Effects of extreme environments on food intake in human subjects

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Effects of extreme environments on food intake in human subjects are analysed as behavioural and physiological adaptations to annual and circadian rhythms, temperature and altitude. Effects of the environment on food intake through food availability have direct consequences on energy balance and body weight. Different geographical regions show variations in the composition of dietary foods, i.e. the relative proportions of carbohydrate, protein and fat. In developing countries the annual cycle appears to affect body weight through dependence on food availability. In West-European countries this effect appears to depend on physical activity. Energy and macronutrient intakes appear to follow a circadian pattern, with breakfast being relatively high in carbohydrate and dinner being relatively high in fat. In cold conditions, maintaining an adequate food intake is important in sustaining normal physiological responses to cold. Evidence for a possible coldinduced increase in appetite is poor. A condition influencing level of intake is the palatability of the food. High altitude, i.e. hypobaric hypoxia, appears to reduce appetite, energy intake and body mass, irrespective of acute mountain sickness (AMS). Meal size is reduced and meal frequency increased. Under circumstances of AMS, dissociation between appetite and hunger occurs. Thus, spontaneous adaptation to extreme environments requiring increased energy intake occurs first by adaptation of body weight to a new energy balance. In general, prevention of a negative energy balance occurs by learning with respect to food intake. After return to normal, adjustment of energy intake to the original energy balance occurs with restoration of body weight.

Energy balance: Body weight: Hypobaric hypoxia: Macronutrients: Seasonal effects

The environment: biotic and abiotic factors

Ecologically, the environment is characterized by abiotic and biotic factors. The fluctuations, range and interplay of these factors at a certain place determine the habitat of an individual (Bakker *et al.* 1995). Abiotic factors include temperature, humidity, pressure and day length, also represented by climate, altitude and latitude. Ambient temperature and humidity mainly depend on latitude and a more terrestrial or marine situation, pressure mainly depends on altitude. The abiotic factors day length and rhythmicity depend on latitude.

Biotic factors are represented by the other organisms that are present in the same habitat. Their roles range from providing food, shelter or clothing, to being a predator. Distribution and abundance of organisms in a certain habitat are determined by biotic and abiotic factors, as well as by their interplay (Lack, 1954). Adaptation to the environment may take place to a certain extent, and over shorter or longer periods of time, since adaptation can be behavioural,

physiological or genetic (Krebs & Davis, 1978; van Rhijn & Westerterp-Plantenga, 1989; Bakker *et al.* 1995).

As such, an ecosystem is dynamic rather than rigid, evolving continuously. Thus, from an ecological point of view, 'effects of extreme environments on food intake' can be perceived as an example of behavioural and physiological adaptations to extreme environments. In this paper, I will discuss behavioural and physiological adaptations of human subjects to annual and circadian rhythms, temperature and altitude. However, since food is also a biotic factor, and food availability itself depends on other biotic and abiotic factors, therefore I will deal first with the effect of food intake on the environment.

Effects of food intake on the environment

The effects of food intake on the environment consist mainly of the effects of exploitation of ecosystems (van Rhijn & Westerterp-Plantenga, 1990). Food availability

Abbreviation: AMS, acute mountain sickness

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used to depend completely on the actual exploitation of ecosystems, and therefore it was time- and place-dependent. However, since human subjects prefer to live independently of food availability, we expend energy and raw materials to sustain a food culture which is independent of time and place (Westerterp-Plantenga, 1994). This system seems to improve security and self-confidence, and to reduce fear of food shortage, at least in the short term. This system also implies an increasing demand on ecosystems, from relatively modest during pre-history, to rather severe as the result of the introduction of agriculture and the Industrial Revolution (van Rhijn & Westerterp-Plantenga, 1990).

