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REVIEW

CENTENARY ARTICLE 100 YEARS OF DISCOVERY

# The fire of evolution: energy expenditure and ecology in primates and other endotherms

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## ABSTRACT

Total energy expenditure (TEE) represents the total energy allocated to growth, reproduction and body maintenance, as well as the energy expended on physical activity. Early experimental work in animal energetics focused on the costs of specific tasks (basal metabolic rate, locomotion, reproduction), while determination of TEE was limited to estimates from activity budgets or measurements of subjects confined to metabolic chambers. Advances in recent decades have enabled measures of TEE in free-living animals, challenging traditional additive approaches to understanding animal energy budgets. Variation in lifestyle and activity level can impact individuals' TEE on short time scales, but interspecific differences in TEE are largely shaped by evolution. Here, we review work on energy expenditure across the animal kingdom, with a particular focus on endotherms, and examine recent advances in primate energetics. Relative to other placental mammals, primates have low TEE, which may drive their slow pace of life and be an evolved response to the challenges presented by their ecologies and environments. TEE variation among hominoid primates appears to reflect adaptive shifts in energy throughput and allocation in response to ecological pressures. As the taxonomic breadth and depth of TEE data expand, we will be able to test additional hypotheses about how energy budgets are shaped by environmental pressures and explore the more proximal mechanisms that drive intra-specific variation in energy expenditure.

KEY WORDS: Energetics, Evolution, Ecology, Environment, Trade-off

## Introduction

Biologists have long recognized the importance of energetics, metabolism and what early scientists termed 'vital heat' in sustaining life. Antoine Lavoisier conducted the foundational animal experiments in 1782–1783 that launched the modern field of metabolic science (Underwood, 1944). Placing a guinea pig in a double-walled metal container with snow packed between the walls, he measured the amount of carbon dioxide produced and the mass of ice melted by the guinea pig, and then compared these rates with those produced from burning charcoal placed inside the same chamber. Lavoisier's guinea pigs demonstrated that aerobic respiration followed the same principles as a burning fire, leading to his insight 'la respiration est une combustion' (respiration is combustion).

Though his experiments took place over two centuries ago, the fundamentals of Lavoisier's insights are still relevant today, and much modern energetics research seeks to understand what drives variation in energy expenditure within and between species and individuals. Nineteenth-century experimental work quantified oxygen consumption, carbon dioxide output and energy balance in humans, dogs and other mammals using closed-circuit metabolism chambers and respiration calorimetry (see Glossary; Webb, 1991). The same basic science underpins modern respirometry and indirect calorimetry techniques [direct calorimetry, which measures the heat produced by an organism (Kenny et al., 2017), is less commonly used]. These methods, which measure carbon dioxide production and/or oxygen consumption, are widely used in laboratory settings to assess resting or maintenance energy expenditure, as well as activity energy expenditure, across a broad range of species, from insects to elephants (Chaui-Berlinck and Bicudo, 1995; Hawkins et al., 2000; Holmér, 1972; John et al., 2021; Langman et al., 1995; Lighton and Duncan, 1995, 2002; Taylor et al., 1982; Vleck, 1979; Walsberg and Wolf, 1995; Ward et al., 2003; Williams, 1983, 1999; Williams et al., 1991).

Quantifying energy expenditure in wild-living or free-ranging individuals is not possible with mask- or chamber-based methods that confine subjects to the lab. Instead, assessments of total energy expenditure (TEE) in the early and mid-twentieth century relied wholly on combining daily activity budgets with lab-based estimates of activity costs to estimate TEE. This 'additive' approach, while still used in many contexts, is problematic because it imparts error in the estimation of daily activity costs and because of the difficulty in capturing the costs of reproduction, immune function, stress response, thermoregulation or other tasks with energy costs that are poorly characterized experimentally or difficult to assess in free-ranging organisms.

Lifson and colleagues (1949, 1955) overcame the challenge of measuring TEE in free-living subjects by developing the doubly labeled water (DLW) method, which has revolutionized the study of energetics and total body metabolism (see Box 1). In the years since Lifson and colleagues' (1949, 1955) initial work on rodents, the DLW method has been applied to a wide range of taxa, from bats to dolphins, birds and humans (Bourne et al., 2019; Hawkins et al., 2000; Jeanniard-du-Dot et al., 2016; Nie et al., 2015; Rimbach et al., 2021; Schoeller and van Santen, 1982; Schoeller et al., 1986; Speakman and Racey, 1991). These studies have proven foundational in understanding the causes and consequences of variation in TEE (MJ day$^{-1}$ or kcal day$^{-1}$), an organism's total energy budget.

Here, we review key studies of energy expenditure across mammals, focusing on measures of TEE. TEE integrates energy allocation across tasks and systems, so we explore both the determinants of TEE and key trade-offs in allocation to different tasks. We will conclude by highlighting work on daily energy expenditure in primates.

