

Maximal sustained energy budgets in humans and animals

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Why are sustained energy budgets of humans and other vertebrates limited to not more than about seven times resting metabolic rate? The answer to this question has potential applications to growth rates, foraging ecology, biogeography, plant metabolism, burn patients and sports medicine.

The highest measured daily energy budgets maintained by any humans over long periods were achieved in the 1984 Tour de France race¹. For 22 days the world's best cyclists, in peak physical condition and fanatically motivated, pedalled up and down 34 mountains and over 3,826 km. Metabolic studies of four of those who completed the race showed that they expended energy at an average rate of 7,000 kcal per day. Nevertheless, throughout the day they gulped so many energy-rich drinks, and at night they bolted down so much pasta, bread and butter, and sweet cakes, that their body mass and fat content at the race's conclusion were virtually the same as at the start. That is, they fuelled their energy expenditure by concurrent energy intake, not by depleting body energy reserves.

To most of us 'couch potatoes', 7,000 kcal d⁻¹ sounds impressive. It is about 4.3 times the basal metabolic rate (BMR) of 1,640 kcal d⁻¹ expected for 70-kg men such as these athletes, BMR being the energy budget of someone fasting and lying motionless in bed all day and night. Actual energy budgets for sedentary men—such as typical laboratory scientists, bankers and *Nature* readers—are barely 70% higher than BMR, namely 2,800 kcal d⁻¹. Budgets are still only 3,800 kcal d⁻¹ even for miners, 4,100 kcal d⁻¹ for army recruits in training, and 5,000 kcal d⁻¹ for Robert Scott and his ill-fated companions man-hauling heavy sleds up glaciers in the Antarctic cold².

Yet, rather than being impressed by the Tour de France cyclists' high energy budgets, we have to wonder why they were not even higher. If any of those athletes had been able to digest 17,000 kcal d⁻¹ instead of 7,000, and to convert it to muscular work, he would have left his competitors behind in the dust. The fact that even such motivated fanatics did not achieve such high budgets strongly suggests that they were incapable of doing so. Are humans really restricted to time-averaged energy budgets below about five times BMR? If so, why?

Energy budgets of animals

Sustained metabolic rate (SusMR) may be defined as the time-averaged energy budget that an animal or human maintains over times sufficiently long that body mass remains constant because time-averaged energy intake equals time-averaged energy expenditure. Much higher metabolic rates can of course be achieved over short times (for example, the time required for a 200-m dash), but they are fuelled by consumption of body energy reserves and not sustained by concurrent energy intake.

Table 1 lists measurements of daily energy budgets (SusMR) in 50 active wild vertebrate species. To normalize for species differences in body size and also in basal energy expenditure, SusMR is divided by resting metabolic rate (RMR) to obtain the ratio SusMR/RMR, termed sustained metabolic scope (SusMS). (RMR would equal BMR if the animal were fasting and not growing or producing new biomass, but these conditions cannot automatically be assumed to apply to a wild-caught animal.) Measured metabolic scopes of active wild animals fall in the range 1.3 to 7.0. Of the 50 species studied, 11 achieved scopes modestly exceeding that of Tour de France cyclists,

but no scope measured to date exceeds 7.0. Yet some of these scope measurements apply to animals that one might expect to have been maximally motivated, just as are Tour de France cyclists: for example, birds foraging from dawn to dusk to gather food for their nestlings, or small mammals nursing pups or active at low environmental temperatures. Thus, Table 1 suggests that energy budgets of wild animals may be constrained by a ceiling similar to that limiting human athletes³. What factors could impose that ceiling?

Factors that might impose metabolic ceilings

If one accepts that sustained metabolic ceilings exist, four hypotheses about the responsible proximate factors suggest themselves.

First, ceilings might be imposed by food availability and not by any property of animals' bodies. This hypothesis is difficult to exclude in studies of wild animals, whose available food supply is generally unmeasurable: perhaps their budgets would have been higher if more food had been available. However, this hypothesis cannot apply to Tour de France cyclists, who certainly have access to unlimited food.

