

Influence of different planes of energy supply prior to the breeding season on blood metabolites in female mink (*Mustela vison*)

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Abstract – Metabolic blood profiles were studied in a total of 30 female mink (*Mustela vison*) at different planes of nutrition prior to the breeding season in a control (CON; $n = 10$), a flushed (FLUSH; $n = 10$) and a negative energy balance group (NEG; $n = 10$). The animals were kept in metabolism cages or under normal farm conditions, respectively. The experiment, which was divided into six 1-week periods, started on 6 February and continued until 20 March. Flushing was performed by restricted feeding in periods 2 and 3 and refeeding in periods 4 and 5. The animals were weighed weekly and blood sampled at the end of periods 1, 2 and 4, 1 week after changes in the food supply of the FLUSH group. Plasma was analysed for insulin, insulin-like growth factor-1, total triiodothyronine, total thyroxine, free thyroxine, glucose and fructosamine. Generally, within the FLUSH group, animal live weights and blood metabolites were strongly influenced by energy supply, these variables remained almost constant in the CON group. In the NEG group the live weight, total triiodothyronine, total thyroxine, insulin and glucose concentrations decreased significantly. Differences in blood metabolites between the FLUSH and CON groups were non-significant, reflecting only small differences when considered over the total experimental period, thus reflecting an acute response to a varied energy supply, while the differences between the NEG group and the CON and FLUSH groups were significant, indicating a considerable chronic response in all metabolites to a constantly low energy supply. © Inra/Elsevier, Paris

energy supply / live weight / insulin / IGF-1 / thyroid hormones

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Résumé – Effet de différents apports énergétiques sur le métabolisme du vison. Trois niveaux nutritionnels (contrôle ; CON, supplémenté : FLUSH, rationné : NEG) ($n = 10$ femelles par groupe) ont été fournis à des visons avant la saison sexuelle et les conséquences de ce rationnement sur des marqueurs métaboliques ont ensuite été étudiées. Les animaux étaient soit en cage-métabolisme soit en conditions de terrain. Au cours de l'expérience (d'une durée de 6 semaines), les animaux subissaient une pesée hebdomadaire et des prélèvements sanguins à la fin des première, deuxième et quatrième semaines. Le flushing était réalisé au cours des quatrième et cinquième semaines après un rationnement au cours des 2 semaines précédentes. Les paramètres mesurés étaient l'insuline, l'IGF₁, la triiodothyrosine, la thyroxine totale et libre, le glucose et la fructosamine. Dans le lot CON, les variables étudiées étaient stables alors que dans le FLUSH, les poids vifs et les métabolites sanguins étaient modifiés par l'apport alimentaire. Dans le lot NEG, la triiodothyronine, la thyroxine totale, l'insuline et le glucose présentaient des niveaux diminués. D'une façon générale, les différences entre les lots CON et FLUSH étaient réduites et non significatives alors que celles entre le NEG et les deux autres étaient plus marquées, montrant l'importance d'une restriction chronique de l'apport alimentaire. (© Inra/Elsevier, Paris.)

apport énergétique / poids vif / insuline / IGF₁ / hormones thyroïdiennes

1. INTRODUCTION

The mink is a seasonal breeder, with one annual breeding season concentrated within a very limited time period of about 3 weeks in March in the northern hemisphere. For experimental purposes this is favourable since it makes it possible to study a considerable group of animals simultaneously. Moreover, the mink responds to changes in energy supply by rapid increase and decrease in body weight, and it is well-documented that energy supply and body condition have a profound influence on the reproductive processes [29]. Because of this, the mink may serve as a suitable experimental model for other species regarding interaction between energy supply, concentrations of blood metabolites and reproductive performance.

Responses to changes in nutritional status generally fall into two categories, those that occur within a few days (acute) and those that occur after several days or weeks (chronic). Chronic effects are nearly always associated with major shifts in body condition, while acute responses to nutrition include short-term increases in dietary energy supply, flushing [11]. Flushing is defined as a period of restricted

feeding followed by refeeding, preceding the oestrous period or breeding season [13], and occurs over such a short period that there is usually not a significant change in female body composition [5, 11]. Flushing has shown positive effects on reproductive performance in different species (gilt: Flowers et al. [18]; Beltrarena et al. [5]; ewe: Haresign [21] and mink: review by Tauson [29]), and because of responsiveness to nutritional changes, it has been hypothesized that some metabolic factors may provide the links between nutrition and reproduction [23].

