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SOME BIOCHEMICAL EFFECTS OF STARVATION IN ARCTIC BLUE FOXES (*ALOPEX LAGOPUS*)*

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Abstract

Morphological blood indices – erythrocyte content, haemoglobin concentration, total activities of enzymes – ASAT (EC 2.6.1.1.), ALAT (EC 2.6.1.2.), LDH (EC 1.1.1.27), AP (EC 3.1.3.1.), amylase (EC 3.2.1.1) and protease (EC 3.4.21) in blood serum, LDH-isoenzymes in some organs, amylase and protease in pancreas and small intestine homogenates were investigated in farmed arctic blue foxes starved for 8 days. No significant changes in blood and organ enzyme activities after 8-day starvation in foxes were revealed. The starvation has been shown to cause adaptive and compensatory alterations in intestine enzymatic topography. The starvation caused no deleterious effects on the health of the arctic blue foxes.

Key words: arctic blue foxes, starvation, blood indices, enzymes, LDH-isoenzymes of organs, intestine enzymatic topography.

The blue fox is a blue-gray colour type of the wild arctic fox (*Alopex lagopus* L. 1758; Canidae). It descends from Alaskan and Greenland arctic foxes and has been farmed for its fur in the USSR since 1924. As an inhabitant of tundra, its wild populations fluctuate widely in association with temporal changes in food availability. The ability of arctic blue foxes adapted to severe conditions of the Arctic to overcome starvation is a reflection of the species ecology and its relations with the environment (Prestrud, 1991; Mustonen et al., 2006 b).

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Starvation – a physiological status of organism caused by the absence or shortage of nutrients – is widespread in seasonal mammals in the wild (Barboza and Hume, 2006; McCue, 2007; Fuglei et al., 2000; John, 2005). Ability of mammals to sustain alimentary starvation is determined by accumulation of exogenous lipids in white adipose tissue (WAT) and carbohydrate metabolites during a period of abundant feeding and active digestion, while under food deficiency conditions this ability is connected with selective mobilization and oxidation of substrates, obtained from fat reserves and economical consumption of proteins (Mustonen et al., 2005, 2006, 2007).

The farmed arctic blue fox is a semi-domesticated carnivore. As a circannually active and easily accessible starved animal, it can be used as an excellent model to study biochemical mechanisms of adaptation to food deprivation (Mustonen et al., 2006). The objective of this study was to determine some morphological and biochemical indices after 8-day starvation experiment in blood serum and some organs of farmed arctic blue fox.

Material and methods

Animals

Twenty farm-bred blue foxes (12 males and 8 females born in early May) with a mean body mass (BM) of 6–7 kg (28 October) were randomly assigned to two groups consisting of 6 males and 4 females. The fed group 1 included animals fed *ad libitum* throughout the autumn, and the starved group 2 consisted of animals starved for 8 days with access to water *ad libitum*. The starvation experiment was conducted between 28 October and 4 November. The animals were housed in individual cages under roof at natural temperature and photoperiod in the Kondopozhskiy Zverovod fur farm located 70 km to the north of Petrozavodsk, Russia. The experiment complied with the current laws of the Russian Federation and the European Convention (1991).

Sample collection and chemical analysis

Blood samples were collected without anaesthesia from plantar vein (Berestov, 2005) at 09.30 and 11.00 a.m. The samples of heart, kidney, lung, spleen, liver, stomach, pancreas, small intestine and skeletal muscle were obtained from carcass 1–2 h postmortem. Samples of tissues were stored at –25°C prior to the beginning of analysis.

The serum enzyme activities of aspartate aminotransferase ASAT (EC 2.6.1.1.), alanine aminotransferase ALAT (EC 2.6.1.2.), lactate dehydrogenase LDH (EC 1.1.1.27) and alkaline phosphatase AP (EC 3.1.3.1.) were determined by the microexpress method (Berestov, 2005). Multiple molecular forms of lactate dehydrogenase in organ extracts were analysed by agar gel electrophoresis (Tyutyunnik et al., 2005). Amylase activity (EC 3.2.1.1) was determined by the decrease in starch level. Total proteolytic activity (TPA) was measured according to hydrolysis of haemoglobin, as previously described (Oleinik, 1995). Glycyl-leucine dipeptidase activity (EC 3.4.13.2) was determined by the decrease in glycyl-leucine. Monoglyceride lipase

activity (EC 3.1.1.23) was determined by the increase in glycerin concentration after tributyrin hydrolysis. Sucrase activity (EC 3.2.1.48) was measured by the increase in glucose level after sucrose hydrolysis (Oleinik et al., 1999).