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## Glossary

**Allometry**

Biological scaling; the study of how processes change and scale with body size.

**Closed-circuit metabolism chambers**

An airtight system that measures the concentration of oxygen and carbon dioxide in inlet and outlet airstreams. This allows one to calculate the energy expenditure of a participant within the chamber.

**Defended core body temperature**

A maintained core body temperature that allows an endotherm to maintain normal body function and maintain natural tissue mechanics.

**Evolutionary radiation**

A rapid increase in the diversity of a clade, often one that allows organisms to fill new niches.

**First principles**

The fundamental building blocks of a science that cannot be further deduced and form the foundation for all other theories, e.g. Newtonian mechanics.

**Metabolic ceiling**

The maximum total energy expenditure that an organism cannot sustainably surpass.

**Respiration calorimetry**

A method of measuring energy expenditure using oxygen consumption and carbon dioxide production (in contrast to direct calorimetry, which measures heat production).

**Thermoneutral**

A state in which heat production and heat loss are balanced, so the body can maintain core body temperature with minimal metabolic regulation; the thermoneutral zone is the range of temperatures at which this is possible.

**Thermal conductivity**

A measure of a material's ability to conduct heat.

## Box 1. Doubly labeled water method

Now considered the gold standard for measuring total energy expenditure (TEE) in many free-living organisms, the doubly labeled water (DLW) method relies on differences in the elimination rate of labeled hydrogen (deuterium) and oxygen (oxygen-18) isotopes from the body water pool. These isotopes are given (injected or ingested) to subjects as a single dose of water, and then lost from the body over time (the typical time frame for study is several days). The hydrogen isotope is excreted from the body only as water, but oxygen is lost as both water and carbon dioxide. Differences in the elimination rate of the two isotopes therefore allow carbon dioxide production and, consequently, TEE to be calculated over the measurement period.

Lifson and colleagues' (1949, 1955) approach was initially limited to mice and other small-bodied species because of the cost of isotopes and the precision of mass spectrometers (Mullen, 1970, 1971; Nagy and Shoemaker, 1975; Westerterp and Bryant, 1984). Advances in mass spectrometry and isotope production reduced these costs, and in the early 1980s the technique was adapted by Schoeller and van Santen (1982) for humans. In the subsequent decades, further reductions in the cost of isotopes and advancements in mass spectrometry have expanded DLW studies across a broad range of endothermic species and with different ecologies. The DLW method has been applied to study energy expenditure in many taxa, from rodents and humans (Lifson et al., 1949, 1955; Schoeller and van Santen, 1982; Schoeller et al., 1986) to bats (Speakman and Racey, 1991), giant pandas (Nie et al., 2015), dolphins (Rimbach et al., 2021), fur seals (Jeanniard-du-Dot et al., 2016), birds (Bourne et al., 2019; Hawkins et al., 2000) and more (Nagy, 2005; Nagy et al., 1999). Although the DLW does have some limitations (it may not be suitable for marine reptiles, for example; Jones et al., 2009), it is indispensable for measuring TEE across taxa.

## TEE

### Determinants of TEE: size, phylogeny and ecology

Both within and between species, body size is the strongest predictor of TEE (Fig. 1). Within species, body mass-adjusted TEE and total energy throughput vary with age, environment and reproductive state (Hammond and Diamond, 1997; Lailvaux and Husak, 2017; Speakman, 2008). Body composition is an important determinant, particularly within species, as organs and tissues vary widely in their mass-specific expenditures: the liver, kidney and brain have high energy demands, whereas fat, bone and skin have low mass-specific requirements (Elia, 1992; Wang et al., 2001). Even in analyses controlling for body size and composition, inter-individual variability in TEE is substantial (Pontzer et al., 2021), and these differences are stable and repeatable over time (Rimbach et al., 2022). Though variation in mitochondrial efficiency (the ratio of oxygen consumed to ATP produced) will lead to variability in metabolic rates measured from oxygen consumption or $CO_2$ production, the magnitude of its effect is not well characterized (Salin et al., 2015). Instead, apart from body size and composition, the main determinants of variation in TEE are thought to be behavioral, ecological and life-history factors.

On short time scales (e.g. days, weeks or seasons), ambient temperature (Nespolo et al., 2003; Speakman et al., 2021), physical activity (Thurber et al., 2019; Zub et al., 2009) and food composition (Zanotto et al., 1997) can affect metabolism and energy throughput. Reproductive status also affects TEE, as reproduction (particularly lactation) is the costliest activity for eutherian mammals after physical activity (Prentice and Prentice, 1988; Speakman, 2008). Across a sample of eutherians, pregnancy increases metabolic rates by approximately 25% relative to non-reproductive rates, with lactation costs even higher (McNab, 2002).

