Maintenance Energy Requirement and Net Energetic Efficiency in Mice with a Major Gene for Rapid Postweaning Gain

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ABSTRACT Previous research in this laboratory demonstrated the existence of a major gene (hg), expressed as a homozygous recessive, which increases postweaning growth by 60% in C57Bl/6 mice (line Ch) compared to the same genetic stock without the major gene (line CH). The effect of the hg gene on the maintenance energy requirement and net energetic efficiency of mice between 21 and 42 d of age was examined in a comparative slaughter experiment. Regressions of changes in body energy per kilogram^{0.75} on metabolizable energy intake per kilogram^{0.75} indicated that the maintenance energy requirements averaged 164 kcal/(kg0.75 • d) and 155 kcal/(kg0.75 • d) for lines CH and Ch, respectively. Net efficiency of energy utilization was 38.5 and 49.5% for lines CH and Ch, respectively. Ad libitum-fed mice of line Ch gained 46% more total body energy per unit of metabolic body weight (kilogram^{0.75}) than ad libitumfed mice from line CH while their energy intake per kilogram^{0.75} was equal. It was estimated that the decreased maintenance energy requirement and increased net energetic efficiency accounted for approximately 25 and 75%, respectively, of the increased energy gain of ad libitum-fed mice of line Ch as compared to CH. The increased energy gain of line Ch was largely (78%) due to an increase fat energy deposition. Regressions of fat energy gain per kilogram^{0.75} on metabolizable energy intake per kilogram^{0.75} indicated that the increased fat energy gain was due to an increased efficiency of fat deposition and/or an increased proportion of metabolizable energy available for gain used for fat gain. J. Nutr. 116: 419-428, 1986.

INDEXING KEY WORDS mice • major gene • maintenance energy requirement • energetic efficiency • fasting heat production

Previous research in this laboratory has demonstrated the existence of a major gene in mice that increases postweaning growth rate and body weight at 42 d of age by 60 and 40%, respectively (1). This condition is due to an autosomal recessive gene, for which the symbol hg (high growth) has been proposed (2). The hg/hg genotype results in rapid postweaning gain by comparison to Hg/Hg and Hg/hg, which are not distinguishable from each other based on postweaning gain or body weight at 42 d of age (1, 2).

The hg gene has a general influence on all chemical components of growth without altering the chemical composition of the carcass (1, 3). This observation was considered unique given that all single genes known to increase rodent weight gain result in obesity (4). A large number of reports also indicates that selection for growth results in increased fat deposition although some reports do not support this conclusion (5).

Calvert et al. (6) observed that the hg

^{© 1986} American Institute of Nutrition. Received for publication: 9 August 1985. Accepted for publication: 7 November 1985.

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gene increased food intake and gross energetic efficiency by 28 and 33%, respectively. Gross energetic efficiency could be improved by an increase in food intake and/or an increase in net energetic efficiency and/or a decrease in energy requirement for maintenance. Everything else being equal, an increase in food intake can increase gross energetic efficiency simply by providing a greater amount of energy available for gain (7, 8). However, Calvert et al. (6) calculated that the increased food intake of hg/hg mice could not account for their increased gross energetic efficiency and that the hg gene must alter maintenance energy requirement and/or net energetic efficiency. The objective of the present report was to examine these possibilities by determining energy required for maintenance and efficiency of energy utilization above maintenance in hg/hg (line Ch) and Hg/Hg (line CH) mice.

MATERIALS AND METHODS

Animals and diets. A complete history of the lines of mice used in this study has been presented elsewhere (2, 3, 6). Briefly, heterozygous animals (Hg/hg) carrying 87.5%C57Bl/6 genes were intermated. Large segregates (hg/hg) were intermated to form line Ch and normal segregates (Hg/Hg and Hg/hg) were intermated to form line CH. In line CH, litters with large segregates were discarded so that after generation 5 no large segregates were detected. The current experiment was conducted with generation 10 of lines Ch and CH.

All mice were kept in a room maintained at 24 ± 2°C with lights on 14 h (0530-1930 h) per day. Breeding pairs were fed a nonpurified mouse diet (Simonsen Laboratories, Gilroy, CA) with a guaranteed analysis of a minimum of 24% crude protein and 6% fat and a maximum of 3.5% crude fiber. Litters were counted on the day of birth and those with more than 10 pups were reduced to 10 at 2 d of age. Young were weaned and weighed to the nearest 0.1 g at 21 d of age. A total of 40 male weanling mice of each line (Ch and CH) were randomly selected from 17 litters of each line at weaning. Animals were randomly allotted to one of five levels of dietary intake and fed a purified diet (table 1) from 21 to 42 d of age. For

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Diet composition

| Component | Amount | |
|--|--------|--|
| | % | |
| Ingredient | | |
| Casein ¹ | 30.0 | |
| L-Methionine | 0.3 | |
| Glucose | 57.0 | |
| Corn oil | 8.0 | |
| AIN mineral mix ² | 3.5 | |
| AIN vitamin mix ³ | 1.0 | |
| Choline chloride (70%) | 0.2 | |
| Analysis | | |
| Drv matter | 96 | |
| Protein (% N \times 6.25) ⁴ | 26.8 | |
| Fat ⁴ | 8.2 | |

¹High nitrogen casein (U.S. Biochemical Corp., Cleveland, OH). ²AIN-76[™] mineral mix (ref. 9). ³AIN-76[™] vitamin mix (ref. 9). ⁴Expressed on a dry matter basis.

each line, one group of eight animals was fed ad libitum while four other groups of eight animals each were fed individually as a function of their body weight 90, 80, 70 or 60% of the average food intake per unit of body weight of the respective ad libitumfed group on the previous day. The daily food intake of restricted mice was offered in two equal meals at 0700 and 1800 h. Mice were individually housed in hanging cages with wire-mesh bottom containing a feeder that minimized spillage and had ad libitum access to water. Body weight and food intake of each mouse were recorded daily.

Measures and calculations of energy values. We assumed that the metabolizable energy (ME) values of fat and glucose averaged 9 and 3.7 kcal/g. The ME value of protein was assumed to be 4 kcal/g when no protein gain occurred, but for mice gaining protein 1.4 kcal/g of protein gain was added to total ME intake (MEI). The calculated ME content of the diet for maintenance was 3.834 kcal/g.

