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GLYCOGEN METABOLISM IN A SUB-TROPICAL, SOCIAL BIRD: WHITE-HEADED JUNGLE BABBLER DURING BREEDING AND NON-BREEDING STATES

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Abstract. The energy required by different tissues, depending on their role show fluctuations in the levels of metabolites and enzymes as the bird undergoes adaptive changes during its breeding activities. Certain enzymes *viz.* Glycogen phosphorylase (GP), Glucose-6-phosphatase (G6Pase), Succinate dehydrogenase (SDH) and ATPase involved in carbohydrate metabolism and energy releasing processes along with glycogen are studied in extra-gonadal tissues. GP a catalytic enzyme in glycogenolysis increases with increased glycogenolysis. The hepatic as well as intestinal glycogen levels in the breeders is high, correspondingly the GP activity is also high in them indicating that the enzyme activity is modulated parallel to the metabolic load. In non-breeders, it shows decrease in liver and intestine but increase in kidney as is reflected by the increased GP activity. G6Pase plays an important role in glucose release from liver and kidney and in Jungle Babblers it is reflected by non-significant lower G6Pase level in breeders and helper females and accumulation of glycogen too. The progressive increase in liver glycogen with concomitant decrease in hepatic G6Pase activity. ATPase and SDH both are involved in cell metabolism wherein ATPase carries the catabolic reaction and SDH keeps up the supply of ATP molecules. The non-significantly high levels of hepatic and intestinal SDH and ATPase is seen in breeders compared to non-breeders suggest an active synthesis as well as hydrolysis of ATP for various energy costing reproductive activities. Thus, the Jungle Babbler, a social breeder, individuals of the flock share all the reproductive activities.

Key words: White-headed Jungle Babbler, *Turdoides striatus*, GP, G6Pase, SDH, ATPase.

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Метаболизм гликогена у субтропической социальной птицы: белоголовая джунглевая тимелия в гнездовой и негнездовой периоды. - Б. Баруча, Дж.С. Падате. - Беркут. 14 (2). 2005. - Изучалось содержание во внегонадальных тканях ряда ферментов, участвующих в метаболизме углеводов: гликогенфосфорилазы, глюкозо-6-фосфатазы, сукцинатдегидрогеназы и аденозинтрифосфатазы. Обнаружены различия у размножающихся и неразмножающихся птиц, что связано с разным потреблением энергии. У участвующих в размножении особей выше уровень содержания гликогена и активность гликогенфосфорилазы.

INTRODUCTION

Carbohydrate is an essential nutrient for all the animals. Glucose is the most abundant and common carbohydrate, acts as a major energy source for all cells which in turn depend on the blood stream for its steady supply. The liver plays a central role in this process by balancing the uptake and storage of glucose via glycogenesis and the release of glucose via the glycogenolysis and gluconeogenesis. The general pathways of the glycogen synthesis and glycogenolysis are identical in all tissues and the glycogen metabolizing enzymes in the liver enable it to act as a lever of blood glucose and to store and mobilize glycogen according to the peripheral needs for later metabolic use (Bollen et al., 1998). The regulation of glucose synthesis, storage, mobilization and catabolism is elaborate and sensitive to the immediate and long term energy needs of the organism.

The opposing processes of glycogen synthesis and degradation, and of glycolysis and gluconeogenesis are reciprocally regulated *i.e.* one is largely turned on while the other is largely turned off (Voet et al., 1998). Glycogenolysis require three enzymes of which one of the important one is glycogen phosphorylase (GP) which catalyses glycogen to yield glucose-1-phosphate which can be used for the production of ATP (Biorn, Graves, 2001). GP plays a strategic role in glycolytic pathway. It leads to phosphorylative degradation and utilization of glycogen and the glycogen phosphorylase levels in the tissue would apparently indicate the rate of glycolysis of the tissue.