Interspecific analyses of TEE scaling patterns have focused on taxonomic differences and ecological influences. The allometry (see Glossary) of TEE varies somewhat among clades but is broadly consistent with the 3/4 power scaling seen in basal metabolic rate (BMR) (Nagy et al., 1999). The increase in energy requirements with size makes sense from first principles (see Glossary), as larger animals are made of more cells, which, in turn, require more energy. However, these energetic requirements do not scale isometrically with body size: a 10 kg animal does not require 10 times the energy of a 1 kg animal. Because BMR accounts for a significant portion of TEE (Pontzer et al., 2014), much of the interspecific variation in TEE can be explained by the allometry of BMR. The determinants of BMR allometry remain a longstanding focus of debate, as discussed below.

Some, but not all, of the taxonomic differences in BMR are apparent in TEE. TEE is much lower among reptiles than among mammals and birds, and metatherians (marsupials) have lower TEE than eutherians, echoing patterns seen in BMR (Nagy, 2005; Nagy et al., 1999). Within birds, TEE among Passeriformes and Procellariformes is generally greater than that of Galliformes (Nagy, 2005). Within eutherian mammals, primates have unexpectedly low TEE for their body size, even though their BMR is generally similar to that of other mammals (Pontzer et al., 2014).

Some of the variation in TEE among species and clades may reflect energetic requirements and challenges imposed by different environments. For example, among mammals and birds, desert species tend to have lower TEE than non-desert species (Nagy, 2005; Nagy et al., 1999). Some have argued that TEE may be restricted by low resource availability or poor digestive efficiency, either of which could limit the energy available for maintenance,

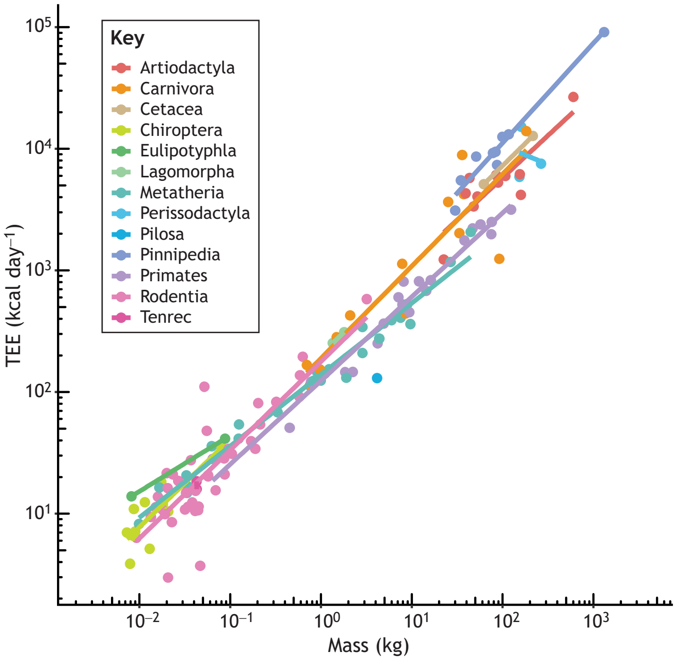

**Fig. 1. Total energy expenditure as a function of body mass in mammals.** Across mammals, body mass is the strongest predictor of total energy expenditure (TEE) (*n*=271 species; number of individuals unknown for all species; analyses unweighted). Some clades, such as Pinnipedia and Cetacea (seals and whales, dolphins and porpoises) have higher than expected TEE for their body mass, likely as a result of the demands of their marine environment.

growth and reproduction (Bozinovic et al., 2007; Burton et al., 2011; Nie et al., 2015; Speakman et al., 2003). Consistent with this view, TEE in the desert-living Arabian oryx (*Oryx leucoryx*) is twice as high during spring rains when grass is abundant as during the summer when food is scarce (Williams et al., 2001b), and *Peromyscus* mice in high primary productivity environments have higher BMR and food intake than those from lower productivity environments (Mueller and Diamond, 2001).

Interestingly, although total energetic demands may be reduced in food-insecure environments, there also may be physiological mechanisms that enable animals to remain in positive energy balance under such conditions. For example, although European starlings (*Sternus vulgaris*) challenged with food insecurity eat less, their body mass increases, possibly as a result of increased energy assimilation and energetic efficiency (Bateson et al., 2021). Future research on the mechanisms underlying this phenomenon, as well as its applicability across taxa, is needed.

Alternatively, based on evidence from voles (*Microtus agrestis*; Speakman et al., 2003) and blue tits (*Parus caeruleus*; Thomas et al., 2001), individuals living in poor-quality environments characterized by low resource availability may have higher energetic demands because they are forced to travel farther to forage (Speakman et al., 2003). This effect, however, may not be generalizable to all foraging scenarios. Although starling (*Sternus vulgaris*) daily energy expenditure (as estimated from food consumption, waste production and mass change) increases when birds are experimentally required to fly farther to find food (Wiersma et al., 2005), for example, forcing zebra finches (*Taeniopygia guttata*) to increase foraging effort by cutting food with chaff is associated with decreased TEE (Wiersma and Verhulst, 2005). These differences suggest that the effect of resource availability on TEE is likely to be mediated by the energetic cost and nature of food-acquisition activities. Furthermore, because foraging often exposes animals to predators, the benefits of increased foraging must be balanced with the costs of increased predation risk.