At the beginning of the experiment, 14 Ch and 15 CH 21-d-old mice were weighed, then killed by cervical dislocation, and gastrointestinal tract contents were removed. The 42-d-old mice were likewise killed at the end of the experiment. Body water was determined by freeze-drying the carcasses to a constant weight. Carcass lipid content was quantified as the difference in the weights of the dried carcasses before and after extraction with anhydrous diethyl ether for 7 d followed by 4 d extraction with acetone. Body protein was determined by Kjeldahl N \times 6.25 using dry fat-free carcasses that had been ground in a laboratory Wiley mill with a 40-mesh screen. Energy content of a pooled fat sample and of individual fat-free carcasses was determined by using a bomb calorimeter (Gallenkamp, model APP CB-110/1, London, England). The energy content the pooled fat sample was 9.03 kcal/g. Lean body mass energy (LE) was calculated as the product of dry fat-free carcass weight (grams) times fat-free carcass energy content (kilocalories/gram). Fat energy (FE) was calculated as carcass lipids (grams) \times 9.03 kcal/g.

Regression equations developed from data generated by mice killed at 21 d of age were used for each line of mice to express body protein (BP), LE and FE as a linear function of live body weight (BW) at 21 d of age. When there was no significant difference between regressions for line Ch and CH, a pooled equation was calculated. The following equations were derived (BW in grams): for line CH and Ch, LE (kilocalories) $= 0.879 \times BW + 0.640 (n = 29; r = 0.99;$ P < 0.001; for line CH and Ch, BP (grams) $= 0.147 \times BW + 0.165 (n = 29; r = 0.99;$ P < 0.001; for line CH, FE (kilocalories) $= 0.986 \times BW - 3.980 (n = 15; r = 0.96;$ P < 0.001; for line Ch, FE (kilocalories) $= 1.07 \times BW - 3.491 (n = 14; r = 0.93;$ P < 0.001). By using 21-d-old BW, these equations were then used to predict initial values of BP, LE and FE at 21 d of age in those mice killed at 42 d of age. Changes in body protein (Δ BP), lean body energy (Δ LE) and fat energy (ΔFE) were calculated as the difference between the 42-d-old value (measured) and the 21-d-old value (predicted). Change in total-body energy (ΔBE) was calculated as the sum of ΔLE and ΔFE . Heat production (HP) was calculated as the difference between MEI and BE. Energy changes (ΔLE , ΔFE and ΔBE), HP and MEI were all divided by metabolic body size and expressed as kilocalories/(kilogram^{0.75} · d). Metabolic body size (kilogram^{0.75}) of each mouse was calculated by raising to the 0.75

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power its average body weight calculated over the 21 d of experiment.

Energy requirement for maintenance as defined by the MEI producing no change in body energy was determined by the x-axis intercept of the regression of $\Delta BE/BW^{0.75}$ over MEI/BW^{0.75}. Net efficiency of energy utilization above maintenance was given by the slope of this same regression. Fasting heat production (FHP) as defined by the heat production when energy intake is zero was estimated by extrapolation from the regression of logarithm heat production/ BW^{0.75} over MEI/BW^{0.75} (10).

Statistical analysis. Regression analysis was used for statistical interpretation of the results. From correlation coefficients (r) corresponding t-values were computed to test the statistical significance of correlation. Standard errors of the y-axis intercept and regression coefficient were computed (11). Regression lines for both lines of mice were tested for equality of slopes (11). Given the standard regression equation y = a + bx, the x-axis intercept was calculated as -a/b. The variance of the x-axis intercept was approximated as $(-a/b)^2 \times [V(a)/a^2 + V(b)/b^2$ $-2 \times \text{COV}(a,b)/a \times b$ where COV(a,b)is the covariance of a and b; V(a) and V(b)are the respective variances of a and b (12). The x-axis intercepts for both lines of mice were compared by computing a *t*-value from their mean and variances. Differences between means for food intake, energy changes and gross energetic efficiency of ad libitumfed mice of lines CH and Ch were tested for significance by Student's t-test.

RESULTS AND DISCUSSION

Gross energetic efficiency as defined by the ratio of ΔBE over MEI was significantly improved by the major gene for rapid postweaning growth in ad libitum-fed mice (table 2). Mice of line Ch had a 46.2% higher gross energetic efficiency than mice from line CH. Similar differences in gross energetic efficiency between line Ch and CH was observed by Calvert et al. (6). Gross energetic efficiency may be improved simply by increasing energy intake thus providing a greater amount of energy available for gain (7, 8). MEI of ad libitum-fed mice was 36.7% higher (P < 0.001) in line Ch as

Weight gains, energy intakes and body energy changes from 21 to 42 d of age in mice from line CH and Ch^{1}