Insulin, stimulated by glucose administration and suppressed by under-nutrition, may be a candidate for metabolic signalling to the reproductive system. Previous studies with sheep [22] and mink [17] demonstrated a close relationship between food intake and insulin concentration. Similar responses in IGF-1 concentrations have been seen in beef heifers [34] and pigs [5]. Blood glucose is the primary energy substrate used at the cellular level, and reduced concentrations may influence body composition [26].

Results by Tauson [30] indicated that, as in for instance the red deer [24], thy-

roid hormones may be involved in the seasonal regulation of food intake also in the mink, and that plasma concentration of triiodothyronine (T_3) and thyroxine (T_4) [17] varies in the same way as that of insulin secretion in response to changes in energy supply, confirming results in pigs by Evans and Ingram [16]. Fasting is thus associated with low secretion rates and low plasma concentrations of T_3 and T_4 [2, 25, 26, 33].

Knowledge of the interaction between energy supply and blood metabolites is a very important component in the understanding and explaining of the reproductive response to different planes of energy supply, and especially flushing. In the present investigation the female mink was used as an experimental model in order to further elucidate the mechanisms underlying a chronic (low energy supply) or an acute (flushing) response to nutritional status as monitored by some blood metabolites which are believed to be important in signalling nutritional status to the reproductive axis.

2. MATERIALS AND METHODS

The influence of different planes of nutrition on some blood metabolites and animal performance during a conditioning period prior to the breeding season was studied in 30 yearling female mink of the standard black (Scanblack) colour type, for 12 of them in the laboratory

by means of balance and respiration experiments, results from which study will be reported elsewhere, and for the remaining 18 females under normal farm conditions (55° N, 12° E).

Weighing and grouping of the animals into a control group (CON) (pursued to be in energy balance), a flushed group (FLUSH) and a third group (NEG) (pursued to be in negative energy balance) was carried out in late January. The experiment was divided into six 1-week periods starting on 6 February and continuing until 20 March. Details on the experimental design are given in *table I*.

The food was purchased from a commercial mink food kitchen (Stårup fodercentral, Højby Sjælland) on a single occasion and weighed out into daily portions in plastic bags and immediately frozen. Food was taken out of the freezer the day before use and thawed over night. Analysed chemical composition of the diet is given in *table II*. Collection of food residues was carried out once a day and the amount of food consumed was calculated for the individual animals. The food supply of 200 g per animal and day for the CON group corresponded to ca 850 kJ metabolizable energy (ME) \cdot d $^{-1}$ and was supposed to provide ad libitum food supply. For the FLUSH group food supply during the restriction periods 2 and 3 corresponded to ca 450 kJ ME \cdot d $^{-1}$ and in the refeeding periods 4 and 5 to ca 1 300 kJ ME \cdot d $^{-1}$. The daily food supply of 125 g for the NEG group corresponded to ca 525 kJ ME \cdot d $^{-1}$.

The animals were weighed weekly at the end of each period. Blood samples, by puncture of Vena cephalica antebrachii as described by Blixenkroner-Møller et al. [7], were taken at the end of periods 1, 2 and 4, the two latter occasions corresponding to 1 week after

Table I. Daily food supply (g \cdot animal $^{-1}$ \cdot d $^{-1}$) in the six experimental periods for mink females given food ad libitum (CON), food restricted and re-fed (FLUSH) and food restricted (NEG).

Period	Treatment		
	CON	FLUSH	NEG
1	200	200	125
2-3	200	100	125
4-5	200	300	125
6	200	200	125

Table II. Results of chemical analyses of the diet.

Chemical composition	
Dry matter (DM), g·kg ⁻¹	307
Ash g·kg ⁻¹ DM	111
Crude protein, g·kg ⁻¹ DM	567
Fat, g·kg ⁻¹ DM	157
Gross energy, MJ·kg ⁻¹	22.6

changes in the food supply of the flushing group took place. To avoid diurnal variation in hormone concentrations, blood was sampled from 0900 to 1130 hours and collected into heparinized tubes. The separated plasma was stored in plastic tubes at -18 °C until assay.

