Sustained metabolic scope

(metabolic rate/doubly labeled water/metabolic ceiling/symmorphosis/exercise)

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ABSTRACT   Sustained metabolic rates (SusMR) are time-averaged metabolic rates that are measured in free-ranging animals maintaining constant body mass over periods long enough that metabolism is fueled by food intake rather than by transient depletion of energy reserves. Many authors have suggested that SusMR of various wild animal species are only a few times resting (basal or standard) metabolic rates (RMR). We test this conclusion by analyzing all 37 species (humans, 31 other endothermic vertebrates, and 5 ectothermic vertebrates) for which SusMR and RMR had both been measured. For all species, the ratio of SusMR to RMR, which we term sustained metabolic scope, is less than 7; most values fall between 1.5 and 5. Some of these values, such as those for Tour de France cyclists and breeding birds, are surely close to sustainable metabolic ceilings for the species studied. That is, metabolic rates higher than 7 times RMR apparently cannot be sustained indefinitely. These observations pose several questions: whether the proximate physiological causes of metabolic ceilings reside in the digestive tract's ability to process food or in each tissue's metabolic capacity; whether ceiling values are independent of the mode of energy expenditure; whether ceilings are set by single limiting physiological capacities or by coadjusted clusters of capacities (symmorphosis); what the ultimate evolutionary causes of metabolic ceilings are; and how metabolic ceilings may limit animals' reproductive effort, foraging behavior, and geographic distribution.

Most studies of peak metabolic rates have dealt with brief bursts of activity. As is well known, the shorter the burst, the higher the metabolic rate or power output that can be sustained (see Fig. 1). For instance, the power output and speed of a human sprinter exceed those of a miler, whose output and speed in turn exceed those of a marathon runner.

Energy expenditure during a few seconds of maximal exertion by a human may be 100 times the level of the same person's energy expenditure at rest (1). Most of this expenditure during maximal exertion is fueled by anaerobic ATP production and cannot be kept up for more than a minute or so because of toxic effects of lactic acid buildup (2). Aerobically supported energy expenditure can be sustained for minutes or hours at somewhat lower levels of up to 32 times the resting metabolic rate (RMR) in wolves and other canids, up to 20 times RMR in trained humans and race horses, and at various lower multiples of RMR in birds, rodents, and ectothermic vertebrates (3). [Throughout this paper we use RMR to refer generically to any metabolic rate(s) measured in animals at rest, including basal metabolic rate (BMR), standard metabolic rate, and/or total resting metabolism.]

However, even these maximal aerobic energy expenditures cannot be sustained indefinitely, because the animals or humans are not in energy balance during the exertion. Instead, much of their energy expenditure is powered by
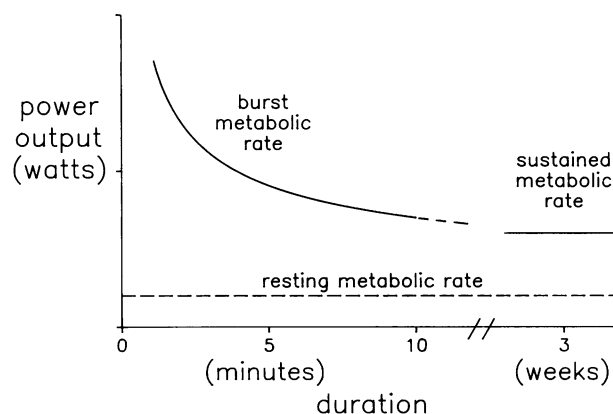

FIG. 1. Burst metabolic rate equals maximum power output maintained by a human (e.g., a runner) or animal, as a declining function of the duration that the individual is able to sustain that output. The dashed line is the RMR of the same individual. The present paper argues that power output declines to an asymptotic value at long times—a maximal achievable value of time-averaged SusMR—that is only a few times the RMR.

stored energy reserves, which eventually become depleted. Is there a ceiling on the time-averaged metabolic rate that an animal or human can sustain indefinitely, for days or weeks, while remaining in energy balance through food intake? (Naturally, to pursue the example of a human athlete, we are not picturing a runner as jogging uninterruptedly day and night for weeks, but instead as alternately running, resting, eating, and sleeping and thereby achieving some time-averaged metabolic rate on a maximal training regimen.) In other words, does the curve of Fig. 1 eventually decline to an asymptote that could be termed the sustained metabolic rate (SusMR)?