| $\begin{tabular}{ c c c c c c } \hline Parameter & Ad libitum^3 & 90\% & 80\% & 70\% & 60\% \\ \hline \\ \hline \\ \hline \\ Line CH (Hg/Hg) \\ \hline \\ \hline \\ \hline \\ \hline \\ Parameter & Ad libitum^3 & 90\% & 80\% & 70\% & 60\% \\ \hline \\ $ | Parameter | Intake level ² | | | | | |
|--|---|---------------------------|-------------------|---------------------|-------------------|-------------------|--|
| $\begin{tabular}{ c c c c c } Line CH (Hg/Hg) \\ \hline No. of animals^4 & 8 & 8 & 7 & 7 \\ Body wt gain, g & 17.2 \pm 1.9 & 10.4 \pm 4.4 & 4.2 \pm 4.0 & 0.01 \pm 1.5 & -1.6 \pm 1.1 \\ Arg metabolic body wt, kg^{0.73} & 0.049 \pm 0.003 & 0.043 \pm 0.01 & 0.038 \pm 0.008 & 0.032 \pm 0.007 & 0.030 \pm 0.003 \\ Metabolizable energy intake, \\ kcal/(kg^{0.73} \cdot d) & 258 \pm 14 & 225 \pm 14 & 198 \pm 16 & 169 \pm 12 & 144 \pm 6 \\ Change in lean body energy, \\ kcal/(kg^{0.73} \cdot d) & 19.5 \pm 1.5 & 13.5 \pm 3.4 & 8.1 \pm 4.3 & 2.9 \pm 2.7 & 0.7 \pm 1.8 \\ Change in total body energy, \\ kcal/(kg^{0.73} \cdot d) & 17.7 \pm 4.4 & 12.8 \pm 7.7 & 1.1 \pm 5.7 & -3.1 \pm 2.7 & -5.7 \pm 1.8 \\ Change in total body energy, \\ kcal/(kg^{0.73} \cdot d) & 37.2 \pm 4.7 & 26.3 \pm 10.4 & 9.2 \pm 9.4 & -0.2 \pm 4.5 & -5.0 \pm 3.2 \\ Gross energetic efficiency, \% & 14.5 \pm 1.9 & 11.6 \pm 4.3 & 4.5 \pm 4.4 & -0.2 \pm 2.5 & -3.5 \pm 2.3 \\ \hline No. of animals^4 & 8 & 8 & 8 & 8 & 5 \\ Body wt gain, g & 29.8 \pm 2.8^* & 10.4 \pm 8.9 & 5.1 \pm 2.6 & 1.0 \pm 1.1 & -0.5 \pm 0.9 \\ Arg metabolizable energy intake, \\ kcal/(kg^{0.73} \cdot d) & 0.068 \pm 0.003^* & 0.043 \pm 0.013 & 0.039 \pm 0.006 & 0.031 \pm 0.003 & 0.027 \pm 0.003 \\ \hline Metabolizable energy intake, \\ kcal/(kg^{0.73} \cdot d) & 257 \pm 9 & 207 \pm 20 & 187 \pm 8 & 160 \pm 5 & 130 \pm 9 \\ \hline Change in lean body energy, \\ kcal/(kg^{0.73} \cdot d) & 257 \pm 9 & 207 \pm 20 & 187 \pm 8 & 160 \pm 5 & 130 \pm 9 \\ \hline Change in lean body energy, \\ kcal/(kg^{0.73} \cdot d) & 23.2 \pm 1.2^* & 12.8 \pm 6.3 & 9.2 \pm 3.1 & 4.1 \pm 1.6 & 1.2 \pm 1.7 \\ \hline Change in lean body energy, \\ kcal/(kg^{0.73} \cdot d) & 31.2 \pm 4.3^* & 9.5 \pm 11.3 & 2.5 \pm 3.0 & -4.0 \pm 1.2 & -4.7 \pm 2.0 \\ \hline Change in total body energy, \\ kcal/(kg^{0.73} \cdot d) & 31.2 \pm 4.3^* & 9.5 \pm 11.3 & 2.5 \pm 3.0 & -4.0 \pm 1.2 & -4.7 \pm 2.0 \\ \hline Change in total body energy, \\ kcal/(kg^{0.73} \cdot d) & 31.2 \pm 4.3^* & 9.5 \pm 11.3 & 2.5 \pm 3.0 & -4.0 \pm 1.2 & -4.7 \pm 2.0 \\ \hline Change in total body energy, \\ kcal/(kg^{0.73} \cdot d) & 31.2 \pm 4.3^* & 9.5 \pm 11.3 & 2.5 \pm 3.0 & -4.0 \pm 1.2 & -4.7 \pm 2.0 \\ \hline Change in total body energy, \\ kcal/(kg^{0.73} \cdot d) & 31.2 \pm 4.3^* & 9.5 \pm 11.3 & 2.5 \pm 3.0 & -4.0 \pm 1.2 & -4.7 \pm 2.0 \\ \hline C$ | | Ad libitum ³ | 90 % | 80 % | 70 % | 60 % | |
| No. of animals ⁴ 8 8 8 8 7 7 Body wt gain, g 17.2 ± 1.9 10.4 ± 4.4 4.2 ± 4.0 0.0 ± 1.5 -1.6 ± 1.1 Avg metabolic body wt, kg ^{0.73} 0.049 ± 0.003 0.043 ± 0.01 0.038 ± 0.008 0.032 ± 0.007 0.030 ± 0.003 Metabolizable energy intake, kcal/dg ^{0.75} · d) 12.73 ± 0.44 9.73 ± 0.97 7.73 ± 0.77 5.55 ± 0.59 4.34 ± 0.22 Metabolizable energy intake, kcal/(kg ^{0.75} · d) 19.5 ± 1.5 13.5 ± 3.4 8.1 ± 4.3 2.9 ± 2.7 0.7 ± 1.8 Change in fat energy, kcal/(kg ^{0.75} · d) 19.5 ± 1.5 13.5 ± 3.4 8.1 ± 4.3 2.9 ± 2.7 0.7 ± 1.8 Change in total body energy, kcal/(kg ^{0.75} · d) 17.7 ± 4.4 12.8 ± 7.7 1.1 ± 5.7 -3.1 ± 2.7 -5.7 ± 1.8 Change in total body energy, kcal/(kg ^{0.73} · d) 37.2 ± 4.7 26.3 ± 10.4 9.2 ± 9.4 -0.2 ± 4.5 -5.0 ± 3.2 Gross energetic efficiency, % 14.5 ± 1.9 11.6 ± 4.3 4.5 ± 4.4 -0.2 ± 2.5 -3.5 ± 2.3 Line Ch (hg/hg) 0.003 ± 0.003* 0.0043 ± 0.013 0.039 ± 0.006 0.031 ± 0.003 0.027 ± 0.023 Avg metaboli | | Line CH (Hg/Hg) | | | | | |
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| Change in lean body energy, kcal/(kg ^{0.75} · d) 19.5 ± 1.5 13.5 ± 3.4 8.1 ± 4.3 2.9 ± 2.7 0.7 ± 1.8 Change in fat energy, kcal/(kg ^{0.75} · d) 17.7 ± 4.4 12.8 ± 7.7 1.1 ± 5.7 $-3.1 \pm 2.7 -5.7 \pm 1.8$ Change in total body energy, kcal/(kg ^{0.75} · d) 37.2 ± 4.7 26.3 ± 10.4 9.2 ± 9.4 $-0.2 \pm 4.5 -5.0 \pm 3.2$ Gross energetic efficiency, % 14.5 ± 1.9 11.6 ± 4.3 4.5 ± 4.4 $-0.2 \pm 2.5 -3.5 \pm 2.3$ Line Ch (hg/hg) No. of animals ⁴ 8 8 8 8 8 5 Body wt gain, g 29.8 ± 2.8* 10.4 ± 8.9 5.1 ± 2.6 1.0 ± 1.1 -0.5 ± 0.9 Avg metabolic body wt, kg ^{0.73} Metabolizable energy intake, kcal/(kg ^{0.75} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.75} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in fat energy, kcal/(kg ^{0.75} · d) 31.2 ± 4.3* 9.5 ± 11.3 2.5 ± 3.0 $-4.0 \pm 1.2 -4.7 \pm 2.0$ Change in total body energy, kcal/(kg ^{0.75} · d) 54.4 ± 4.8* 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 | $kcal/(kg^{0.75} \cdot d)$ | 258 ± 14 | 225 ± 14 | 198 ± 16 | 169 ± 12 | 144 ± 6 | |
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| Change in fat energy, kcal/(kg ^{0.75} · d) 17.7 ± 4.4 12.8 ± 7.7 1.1 ± 5.7 -3.1 ± 2.7 -5.7 ± 1.8 Change in total body energy, kcal/(kg ^{0.75} · d) 37.2 ± 4.7 26.3 ± 10.4 9.2 ± 9.4 -0.2 ± 4.5 -5.0 ± 3.2 Gross energetic efficiency, % 14.5 ± 1.9 11.6 ± 4.3 4.5 ± 4.4 -0.2 ± 2.5 -3.5 ± 2.3 Line Ch (hg/hg) No. of animals ⁴ 8 8 8 8 5 Body wt gain, g 29.8 ± 2.8 [*] 10.4 ± 8.9 5.1 ± 2.6 1.0 ± 1.1 -0.5 ± 0.9 Avg metabolic body wt, kg ^{0.75} 0.068 ± 0.003 [*] 0.043 ± 0.013 0.039 ± 0.006 0.031 ± 0.003 0.027 ± 0.003 Metabolizable energy intake, kcal/(kg ^{0.75} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.75} · d) 23.2 ± 1.2 [*] 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, kcal/(kg ^{0.75} · d) 31.2 ± 4.3 [*] 9.5 ± 11.3 2.5 ± 3.0 $-4.0 \pm 1.2 - 4.7 \pm 2.0$ Change in total body energy, kcal/(kg ^{0.75} · d) 54.4 ± 4.8 [*] 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % 21.2 ± 1.9 [*] 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | $k_{cal}/(k_{g}^{0.75} \cdot d)$ | 19.5 ± 1.5 | 13.5 ± 3.4 | 8.1 ± 4.3 | 2.9 ± 2.7 | 0.7 ± 1.8 | |
