

CHAPTER 11

GENERAL CONSIDERATIONS

The physiology of bird migration is a subject in which much remains unexplored. What little we know about the magnitudes of physiological changes that take place in a migratory bird is not sufficient enough to make clear the complex nature of such processes. While we know something about the major changes that are seen in a migratory bird, such as enormous deposition of fat prior to migration, the effect of environmental factors on the neuroendocrine system and gonadal development, an integrated picture of the various physiological changes and the mechanisms by which such changes are brought about has not yet emerged. The journey between the breeding grounds and wintering areas^a necessitates a sufficient store of fuel and many of the physiological adjustments in the premigratory bird are geared to ensure the synthesis and storage of large amounts of fat for muscular fuel. But the migratory bird is faced with many other challenges too, during the course of migration, such as adverse climatic conditions and ecological barriers. Their success in completing the journey facing all such detrimental forces is a complement to the co-ordinated physiological processes that equip the animal to confront such conditions.

It is obvious that the physiological mechanisms are controlled by the neuroendocrine system. Hence a knowledge of the changes in the activities of various endocrine glands of

these birds in connection with the migratory preparations, is essential to correlate all the physiological changes. The studies by Dr.J.C.George and his colleagues on the Rosy Pastor have thrown light on the neuroendocrine mechanisms and some physiological manifestations in these birds during the premigratory period.

It is interesting to note that the pituitary, which could control all other glands exhibited higher capacity to produce various hormones as the number of different types of cells which are the sites of production of different hormones was found to increase, synchronized with the time they prepare for the migration (Naik and George,1965). Therefore an increased secretion of ACTH, LTP (prolactin), FSH, TSH etc., can be expected in this period. Increased hyperplasia and colloidal release in the thyroid gland (George and Naik,1964a), hyperactivity of adrenal gland (Naik and George,1965), increased number of insulin producing islet cells in the pancreas (George and Naik,1964b) and gonadal development (Naik and George,1964) were also noted in the premigratory period. Combined with the release of neurosecretory materials from the hypothalamus (George and Naik,1965) the different hormones from the various glands bring about essential changes in the physiological apparatus of the body, thus preparing the birds for migration and finally trigger the migration itself.

Some of the various physiological changes in the Rosy Pastor during the premigratory period are also known. Increased

deposition of fat in the liver (Naik,1963) and of fat and glycogen in the muscle (Vallyathan,1963; Vallyathan and George, 1964) were found to take place in these periods. Information regarding changes in the concentration of certain amino acids in the brain which are precursors of neurosecretory materials, changes in the amount of cholesterol in the liver, and ascorbic acid content of the adrenal gland are also available (John,1967). The present investigations have revealed that fat is synthesized de novo in the liver as well as in the adipose tissue during the day time and that the rate of synthesis is controlled by the amounts of glucose available (Chapter 1). It has also been shown that certain changes in the ionic concentrations provide the necessary background or stimuli for increased fat synthesis (Chapter 2&3). A decreased phospholipid content in the liver was observed during the premigratory period (Chapter 3). The Rosy Pastor stores a large quantity of iron in the liver which was found to be mobilized during the premigratory period, while the iron content of the muscle slightly increased (Chapter 4). Elevated number of precursor cells in the bone marrow and increased red blood cell count and haemoglobin level in the blood showed an increased erythropoiesis during this period (Chapter 5). Lymphocytes were produced in large numbers in the liver as well as in spleen along with an increased fat deposition in liver and adipose tissue (Chapter 6). The liver ascorbic acid level was found to rise towards April (Chapter 7). Tyrosine level in blood which could be taken as an index of thyroid activity was found to increase

and at the same time oxygen consumption of the muscles also increased (Chapter 8). Both the cholinesterases (specific and non-specific) were found to be very active in the premigratory period with a diurnal rhythm for peak activity of AChE (Chapter 9). The pectoral muscle of Rosy Pastor, in an evolutionary stand point, is found to be far advanced than that of akin species that are non-migratory (Chapter 10). The capacity of the muscles to oxidize fatty acids was found to diminish in the premigratory period (George and Vallyathan, 1964). A slightly reduced lipase activity (Vallyathan, 1963), increased phosphorylase activity (Vallyathan and George, 1964) and diurnal and seasonal variations in the activities of lipase and SDH in the various particulate fractions of the muscle (George and Vallyathan, 1964) were also noticed in the premigratory period.