Ecosystems are mainly vulnerable to and affected by human behaviour (van Rhijn & Westerterp-Plantenga, 1989). In small closed groups, human behaviour is determined to a great extent by a system of reciprocity, thus individuals share in the prosperity of the group. Over many generations the same ecosystem was exploited by the same group, therefore human behaviour was adapted to a sustained relationship with the ecosystem. Nowadays, in large societies containing subgroups with conflicting interests, this system of reciprocity has become unsustainable, and has lost its impact. In the social situation of modern society a sustained relationship with the ecosystem can no longer be the delegated responsibility of individual group members. Management of ecosystems has become largely the responsibility of authorities (van Rhijn & Westerterp-Plantenga, 1990).

Effects of the environment on food intake

Energy intake

The presence of an effect of the environment on food intake through food availability implies a balance between eating to live, or living to eat (Westerterp-Plantenga, 1994). Eating to live is a physiological condition; living to eat illustrates the process of civilization as applied to eating, as has taken place, for example in Europe, especially from the nineteenth century onwards (for example, see van Otterloo, 1990). Eating to live represents a food intake necessary to meet the metabolic needs of the body, and to maintain body weight. Living to eat concentrates on the question of why human subjects eat what they eat, and how and why eating habits and appreciation change. Here socio-cultural aspects appear to dominate (Westerterp-Plantenga, 1994).

We consume food, the availability of which is both dependent and independent of time and place of harvesting. The dependence on time and place of harvesting can have considerable consequences for body weight during periods of food shortage. An example of this dependency will be discussed later as an effect of annual cycling. The independence of time and place of harvesting can lead to over-abundance and unlimited supply (Westerterp-Plantenga, 1994). In the present affluent Western societies this situation, in combination with reduced physical activity, might contribute to obesity (Pasman *et al.* 1999). Thus, one of the effects of extreme environments, by means of food availability, is recognized as a body-weight effect.

Macronutrient intake

The distribution of food energy among the macronutrients differs between cultures and countries (Bellisle *et al.* 1998). Extreme variations in the composition of foods selected by human subjects can be found in different geographical regions. For instance, there is a fairly wide range of carbohydrate: protein: fat values within which energy balance can be maintained. Carbohydrate intakes range from 3 to 82 % dietary energy and fat intakes from 6 to 54 % dietary energy, while protein intakes are generally at least 11 % dietary energy (Westerterp, 1994). In addition to this factor, dietary changes take place with changes in food supply, within a culture or country.

Kuhnlein *et al.* (1996) compared the effect of food source (traditional or market) and season (six seasons) on dietary nutrient patterns of Inuit living in Baffin Island, Canada. They conducted 24 h recall interviews with all residents who had lived for ≥3 years in this one community in each of six seasons. The Inuit community of Qikiqtarjuaq harvests the highest quantity of wildlife *per capita* of all Baffin communities. Food source made a significant difference to nutrient intakes; traditional food contributed more protein, and market food contributed greater amounts of dry weight, energy, fat and carbohydrate. Thus, food consumption appears to depend on food availability, and to encompass a considerable range of % dietary energy derived from the different macronutrients.

Annual cycles

Annual cycles in energy balance were studied by Van Staveren *et al.* (1986). A random sample of 114 women aged 29–32 years was selected from a small industrial town in The Netherlands. Food consumption was estimated once monthly with a 24 h recall method. The subjects weighed themselves without clothes every day using a high-accuracy balance ($\pm 0.5 \, \mathrm{kg}$) which was supplied.

The study did not demonstrate systematic changes in energy intake throughout the year, although there was a relatively lower fat consumption in the summer months $(37.2\% \text{ energy } v.\ 39.4\% \text{ energy in winter})$. Body weight showed small seasonal fluctuations (Fig. 1), with an increase before winter and a decrease before summer. This result was suggested to be a consequence of changes in physical activity, since the subjects were more physically active in spring and summer than in winter and autumn; food availability did not differ between the seasons.

