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Limits to sustainable human metabolic rate

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Summary

There is a limit to the performance of an organism set by energy intake and energy mobilization. Here, the focus is on humans with unlimited access to food and for whom physical activity can be limited by energy mobilization. The physical activity level (PAL) in the general population, calculated as doubly-labelled-water-assessed average daily metabolic rate as a multiple of basal metabolic rate, has an upper limit of 2.2–2.5. The upper limit of sustainable metabolic rate is approximately twice as high in endurance athletes, mainly because of long-term exercise training with simultaneous consumption of carbohydrate-rich food during exercise. Endurance athletes have an increased fat-free mass and can maintain energy balance at a PAL value of 4.0–5.0. High altitude limits exercise performance as a result of combined effects on nutrient supply and the capacity to process nutrients. Thus, trained subjects climbing Mount Everest reached PAL values of 2.0–2.7, well below the observed upper limit at sea level.

Key words: doubly labelled water, food intake, energy expenditure, energy balance, body composition, physical activity, exercise, high altitude.

Introduction

Sustainable metabolic rate may be defined as the time-averaged energy budget that an animal or human maintains over periods sufficiently long that body mass remains constant because time-averaged energy intake equals time-averaged energy expenditure (Hammond and Diamond, 1997). Thus, there is a limit to the performance of an organism set by energy intake and energy mobilization. Here, we focus on limits of performance observed in humans with access to unlimited food and where limits are set by energy mobilization.

Daily energy expenditure consists of four components, the sleeping metabolic rate (SMR), the energy cost of arousal, the thermic effect of food, or diet-induced energy expenditure (DEE), and the activity-induced energy expenditure (AEE). Daily energy expenditure is sometimes divided into three components, taking sleeping metabolic rate and the energy cost of arousal together as energy expenditure for maintenance or basal metabolic rate (BMR). BMR is usually the main component of average daily metabolic rate (ADMR). DEE is assumed to be 10 % of ADMR in subjects consuming the average mixed diet and being in energy balance. AEE is the remaining and most variable component of ADMR. Physical activity can be limited by sustainable metabolic rate.

The doubly labelled water method has provided truly quantitative estimates of AEE in daily life. Subsequently, however, there is no consensus on the way to normalize AEE for differences in body size. A frequently used method to quantify physical activity is by expressing ADMR as a multiple of BMR or SMR (FAO/WHO/UNU, 1985). This assumes that variations in ADMR are due to body size and physical activity. The effect of body size on ADMR is corrected for by expressing ADMR as a multiple of BMR or SMR. Physical activity level (PAL) is equal to ADMR/BMR or ADMR/SMR.

The focus of the current review is on PAL in the general population, exercise-induced possibilities to increase energy intake and thus to increase PAL, changes in body composition and limits to PAL at high altitude.

Physical activity level in the general population

Black et al. (Black et al., 1996) described the metabolic rate in people from affluent societies on the basis of all doubly-labelled water estimates of ADMR available in the literature (*N*=574). They suggested a range for PAL of 1.2–2.5 for ‘sustainable lifestyles’. Fig. 1 shows the frequency distribution of PAL of all subjects measured with doubly labelled water in our laboratory, excluding the following characteristics: age below 20 and above 50 years, an intervention in energy intake, an intervention in physical activity including athletic performance, pregnancy, lactation and disease. Basal metabolic rate (BMR) was measured with a ventilated hood or in a respiration chamber. The range for PAL is similar to that of Black et al. (Black et al., 1996), with an upper limit just over 2.0.