In the light of the above studies it would be interesting to make an attempt to correlate the observed physiological changes with the activities of various endocrine glands during premigratory period and to digress on the cause-effect relationship among the various physiological changes.

Since, the liver has the most important role in any adjustments or adaptations with regard to metabolic processes, most of the endocrine secretions should be expected to exert their primary influence on the liver (Fig.1). When dealing with the metabolic activities of a migratory bird the first to attract our attention is that concerned with the synthesis of

fat. Many hormones are known to stimulate increased fat synthesis in the liver. But how they bring about this ~~is~~ still remains obscure. The liver has all the necessary set up in its component cells for lipogenesis. Prior to migration there must be some basic adjustments in the liver which would facilitate not only an increased production of fat, but also a diminished breakdown of fat. Bleicher et al. (1966) suggested that Na^+/K^+ flux could influence the metabolism of fat to take anabolic or katabolic directions. In the present study, the muscle and kidney showed an outflux of K^+ and an influx of Na^+ and the liver an outflux of K^+ . This may be attributed to the influence of adrenocortical hormones. Nejad and Chaikoff (1964) found that the adrenocortical hormones increased the synthesis of fat in the liver of rats. Thus it can be suggested that enhanced fat synthesis may take place when certain specific ionic or osmotic changes occur which itself is under the influence of certain hormones. Increased fat retaining (storing) capacity of the liver could also be like wise under the hormonal control. Anterior pituitary extracts causes ^{an} increased accumulation of fat in the liver (Levin and Farber, 1952). This could be similar to the fatty infiltration caused by CCl_4 . The CCl_4 reduced the osmotic pressure (Popper and Schaffner, 1957) and decreases the potassium content (Kume, 1962). Putting these observations together it could be assumed that CCl_4 by reducing ionic concentration which in turn reduces the water content also, brings the osmotic pressure to a low level. This must be

the reason for the accumulation of fat when CCl_4 is administered, since the sites vacated by water are normally filled up by fat (Adolf, 1947). Hence the influence of certain anterior pituitary hormones and adrenocortical hormones may be the cause of increased synthesis and storage of fat in the liver. Some what similar processes might influence the adipose tissue to increase its fat producing activity.

However, though some hormones help bring about the necessary changes in the liver preparing it for ^{an} elevated lipogenesis, the actual rate of synthesis of fat depends upon the availability of glucose. A higher amount of glucose in the pre-migratory period is ensured by the change of diet (fruits). This change may be effected by the hypothalamic 'feeding centre' which is under the direct control of environmental conditions (Farner, 1965). Increased uptake of carbohydrates by the intestine is influenced by thyroxine (Holliday et al., 1962). Since an increased number of islet cells were seen in the pancreas at this period (George and Naik, 1964) an increased output of insulin could also be expected. The insulin therefore should help in bringing about an increased concentration of glucose in the liver and in the adipose tissue. When these tissues are confronted with such heavy load of glucose, adaptive hyperlipogenesis sets in as suggested by Tepperman and Tepperman (1965a). The concentration of glucose should be highest in the day time when the birds ingest a lot of carbohydrate food. Since the amount of fat in the liver was found to be highest in the evening than

in the morning, it could be concluded that the synthesis of fat occurs in the day time when an elevated level of glucose is available. The synthesis of fat is obviously not at the expense of glycogen since glycogen depletion during night was not accompanied by a rise in the amount of fat in the liver. Thus, the adaptive hyperlipogenesis is to be conceived as a combined effect of so many factors.

Enhanced lipogenesis requires a good supply of NADPH_2 . It is known that thyroxine perhaps in a certain concentration can activate the HMP- shunt dehydrogenases as well as malic enzyme, which in turn produce enough NADPH_2 (Tepperman and Tepperman, 1964). Increased carbohydrate intake also elevates the activities of these enzymes (Willmer and Foster, 1962). The major part of the amount of glucose then may break-down via direct oxidative pathway while most of the other part may take the Embden-Meyerhof pathway and only the rest may be utilized for glycogen synthesis. This naturally reduces the glycogen level in the liver during the period when active lipogenesis occurs (first and second week of April). But, by the last weeks of April, the amount of glycogen was found to increase which should indicate that in this period more glucose is available for conversion to glycogen. This is either due to the inability of the liver to cope up with the ⁿconversion to fat of the overwhelming supply of glucose or due to the suspension of fatty acid synthesis.