Prentice *et al.* (1981) observed a more pronounced annual cycle of body weight in developing countries where food availability changes throughout the year. In the Gambia energy intake in the wet season was clearly inadequate, while in the dry season intake almost met energy requirements. Thus, most adults undergo seasonal body-weight changes, with weight loss during the wet season and weight regain during the dry season when food supplies are relatively abundant. Data obtained by weighing all non-pregnant non-lactating women of child-bearing age in a rural subsistence farming community at 2-month intervals illustrate this annual pattern of weight change (Fig. 2). In

pregnant women an inadequate gain of 0.4 kg per month during the wet season was found, compared with a 1.4 kg per month weight gain (which is in accordance with conventional standards) during the dry season. All women, including women at different stages of pregnancy, utilized body fat during the wet season, as measured by the sum of skinfold thicknesses.

When the annual cycle of body weight in a European country is compared with that in a developing country where food availability is suboptimal for part of the year, the difference is pronounced. The women in the Gambia show a mean annual weight change of 1.5 kg, while for a comparable group of Dutch women it is only 0.5 kg. The situation in the Gambia illustrates the importance of body fat reserves in women in order to allow for reproduction, including pregnancy and a lactation period of more than 1 year.

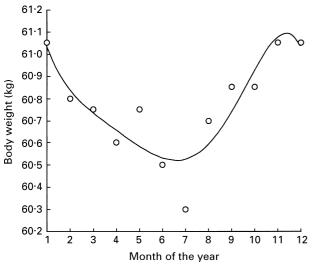


Fig. 1. Mean fluctuation of body weight in young adult women in the Netherlands as assessed monthly throughout 1 year (*n* 114). (From Westerterp-Plantenga *et al.* 1994; adapted from van Staveren *et al.* 1985).

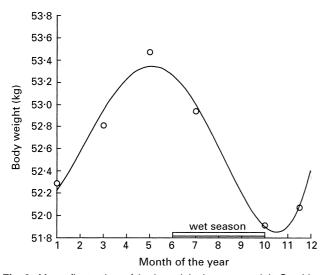


Fig. 2. Mean fluctuation of body weight in young adult Gambian women as assessed bi-monthly throughout 1 year (*n* 53). (From Westerterp-Plantenga *et al.* 1994; adapted from Prentice *et al.* 1981).

The function of body fat reserves in women is used mostly to explain the sex differences in body composition. The function of fat is more than to make a woman look attractive. In evolution it has been important as a determinant of reproductive success, which explains why women have more fat than men from puberty onwards.

Here we conclude again that if food consumption depends on food availability, body weight adapts to a new energy balance.

Circadian rhythms

Compared with the annual effects, circadian effects appear to be more short-term effects. Under normal circumstances, energy and macronutrient intakes follow a circadian pattern, with breakfast being relatively high in carbohydrate and dinner being relatively high in fat. This pattern appears to hold true for lean as well as obese subjects (Westerterp-Plantenga et al. 1996a,b). Selection in macronutrient intake throughout the day occurred as follows: macronutrient specific satiety for protein occurred by means of a significantly (P < 0.05) increased satiety per kJ ingested; for fat there was a significant (P < 0.05) drop in hedonic value; for carbohydrate there was a significantly (P < 0.05) increased desire for a different taste (Westerterp-Plantenga et al. 1996b). Moreover, compensation, i.e. a correction afterwards for an earlier unusual macronutrient composition, occurred at dinner, resulting in a more-or-less stable macronutrient intake during an average day (Westerterp-Plantenga et al. 1996b).

