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Effect of high-fat diet on body mass and energy balance in the bank vole

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Abstract

We tested the hypothesis that animals that reduce their body mass in response to decreased photoperiod do not develop diet-induced obesity (DIO) when fed a high-fat diet (HFD). Bank voles (*Clethrionomys glareolus*) fed a diet with fat content of 13.5% by mass and 28.2% by energy, for 5 weeks, did not develop hyperphagia and were resistant to DIO, consistent with predictions. There was no significant difference between food (g/day) or energy intake (kJ/day) between the experimental or control group (fed a standard diet with fat content of 5.4% by mass and 12.3% by energy) over the duration of the experiment. However, as a result of a higher apparent energy assimilation efficiency (AEAE), voles fed the HFD assimilated significantly more energy over the 5-week period. Furthermore, they consumed twice as much fat per day as controls. There were no significant differences in resting metabolic rate (RMR) over time or between groups over the 5-week period. In conclusion, bank voles achieved resistance to DIO despite assimilating more energy than control animals fed the standard diet and taking in twice as much fat. Resistance did not occur by modification of RMR, implicating differences in activity levels.

Keywords: Diet-induced obesity; High-fat diet; Resting metabolic rate (RMR)

1. Introduction

It has been suggested that animals that display different strategies in seasonal variation in fat deposition also show contrasting responses to a high-fat diet (HFD) [1]. Those species that increase their body or fat mass in response to a decrease in photoperiod (e.g., the collared lemming, *Dicrostonyx groenlandicus* [2], and the Syrian hamster, *Mesocricetus auratus* [3]) also develop diet-induced obesity (DIO) when fed an HFD [3]. Conversely, species that exhibit a decrease in body or fat mass in response to short day lengths (e.g., Shaw's jird, *Meriones shawi* and the Siberian hamster, *Phodopus sungorus sungorus*) do not appear prone to obesity when fed an HFD [1,4].

The mechanisms involved in body mass responses to photoperiod and diet in seasonal rodents are relatively unexplored in species other than the Siberian and Syrian hamster. The reduction in body mass in response to decreased photoperiod of at least two rodent species precedes or is not dependent on a reduction in food intake [5,6]. Furthermore, when fed a diet high in fat, Syrian hamsters develop obesity without a corresponding increase in food intake [7] and conversely Siberian hamsters develop hyperphagia with no gain in body mass [4]. These observations suggest that changes in energy expenditure rather than energy intake may be of primary importance in the regulation of body mass and fat balance in the seasonal responses of these animals.

Variation in resting metabolic rate (RMR), a major component of total energy expenditure, may be important in the regulation of energy balance in response to changes in diet or photoperiod [2,5]. The aim of our experiment was to determine the effects of an HFD on the body composition, food intake, RMR, and apparent energy assimilation efficiency (AEAE) of bank voles (*Clethrionomys glareolus*). This species exhibits a decrease in body mass in response to a decrease in photoperiod [8] and were, therefore, expected not to develop DIO in response to an HFD. In addition, we hypothesised that resistance to obesity would involve adjustments of RMR, or some other component of energy expenditure rather than, or instead of, a decrease in food intake.

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2. Methods

2.1. Animals

Thirty-nine bank voles (20 males, 19 females) aged 3–5 months were selected from a laboratory breeding colony, which were maintained in a 12L:12D photoperiod at an ambient temperature of 20 ± 2°C. From weaning, voles were kept in single-sex cages of 4–6 individuals and supplied pelleted Rodent Maintenance Diet 3 (RM3 — Special Diets Services) and water ad libitum. One week before the preexperimental measurements were measured, voles were separated, housed individually in cages (28 × 11 × 12 cm), and randomly assigned a number. The HFD used in the experiment was in meal form, therefore, a glass jar containing ground RM3 was placed inside each cage 4 days before the beginning of the experiment to allow animals to adjust to the new feeding method. Animals appeared to have no difficulties feeding from these jars. The voles were divided into two groups matched for body mass: six males and six females formed the control group while all other animals (n = 14 males, 13 females) were the experimental group.