TEE has been linked to predation, which can affect behavior and energy expenditure as individuals flee or hide from predators, experience physiological stress or restrict foraging (McNab, 1986; Pettett et al., 2017). Pettett and colleagues (2017) reported lower TEE for European hedgehogs (*Erinaceus europaeus*) in the presence of predators and higher TEE in the presence of low food availability. Energy conservation strategies may be favored when predation risk reduces food intake; in the absence of predators, low food availability may necessitate increased foraging effort that increases TEE (Pettett et al., 2017). Although not a direct test of the relationship between predation and TEE, across taxa, internal energy stores (i.e. adipose tissue) decrease as true or perceived predation pressure increases (Macleod et al., 2005; Speakman, 2018; Zimmer et al., 2011), suggesting that increased predation does not favor positive energy balance. The decreased energetic requirements of smaller size reduce foraging investment, which in turn reduces exposure to predation. Smaller bodies, especially smaller fat stores, may also be selected for under higher predation pressure to improve performance and facilitate escape from predators (McNamara and Houston, 1990; Speakman, 2018; Witter and Cuthill, 1993; Zimmer et al., 2011). Further work on the relationship between predation pressure, locomotor performance, foraging effort and total energy budget in wild populations would help untangle the effects of different pressures.

Lower quality environments may also be characterized by high pathogen or disease burden, not simply limited food resources. Although experimental immune challenges raise resting or metabolic rate in many marine and avian taxa (e.g. Cutrera et al., 2010; Eraud et al., 2005; Martin et al., 2003; Ots et al., 2001), other experiments fail to identify a significant effect (e.g. Pilorz et al., 2005). As many of these experiments measure basal or resting metabolism, it is unclear whether increased immune activity truly elevates TEE or simply forces trade-offs in energy allocation between competing demands (e.g. Amat et al., 2007; Demas et al., 1997; Derting and Compton, 2003; Urlacher et al., 2019; see ‘Trade-offs: maintenance, growth and reproduction’, below). Additional work that directly measures TEE in response to immune challenges is needed to understand how immune activity in response to disease- and pathogen-linked mortality risk shapes overall energy throughput.

Marine mammal radiations (an evolutionary radiation, see Glossary) provide further insights into interactions between resource availability and other evolutionary and ecological selective pressures on TEE. Though two marine mammal lineages (cetaceans and pinnipeds) evolved from independent terrestrial ancestors, many taxa from both lineages have high TEE relative to that of terrestrial mammals of similar body mass (Rimbach et al., 2021). The high TEEs of marine mammals are often attributed to the high costs of homeothermy (the same argument used to explain their high BMRs; see below) in marine environments (Williams et al., 2001a). However, not all marine mammals have elevated TEE or BMR relative to terrestrial mammals. Harbor porpoises (*Phocoena phocoena*) and Galapagos fur seals (*Arctocephalus galapagoensis*), for example, have lower TEEs than expected for their size (John et al., 2021; Pedersen et al., 2020; Rimbach et al., 2021). Some marine mammals (e.g. manatees) may face challenges to maintaining daily energy balance because of the lower primary productivity of marine environments with fewer plants, increased competition from ectotherms (Tittensor et al., 2010) or anthropogenic impacts on food resources and foraging behavior (DeMaster et al., 2001; John et al., 2021; Nowacek et al., 2004). The variability in TEE among marine mammals highlights the complexity of interactions between ecological, trophic-level (e.g. carnivore versus herbivore) and locomotor correlates of total energy throughput across taxa.

Although environmental and ecological pressures clearly shape TEE, the relationship between environment and energy allocation to different tasks is complex. Co-variation between the environment and TEE may not always reflect resource availability and is mediated by other extrinsic and intrinsic factors such as predation, disease and thermoregulatory demands. The answers to questions about whether a higher energy budget is forced by a poor-quality environment or enabled by a favorable one depend in part on the conditions used to define environmental quality, as well as the strength of competing selective pressures. In high primary productivity environments, for example, where some resource acquisition costs are relaxed, or in more temperate environments where endotherms' thermoregulatory costs are relaxed, some animals may be freed to reduce overall expenditure, and TEE across taxa may vary more widely. In support of this, Anderson and Jetz (2005) found that mammals and birds inhabiting high latitudes invariably had high TEEs, whereas animals living closer to the equator exhibited a wider range of TEE and pushed the lower bound of daily TEE. This suggests that the lower limit of energy expenditure is driven by environmental factors, with the upper limit determined by physiological constraints (Anderson and Jetz, 2005).