Indeed, there is evidence for an upper limit of sustainable

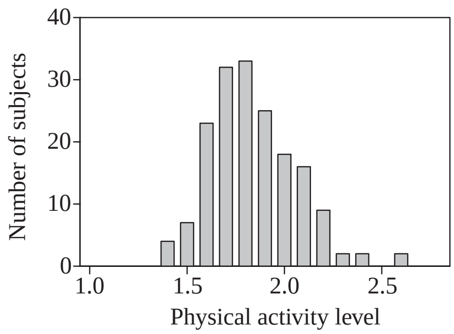

Fig. 1. Frequency distribution of physical activity level (see text) in a sample (*N*=173) of the general population aged 20–50 years.

metabolic rate in the general population. Novice athletes starting a training programme to run a half-marathon increased their PAL from an initial value of 1.66±0.07 (close to the value of 1.54 for sedentary subjects; FAO/WHO/UNU, 1985) to 2.03±18 (means ± S.D., *N*=7) after 8 weeks of training (Westerterp et al., 1992b). Surprisingly, after the initial increase, PAL remained stable while the subjects doubled their training intensity. It was postulated that the subjects had already reached the natural limit of their daily energy turnover at the start of the training period. Five studies on soldiers during field training, together including 66 subjects with a mean PAL of 2.40±0.46 (mean ± S.D.), all reported a negative energy balance over the observation period (Westerterp, 1998). The body mass loss ranged from 0.4 to 2.3 kg week^{-1}.

Exercise-induced changes in energy intake

An important aspect of the maintenance of energy balance during high-intensity endurance exercise is the adaptation of food intake to high energy requirements. Edholm et al. (Edholm et al., 1955) showed that intake tends to be low on days when the expenditure is very high and that the difference was made up some days later when expenditure was lower. Apparently, very high levels of exercise reduce appetite, and subjects need time to adjust their energy intake to increased energy requirements. Woods (Woods, 1996) hypothesized that food provides a potential threat to the organism and that defence mechanisms against an increased energy intake may become activated. The average discrepancy between energy intake and energy expenditure in the studies on soldiers during field training cited above ranged from 2 to 8 MJ day^{-1} or 20–90 MJ over the observation period of 7–25 days.

The upper limit of power output during endurance activities can be increased when energy-dense, carbohydrate-rich food is eaten during the exercise, a practice common in endurance sports. Energy-rich drinks make up a substantial proportion of energy intake in professional athletes. Sjödin et al. (Sjödin et al., 1994) reported a contribution of 16 % of energy intake and 25 % of carbohydrate consumption by carbohydrate-rich formulae in athletes with a PAL of up to 4.5 over a 6-day training period. Subjects were cross-country skiers in the Swedish national team studied in a training camp. It was shown that energy intake matched energy turnover at the high PAL. The mean difference between energy turnover and energy intake for the group of four women and four men was 0.1±1.9 MJ day^{-1}. In the ‘Tour de France’ of 1984, athletes maintained energy balance at a PAL of 3.5–5.5 (Westerterp et al., 1986). Body mass and body composition did change significantly over the 23-day race. None of the studies of soldiers during field training mentions the use of energy-dense, carbohydrate-rich liquid formulae during exercise.

The question remains as to whether a further increase in food intake would result in an upward shift of the limit of sustainable PAL of approximately 5, the value achieved in professional athletes. The capacity to eat and process food certainly limits the energy supply. The absorption capacity of the small intestine is thought to be a limiting factor. The evolutionary design of the intestinal nutrient absorption system is adequate but not too great (Diamond, 1991). Brouns et al. (Brouns et al., 1989) showed that athletes maintained energy balance during a ‘Tour de France’ simulation in a respiration chamber on a conventional solid diet with a high carbohydrate content and supplemented with a 20 % enriched carbohydrate liquid. The energy intake was 5–10 MJ day^{-1} too low when the same diet was available *ad libitum* without the supplement.

In conclusion, the upper limit of sustainable metabolic rate in professional athletes is twice the upper limit in the general population. Two important contributors to the upward shift in PAL are that endurance athletes have learned to ingest large amounts of food and incorporate a significant amount of carbohydrate-rich drinks in their diet. They often follow a continuous eating pattern consisting of many small ‘meals’ at short intervals.

Exercise-induced changes in body composition

Exercise training has a positive effect on performance through changes in body composition. Effects on digestive capacity, the cardiovascular system, the ventilatory system, muscle mass and muscle function have been described. Here, the focus is on two components of the body, fat-free mass (FFM) and fat mass (FM), where muscle mass is the main component of FFM. A reflection of function is the sustainable level of metabolic rate. The level of SMR and BMR is thought to be a reflection of body function as well. Body composition and BMR of subjects with a PAL greater than 3 are compared with those of subjects in the normal PAL range. In addition, changes in body composition and SMR for subjects participating in a long-term exercise intervention study in which PAL increased from a sedentary level to the upper limit observed in the general population are presented.