Ambient temperature

Very few data have been reported on the effect of extreme temperatures on food intake in human subjects. Marriot & Carlson (1996) discussed nutritional needs in cold environments with respect to applications for military personnel in field operations. It appears that heat loss in a cold environment is considerably reduced through thermoregulation, clothing and behaviour, i.e. seeking shelter whenever possible, and creating or moving to warmer environments. Moreover, skeletal muscle contractions, either during voluntary exercise or involuntary shivering, are the major source of the metabolic heat produced to protect against cold stress (Marriot & Carlson, 1996). Heat production parallels an increase in O_2 uptake, the magnitude of which depends on the proportion of the muscle mass engaged in shivering or work and the duration and severity of the work being done. Shivering alone can produce only a fourfold increase above basal rates of heat production, and even the greatest increases in heat production due to shivering alone are less than one-quarter of a muscle's maximum contractile activity (Marriot & Carlson, 1996). The increase in O₂ uptake during shivering thermogenesis is also accompanied by an increase in cardiac output. This increase is due almost entirely to an increase in stroke volume, which appears to be the result of the increased central blood volume that is associated with cold-induced peripheral vasoconstriction. Resting heart rate remains unchanged (Muza et al. 1988). The effect of the mechanisms used to protect against heat loss depends on the body surface area in comparison with body mass (Young, 1991). Thus, problems may arise in malnourished subjects who have lost both body fat and muscle mass. Effects of sex and age also depend on differences in the body surface area in comparison with body mass, and on differences in muscle mass. This factor may explain why the elderly, the malnourished and women are relatively more vulnerable to hypothermia than younger well-nourished human subjects, especially men.

Cold acclimatization can occur in human subjects, but it is minimal. An important modifying factor on the thermoregulatory response to cold is the individual's provision of subcutaneous fat, since fat reduces thermal conductance from the core to body surfaces (Toner & McArdle, 1988). Physical fitness has mixed effects; the fittest individuals show the greatest heat production, but they are also the leanest, and this factor combined with their higher skin temperatures from increased heat production, causes them to lose heat more quickly. Severe losses of body weight in a cold environment due to physical activity could also complicate the normal physiological responses to cold. Thus, maintaining an adequate intake in a cold environment, especially under physically-active conditions, is important to sustain normal physiological responses to cold.

How does cold exposure influence appetite? Anecdotally, cold climatic conditions lead to an increase in appetite. The evidence for this conclusion is derived from changes in body weight, self-scored questionnaires and food intake records

in cold environments at sea level. However, the reported increase in appetite is also associated with changes in other aspects of the subjects' environment such as altered activity levels, social isolation, reduced social interaction and modifications in diet (Marriot & Carlson, 1996). Although it seems that food intake is generally increased with cold exposure, this finding appears to be based on little evidence. The reasoning is that as the result of cold exposure energy expenditure increases (in order to maintain body temperature) to, for example, two to three times BMR (Marriot & Carlson, 1996), and therefore energy intake needs to increase. Often, this cold-induced energy expenditure is difficult to discriminate from energy expenditure due to activity, which also requires increased energy intake.

In animals it has been reported that in a cold environment the increase in energy expenditure caused by increased thermogenesis is compensated for by increased energy intake (Louis-Sylvestre, 1987).

However, in human subjects increased energy intake requirements do not always trigger an increased energy intake and appetite immediately. The phenomenon of short-term exercise-induced anorexia is well known (Fig. 3; Westerterp-Plantenga *et al.* 1997), and also the higher dietinduced energy expenditure (14·6 (SD 2·9) % on the high-protein high-carbohydrate diet v. 10·5 (SD 3·8) % on the high-fat diet; P < 0.01) coinciding with the higher satiety,

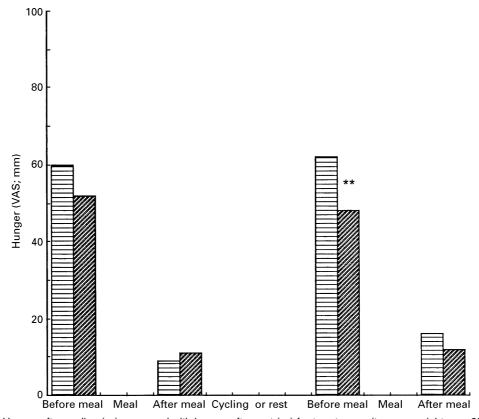


Fig. 3. Hunger after cycling (∞) compared with hunger after rest (\equiv) for twenty men (ten overweight: age 25 (SD 6) years, BMI 28·5 (SD 1·9) kg/m²; ten lean: age 27 (SD 7) years, BMI 22·8 (SD 1·6) kg/m²) who cycled for 2 h at 60 % of the individual W_{max}, which was on average 144 (SD 19·2) W for overweight men and 211 (SD 27·9) W for lean men. Mean value was significantly different from that after rest: **P<0·01. VAS, visual analogue scale (100 mm). (From Westerterp-Plantenga *et al.* 1997.)

