Chapter 4

INFLUENCE OF INDUCED FUNCTIONAL ATHYREOSIS ON HISTOPHYSIOLOGY OF DEVELOPING FEATHERS IN THE PIGEON, *COLUMBA LIVIA*

Dependence of moult, growth, and pigmentation of plumage on various endocrine factors is well documented. Preeminant among these is the thyroid gland, the role of which has been extensively investigated (for a comprehensive review, see Voitkevich, 1966). Administration of thyroxine or its analogues is reported to induce moult in various avian species (Juhn, 1963; Voitkevich, 1966). Hypothyroidism and athyreosis are known to retard development of body feathers (Schwarz, 1931; Chu, 1938; Blivaiss, 1947), whereas replacement thereapy restores the process to normalcy (Voitkevich, 1966). Various suggestions as to the mode in which thyroxine initiates moult and influences plumage development have been advanced, including its local stimulatory effects on the papillae (Juhn, 1963) as well as its action through general physiological changes in the body (Voitkevich, 1966). Yatvin (1966a,b) has suggested endocrine dependence of some subcellular aspects of keratinization in the embryonic chick skin. However, no attempts to analyse possible alternations in the metabolic pattern of the feather forming tissues under functional athyreosis have been made so far. Morphological events such

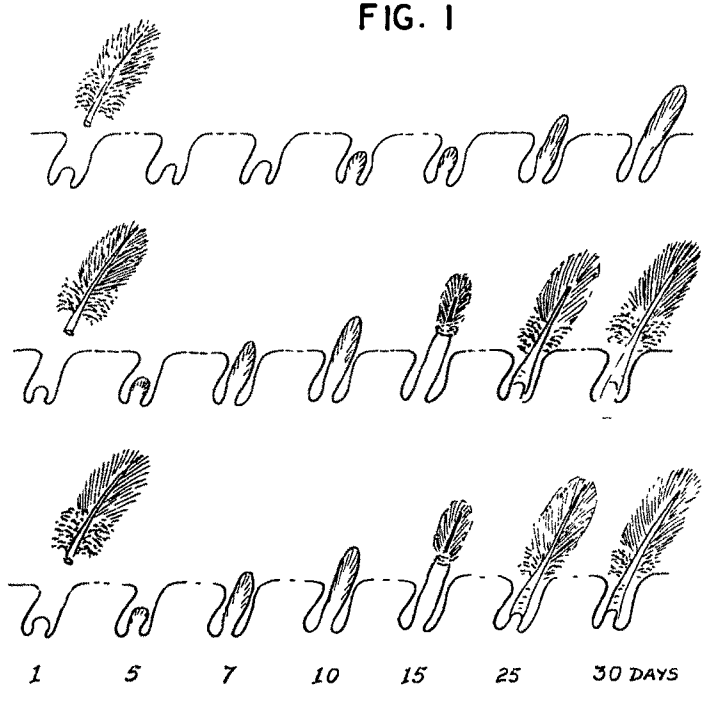
as plumage development, differentiation and growth are subjected to modifications by a variety of regulatory factors, as the manifestations of these processes are dependent on various metabolic reactions translated to effectiveness through the participation of enzymes. Shah and Menon (1971, 1972, 1973, 1974a,b,1976) and Menon and Shah (1975) explored the histoenzymological profile of avian integument and established the significance of activities of a number of enzymes during various stages of contour feather development. It was deemed profitable to look for the possible influence of thyroid hormones on the enzyme complements involved in regulation of feather development. Hence the present histochemical investigations on certain enzymes viz., alkaline and acid phosphatases; glucose-6-phosphate, succinate, malate and lactate dehydrogenases in the integument under experimental athyreosis in the feral blue rock pigeon, Columba livia were undertaken.