To allow comparisons of FFM and FM among subjects, the components need to be corrected for differences in body height. FFM and FM are expressed as indices, FFMI and FMI, respectively, where FFMI=FFM/height^2 and FMI=FM/height^2 (FM and FFM are in kg and height is in m). The correction is by analogy with the body mass index (BMI; Quetelet, 1871): BMI=FFMI+FMI. In the normal, sedentary population, there

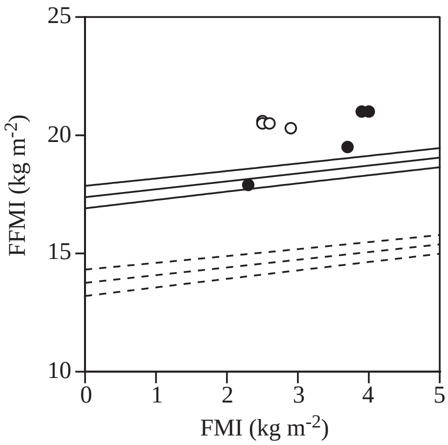

Fig. 2. Fat-free mass index (FFMI) as a function of fat mass index (FMI) in women (broken lines, *N*=61) and men (continuous lines, *N*=112). The regression lines with 95 % confidence limits are calculated for the subjects with the physical activity levels presented in Fig. 1 (women, r^2=0.61, P<0.0001; men, r^2=0.44, P<0.0001). Data for elite athletes, four women (filled symbols) and four men (open symbols) from the Swedish national cross-country ski team (Sjödin et al., 1994) are plotted in the same figure.

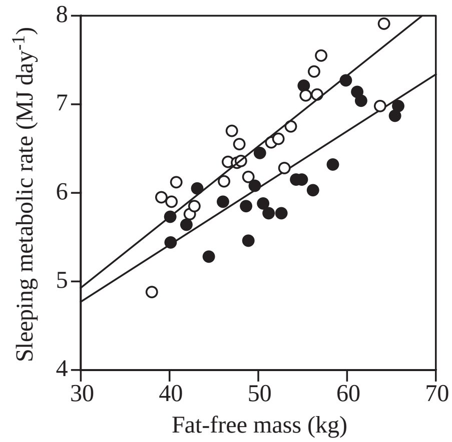

Fig. 3. Sleeping metabolic rate as a function of fat-free mass in novice athletes (*N*=23) before (open symbols; r^2=0.78, P<0.0001) and after (filled symbols; r^2=0.65, P<0.0001) 40 weeks of exercise training.

is a highly significant relationship between FFMI and FMI in both sexes (Westerterp et al., 1992c). Subjects with a higher FM have a higher FFM. Plotting FFMI against FMI in a linear regression analysis resulted in approximately the same slope for both sexes. The slope of the regression of 0.26–0.36 meant that a subject with 1.00 kg more FM has on average 0.26–0.36 kg more FFM, comparable with the composition of mass gain in obese subjects. Fig. 2 shows the calculated linear regression lines for FFMI plotted against FMI for the subjects with PALs presented in Fig. 1. Data for elite athletes, four women and four men from the Swedish national cross-country ski team, are also plotted. PAL was 3.4±0.3 for the female skiers and 4.0±0.5 (means ± S.D.) for the male skiers (Sjödin et al., 1994). The athletes clearly show an increased FFMI, adjusted for FMI. All subjects, women as well as men, fall well above the sex-specific regression line and the upper 95 % confidence limits for the general population. The lower value for one of the four women was for a subject with a previous history of anorexia nervosa.

FFM is the main determinant of BMR. Energy balance is an extrinsic factor known to influence BMR. The BMR of the athletes from the Swedish national cross-country ski team with a PAL of 3.0–4.5 was compared with that of sedentary non-athletic controls matched for sex and FFM (Sjödin et al., 1996). Comparisons with theoretical calculations of BMR were also made. The athletes had a 13 % higher (P<0.001) BMR than controls if related to FFM and a 16 % higher (P=0.001) BMR if related to both FFM and FM. Possible explanations included an increased substrate flux in the athletes, even during the non-exercise phase, during recovery and in anticipation of exercise.

