Effects of Seasonality and Fasting on the Body Mass and Plasma Growth Hormone Concentrations of the Raccoon Dog (*Nyctereutes procyonoides*) and the Blue Fox (*Alopex lagopus*)

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Growth hormone (GH) promotes growth and endochondral ossification, but it is also important in the response to fasting due to its effects of increasing gluconeogenesis and lipolysis. In this study eleven raccoon dogs and blue foxes were followed for six months and their body mass and GH levels were measured. In November half of the animals of both species were put to a three-week fast. There were no significant differences in the GH levels between the animals of different ages and the subadults and adults both had quite low GH levels in the summer. Fasting had no effect on the GH levels of the raccoon dogs, but the fasting blue foxes had lower GH concentrations than the controls in Nov 16th. The control blue foxes experienced a significant increase in the GH levels in early November and the fasting blue foxes in late November. The GH concentrations of all the raccoon dogs rose in early December. As fasting did not cause an elevation in the GH levels but the concentrations increased with decreasing temperature and shortening daylength, the autumnal GH secretion of these species could be regulated by endogenous seasonal rhythms entrained by exogenous *Zeitgebers* such as temperature or photoperiod. The autumnal increase of GH levels contributes to the response to fasting as an adaptation to survive the winter months with inadequate nutrition. The raccoon dog which spends the coldest part of the winter in winter sleep seems to be better adapted to a total fast than the actively wintering blue fox.

Introduction

The raccoon dog (*Nyctereutes procyonoides*, Gray, 1834, Canidae, Carnivora) is a middle-sized mammal originating from Eastern Asia. It was introduced to north-western Russia as a game animal for the fur trade, and from there it has spontaneously dispersed to Finland, where it is now quite common. Its northern distribution limit lies between 65°N and the Arctic Circle (Kauhala, 1992). In Europe the raccoon dog has spread to Germany and crossed the Rhine as well (Nowak, 1992). It is also reared commercially for the fur trade in Finland, where raccoon dog farming began in the early seventies with animals originating from wild stock (Mäkelä, 1973).

The raccoon dog is ecologically an omnivore. Its diet consists mainly of small mammals and berries, but it shows no strong preference to any food items (Korhonen, 1987). It has a tendency of excessive fattening in the autumn in preparation for the winter rest (Heptner *et al.*, 1974). The animals present with a rapid weight gain during July-October and the fat reserves are the greatest in October-December and the lowest in May (Kauhala, 1992). The inner fat reserves in May are only 25% of those in late autumn.

During the winter the animal exhibits winter sleep in a borrow or a den (Nowak, 1992). There may be occasional periods of arousal and feed intake but generally the raccoon dog fasts during the winter sleep. The animal enters the winter sleep when the ambient temperature drops below freezing – usually in November in Finland. At the onset of the winter sleep about 25% of the raccoon dog's body mass is subcutaneous fat accumulated during the autumn. In general the animals do not exhibit winter sleep on fur farms mostly due to the lack of available nests (Korhonen, 1987).

The blue fox (*Alopex lagopus*, L., 1758, Canidae, Carnivora) is a variant of the arctic fox reared for fur production. The arctic fox has a circumpolar distribution (Pulliainen, 1992). The Fennoscandian arctic fox population is very small even though the

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species has been protected for about 60 years. The arctic fox is an opportunistic omnivore, whose diet consists of rodents, especially lemmings (*Lemmus lemmus*), birds, eggs, leftovers of larger predators (Fay and Stephenson, 1989; Hersteinsson *et al.*, 1989; Hersteinsson and MacDonald, 1996) as well as cadavers and berries (Pulliainen, 1992). In contrast to the raccoon dog the arctic fox does not exhibit winter sleep, but like the raccoon dog it also experiences quite long periods of naturally occurring (involuntary) fasting during the winter when the food is scarce. The arctic fox is better protected from the cold than the raccoon dog due to its well-developed peripheral and total insulation (Scholander *et al.*, 1950a,b,c). Thus the metabolic response to cold is not very intense in the arctic fox even though its metabolic rate increases when temperatures drop to about −24 °C.