OBSERVATIONS

Morphological

Control birds not treated with thiouracil (Group B) and those under replacement therapy (Group C), showed the emergence of developing feather stubs at the skin surface on the 7th day after plucking, and the feathers were fully developed by the 30th day. However, those birds (Group A) which were rendered functionally athyroidic with thiouracil treatment before

FIG. 1



Group A

Significant reduction	Alk.Pase – G-6-PDH, SDH & MDH
Active	Acid. Pase, LDH

Group B

Active	Alk. Pase, Acid. Pase, G-6-PDH, SDH, MDH & LDH

Group C

Active	Alk. Pase, Acid. Pase, G-6-PDH, SDH, MDH & LDH

plucking of the feathers showed delayed emergence of feathers and retarted development(i.e. feather emergence and its full development were seen only by about the 25th and 60th days respectively). Besides, the feathers in this case when fully formed were duller in colouration and imperfect in the formation of vanes.

Histochemical

Histochemically demonstrated activities of the enzymes, like alkaline phosphatase, and, glucose-6-phosphate, succinate and malate dehydrogenases were found to be considerably low in the integument and feather follicles of the birds of Group A as compared to the high activity of these enzymes in the corresponding tissues of the control birds (Group B) as well as those under replacement thereby (Group C). On the other hand, no noteworthy differences could be seen among birds of all the three groups as far as the reactivities of acid phosphatase and LDH were concerned. A schematic representation, comparing temporal relation of developmental events during feather restoration in the three groups of pigeons, and the state of activities of the enzymes studied, is given in Fig. 1. The relative state of activities of the enzymes in the three groups of birds is presented in Table-1. Only the generalised state of enzyme activities are considered here for comparison.

DISCUSSION

Results of the present study show that the active

TABLE.I

RESULTS

State of enzyme activity during feather development after inducing moult under experimental conditions.

Enzymes	Athyroidic	Control	Replacement therapy
Alk. Pase	+	+++	+++
G-6-PDH	+	+++	+++
SDH	+	+++	+++
MDH	+	+++	+++
Acid Pase	+++	+++	+++
LDH	+++	+++	+++

principles of thyroid gland are indispensible for the normal process of development and restoration of definitive feathers and that, in their absence, feather development gets retarded. These findings gain support from the works of Schwarz (1931), Chu (1938), Blivaiss (1947) and Voitkevich (1966). The concurrent alterations in the histoenzymological profile of the feather forming tissues during functional athyreosis noted herein, as well as the restoration of normal enzymological pattern and the time span needed for complete restoration of these cutaneous appendages with replacement therapy, prove that thyroid mediated metabolic events are significant factors influencing development, differentiation and growth of feathers. Observations of similar morphological and histological effects of athyreosis and replacement therapy on differentiation of avian scales by Laurenz and Johnson (1970) and that of Chapman et al.(1974) on development of wool follicles in sheep, clearly underscore the significance of thyroid hormone in growth and differentiation of cutaneous appendages of vertebrates in general. Present findings lend credulence to the suggestion of Juhn and Harris (1955) that the thyroid hormone influences feather development by its local effects on the feather follicles. Since the two major developmental events, viz., cellular proliferation and differentiation, are not mutually exclusive in developing systems like feathers (Cameron and Jetter, 1971) but overlap to a large extent, a

number of metabolic pathways operate simultaneously in the feather forming tissues during feather development and growth, supporting differentiation and/or growth (Menon, 1974). Hence, activities of key enzymes when altered by endocrine factors could be expected to bring about changes in the histomorphological profile as well as in the time span needed for development of these cutaneous appendages. A direct correlation between retardation of feather restoration and decreased activities of the enzymes studied (except acid phosphatase and LDH) becomes quite obvious, when viewed in the light of their known involvements in the metabolic events underlying feather development. Alkaline phosphatase shown to be essential for proper differentiation of down feathers (Hamilton, 1965) plays a multifarious role during development and regeneration of definitive feathers (Shah and Menon, 1974). In general, this enzyme is known to accumulate in tissues prior to functional differentiation (Moog, 1965). It is also known to aid in proliferative activities of the epithelial cells of the feathers. The quiescent feather papillae too exhibit activity of this enzyme, and these are the only components of pigeon skin that show the enzyme reactivity during non-moulting period. Voitkevich (1966) views this enzyme as an 'activator' substance; Shah and Menon (1974) have noticed characteristic fluctuations in its activity directly related to the histomorphological events of feather development. Moog (1965) has suggested that this enzyme is an inducible one. This contention is