A study of the diurnal variations in the fat content

of the liver revealed that a certain amount of fat is always removed from the liver during the resting period (night). This fat is certainly transported to the peripheral tissues, mostly to the depot. Though this transported fat is in triglyceride form, usually a protein molecule is added from the liver or it may get bound with plasma proteins to form lipoproteins. The lipoproteins reaching the capillaries of the adipose tissue is acted upon by lipoprotein lipase to release fatty acids which then enter the adipose tissue and get converted to fat again (Ball and Jungas, 1964). Such lipotropic affects, shown by choline, methionine etc., prevent the excessive accumulation of fat in the liver. The choline, being essential to form lipoproteins, can be made available by releasing choline from its bound form (esters of choline). The increased activities of cholinesterases, especially that of non-specific ChE can be then accounted for. When choline and similar substances are increasingly utilized to produce lipoproteins the synthesis of phospholipids may suffer. This might be the reason for the reduced level of phospholipids during the premigratory period (Chapter 3).

The increased mobilization of fat from adipose tissue during migration is also under the influence of hormones. Sympathetic nerve stimulation is also effective in mobilizing fat. Catecholamines, thyroxine (in high concentration), thyrotropin, glucagon etc. are all fat mobilizing agents. Release of greater amounts of free fatty acids from adipose tissue naturally causes an inhibition of glycolysis and fatty acid synthesis and

thus the tissues are persuaded to utilize fatty acids for energy purposes. This switch over to fat catabolism and the elevation of QO_2 by thyroxine necessitates a high requirement of oxygen by various tissues. Burning of fat fuel also means an active Krebs cycle pathway. The increased amount of ascorbic acid can maintain the tempo of the enzymes in the Krebs cycle (Banerjee, et al., 1959).

The increased demand of oxygen is effectively met by these birds by producing more erythrocytes in the marrow during the premigratory period. This means additional synthesis of haemoglobin too. The liver of Rosy Pastor stores a large amount of iron in comparison with that of non-migratory birds (in the Rosy Pastor a maximum of 82 mg/100g fresh tissue was noted in February while the liver of Brahminy Myna contained only 35.4 mg per 100 g fresh tissue in any season). This stored iron is released in the premigratory period as noted in chapter 4, evidently to facilitate increased haemoglobin synthesis. The process of release of iron from haemosiderin or transferrin is greatly assisted by the ascorbic acid in the liver. It may be noted that thyroxine which is released in the premigratory period is also known to elevate erythropoiesis (Fisher and Cook, 1962; Waldman et al., 1962).

Evidently, for increased erythrocyte production more stem cells are required. Perhaps the lymphocytes that are abundantly produced in the liver as well as in the spleen during the premigratory period are transformed to stem cells in the bone



marrow. As the lymphocytes are known to undergo transformation into fat cells (Wasserman, 1926; Chang, 1940) and mast cells (Michels, 1938; Asboe-Hansen, 1954; Csaba et al., 1960), the elevated production of lymphocytes can also contribute to the production of fat and mast cells.