If the limit resides in properties of animals' bodies rather than in the food supply, one can then distinguish two further hypotheses: so-called peripheral limitations associated with energy-consuming machinery, and so-called central limitations associated with energy-supplying machinery. As for the former (our second hypothesis), energy budgets might be limited during physical exercise by work properties of skeletal muscle, during lactation by the milk-producing capacity of mammary glands or by availability of limiting nutrients, and during cold exposure by the capacities of brown fat or muscle shivering for heat production. Perhaps the gut and other central energy-supplying organs could supply calories faster, but those peripheral organs cannot (supposedly) convert the calories to work and heat faster. If so, one might expect in a given animal species different values of the metabolic ceiling for different modes of energy expenditure, depending on the particular properties of skeletal muscle or mammary glands or brown fat in that species.

The third hypothesis conversely attributes metabolic ceilings to bottlenecks in shared central machinery for acquiring, processing and distributing calories to any and all energy-consuming organs⁴. For example, the bottleneck could reside in the gut's capacity to digest and absorb food, or in the liver's capacity to process the absorbed foodstuffs, or in the lungs' capacity to take up O₂ or exhale CO₂, or in the heart's capacity to pump around the O₂ or nutrients, or in the kidneys' capacity to excrete the resulting wastes. Perhaps muscles could work faster and mammary glands could secrete milk faster, if only the rest of the body could supply nutrients and remove wastes faster. If such central limits applied, a given animal species might exhibit the same value of metabolic ceiling for different modes of energy expenditure.

Finally, animals might have evolved such that capacities of several of these potential limiting factors are matched to each other, a possibility termed symmorphosis⁵. For instance, the maximal rates

Table 1 The highest values of sustained metabolic scope (SusMS) reported for 50 vertebrate species