Glucose-6-phosphatase is a crucial enzyme of glucose homeostasis since it catalyses the ultimate biochemical reaction of both glycogenolysis and gluconeogenesis (Plewka et al., 2000). It allows the gluconeogenic tissues, in which it is specifically expressed to release glucose in blood. Glucose-6-phosphatase plays an important role in the glucose release by the liver and the kidney through mechanisms involving either gene expression and/or biochemical inhibitions of its enzymatic activity (Haber et al., 1995; Minassian et al., 1996; Mithieux et al., 1996, as cited by Mithieux et al., 1998). The glucose-6-phosphate produced by glycogen breakdown continues along the glycolytic pathway in liver, and is made available to other tissues but since G-6-Pase cannot pass through the cell membrane, to yield glucose, it is first hydrolyzed by G-6-Pase. Therefore, glucose-6-phosphatase is an enzyme which generates glucose in the liver.

The increased or decreased intensity of aerobic glycolysis, TCA cycle and ATP usage could be inferred from the activities of the enzymes such as Succinate dehydrogenase (SDH) and Adenosine triphosphatase (ATPase). SDH and ATPase both are actively involved in cell metabolism, wherein SDH keeps up the supply of energy rich substrate ATP molecules for ATPase. ATPase generally carries the catabolic reactions to yield energy rich ATP. Being an important enzyme of TCA cycle, the quantitative measurement of SDH activity is one of the reliable indices of oxidative metabolism and the production of ATP molecules of any metabolically active organ.

An active synthesis of ATP and its enzymic hydrolysis is the characteristic feature of the metabolically active tissue and the ATPase is actively involved in high energy phosphate metabolism. The total activity of ATPase indicates active transport of Na^+ and K^+ ions as well as essential metabolites like glucose and amino acids in tissues and also their involvement in the energy metabolism (Patel, 1982).

As birds face tremendous stress during breeding, the energy requirement of these birds should vary and should be indicated by the variations in the enzyme activities of the tissues during different breeding states. Glycogen phosphorylase and Glucose-6-phosphatase, enzyme of citric acid cycle *viz.* SDH and adenosine triphosphatase (ATPase) along with glycogen were assayed in the three extra gonadal tissues in the breeding and non-breeding males and females and helper females of White-headed Jungle Babbler (*Turdoides striatus*), a social sub-tropical bird with long favorable breeding period.

MATERIAL AND METHODS

Normal and healthy Jungle Babblers of both the sexes were obtained from the local animal dealer from the wild in breeding and non-breeding states. They were housed in an aviary providing food and water *ad-libitum*. Before sacrificing they were weighed and specific parts of liver, kidney, and intestine (duodenum) were taken out and blotted free of blood and tissue fluids and weighed for individual quantitative biochemical estimation of glycogen and the above mentioned enzymes.

(1) Glycogen: Different dilutions were taken for the estimation of glycogen by the Anthrone method of Seifter et al., (1950). It expressed in mg glycogen/ 100 mg of tissue.

(2) Glycogen phosphorylase (EC: 2.4.1.1): Phosphorylase activity was assayed by a modification of the method of Cori et al., (1943) and adapted by Cahill et al., (1957). The inorganic phosphate released is measured according to the method of Fiske and Subbarow (1925). The enzyme activity was expressed as μg of phosphorous released/ mg protein/ 10 minutes.

(3) Glucose-6-phosphatase (EC: 3.1.3.9): G-6-Pase was estimated by the method described by Harper (1963). Inorganic phosphate released was measured employing the method of Fiske and Subbarow (1925). The activity

Table 1

Variations in the levels of glycogen and some metabolizing enzymes in male Jungle Babblers

Вариации уровня гликогена и некоторых метаболизирующих энзимов у самцов джунглевой тимелии