| $\begin{array}{c c c c c c c c c c c c c c c c c c c $ | Change in fat energy. | | | | | | |
| Change in total body energy, kcal/(kg ^{0.75} · d) 37.2 ± 4.7 26.3 ± 10.4 9.2 ± 9.4 $-0.2 \pm 4.5 -5.0 \pm 3.2$ Gross energetic efficiency, % 14.5 ± 1.9 11.6 ± 4.3 4.5 ± 4.4 $-0.2 \pm 2.5 -3.5 \pm 2.3$ Line Ch (hg/hg) No. of animals ⁴ 8 8 8 8 5 Body wt gain, g 29.8 ± 2.8 [*] 10.4 ± 8.9 5.1 ± 2.6 1.0 ± 1.1 -0.5 ± 0.9 Avg metabolic body wt, kg ^{0.75} 0.068 ± 0.003 [*] 0.043 ± 0.013 0.039 ± 0.006 0.031 ± 0.003 0.027 ± 0.003 Metabolizable energy intake, kcal/d 17.40 ± 0.44 [*] 9.09 ± 1.26 7.33 ± 0.49 5.01 ± 0.23 3.48 ± 0.24 Metabolizable energy intake, kcal/(kg ^{0.75} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.75} · d) 31.2 ± 4.3 [*] 9.5 ± 11.3 2.5 ± 3.0 $-4.0 \pm 1.2 - 4.7 \pm 2.0$ Change in total body energy, kcal/(kg ^{0.75} · d) 54.4 ± 4.8 [*] 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % 21.2 ± 1.9 [*] 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | $k_{cal}/(k_g^{0.75} \cdot d)$ | 17.7 ± 4.4 | 12.8 ± 7.7 | 1.1 ± 5.7 | -3.1 ± 2.7 | -5.7 ± 1.8 | |
| kcal/(kg^{0.73} \cdot d) 37.2 ± 4.7 26.3 ± 10.4 9.2 ± 9.4 -0.2 ± 4.5 -5.0 ± 3.2 Gross energetic efficiency, % 14.5 ± 1.9 11.6 ± 4.3 4.5 ± 4.4 -0.2 ± 2.5 -3.5 ± 2.3 Line Ch (hg/hg)No. of animals ⁴ 8888Body wt gain, g $29.8 \pm 2.8^{*}$ 10.4 ± 8.9 5.1 ± 2.6 1.0 ± 1.1 -0.5 ± 0.9 Avg metabolic body wt, kg ^{0.73} $0.068 \pm 0.003^{*}$ 0.043 ± 0.013 0.039 ± 0.006 0.031 ± 0.003 0.027 ± 0.003 Metabolizable energy intake, kcal/(kg ^{0.75} · d) $17.40 \pm 0.44^{*}$ 9.09 ± 1.26 7.33 ± 0.49 5.01 ± 0.23 3.48 ± 0.24 Metabolizable energy intake, kcal/(kg ^{0.73} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.73} · d) $31.2 \pm 4.3^{*}$ 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, kcal/(kg ^{0.73} · d) $54.4 \pm 4.8^{*}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Cross energetic efficiency, % $21.2 \pm 1.9^{*}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | Change in total body energy. | | | | | | |
| Gross energetic efficiency, %14.5 \pm 1.911.6 \pm 4.34.5 \pm 4.4-0.2 \pm 2.5-3.5 \pm 2.3Line Ch (hg/hg)No. of animals ⁴ 8888Body wt gain, g29.8 \pm 2.8°10.4 \pm 8.95.1 \pm 2.61.0 \pm 1.1-0.2 \pm 2.5-3.5 \pm 2.3Line Ch (hg/hg)No. of animals ⁴ 8885Body wt gain, g29.8 \pm 2.8°10.4 \pm 8.95.1 \pm 2.61.0 \pm 1.1-0.5 \pm 0.9Avg metabolic body wt, $kg^{0.75}$ 0.068 \pm 0.003°0.043 \pm 0.0130.039 \pm 0.0060.031 \pm 0.0030.027 \pm 0.003Metabolizable energy intake, $kcal/(kg^{0.75} \cdot d)$ 17.40 \pm 0.44°9.09 \pm 1.267.33 \pm 0.495.01 \pm 0.233.48 \pm 0.24Metabolizable energy intake, $kcal/(kg^{0.75} \cdot d)$ 23.2 \pm 1.2°187 \pm 8160 \pm 51300 \pm 9Change in lean body energy, $kcal/(kg^{0.75} \cdot d)$ 23.2 \pm 1.2°12.8 \pm 6.39.2 \pm 3.14.1 \pm 1.61.2 \pm 1.7Change in lean body ener | $kcal/(kg^{0.75} \cdot d)$ | 37.2 ± 4.7 | 26.3 ± 10.4 | 9.2 ± 9.4 | -0.2 ± 4.5 | -5.0 ± 3.2 | |
| Line Ch (hg/hg)No. of animals ⁴ 8885Body wt gain, g $29.8 \pm 2.8^{\circ}$ 10.4 ± 8.9 5.1 ± 2.6 1.0 ± 1.1 -0.5 ± 0.9 Avg metabolic body wt, kg ^{0.75} $0.068 \pm 0.003^{\circ}$ 0.043 ± 0.013 0.039 ± 0.006 0.031 ± 0.003 0.027 ± 0.003 Metabolizable energy intake, kcal/d $17.40 \pm 0.44^{\circ}$ 9.09 ± 1.26 7.33 ± 0.49 5.01 ± 0.23 3.48 ± 0.24 Metabolizable energy intake, kcal/(kg ^{0.75} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.73} · d) $23.2 \pm 1.2^{\circ}$ 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, kcal/(kg ^{0.73} · d) $31.2 \pm 4.3^{\circ}$ 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, kcal/(kg ^{0.73} · d) $54.4 \pm 4.8^{\circ}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | Gross energetic efficiency, % | 14.5 ± 1.9 | 11.6 ± 4.3 | 4.5 ± 4.4 | -0.2 ± 2.5 | -3.5 ± 2.3 | |
| No. of animals ⁴ 88885Body wt gain, g $29.8 \pm 2.8^{\circ}$ 10.4 ± 8.9 5.1 ± 2.6 1.0 ± 1.1 -0.5 ± 0.9 Avg metabolic body wt, kg ^{0.73} $0.068 \pm 0.003^{\circ}$ 0.043 ± 0.013 0.039 ± 0.006 0.031 ± 0.003 0.027 ± 0.003 Metabolizable energy intake, kcal/(kg ^{0.73} · d) $17.40 \pm 0.44^{\circ}$ 9.09 ± 1.26 7.33 ± 0.49 5.01 ± 0.23 3.48 ± 0.24 Metabolizable energy intake, kcal/(kg ^{0.73} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.73} · d) $23.2 \pm 1.2^{\circ}$ 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, kcal/(kg ^{0.73} · d) $31.2 \pm 4.3^{\circ}$ 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, kcal/(kg ^{0.73} · d) $54.4 \pm 4.8^{\circ}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Cross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | | Line Ch (hg/hg) | | | | | |
| Note that Body wf gain, g $29.8 \pm 2.8^{\circ}$ 10.4 ± 8.9 5.1 ± 2.6 1.0 ± 1.1 -0.5 ± 0.9 Avg metabolic body wt, kg ^{0.73} $0.068 \pm 0.003^{\circ}$ 0.043 ± 0.013 0.039 ± 0.006 0.031 ± 0.003 0.027 ± 0.003 Metabolizable energy intake, kcal/(kg ^{0.73} · d) $17.40 \pm 0.44^{\circ}$ 9.09 ± 1.26 7.33 ± 0.49 5.01 ± 0.23 3.48 ± 0.24 Metabolizable energy intake, kcal/(kg ^{0.73} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.73} · d) $23.2 \pm 1.2^{\circ}$ 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, kcal/(kg ^{0.73} · d) $31.2 \pm 4.3^{\circ}$ 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, kcal/(kg ^{0.73} · d) $54.4 \pm 4.8^{\circ}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Cross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | No. of animals ⁴ | 8 | 8 | 8 | 8 | 5 | |