Species	Condition	Body mass (g)	RMR (kJ g ⁻¹ d ⁻¹)	SusMR (kJ g ⁻¹ d ⁻¹)	SusMS	Reference
MAMMALS						
Rodents						
<i>Acomys cahirinus</i>	Lactating (3 pups)	40	0.49	3.25	6.7	30
<i>Acomys russatus</i>		51	0.37	1.07	2.7	2
<i>Ammospermophilus leucurus</i>		96	0.49	0.99–1.43	1.7–2.6	2
<i>Apodemus flavicollis</i>	Cold (–10 °C)	28.4	1.13	4.16	3.7	31
<i>Microtus agrestis</i>	Cold (5 °C)	23.7	2.34	6.68	2.9	32
<i>Mus musculus</i>	Lactating (14 pups)	38.2	1.16	7.57	6.5	K.A.H. (unpubl.)
<i>Peromyscus leucopus</i>		21	0.76	3.28–4.28	3.9–5.0	2
<i>Peromyscus maniculatus</i>	Cold field measurements	20.6	0.42	2.72	6.4	33
<i>Sekeetamys calurus</i>		41	0.37	1.07	2.9	2
<i>Spermophilus saturatus</i>	Lactating (5 pups in the field)	232	0.43	1.59	3.7	34
<i>Thomomys bottae</i>		143	0.40	1.28–1.37	2.8–3.0	2
Marsupials						
<i>Antechinus stuartii</i>		37	0.46	2.72	4.6	2
<i>Gymnobelideus leadbeateri</i>		166	0.29	1.87–1.98	5.6–5.8	2
<i>Macropus eugenii</i>		4,800	0.14	0.27	1.9	2
<i>Petaurus breviceps</i>		128	0.32	1.37–1.71	4.0–4.4	2
<i>Phascolarctos cinereus</i>		4,770	0.20	0.26	2.3–3.0	2
<i>Pseudocheirus peregrinus</i>		860	0.16	0.78	4.7	2
<i>Setonix brachyurus</i>		2,510	0.15	0.32–0.44	1.8–1.9	2
<i>Sminthopsis crassicaudata</i>		14	0.64	4.06	6.9	2
Other mammals						
<i>Alouatta palliata</i>		4,670	0.21	0.35–0.89	1.5–2.0	2
<i>Bradypus variegatus</i>		3,790	0.09	0.13–0.19	1.4–2.0	2
<i>Echinops telfairi</i>	Lactating (1 pup)	262.6	0.11	0.23	2.2	35
<i>Homo sapiens</i>	Tour de France cyclist	68,500	0.10	0.42–0.56	42.–5.6	2
BIRDS						
<i>Aethia pusilla</i>	Rearing chicks	83	1.38	4.32	3.1	36
<i>Alectoris chukar</i>		475	0.36	0.65–1.16	1.6–2.4	2
<i>Callipepla gambelii</i>		126	0.52	0.63	1.3	2
<i>Delichon urbica</i>		21	1.48	3.90–4.21	2.6–2.8	2
<i>Diomedea exulans</i>		8,130	0.22	0.36–0.54	1.6–2.0	2
<i>Eudypetes chrysolophus</i>		3,870	0.19	1.12	5.8	2
<i>Falco tinnunculus</i>		108	0.66	1.56	2.9	2
<i>Hirundo tahitica</i>	Rearing chicks	14	1.09	4.25	3.9	37
<i>Macronectes giganteus</i>		4,780	0.24	1.16–1.32	4.3–4.4	2
<i>Merops viridis</i>	Rearing chicks	34	0.76	2.55	3.4	2
<i>Oceanites oceanicus</i>	Rearing chicks	42.2	0.87	3.72	4.3	38
<i>Oenanthe oenanthe</i>	Rearing chicks	24	1.54	3.67	2.4	10
<i>Pelecanoides urinatrix</i>	Rearing chicks	132	0.96	4.28	4.5	10
<i>Pelecanoides georgicus</i>	Rearing chicks	119	1.02	3.89	3.9	10
<i>Puffinus pacificus</i>		338	0.38	1.60	4.3	2
<i>Pygoscelis adeliae</i>		3,970	0.27	1.03	3.8	2
<i>Pygoscelis papua</i>		6,290	0.26	0.59–0.64	2.3–2.5	2
<i>Rissa tridactyla</i>		386	0.81	2.27	2.8	2
<i>Sterna fuscata</i>		148	0.47	1.30	3.0	2
<i>Sula bassanus</i>	Rearing chicks	3,210	0.23	1.52	6.6	39
<i>Sula capensis</i>	Rearing chicks	2,575	0.32	1.31	4.7	40
<i>Sula sula</i>	Breeding and free-ranging	1,070	0.78	1.21	1.6	41
REPTILES						
<i>Amblyrhynchus cristatus</i>		965–2,250	0.04–0.08	0.06–0.13	1.7	2
<i>Cnemidophorus tigris</i>		16	0.13	0.21	1.6	2
<i>Cnemidophorus hyperythrus</i>		3.9–4.4	0.17–0.21	0.22–0.37	1.3–1.8	2
<i>Dipsosaurus dorsalis</i>		3.5–57	0.13–1.15	0.21–2.34	1.0–2.6	2
<i>Sceloporus virgatus</i>		5.5–76	0.04–0.08	0.13–0.21	2.1–4.6	2

SusMS is calculated as the ratio SusMR/RMR. Most values of SusMR and RMR were measured in the same individual animals, except for some of the values from ref. 2. The condition of the animals is listed if it is known.

Table 2 Sustainable metabolic scopes (SusMS), measured in the same species under several different types of energy demand

Taxa	Condition	Body mass (g)	RMR (kJ g ⁻¹ d ⁻¹)	SusMR (kJ g ⁻¹ d ⁻¹)	SusMS	Reference
MAMMALS						
Rodents						
<i>Acomys cahirinus</i>	Non-lactating, non-cold	42	0.52	1.37	2.5	2
	Cold (3°C)	37.8	0.49	1.845	3.8	30
	Lactating (3 pups)	40	0.49	3.25	6.7	30
	Cold (–10°C)	28.4	1.13	4.16	3.7	30
<i>Peromyscus maniculatus</i>	Lactating (3–5 pups)	24.7	0.88	4.05	4.6	42
	Cold (–10°C)	21.4	0.90	5.45	6.1	43
<i>Mus musculus</i>	Non-pregnant, non-lactating	30.8	0.79	1.81	2.3	8
	Strenuous exercise (running 6 h d ⁻¹)	25.2	0.81	2.94	3.6	I. Choshniak <i>et al.</i> (unpublished results)
	Cold (5°C)	30.7	0.90	3.59	4.0	K.A.H. (unpublished results)
	Cold (–10°C)	26.9	1.06	5.09	4.8	7
	Lactating (5 pups)	35.9	0.94	5.77	6.1	K.A.H. (unpublished results)
	Lactating (14 pups)	38.2	1.16	7.57	6.5	K.A.H. (unpublished results)
Humans						
Nepali women Nov–Dec	Light physical activity	46,670	0.11	0.18	1.6	44
Nepali women July–Sept	Pregnancy and heavy physical activity	52,000	0.10	0.19	1.9	44
	Lactation and heavy physical activity	47,900	0.11	0.20	1.9	44
	Very heavy physical activity	46,670	0.11	0.22	2.0	44
BIRDS						
<i>Oceanites oceanicus</i>	Incubation and brooding of eggs	42.2	0.87	2.81	3.2	38
	Rearing chick and at sea	42.2	0.87	3.72	4.3	38