### Upper limits to TEE

Even with unlimited food availability, TEE in wild and lab populations is limited by intrinsic constraints that impose a 'metabolic ceiling' (see Glossary) on daily energy expenditure (Drent and Daan, 1980; Elliott et al., 2014; Hammond and Diamond, 1997; Speakman, 1997; Speakman et al., 2003; Tinbergen and Verhulst, 2000). TEE constraints are perhaps most evident during periods of elevated energy expenditure associated with reproduction. Drent and Daan (1980), in a classic paper on energy limits, showed that TEE in wild birds was limited to ∼4 times BMR during the peak period of activity to provision nestlings. Perrigo (1987), in a series of laboratory studies in rodents, showed that maternal TEE was limited such that increasing the energy required for daily physical activity led to reduced offspring growth or even the cannibalization of pups. Król and colleagues (Król and Speakman, 2003; Król et al., 2007) demonstrated that, at least in mice, the metabolic ceiling for nursing mothers could be raised by cooling them, suggesting that TEE limits are (at least in mice) a function of heat dissipation.

These and other studies led to a series of analyses debating both the level and underlying mechanisms of peak sustainable TEE across different species (Drent and Daan, 1980; Hammond and Diamond, 1997; Król and Speakman, 2003; Peterson et al., 1990; Thurber et al., 2019). Proponents of the 'central limitation' or 'peripheral limitation' hypotheses argue that peak energy expenditure is limited by the physiology of energy-supplying and energy-consuming organs, such as the ability of the gastrointestinal tract to absorb energy (e.g. Hammond and Diamond, 1997; Thurber et al., 2019) or peripheral tissues to consume energy (e.g. Hammond and Diamond, 1997). An alternative hypothesis extends output-based hypotheses to propose that the ability of an animal to dissipate heat is what limits maximum energy expenditure (e.g. Król and Speakman, 2003; Speakman and Król, 2010).

Notably, work across endothermic species suggests that constraints on TEE may arise well before individuals reach peak sustainable TEE (Pontzer, 2015, 2018). In laboratory studies on rodents challenged with increased activity workload, TEE does not increase as expected with rising locomotor energy expenditure (O'Neal et al., 2017; Perrigo, 1987). In human exercise intervention studies, observed TEE increases are generally less than expected from imposed physical activity workloads, which suggests some degree of compensation to maintain habitual TEE within a narrow range (Donnelly et al., 2003; Goran and Poehlman, 1992; Martin et al., 2019; Pontzer, 2015; Pontzer et al., 2018; Wang et al., 2017; Willis et al., 2014). Indeed, in some cohorts in these studies, TEE at the end of a months-long exercise intervention is statistically indistinguishable from baseline measures, even though TEE is far below maximum sustainable levels (Pontzer, 2015, 2018).

The mechanisms underlying energy compensation and TEE constraint are not well understood. In principle, such constraints could arise from any combination of limits on energy absorption (e.g. rate of digestion), whole-body energy expenditure (e.g. heat dissipation limits) or the rate of energy expenditure in peripheral tissues (e.g. mammary glands or muscle) (Pontzer and McGrosky, 2022). Król and Speakman's (2003) laboratory work supports a heat dissipation limit on whole-body energy expenditure for mice, but tests in other species and settings are needed. Whatever the mechanism, constraints on TEE imply trade-offs, as organisms must allocate limited energy across competing tasks.

## Energy allocation

TEE represents the total energy allocated to growth, reproduction and body maintenance as well as the energy that an animal expends on physical activity (Fig. 2; Pontzer and McGrosky, 2022). We should expect natural selection to favor behavioral and physiological strategies that allocate energy across these competing domains in ways that maximize fitness (Stearns, 1989). To understand how the total energy budget is allocated, however, we must first explore these domains – basal metabolism, thermoregulation, physical activity, body maintenance, body growth and reproduction.

### BMR

BMR, or the energy expended when an animal is at rest in a thermoneutral (see Glossary), post-absorptive (i.e. non-digestive) state, corresponds to the minimum costs of body maintenance. Comparisons of magnetic resonance imaging and BMR across large samples of human subjects have demonstrated that BMR reflects the