Plasma samples were analysed for total triiodothyronine (TT₃), total thyroxine (TT₄) and free thyroxine (FT₄) by use of a commercial chemiluminescence immunoassay (Amerlite, Johnson and Johnson, Amersham, UK). Serial dilutions of mink plasma with high concentrations of TT₃, TT₄ and FT₄ produced displacement curves parallel to the standard curves of the respective assays. The within assay coefficients of variation for TT₃ were below 10 % for all concentrations, and the corresponding between assay coefficients of variation were 21.8 % for samples with low concentration (mean = 1.1 nmol·L⁻¹) and 10.2 % (mean = 3.0 nmol·L⁻¹) and 8.0 % (mean = 6.1 nmol·L⁻¹) for samples with medium and high concentrations, respectively. For TT₄ the within assay coefficients of variation were 14.3 % for samples with low concentration (mean = 6.0 nmol·L⁻¹), 6.0 % (mean = 20.6 nmol·L⁻¹) for medium concentrations and 4.1 % (mean = 73.4 nmol·L⁻¹) for samples with high concentration, and the between assay coefficients of variation were 26.1 % for low, 3.6 % for medium and 5.0 % for high concentrations, respectively. For FT₄, finally, within assay coefficients of variation were below 10 % for all concentrations, and the corresponding between assay coefficients of variation were 18.8 % for samples with low concentration (mean = 12.2 pmol·L⁻¹), and below 10 % for samples with medium (mean = 21.9 pmol·L⁻¹) and high (mean = 41.9 pmol·L⁻¹) concentrations, respectively. Plasma concentrations of insulin were determined by radio immunoassay (Pharmacia insulin RIA, Kabi-Pharmacia, Upp-

sala, Sweden). Serial dilutions of mink plasma containing high concentrations of insulin produced a dose-response curve parallel to the standard curve. The within assay coefficients of variation for quality control samples were 5.4 % (mean = 12 µU·L⁻¹), 5.3 % (mean = 42 µU·L⁻¹) and 5.3 % (mean = 117 µU·L⁻¹). The corresponding between assay coefficients of variation were 7.8, 2.2 and 6.7 %. IGF-1 was determined by radioimmunoassay according to the manufacturers recommendations (IGF-1, cat. no.: 53065, Incstar Corporation, Stillwater, MI, USA). Plasma was extracted with ODS-silica columns before assay. Serial dilutions of mink plasma with high concentrations of IGF-1 produced displacement curves parallel to the human standard curve. The within assay coefficient of variation, calculated from the precision profiles of five assays, was below 12 % for IGF-1 concentrations between 2.9–82.5 nmol·L⁻¹. The between assay coefficients of variation for two control samples were 19 % (mean = 10 nmol·L⁻¹) and 21 % (mean = 28 nmol·L⁻¹). The minimum detectable amount of IGF-1 was set to 2 nmol·L⁻¹ (average 10 % fall from '0'-binding of five assays). Plasma glucose and fructosamine concentrations were analysed in a computerized multichannel spectrophotometer (Cobas Mira, Hoffmann-La Roche & Co., Switzerland). Analysis of glucose was performed according to Bondar and Mead [8] and fructosamine was analysed by measuring formazane at 550 nm [4]. The between assay coefficients of variation were 1.6 and 3 %, respectively.

Statistical analyses were carried out according to the GLM procedure of SAS [28]. The dependent variables were analysed according to a model comprising the fixed effects of treatment group and period, the interaction between treatment group and period and random animal within treatment group. When evaluating effects of treatment group, animal within treatment group was used as error term. Results are given as least-squares means.

3. RESULTS

3.1. Food intake and animal live weights

The food intake was fairly stable in the CON group with an average of 180 g

(range 152–196) and in the NEG group, in which the total supply was consumed, hence 126 g (range 124–132). The intake being above 125 g is explained by the fact that the food allowance had to be raised in period 6 since weight losses in some of the animals were too large. The FLUSH group consumed the total food allowance (100 g) during restriction in periods 2 and 3 and about 35 % above the level in the CON group (242 g) during the first week

of flushing in period 4. The following week (period 5), food intake decreased to under the level of the CON group (143 g) (*figure 1a*).

