Chapter 8

INCUBATION PATCH FORMATION IN HOUSE SPARROW, *PASSER DOMESTICUS* : DISTRIBUTION PATTERN OF LACTATE, SUCCINATE AND MALATE DEHYDROGENASES

Anaerobic glycolysis has been recognized as the major pattern of metabolism in the avian integument (Shah and Menon, 1974b). Significance of LDH as a regulatory enzyme of EMP pathway of glycolysis (Racker, 1965; Nelson and Wakefield, 1973) is apparent from the fact that during the reaction, catalised by LDH, reduced Nicotinamide Adenine Dinucleotide (NADH) is oxidised and NAD (an essential co-factor needed for the continued operation of the EMP pathway) is regenerated. Variations in the activity of this enzyme have been well investigated in developing systems like, chick liver (Conklin, 1965), hatching muscle of chick (Klicka and Kaspar, 1970), mammalian tooth (Fullmer, 1963), kidney (Smith and Kissane, 1963), cerebral cortex (Flexner *et al.*, 1960), regenerating amphibian limb (Schmidt, 1968), lacertilian tail regeneration (Shah and Ramchandran, 1970; Magon, 1970), feather development in pigeon (Shah and Menon, 1974b) and during general development and organogenesis in amphibians (Adams and Finnegan, 1965).

Significance of the operation of Tricarboxylic Acid Cycle (TCA Cycle), during organogenesis of vertebrate cutaneous

appendages is also well recognised (Montagna, 1962; Shah and Menon 1973; Adachi and Uno, 1968). Histochemically demonstrated activities of succinate and malate dehydrogenases (SDH and MDH) are considered to be indicators of the operation of this metabolic pathway. The role of SDH in normal metabolic processes in epithelial tissues, like corneal epithelium (Ehlers, 1970) and in integumentory system (Montagna and Formissano,1955; Michael, 1965; Sasai, 1974) has been well documented. Apart from this role its importance in the development of chick down feather (Koning and Hamilton, 1964), mammalian tooth (Fullmer, 1963), regenerating urodele limb (Schmidt, 1968) and lacertilian tail regeneration (Shah and Chakko, 1969; Shah and Ramchandran, 1976) and Pigeon definitive feathers during post-hatching, induced and regenerative modes of development (Shah and Menon, 1973) has been reported. Studies on distribution pattern and activity of MDH have been carried out in developing chick liver (Solomon, 1959; Greenfield and Boell, 1970), hatching muscle of chick (Klicka and Kaspar, 1970), developing sea urchin embryos (Gustafson, 1954; Billier et al., 1966), mammalian tooth (Fullmer, 1963), regenerating urodele limb (Schmidt, 1968) and lacertilian tail (Shah and Ramchandran, 1970) and pigeon definitive feather (Shah and Menon, 1973). The present investigations were undertaken with a view to evaluate relative significance of the two metabolic pathways viz., anaerobic glycolysis and operation of TCA cycle in the metabolic processes associated with different aspects of development,

EXPLANATION FOR FIGURES

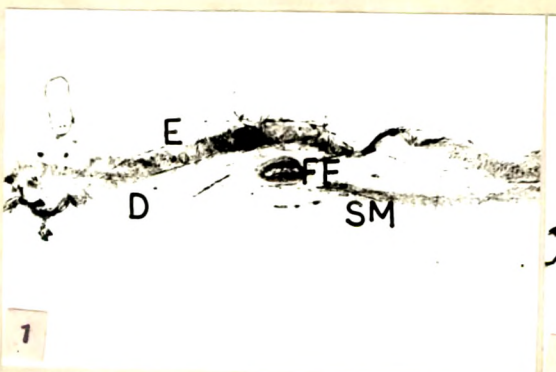
Figs. 1 to 4 : Photomicrographs of V.S. of Ventral skin, showing histochemical distribution pattern of LDH activity in various phases of incugation patch formation in female House Sparrow. All 76 X.

Fig.1 Non-breeding phase.

Fig.2 Nest building phase.

Fig.3 Fully formed patch.

Fig.4. Regressing phase.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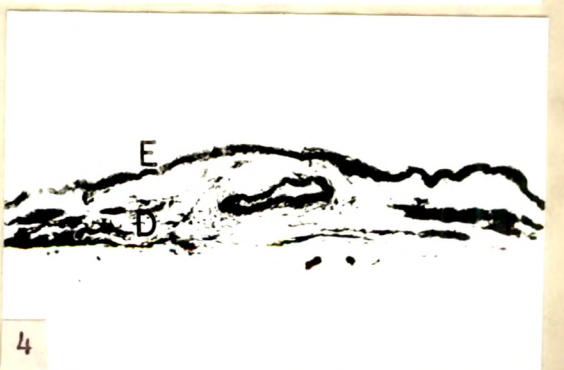
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maintenance and regression of the incubation patch in the House Sparrow, Passer domesticus where suppression of feather development occurs in the patch during its functional state. For this, histochemical studies on LDH, MDH and SDH in the incubation patch of the house sparrow have been conducted.

