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Hormones and metabolites of arctic foxes (*Alopex lagopus*) in response to season, starvation and re-feeding

E. Fuglei [a,*], M. Aanestad [b], J.P. Berg [b]

[a] *Norwegian Polar Institute, N-9296 Tromsø, Norway*
[b] *Hormone Laboratory, Aker University Hospital, N-0514 Oslo, Norway*

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Abstract

Svalbard's arctic foxes experience large seasonal variations in light, temperature and food supply throughout the year, which may result in periods of starvation. The aim of this work is to investigate if there are seasonal variations in post-absorptive plasma thyroid hormones (free thyroxin (fT_4), free triiodothyronine (fT_3) and reverse triiodothyronine (rT_3)) and metabolites (free fatty-acids (FFA) and β-hydroxybutyrate (β-OHB)) with season and their response to starvation and re-feeding. The concentrations of post-absorptive free triiodothyronine were significantly higher in November than May, while those of thyroxin, reverse triiodothyronine, free fatty-acids and β-hydroxybutyrate remained unchanged. Possible explanations for the seasonal variations in free triiodothyronine are discussed. There were no significant changes from post-absorptive concentrations of thyroxin and reverse triiodothyronine in starved and re-fed foxes. However, free triiodothyronine concentrations decreased during starvation and increased again with re-feeding both in May and November. Starvation induced high levels of free fatty acids in both May and November, indicating increased lipolysis. There was a significant increase in β-hydroxybutyrate in November only, indicating that arctic foxes are capable of protein conservation during starvation.

Keywords: Arctic foxes; β-hydroxybutyrate; Fasting; Free fatty-acid; Reverse-triiodothyronine; Svalbard; Thyroxin; Triiodothyronine

1. Introduction

The arctic fox (*Alopex lagopus*) is a non-hibernating circumpolar inhabitant of the Arctic. On Svalbard (74–81°N), they are widespread throughout the archipelago. Due to the high latitude, the sun remains below the horizon from late October to mid February, with complete darkness from mid November to the end of January, and frequent temperatures below freezing from September to mid May (Steffensen, 1982). Summer gives the opposite extremes with continuous daylight from late April to August (Steffensen, 1982). In spring and summer, food items are in excess when hundreds of thousands of seabirds arrive to the numerous bird cliffs together with geese, ducks and other birds. However, access to food becomes limited during autumn and winter because most birds leave Svalbard by October. Carcasses of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and other foxes, together with food stored during spring and summer, are potential food items for foxes during the dark winter, but their occurrence is low (Frafjord, 1993; Prestrud, 1993). Thus, during the harshest winter months, with complete darkness, low tempera-

* Corresponding author. Tel.: +47-77-750528; fax: +47-77-750501.
E-mail address: eva.fuglei@npolar.no (E. Fuglei)

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tures and occasional winter storms that can last for weeks, the arctic fox may undergo periods of starvation.

When animals go through periods with limited food, they have to rely on their body reserves to provide energy for body functions. Adaptations to periods of starvation, thus represent adjustments both in hormones and in the mobilisation of fuel substrates. There is no information available on starvation-induced hormonal changes or changes in metabolites in the arctic fox. Thyroid hormones are thought to play a role in energy conserving processes and maintaining homeostasis in a starving organism (Shetty, 1990). Changes in the levels of the different thyroid hormones in response to starvation differ among species. Starvation reportedly increases the level of thyroxin (T_4) in broiler chickens (May, 1978), decreases it in Wistar and Sprague–Dawley rats (Wimpfheimer et al., 1979; Goodman et al., 1980), but has no effect in humans (Vagenakis et al., 1975; Marine et al., 1991). In all the above-mentioned species, concentrations of total triiodothyronine (T_3) and/or free T_3 (fT_3) decline during starvation (Vagenakis et al., 1975; May, 1978; Wimpfheimer et al., 1979; Goodman et al., 1980; Marine et al., 1991). The starvation-induced lowering of T_3 has been associated with the starvation-induced reduction of resting metabolic rate (RMR), also called metabolic depression and the conservation of proteins (Cahill, 1976; Cox et al., 1984). Additionally, the concentration of reverse T_3 (rT_3) increases during starvation in humans (Vagenakis et al., 1975; Marine et al., 1991) and is also suggested to cause metabolic depression (Lynch et al., 1985).