Animal live weights were almost stable in the CON group with an average of 1.165 kg (range 1.155–1.184). The live weights in the FLUSH group decreased ($P < 0.001$) from 1.158 kg to 1.026 and 0.949 kg during the restriction in periods 2 and 3, and then increased ($P < 0.001$)

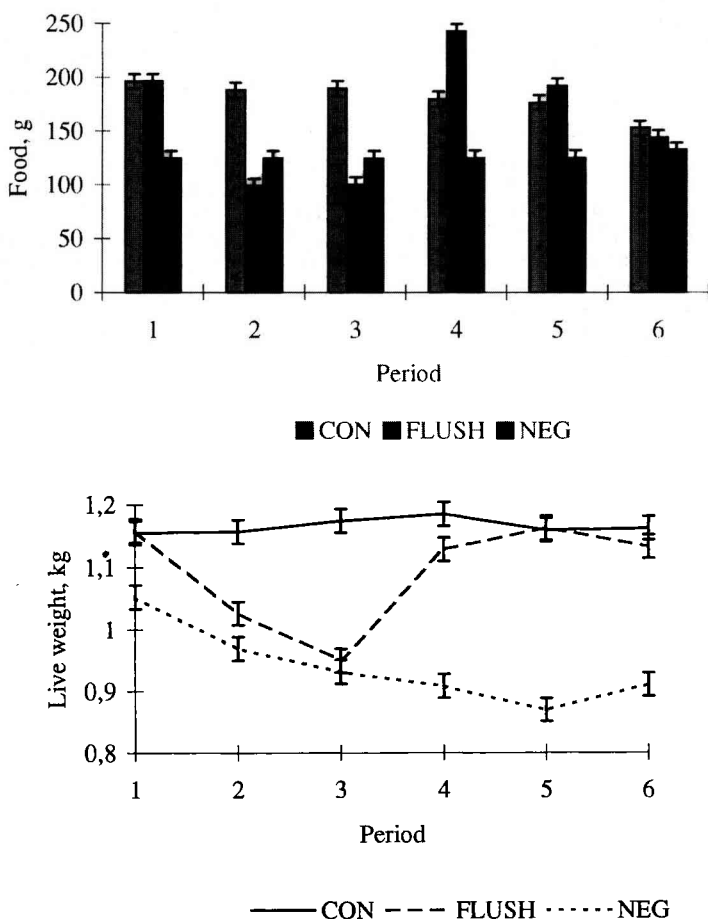


Figure 1a, b. Food consumption and animal live weights during the six experimental periods for mink females given food ad libitum (CON), food restricted in periods 2 and 3 and refed in periods 4 and 5 (FLUSH), and restricted during periods 1–6 (NEG), respectively.

to 1.162 kg during flushing in period 5. The live weight in the NEG group decreased significantly ($P < 0.001$) from 1.052 kg in period 1 to 0.909 kg after period 6 (*figure 1b*).

3.2. Blood metabolites

Plasma concentrations of the analysed blood metabolites are presented in *table III*. The TT_3 and TT_4 concentrations remained almost constant in the CON group, while the values in the FLUSH group decreased significantly (TT_3 ; $P = 0.01$) and (TT_4 ; $P = 0.001$), respectively, during restriction in period 3 and increased (TT_3 ; $P < 0.001$), (TT_4 ; $P < 0.001$) during refeeding in period 5. Also the FT_4 concentrations were significantly ($P = 0.03$) lower in period 3 than in period 1 in the FLUSH group. The insulin concentration in plasma was almost constant for the CON group. In the FLUSH group it decreased ($P = 0.05$) and increased ($P = 0.04$) significantly during restriction and refeeding, respectively. Plasma concentration of IGF-1 was also fairly stable in the CON group, but decreased ($P = 0.006$) and increased ($P < 0.001$) significantly during restriction and refeeding, respectively, in the FLUSH group. Despite the values being significantly different between periods within the FLUSH group (*table III*), there were no significant differences between the CON and FLUSH groups when data were considered over the total experimental period. For the NEG group the values for TT_3 , TT_4 , insulin and glucose decreased significantly ($P < 0.05$) from period 1 to the end of the experiment in period 6. Values for fructosamine showed no significant differences both when considered within group between periods, and between treatment groups (*table III*). Only values for TT_3 were significantly different between all treatment groups ($P < 0.02$).