which is shown in Fig. 4 (Westerterp-Plantenga et al. 1999a). Obviously, if it happens, it takes time for the appetite to adjust to the changes in energy expenditure. In situations that require sustained performance, e.g. during a cycling race like the Tour de France, learning with respect to food intake occurs to prevent a negative energy balance. One of the conditions for increasing food intake is the palatability of the food. The effect of palatability of the food is nicely illustrated by a study by Rode & Shephard (1992), who showed that the subcutaneous fat layer of 9-19-yearold Eskimos was twice as large in 1990 as it was in 1970. This difference was explained by the fact that in 1970 youngsters were fed on the traditional Eskimo diet characterized by high protein and fat content and the absence of carbohydrates, whereas in 1990 they ate typical modern Western food such as sweets, popcorn, chocolate bars, ice cream, and soft drinks. In addition to the palatability of the food, learning has been applied in a military situation. During a field study in Alaska the soldiers were given a ready-to-eat supplemental pack of 3 MJ as palatable foods, which they were taught to consume. This process resulted in a reduction in the usual body weight loss under these conditions (Edwards & Roberts, 1991)

More research is needed to explain if and how appetite might switch on to meet higher energy requirements. The

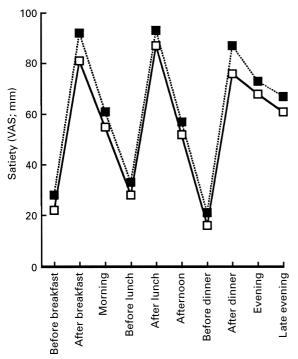


Fig. 4. Satiety during the day for eight female subjects (age 23–33 years, BMI 23 (SD 3) kg/m², % body fat 29 (SD 6)) receiving a high-fat diet or high-protein high-carbohydrate diet in which the % energy from protein, carbohydrate and fat alues were 9, 30 and 61, and 29, 61 and 10 respectively. The area under the curve (AUC) was calculated over 24 h, interpolating the value in the late evening to the early morning value, thus correcting for the part of the visual analogue scale (VAS; 100 mm) that is never used by the individual subject. The AUC for the high-protein high-carbohydrate diet was compared with that for the high-fat diet using ANOVA repeated measures and the values were significantly different (*P*<0.01). (From Westerterp-Plantenga *et al.* 1999*a*).

short-term alternative is the adaptation of body weight to the new energy balance, which has been shown to depend on food availability.

High altitude

Finally, the effect of high altitude on food intake will be discussed.

One of the most common observations made on a short stay by human subjects at high altitude is an initial loss of body weight. Many studies have shown that subjects lose significant amounts of body mass (fat mass as well as fatfree mass) during a climb to and/or a stay at altitudes of \geq 3600 m. The amount lost depends on the altitude reached and the time period spent there (Boyer & Blume, 1984; Guilland & Klepping, 1985; Rose et al. 1988). Several hypotheses have been formulated to explain this phenomenon, e.g. appetite suppression, malnutrition, loss of body water and intestinal malabsorption. Moreover, acute mountain sickness (AMS) contributes to reduced energy intake by appetite suppression, i.e. the inability to eat or drink due to nausea (The Lake Louise Consensus, 1992). However, appetite suppression persists after other AMS symptoms have disappeared.

Malnutrition. With regard to malnutrition, there is evidence that subjects can more or less maintain energy balance during a stay at high altitude. This process does not occur spontaneously, but only if supported by the provision of special foods, which the subjects are taught to consume (Butterfield *et al.* 1992). During a 1 month stay at 5050 m, it was shown that, in the presence of sufficient physical comfort and palatable food, weight loss can partly be prevented (Kayser, 1991).