at which the gut could absorb calories, the lungs could take up the O₂ necessary to burn them aerobically, and the muscles could convert the calories to work might have evolved to be about the same.

Experimental tests of ceilings in animals

A key step in confirming the suggested reality of metabolic ceilings and distinguishing between hypotheses about their origin has been laboratory studies in which animals, in the presence of excess quantities of available food, have been pushed to maximal SusMRs through different modes of energy expenditure. These studies serve three purposes: they exclude food availability as a potential limitation; they test whether rates of energy expenditure in fact increase up to a ceiling or continue to increase with increasing demands; and they test whether, within a given species, that ceiling value (if it exists) differs among different modes of energy expenditure, as predicted by the peripheral limitation hypothesis but not by the central limitation hypothesis. In effect, these experiments seek to study animals under conditions of maximal motivation, similar to those prevailing for Tour de France cyclists.

These studies do reveal maximal energy budgets with increasing 'motivation'. For instance, laboratory mice held at lowered ambient temperature counter their increased heat loss with increased heat production by non-shivering thermogenesis, yet maintain body mass by correspondingly increasing their food intake to fuel that increased metabolic rate^{6,7}. Their food intake increases with decreasing ambient temperature down to –15°C, below which they lose body mass and die in the presence of excess food. Thus, even given the maximal possible motivation of saving their lives, they do not

increase food intake and heat production further. Similarly, mice motivated by motherly love increase their food intake 4.9-fold to produce milk for a normal litter of 8–10 pups⁸. They increase food intake and milk output slightly more as motivation is experimentally increased by cross-fostering additional pups from another litter of the same age, or by experimentally requiring the mother to nurse her pups beyond the usual age of pup weaning until pups weigh double their usual mass at weaning^{8,9}. But food intake with either of these two experimentally increased appeals to motherly love still reaches a ceiling, in the presence of excess food, of 5.5 times non-lactating food intake. Finally, mice required to run on treadmills increase their food intake and run for up to 6 h d⁻¹, after which they become exhausted and run no further despite the availability of excess food (I. Choshniak *et al.*, unpublished observations).

Table 2 depicts the results of such studies for five vertebrate species in which ceilings were sought experimentally by more than one mode of energy expenditure. These results yield the following conclusions.

(1) Ceiling values of the ratio SusMS fall in the range of 4.3–6.7 (Table 2), no higher than values measured in the field for some wild animals (Table 1). Hence some of the wild animals studied in Table 1 were also probably at or near their metabolic ceilings.

(2) In each animal species, the ceiling value differs for different modes of energy expenditure. For instance, in laboratory mice peak SusMS is 3.6 for physical exercise, 4.8 for heat production at low ambient temperature, and 6.5 for lactation. This agrees with the peripheral limitation hypothesis and disagrees with the central limitation hypothesis, for all those modes whose scope value is surpassed during some other mode in the same species (such as