| Avg metabolic body wt, $kg^{0.75}$ 0.068 ± 0.003*0.043 ± 0.0130.039 ± 0.0060.031 ± 0.0030.027 ± 0.003Metabolizable energy intake, kcal/d17.40 ± 0.44*9.09 ± 1.267.33 ± 0.495.01 ± 0.233.48 ± 0.24Metabolizable energy intake, kcal/(kg^{0.75} · d)257 ± 9207 ± 20187 ± 8160 ± 5130 ± 9Change in lean body energy, kcal/(kg^{0.75} · d)23.2 ± 1.2*12.8 ± 6.39.2 ± 3.14.1 ± 1.61.2 ± 1.7Change in fat energy, kcal/(kg^{0.75} · d)31.2 ± 4.3*9.5 ± 11.32.5 ± 3.0-4.0 ± 1.2-4.7 ± 2.0Change in total body energy, kcal/(kg^{0.75} · d)54.4 ± 4.8*22.3 ± 17.011.8 ± 5.60.1 ± 2.6-3.6 ± 3.6Cross energetic efficiency, %21.2 ± 1.9*10.2 ± 7.16.2 ± 2.70.0 ± 1.6-2.9 ± 3.2 | Body wt gain, g | $29.8 \pm 2.8^{*}$ | 10.4 ± 8.9 | 5.1 ± 2.6 | 1.0 ± 1.1 | -0.5 ± 0.9 | |
| Metabolizable energy intake, kcal/d 17.40 \pm 0.44* 9.09 \pm 1.26 7.33 \pm 0.49 5.01 \pm 0.23 3.48 \pm 0.24 Metabolizable energy intake, kcal/(kg ^{0.75} · d) 257 \pm 9 207 \pm 20 187 \pm 8 160 \pm 5 130 \pm 9 Change in lean body energy, kcal/(kg ^{0.75} · d) 23.2 \pm 1.2* 12.8 \pm 6.3 9.2 \pm 3.1 4.1 \pm 1.6 1.2 \pm 1.7 Change in fat energy, kcal/(kg ^{0.75} · d) 31.2 \pm 4.3* 9.5 \pm 11.3 2.5 \pm 3.0 -4.0 \pm 1.2 -4.7 \pm 2.0 Change in total body energy, kcal/(kg ^{0.75} · d) 54.4 \pm 4.8* 22.3 \pm 17.0 11.8 \pm 5.6 0.1 \pm 2.6 -3.6 \pm 3.6 Cross energetic efficiency, % 21.2 \pm 1.9* 10.2 \pm 7.1 6.2 \pm 2.7 0.0 \pm 1.6 -2.9 \pm 3.2 | Avg metabolic body wt. $kg^{0.75}$ | 0.068 ± 0.003 | 0.043 ± 0.013 | 0.039 ± 0.006 | 0.031 ± 0.003 | 0.027 ± 0.003 | |
| kcal/d 17.40 \pm 0.44* 9.09 \pm 1.26 7.33 \pm 0.49 5.01 \pm 0.23 3.48 \pm 0.24 Metabolizable energy intake, kcal/(kg^{0.75} \cdot d) 257 \pm 9 207 \pm 20 187 \pm 8 160 \pm 5 130 \pm 9 Change in lean body energy, kcal/(kg^{0.75} \cdot d) 23.2 \pm 1.2* 12.8 \pm 6.3 9.2 \pm 3.1 4.1 \pm 1.6 1.2 \pm 1.7 Change in fat energy, kcal/(kg^{0.73} \cdot d) 31.2 \pm 4.3* 9.5 \pm 11.3 2.5 \pm 3.0 -4.0 \pm 1.2 -4.7 \pm 2.0 Change in total body energy, kcal/(kg^{0.73} \cdot d) 51.4 \pm 4.8* 22.3 \pm 17.0 11.8 \pm 5.6 0.1 \pm 2.6 -3.6 \pm 3.6 Cross energetic efficiency, % 21.2 \pm 1.9* 10.2 \pm 7.1 6.2 \pm 2.7 0.0 \pm 1.6 -2.9 \pm 3.2 | Metabolizable energy intake. | | | | | | |
| Metabolizable energy intake, $kcal/(kg^{0.73} \cdot d)$ 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, $kcal/(kg^{0.73} \cdot d)$ 23.2 ± 1.2* 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, $kcal/(kg^{0.73} \cdot d)$ 31.2 ± 4.3* 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, $kcal/(kg^{0.73} \cdot d)$ 54.4 ± 4.8* 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % 21.2 ± 1.9* 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | kcal/d | $17.40 \pm 0.44^{\circ}$ | 9.09 ± 1.26 | 7.33 ± 0.49 | 5.01 ± 0.23 | 3.48 ± 0.24 | |
| kcal/(kg ^{0.73} · d) 257 ± 9 207 ± 20 187 ± 8 160 ± 5 130 ± 9 Change in lean body energy, kcal/(kg ^{0.73} · d) $23.2 \pm 1.2^{\circ}$ 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, kcal/(kg ^{0.73} · d) $31.2 \pm 4.3^{\circ}$ 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, kcal/(kg ^{0.73} · d) $31.4 \pm 4.8^{\circ}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | Metabolizable energy intake. | | | | | | |
| Change in lean body energy, $kcal/(kg^{0.73} \cdot d)$ 23.2 ± 1.2 [•] 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, $kcal/(kg^{0.73} \cdot d)$ 31.2 ± 4.3 [•] 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, $kcal/(kg^{0.73} \cdot d)$ 54.4 ± 4.8 [•] 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % 21.2 ± 1.9 [•] 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | $k cal/(k g^{0.75} \cdot d)$ | 257 ± 9 | 207 ± 20 | 187 ± 8 | 160 ± 5 | 130 ± 9 | |
| kcal/(kg ^{0.73} · d) $23.2 \pm 1.2^{\circ}$ 12.8 ± 6.3 9.2 ± 3.1 4.1 ± 1.6 1.2 ± 1.7 Change in fat energy, kcal/(kg ^{0.73} · d) $31.2 \pm 4.3^{\circ}$ 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, kcal/(kg ^{0.73} · d) $54.4 \pm 4.8^{\circ}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | Change in lean body energy. | | | | | | |
| Change in fat energy, $kcal/(kg^{0.73} \cdot d)$ 31.2 ± 4.3° 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, $kcal/(kg^{0.73} \cdot d)$ 54.4 ± 4.8° 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % 21.2 ± 1.9° 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | kcal/(kg ^{0.75} • d) | $23.2 \pm 1.2^{\circ}$ | 12.8 ± 6.3 | 9.2 ± 3.1 | 4.1 ± 1.6 | 1.2 ± 1.7 | |
| $kcal/(kg^{0.73} \cdot d)$ $31.2 \pm 4.3^{\circ}$ 9.5 ± 11.3 2.5 ± 3.0 -4.0 ± 1.2 -4.7 ± 2.0 Change in total body energy, $kcal/(kg^{0.73} \cdot d)$ $54.4 \pm 4.8^{\circ}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Cross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | Change in fat energy. | | | | | | |
| Change in total body energy, $kcal/(kg^{0.73} \cdot d)$ 54.4 ± 4.8 [*] 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 - 3.6 ± 3.6 Gross energetic efficiency, % 21.2 ± 1.9 [*] 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 - 2.9 ± 3.2 | $k_{cal}/(k_{\sigma}^{0.78} \cdot d)$ | $31.2 \pm 4.3^{*}$ | 9.5 ± 11.3 | 2.5 ± 3.0 | -4.0 ± 1.2 | -4.7 ± 2.0 | |
| kcal/(kg^{0.73} \cdot d) $54.4 \pm 4.8^{\circ}$ 22.3 ± 17.0 11.8 ± 5.6 0.1 ± 2.6 -3.6 ± 3.6 Gross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | Change in total body energy. | | | | | | |
| Gross energetic efficiency, % $21.2 \pm 1.9^{\circ}$ 10.2 ± 7.1 6.2 ± 2.7 0.0 ± 1.6 -2.9 ± 3.2 | kcal/(kg ^{0.75} · d) | $54.4 \pm 4.8^{\circ}$ | 22.3 ± 17.0 | 11.8 ± 5.6 | 0.1 ± 2.6 | -3.6 ± 3.6 | |
| | Gross energetic efficiency. % | $21.2 \pm 1.9^{\circ}$ | 10.2 ± 7.1 | 6.2 ± 2.7 | 0.0 ± 1.6 | -2.9 ± 3.2 | |