Human experience makes it obvious that such an asymptotic ceiling must exist. For example, the athletes who compete in the annual Tour de France bicycle race are highly motivated to maximize their time-averaged power output. The race covers 3826 km and crosses 34 mountains in 22 days. The cyclists fuel their power output by consuming more food than does a normal person, and four cyclists studied by physiologists thereby managed to maintain body mass constant over the whole duration of the race (4). Yet that food consumption and hence power output were only 5 times BMR, although any cyclist who could have sustained a food consumption and power output of 20 times BMR would thereby have "wiped out" the competition. Why did these highly motivated athletes not achieve a higher SusMR?

Asymptotic ceilings on SusMR are central not only to exercise physiology but also to ecology and evolutionary biology, since metabolic ceilings might limit reproductive

Abbreviations: RMR, resting metabolic rate(s); SusMR, sustained metabolic rate(s); SusMS, sustained metabolic scope(s); FMR, field metabolic rate(s); BMR, basal metabolic rate(s).

effort, foraging activity, and ability to withstand cold. For example, it seems unlikely that the litter size of lactating female mammals or the clutch size of parent birds feeding nestlings could be increased indefinitely merely by providing the parents with more food. Similarly, it seems unlikely that all animals, given unlimited access to food, could increase their heat production indefinitely, maintain a constant body temperature in any environment no matter how cold, and extend their geographic range to the coldest climates.

Many authors have suggested that SusMR of various wild animals may be constrained to only a few times RMR (5–12) and that this ceiling may in some cases limit litter size or polar range boundaries (e.g., ref. 13). These previous comparisons of SusMR and RMR values were suggestive of a ceiling on the ratio of SusMR to RMR, which we term "sustained metabolic scope" (SusMS). However, these comparisons were limited in four respects: (*i*) values for only a few selected species were considered; (*ii*) most SusMR values were estimated indirectly, rather than measured; (*iii*) most RMR values were also not measured, but were instead calculated from interspecific allometric equations, from which individual species deviate by as much as -70% to $+250\%$ (14); and (*iv*) the animals were seldom demonstrated to be in a state of energy balance (inferred from constant body mass) during the period when SusMR values were being measured.

We have therefore systematically tested for the existence of a ceiling on SusMS by comparing SusMR and RMR values for all species in which both have actually been measured and that had been shown to be maintaining constant body mass during the period of SusMR measurements. We found 36 vertebrate species other than humans meeting these criteria, including both endotherms and ectotherms, representing three vertebrate classes. Although RMR itself varies 30,000-fold among the species analyzed, all values of SusMS (i.e., the ratio of SusMR to RMR) prove to be less than 7; most values fall between 1.5 and 5 (Tables 1 and 2). Ratios for humans fall in the same range (Table 3). These observations raise a series of questions concerning the proximate and ultimate limiting factors that set a ceiling on SusMS and the significance that ceilings may possess for animals' lives.

DATA

Table 1 presents the data for endothermic vertebrates other than humans; Table 2, for ectothermic vertebrates (lizards); and Table 3, for humans. The data were obtained as follows.

Table 1. SusMS values in endothermic vertebrates

Taxon	BMR body mass, g	BMR, kJ/day	Ref.	SusMR body mass, g	SusMR, kJ/day	Ref.	SusMS
Eutherian mammals							
Mus musculus	15	12	15	13	40	19	3.7
Peromyscus maniculatus	19	18	14	18	46–68	20	2.6–3.9
Peromyscus leucopus	21	16	15	18–24	59–77	21	3.9–5.0
Acomys cahirinus	42	22	14	38	52	19	2.5
Sekeetamys calurus	41*	15	16	41	44	19	2.9
Acomys russatus	51	19	14	45	48	19	2.7
Ammospermophilus leucurus	96	47	14	80–96	79–114	19	1.7–2.6
Thomomys bottae	143	57	15	99–108	127–136	19	2.8–3.0
Bradypus variegatus	3790	324	14	3830–4450	490–739	19	1.4–2.0
Alouatta palliata	4670	970	15	3200–8420	1110–2860	19	1.5–2.0
Marsupial mammals							
Sminthopsis crassicaudata	14	9	14	17	69	19	6.9
Antechinus stuartii	37	17	14	18	49	19	4.6
Petaurus breviceps	128	41	14	112–135	153–192	19	4.0–4.4
Gymnobelideus leadbeateri	166	48	14	117–133	219–232	19	5.6–5.8
Pseudocheirus peregrinus	860	134	14	717	556	19	4.7
Setonix brachyurus	2510	379	14	1510–2470	486–662	19	1.8–1.9
Macropus eugenii	4800	657	14	4560	1230	19	1.9
Phascolarctos cinereus	4770	970	14	7800–10,800	2030–2050	19	2.3–3.0
Birds							
Delichon urbica	21	31	17	19	74–80	22	2.6–2.8
Callipepla gambelii	126	65	17	145	91	19	1.3
Sterna fuscata	148	69	17	186	241	19	3.0
Falco tinnunculus	108	71	17	220	343	23	2.9
Puffinus pacificus	338	129	17	384	614	19	4.3
Rissa tridactyla	386*	314	18	386	876	18	2.8
Alectoris chukar	475	170	17	359–498	232–416	24	1.6–2.4
Sula bassana	3030	701	10	3210	4865	10	6.7
Pygoscelis adeliae	3970	1060	17	3870	4000	19	3.8
Eudyptes chrysolophus	3870	747	17	3900	4380	25	5.8
Macronectes giganteus	4780	1160	17	3580–4510	4150–4740	19	4.3–4.4
Pygoscelis papua	6290	1610	17	6100	3580–3890	25	2.3–2.5
Diomedea exulans	8130	1760	17	7360–9440	2630–3970	19	1.6–2.0