To summarize, in elite endurance athletes, maintenance metabolic rate is increased for two reasons: FFM is higher than in subjects with a lower PAL (Fig. 2), and maintenance metabolic rate adjusted for FFM is also higher. The suggestion that an increased substrate flux is a determinant of the increased maintenance metabolic rate is confirmed by the value of BMR for the skier with a previous history of anorexia nervosa. She had a much lower BMR (by 16 %) than those of the other female skiers but matched the sedentary controls as well as theoretical calculations (Sjödin et al., 1996). The effect of exercise on maintenance metabolic rate was not observed in intervention studies in which (sedentary) subjects reached a PAL in the range 2.0–2.5, the upper limit observed in the general population (Fig. 1; Westerterp, 1998).

The absence of a long-term effect of exercise on RMR is surprising. Most studies show an exercise-induced change in FFM, the main determinant of RMR. We induced an increase in FFM from 49.5±7.3 to 52.2±7.6 kg (means ± S.D., *N*=23, P<0.001) in novice athletes participating in a 44-week training programme to run a half-marathon. SMR did not increase; in fact, the opposite occurred: SMR decreased by 0.3±0.5 MJ day^{-1} (mean ± S.D., *N*=23, P<0.05; Westerterp et al., 1994). SMR as a function of FFM was lower after 40 weeks of exercise training than before training (Fig. 3). The decrease in SMR was related to a decrease in body mass (r=0.62, P<0.01), possibly as a defence mechanism by the body to maintain body mass. The results contrast with findings for elite athletes, who maintain their body mass at extremely high values of PAL.

Limits to sustainable metabolic rate at high altitude

Sustainable metabolic rate at high altitude is a function of energy balance. It seems to be difficult, if not impossible, to maintain energy balance at altitudes over approximately 5000 m. Kayser (Kayser, 1992) managed to prevent weight loss at 5050 m by supplying subjects with highly palatable diets; however, because the subjects were mainly sedentary, energy turnover was low. A negative energy balance at high altitude

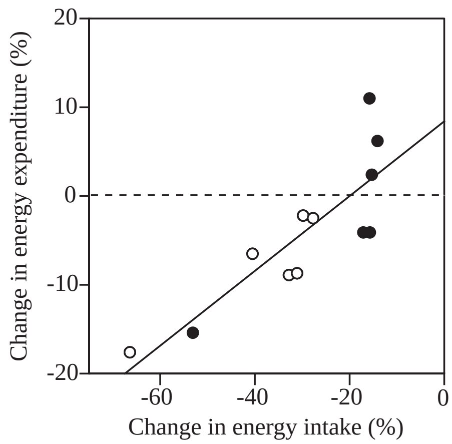

Fig. 4. Change in energy expenditure [100(hypoxic expenditure minus normoxic expenditure)/normoxic expenditure] as a function of the change in energy intake [100(hypoxic intake minus normoxic intake)/normoxic intake] from normoxia to progressive hypoxia in a hypobaric chamber (*N*=6; first 15-day interval, filled symbols; second 15-day interval, open symbols; r^2=0.73, P<0.001).

is mainly the result of malnutrition. Westerterp-Plantenga et al. (Westerterp-Plantenga et al., 1999) assessed the effect of long-term hypobaric hypoxia *per se* on appetite in eight men exposed to a 31-day simulated stay at several altitudes up to the peak of Mount Everest (8848 m). Palatable food was provided *ad libitum*, and stresses such as cold exposure and exercise were avoided. Body mass loss was mainly because of a reduction in energy intake. Meal size was reduced by a more rapid increase in satiety. Initially, meal frequency was increased; however, the increase in the number of meals did not prevent the decrease in total energy intake, resulting in a mean mass loss of 5±2 kg (mean ± S.D., P<0.001) over the 31-day period.