Statistical analysis

Comparisons between two study groups were performed with the Student's t-test for parametric data (Ivanter and Korosov, 2003). As there were no gender-related differences in the measured parameters, the values of the male and female participants were pooled together. The P value less than 0.05 was considered to be statistically significant. The results are presented as $\bar{x}$±SD.

Results

Starvation resulted in a reduction of the mean body mass (BM) of starved blue foxes from 6.66±0.29 to 5.76±0.26 kg ($P<0.05$) after the 8-day fasting, with a weight loss of 900 g. At the beginning of the study the mean BM of the fed blue foxes (control group) was 7.21±0.17 kg and it increased to 7.48±0.19 kg after the 8-day feeding. This occurred obviously due to autumn fat accumulation.

Our study has shown that morphological blood indices (erythrocyte content, haemoglobin concentration) in animals of the starved and fed groups did not differ from one another at the end of the starvation period (Table 1).

Table 1. Morphological and biochemical blood parameters in arctic blue foxes after starvation, $\bar{x}$±SD

Parameters	Fed	Starved
Erythrocytes (T/L)	7.0±0.23	7.4±0.14
Haemoglobin (g/l)	144.3±4,21	147.2±4.73
ASAT (mmol/h · 1)	0.19±0.01	0.26±0.04 x
ALAT (mmol/h · 1)	0.45±0.02	0.46±0.06
LDH (mmol/h · 1)	2.7±0.52	3.0±0.42
AP (mmol/h · 1)	2.1±0.14	2.6±0.32

x Significant difference between the starved and the fed group (t-test, $P<0.05$).

The serum ASAT activities of the starved blue foxes were higher than those of the fed animals (Table 1). The 8-day starvation did not affect the serum ALAT, LDH, and AP activities of the blue foxes.

Lactate dehydrogenase (LDH), an enzyme of carbohydrate metabolism, reversibly catalyzes the oxidation of lactate to pyruvate. Our investigation has shown that in tissues of the starved and fed arctic blue foxes lactate dehydrogenase presented in 3-5 molecular forms: from anodic fraction LDH-1 to cathodic fraction LDH-5. It has been previously noted that patterns of isoenzymatic LDH spectrum are distinctly correlated with metabolic type of tissues (Tyutyunnik et al., 2005). Anodic fractions, i.e. isoenzymes dominated by H-subunits such as LDH-1 and LDH-2 are most active in heart and kidney tissues with predominantly aerobic type of metabolism. How-

ever, the isoenzyme LDH spectra of the latter organs were not affected by starvation (Table 2). At the same time, in tissues clearly capable of anaerobiosis (skeletal muscles) the relative content of LDH-5 isoenzyme increased from 48.1 to 55.2% of the total enzyme activity. The last result is considered to be an evidence of carbohydrate anaerobic degradation processes in this organ. Similar patterns for stimulation of anaerobic carbohydrate transformation were observed for isoenzymatic LDH spectra of spleen and lungs (tissues with the highest relative content of intermediate forms of enzymes) in starved arctic blue foxes (Table 2). Thus, in the isoenzymatic spectrum of lung tissues the levels of LDH-5 were higher in the starved foxes. Moreover, the fasted animals had lower spleen LDH-1 content. The latter demonstrated fasting-induced reduction in aerobic metabolism in starved blue foxes.

Table 2. Effects of 8-day starvation on isoenzymatic LDH-spectra of tissues of blue foxes

Groups	Fractions LDH, % ($\bar{x}$±SD)				
	LDH-1	LDH-2	LDH-3	LDH-4	LDH-5
Heart					
Fed	54.5±0.88	40.9±0.40	4.7±0.74	0	0
Starved	54.4±0.63	41.3±0.59	4.3±0.78	0	0
Kidney					
Fed	30.9±1.53	15.7±0.61	9.5±0.54	9.5±0.87	34.5±0.98
Starved	32.1±0.88	17.1±0.86	9.2±0.35	9.5±0.81	32.1±1.59
Liver					
Fed	5.7±0.93	5.4±0.44	9.5±0.67	10.1±0.77	69.4±1.46
Starved	4.6±0.50	3.7±0.40	8.5±1.11	15.3±1.57	67.9±2.23
Skeletal muscle					
Fed	8.8±3.2	18.9±1.8	14.2±2.3	10.1±1.9	48.1±2.0
Starved	8.5±2.2	16.2±2.2	11.3±1.6	8.8±1.5	55.2±2.6 x
Lungs					
Fed	11.6±1.31	23.8±1.31	25.7±0.62	14.4±2.04	24.5±1.40
Starved	7.9±0.80	23.1±1.19	29.1±1.57	10.1±1.89	29.9±2.38 x
Spleen					
Fed	9.8±1.45	30.1±0.74	32.7±1.15	9.1±0.60	18.3±1.60
Starved	5.3±0.38 x	28.0±0.87	36.5±1.39	10.7±0.58	19.5±1.02