Table 1
Experimental set-up showing when the blood samples where taken from each of the eight foxes from 1993 to 1995

Fox no.	1993		1994		1995
	May	November	May	November	May
1	X	X	X	X	X
2	–	X	X	X	X
3	–	–	–	X	X
4	–	–	–	–	X
5	–	–	–	X	X
6	–	–	–	X	X
7	X	Dead	–	–	–
8	X	Released	–	–	–

Seasonal variations in body fattening (Prestrud and Nilssen, 1992) and body weight (Fuglei and Øritsland, 1999a) have been reported in arctic foxes on Svalbard, with the highest levels of body fat in November and December (20%) and lowest in June and July (6%). This indicates the adaptive significance of fat storing, the fat reserve in an average-sized fox in November and December approximated an energy storage of 15 640 kJ (Prestrud and Nilssen, 1992), enough energy to survive for $\approx$19 days without food at RMR levels. Thus, the arctic fox may be capable of enduring long periods of starvation, especially in winter when food is scarce. Generally, fat is the main source of metabolic energy during starvation (Cahill, 1976; Goodman et al., 1980; Nordøy et al., 1993). This is likely to be the case in the arctic fox, although no previous studies have quantified it in this species.

To better understand how the arctic fox is adapted to living at high latitudes, this study investigated if there are seasonal variations in post-absorptive plasma thyroid hormones and metabolites, and their response to starvation and re-feeding. Blood chemistry profiles were examined during the period of the 'midnight sun' in May, during complete darkness in November, and during starvation and re-feeding. The parameters investigated were plasma concentrations of fT_4, fT_3, rT_3, free fatty-acid (FFA) and β-hydroxybutyrate (β-OHB) in blood samples taken from arctic foxes exposed to natural light and temperature conditions in high Arctic Svalbard.

2. Materials and methods

Eight male adult arctic foxes were caught in the area around Ny-Ålesund on Svalbard (78°55′ N, 11°56′ E) during 1993 and 1995. The foxes were kept year-round in separate, adjacent, outdoor steel cages (2.5 × 2 × 2 m length × width × height) at the Norwegian Polar Institute Research Station in Ny-Ålesund. Each cage was furnished with a wooden sleeping box (0.5 × 0.5 × 1 m length × width × height). The foxes were fed ad libitum with commercial fox pellets (FK-Revepellets, Felleskjøpet, Norway) softened in water. Water was always provided ad libitum. Heating elements in the food cups prevented the food and water from freezing.