4. DISCUSSION

The differences in body weight and plasma metabolite concentrations were significant between periods in the FLUSH group, but not between the FLUSH and the CON groups when considered over the total experimental period, confirming that flushing is an acute response [11] inducing fluctuation in energy status, hormone and metabolite concentrations of the animal despite absence of major changes in the total nutritional status or body reserves. However, the responses in the NEG group were chronic and associated with considerable shifts in live weight and body condition [11], leading the differences between treatment groups to be significant.

The metabolizable energy requirement for maintenance (MEM) has been estimated to be $527 \text{ kJ}\cdot\text{kg}^{0.75}$ for adult male mink in positive energy balance and in termoneutral zone (20°C) [14]. In relation to this, the food supply in the CON group should sustain maintenance requirements, which was confirmed by the animals' fairly constant live weights. The decrease and increase in animal live weights in the FLUSH group indicated that the food intake was less than required for maintenance during restriction, while the energy intake during the refeeding exceeded the requirement. These results were in agreement with calculations on substrate oxidation in animals exposed to a similar feeding regime [31] which showed a high level of fat oxidation during periods of restriction, whereas protein oxidation provided the major contribution to the total heat production when the food supply was ample, and with results by Fink and Tauson [17] showing negative values for retained energy and weight loss during the restriction period preceding refeeding in flushed animals. The weight losses during the experiment in the NEG group confirmed that the animals were in

Table III. Plasma concentrations (\pm SEM) of total triiodothyronine (TT₃), total thyroxine (TT₄), free thyroxine (FT₄), insulin, insulin-like growth factor I (IGF-I), glucose and fructoseamine for mink females given food ad libitum throughout the six experimental periods (CON), food restricted in periods 2 and 3, and re-fed in periods 4 and 5 (FLUSH) and food restricted in periods 1–6 (NEG).

	Treatment								
	CON			FLUSH			NEG		
	Ad libitum	Ad lib.	Restriction	Restriction	Flushing	Restriction	Restriction	Restriction	
TT ₃ , nmol·L ⁻¹	0.59 ± 0.05	0.66 ± 0.04	0.61 ± 0.07	0.57 ^a ± 0.08	0.41 ^b ± 0.08	0.69 ^c ± 0.04	0.54 ^a ± 0.04	0.40 ^b ± 0.07	0.26 ^c ± 0.08
TT ₄ , nmol·L ⁻¹	16.6 ± 1.40	17.5 ± 1.20	18.5 ± 1.98	18.8 ^a ± 1.15	13.3 ^b ± 1.11	18.8 ^a ± 1.55	20.8 ^a ± 2.13	17.1 ^b ± 1.25	17.6 ^{ab} ± 1.62
FT ₄ , pmol·L ⁻¹	21.1 ± 0.88	21.5 ± 1.03	21.9 ± 0.86	22.4 ^a ± 0.85	20.7 ^b ± 0.68	21.9 ^{ab} ± 0.97	23.4 ± 0.88	23.2 ± 0.96	23.9 ± 1.40
Insulin, μ U·L ⁻¹	7.3 ± 0.69	8.6 ± 1.25	8.6 ± 1.01	9.2 ^a ± 1.55	5.2 ^b ± 0.93	9.2 ^a ± 1.00	11.0 ^a ± 2.58	5.5 ^b ± 0.94	5.9 ^b ± 1.06
IGF-I, nmol·L ⁻¹	34.3 ± 5.78	36.8 ± 4.81	34.0 ± 3.54	39.8 ^a ± 5.58	24.0 ^b ± 3.22	45.7 ^a ± 5.45	29.2 ± 3.12	27.9 ± 5.08	23.2 ± 3.16
Glucose, mmol·L ⁻¹	10.1 ± 0.73	12.7 ± 0.86	11.9 ± 0.74	9.5 ± 1.33	11.2 ± 1.90	10.4 ± 0.55	9.8 ^{ab} ± 0.65	10.7 ^b ± 0.49	8.3 ^a ± 0.41
Fructosamine, μ mol·L ⁻¹	286 ± 17.1	320 ± 18.6	308 ± 25.2	273 ± 21.9	296 ± 29.3	262 ± 7.4	297 ± 18.2	282 ± 17.6	273 ± 19.1