	Glycogen			Glycogen Phosphorylase			SDH			ATPase			G6Pase
	Liver	Intestine	Kidney	Liver	Intestine	Kidney	Liver	Intestine	Kidney	Liver	Intestine	Kidney	Liver
Breeding	0.122 ± 0.012	0.067 ± 0.008	0.051 ± 0.007	22.05 ± 0.70	20.16 ± 0.75	18.00* ± 0.72	5.55 ± 0.80	6.75 ± 0.90	5.05 ± 0.74	144.68 ± 0.72	138.23 ± 0.84	138.06** ± 0.63	2.25 ± 0.50
Non-Breeding	0.088 ± 0.013	0.041 ± 0.007	0.062 ± 0.007	18.09** ± 0.65	19.04 ± 0.80	19.89 ± 0.66	4.55 ± 0.70	5.83 ± 0.82	5.78 ± 0.79	140.8*** ± 0.61	136.08* ± 0.75	140.56 ± 0.73	3.10 ± 0.65

* P < .05 ** P < .005 *** P < .0005

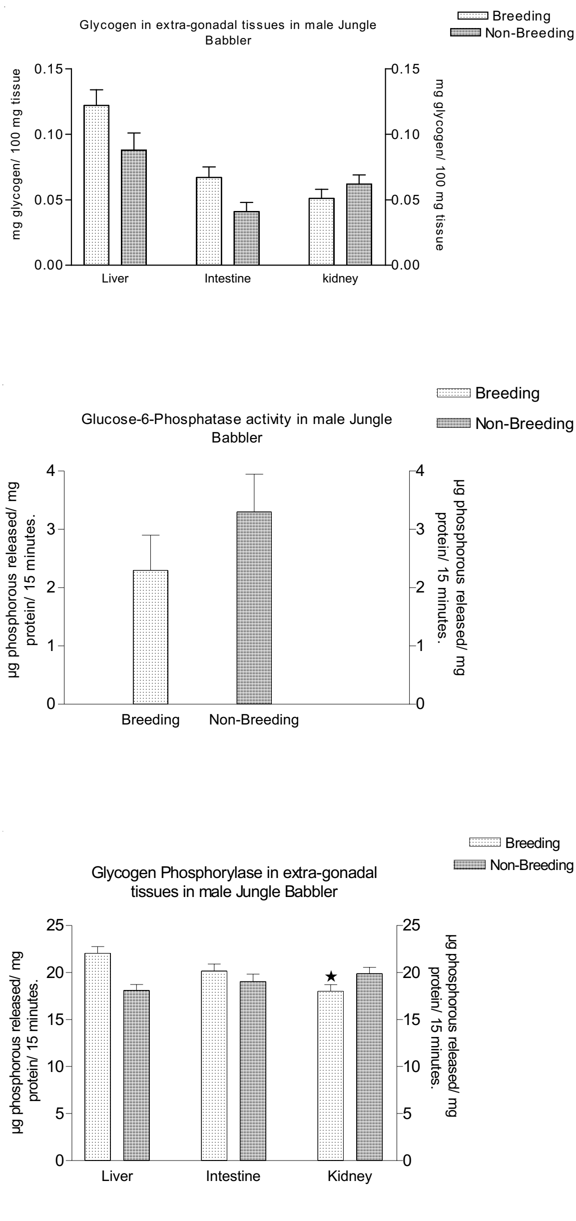


Fig. 1. Glycogen, GP, G-6-Pase levels in extra-gonadal tissues of breeding and non-breeding male Jungle Babblers.

Рис. 1. Уровни гликогена, гликогенфосфорилазы и глюкозо-6-фосфатазы во внегонадальных тканях размножающихся и неразмножающихся самцов джунглевой тимелии.

of the enzyme was expressed as µg phosphorous released/ mg protein/ 15 minutes.

(4) Succinate dehydrogenase (EC: 1.3.99.1): SDH activity was assayed by the method described by Kun and Abood (1947). The enzyme activity is expressed as µg formazon formed/ mg protein/ 20 minutes.

(5) Adenosine triphosphatase (EC: 3.6.1.3): ATPase activity was measured quantitatively adapting the method of Umbriet et al., (1957). Inorganic phosphate released was estimated according to the method of Fiske and Subbarow (1925). The enzyme activity was expressed as µg of phosphorous released/ mg protein/ 10 minutes.