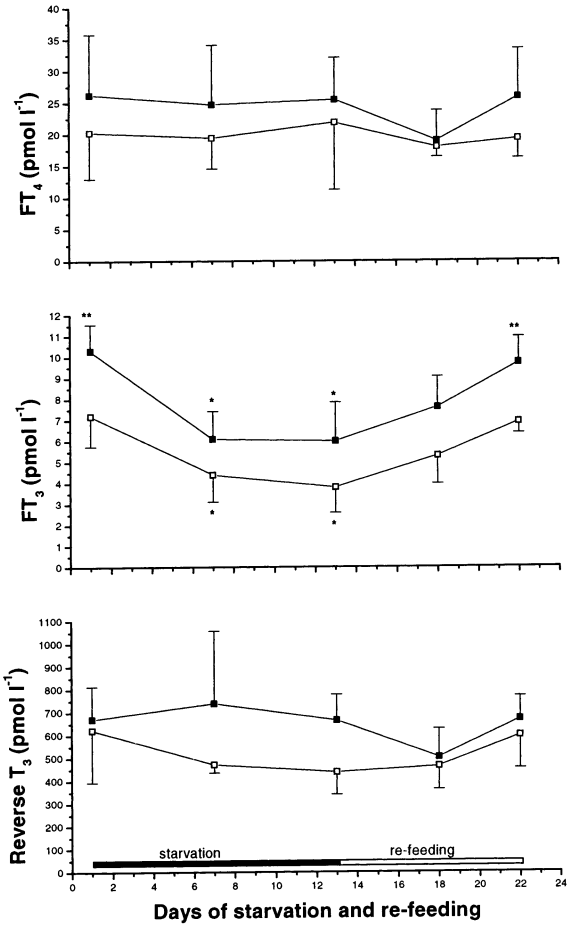

Fig. 1. Average plasma concentrations of free thyroxine (fT_4), free triiodothyronine (fT_3) and reverse triiodothyronine (rT_3), presented as mean ± S.E.M., measured during starvation and re-feeding in arctic foxes in May ($n = 6$; open symbols) and November ($n = 5$; filled symbols). **, significantly difference between May and November; *, significantly different from post-absorptive levels.

A total of eight foxes were used for the whole study (see details in Table 1). In May, starvation experiments were conducted on three foxes (1993), two foxes (1994) and six foxes (1995), while in November, two foxes (1993) and five foxes (1994) were used. Experiments were carried out according to the following protocol: food was withdrawn from the foxes for 13 days, after which they were re-fed ad libitum. Twenty hours after food was withdrawn, called day 1, the first blood sample was taken and was used as the post-absorptive level. Thereafter, blood was sampled on day 7 and 13 of starvation, and again on day 2 and 9 of re-feeding, both in May and November. The blood samples were obtained from the cephalic vein using a syringe (needle 1.2 × 40 mm) and heparin was used as an anticoagulant. To reduce the influence of possible circadian variation in plasma hormone and metabolite levels, blood was sampled only in the afternoon. Blood was centrifuged (10 min at 3000 rpm) immediately after the samples were collected, and plasma was separated and stored at −20°C. When blood samples were taken from one animal in the same season, May or November, in more than 1 year the mean value was calculated for that animal.

Hormone analyses were conducted at the Hormone Laboratory, Aker University Hospital, Oslo, Norway. Free T_4 and fT_3 were measured by time-resolved fluoroimmunoassay with europium as a marker (Delfia, Wallac Oy, Turku, Finland). Reverse T_3 was measured by a radioimmunoassay with ^{125}I-rT_3 as a marker (Serono Diagnostics GmbH, Germany). Measurements of hormones were made in replicates and the means of the two values were used in statistical analyses. The inter-assay coefficient of variation was 5% for fT_4, 6% for fT_3 and 10% for rT_3.

Plasma FFA and β-OHB were measured on a Technicon Axon® System (Bayer, Tarrytown, NY, USA) with FFA reagents (Wako Chemicals GmbH, Germany), and β-OHB reagents (Sigma Diagnostics, USA) at the Norwegian College of Veterinary Medicine, Oslo, Norway. The inter-assay coefficient of variation was 5% for both FFA and β-OHB.

Statistical tests were performed using Sigma Stat software v. 2.03 (Erkrath, Germany). Data are presented as mean ± S.E.M. Variance between season and days was analysed by two-way ANOVA, where days of starvation and re-feeding were used as one variable and the season, May and November, as the other. Differences in hormone and metabolite concentrations were compared using a Student–Newman–Keuls test. P values < 0.05 were considered statistically significant.

3. Results

There were no significant differences in post-absorptive (day 1) fT_4 concentrations between May and November. Starvation and re-feeding produced no significant deviations from post-absorptive levels ($P > 0.05$, Fig. 1).

Levels of post-absorptive fT_3 were significantly lower in May than in November ($P < 0.05$). Free T_3 levels were significantly reduced after 7 and 13 days of starvation in both seasons and increased significantly with re-feeding ($P < 0.05$, Fig. 1).