strengthened by the present findings in that the functional athyreosis adversely affects the activity of alkaline phosphatase in the skin, and replacement therapy restores the enzyme reactivity to normalcy. Taking all these facts into account, the significance of alterations in the enzyme reactivity noted presently in the retardation of feather development in athyroidic birds becomes self explanatory.

Glucose-6-phosphate dehydrogenase is an indicator of the operation of hexose monophosphate pathway, a metabolic route acknowledged to be of prime significance for developing systems (Papaconstantinou, 1967). Activity of this enzyme is also the controlling site of the pathway (Anstall and Trujillo, 1967). The implication of declined reactivity of G-6-PDH in retardation of feather development under functional athyreosis can be readily appreciated when the role of G-6-PDH in regulation of various developmental events is considered. Shah and Menon (1976) implicated the activity of G-6-PDH in metabolic regulation underlying cell proliferation and differentiation in pigeon contour feathers during their development. Recently, a temporal relation between G-6-PDH activity and DNA synthesis has been demonstrated by Coulton (1977) and a direct stimulatory effect of thyroid hormone on cell proliferation has been proposed by Bommer et al., (1977). Present observations on restoration to normalcy in the pattern of feather development, as well as G-6-PDH activity in the

feather forming tissues following replacement therapy underscore the fact that alterations in the operation of hexose monophosphate pathway forms part of the regulatory mechanisms of plumage development influenced by thyroid principles. In the feather forming tissues, activities of SDH and MDH (indicators of operation of oxidative metabolism in tissues in general), are also adversely affected under functional athyreosis. Oxidative metabolism is highly significant from the energetic point of view, in ensuring normal developmental processes of definitive feathers (Shah and Menon,1974). It is also well known that anaerobic processes cannot support continued development. The normalization of activities of these enzymes as well as those of the sequential events in plumage replacement following replacement therapy in functionally athyroidic birds further reveal that the growth regulating effects of thyroid on the developing systems are through modulation of metabolic pathways that are crucial in ensuring continued and proper development. Results of a similar histochemical study conducted on the enzyme complements of rat sciatic nerves under hypothyroidic condition as well as replacement therapy by Amenta and Cavallotti (1977) also show that activities of a number of dehydrogenases are adversely affected by thyroxine deprivation and that they could be returned to normalcy by replacement therapy. In this light it is interesting to note that though feather development was retarded in the

functionally athyroidic group of birds, activities of Acid phosphatase and LDH did not get altered noticeably under the three experimental conditions. Acid phosphatase is known to be a constitutive enzyme unlike Alkaline phosphatase which is inducible and readily influenced by hormonal factors (Moog, 1965). LDH being an enzyme concerned with anaerobic metabolism is not probably influenced by thyroid principles which have a considerable control over the oxidative processes of tissues. Though much caution should be exercised in interpreting the pattern of activity of these two enzymes in the feather forming system under the present experimental regimes, it is tempting to view it, as an instance of the organism's adaptive devices to ultimately overcome the restrictions placed on the discharge of normal functions by the control measures such as endocrine factors. Thus we find that despite the absence of thyroid hormones restoration of plumage occurs, though with a considerable delay. The metabolic pattern of feathers developing under such conditions could be anaerobic, which explains the delay in plumage restoration. However, acid phosphatase activity in athyroidic birds, which remains unaltered, could be visualised as assisting in the developmental activities, though relatively in a less effective way as compared to what is done by alkaline phosphatase in the normal condition.