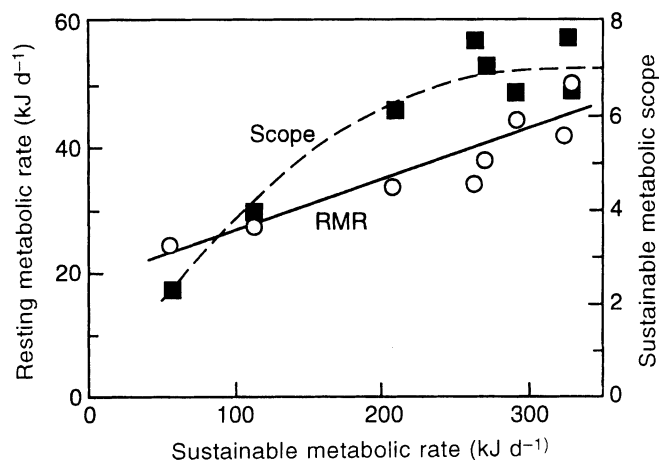


Figure 1 Measured or estimated values of RMR, and calculated values of SusMS (metabolic scope), in female mice, plotted as a function of SusMR. SusMR was manipulated experimentally by applying cold stress, lactation with various litter sizes from 5 to 14 pups, or cold stress plus lactation. The left-most point is for virgin mice at 23 °C; the right-most point, for mice nursing 14 pups at 5 °C. Note that both RMR and SusMS increase with SusMR. The straight line through RMR values, and the curve fitted by eye through SusMS values, serve merely to summarize trends and have no theoretical significance. Data are from ref. 8 and our unpublished measurements.

exercise and heat production in laboratory mice). However, the central limitation hypothesis is not thereby excluded for the mode yielding the highest scope value in a given species (such as lactation in laboratory mice).

(3) Different species excel for different modes of energy expenditure. For instance, the highest values of SusMS are achieved during lactation by laboratory mice, at low ambient temperatures for a wild mouse population (*Peromyscus maniculatus*), and during physical exercise for humans. These differences are obviously related to each species' lifestyle: the wild mouse populations studied live without clothing in cold environments, and traditional human populations were physically vigorous but did wear clothing in cold environments and gave birth to a litter of only one, whereas laboratory mice have been selected for the ability to rear large litters.

RMR increases at high SusMR

A clue as to why SusMS reaches a ceiling emerged from a study applying a combination of two energy stresses (cold and lactation) to laboratory mice⁹. Food intake and SusMS reached an upper limit during maximal tolerated cold stress, and reached a higher limit during maximal lactation. But when cold stress and lactation were applied simultaneously, food intake increased even further (by 16%) above the lactational ceiling, by an absolute increment roughly equal to that measured for cold exposure of non-lactating mice. Evidently, even though food intake did not increase any further under the stress of lactation alone, lactating mice were still capable of processing more food energy and expending it for a different purpose. Nevertheless, SusMS (= SusMR/RMR) was no higher in cold lactating mice than in lactating mice at room temperature, because RMR as well as SusMR proved to be higher in cold lactating mice.

Figure 1 illustrates that RMR and SusMS of mice increase with increases of SusMR elicited experimentally by any means. As SusMR increases sixfold, RMR increases twofold, and SusMS reaches values near seven. These results suggest that SusMR and RMR are obligatorily somehow coupled to each other, in such a way that values of their ratio are highest at high SusMR (Fig. 1).

One test of this hypothesis has involved analysing SusMR and RMR values for a wide variety of mammal and bird species under

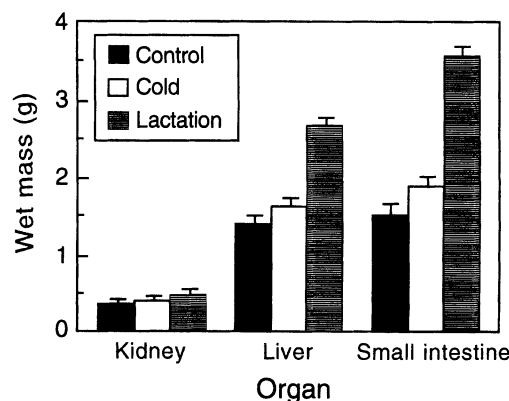


Figure 2 Changes in wet mass of kidney, liver and small intestine in mice with three increasing levels of energy demand (from left to right: control or virgin females, acclimation to 5 °C, and lactation with a litter of 8 pups). Within each organ, changes of organ mass with energy demand are statistically significant at $P < 0.05$ by ANOVA. Data are from ref. 8.

a wide variety of conditions (see for example, refs 10–12). Perhaps not surprisingly, those analyses have yielded at best equivocal evidence for a coupling between SusMR and RMR, because of likely species differences in the form of the relation and because of the modest range of mass-specific SusMR and RMR values observed for different mammal and bird species of a given body size. However, the hypothesis is supported by the much greater contrast between endothermic and ectothermic vertebrate species: endotherms (mammals and birds) have both SusMR values and RMR values an order of magnitude higher than those of ectotherms (reptiles, amphibia and fish) of the same body size (see for example, refs 13–15).