The decrease in energy intake at high altitude is probably one of the determinants of a reduction in sustained metabolic scope. The average daily metabolic rate of the men exposed to a 31-day simulated stay at several altitudes up to the peak of Mount Everest, as described above, was higher than their energy intake, and the discrepancy increased during the exposure (Westerterp et al., 2000). Fig. 4 shows the change in energy expenditure as a function of the change in energy intake from normoxia to progressive hypoxia. The reduction in ADMR was on average approximately one-third of the reduction in energy intake. A reduction in ADMR in a hypoxic environment where stresses such as cold exposure and exercise were avoided implicates mainly a reduction in energy expenditure for physical activity. Maintenance requirement at altitude is thought to be increased (Mawson et al., 2000) and, thus, at a given level of energy expenditure, there is less energy available for diet-induced and activity-induced energy expenditure. Only approximately 10 % of the reduction in energy intake can be explained by a reduction in DEE because DEE is assumed to be 10 % of ADMR in subjects consuming the average mixed diet and being in energy balance. The major proportion of a reduction in ADMR at high altitude will therefore be due to a reduction in AEE.

Exposure to high altitude limits exercise performance by its combined effects on nutrient supply and the capacity to process nutrients by taking up O_2 and exhaling CO_2. Even elite high-altitude climbers do not have physiological adaptations to overcome the consequences of the reduction in partial O_2 pressure (Oelz et al., 1986). We measured PAL values of 2.0–2.7 in subjects climbing Mount Everest, well below the values of up to 5.0 reported for elite endurance athletes at sea level (Westerterp et al., 1992a).

Discussion

An important limit to sustainable metabolic rate is the energy supply. In the general population with unlimited access to food, metabolic rate reaches an upper limit at a PAL value just over 2. Subjects trying to increase PAL further get into a negative energy balance, with consequences for performance. Endurance athletes manage to increase the energetic ceiling of performance to a level of more than twice the limit observed in the general population.

There are at least three explanations for the increase in the energetic ceiling in professional athletes. First, professional athletes are a selection of the population. Few people are born to be athletes. Second, they have to train for many years to reach their high level of performance. For many sports, training has to start at a young age for athletes to be able to compete successfully. Third, training includes exercise and the maintenance of energy balance at a high level of energy turnover. The latter implicates the supplementation of the diet with carbohydrate-rich liquid formulae. Highly trained athletes have learned how to eat the maximum amount of food during hard physical work.

An important aspect of performance at a high level of energy turnover is the 'machinery of the power supply'. There are few data on endurance exercise and energy balance and fat-free mass. Fig. 2 compares data for highly trained athletes with data for subjects from the general population. Endurance athletes are characterized by a high FFM adjusted for height and FM. Values for two of the four women were comparable with those for the four men, although women generally have a considerably lower FFM than men. Sustainable metabolic rate is probably limited by FFM. Maintaining FFM requires exercise training and energy balance. The resulting substrate flux increases BMR, even after adjustment for the enlargement of the FFM. The absolute value of BMR of 7–9 MJ day^{-1} (Sjödin et al., 1996) is equivalent to ADMR for a sedentary subject. Subjects such as novice athletes preparing for a half-marathon run increased FFM but did not show the FFM-adjusted increase in SMR (Fig. 3) observed in professional athletes. This might be a reflection of the limitations of subjects from the general population to increase the substrate flux and thus the normal PAL ceiling of 2.0–2.5.

At high altitude, FFM usually goes down. The decrease is a consequence of the reduced PAL and of negative energy balance. It is difficult to separate the effects of the change in PAL and the energy deficit. We know from mass loss studies that subjects inevitably lose FFM during negative energy balance, even when an energy-restricted diet is combined with an exercise programme.

References

Black, A. E., Coward, W. A., Cole, T. J. and Prentice, A. M. (1996). Human energy expenditure in affluent societies: an analysis of 574 doubly-labelled water measurements. *Eur. J. Clin. Nutr.* **50**, 72–92.

Brouns, F., Saris, W. H. M., Stroecken, J., Beckers, E., Thijssen, R., Rehrer, N. J. and Ten Hoor, F. (1989). Eating, drinking and cycling. A controlled Tour de France simulation study. II. Effect of diet manipulation. *Int. J. Sports Med.* **10**, S41–S48.