2.2. Experimental design

The following preexperimental measurements were made to ascertain any differences between the two groups at the beginning of the experiment. Body mass and food intake were measured daily over a period of 5 days, during which time faecal samples were collected for energy analysis. RMR and body composition were recorded the following week. RMR was measured once for each animal using an open circuit respirometry system (Servomex) as previously described in Redman et al. [9]. Access to food and water was not denied before respirometry measurements were taken. Voles were placed in a sealed Perspex chamber within an incubator (INL-401N-010, Gallenkamp) at a temperature of 25 ± 0.5°C, which is within the thermoneutral zone of these animals. Air was dried using silica gel (BDH, UK) and pumped through the system (Charles Austin Pumps) at a rate of 400–600 ml/min (Alexander Wright flowmeter DM3A). A 150-ml sample of dried excurrent air was subsequently passed through an oxygen analyser and the mean measurements recorded on a microcomputer at 30-s intervals. Carbon dioxide was not absorbed prior to gas analysis to minimise error in the conversion of oxygen consumption to energy expenditure [10]. The 10 lowest consecutive readings, equivalent to 5 min within the respirometry chamber, were used to estimate RMR for each measurement, using the appropriate equation from Hill [11], with values corrected for temperature and pressure. Body composition was measured using total body electrical conductivity (TOBEC) with an ACAN-2 small animal body composition analyser (Jagmar, Poland). All TOBEC measurements were taken at an ambient temperature of 20 ± 2°C immediately prior to respirometry.

Immediately before the diet was changed, the body composition of all animals was measured. A known quantity of approximately 60 g of either HFD or standard RM3 (control group) was then supplied. For comparison of diet specifications, see Table 1. The following experimental regime was carried out over the next 5 weeks: body mass and food intake were recorded daily over a 4-week period; RMR and body composition (by TOBEC) were measured in Weeks 2 and 5; and faecal samples were collected over a period of 5 days in Week 4 to establish any differences in the digestibility between the two types of diet.

2.3. Energy analysis

The gross energy (GE) content of each diet and of faecal samples from 10 individuals (five from each group; collected during the preexperimental and 4-week collection periods) were measured by adiabatic bomb calorimetry. Dry mass digestibility (DMD) and AEAE were then determined as (Eqs. (1) and (2)):

$$\mathrm{DMD} = \frac{\text{Dry food intake (g)} - \text{Dry faeces mass (g)}}{\text{Dry food intake (g)}} \quad (1)$$

$$\mathrm{AEAE} = \frac{(\text{Dry FI} \times \text{GE food}) - (\text{Dry faeces mass} \times \text{GE faeces})}{(\text{Dry FI} \times \text{GE food})} \quad (2)$$

where FI = food intake.

2.4. TOBEC calibration

The use of TOBEC for the calculation of body composition relies on a calibration equation, which is both machine- and species-specific [12]. For this reason, a predictive equation for bank voles was formulated. TOBEC indices were taken for 38 animals. They were then sacrificed, their brains removed (for neuroendocrinological analyses), and the remaining carcasses dried in an oven at 60°C for 2 weeks until a stable dry mass was obtained. Fat was extracted from the carcasses, using the Soxhlet method, to determine the lean mass that was then subtracted from the total body mass to calculate the fat mass. Because we removed the brains prior to composition

Table 1
Comparison of dietary specifications of the HFD and standard diet

Nutrient	HFD	Standard diet
GE (kJ/g)[a]	18.93	17.33
Total fat (% by mass)[a]	13.45	5.39
Total fat (% by energy)[a]	28.16	12.31
Carbohydrate (%)	46.00	51.20
Crude protein (%)	22.30	19.19
Crude fibre (%)	3.73	4.50
Ash (%)	6.03	7.70

[a] Analysis carried out at the Rowett Research Institute, Aberdeen. All other nutrients analysed by SDS.

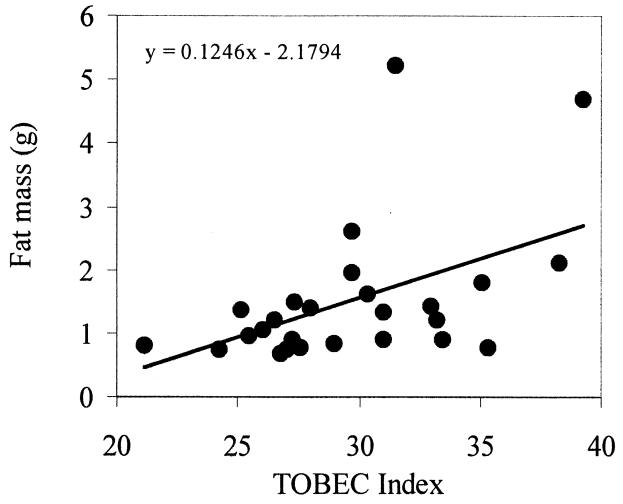

Fig. 1. Linear least square regression of fat mass and TOBEC index for bank voles ($n=26$) ($r^2=.233$; $F=7.30$, $P=.01$).

analysis, the estimated lean and fat masses referred to the total body mass excluding the brain tissue. We adjusted the estimates of lean and fat masses upwards to give the total fat and lean contents of the bodies (including the brains) using the known masses of the brains (±0.0001 g, Ohaus Analytical Plus) and by assuming the composition of the brain was the same as the rest of the body. Twenty-six animals were chosen at random to produce a regression equation to predict fat mass from the TOBEC index. The remaining 12 animals were used for a cross-validation of the equation.