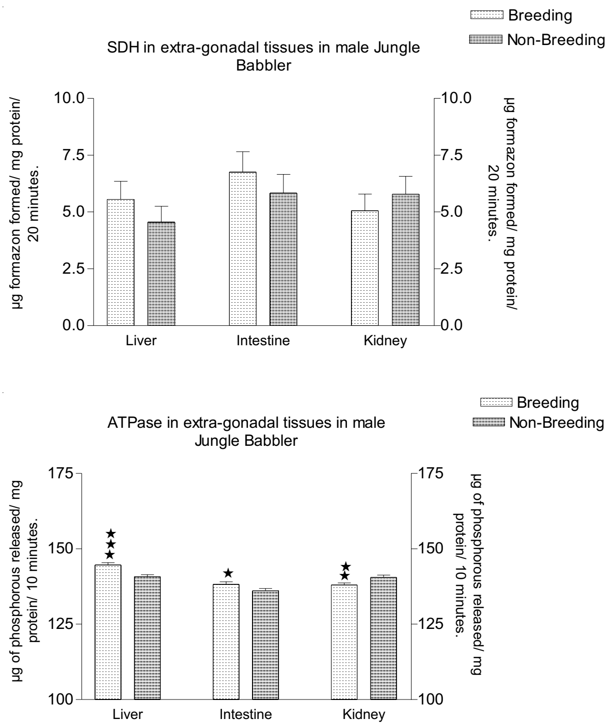


Fig. 2. SDH and ATPase levels in extra-gonadal tissues of breeding and non-breeding male Jungle Babblers.

Рис. 2. Уровни сукцинатдегидрогеназы и аденозинтрифосфатазы во внегонадальных тканях размножающихся и неразмножающихся самцов джунглевой тимелии.

RESULTS

Male Jungle Babblers

The Glycogen, Glycogen phosphorylase (GP), Glucose-6-phosphatase (G-6-Pase), Succinate dehydrogenase (SDH) and Adenosine triphosphatase (ATPase) for male Jungle Babbler are given in Table 1, Figures 1 and 2.

Glycogen: Among the three tissues studied after the liver, intestine had the higher glycogen content followed by the kidney in the breeding males whereas among the non-breeding males kidney had higher glycogen content than the intestine. The mean hepatic glycogen level in breeding males was 0.122 ± 0.012 (mg glycogen/100 mg tissue wt) which decreased non-significantly in the non-breeding males to 0.088 ± 0.013 mg. The glycogen content in the intestine of the breeding males was at 0.067 ± 0.008 mg which also decreased non-significantly in non-breeding males to 0.041 ± 0.007 mg, whereas in kidney it was low at 0.051 ± 0.007 mg in breeding birds which increased non-significantly in the non-breeding males to 0.062 ± 0.007 mg.

Glycogen phosphorylase (GP): The hepatic GP in breeding males was significantly higher at 22.05 ± 0.70 (µg of phosphorous released/ mg protein/ 10 minutes) while in the non-breeding males it was significantly low at 18.09 ± 0.65 µg. Intestinal GP in breeding males was high at 20.16 ± 0.75 µg while in the non-breeding males it was non-significantly lower at 19.04 ± 0.80 µg whereas renal GP levels in breeding males were 18.00 ± 0.72µg and significantly high in the non-breeding males at 19.89 ± 0.66 µg.

Glucose-6-phosphatase (G-6-Pase): As G6Pase is mainly present in liver, hence, it was estimated only in the liver. The hepatic G-6-Pase was significantly lower in the breeding

Table 2

Variations in the levels of glycogen and some metabolizing enzymes in female Jungle Babblers

Вариации уровня гликогена и некоторых метаболизирующих энзимов у самок джунглевой тимелии