¹Values are means \pm SEM. ³Mice of each line were fed individually as a function of their body weight either 90, 80, 70 or 60% of the average food intake per unit of body weight of their respective ad libitum-fed group on the previous day. ³Significantly (*P < 0.001) greater mean for ad libitum-fed mice from line Ch as compared to ad libitum-fed CH mice. ⁴A value smaller than eight indicates that some animals in this intake group died.

compared to line CH (table 2). However, average metabolic body size (BW^{0.75}) was also 38.8% higher (P < 0.001) in ad libitumfed Ch mice such that energy intake per unit of metabolic body size was the same in nonrestricted animals of both lines (table 2). Energy intake being the same, the increased gross energetic efficiency of line Ch by comparison to line CH was due to a 46.2% increase (P < 0.001) in energy retention (table 2). Increased energy gain at equal MEI must be due to a decreased maintenance energy requirement and/or an increased net energetic efficiency.

Determination of maintenance energy requirement and net energetic efficiency were obtained by regressing ΔBE over MEI (fig. 1). Net efficiency of energy utilization was 38.5 and 49.5% for lines CH and Ch, respectively. The hg/hg genotype resulted in a 28.6% greater (P < 0.005) efficiency of utilization of metabolizable energy available for gain (MEA). Maintenance energy requirement of mice from lines CH and Ch was 164 kcal/ (kg^{0.75} · d) and 155 kcal/(kg^{0.75} · d), respectively. Mice of line Ch had a 5.1% lower (P < 0.01) maintenance requirement than mice from line CH. Energy intake of ad libitum-fed mice of both lines averaged about 1.5 times the maintenance energy requirement (table 2). An estimate of the quantitative contribution of decreased maintenance energy requirement to increased gross energetic efficiency of ad libitum-fed Ch mice