Growth hormone (GH) or somatotropin is a peptide secreted by the anterior hypophysis (adenohypophysis) (Brück, 1983). GH is essential for young animals promoting e.g. growth by increasing endochondral ossification, which makes the bones grow in length. The response of the organism to GH is biphasic. There is an acute insulin-like effect increasing glucose uptake in skeletal muscle and fat, stimulating uptake of amino acids and protein synthesis in liver and muscle and inhibiting lipolysis in adipose tissue. This rapid effect is replaced in a few hours by the slow response. This response is diabetogenic causing inhibition of glucose uptake, increased levels of plasma glucose and free fatty acids and increased lipolysis and gluconeogenesis.

In humans plasma GH levels increase during fasting and GH contributes with cortisol, adrenaline and glucagon to the organism's adaptation to fasting or inadequate nutrition (Harris and Crabb, 1986; van Pilsum, 1986). GH is secreted in a rhythmic pattern and the circadian peak of GH production occurs at night and is associated with the phase of deep sleep (Brück, 1983). GH secretion is also influenced by blood chemistry. Hypoglycemia increases the rate of GH secretion e.g. at times of inadequate nutrition.

The aim of this study was to investigate how GH contributes to the survival of mammals during the autumn and winter months. As GH is considered to be important in the response to fasting it could have a role in the seasonal adaptation of mammals at the onset of winter and during the winter metabolism. Thus the secretion of GH should show seasonal patterns. The raccoon dog and the blue fox were chosen for this study to represent two different wintering strategies – winter sleep (wait it out) and the active kind of wintering. To get insight into the regulation of GH secretion by e.g. the decreasing adipose tissue mass during the winter, half the animals were fasted during this experiment to mimic natural phenomena of the species.

Materials and Methods

Eleven raccoon dogs (six males and five females) and eleven blue foxes (four males and seven females) of the Siikasalmi Research Station fur farm of the University of Joensuu (62 °N) were selected for this study. Handling of the animals was approved by the Animal Care and Use Committee of the University of Joensuu and conformed with the European convention for the protection of vertebrate animals for experimental and other scientific purposes. Most of the animals were juveniles born in the same spring. Two of the raccoon dogs and three of the blue foxes represented the previous generation. All the animals were caged singly under roof but in natural temperatures and photoperiod and fed *ad libitum*. The diet was the standard diet of the Finnish fur farms according to the regulations of the Finnish Fur Breeders' Association. Water or snow was available *ad libitum*.

The follow-up period was from the beginning of June to December 7th 1999 (Fig. 1). The weight gain of the animals was measured monthly. Blood samples were also taken monthly between June and October. The samples were drawn from the superficial vein of the shank of the left hind leg using sterile needles and syringes.

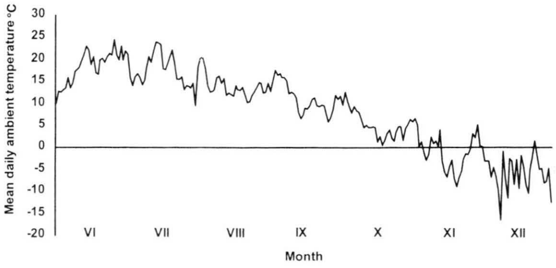

Fig. 1. Mean daily ambient temperature (°C) in the study area from June to December 1999.