The BMR were measured for individuals of the mean body mass given in column 2; these data were taken from the references listed in column 4. The SusMR were measured for individuals of the mean body mass given in column 5; these values were taken from the references given in column 7 (for FMR values collected from ref. 19, information on body mass maintenance was gleaned from references cited therein). The SusMS values given are the ratios of SusMR to BMR after an allometric equation (calculated for the species of that vertebrate class in this table) was used to adjust the BMR values (column 3) to individuals of the body mass used for SusMR measurements (column 5).
*Estimated body mass.

Table 2. SusMS values in ectothermic vertebrates (lizards)

Species	Body mass, g	TRM, kJ/day	SusMR, kJ/day	Ref.	SusMS
Cnemidophorus hyperythrus	3.9–4.4	0.65–0.80	0.85–1.45	26	1.3–1.8
Sceloporus virgatus	5.5–7.6	0.23–0.43	0.72–1.13	27	2.1–4.6
Cnemidophorus tigris	16	2.04	3.28	28	1.6
Dipsosaurus dorsalis	3.5–57	0.46–4.02	0.75–8.2	29	1.0–2.6
Amblyrhynchus cristatus	965–2250	40.5–73.6	58.4–124	30	1.7

TRM, total resting metabolism. The SusMS values given are the ratios of SusMR to TRM.

SusMR. As published values of SusMR for wild animals and Tour de France cyclists, we used field metabolic rates (FMR) measured by the doubly labeled water technique, which yields total aerobic metabolism from the time that an animal is captured and injected with doubly labeled water (e.g., $^3H_2^{18}O$) until the time (typically 1–10 days later) that the animal is recaptured to determine H and O isotope turnover (34, 35). To ensure that these FMR values represent sustained metabolism powered by food intake rather than by energy reserves, we restricted this analysis to studies in which the animals' body masses were reported to change by <1% per day. SusMR values for humans other than cyclists were taken from energy balance studies of European adults, lasting 5–14 days, during which energy expenditure approximately balanced intake (31, 32). Estimates of energy expenditure based on the doubly labeled water technique and on energy balance studies agree in humans within 2% (36).

RMR. Published values for resting (basal) metabolic rates of endothermic vertebrates (column 3 of Table 1) were measured by O_2 consumption in normothermic, fasted, captive animals at rest within their zone of thermoneutrality during their period of normal daily inactivity. Ideally, BMR and SusMR would have been measured in the same individual, but usually the values were from separate studies, inevitably on individuals of slightly differing body mass. Hence we used the empirical allometric slope for BMR vs. mass for the analyzed species of that vertebrate class to adjust reported BMR values to the mass of the individuals used for SusMR studies (column 5 of Table 1). The adjustment ranged from −39% to +79%, with a mean absolute value of 14%. The uncertainty due to this allometric adjustment of measured BMR values is less than the uncertainty introduced by not measuring BMR values at all and instead relying entirely on interspecific allometric equations, because the former procedure retains species-level variation in BMR relative to body mass.