Diamond, J. (1991). Evolutionary design of intestinal nutrient absorption: enough but not too much. *News Physiol. Sci.* **6**, 92–96.

Edholm, O. G., Fletcher, J. G., Widdowson, E. M. and McCance, R. A. (1955). The energy expenditure and food intake of individual men. *Br. J. Nutr.* **9**, 286–300.

FAO/WHO/UNU (1985). *Energy and Protein Requirements*. WHO Technical Report Series 724. Geneva: World Health Organization.

Hammond, K. A. and Diamond, J. (1997). Maximal sustained energy budgets in humans and animals. *Nature* **386**, 457–462.

Kayser, B. (1992). Nutrition at high altitude. *Int. J. Sports Med.* **13**, 129–131.

Mawson, J. T., Braun, B., Rock, P. B., Moore, L. G., Mazzeo, R. and Butterfield, G. E. (2000). Women at high altitude: energy requirement. *J. Appl. Physiol.* **88**, 272–281.

Oelz, O., Howald, H., Prampero, P. E., Hoppeler, H., Claassen, H., Jenni, R., Bühlmann, A., Ferretti, G., Brückner, J.-C., Veicsteinas, A., Gussoni, M. and Cerretelli, P. (1986). Physiological profile of world-class high-altitude climbers. *J. Appl. Physiol.* **60**, 1734–1742.

Quetelet, L. A. J. (1871). *Antropométrie ou Mesure des Différences Facultés de l'Homme*. Brussels: Musquardt.

Sjödin, A. M., Andersson, A. B., Högberg, J. M. and Westerterp, K. R. (1994). Energy balance in cross country skiers. A study using doubly labelled water. *Med. Sci. Sports Exerc.* **26**, 720–724.

Sjödin, A. M., Forslund, A. H., Westerterp, K. R., Andersson, A. B., Forslund, J. M. and Hambraeus, L. M. (1996). The influence of physical activity on BMR. *Med. Sci. Sports Exerc.* **28**, 85–91.

Westerterp, K. R. (1998). Alterations in energy balance with exercise. *Am. J. Clin. Nutr.* **68**, 970S–974S.

Westerterp, K. R., Kayser, B., Brouns, F., Herry, J. P. and Saris, W. H. M. (1992a). Energy expenditure climbing Mt. Everest. *J. Appl. Physiol.* **73**, 1815–1819.

Westerterp, K. R., Meijer, E. P., Rubbens, M., Robach, P. and Richalet, J.-P. (2000). Operation Everest III: Energy and water balance. *Eur. J. Physiol.* **439**, 483–488.

Westerterp, K. R., Meijer, G. A. L., Janssen, E. M. E., Saris, W. H. M. and Ten Hoor, F. (1992b). Long term effect of physical activity on energy balance and body composition. *Br. J. Nutr.* **68**, 21–30.

Westerterp, K. R., Meijer, G. A. L., Kester, A. D. M., Wouters, L. and Ten Hoor, F. (1992c). Fat-free mass as a function of fat mass and habitual activity level. *Int. J Sports Med.* **13**, 163–166.

Westerterp, K. R., Meijer, G. A. L., Schoffelen, P. and Janssen, E. M. E. (1994). Body mass, body composition and sleeping metabolic rate before, during and after endurance training. *Eur. J. Appl. Physiol.* **69**, 203–208.

Westerterp, K. R., Saris, W. H. M., Van Es, M. and Ten Hoor, F. (1986). Use of the doubly labeled water technique in humans during heavy sustained exercise. *J. Appl. Physiol.* **61**, 2162–2167.

Westerterp-Plantenga, M. S., Westerterp, K. R., Rubbens, M., Verwegen, C. R. T., Richalet, J.-P. and Gardette, B. (1999). Appetite at 'high altitude' [Operation Everest III (Comex-'97)]: a simulated ascent of Mount Everest. *J. Appl. Physiol.* **87**, 391–399.

Woods, S. C. (1996). The eating paradox: how we tolerate food. *Psychol. Rev.* **98**, 488–505.