Samples were taken at the end of periods 1, 2 and 4, the two later occasions corresponding to 1 week after changes in food supply of the FLUSH group took place. a-c Values that share no common superscript differ significantly ($P < 0.05$) between periods within the FLUSH and NEG groups, respectively.

negative energy balance. However, the weight losses in the NEG group occurred at a slower rate than the rapid weight loss imposed by the restriction in the FLUSH group, which may indicate that the low rate of weight loss was caused by an adaptation of the basal metabolism to a constantly low energy supply [6].

Data on effects of food supply on metabolic hormones are scarce for mink, and therefore few within species comparisons can be made. In other species (pigs: Flowers et al. [18], Beltranena et al. [5]; lambs: Hileman et al. [22]) changes in insulin, IGF-1 and glucose by flushing have been demonstrated. Thus, the close relationship between food intake and plasma concentrations of insulin found here confirm results in lambs by Hileman et al. [22] showing direct proportionality between insulin and level of food intake, and own previous results in mink [17]. In the NEG group the insulin concentration decreased to a very low level confirming [1] that insulin is suppressed by under-nutrition.

No previous results on IGF-1 concentrations in mink have, to our knowledge, been presented in the literature, but our results showed that in mink, as in other species, (pig: Buonomo and Baile [12]; heifer: de Boer et al. [15]; Granger et al. [20], I'Anson et al. [23], and human: Thissen et al. [32]; Yambayamba et al. [34]) the plasma IGF-1 concentrations are responsive to nutritional changes, decreasing and increasing during restriction and realimentation, respectively. Plasma IGF-1 concentrations, however, responded more slowly to change in food intake than that of insulin, which is in agreement with the concept that, compared with insulin, plasma IGF-1 would be a longer-term mediator of metabolic effects on reproduction [9].

The significant differences in TT₃ and TT₄ concentrations in the FLUSH, and the stable level in the CON group, confirm

our own previous results in mink [17], pig [16] and sheep [27] showing that fluctuations in TT₃ and TT₄ are regulated not only by seasonal variations, but also in close interaction with food intake. In the NEG group TT₄ and especially TT₃ decreased, which is in agreement with results from several workers who showed that fasting is associated with low secretion rates and low plasma concentrations of T₃ and T₄ [2, 17, 25, 26, 33]. The low concentrations of thyroid hormones and the slow rate of weight loss in the NEG group are in agreement with the hypothesis, that the animals can adapt their basal metabolism to changes in energy supply, and thus help the organism to survive periods of scarcity.

Generally, the plasma glucose concentration was high compared with values found in mink fitted with permanent catheters [10], which probably was caused by the handling in connection with blood sampling (mink: Børsting and Damgaard [10] and rat: Gärtner et al. [19]). The differences in glucose were, however, small throughout the experiment, confirming the results of Armstrong and Britt [3] showing that homeostatic mechanisms maintain plasma glucose concentrations within fine limits, and therefore even during chronic under-nutrition and weight loss, plasma glucose concentrations may be normal. Fructosamine may be a useful indicator for long-term nutritional status of an animal, but in our experiments (present data and Fink and Tauson [17]) it has not been shown to be responsive to the levels or time periods applied for the varied food supply.

In conclusion, the present investigation implies that, acute metabolic responses include rapid changes in live weight and plasma concentrations of insulin, and somewhat slower responses in IGF-1 and thyroid hormones. Chronic responses to a low energy supply include loss of body weight and body fat reserves, however, at

a slower rate than caused by an acute response. Metabolic status could be monitored by decreased plasma concentrations of insulin, IGF-1 and thyroid hormones, confirming results found in other species and thus suggesting that the mink may be used as a suitable model for studies both on acute and chronic responses to nutritional status.

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