OBSERVATIONS

Non-Breeding Phase : (Figs. 1, 5, and 10)

The ventral skin (prospective incubation patch area) is well covered with feathers and has all histological characteristics typical of avian integument. General pattern of localization and distribution of the three enzymes viz., LDH, SDH and MDH, in the ventral skin of the House Sparrow are almost identical. However, the intensity of SDH and MDH is found to be more as compared to that of LDH. Of the component parts of the skin, highest concentration of all the three enzymes was noted in the feather germs. Structural elements of the dermis showed a relatively low reactivity for the enzymes while, the epidermis depicted an intermediate level for all three enzymes.

Nest Building Phase (Figs. 2, 6 and 11)

During this phase intensity of reactivity of all the three enzymes gradually increased in the interplumar epidermis as well as the dermis in general. However, the feather germs maintained the same level of the enzymes' concentration as was noted in the non-breeding phase.

EXPLANATION FOR FIGURES

Figs. 5 to 9 : Photomicrographs of V.S. of ventral skin, showing histochemical distribution pattern of SDH activity in various phases of incubation patch formation in female house sparrow. All 76 X.

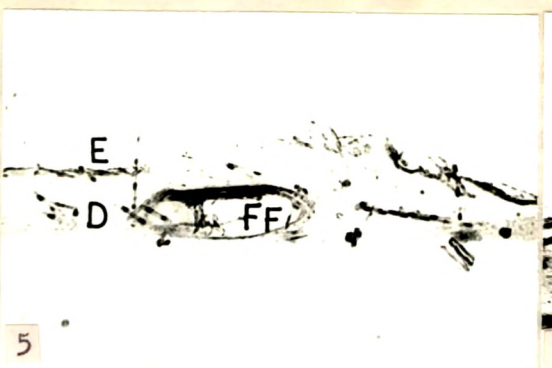
Fig.5 Non-breeding phase

Fig.6 Nest building phase

Fig.7 Defeathered and vascularized phase.

Fig.8 Fully formed patch.

Fig.9 Refeathering phase.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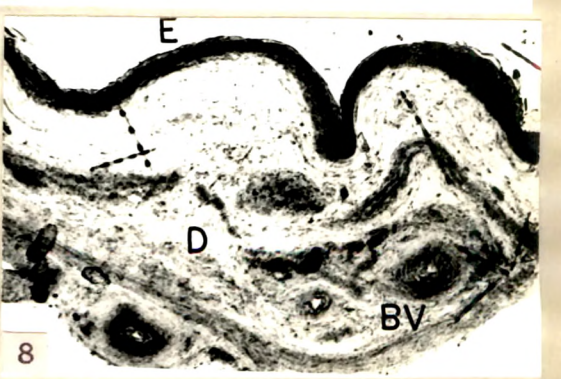
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Defeathering Phase

With the onset of defeathering, there was a general decline in the reactivities of all the three enzymes in the component parts of the skin. However, the decline was more noticeable in the feather germs.

Defeathered and Vascularized Phase (Figs. 7 and 12)

Once the defeathering of the skin is complete and high vascularization of the dermis has been established, the enzymes viz., LDH, SDH and MDH showed increased reactivities in all the component parts of the skin except the feather germs. Of the TCA cycle enzymes studies viz., SDH and MDH, the activity of the former was relatively lower than the latter.

Fully Formed Incubation Patch (Figs. 3, 8 and 13)

With the formation of the incubation patch as marked by the establishment of an edematous condition as well as further vascularization, all the three enzymes registered their high peak level of activity in all the components of the patch skin excepting for the feather germs (dormant) in which the enzyme activities remained very low. During this phase too, SDH concentration was relatively lower than that of the other two enzymes viz., MDH and LDH.

Regressing Phase : (Figs. 4 and 14).

Once the functional role of the patch is over, its regression commences; the edema, its high vascularity and hyperplastic state of the epidermis and dermis gradually

EXPLANATION FOR FIGURES

Figs.10 to 15 : Photomicrographs of V.S. of ventral skin, showing histochemical distribution pattern of MDH activity in various phases of incubation patch formation in female House Sparrow. All 76 X.

Fig. 10 Non-breeding phase

Fig.11 Nest building phase

Fig.12 Defeathered and vascularized phase.