	Glycogen			Glycogen Phosphorylase			SDH			ATPase			G6Pase
	Liver	Intestine	Kidney	Liver	Intestine	Kidney	Liver	Intestine	Kidney	Liver	Intestine	Kidney	Liver
Breeding	0.126 ± 0.018	0.076 ± 0.012	0.056 ± 0.017	30.16 ± 0.55	28.18 ± 0.82	27.89* ± 0.70	5.75 ± 0.64	6.95 ± 0.90	5.05* ± 0.64	145.23 ± 0.81	133.69 ± 0.73	125.05 ± 0.70	2.30 ± 0.60
Non-Breeding	0.028 ± 0.008	0.041 ± 0.005	0.057 ± 0.007	27.14** ± 0.65	26.72 ± 0.74	29.89 ± 0.82	4.90 ± 0.62	5.60 ± 0.80	6.75 ± 0.68	143.31* ± 0.75	130.2** ± 0.75	126.45 ± 0.80	3.30 ± 0.70
Helper	0.156 ± 0.017	0.056 ± 0.011	0.047 ± 0.005	28.15# ± 0.67	26.79 ± 0.88	28.65 ± 0.76	4.50 ± 0.70	5.10 ± 0.70	5.23 ± 0.69	142.65# ± 0.85	130.75## ± 0.80	124.35# ± 0.82	2.50 ± 0.60

* NB/BR # BR/helper */# $P < 0.05$ **/## $P < 0.005$ ***/### $P < 0.0005$

males at 2.25 ± 0.50 (µg of phosphorous released/ mg protein/ 15 minutes) which increased to 3.1 ± 0.65 µg in the non-breeding males.

Succinate dehydrogenase (SDH): Mean hepatic SDH level in breeding males was 5.55 ± 0.80 (µg of formazan formed/ mg protein/ 30 minutes) and in non-breeding males, it was non-significantly lower at 4.55 ± 0.70 µg. Intestinal SDH levels in breeding males were also high at 6.75 ± 0.90 µg which decreased non-significantly in non-breeding males to 5.83 ± 0.82 µg whereas in kidney the SDH levels were almost maintained at 5.05 ± 0.74 µg and 5.78 ± 0.79 (µg of formazan formed/ mg protein/ 30 minutes) respectively.

Adenosine triphosphatase (ATPase): Hepatic ATPase levels in breeding males was significantly high at 144.68 ± 0.72 (µg of phosphorous released/ mg protein/ 10 minutes) compared to the non-breeding males at 140.8 ± 0.61 µg ($p<0.0005$). In intestine also ATPase was significantly higher at 138.23 ± 0.84 µg in the breeding males compared to the non-breeding males at 136.08 ± 0.75 µg ($p < 0.05$). However renal ATPase in breeding males was significantly lower ($p < 0.005$) then in the non-breeding males at 138.06 ± 0.63 µg and 140.56 ± 0.73 (µg of phosphorous released/ mg protein/ 10 minutes) respectively.

Female Jungle Babblers

The Glycogen, Glycogen phosphorylase (GP), Glucose-6-phosphatase (G-6-Pase), Succinate dehydrogenase (SDH) and Adenosine triphosphatase (ATPase) for breeding, non-breeding and helper female Jungle Babblers are given in Table 2, Figures 3 and 4.

Glycogen: The mean hepatic glycogen in breeding females was equal to that found in breeding males i.e. 0.126 ± 0.018 (mg glycogen/100 mg tissue wt) which decreased significantly in the non-breeding females to 0.028 ± 0.008 mg. The decrease was sharp in the female Jungle Babblers as compared to the male Jungle Babblers. Helper females showed non-significantly higher levels than the breeding females at 0.156 ± 0.017 mg. Intestinal glycogen in breeding females was 0.076 ± 0.012 mg which decreased non-significantly in the non-breeding females to 0.041 ± 0.005 mg while in the helper females intermediate level at 0.056 ± 0.011 mg was noted. However compared to males renal glycogen levels in females were maintained both in breeding and non-breeding females at 0.056 ± 0.017 mg and 0.057 ± 0.007 mg respectively, while the helper females had 0.047 ± 0.005.