Since endothermic vertebrates (including humans) maintain constant body temperature physiologically, their BMR represents a minimal metabolic rate that is fairly constant throughout the day, so that BMR measurements translate directly into total daily resting metabolism for use as a baseline to compare with SusMR. For lizards, however, whose body temperature and hence RMR vary throughout the day, no such minimal baseline metabolic rate exists, and the translation of RMR into total daily resting metabolism is more complex. As a measure of RMR for lizards (column 3

of Table 2), we used total resting metabolism, the cumulative daily metabolic rate of a lizard at rest under the thermal regime normally experienced by that species in the field at the season of the SusMR measurements. The total resting metabolism was calculated from body temperatures and time budgets measured in the field, combined with RMR measured on lizards at those body temperatures in the laboratory (30). [RMRs were measured in fed lizards but would be lower in fasted lizards, by up to 50% (37), so that SusMR for lizards should probably be somewhat higher than the values shown in Table 2.]

Human BMR values (column 3 of Table 3) were taken as 6870 or 5990 kJ/day, the values for average European adult males or females, respectively (33).

RESULTS

Tables 1–3 show that RMR or SusMR values themselves vary 30,000-fold or 53,000-fold, respectively, among the species analyzed. As is well known, most of this variation is correlated with body mass (which varies 20,000-fold among our species) and status as endotherms or ectotherms [metabolic rates are typically ≈17 times higher in endotherms than in ectotherms of similar mass (19)].

Despite this great interspecific variation in both RMR and SusMR, the ratios of SusMR to RMR—the SusMS—fall within a modest range. Most ratios are 1.5–5, and the highest we found were 6.7 for a large seabird (the gannet *S. bassana*) and 6.9 for a small marsupial (the marsupial "mouse" *S. crassicaudata*). The highest human ratios that we found, those of 4.1–5.6 for Tour de France cyclists, were similar to the higher nonhuman values. The most vigorous cyclist was topped in this respect by only 4 of the 36 nonhuman species that we studied: the above-mentioned gannet and marsupial mouse, another small marsupial (the Australian possum *G. leadbeateri*), and the Macaroni penguin (*E. chrysolophus*).

DISCUSSION

Tables 1–3 yield seven sets of conclusions or questions.

Species Comparisons. The tables yield the first-order conclusion that values of SusMS for lizards, birds, marsupials, and eutherians (including humans) fall within similar ranges. However, second-order differences among groups of species may emerge, as in other interspecific comparisons of metabolic parameters (17, 19, 38, 39). We believe that testing for

Table 3. SusMS values in humans

Sex	Activity	BMR, kJ/day	SusMR, kJ/day	Ref.	SusMS
Female	Scientist	5990	8400–8600	31	1.4
Female	Pregnant	5990	9830–10700	31	1.6–1.8
Male	Scientist or banker	6870	11700–12000	31	1.7–1.8
Male	Miner	6870	15300–16900	31	2.2–2.5
Male	Army soldier	6870	13500–21000	31	2.0–3.1
Male	Antarctic explorer	6870	18500–23000	32	2.7–3.4
Male	Tour de France cyclist	6870	28400–38400	4	4.1–5.6

BMR values are for average European adult males or females (33).

such second-order effects will require data more accurate than those of Tables 1–3. Especially, SusMR and RMR should be determined in the same individuals at the same time. Because almost none of the studies used in Tables 1–3 did this, we had to make small allometric adjustments of RMR to the body mass of the conspecific individuals in which SusMR was determined. In addition, RMR varies seasonally by up to 50% (40), but conspecific SusMR and RMR values were not necessarily measured at the same season. These differences between the individuals used for SusMR and RMR studies must contribute some scatter to Tables 1–3.

Do These SusMR Values Constitute Metabolic Ceilings? Within a given species, SusMR varies severalfold with season or activity levels. For example, it is higher in physically vigorous than sedentary people, in breeding than nonbreeding animals, and in pregnant than non-pregnant human females. Thus, some values of Tables 1–3 certainly do not constitute ceilings.

However, human experience shows that even motivated athletes in training, soldiers, and explorers with unlimited available food cannot maintain chronic activity levels much beyond 40,000 kJ/day. More food does not permit Tour de France cyclists to triple their mileage or people to maintain body temperature while living naked outdoors in Arctic climates. For those animal species of Tables 1 and 2 for which ranges of values are given, most of the higher values refer to periods of reproductive activity (e.g., birds feeding nestlings), when time budget studies often indicate nearly full-time daylight activity (e.g., ref. 22). Several laboratory studies that manipulated animals' energy requirements experimentally by varying ambient temperature found that energy intake and expenditure reached a plateau with decreasing temperature (41–43).