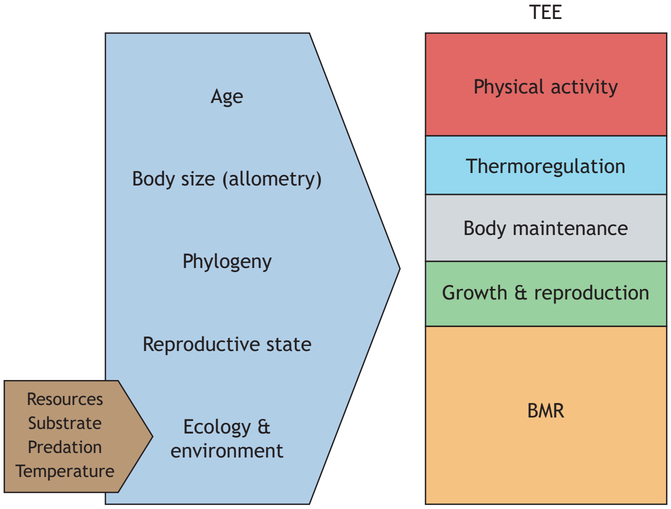

**Fig. 2. Components and determinants of TEE.** Components of TEE [basal metabolic rate (BMR) and energy allocated to reproduction, growth, maintenance, physical activity and thermoregulation] are not to scale, but for many taxa, BMR (measured in a post-digestive, thermoneutral state at rest) is the largest component. Known determinants of TEE are shown in the blue arrow, with some specific ecological and environmental pressures highlighted in the brown arrow. Determinants do not affect all components of TEE equally. Ambient temperature, for example, plays a large role in determining energy allocated to thermoregulation, but is not known to appreciably impact energy allocated to growth and reproduction.

size- and tissue-specific metabolic rates of the organs at rest (Wang et al., 2010).

The scaling of BMR has long been of interest to biologists, with Sarrus and Rameaux (1838) suggesting that the relationship between body mass and metabolism may reflect the physics of heat dissipation across the body surface and thus that metabolic rate would be proportional to body mass$^{2/3}$ (White and Seymour, 2005). Rubner (1883) subsequently provided empirical measurements of metabolic rate in dogs to support the 2/3 power scaling of metabolic rate with body mass (Hoppeler and Weibel, 2005). Rubner's (1883) 2/3 power scaling was generally accepted until Kleiber's (1932, 1947, 1961) foundational work on BMR indicated an exponent closer to 3/4 across mammals (Benedict, 1938; Brody, 1945; Gillooly et al., 2001; Hemmingsen, 1960; Schmidt-Nielsen, 1984). Kleiber's Law of a mass$^{0.75}$ scaling for BMR remains widely accepted today, although considerable variation has been reported in allometric studies (see Box 2).

Between species, there is a well-supported relationship between environment and metabolic rate after controlling for body mass, with colder temperatures associated with higher BMR in birds (e.g. Jetz et al., 2008; Kang et al., 1963; White et al., 2006) and mammals (e.g. Careau et al., 2007; Clarke et al., 2010; Lovegrove, 2003). The relatively lower BMR of hot-adapted endothermic taxa may be necessary because high temperatures limit metabolism (Speakman and Król, 2010) or because relying on environmental temperature to help maintain body temperature reduces endogenous heat production requirements and thus saves energy and water (White and Kearney, 2013). For cold-dwelling taxa, a higher metabolic rate may be necessary to maximize heat production and maintain homeothermy (Heldmaier et al., 1990; Rezende et al., 2004). It is important to note, however, that BMR by definition does not include energy allocated to thermoregulation, so some studies on temperature effects may actually be capturing temperature-linked differences in resting metabolic rate (RMR).

**Box 2. Basal metabolic rate scaling**

Biologists have proposed various hypotheses to explain the scaling of basal metabolic rate (BMR). West and colleagues (1997) hypothesized that Kleiber's 3/4 scaling of BMR results from the fractal geometries of the vascular systems that provide nutrients to the body. Others have disagreed, arguing that when only true BMR measurements (i.e. those collected following strict BMR measurement criteria, which require adult participants in an inactive, fasted, non-reproductive thermoneutral state) are included in analyses, the scaling is closer to Rubner's (1883) 2/3 value and therefore a function of surface area scaling (White and Seymour, 2003, 2005). Phylogenetically informed analyses suggest that the scaling exponent of BMR varies between lineages, with some closer to Rubner's (1883) 2/3 value and others closer to Kleiber's (1932, 1947, 1961) 3/4 value (White et al., 2009). Some have argued that this observed variation in allometric exponents among clades (e.g. differences in scaling patterns between endothermic and exothermic taxa) precludes a unifying explanation for BMR scaling (Capellini et al., 2010). More recently, White et al. (2022) have hypothesized that the allometry of BMR reflects optimization of life history parameters, balancing energy investment in growth, reproduction and maintenance. Resolving the debate around the scaling of BMR is beyond the scope of this Review (see White and Kearney, 2013), but will presumably inform our understanding of TEE scaling, as BMR comprises a large portion of TEE for most species.