There were no significant changes in post-absorptive levels of rT_3 between May and November, and the concentrations did not differ significantly from day 1 values during starvation and re-feeding ($P > 0.05$, Fig. 1).

Post-absorptive concentrations of FFA did not differ significantly between May and November ($P > 0.05$). Starvation induced significant increases in FFA levels in both May and November ($P < 0.05$, Fig. 2). The levels of FFA were significantly higher in November than May at starvation day 13 ($P < 0.05$, Fig. 2). Re-feeding of the foxes reduced the FFA levels again, which by re-feeding day 5 were significantly lower than the levels after 13 days of starvation both in May and November ($P < 0.05$, Fig. 2).

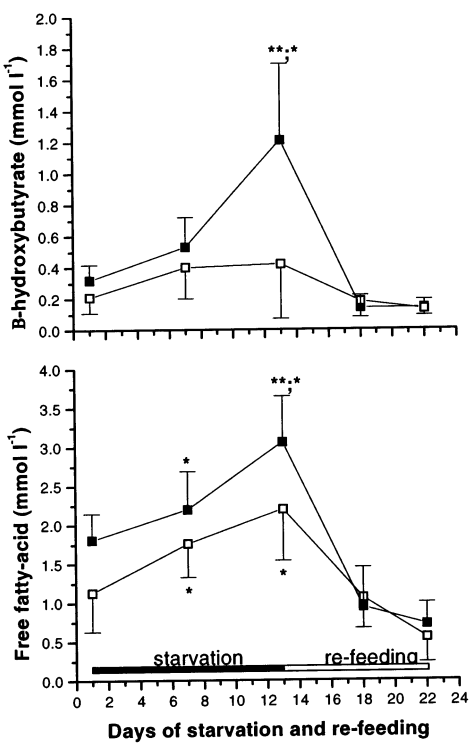

Fig. 2. Average plasma concentrations of free fatty acid (FFA) and β-hydroxybutyrate (β-OHB), presented as the mean ± S.E.M., during starvation and re-feeding in arctic foxes in May ($n = 7$; open symbols) and November ($n = 5$; filled symbols). **, significantly difference between May and November; *, significantly different from post-absorptive levels.

β-OHB levels of post-absorptive foxes were not significantly different between May and November ($P > 0.05$). Starvation induced an increase in β-OHB in both months. However, the increase was statistically significant only in November ($P < 0.05$, Fig. 2) and became significantly higher than the May levels after 13 days ($P < 0.05$). After re-feeding, β-OHB levels decreased again in November and were significantly lower after 5 and 9 days when compared to the peak level on day 13 during starvation ($P < 0.05$, Fig. 2).

4. Discussion

Post-absorptive thyroid hormone levels in arctic foxes were within the range of values found in humans and dogs (humans: 9.0–19.4 pmol·l^{-1} for fT_4, 2.9–7.7 pmol·l^{-1} for fT_3 and 123–539 pmol·l^{-1} for rT_3 (Becker, 1995); dogs: 7–47 pmol·l^{-1} for fT_4 (Dietl and Kraft, 1994; Peterson et al., 1997; Behrend et al., 1998)). With the exception of fT_3, which was lower during May than November, the post-absorptive (day 1) values of fT_4 and rT_3 were similar in May and November (Fig. 1). Given that high levels of thyroid hormones, in particular fT_3, are thought to be associated with elevated metabolic rates (Lynch et al., 1985) and high food intake (Ryg and Jacobsen, 1982), lower fT_3 in May than November in the present study did not coincide with the seasonal variation in RMR and food intake previously found in arctic foxes (higher RMR and food intake in summer than in winter (Fuglei and Øritsland, 1999a)). However, thyroid hormones may also be associated with other physiological mechanisms such as reproduction and moulting. An inverse phase relationship between the seasonal thyroid cycle and the reproductive cycle has been suggested for birds (Jallageas et al., 1978) and red foxes (Maurel and Boissin, 1981). In semi-domesticated blue foxes, testosterone concentrations increase from the end of January to the middle of April and are low for the rest of the year (Smith, 1987). Arctic foxes mate in early spring and a similar testosterone pattern may also occur in Svalbard's arctic foxes, thus relating it to the low fT_3 levels in May and high fT_3 in November. Increased thyroid hormone levels have also been associated with regeneration of pelage during the annual moult in seals (John et al., 1987) and in Svalbard ptarmigan (Stokkan et al., 1985).

