colvin, 1964; Michel, 1971; Akester, 1986). Rhythmic contractions of the ventricular muscles occur two or three times per minute (Dzuike and Duke, 1972), resulting in the food being crushed into fine pieces (Akester, 1986).

Among all internal organs of birds, the stomach complex exhibits the greatest range of variations in its structural and functional differentiation (Farner and King, 1972; Hodges, 1974). The lumen of the glandular stomach of piscivorous or frugivorous species is large and the graminivorous species which eat predominantly seeds have large lumina (Hodges, 1974). The muscular stomach of birds is frequently considered as a compensatory organ for the lack of chewing apparatus. It functions as a storage organ until the gastric juice penetrates sufficiently to affect the acid proteolysis or until it is passed into the intestine. However, the grinding function of this organ is the most striking (as an accessory device in this function the muscular stomach of many species contains many stones). It has a role in propelling food into the intestine and filtering the undigestible materials that can be formed into the pellets and are, from time to time regurgitated (Howard, 1958; Grimm and Whitehouse, 1963).

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The nature of the feed and amount of food passing through the digestive tract has an influence on the thickness and firmness of the ventriculus musculature. Heavily muscular and large sized ventriculus is found in those birds that feed on grains and seeds, while the ventriculus of birds of prey is relatively less muscular. Intermediate form of ventriculus, for their degree of muscularity and size is seen in birds that feed on mixed diet and in all frugivores (Shah and Paniker, 1975). Such morphological variations exhibited by the stomach should, logically reflect on their physiological activities too. With varied force for grinding which would be required to treat the food of different consistency, variations in the activities of the stomach could naturally be expected.

Precocial and Altricial Mode of Development: Morphophysiological Characteristics

There are important differences between precocial and altricial birds in the development and activities of their digestive system into completely functional organ system. Precocial birds are those birds which are born live with feathers, without parental care, highly self sufficient in feeding, grows slowly, well developed down feathers, more matured, short incubation period, early mature functioning, large proportion of non lipid dry matter and less water in their bodies, whose young can maintain their own body temperature and presumably escape some predation. In contrast, altricial birds are those birds born live without feathers, cannot regulate their body temperature at hatching, cannot fly, less matured at hatching, have rapid growth, long incubation period, small proportion of non lipid dry matter and more water in their bodies (Wetherbee, 1961; Ricklefs, 1967, 1973, 1974, 1979; Spiers *et al.*, 1974; Dunn, 1975). A comparison of organ growth showed that the precocial birds are at a more completely developed stage than altricial species (Dunn, 1975). Growth of digestive system after hatching is initially rapid in the altricial species whereas it is slow in case of precocial birds. This initial enlargement in the digestive system allows nestlings 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). As precocial chicks are much more mature at hatching than altricial young, it is not surprising that the internal and external development differs (Ricklefs, 1973, 1974). But growth processes also vary among species of the same developmental mode (Dunn, 1973, 1975) and hence, detailed studies should be of value in analysing differences in ecological adaptation.

Most of the earlier studies on avian developing stomach were mainly confined to chicks or adult fowl (Blessing and Müller, 1974; Okuro and Ikeda, 1974; Nishida, 1976; Nishida and Nishida, 1978, 1985; Akester, 1986). However, the generality in the pattern of development of stomach of other precocial species is scantily understood. When Japanese quail (one of the smaller precocial birds) is considered, it has more advantages than fowl.

The advantages are:

1. General care of this species is very easy because of its small body size.
2. Has low feed requirement.
3. Has more rapid growth, earlier sexual maturity.
4. Has greater laying ability and shorter time of hatching as compared to chickens (Wilson *et al.*, 1961 and El-ibiary *et al.*, 1966).
5. Has shorter generation interval (Sadjadi and Becker, 1980).