Despite a negative correlation between metabolic rate and environmental temperature across taxa, analyses of the environmental and ecological correlates of BMR and RMR within species have produced mixed results (Lovegrove, 2009; White and Seymour, 2004). Cold acclimation can raise metabolic rates in mammals (Chi and Wang, 2011; Song and Wang, 2006) and birds (Klaassen et al., 2004; McKechnie et al., 2007; Williams and Tieleman, 2000). BMR and RMR may also vary with environment and season (Bech et al., 2002; Kersten et al., 1998), as some animals reduce metabolic rate in response to resource unpredictability or other events that limit food availability (e.g. reproduction, hibernation, migration) (Halsey, 2018; Secor and Carey, 2016). Work on birds has shown that waders that winter in the tropics have depressed BMR compared with conspecifics that winter in more temperate regions, likely through a combination of metabolically active tissue size reduction and hormonal changes (Kersten et al., 1998). Though many intraspecific changes in BMR are largely a secondary consequence of changes in body mass (e.g. Bech et al., 2002; Schaeffer et al., 2020), some may also have adaptive benefits. For example, kittiwakes (*Rissa tridactyla*) reduce body mass, and thus BMR and their own maintenance costs, during costly chick-rearing periods, which may allow them to allocate more energy to provisioning their offspring to ensure the survival of both generations (Bech et al., 2002; Tremblay et al., 2022; Welcker et al., 2013). Similarly, starlings (*Sternus vulgaris*) that are required to fly farther to earn food (a proxy for a 'poor' environment) reduce body mass, BMR and pectoral muscle size, which likely saves energy to blunt the observed foraging cost-driven increase in daily energy expenditure (Wiersma et al., 2005).

### Thermoregulation

For endotherms, particularly those in cold climates or marine environments, maintaining core body temperature represents a substantial component of TEE. Species in cold climates have evolved mechanisms to conserve energy and thus reduce thermoregulatory costs, such as increased insulation (e.g. denser fur, more subcutaneous fat), sometimes in conjunction with torpor or hibernation that suppresses metabolic rate (Scholander et al., 1950; Speakman, 2018; Speakman and Rowland, 1999). Thermoregulation is a particular challenge for cold-dwelling small-bodied animals because of their high surface area-to-volume ratio or marine animals because of the high thermal conductivity (see Glossary) of water. In the marine environment, many marine mammals have a higher BMR than terrestrial mammals of similar body mass (Williams et al., 2001a; Wright et al., 2021). Consistent with this interpretation, John and colleagues (2021) found that species belonging to two independent lineages of warm-water marine mammals, monk seals (*Neomonachus shauinslandi*) and manatees (*Trichechus manatus latirostris*), exhibited lower BMRs than similarly sized marine mammals living in cooler waters. These authors suggested diet may also influence BMR evolution, noting that the reduced BMR of monk seals is likely to be an adaptation to low prey availability in tropical waters and represents a relatively modest reduction in BMR relative to that of cold-adapted marine mammals (John et al., 2021).

Thermoregulatory demands also affect energy budgets intraspecifically. Among free-ranging adult least weasels (*Mustela nivalis*), TEE is negatively correlated with ambient temperature after adjusting for body mass, activity and habitat (Zub et al., 2009). The range of variation in mass- and activity-adjusted TEE decreases with temperature, likely because survival at the lowest temperatures requires animals to maintain some minimum TEE to permit sufficient thermoregulation (Zub et al., 2009). At higher ambient temperatures, the thermoregulatory costs of endotherms are reduced, permitting more flexibility in energy allocation within the total energy budget, resulting in greater variation in mass- and activity-adjusted TEE (Zub et al., 2009).

While the increased subcutaneous fat and fur of many cold-adapted animals serves as a physical insulator (Scholander et al., 1950), physiological mechanisms can also seasonally reduce energetic demands. Lower TEE in cold conditions can be accomplished by hibernation, torpor and/or lowering the defended core body temperature (see Glossary), thereby reducing the temperature gradient with the ambient air and thus lowering thermoregulatory demands (Speakman, 2018; Speakman et al., 2021). During the winter, pikas (*Ochotona curzoniae*) living on the Tibetan plateau, where temperatures can drop to below −30°C, suppress BMR and TEE by reducing body temperature and physical activity (Speakman et al., 2021). Common shrews (*Sorex araneus*) also experience an absolute energy expenditure reduction in the winter via a reduction in body mass that helps them to survive harsh conditions with lower resource availability, despite the thermoregulatory challenges posed by small body size (Schaeffer et al., 2020). A similar temperature-driven reduction in TEE has been observed in red squirrels (*Tamiasciurus hudsonicus*; Fletcher et al., 2012; Humphries et al., 2005), llamas (*Llama glama*; Riek et al., 2017; Riek et al., 2019) and Shetland ponies (*Equus caballus*; Brinkmann et al., 2014) during cold seasons. As acclimation to cold temperatures is often hypothesized to raise metabolic rates (e.g. Chi and Wang, 2011; Klaassen et al., 2004), further investigation of the relationship between BMR and/or RMR and TEE in cold environments would be valuable.

There are also many non-hibernating mammals inhabiting temperate climates for which TEE does not significantly vary between seasons (Speakman, 1999; Zub et al., 2009). These species appear to reduce expenditure on other components of the total energy budget (e.g. physical activity). Among least weasels, for example, after accounting for body mass, activity time is the strongest predictor of TEE; their TEE is not significantly different between summer and winter, presumably because energy that was spent on thermoregulation in the winter was re-allocated to activity costs during the summer (Zub et al., 2009). This highlights both the costs of physical activity and the role of trade-offs in energy allocation.