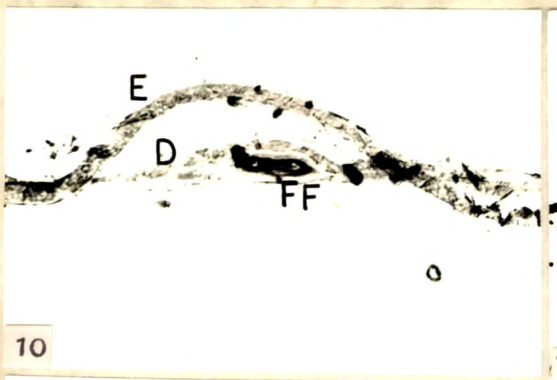
Fig.13 Fully formed patch.

Fig.14 Regressing phase.

Fig.15 Refeathering phase.

ABBREVIATIONS

BV- Blood Vessels, D- Dermis, DF- Down feather; E- Epidermis; FF- Feather follicle; FG- Feather germ, FP- Feather popillae; FW- Follicular wall; SG- Stratum germination, SM- Smooth muscles.



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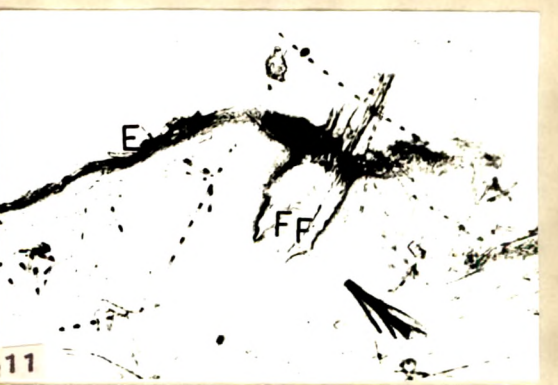

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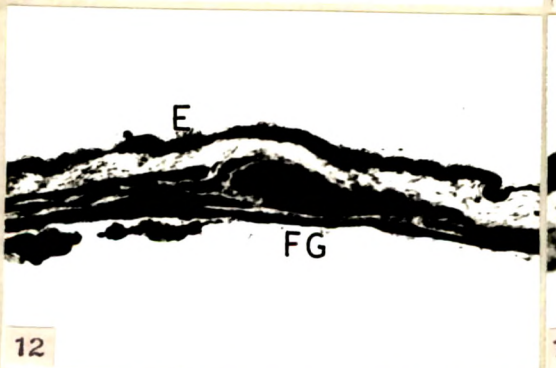

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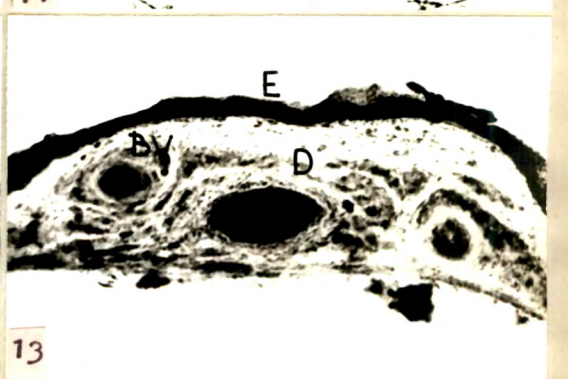

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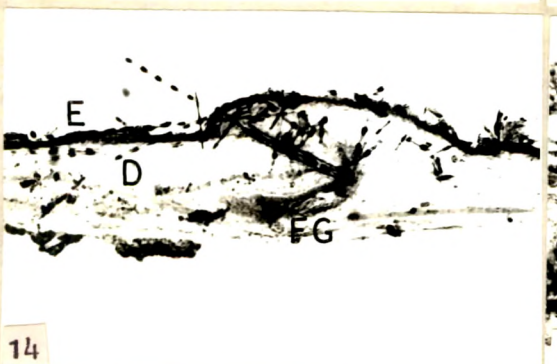

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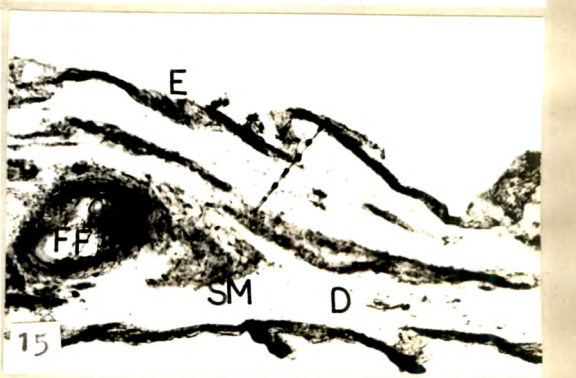

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reduce and return to the state of the skin originally present in non-breeding conditions. During the regressing period, the structural components of the patch skin presented a metabolic picture, where LDH, MDH and SDH showed a general decline in their reactivities. Nevertheless, the feather germs, epidermis and the walls of the blood vessels presented a picture wherein the activities of the three enzymes were higher than those seen in the other component structures of the patch skin. Of the three enzymes, relatively speaking, MDH reactivity was considerably lower than that of LDH and SDH.