Hence, the present study is planned to determine whether a common pattern of growth, development and metabolic adaptations exists in the two developing and adult precocial species viz., Domestic Fowl (*Gallus gallus domesticus*) (plate 1a and 1b) and Japanese Quail (*Coturnix coturnix japonica*) (plate 2a and 2b). The study is also extended to certain adult birds, such as House Swift (*Apus affinis*) (plate 3a), House Sparrow (*Passer domesticus*) (plate 3b) and Blue Rock Pigeon (*Columba livia*) (plate 4) [with altricial mode of development], to lay a basic ground work for the evaluation and elucidation of the various metabolic aspects aimed and planned at, by the application of suitable histophysiological techniques and compare these metabolic and enzymatic peculiarities exhibited by the above mentioned precocial and altricial birds. These birds are also studied in a different perspective, i.e. their preferential food habits.

In the present study, the posthatched developing birds of 0, 5, 10, 20, 30 days of age and adult birds were used. Such grouping would give a better understanding of any significant variation in morphophysiological characteristics, such as increase or decrease in body weight, organ weight and different components of the organs as well as differences in the concentration and distribution of few metabolites and enzymes, taking place during this time interval. As the developmental process involves much cellular changes and organization, intriguing metabolic

Plate Ia.

Bird	: 0 day old chick
Scientific name	: <i>Gallus gallus domesticus</i>
Height	: 9 cm
Length	: 10.5 cm
Weight	: 30 gm

Plate Ib.

Bird	: Domestic fowl (R)
Scientific name	: <i>Gallus gallus domesticus</i>
Height	: 44 cm
Length	: 54 cm
Weight	: 1.85 kg
Habitat	: Poultry bird (commensal of man in cities and villages)
Feeding habit	: Graminivore
Distribution	: All over India (Subcontinent)



Plate IIa.

Bird	: 0 day old quail
Scientific name	: <i>Coturnix coturnix japonica</i>
Height	: 3.5 cm
Length	: 6.5 cm
Weight	: 4.5 gm

Plate IIb.

Bird	: Japanese quail (R)
Scientific name	: <i>Coturnix coturnix japonica</i>
Height	: 7.6 cm
Length	: 21 cm
Weight	: 100 gm
Habitat	: Grassland and standing crops
Feeding habit	: Graminivore
Distribution	: Japan, Korea, France, Italy, Hong Kong, UK, UP, Gujarat etc.



Plate IIIa.

Bird	: House swift
Scientific name	: <i>Apus affinis</i>
Height	: 4.5 cm
Length	: 13 cm
Weight	: 20 gm
Habitat	: High cliffs, buildings
Feeding habit	: Insectivore
Distribution	: N. Baluchistan, Himalayas, Western Ghats from Nasik to Kerala, Madhya Pradesh, Sri Lanka

Plate IIIb.

Bird	: House sparrow
Scientific name	: <i>Passer domesticus</i>
Height	: 5 cm
Length	: 15.5 cm
Weight	: 22 gm
Habitat	: A ubiquitous commensal of man in cities, suburbs, villages, etc.
Feeding habit	: Omnivore
Distribution	: Subcontinent



Plate IV.

Bird	: Blue rock pigeon
Scientific name	: <i>Columba livia</i>
Height	: 12 cm
Length	: 32.5 cm
Weight	: 260 gm
Habitat	: Cliffs and gorges and around habitation and cultivation
Feeding habit	: Graminivore
Distribution	: All over India (Subcontinent)



changes could be expected to occur. Such changes might be of significance during posthatching development, as the tissues are undergoing fast changes in their attempt to acquire the adult pattern of structure and function.

Although body weights are relevant to many branches of avian biology, they have not been reviewed recently. Clark (1979) did survey sources and uses for weight data with reference to many parameters such as food size, habitat, ^{and} migration (etc). He considered uses of weight as standard for body size, in systematics, in assessing the physiological condition of individuals and in analysis of ecological communities. Ricklefs (1968 and 1973) has emphasized growth studies to be traditionally concentrated on changes in body weight. Growth and development, however, involve changes not only in gross weights but also in the relative sizes of component parts. ^{naturally} Hence, morphometric studies are carried out on the proventriculus and ventriculus, keeping in mind the external dimensions, thickness of the four layers of proventriculus and ventriculus of developing and adult birds.