At the beginning of November the animals of both species were randomly divided into two groups. The fasting groups of five individuals each were put to a total three-week fast, and the control groups of six animals continued to feed on the standard diet. The fasting group of the raccoon dogs consisted of three subadults and two adults and the control group of six subadults. The fasting group of the blue foxes had one adult and four subadults and the control group two adults and four subadults, respectively. None of the animals showed any adverse effects due to the fast, except the lowering of their body weight. During the fast the blood samples were taken weekly from all the experimental groups. After three weeks the fasting groups resumed eating for two weeks. Thereafter the animals were sacrificed electrically as they were normal fur-producing animals of the research fur farm with mature winter pelage. The final blood samples were obtained with cardiac punctures using sterile syringes. All the blood samples were taken into test tubes containing EDTA to prevent clotting and centrifuged at 1000 g. The obtained plasma was stored at –80° C.

The plasma GH levels were determined using *the Human Growth Hormone* (hGH) *Double Antibody kit* by Diagnostic Products Corporation, Los Angeles, USA. The results of the GH measurements are represented as ng/ml ± SE.

The body mass index (BMI) was calculated by the formula: weight (kg)/length (m^3). The formula is the same as for human infants and toddlers due to the larger skin area in mammals of small weight when compared with e.g. large mammals or adult humans (the formula for adult humans is weight (kg)/ length (m^2)). The statistical analysis was performed with the SPSS program using the one-way analysis of variance (ANOVA) followed by a *post hoc* Duncan's test ($p < 0.05$). The normality of distribution and the homogeneity of variances were tested with the Kolmogorov-Smirnov test and the Levene test, respectively. For nonparametric data the Mann-Whitney U test ($p < 0.05$) was performed. The results are expressed as the mean ± SE.

Results

The body weights of both species steadily increased during the summer and early autumn (Figs. 2–3, Tables I–II). The weight gain of the control groups levelled off at the beginning of November. The fasting raccoon dogs lost body mass at a rate of 600 g/week but the differences between the fasters and the controls were not statistically significant (Fig. 2, Table I). The blue foxes lost their body mass faster (700–900 g/week) and this weight loss was statistically significant after two weeks of fast and remained marginally significant during the two weeks after the fast (Fig. 3, Table II). There were no differences in the lengths or BMIs of the study groups at the end of the experiment (Table III).

The GH levels of the adult raccoon dogs were relatively high in the summer. There was a decreasing trend in the concentrations towards the end of the year. The GH levels of the raccoon dog puppies were quite low in July but the concentrations slightly increased during the autumn. The GH levels of the adults and pups differed in July and in October the concentrations being higher in the adults (Mann-Whitney U test, $p < 0.037$). At the beginning of December the GH concentrations of all the raccoon dogs increased to significantly higher levels (Mann-Whitney U test, $p < 0.0004$) (Fig. 2, Table I). There were no differences between the GH levels of the controls and the fasting raccoon dogs.

Table I. Mean weight (kg) and plasma GH concentrations (ng/ml) ± SE of the eleven raccoon dogs. November 2nd 5 individuals were put to a total three-week fast and the remaining six animals continued to feed on the standard diet. Two of the raccoon dogs were adults, the others juvenile animals born the same spring.

Time	Weight [kg]	GH [ng/ml]
VI	3.57 ± 0.93 A	2.4 ± 0.01
VII	5.51 ± 0.65 B	1.5 ± 0.25
VIII	7.89 ± 0.53 C	1.3 ± 0.13
IX	9.92 ± 0.42 DE	1.7 ± 0.18
X	11.02 ± 0.38 DE	1.6 ± 0.12
Nov. 2.	11.53 ± 0.36 E	1.6 ± 0.10
Nov. 16. controls	11.61 ± 0.50 E	1.8 ± 0.10
Nov. 16. fasting	10.85 ± 0.65 DE	2.0 ± 0.07
Nov. 30. controls	11.13 ± 0.99 E	1.7 ± 0.16
Nov. 30. fasting	9.74 ± 1.23 DE	1.8 ± 0.16
Dec. 7. controls	11.06 ± 0.45 E	2.6 ± 0.23*
Dec. 7. fasting	10.18 ± 0.61 DE	2.6 ± 0.17*

The means with no common letter differ at $p<0.05$ (ANOVA *post hoc* Duncan's test), * = statistically significant difference from the previous measurement (Mann-Whitney U test, $p<0.05$).