Glycogen Phosphorylase (GP): Hepatic GP in breeding female Jungle Babblers was higher than the breeding males and significantly higher than the non-breeding females. In breeding females in liver it was 30.16 ± 0.55 (μg of phosphorous released/ mg protein/ 10 minutes) and in non-breeding females had 27.14 ± 0.65 μg, while in the helper females it was at intermediate level at 28.15 ± 0.67 μg. Intestinal GP level in breeding females was non-significantly higher at 28.18 ± 0.82 μg compared to the non-breeding females and helpers. These two later groups had equal GP content at 26.72 ± 0.74 μg and 26.79 ± 0.88 μg respectively. Breeding females had significantly low GP activity in kidney compared to the non-breeding females in which it was 27.89 ± 0.70 μg and 29.89 ± 0.82 μg respectively, while helpers showed intermediate levels at 28.65 ± 0.76 μg.

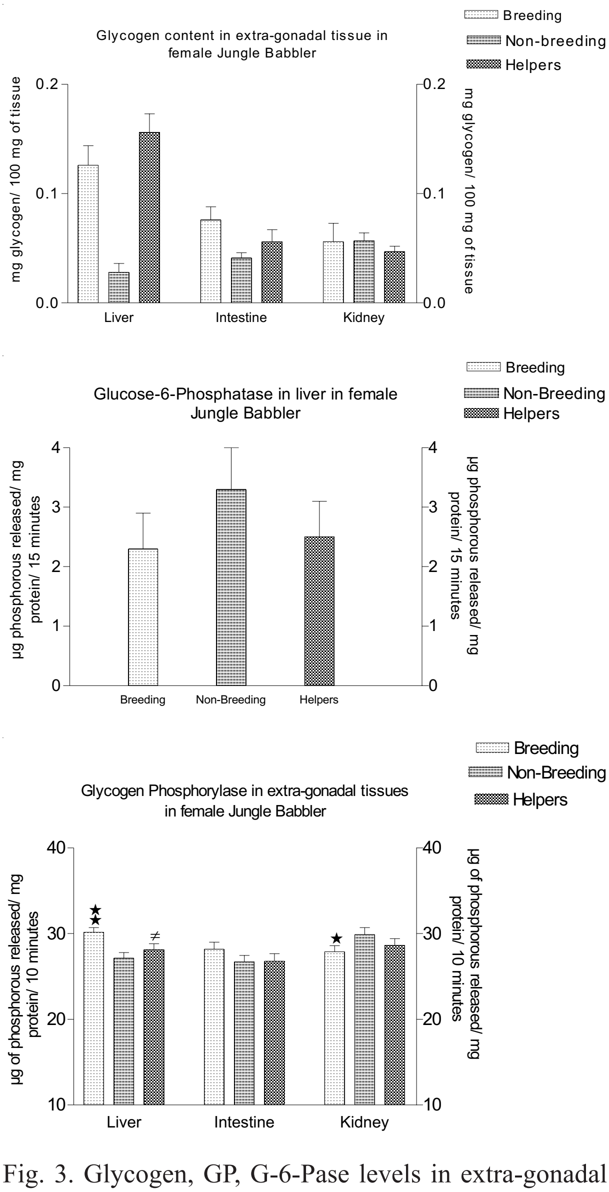
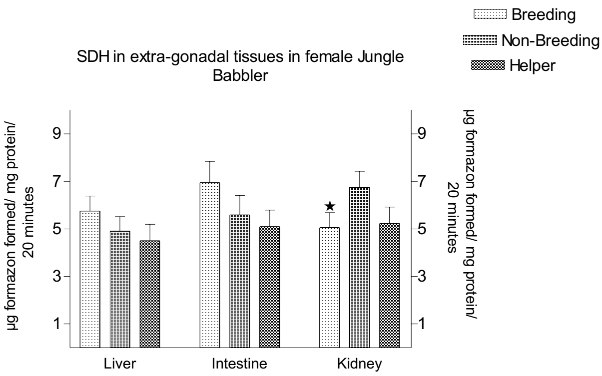


Fig. 3. Glycogen, GP, G-6-Pase levels in extra-gonadal tissues of breeding, non-breeding and helper female Jungle Babblers.