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Fig. 1 Change in total body energy (ΔBE) as a function of metabolizable energy intake (MEI) in CH (\Box) and Ch (\triangle) mice. Each symbol represents one mouse. Standard error of the parameter estimates are given in parentheses (\pm SE). The regression line for CH (- -) is described by $\Delta BE = 0.385 (\pm 0.026)$ MEI - 62.94 (± 5.35) (x,y = 38) with an x-axis intercept of 163.66 (± 3.55). The correlation coefficient (r) is 0.93 (P < 0.001). For line Ch (-), the regression equation is $\Delta BE = 0.495 (\pm 0.028)$ MEI - 76.88 (± 5.46) (x,y = 37) with an x-axis intercept of 155.36 (± 3.38). (r = 0.95; P < 0.001.) The slopes of the regression equations for each line are significantly different (P < 0.005). The x-axis intercepts of the regression lines are also significantly different (P < 0.01).

was calculated. The difference between the predicted values of $\Delta BE/BW^{0.75}$ of ad libitum-fed Ch and CH mice from measured MEI (table 2) and the regression equations in figure 1, was 14 kcal/(kg $^{0.75}$ · d). The difference between the maintenance energy requirement of line CH and Ch, representing the supplementary MEA for line Ch due to a decreased maintenance requirement, was 9 kcal/(kg $^{0.75}$ · d). If this supplementary MEA was used with the 38.5% net energetic efficiency of line CH, it would account for 3.5 $kcal/(kg^{0.75} \cdot d)$ of energy gain or 25% of the predicted difference in retained energy. The 46% difference in gross energetic efficiency between the two lines of mice was largely (75%) due to a 28% increase in net energetic efficiency even though the small difference in maintenance requirement may account for as much as 25% of the increase in gross energetic efficiency.

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In a similar experiment, Canolty and Koong (13) observed that mice selected for rapid postweaning gain and their control line had equal maintenance energy requirements of 176 kcal/(kg^{0.75} · d). From the same diet, our estimates of maintenance requirement [155 and 164 kcal/(kg^{0.75} · d) for Ch and CH] were slightly lower than their value of 176 kcal/(kg^{0.75} · d). Very likely

their value for maintenance energy requirement was slightly overestimated by assuming an ME value of 4 kcal/g for glucose while the heat of combustion of glucose is 3.74 kcal/g (13, 14). Webster (15) reported that the maintenance requirement of adult mice maintained at 24 °C was 161 kcal/(kg^{0.75} · d). Lower estimates of maintenance energy requirement averaging 73 kcal/ $(kg^{0.75} \cdot d)$ for obese (ob/ob) mice and 118 kcal/(kg^{0.75} · d) for lean mice fed a high carbohydrate diet have been reported (16). The lower estimates may be partly explained by utilization of female mice maintained at a higher environmental temperature of 30°C for the first week postweaning and 26°C for the two following weeks (16). Sex may influence the maintenance requirement of animals. It has been observed that female rats have a lower maintenance energy requirement than male rats (17). Environmental temperature is also an important determinant of maintenance requirement. Webster (15) observed that energy metabolism of laboratory mice is enormously sensitive to subtle environmental variations. When room temperature was increased from 24 to 28 °C, heat production of mice decreased 21% (15). Many other factors, such as age, body composition, diet composition and meal frequency have also been reported to affect maintenance energy requirement (15, 16, 18–21). As a result, estimates of maintenance energy requirement may vary widely from one study to another. For example, experimental estimates of maintenance requirements of growing pigs vary from 85 to 163 kcal/(kg^{0.75} · d) (22).

Net energetic efficiencies in our experiment were similar to other values reported for mice. The net energetic efficiencies of Ch mice (fig. 1), obese mice (16) and mice selected for rapid postweaning growth (13) were 49.5, 51 and 49.7%, respectively, while values for their respective control lines were 38.5, 42 and 23%. The low net energetic efficiency of the control line of Canolty and Koong (13) is difficult to explain, but it is possible that differences in genetic background of mice used in different studies were involved. In their experiment, they used mice derived from a four-way cross of common inbred lines (AKR, C3H, C57BL/6 and DBA/2) (2) while in our experiment and the Lin et al. (16) trial, mice were derived from C57Bl/6 inbred mice. The hg gene appears to have an effect similar to that of the ob gene and selection for growth with respect to increasing net energetic efficiency. However, this does not imply that the underlying mechanism for the three genetic models of improved energetic efficiency is the same.

Decreased protein turnover and Na⁺,K⁺-ATPase activity are two possible ways of increasing net energetic efficiency. Protein turnover and Na⁺, K⁺-ATPase activity have been observed to increase with level of feeding and are important contributors to the heat increment of feeding above maintenance (15, 23, 24). Obese mice have a normal or elevated protein turnover rate (25) but only 50% of the Na⁺, K⁺-ATPase units in skeletal muscle as compared to their lean controls (26). Mice selected for small body size had decreased protein accretion but increased protein synthesis and degradation rates compared to larger mice (27). This suggests that the increased energetic efficiency of obese mice and mice selected for rapid gain result from different mechanisms. The mechanism for the increase in energetic efficiency of mice from line Ch is unknown and cannot be determined from the present experiment.

Fasting heat production was estimated from regressing logarithm of heat production/BW^{0.75} over MEI/BW^{0.75} (fig. 2). Estimates of fasting heat production were 94 and 97 kcal/(kg^{0.75} \cdot d) for line CH and Ch, respectively. The FHP of hg/hg mice was significantly higher than their controls (fig. 2). Efficiency of energy utilization below maintenance was not measured but



Fig. 2 Logarithm of heat production (LogHP) as a function of metabolizable energy intake (MEI) in CH (\Box) and Ch (\triangle) mice. Each symbol represents one mouse. Standard error of the parameter estimates are given in parentheses (\pm SE). The regression line for CH (- -) is described by LogHP = 0.0015 (\pm 0.0001) MEI + 1.975 (\pm 0.013) (x,y = 38). (r = 0.97; P < 0.001.) For line Ch (---), the regression equation is LogHP = 0.0013 (\pm 0.0001) MEI + 1.989 (\pm 0.016). (r = 0.94; P < 0.001.) The slopes of the regression equations are significantly different (P < 0.001). Assuming equal slopes, the y-axis intercepts are significantly different (P < 0.05).

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can be derived from estimates of FHP and maintenance energy requirement (28). Using this approach, the efficiency of energy utilization below maintenance was 55.6 and 61.0% for lines CH and Ch, respectively. Although the efficiency of mice from line Ch appeared to be 10% higher than line CH, no statistical comparison of these estimates was possible.