Malabsorption. With regard to malabsorption, it appears that at $\leq 5000-5500$ m intestinal absorptive function for macronutrients remains normal (Kayser, 1991; Butterfield *et al.* 1992). The available evidence at higher altitude (>6300 m) from a study of three subjects during a Mount Everest expedition is unsubstantial (Boyer & Blume, 1984), and it remains unclear whether malabsorption would play a significant role in energy balance at altitudes of > 5500 m.

Appetite. The previously mentioned studies on energy balance at high altitudes, reporting body weight loss due to reduced energy intake, discussed the possibility of reduced appetite. Since possible loss of appetite due to hypobaric hypoxia had not been separated from possible changes in appetite due to overexerting, cold, stress or a qualitatively-or quantitatively-limited food supply, we studied appetite under hypobaric hypoxia *per se*, i.e. during a simulated ascent of Mount Everest (Westerterp-Plantenga *et al.* 1999b).

The subjects who participated in this simulation study were eight men with the following characteristics: age 26 (SD 4) years, height 1·80 (SD 0·07) m, weight 74·3 (SD 6·6) kg. They had been at an altitude of 5000 m or higher before the experiment. The experiments were carried out in a hypobaric chamber, which consisted of a bedroom, a small bathroom and an exercising room. Temperature and humidity were well controlled and kept at a constant level of 23° and 41 % relative humidity. The observation started with baseline measurements over 7 d (Marseille, France),

referred to as the normoxia period. Thereafter, subjects were transported to the field station on Mont Blanc (Observatoire Vallot, 4350 m) in the French Alps, where they stayed for 1 week to acclimatize. Then, they travelled back to Marseille. On arrival subjects went straight into the hypobaric chamber, where they stayed for a subsequent period of 31 d. During this period the ascent of Mount Everest (8848 m) was simulated. Ambient pressure created hypobaric simulations of 0, 5000, 6000, 7000, 8000 and 8848 m. Over the entire ascent the body mass of the subjects was reduced significantly (P < 0.05), by 5.0 (SD 2.0) kg, being exposed only to hypobaric hypoxia and not to other factors that are usually part of the rigours of climbing high mountains.

During the 4 d recovery period body mass increased immediately to an average of $-2 \, \text{kg}$ compared with the start of the experiment. The average reduction in body mass throughout the experiment was obviously the result of a negative energy balance. This negative energy balance was mainly due to the decreased energy intake, since energy expenditure was low (Fig. 5, Westerterp-Plantenga *et al.* 1999b). The downward trend in these energy intake values, i.e. up to 55 % energy intake reduction during a simulation of 8000 m compared with the energy intake during the normoxia period, was about the same as that during mountain stays of up to 26 d in duration (Boyer & Blume, 1984; Guilland & Klepping, 1985; Westerterp *et al.* 1992, 1994b; Dinmore *et al.* 1994).

The reduced energy intake during simulations of 5000 and 6000 m also appeared to be due to reduced appetite (measured by the different features of the appetite profile)

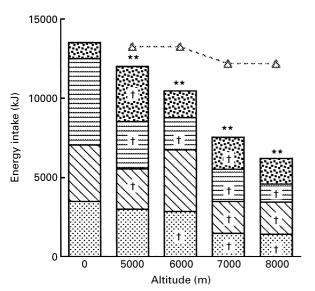


Fig. 5. Energy intake at different eating occasions (breakfast (\blacksquare), lunch (\bowtie), dinner (\blacksquare) and snacks (\blacksquare), and energy expenditure at different simulated altitudes (\triangle). Values for total daily energy intake were significantly different from those during the normoxia period (baseline): **P<0.01. Energy intakes during meals or snacks were significantly different from those during the normoxia period: † P<0.05. For details of subjects and procedures, see Westerterp-Plantenga *et al.* (1999*b*).

when symptoms of AMS were not present or were negligible (Westerterp-Plantenga *et al.* 1999*b*).