Рис. 3. Уровни гликогена, гликогенфосфорилазы и глюкозо-6-фосфатазы во внегонадальных тканях размножающихся, неразмножающихся самок и самок-помощников джунглевой тимелии.

Glucose-6-phosphatase (G-6-Pase): The hepatic G-6-Pase was significantly lower in the breeding females at 2.3 ± 0.6 (μg of phosphorous released/ mg protein/ 15 minutes) which increased non-significantly to 3.30 ± 0.70 μg in the non-breeding females while in the helper females it was almost equal to that of the breeding females at 2.5 ± 0.6 μg.

Succinate dehydrogenase (SDH): The



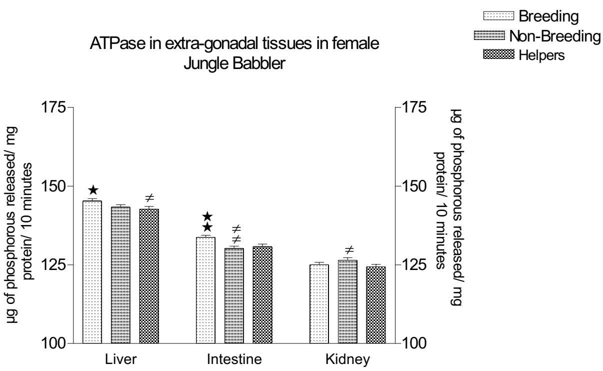


Fig. 4. SDH and ATPase levels in extra-gonadal tissues of breeding, non-breeding and helper female Jungle Babblers.
Рис. 4. Уровни сукцинатдегидрогеназы и аденозинтрифосфатазы во внегонадальных тканях размножающихся, неразмножающихся самок и самок-помощников джунглевой тимелии.

breeding females had non-significantly higher hepatic SDH at 5.75 ± 0.60 (µg of formazon formed/ mg protein/ 30 minutes) compared to the non-breeding females and helper females which had 4.90 ± 0 0.62 µg and 4.50 ± 0.70 µg respectively. Similarly intestinal SDH levels in the breeding females was non-significantly higher at 6.95 ± 0.90 µg compared to the non-breeding females and helpers at 5.6 ± 0.8 µg and 5.1 ± 0.7 µg respectively. The renal SDH levels were significantly low at 5.05 ± 0.64 µg in the breeding females which increased to 6.75 ± 0.68 µg in non-breeding females. In helper females the levels were almost equivalent to those of the breeding females at 5.23 ± 0.69 µg.

Adenosine triphosphatase (ATPase) Compared to the breeding females, in non-breeding females the hepatic ATPase levels were significantly lower at 143.31 ± 0.75 (µg of phosphorous released/ mg protein/ 10 minutes) nearly equal to the helpers at 142.65 ± 0.85 µg. The breeding females had 145.23 ± 0.81 µg ATPase in the liver. The intestinal levels of ATPase were equal and significantly lower at 130.2 ± 0.75 µg and 130.75 ± 0.80 µg respectively in non-breeding and helper females when compared to the breeding females which had 133.69 ± 0.73 µg. The renal ATPase activity in all the three females i.e. breeding, non-breeding and helpers showed nearly equal levels at 125.05 ± 0.70 µg, 126.45 ± 0.80 µg and 124.35 ± 0.82 (µg of phosphorous released/ mg protein/ 10 minutes) respectively.