Refeathering Phase : (Figs. 9 and 15)

With the total regression of incubation patch, refeathering of the patch skin commences. During the refeathering phase, there is a spurt in the reactivity of all the three enzymes in the feather germs whereas, in the other component structures of the skin they showed a gradual acquisition of the normal conditions (i.e. returning to the state of enzyme concentration as was seen during the normal feathered state of the skin during non-breeding period.) Finally, as the feathers get fully developed, the feather germs also attain normal characteristic (non-breeding state) histochemical concentrations of SDH, MDH and LDH.

DISCUSSION

High reactivity of LDH in the feather germs and most of the other components of the ventral skin of female House

Sparrow during its non-breeding phase (when incubation patch is not formed) as well as during the process of refeathering after regression of the incubation patch, suggests, that the normal skin of the bird has anaerobic glycolysis as a dominant feature in its metabolic adaptations. This suggestion finds support from the reports of work on integument of pigeon (Shah and Menon, 1974), reptiles (Shah and Ramchandran, 1972) and mammals (Adachi and Uno, 1968; Sasai, 1974) where similar metabolic pattern is known to prevail. The relatively low MDH and SDH activities in comparison to that of LDH in the integumentary components of the sparrow might be indicative that the TCA cycle operation per se is in low gear.

With the transformation of the ventral skin (during breeding period) into an incubation patch, a notable change in its metabolic pattern becomes evident. During nest building and defeathering phases of the patch formation, gradual but significant increase in SDH and MDH reactivities in the epidermis and dermis becomes discernible. Thus it appears that gradual but effective operation of the aerobic pattern of metabolism sets in, along with the existing anaerobic one. This suggests that high energy requirements of most of the skin components are being realised. It seems that, during these two phases of the incubation patch formation, metabolic reactions are being geared up in advance to meet the high demand of energy required for the active cellular proliferation

(in epidermis and dermis), and increase in capillarization (of the dermis), that are to occur during the ensuing phases of the patch formation. However, it is also equally interesting to note, that, there is a gradual decline in the reactivity of all the three enzymes (viz., LDH, SDH and MDH) in the feather germs of the transforming incubation patch skin. Here it should be recalled that the feather germs in the patch skin gradually enter into a state of dormancy with defeathering and remain in a completely dormant state in the fully formed patch. Such functional inactivity of the feather germs is well reflected in their metabolic dormancy marked by low reactivities of LDH, SDH and MDH. It is also known that the dormant feather germs in a well formed incubation patch are indifferent to hormonal (e.g. thyroxine, see Chapter 10) or other activating agents. Thyroxine is known to have a positive influence on the activity of enzymes like SDH, G-6-PDH and alkaline phosphatase (Chapters 4,10). This insensitivity of the feather germs to thyroxine and possibly to other hormones as well, when coupled to the present observations of subnormal activities of the enzymes becomes self explanatory. Thus, the low reactivity of SDH, MDH and LDH in the dormant feather germs in a fully formed incubation patch suggests the low metabolic state justifying its probable role in the maintenance of the functional dormancy of the feather germs.

High incidence of LDH, SDH and MDH reactivities in the

epidermis and dermis (except feather germs) during the late phase of incubation patch formation as well as in the fully formed state, is considered as indicative of increased energy production related to highly active cellular proliferation in all the components (of course, except the feather germs) of the patch skin.

Active metabolic state of the fully formed incubation patch skin is well justified, when correlated with the fact that such a state would generate considerable amount of heat which is quite essential for the incubation of eggs as well as keeping the nestlings warm during their early nesting period.

During regression of the incubation patch, reduction in vascularization, cessation of cellular proliferation, casting off of epidermal cells from the highly stratified epidermis, and loss of edematous condition occur. Under these conditions it is obvious that the energy requirement of the concerned tissues gets reduced. Such a state of metabolic activity is evident from the declining reactivities of LDH, SDH and MDH. It is necessary to recall here that in a fully formed incubation patch, excepting for feather germs which were functionally dormant and had the lowest level of enzyme reactivities, all other components exhibited peak level of activity of all the three enzymes. But as regression of the patch progresses these enzymes again become gradually active in the feather germs.

Finally, with complete regression of the incubation patch

refeathering of the bare areas commences. The feather development from hitherto dormant but now activated feather germs can be well correlated with the presently observed increasing activities of the LDH and TCA cycle enzymes (viz., SDH and MDH) during this phase. The findings can be well supported by the reports of Shah and Menon (1973) and Menon (1974) where they have shown that concentration of these enzymes increases during the development of feathers in pigeon. Similarly, it is known that during hair development also, TCA cycle enzymes are quite active (Montagna and Formissano, 1955).