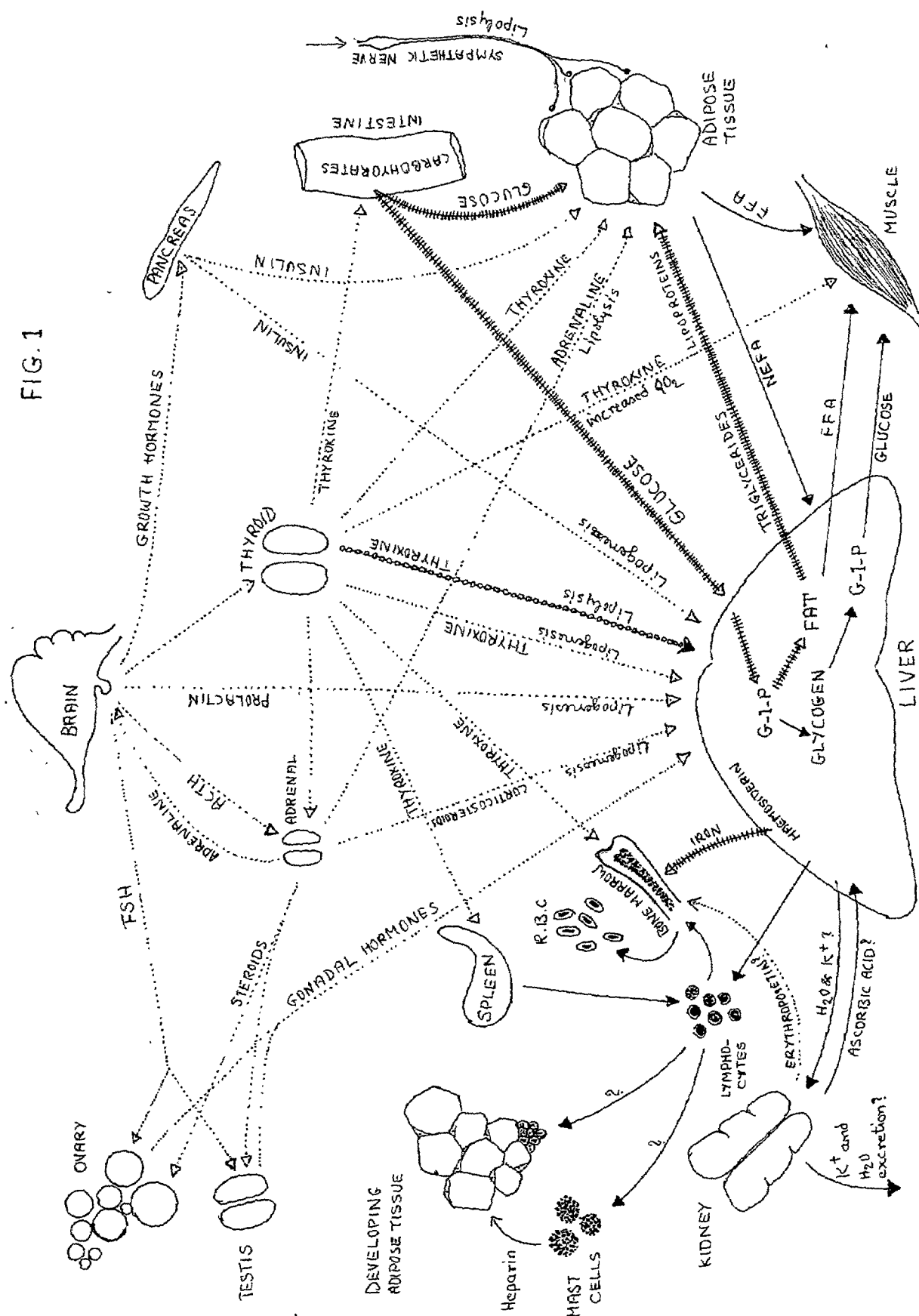
Certain physiological changes in the muscle tissue of Rosy Pastor have ^{been} noted during the premigratory period. During this period the capacity of fatty acid oxidation of the breast muscles was found to decrease which in turn reduces the utilization of fat (George and Vallyathan, 1964). Oxygen uptake of the muscle has also been shown to increase during this period (Chapter 8). This increased requirement of oxygen is effectively met not only by increasing the number of erythrocytes, haemoglobin level and the vascularization of the muscles, but also by elevating the capacity of muscles to take up and utilize more oxygen. This is brought about by providing muscles with more myoglobin, cytochromes, SDH and other iron containing compounds and enzymes. The efficiency of pectoral muscles of Rosy Pastor for long distance flight utilizing fat for fuel is greater than that of non-migratory ones. Apart from the above mentioned adaptations it may also be noted that the fibre distribution in the pectoralis exhibits an evolutionary advance (Chapter 10). The white fibres are reduced in number and size and are grouped more to the superficial parts. This gives more freedom and force to the red fibres to contract as interference from the slowly contracting white fibres are minimized. The distribution

Fig.1. Diagrammatic representation of hormonal, metabolic and physiological interplay of events that have great influence on the functions of the liver during premigratory period.

-> stimulation or influence of hormones
- oooooooooooooooo> High amount of hormone.
- ++++++++++++> Highly active pathway or transport of
very high amount of substance.

.- Not established suggestions.