2.5. Statistical analysis

Two-sample t tests were used to establish if there were any differences between the experimental and control groups prior to the start of the experiment. The effects of diet and time on all variables were established using two-sample t tests of means and repeated measures one-way analysis of variance (ANOVA), respectively, using a statistical package (Minitab Version 11). Least square regression analysis was used to determine whether linear trends or daily variability were responsible for significant time effects in the ANOVAs. Fisher's pairwise comparisons were employed as post hoc tests where appropriate.

3. Results

There was no significant difference between the experimental and control groups in any preexperimental variables measured (body mass: $t=-0.05$, $P=.96$; food intake: $t=-0.72$, $P=.48$; RMR: $t=-0.57$, $P=.58$; fat mass: $t=0.03$, $P=.97$). Furthermore, there were no significant differences between male and females for any trait; therefore, data was pooled across the sexes.

3.1. TOBEC validation

There was a significant relationship between fat mass (g) and TOBEC index (Fig. 1; $r^2=.233$, $F=7.30$, $P=.01$). The resulting predictive equation was (Eq. (3)):

$$\text{Predicted fat mass} = (0.1246 \times \text{TOBEC index}) - 2.1794. \quad (3)$$

There was no significant difference between observed fat mass and the predicted fat mass of voles used for the cross-validation (paired t test, $n=12$, $t=-0.70$, $P=.50$).

3.2. Body mass and body composition

Over the first 7 days following food manipulation, there was a significant loss of body mass in both the HFD and control groups (Fig. 2; repeated measures one-way ANOVA, HFD: $F(6,188)=3.64$, $P=.002$; RM3: $F(6,83)=3.00$, $P=.011$). Voles fed the HFD decreased in mass from 15.5±0.42 g to 15.0±0.41 g and control animals decreased from 15.4±0.80 g to 14.9±0.73 g. This amounted to approximately 3.3% of body mass in both groups. Between Days 7 and 28, control animals significantly increased their body mass back to levels comparable to those at the start of the experiment [repeated measures one-way ANOVA: $F(21,261)=2.23$, $P=.002$; least square regression: $F(1,21)=12.40$, $P=.002$]. This trend was not seen in voles fed the HFD whose body mass remained relatively constant at approximately 14.95±0.03 g during this period [repeated one-way ANOVA: $F(21,593)=2.49$, $P<.001$; least square regression: $F(1,21)=0.03$, $P=.863$].

Significant changes in fat mass corresponded with the aforementioned adjustments in body mass (Fig. 3). The control group significantly reduced their fat mass by Week 2 and this subsequently recovered by Week 5 [repeated one-way ANOVA: $F(2,35)=14.14$, $P<.001$; Fisher's pairwise comparisons: $P<.05$]. Voles fed the HFD had a significantly higher fat mass at the start of the experiment than in either Week 2 or 5. There was no significant difference in fat mass for this group between Weeks 2 and 5 [repeated one-way

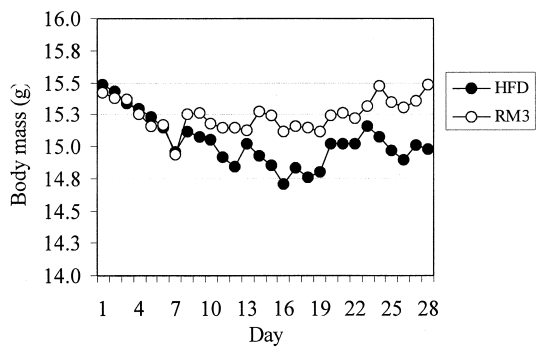

Fig. 2. Mean body mass of voles fed HFD ($n=27$) or standard diet (RM3; $n=12$) for over 28 days.