The efficiency of glucose utilization below maintenance is close to 100% and assuming that nutrients replace one another on the basis of the amount of energy (heat of combustion) required per mole of ATP synthesized, a theoretical efficiency below maintenance of 93% was calculated for the experimental diet (29, 30). This estimate did not include costs associated with food prehension, digestion and nutrient storage. In extreme cases of storage, these costs may represent 20% of MEI (30). Considering that the mice were fed only twice a day, storage was likely to be an important cost. After correction for these costs, the theoretical energetic efficiency below maintenance was approximately 75%, which is still higher than the estimates of 56 and 61% for line CH and Ch. This discrepancy may be due to underestimation of FHP or because the theoretical calculation of efficiency did not include all energetic costs. Animals fed the lowest level of energy were systematically below the regression lines used to predict FHP (fig. 2), suggesting that FHP was probably underestimated by these equations.

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Although these estimates of fasting heat production were probably too low, they were higher than $70 \text{ kcal/(kg}^{0.75} \cdot d)$, which is the suggested interspecific mean basal metabolic rate of adult animals maintained at thermoneutrality (31, 32). The mice in the present experiment were housed at 24 °C while the thermoneutral zone of mice is 29-31°C (33, 34). Bailey et al. (33) have observed that when environmental temperature was decreased from 30 to 24°C, FHP of mice increased by 39%. Applying this increase to the interspecific mean of 70 kcal/ $(kg^{0.75} \cdot d)$, an estimate of 97 kcal/ $(kg^{0.75} \cdot d)$ is obtained. This is close to the predicted FHP obtained by regression for lines CH and Ch. It is also possible that the higher FHP estimates were related to the use of immature growing mice. FHP per unit of metabolic body weight has been shown to decrease with age in mice (33). It is clear that many factors affect FHP and that systematic deviations from the interspecific mean have been observed (21). For example, reported values for FHP of sheep are consistently below while cattle are consistently above the interspecific mean (15, 29). Still, after correction for environmental temperature estimates of FHP for lines CH and Ch appear to agree with the interspecific mean and values reported for mice (31, 32). However, direct measurements of FHP appear to be required in order to better understand energy utilization below maintenance in these two lines of mice.

Changes in total body energy can be partitioned between changes in lean body energy and fat energy. Regressions of changes in LE/BW^{0.75} over MEI/BW^{0.75} are presented in figure 3. The x-axis intercept of this regression line is an estimate of the amount of ME necessary to maintain zero energy balance in the lean body. The slope of this regression is the product of the proportion of MEA used for LE gain by the efficiency of utilization of MEA for lean gain. This composite term is called the lean energy deposition coefficient (13). Lean energy deposition coefficients for mice of line CH and Ch were 16.9 and 18.5% and were not statistically different from each other (fig. 3). However, the MEI required to have no change in LE was 7.6% lower (P < 0.01) in mice with the hg/hg genotype. As a result, ad libitum-fed mice from line Ch had an 18.9% greater (P < 0.001) lean energy gain per unit of metabolic weight than mice from line CH (table 2). Regressions of changes in fat energy/ $BW^{0.75}$ over MEI/ $BW^{0.75}$ are presented in figure 4. MEI needed to maintain fat energy was estimated by the x-axis intercept of the regression line. Fat energy deposition coefficients, as defined by the product of proportion of MEA used for fat gain times efficiency of utilization are the slopes of the regression lines, 21.6 and 31.0% for lines CH and Ch, respectively. Mice from line Ch had a 43.5% higher (P < 0.002) fat energy deposition coefficient than mice from line CH. The amount of energy required to maintain fat energy balance was also 5.6% lower (P < 0.01) in line Ch as compared to line CH. As a result, ad libitum-fed



Fig. 3 Change in lean body energy (Δ LE) as a function of metabolizable energy intake (MEI) in CH (\Box) and Ch (\triangle) mice. Each symbol represents one mouse. Standard error of the parameter estimates are given in parentheses (\pm SE). The regression line for CH (- -) is described by Δ LE = 0.169 (\pm 0.009) MEI - 24.58 (\pm 1.93) (x,y = 38) with an x-axis intercept of 145.75 (\pm 3.75). (r = 0.95; P < 0.001.) For line Ch (—), the regression equation is Δ LE = 0.185 (\pm 0.008) MEI - 24.94 (\pm 1.63) (x,y = 37) with an x-axis intercept of 134.66 (\pm 3.32). (r = 0.97; P < 0.001.) The slopes of the regression lines are not significantly different (P > 0.10) but the x-axis intercepts are significantly different (P < 0.01).

mice from line Ch had a 76.3% increase (P < 0.001) in fat energy gain per unit of metabolic weight in comparison to line CH (table 2).

For both lines of mice, the amount of energy required to maintain lean energy balance was smaller than the amount required for fat energy balance (fig. 3, 4). Mice fed close to maintenance gained lean body energy but lost fat energy (table 2). Similar observations have been reported for normal mice and mice selected for rapid



Fig. 4 Change in fat energy (ΔFE) as a function of metabolizable energy intake (MEI) in CH (\Box) and Ch (\triangle) mice. Each symbol represents one mouse. Standard error of the parameter estimates are given in parentheses (\pm SE). The regression line for CH (- -) is described by $\Delta FE = 0.216$ (± 0.020) MEI - 38.35 (± 4.07) (x,y = 38) with an x-axis intercept of 177.64 (± 4.01). (r = 0.88; P < 0.001.) For line Ch (—), the regression equation is $\Delta FE = 0.310$ (± 0.022) MEI - 51.94 (± 4.31) (x,y = 37) with an x-axis intercept of 167.76 (± 3.82). (r = 0.92; P < 0.001.) The slopes of the regression lines are significantly different (P < 0.002) and the x-axis intercepts are significantly different (P < 0.001).

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growth (13). When food intake of growing animals is restricted, they tend to maintain protein deposition at the expense of fat (15). The energy deposition coefficients indicated that the increased net energetic efficiency of mice from line Ch was primarily due to increased fat deposition per unit of MEA. No conclusions as to whether the hg gene was affecting the proportion of energy used for fat and lean gain and/or its efficiency of utilization were possible because the energy deposition coefficients are a combination of these two terms.

The results of this experiment demonstrate that the single gene for rapid postweaning growth increased fat energy deposition and to a lesser extent lean body energy deposition. This increase in fat energy deposition caused an increase in net energetic efficiency. The hg gene also produced a small decrease in maintenance energy requirement. It was estimated that the decreased maintenance requirement accounted for approximately 25% of the increased gross energetic efficiency of line Ch. Further experiments are needed to understand the metabolic basis of the increased energetic efficiency observed in hg/hg mice.

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