FIG. 1



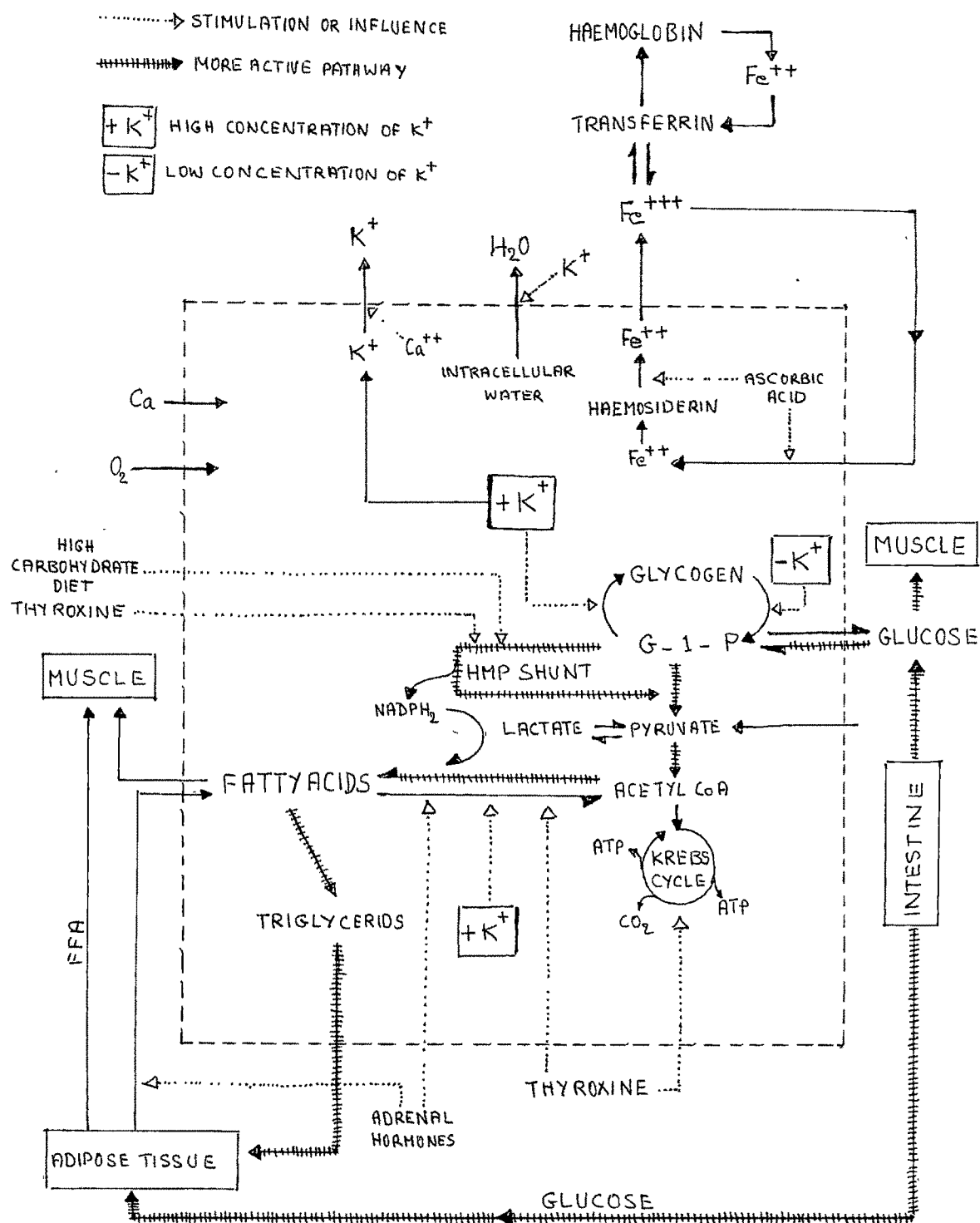


FIG.2. SCHEMATIC DIAGRAHM OF MAJOR REACTIONS IN THE LIVER DURING PREMIGRATORY PREPARATIONS OF ROSY PASTOR AND FACTORS THAT INFLUENCE THEM

of the red fibres in the deeper part may also ensure a good supply of oxygen and nutrients.

The above discussion on the physiological adaptations of the migratory bird is based on several observations made on the Rosy Pastor. Since, the metabolic pathways and factors regarding synthesis of various metabolites are more or less universal, an attempt has been made here to piece together the various observations and present an integrated picture of the physiological processes in this migratory bird. A schematic representation of the various phenomena and their interrelationships discussed above, is presented in Figures 1 and 2. Perhaps many of the conclusions are rather speculative. Speculation in a way is good since it calls forth more research to prove or disprove it.

It is indeed necessary to mention that the studies presented in this thesis are rather preliminary and more readily stress the fact that only with further experiments and observations the complex nature of the physiological processes in the migratory bird could be unravelled.