x – significant difference between the starved and the fed group (t-test, $P<0.05$).

The 8-day starvation did not affect the serum trypsin activities of the blue foxes, but amylase activities of the fasted foxes were lower than in the fed group at the end of the starvation (Table 3). The patterns of changes in the enzymic activities in pancreas tissue under starvation were very similar to those observed in blood serum (Table 3).

In starved animals, pancreas induced a reduction in protease (11%) and amylase (46%) activities. Moreover, lipase activities in the pancreas were higher in the starved arctic blue foxes (34%). Total protease activities (TPA) and amylase levels were higher in the fasted animals by 53% and 78% compared to the fed group. The differences in activities of other enzymes between the fasted and fed animals were not significant (Table 3).

Table 3. Changes in digestive hydrolases activities in arctic blue foxes starved for 8 days, $\bar{x}$±SD.

Enzyme, unit	Fed	Starved
	Serum	
Amylase (g/h · 1)	72.4±4.78	54.4±1.48 x
Trypsin (E/h/ml)	10.4±1.10	9.9±1.18
	Pancreas	
Amylase (mg/min/g)	287.3±22.40	154.8±14.11 x
Protease (µmol/min/g)	90.0±2.18	80.3±4.58 x
Lipase (µmol/min/g)	1.1±0.10	1.5±0.07
	Small intestine[1]	
Amylase (mg/min/g)	1.3±0.08	2.4±0.31 x
TPA (µmol /min/g)	2.2±0.18	3.4±0.45 x
Lipase (µmol /min/g)	0.07±0.01	0.10±0.01
Sucrase (µmol /min/g)	9.0±1.36	11.7±1.25
Dipeptidase (µmol /min/g)	4.9±0.38	5.7±0.44

x – significant difference between the starved and the fed group (t-test, $P<0.05$).
[1] average activity in 5 parts of intestine.

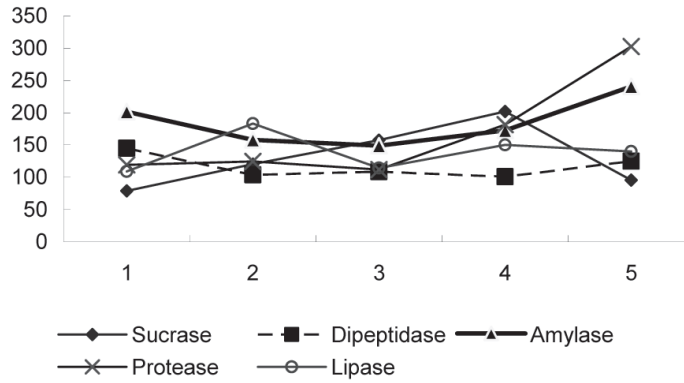

Figure 1. Effects of 8-day starvation on enzyme activities in mucosa of different segments of arctic blue foxes intestine
Axis of abscisses – segments of intestine (1–5); ordinate axis – activity (% to fed group)

Although starvation did not affect the enzymatic activity in small intestine mucosa, it changed the distribution of the studied activities across the intestine (Figure 1). The amylase activities decreased abruptly in the proximal-medial direction, then increased in the caudal direction. Similar topography changes upon starvation were detected for TPA in both cases – with minimal activity in the medial segments and maximal in the caudal ones. The changes of proximal-distal gradient of monoglyceride lipase activities fluctuated with a maximum in the second and a minimum in the third section of small intestine. The dipeptidase activities were decreased in the proximal-distal segments and increased in the caudal ones. The maximum saccharase activities in arctic blue foxes starved for 8 days shifted the enzyme activities

towards proximal-distal direction, with the minimum moving to the caudal segment. It can be seen from Figure 1 that the distribution of enzymatic activity across intestine in arctic blue foxes starved for 8 days was quite different. Nonetheless, the activity gradient in both cases shifted towards distal parts.