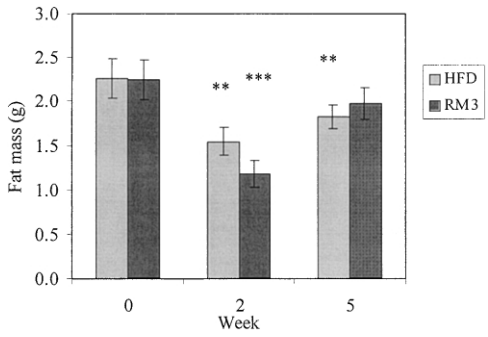

Fig. 3. Change in fat mass of bank voles fed HFD ($n=26$) or standard diet (RM3; $n=12$) for over 5 weeks. Mean values ± S.E.M. $^{**}P=.001$, $^{***}P<.001$ compared to Week 0 (repeated two-way ANOVA).

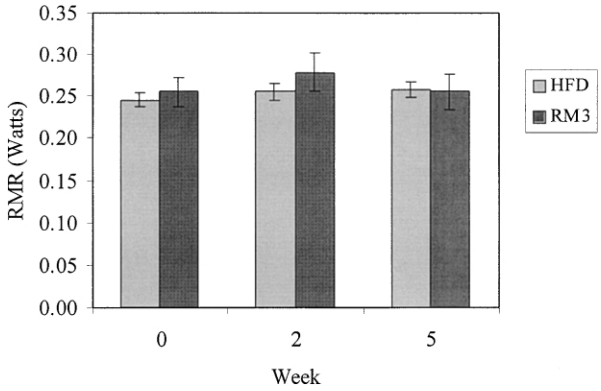

Fig. 4. Effect of HFD ($n=26$) or standard diet (RM3; $n=12$) on RMR of bank voles. Mean values ± S.E.M.

ANOVA, $F(2,77)=7.13$, $P=.001$; Fisher's pairwise comparisons $P>.05$].

3.3. DMD and AEAE

After 4 weeks on the dietary regimes, DMD and AEAE were significantly greater for voles fed the HFD than those fed the standard diet [Table 2; two-sample t test, DMD: $t=2.97$, $P=.031$, $df=8$; AEAE: $t=4.60$, $P=.004$, $df=8$]. Furthermore, those voles whose diet was switched from standard to HFD had a significantly higher AEAE (mean ± S.E.) on the HFD (86.4 ± 0.97%) than on the standard diet (82.93 ± 0.46%; paired t test: $n=5$, $t=-6.15$, $P=.004$).

3.4. Food, energy, and fat intake

Food intake (g/day) of animals fed the HFD varied significantly over the duration of the experiment [repeated measures one-way ANOVA: $F(26,727)=2.81$, $P<.001$]. This was due to random day to day variation rather than a general trend over time [least square regression, HFD: $F(1,26)=1.13$, $P=.298$]. There was no significant effect of time on food intake for control animals [repeated measures one-way ANOVA: $F(26,306)=1.01$, $P=.455$]. These results held for both groups even when Days 1–7 and 7–27 were analysed separately (results not given). Voles fed the HFD ate on average 0.15 g (5.3%) less food but 1.51 kJ (3.1%) more energy per day compared to control animals (Table 2). These differences were not significant (two-sample t test of means, food: $t=-1.23$, $P=.24$, $df=36$; energy: $t=0.69$, $P=.50$, $df=36$). There was also no significant difference in the total amount of food or energy consumed by each group over the 28 days (two-sample t test of means, food: $t=-1.24$, $P=.24$, $df=36$; energy: $t=0.72$, $P=.48$, $df=36$).

When AEAE was taken into account, the total amount of energy assimilated by voles fed the HFD was significantly higher than the controls over the duration of the experiment (two-sample t test of means: $t=2.13$, $P=.05$, $df=36$). Furthermore, there was a large and significant difference in the amount of fat consumed by each group, with animals on the HFD eating 0.36 ± 0.01 g/day compared to 0.15 ± 0.01 g/day eaten by controls — more than twice as much (two-sample t test of means: $t=21.57$, $P<.0001$, $df=36$).

Table 2
Food intake and energy variables of bank voles fed HFD or standard diet

Variable	HFD	Standard diet
Mean food intake/day (g) (Days 1–27)	2.67 ± 0.06 (27)	2.82 ± 0.11 (11)
Total food intake (g) for over 28 days	71.9 ± 1.47 (27)	76.0 ± 3.03 (11)
Mean energy intake/day (kJ) (Days 1–27)	50.5 ± 1.06 (27)	49.0 ± 1.91 (11)
Total energy intake (kJ) over 28 days	1360.3 ± 27.8 (27)	1317.5 ± 52.6 (11)
DMD (%)	84.3 ± 1.15 (5)*	80.5 ± 0.56 (5)
AEAE (%)	86.4 ± 0.97 (5)**	81.3 ± 0.52 (5)
Total energy assimilated (kJ) for over 28 days	1175.3 ± 24.0 (27)*	1071.1 ± 42.7 (5)

Mean values ± SE; n-value in parentheses.
* Two-sample t test $P<.05$ compared to the standard diet.
** Two-sample t test $P<.005$ compared to the standard diet.