The carbohydrate metabolism as the primary source of energy for the ^{sustenance?} subservience of animal | ? tissue is, by now an established fact. The circulating blood glucose or the glycogen stored in tissue are the metabolites of choice consumed or broken down during the biochemical reaction characteristics of the carbohydrate metabolism (Shah and Panicker, 1975; Hazelwood, 1986). Importance of lipids as the major fuel for energy during long and sustained muscular activity has been well established (George and Jyoti, 1957; George and Berger, 1966).

Myoglobin is a reddish brown sarcoplasmic chromoprotein predominantly occurring in red muscle than in white ones. The greater contractile power of the red muscles is attributed to the higher concentration of oxygen in its myoglobin and there is added evidence of the occurrence of more myoglobin, fat and lipase in the red muscle in contrast to the white one (Lawrie, 1952). It is present in large amounts in the slow contracting type of fibers and depends primarily on aerobic glycolysis for energy. The oxygen binding muscle protein, myoglobin, functions both in facilitating rapid oxygen transfer from the blood capillaries to the mitochondria and in oxygen storage; consequently, elevated myoglobin concentration occurs in skeletal and heart muscles capable of sustained activity by oxidative phosphorylation (Wittenberg, 1970; Burke *et al.*, 1971;

Wittenberg *et al.*, 1975; Butler and Jones, 1982; Pages and Planas, 1983; Baldwin *et al.*, 1984; Gayeski and Honig, 1986).

The synthesis and utilization of adenosine triphosphate (ATP) occur simultaneously in any living cell and the activity of adenosine triphosphatase (ATPase) is an indication of energy consuming activities of the cells engaged in synthesis and active transport of metabolites across the cell membrane (Silver and Stull, 1982; Hai and Murphy, 1988; Kenney *et al.*, 1990). Na^+ and K^+ dependent ATPase is widely accepted to be intimately associated with the mechanism of transport of ions and metabolites such as glucose, ^{and} amino acid, (etc) across the glandular epithelial tissues and also in other tissues concerned with secretory functions (Ganong, 1989). In metabolic tissues or organs such as stomach, the synthesis and hydrolysis of ATP are characteristic features.

Dietary preferences of birds have brought about drastic adaptive changes in feeding apparatus as well as alimentary canal. Chordate stomach in general, is primarily a store place for food (though for a short time), when modified into ventriculus in birds, has transformed into a grinding mill of varied type for force depending upon the consistency of the food they consume. In contrast to anatomical adaptations that are easily understood, the physiological and biochemical adaptations are very complex to be accounted for. Among the metabolic adaptations the enzymatic one is the foremost, as induction and repression of the enzyme are genetically controlled and as such (as) heritable. Among the enzymes phosphatases have drawn considerable attention in the recent times due to their purported importance in different aspects of cell metabolism (Verzar and McDougall, 1936; Moog, 1946, 1981; Rosenthal *et al.*, 1960; Novikoff, 1961 and 1963; Pilo *et al.*, 1972; Shah and Panicker, 1977; and Yora and Sakagishi, 1986).

The studies mentioned above have created interest and in order to understand such variations, if any, detailed morphophysiological and enzymatic studies have been undertaken on the stomach complex of developing and adult precocial birds and also certain adult altricial birds and the results are discussed in detail.

To assess the growth and metabolic pattern of the birds (as mentioned earlier), the following investigations were carried out.

1. Comparative morphometric studies on proventriculus and ventriculus of postnatally developing domestic fowl and coturnix quail and also certain adult birds.
2. Metabolic profiles.
3. Myoglobin (a muscle protein) usually absent in smooth muscle but the stomach complex of birds are notable exception.
4. Non-specific phosphatases (acid and alkaline phosphatase) in relation to dietary preferences.
5. ATPase as a possible source of energy.