Discussion

The arctic fox is a medium-sized predator, which originally inhabited severe circum-polar tundra regions. Its ability to survive under extreme circumstances is mainly based on its excellent fur coat insulation, seasonally altering energy requirements and behavioural strategies (Prestrud, 1991; Mustonen et al., 2006 b).

Eight-day food deprivation of arctic blue foxes in the period of intensive fat accumulation (in October) evidently did not cause any irreversible and deep changes in morphological and biochemical blood parameters and did not significantly influence their physiological condition. It is known that in the natural habitats of arctic blue foxes the periods of abundant food consumption (summer and autumn) are alternated with periods of scanty feeding, and occasionally with periods of starvation (winter). At the beginning of November foxes in the wild increase their body mass by 30–50% just due to fat reserves (Prestrud, 1991). The ability of seasonal fat accumulation is one of the essential features of animals inhabiting northern and temperate latitudes. Fat deposition is typical of farmed arctic blue foxes as well.

When analysing the results of morphological and biochemical investigation of arctic blue foxes after 8-day starvation it is necessary to take into account that even short absence of food is itself a stressful factor, though it often happens to arctic blue foxes in the wild. In natural habitats, arctic blue foxes realize the stress-reaction through locomotor activity increase in food search that is impossible when these animals are raised in zooculture (Zabolotskikh, 1997). Through the corticosteroid system the starvation stress triggers a number of biochemical reactions, directed to the energy homeostasis maintenance that is connected with redistribution of energy and plastic resources. Food deprivation of the arctic blue foxes investigated most probably represents the emergency adaptation period by classification of starvation periods, the period characterized by glycolysis stimulation, inhibition of protein synthesis and activation of its degradation, and reinforcement of glycogenolysis. In the last process glycogen reserves are exhausted as early as after 12–24 hours of full starvation, but thereafter, several energy production mechanisms begin to work due to glucocorticoid influence; the main of these mechanisms is gluconeogenesis that proceeds with the usage of amino acids, namely with an increase of their transport and transamination. These enzymes initiate the processes of amino acid degradation and ensure, eventually, generation of glucose precursors in gluconeogenesis.

It is well known that rearrangement of metabolism under endogenous feeding consists in gradual transition from carbohydrate to lipid metabolism (Mustonen et al., 2005). In this connection it was important to study not only the total activity of glycolysis key enzyme – LDH – in starved blue foxes, but also the isoenzymatic profile of this enzyme in organs (Toropila et al., 1996). The most mobile source of energy

is glucose dissolved in blood, and its degradation (glycolysis) can be realized in both aerobic and anaerobic manner. Exactly "pure" isoenzymes LDH-1 and LDH-5, the former containing aerobic B(H) subunits and the latter – anaerobic A(M) subunits can serve as evidence for prevalence of one or another alternative pathways of glycolysis in tissues.

Thus, 8-day starvation of the arctic blue foxes resulted in some isoenzymatic changes, shifting the metabolic processes in skeletal muscles, spleen and lungs towards anaerobic glycolysis. The reduction of locomotor activity of farmed arctic blue foxes by the end of starvation period (Zabolotskikh, 1997) as well as the decrease of oxygen access to tissues due to these pathways of anaerobic degradation of carbohydrates acquired a significant place in metabolism of skeletal muscles and lungs (O'Carra and Mulcahy, 1990). Progressing hypodynamia and hypoxia as consequences of starvation, have special effect on arctic blue foxes' immune system by the end of 8-day starvation period. In tissues of spleen, a rearrangement of metabolism also occurred, when anaerobic degradation of carbohydrates became a source of energy, which occurs with oxygen deficit.

Processes of alanine transamination decreased (ALAT activity did not change in starved arctic blue foxes in contrast with the fed ones), but the compensatory increase of serum ASAT activities increased by 40%. The intensity of energy exchange was reduced, but LDH activity had fallen, and judging by LDH isoenzymatic spectra in organs, at the end of 8-day starvation the major part of the glycolytic process in skeletal muscles, lungs and spleen (but not heart and kidney) in starved arctic blue foxes went through its anaerobic pathways, which were the main source of energy in conditions of abrupt reduction of oxidative phosphorylation during phase I of starvation.