We then observed a change in the meal pattern from a gorging to a nibbling style, i.e. an increase in meal frequency. This change in meal pattern was related to a change in appetite profile during the day (Fig. 6). Within this changed meal pattern, meal sizes were reduced due to a more rapid increase in satiety and decrease in hunger across a meal, with a constant decrease in pleasantness of taste with a certain meal type (Fig. 7; Westerterp-Plantenga *et al.* 1999*b*).

The change to a nibbling pattern might be functional in an attempt to meet the energy intake requirements for a sustained energy balance, which is in line with the observation of energy intake compensation in nibblers but not in gorgers (Westerterp-Plantenga et al. 1994b). With respect to macronutrient balance, a relative increase in carbohydrate intake has been shown at simulated altitudes of 5000 and 6000 m. This increase does not cause a difference in the fuel mixture that is oxidized, since loss of body mass consisted mainly of loss of fat mass (Westerterp et al. 1996), allowing fat oxidation from stores. When AMS symptoms were present, the meal pattern remained as a nibbling pattern, but there was a loss of interest in food intake, as was shown from the reduced scores on the cognitive restraint factor of the Three Factor Eating Questionnaire (Stunkard & Messick, 1985). Although hunger was present, appetite was depressed. At a simulation of 7000 m, the features of the appetite profile were uncoupled, in the sense that depressed appetite

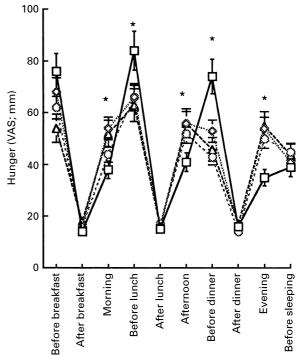


Fig. 6. Hunger scores throughout the day at different simulated altitudes (m; $0 (\Box - \Box)$, $5000 (\diamond \cdots \diamond)$, $6000 (\diamond - \cdot \diamond)$, $7000 (\diamond - \cdot \triangle)$. Values are means and standard deviations represented by vertical bars. Mean values were significantly different from those for the normoxia period (baseline): * P < 0.05. For details of subjects and procedures, see Westerterp-Plantenga *et al.* (1999*b*). VAS, visual analogue scale (100 mm).

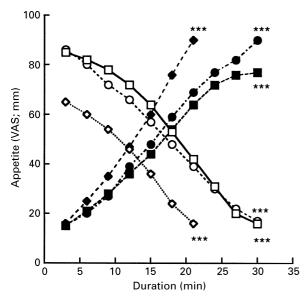


Fig. 7. Appetite during lunch at different simulated altitudes (hunger: 0 m; 0 (□—□), 5000 (⋄···⋄), 6000 (⋄···∘); satiety: 0 m (■-··■), 5000 m (◆-··•)). Mean values were significantly different from those at 3 min: ***P<0.0001. For details of subjects and procedures, see Westerterp-Plantenga *et al.* (1999*b*). VAS, visual analogue scale (100 mm).

prevented the volunteers from reacting to increased hunger (Westerterp-Plantenga *et al.* 1999b).

One of the indications of depressed appetite might have been an increase in the serum leptin level, since leptin is a key mediator in the neuroendocrine regulation of food intake and energy expenditure. Elevated leptin levels at high altitude were found to be associated with loss of appetite and AMS (Tschopp *et al.* 1998). We speculate that leptin may be an important factor in the neuroendocrine dysregulation of energy balance at high altitude.

From the point of view of adaptation to hypobaric hypoxia, we suggest that a change in body mass as well as a change in the appetite profile and in meal pattern might contribute to preventing an even greater negative energy balance. This process was more successful in the absence of AMS than when AMS was present (Westerterp-Plantenga *et al.* 1999*b*).

Thus, under extreme circumstances, when food availability did not play a role and food intake was spontaneous, i.e. not influenced by learning, a dysregulation of energy balance occurred in the short term, and body mass was adapted to the new energy balance. On return to normal conditions appetite was resumed and body mass began to be restored.

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