The arctic fox begins to moult its winter fur in May, having short summer fur in late June, July and August. Regeneration of the winter fur starts in September, continuing to grow until early December (Underwood, 1971). More detailed studies on the thyroid hormone pattern during the year are needed to understand its physiological implications in arctic foxes at high latitudes.

Compared to levels in humans and rats, concentrations of FFA in post-absorptive (day 1) foxes were high (human: 0.42 mmol·l^{-1} (Cahill et al., 1966); rat: 0.35 mmol·l^{-1} (Goodman et al., 1980)). However, the FFA levels observed in arctic foxes were at the same level as found in the domestic dog (1.13 mmol·l^{-1} (Brady et al., 1977)), and in Arctic seals such as grey seal pups (*Halichoerus grypus*) and harp seal pups (*Phoca groenlandica*) (1.09 and 1.4 mmol·l^{-1}, respectively (Nordøy and Blix, 1991; Nordøy et al., 1993)). Post-absorptive levels of β-OHB in arctic foxes were higher than those found in humans, harp seal pups and dogs (humans: 0.02 mmol·l^{-1} (Cahill et al., 1966); harp seal pups: 0.06 mmol·l^{-1} (Nordøy et al., 1993); dogs: 0.01–0.03 mmol l^{-1} (Brady et al., 1977; De Bruijne et al. 1981)). However, the levels of β-OHB found in emperor king penguins (*Aptenodytes forsteri*) and grey seal pups (0.48 and 0.12 mmol·l^{-1}, respectively) (Groscolas, 1986; Nordøy and Blix, 1991) were in agreement with those found in arctic foxes. The relatively high levels of FFA in foxes implies a shift towards lipid utilisation in the post-absorptive state, in agreement with the respiratory exchange ratio (RER; 0.71–0.72) found in post-absorptive arctic foxes (Fuglei and Øritsland, 1999a).

For the arctic fox in the high Arctic environment, where periodic limitations of food are common, the ability to cope with periods of starvation is fundamentally important for survival. Starvation was not found to alter the concentrations of plasma fT_4 and rT_3 from post-absorptive values either in May or November (Fig. 1), while it caused a decrease in the concentration of fT_3 by $\approx 45\%$ (Fig. 1). Identical starvation-induced effects have previously been reported on plasma total T_4, T_3 and rT_3 in dogs (De Bruijne et al., 1981). Similar patterns in fT_4 and fT_3 levels during starvation have also been reported in humans; however, the levels of rT_3 were increased in humans (Vagenakis et al., 1975; Marine et al., 1991). Furthermore, other studies in humans have shown that the concentration of rT_3 does not necessarily increase with starvation, while the concentration of T_3 decreases (Einsenstein et al., 1977). Thus, there seems to be no obligatory reciprocal relation between the pathways that generate either T_3 or rT_3 from T_4 in humans (Einsenstein et al., 1977), which may as well be the case in arctic foxes and dogs. Formation of T_3 is produced by the monodeiodination of the outer ring of T_4, by the action of a 5′-deiodinase enzyme (Surks and Oppenheimer, 1971, Wartofsky and Burman, 1982). Starvation is believed to inhibit the enzyme 5′-deiodinase in humans, resulting in inhibition of conversion of T_4 into T_3 (Spencer et al., 1983). Inhibition of 5′-deiodinase may also be due to the reduced levels of fT_3 in starved arctic foxes. An additional possible mechanism is that the level of T_3 might depend on thyroid stimulating hormone secretion (Shimizu et al., 1991). In humans, low levels of thyroid stimulating hormone are reported together with low concentrations of fT_3 during starvation, indicating inactivation of the hypothalamo-pituitary-thyroid axis (Shimizu et al., 1991). A general energy conserving physiological adaptation to starvation is a lowering of RMR (Keys et al., 1950; Kleiber, 1975; Fuglei and Øritsland, 1999b). It is thought that a reduction of fT_3 may explain the reduction of RMR observed during starvation (Carter et al., 1975). The decline in fT_3 during starvation in the present study coincided with a starvation-induced lowering of RMR found in arctic foxes (Fuglei and Øritsland, 1999a), which implies an association between fT_3 and RMR in arctic foxes during starvation.