Starvation induced modifications in enzymatic topography in small intestine of arctic blue foxes. Although the small intestine functional topography varies in different species, a common feature for them is that enzymatic activity is the highest in the proximal part (Oleinik, 1995). Normally, maximum amylase activity in rats is found in the small intestine proximal part, with an abrupt decrease in the distal part. Such distribution of the enzyme activity has been demonstrated for a number of other animals as well (Bjornvad et al., 2004). Maximum amylase activity in the arctic blue foxes starved for 8 days was found in the caudal segments. In many animals dipeptidase activity is maximal in mid-caudal part of the small intestine, whereas in arctic blue foxes its activity peaked in proximal segment. The monoglyceride lipase activity gradient in small intestine in arctic blue foxes starved for 8 days was similar to that in rats. TPA in small intestine was maximal in distal segments of the starved animals. It is known that the small intestine functional topography is not constant, but depends on a range of factors, and changes under the influence of different diets.

The level of enzymatic activity in distal segments of intestine of starved animals was high. The reason for high enzymatic activity in distal segments of the small intestine in predators is known as "local substratum fed" (Oleinik, 1995). This implies that the proximal-distal topography of enzymatic activities in small intestine mucosa depends on low molecular forms of substrates, which can penetrate into the brush border and interact with digestive enzymes. Since food transport through the intestine is fast in predators, it is obvious that it is in its distal segments that large quantities

of low molecular forms of substrates would come into contact with membranes of enterocytes. High enzymatic activity in the distal part of the intestine in starved arctic blue foxes indicates that this peculiarity is the species genetic trait, rather than the consequence of food availability or absence.

In starved animals, small intestine becomes essential for metabolism and decomposition of endogenous food substrates meant to provide the organism with energy and tissue building material (Bjornvad et al., 2004). The substrates are actively secreted into the intestine and reabsorbed upon hydrolysis. This must be the reason for the increased activity of digestive enzymes in the small intestine of arctic blue foxes starved for 8 days.

Since the activities of most studied enzymes showed no significant changes, one could assume that the organism of arctic blue foxes endured 8-day starvation quite well. Some reduction in amylolytic activity is offset by an increase in saccharase activity in small intestine, as well as by the transformation of the small intestine enzymatic topography, which is one of the most sensitive mechanisms for adaptation of the digestive system to nutritional conditions (Naruse et al., 1999; Oleinik, 1995).

The arctic fox is well adapted to a scarcity of food in Arctic winter conditions, because it is able to store an adequate amount of exogenous lipids in white adipose tissue during autumn (Prestrud, 1991). In the wild animals are adapted to overcome extended periods without access to food in order to survive to next reproductive season and produce offspring. However, the high adiposity of farmed arctic blue fox before reproductive period is abnormal. The excessive obesity is detrimental to reproductive success of the animals (Asikainen et al., 2002; Zabolotskikh, 1997).

Food deprivation did not affect the well-being of the animals, which was confirmed by some blood and organ indices measured in October and November at the end of the fast. There were no significant differences in erythrocyte, haemoglobin, ALAT, LDH, AP or digestive hydrolase activities. These data show that the 8-day period of autumn food deprivation is well tolerated by arctic blue fox with no adverse physiological effects.

The use of 8-day autumn starvation for farmed polar foxes, based on natural phenomena concurs with international recommendations on technology of keeping fur-bearing animals in captivity and is in accordance with modern ethical and humane standards, accepted by the World Society for the Protection of Animals (European Convention, 1991).

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Wybrane biochemiczne skutki głodzenia lisów polarnych niebieskich (*Alopex lagopus*)

STRESZCZENIE

U fermowych lisów polarnych niebieskich głodzonych przez okres 8 dni badano morfologiczne wskaźniki krwi – zawartość erytrocytów, stężenie hemoglobiny, łączną aktywność enzymów ASAT (EC

2.6.1.1.), ALAT (EC 2.6.1.2.), LDH (EC 1.1.1.27), AP (EC 3.1.3.1.), amylazy (EC 3.2.1.1) i proteazy (EC 3.4.21) w surowicy krwi, izoenzymów LDH w niektórych narządach, oraz amylazy i proteazy w homogenatach trzustki i jelita cienkiego. Nie stwierdzono istotnych zmian aktywności enzymów w krwi i narządach lisów po 8 dniach głodzenia. Stwierdzono, że głodzenie powoduje adaptacyjne i kompensacyjne zmiany w topografii enzymów jelita. Głodzenie nie miało negatywnego wpływu na zdrowotność lisów polarnych niebieskich.