DISCUSSION

Birds derive all the energy from the food they eat and to release this energy from the food, catalytic action of certain enzymes is required. The increased enzymic activities could denote a generalized increase in the body metabolism and the activity which corresponds with the different breeding activities (Patel, 1982). As shown in Tables 1 and 2, the hepatic as well as intestinal glycogen levels in breeding Jungle Babblers were high; correspondingly, the glycogen phosphorylase activity was also high in both the sexes indicating that the enzyme activity is modulated parallel to that of the metabolite load. This indicates that carbohydrates are consumed as well as degraded at equal rates. This is possibly complemented by the kidney as it shows opposite trend to that of liver and intestine. Avian kidney is extensively involved in gluconeogenic activities (Krebs, Yoshida, 1963). In Jungle Babbler it seems that carbohydrate metabolism slows down in the liver and intestine of the non-breeding birds of both the sexes and the involvement of kidney in carbohydrate metabolism increases during this time as is reflected by increase in GP activity which had maintained low profile in breeding Jungle Babblers. Kidney becomes a major gluconeogenic organ during prolonged starvation (Mehta, 1985). The non-breeding state of the Jungle Babblers coincides with the colder months of the year with shorter days and many crops like Pigeon pea are grown which are known to be heavily infested with *Helicoverpa armigera* and other insect pest. Jungle Babblers are reported to feed more on insects, rich in protein, during these months (Gaston, 1978; Dhindsa et al., 1994), hence, the carbohydrate consumption decreases influencing the kidney to become the prominent gluconeogenic organ. This is reflected in higher glycogen levels as well as higher GP in the non-breeding kidney. This needs further investigation with the variations in the enzymes like Phosphoenol pyruvate carboxykinase involved in gluconeogenic pathways. In the helper females which share the domestic duties, the energy is not utilized probably equal to that of the breeding birds as they have non-significantly higher glycogen in liver and lower GP in all the three tissues studied. Intestinal glycogen in helpers is non-significantly higher than the non-breeding females but non-significantly lower than the breeding females.

Jungle Babblers are social birds wherein the few birds called helpers forgo their breeding in order to help the breeding pair in all the reproductive activities except the egg formation and egg laying. Thus, the load of the energy expenditure is shared by all the members of the flock; therefore storage of energy is not required. This is reflected in the simultaneous absorption and breakdown of carbohydrate by intestine and storage of glycogen in the liver in these birds during breeding. Also the higher glycogen phosphorylase activity in liver and kidney of breeding birds indicates simultaneous breakdown of glycogen for energy required for various breeding activities.

The extent of glycogen accumulation is inversely related to the glucose-6-phosphatase which is a rate limiting glycogenolytic enzyme (Raheja et al., 1980). This is reflected by non-significantly lower G-6-Pase in liver of breeding and helper females which show accumulation of glycogen too. The helper females showed the intermediate levels. The progressive increase in the liver glycogen concentration is associated with a concomitant decrease in the hepatic glucose-6-phosphatase activity (Raheja et al., 1980).

According to the energy need of the body, the increased or decreased rate of Krebs cycle and the oxidative phosphorylation (for release of energy from ATP), could be inferred from the activities of the enzyme such as SDH and ATPase respectively. The high levels of hepatic and intestinal SDH and ATPase intensities observed in the breeding Jungle Babblers compared to the non-breeding birds are suggestive of an active synthesis as well as hydrolysis of ATP to provide energy in order to fulfill the increased energy demand to carry out several metabolic processes during the breeding state. Both the enzymes are active in breeding male and female Jungle Babblers. Energy released during the process is required for the synthesis of different metabolites as well as for all the physical activities carried out during reproduction. Non-significantly lower SDH and ATPase activities in all the three tissue of the helper females indicate lower energy demands compared to breeding birds. As discussed earlier these birds share almost all the activities except egg laying, hence, non-significantly lower differences. Further, no prominent differences are noted in the kidney too.

In case of Jungle Babblers which are social birds, all the energy demanding breeding activities are performed by the whole flock which consists of a breeding pair and assistants called helpers, the energy expenditure is distributed amongst the flock members and hence, storage of energy in the form of glycogen or lipids is lowest. They rely on the daily supply of food which is reflected in their foraging behavior, wherein they spend their maximum time in search of food. The degree of maintenance of the enzyme activity reflects the physiological role of these enzymes i.e. the physiological need for keeping an animal active. Generally, the enzymes involved in the energy production are preferentially maintained (Szepsi, 1976). It is evident from the present work that the biochemical changes that take place in the body of Jungle Babbler depend on the physiological requirement to obtain energy for maintaining vital functions of the body as well as for the different activities during reproduction.

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