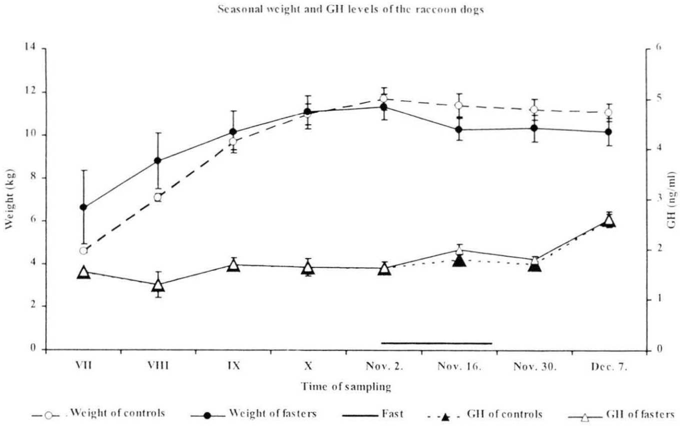

Fig. 2. Seasonal changes in the body mass (kg) and plasma GH levels (ng/ml) of the raccoon dogs. Until November 2nd the GH values of the controls and fasters are treated as one group (mean ± SE).

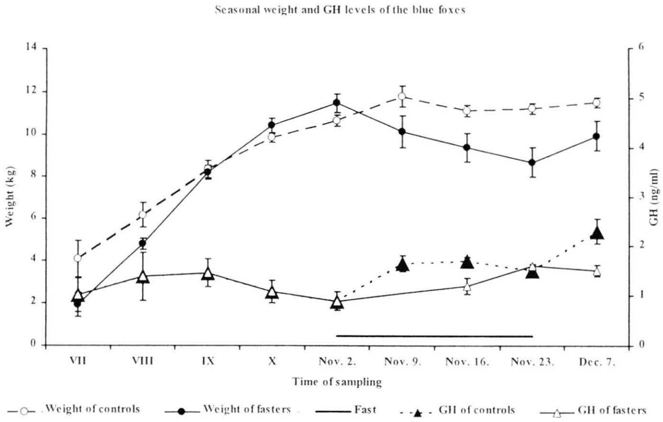

Fig. 3. Seasonal changes in the body mass (kg) and plasma GH levels (ng/ml) of the blue foxes. Until November 2nd the GH values of the controls and fasters are treated as one group (mean ± SE).

Also the GH levels of the adult blue foxes declined to lower levels in July. During the early autumn the concentrations of the puppies remained fairly low and variable. There were no differences between the GH levels of the adults and the pups. At the beginning of November the GH levels of the control blue foxes increased significantly (Mann-Whitney U test, $p < 0.01$) and stayed at a higher level during the rest of the study (Fig. 3, Table II). The GH levels of the fasting blue foxes were significantly lower compared to the controls in Nov 16th (Mann-Whitney U test, $p < 0.018$), but the concentrations increased in late November (Mann-Whitney U test, $p < 0.014$).

Discussion

Our result show a rapid body mass gain of the raccoon dogs and the blue foxes in July-October followed by a steady-state period. This finding is in concordance with the previous results of Korhonen (1988). Seasonal periodicity in the pattern of the gain and loss of body weight is characteristic to both species even when raised in a standard environment with a constant supply of a balanced diet. The autumnal body weight gain mainly results from the increased deposition of subcutaneous fat, which serves as an energy reserve and provides the animals with thermal insulation. At the beginning of the fast the animals of both species had a similar mean body mass. During the fast, however, the blue foxes lost body mass at a higher rate than the raccoon dogs, which normally spend the coldest part of the winter in winter sleep (Heptner *et al.,* 1974). The raccoon dog thus appears to be better adapted to a total fast compared to the actively wintering blue fox.