Mechanism of increased RMR at high SusMR

Although Fig. 1 suggests a formal explanation for an upper asymptote of SusMS, it leaves unanswered the question of the mechanism underlying the observed increase in RMR with increasing SusMR. We suggest that that mechanism depends in large part on mass increases in energy-supplying organs.

As is well known and obvious, the masses of peripheral energy-consuming organs increased selectively and reversibly during conditions of high sustained function. For instance, specific skeletal muscles can be observed to grow in athletes during training; mammary glands grow during lactation; and both organs atrophy again upon resumption of couch-potato or non-lactating status. But there is also, taking place invisibly inside an animal's body during any such condition of high SusMR, a less well-known reversible hypertrophy of central energy-supplying organs. In laboratory mice, the small intestine, kidneys, liver and heart increase in mass during lactation, cold exposure, or both stresses applied simultaneously^{6–9,16} (Fig. 2). These same organs, plus the lungs, stomach and pancreas, increase in mass in snakes and frogs with greatly elevated metabolic rates during digestion of large meals^{17,18}. The reason why these organs must grow under conditions of high food intake and energy budgets is that their masses under resting conditions provide only modest functional reserve capacities that would be unequal to the demands upon them at high SusMR if their masses did not increase^{8,9,16}.

Analogous to these reversible intraspecific mass increases in

energy-supplying organs at high SusMR are the permanent inter-specific mass differences observed in the same organs when one compares species with chronically high or low energy budgets. The largest contrast is between endotherms and ectotherms: associated with their 15–50-fold higher SusMRs, endotherms have intestines, livers, kidneys and hearts several times larger than those of ectotherms of the same body size^{13,15,19}. Temperate-zone birds and mammals tend to have larger hearts, kidneys, livers, intestines, stomachs and pancreases than tropical birds and mammals, which tend to operate at lower SusMRs because of less need for heat production²⁰. Among different species of temperate-zone birds, those with higher SusMRs and RMRs tend to have larger hearts and kidneys¹⁰. If RMR differences may be taken as an indication of corresponding SusMR differences, it is also relevant to note that, among different strains of laboratory mice, those with higher RMRs tend to have larger hearts, kidneys, small intestines and livers²¹.

These central energy-supplying organs, although their masses contribute only a modest fraction of an animal's total body mass, contribute a large fraction of an animal's RMR because of their very high mass-specific metabolic rates. For instance, in laboratory mice the kidneys have a mass-specific metabolic rate 51% higher than that of any other tissue, and the heart, small intestine and liver are not far behind²². Even in a resting animal or human, the kidney has a very high metabolic rate because it is constantly filtering urine and then actively reabsorbing most of the filtrate; the small intestine has a high metabolic rate because its mass turns over every 2–3 d; and the liver is constantly processing nutrients. Although these three organs contribute, respectively, only 0.5, 5 and 7% of a mouse's body mass, in aggregate they account for 24% of RMR²². As another example, the liver and gut account for up to 70% of the metabolic heat production above maintenance in ruminants experiencing high workloads²³. This, too, is a large fraction of the metabolic heat production from a relatively small fraction of the total body mass.

Thus, our suggested mechanistic explanation of Fig. 1, and of the observed ceiling on SusMS, is that high SusMR requires increased mass of energy-supplying organs, but that the high maintenance and operating costs of these organs cause them to contribute disproportionately to RMR, which thus tends to increase with SusMR. That is, high energy budgets depend on energetically expensive metabolic machinery.

Future directions

We conclude by pointing out some questions ripe for study.