3.5. RMR

There was no significant difference in the RMR of animals fed the HFD over time [Fig. 4; 0.245 ± 0.008–0.258 ± 0.009 W; repeated measures one-way ANOVA: $F(2,76)=0.94$, $P=.395$]. In Week 5, the mean RMR of voles fed the HFD and standard diet were 0.258 ± 0.009 and 0.256 ± 0.021 W, respectively. This difference was not significant (two-sample t test: $t=0.09$, $P=.93$, $df=35$).

4. Discussion

The purpose of this study was to establish whether bank voles are resistant to DIO when fed an HFD and to address the role of RMR, a component of energy expenditure, in this resistance. As expected, bank voles did not develop obesity

when fed an HFD. An unexpected result was that after an initial decrease in mass by both groups, the control animals regained their mass to their original value whereas the group fed the HFD maintained their body and fat mass relatively constant at the reduced level. This observation is in part consistent with other studies in which species (Shaw's jird and the domestic cat, *Felis domesticus*) did not change their mass when fed a diet high in fat [1,13].

The principal difference between the two dietary regimes was the amount of dietary fat rather than the energy content of the diet. This is reflected by the fact that neither daily food intake (g) nor energy intake (kJ) differed between voles fed the standard or HFD even though the latter consumed twice as much fat. There is much deliberation as to the role of macronutrients, as opposed to the total energy content of the diet, in the promotion of obesity. Factors such as fat content [14,15], percentage energy from fat [16], and energy density [17] have all been suggested to play a role in the development of obesity. Diets high in fat are known to promote hyperphagia in a number of species including humans [4,18,19]. We found no significant increase in food intake by bank voles fed the HFD; an observation that supports other studies in which animals were not susceptible to DIO [1,13]. The mechanism by which these animals resist hyperphagia may be of importance in the regulation of body fatness. Resistance to hyperphagia and, thus, DIO in small mammals, such as the bank vole, is unlikely to be of adaptive significance in free-living animals. It is doubtful that voles experience such high levels of fat in their natural diet even when feeding on items such as seeds and beech mast in autumn. Resistance may, therefore, be a consequence of the mechanism evolved to prevent weight gain in winter rather than an adaptation against fat content of the diet per se.

Although there were changes in body mass and composition in both groups throughout the experiment, there were no detectable alterations in RMR. This may have been due to the changes being primarily of fat mass, with limited alterations in the lean body mass. It has been well documented that lean mass is considered the major metabolic component of the body with fat mass being relatively metabolically inert [20–23] (but see also Ref. [24]).

Experimental animals increased their energy assimilation efficiency on the HFD, indicating that this was of a higher quality than the standard diet. An observation that suggests the lack of weight gain on the HFD was not due to the inability of the voles to digest the food. There have been mixed reports over the responses of RMR to diet quality [25,26]. Varying results may reflect differing life history strategies of the animals studied. During the seasons when food quality decreases, bank voles reduce their body mass and presumably their energy requirements; for this reason it may not be necessary to further decrease their metabolic rate. However, terrestrial or marine mammals that fast for long periods of time may require the ability to depress their metabolism to ride out these times when food is absent [25].

In conclusion, our study provides additional evidence supporting the hypothesis that seasonal animals that decrease their body mass in response to short photoperiods are not susceptible to DIO when fed an HFD. Voles consumed large amounts of fat without developing the hyperphagia associated with high-fat feeding in other species that are prone to obesity [18,19]. Furthermore they resisted weight gain, seen in the control group, whilst assimilating more energy from their food but without corresponding adjustments in energy intake or RMR. We suggest that an increase in total daily energy expenditure, perhaps advancing the shift in fat oxidation [27], may be a significant factor contributing to the above observations. Increased fat oxidation may reduce hyperphagia [28,29] and furthermore, subjects prone to obesity fail to increase their fat oxidation in response to an HFD [30]. Further study into the mechanisms involved in the seasonal variation of fat deposition in response to changes in photoperiod and diet may prove an important contribution to our understanding of the physiological basis of resistance to obesity on an HFD [31].

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