Starvation also induces alterations in metabolic pathways. Plasma concentrations of FFA increased in starved arctic foxes both in May and November (Fig. 2). The levels were high, but in accordance with findings from harp seal and grey seal pups that had been starved for 13 days (Nordøy and Blix, 1991; Nordøy et al. 1993), and 14 days starved dogs (Brady et al., 1977; De Bruijne et al., 1981). During starvation, when the energy needs of an organism are met by using food reserves in the body, FFA is released from adipose tissue triglyceride stores (Cahill, 1976). The enhanced concentrations of FFA in the arctic fox during starvation might be explained by rates of mobilisation exceeding oxidation rates. Thus, the present study suggests that fat stores have a primary role in energy supply during starvation in

the arctic fox. The starvation-induced increase of FFA was accompanied by increased concentrations of β-OHB; however, the increase was significant in November only (Fig. 2). Increased levels of FFA activate the production of ketone bodies (β-OHB and acetoacetate) by the liver (Felig, 1979). Ketone bodies partially replace glucose as the brain's main source of energy, and enable the adaptive conservation of body protein (Owen et al., 1967; Goodman et al., 1980; Groscolas, 1986). Decreased levels of fT_3 are also reported to limit the breakdown of muscle protein (Gardner et al., 1979). Thus, levels of FFA, β-OHB and fT_3 found in this study indicate increased lipolysis, suggesting that muscle protein conservation occurs during starvation in the arctic fox. This protein conservation capacity has also been found in starved dogs, among several other species (Brady et al., 1977).

The seasonal difference in starvation-induced changes of β-OHB in the arctic fox (Fig. 2) may be attributed to depletion of lipid stores below a critical level (Goodman et al., 1980, Le Maho et al., 1981). Winter adapted foxes have much larger fat stores than foxes in spring and summer (Prestrud and Nilssen, 1992), and a critical fat level may have been reached before starvation day 13 in May, explaining the relatively low β-OHB level in May. Since variations in β-OHB were suggested as a mirror image for changes in nitrogen excretion in geese (Le Maho et al., 1981), the lower level of β-OHB in May than in November in arctic foxes may indicate a seasonal variation in the capacity for protein conservation. Based on this assumption, foxes in May, with lower body fat than November, may tolerate shorter starvation periods than foxes in November. This is supported by the finding of a higher starvation-induced body weight loss in May than November in arctic foxes, suggested to be due to a higher protein conservation capacity in fat foxes (Fuglei and Øritsland, 1999a).

After re-feeding, plasma concentrations of fT_3 increased rapidly and FFA and β-OHB decreased (Figs. 1 and 2), indicating that the changes induced by starvation were rapidly reversed by re-feeding in arctic foxes.

In conclusion, fT_3 in post-absorptive foxes was the only hormone that varied in concentration between seasons, with higher levels in November than May. Seasonal variations in the levels of fT3 are suggested to be related to reproduction and/or moulting. High levels of FFA and β-OHB indicate a shift towards lipid utilisation in post-absorptive foxes. Periods of starvation reduced the levels of fT_3, which increased again with re-feeding, while fT_4 and rT_3 were unchanged both during starvation and re-feeding. FFA and β-OHB increased during starvation, indicating enhanced lipid mobilisation. Large fat stores in winter and a preferential use of these stores with minimised breakdown of muscle proteins are suggested as important strategies for surviving periods of starvation in arctic foxes.

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