Table II. Mean weight (kg) and plasma GH concentrations (ng/ml) ± SE of the eleven blue foxes. November 2nd 5 individuals were put to a total three-week fast and the remaining six animals continued to feed on the standard diet. Three of the blue foxes were adults, the others juvenile animals born the same spring.

Time	Weight [kg]	GH [ng/ml]
VI	6.17 ± 0.25 C	4.0 ± 0.79
VII	3.18 ± 0.60 AB	1.0 ± 0.35
VIII	5.59 ± 0.27 BC	1.4 ± 0.49
IX	8.27 ± 0.33 D	1.5 ± 0.28
X	10.10 ± 0.36 DE	1.1 ± 0.22
Nov. 2.	11.02 ± 0.44 GH	0.9 ± 0.19
Nov. 9. controls	11.77 ± 0.49 HI	1.7 ± 0.16*
Nov. 16. controls	11.09 ± 0.27 I	1.7 ± 0.08†‡
Nov. 16. fasting	9.36 ± 0.68 DEFG	1.2 ± 0.16†
Nov. 23. controls	11.20 ± 0.24 HI	1.5 ± 0.06
Nov. 23. fasting	8.65 ± 0.70 DEF	1.6 ± 0.04‡*
Dec. 7. controls	11.48 ± 0.24 HI	2.3 ± 0.25*‡
Dec. 7. fasting	9.89 ± 0.70 DEFGH	1.5 ± 0.11‡

The means with no common letter differ at $p < 0.05$ (ANOVA *post hoc* Duncan's test). * = statistically significant difference from the previous measurement of the same experimental group (Mann-Whitney U test, $p < 0.05$). † = statistically significant difference between the control group and the fasting group (Mann-Whitney U test, $p < 0.05$). ‡ = statistically significant difference from the GH concentrations of November 2nd (Mann-Whitney U test, $p < 0.05$).

Table III. The mean BMIs and body lengths of the raccoon dogs and the blue foxes ± SE at the end of the experiment, Dec. 7th, 1999.

	BMI [kg/m^3]	Length [cm]
Raccoon dogs	32.5 ± 1.0	68.5 ± 0.5
Blue foxes	30.1 ± 1.5	71.2 ± 1.1

The plasma GH concentrations of the raccoon dogs and the blue foxes fluctuate during the autumn. Seasonal fluctuations in GH concentrations have also been reported in some northern ungulate species. The GH levels of the Norwegian reindeer (*Rangifer tarandus tarandus*) reflect strong seasonal changes. The concentrations are the highest from late winter to early spring (Ryg and Jakobsen, 1982). Also the GH levels of the Spitzbergen reindeer (*Rangifer tarandus platyrynchus*) are higher during the winter compared to the levels during the summer (Ringberg, 1979).

The GH levels of the adult animals were relatively high in the early summer. This might reflect a vernal growth peak and weight gain of sexually mature animals. There were, however, slight differences in the GH levels between the animals of different age. In July and in October the GH levels of the adult raccoon dogs were higher compared to the pups. In the blue foxes no such difference could be seen. The GH concentrations did not correlate with the weight gain of the animals, which has also previously been described in the Norwegian reindeer (Ryg and Jakobsen, 1982). It is intriguing that the GH levels of the raccoon dogs and the blue foxes increase in late autumn when the animals have already achieved their maximum body weight and length. Also the lack of differences in the GH levels between the adults and rapidly growing puppies remains to be explained.