Relationships between potential limiting factors. Depending on the circumstances and on the mode of energy expenditure, SusMR might be limited by the energy-consuming organ involved or by one or more energy-supplying organs. But it might alternatively be limited by several such organs in concert. That is, if natural selection has acted to minimize unutilized reserve capacities, then one might observe a rough match between the intestine's capacity to digest and absorb nutrients, the liver's capacity to process absorbed nutrients, the lungs' capacity to take up the O₂ necessary for their metabolism, the heart's capacity to pump the O₂ and nutrients, the capacity of the highest-capacity energy-consuming organ to utilize the nutrients, and the kidneys' capacity to excrete the resulting wastes. Taylor and Weibel³ refer to this possibility as *symmorphosis*. On the other hand, there are also plausible reasons why natural selection might have led to a different outcome. This central question of evolutionary design is unresolved and in need of study²⁴.

Ecological, biogeographic and behavioural significance of ceilings on SusMS. Physiological ceilings on SusMS imply ceilings on heat production, which might account for observed distributional limits of some species in cold climates (poleward latitudinal boundaries and upper altitudinal boundaries)²⁵. Physiological ceilings may also constrain daily foraging efforts, lactational performance and other life-history attributes.

Interspecific variation in ceilings. One might guess that peak values of SusMS differ among wild animal species: for example, that values may be higher for wolves than for sloths. One could also speculate whether species of relatively constant mesic environments should tend to have higher or lower ceilings than species of unpredictable environments. The data of Table 1 hint at such differences but are equivocal, because many SusMS values in Table 1 may not represent peak values. Comparative studies are badly needed that push numerous species to peaks of SusMS.

Applications to growth. Biosynthesis for growth represents a form of sustained energy expenditure and should therefore be subject to a ceiling that could be compared with ceilings on other forms of energy expenditure. The main practical problem in doing so is to know how to divide the measured energy budget of growing animals into the cost of growth and the cost of maintenance activities. Several experimental solutions to this problem have been proposed, such as restricting food to halt growth, estimating costs of protein synthesis, and administering inhibitors of protein synthesis (see for example ref. 26).

Applications to other forms of biomass production. During physical exercise or heat production, dietary nutrients are ingested, absorbed, and then combusted and converted to work or heat, and the combustion is reflected in O₂ consumption and CO₂ production. However, during biomass production, such as lactation, egg production, fat storage, or somatic growth, some of the ingested and absorbed nutrients are not combusted but are transformed into the nutrients of the produced biomass. Hence daily energy budgets calculated from food assimilation should equal budgets calculated from O₂ consumption or CO₂ production during exercise or heat production but might exceed the latter budgets during biomass production, to a degree depending on costs of production and the metabolic transformations involved. Is such a discrepancy actually observed? If intestinal digestion and absorption were limiting, food intake might be no higher during peak biomass production than during peak exercise or heat production; is that true?

Applications to plants. Can one measure, in photosynthetically active plants, quantities that reflect maintenance costs and total daily energy budget and that are, respectively, analogous to RMR and SusMR of animals? For instance, is dark respiration rate or maintenance respiration of plants analogous to animals' RMR, and growth respiration or total respiration of plants analogous to SusMR? Are these two quantities loosely coupled in plants as they are in animals? Is that coupling reflected in the observed correlation between plant growth rates and respiration rates or calorimetrically measured metabolic heat rates^{27,28}?

Clinical applications. People who have suffered burns over more than 40% of their body surface exhibit large increases in resting metabolic rate (termed 'hypermetabolism') because of two ongoing costly processes: tissue repair and heat production to balance increased heat loss²⁹. Burn patients often receive nutrients intravenously by parenteral nutrition. To speed their healing, their metabolic rate should be as high as possible. What limits their metabolic rate and their capacity to process parenterally administered nutrients?

Sports medicine. The Tour de France is unusual among sports events in that it lasts so long that energy expenditure over the course of the event must be balanced in large part by concurrent energy intake. For any event lasting less than 1 d, energy expenditure instead comes largely from depletion of energy reserves not replenished until after the event. Hence SusMS ceilings are not expected to limit performance in a short event but should certainly limit athletes' training regimes leading up to the event. Are human training regimes really limited by properties of skeletal muscle, as usually assumed, or instead by energy-supplying organs such as the intestine and kidneys? Could knowledge of such limitations help in improving training regimes? Heart enlargement in athletes is well known, but one might also expect enlargement of

athletes' intestines, kidneys and livers, and consequent increase in BMR, by analogy with lactating and cold-exposed animals; is that true? □

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