Thus, upper values of some intraspecific ranges in Tables 1–3 are probably close to ceilings.

Do Metabolic Ceilings Vary with the Mode of Energy Expenditure? Does each individual animal's ceiling depend on how it expends energy? For example, do maximal sustainable levels of heat production in cold environments, during exercise, or during lactation yield similar ceilings of energy expenditure in a given species? The answer to this question will be an important clue to answering the following question.

What Are the Proximate Physiological Causes of Metabolic Ceilings? Perhaps the causes lie within one central system, most likely the digestive tract. That is, the intestine's ability to absorb nutrients or the liver's ability to process absorbed nutrients might set a ceiling on the daily nutrient supply available to the entire body, regardless of the purposes for which metabolic energy was being expended (12). In that case, maximal sustained levels of energy expenditure for lactation, exercise, and heat production in the same individual would all equal each other and would in turn equal the ceiling imposed by intestinal absorption.

Alternatively, the causes of metabolic ceilings might lie peripherally, within each metabolizing tissue itself. That is, the properties of mammary glands might limit daily energy expenditure for lactation, whereas properties of muscle might limit expenditure for exercise. In that case, maximal sustained levels of energy expenditure for lactation, exercise, and heat production in the same individual might differ from each other and be lower than the ceiling theoretically imposed by intestinal absorption.

We suggest attempting to discriminate between these two alternatives by measuring ceilings for different modes of energy expenditure and by comparing measured ceilings with physiological capacities of the digestive system and of energy-consuming tissues (cf. refs. 44 and 45).

Single Limiting Physiological Factors vs. Symmorphosis. Once the limiting organ system has been identified, one can ask whether there is a single limiting factor ("bottleneck") in that system or whether the capacities of different steps in the system have instead become evolutionarily coadjusted to operate up to similar ceilings. Taylor and Weibel (44) refer to the latter possibility as symmorphosis. The underlying reasoning is that natural selection seems unlikely to result in a single step of a pathway constituting a bottleneck, since a slightly increased expenditure of biosynthetic energy devoted to increasing the capacity of that one step would then yield a large payoff in the form of increased capacity of the whole pathway. Conversely, natural selection seems unlikely to result in some steps in a pathway having much greater capacity than other steps, since the surplus unutilizable capacity of the former steps would then represent wasted biosynthetic energy. The most efficient design would be for all sequential steps to have the same capacity (symmorphosis). However, it is disputed whether such design optimization is theoretically likely or is achieved in practice (46).

What Are the Ultimate Evolutionary Causes of Metabolic Ceilings? Regardless of the proximate physiological causes of ceilings, one must also inquire about the ultimate evolutionary reasons why natural selection permitted them to evolve. One might naively expect an increase in SusMR to be beneficial, by permitting an animal to raise more young, survive in colder climates, or sustain higher levels of activity. Why, then, did ceilings nevertheless evolve?

Possible answers may depend on cost/benefit trade-offs; for example, metabolic capacities may have evolved only to those limits that an animal's food supply is likely to be able to fuel, since the biosynthetic energy required for higher capacities would be wasted. Alternatively, the answer may involve a design limitation, such as the concept that a higher SusMR requires more metabolic machinery, the maintenance of which may thus require a higher RMR (2).

Significance of Metabolic Ceilings for Animals' Lives. Root (13) noted that, for more than half of North American songbird species analyzed, the entire length of their northern range boundary during midwinter coincides closely with some isotherm of minimum environmental temperature. For each of those species for which measurements of RMR as a function of ambient temperature were available, Root calculated RMR at the minimum midwinter temperature of that species' northern boundary. That RMR, which represents BMR plus the metabolic expenditure required to maintain body temperature, proved to equal about 2.5 times the BMR (in the zone of thermoneutrality) for each species. The total FMR of those birds must have been somewhat more than 2.5 times basal, since the birds must have been expending energy for digestion, foraging, and other activities as well as for heat production. The implication of Root's analysis is thus that those bird species are limited to wintering in areas where they do not have to raise their resting metabolic rate beyond 2.5 times the basal level—or their total FMR beyond somewhat more than 2.5 times the basal level—in order to stay warm. This factor is compatible with the SusMS values for birds that we have calculated in Table 1.

Root's study exemplifies how ceilings on SusMR may function as proximate factors that limit not only species' geographic distributions (through a ceiling on heat production and hence on survival in cold climates) but also litter size (through a ceiling on lactation rates), foraging (through a ceiling on muscular activities), and other features of animals' lives.

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