Fasting did not affect the GH concentrations of the raccoon dogs. In the blue foxes, however, the GH levels of the fasters were slightly lower compared to the controls two weeks after the beginning of the fast. GH is known to stimulate gluconeogenesis (Brück, 1983) and, on the other hand, hypoglycemia caused by prolonged fasting elevates the circulating GH levels of humans (Roth *et al.,* 1963). In this regard the blue foxes are different in their response to fasting when compared with the species studied previously. GH acts together with other hormones (cortisol etc.) in the neuroendocrine response to fasting enhancing gluconeogenesis and e.g. lipolysis to mobilize the energy reserves needed. The strategy of the blue fox and the raccoon dog to regulate GH secretion in order to overcome periods of energy shortage thus seems to be different from e.g. humans.

The GH levels of the adults and puppies of the both species were, however, elevated in November-December. The earlier increase in the GH levels of the blue foxes may be associated with the more northern geographical distribution of the arctic fox compared to the raccoon dog. It is known e.g. that the winter pelage of the farm-bred blue fox generally matures earlier compared to the raccoon dog (Juha Asikainen, personal communication 2000).

The control blue foxes experienced rising GH levels as the average daily temperature dropped below freezing for the first time in early November (Fig. 1). After a short period of thaw the fasting blue foxes and all the raccoon dogs reacted similarly as more severe cold period S began. During the periods of stress such as starvation (Roth *et* *al.*, 1963) or exposure to cold (Ollsch and Trenkle, 1973) the levels of GH are often elevated as a part of the physiological response to stress. Another possibility is the shortening photoperiod and the increase in melatonin secretion during the dark season. In humans it has been observed that melatonin causes rapid and significant elevations in the serum GH levels (Smythe and Lazarus, 1974). As the GH levels of the blue foxes increased with decreasing temperature and photoperiod but not with fasting, the GH secretion of the species may be regulated by endogenous circannual rhythms entrained by an exogenous *Zeitgeber* rather than by e.g. hypoglycemia induced by fasting.

In the raccoon dogs fasting had no effect on the GH levels. The increase in the GH concentrations was seen in early December about two weeks after the fasting group had resumed feeding. This increase coincided with the beginning of the third cold period (Fig. 1). In this respect the response of the raccoon dogs is similar to the blue foxes suggesting endogenous regulation of GH secretion entrained either by the photoperiod and melatonin secretion or by the ambient temperature. The autumnal melatonin levels of the raccoon dog are known to be the highest in November (Xiao, 1996).

GH might also have a function in the seasonal winter sleep of the raccoon dog. It is known to regulate the sleep of mammals (Toppila, 1999) and the circadian GH secretion peak coincides with deep sleep (Brück, 1983). It has also been observed in transgenic TRrGH mice with abnormally high GH levels that the extra GH causes lethargy and increases the amount of circadian sleep by 3.4 h/d (Lachmansingh & Rollo, 1994). Thus, the increasing GH levels in the raccoon dog could contribute to the winter sleep by decreasing physical activity and increasing the amount of circadian period of sleep. Furthermore, the elevation of the GH levels of the raccoon dogs occurred at the beginning of December (Fig. 2, Table I) and this rise was connected to the suppression of the plasma thyroxine concentrations (Nieminen *et al.*, 2001). The lower thyroxine levels may be associated with metabolic suppression during the winter sleep. The blue fox does not exhibit winter sleep but also its activity levels fall during the winter and contribute to energy preservation helping the animal to overcome the period of inadequate nutrition.

GH is known to increase lipolysis and to inhibit triglyceride accumulation in mammals (Richelsen, 1997). According to this study GH may have a role in maintaining the energy balance of wintering raccoon dogs and blue foxes by promoting lipolysis and gluconeogenesis. A role for GH in winter energy metabolism has also been suggested in the Spitzbergen reindeer (Ringberg, 1979). The GH levels of the blue foxes rise earlier compared to the raccoon dogs, probably due to the more northern geographical distribution of the species. The raccoon dog spends its winter in shallow winter sleep. Fasting had no effect on its GH levels but the increase in the GH concentrations in early December in both the control and the fasting group indicates photoperiodic or temperature-dependent control for the autumnal GH secretion mediated perhaps via melatonin or the ambient temperature.

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