### Physical activity

Energy expended on physical activity is likely the most variable component of TEE across and within populations. Physical activity includes locomotion and smaller motor activities that occur throughout the day while an animal is alert, resting or fidgeting (Karasov, 1992; Levine et al., 2000). Physical activity is often quantified experimentally using accelerometry, but accelerometry-based methods simply provide a measure of physical activity quantity and quality, not the energy expended. In the lab, activity costs can be quantified via indirect calorimetry by measuring expired air during bouts of activity (e.g. Taylor et al., 1982). In the wild, physical activity costs can be inferred from DLW-derived measures by subtracting BMR from TEE (Karasov, 1992) or by calculating the TEE/BMR ratio (Westerterp, 2009). Although these DLW-based measures can be useful in assessing broad trends in activity, it should be noted that these approaches will overestimate daily activity costs because they assume all non-BMR energy expenditure derives from muscle activity and movement, ignoring the energy costs of arousal, thermoregulation or other tasks not captured in BMR.

The ‘cost of transport’ for locomotion (energy expended per unit distance traveled) depends on an animal’s body size, the substrate, and the speed and mode of locomotion. Most locomotor cost derives from muscle energy used to support body weight; thus, larger animals have greater absolute (whole-body) costs of transport (Schmidt-Nielsen, 1972). Swimming, in which body weight is supported by water, is less costly than running, which is in turn less costly than flying (Schmidt-Nielsen, 1972). As with BMR and TEE, larger animals have lower mass-specific costs of transport for swimming, flying and running (Schmidt-Nielsen, 1972). The negative allometry of running cost has been linked to the longer limbs of larger species, which reduce the step cycles and center of mass oscillations used to cover a given distance (Kram and Taylor, 1990; Pontzer, 2007, 2016). Notably, unlike walking, running, swimming and flying, the mass-specific cost of transport for vertical climbing is largely independent of body mass, which may reflect conservation across animals in the efficiency with which muscle converts metabolic energy to mechanical work (Hanna et al., 2008; Pontzer, 2016; Taylor et al., 1972).

Some studies have reported increased TEE with daily travel distance in wild populations (e.g. polar bears; Pagano and Williams, 2019). As discussed above, however, variation in daily physical activity is often not evident in measures of TEE. For example, among human populations, body size-adjusted TEE among highly active hunter-gatherer and horticulturalist populations is indistinguishable from that of more sedentary industrialized populations (Ebersole et al., 2008; Pontzer et al., 2012, 2018; Urlacher et al., 2019, 2021). Captive populations of primates and other mammals have similar TEE to those in the wild (Pontzer et al., 2014). The TEE of carnivores and herbivores scales similarly with body size (Nagy et al., 1999; Fig. 1), even though carnivores travel roughly 4 times farther (Garland, 1983). The lack of correspondence between TEE and daily physical activity underscores the importance of trade-offs, suggesting that animals compensate for changes in physical activity to maintain TEE within a narrow range (Pontzer, 2015, 2018).

### Trade-offs: maintenance, growth and reproduction

The cost of physical activity can be substantial, and evidence of trade-offs between activity energy expenditure and expenditure on other domains can be found across taxa (for reviews, see Pontzer and McGrosky, 2022; Pontzer et al., 2018). Even in the absence of high energy expenditure on activity or changes in physical activity patterns, trade-offs in energy allocation among body maintenance, growth and reproduction are apparent.

Verhulst and colleagues' work with zebra finches shows a negative correlation between maintenance energy expenditure (as measured by immune response) and clutch size (Verhulst et al., 2005), with birds reducing investment in somatic repair during periods of energetic stress (Wiersma and Verhulst, 2005). Trade-offs between clutch size and somatic maintenance or investment have also been observed in tits (Nur, 1984), gulls (Reid, 1987) and kestrels (Daan et al., 1996; Dijkstra et al., 1990).

Experimental induction of immune activity reveals trade-offs between immune system function and adult survival (e.g. Hanssen et al., 2004), breeding effort (e.g. Bonneaud et al., 2003), growth (Soler et al., 2003) and thermoregulation (e.g. Svensson et al., 1998) in eiders, sparrows, magpies and blue tits. Some work (e.g. Burness et al., 2010; Eraud et al., 2005; Nord et al., 2014), however, has questioned the idea that the energetic cost of mounting an immune response is sufficient to require energy reallocation. In one experiment, challenging the immune system of blue tits (*Cyanestes caeruleus*) did not reduce survival to the next breeding season, but instead seemed to encourage birds to accept a higher predation risk in order to conserve energy in cold temperatures (Nord et al., 2014). Further experiments in birds focused on more proximate mechanisms, suggesting that reduced body condition or within-body competition for shared resources (such as proteins) between the immune and other physiological systems may drive immunocompetence trade-offs in some species (Adamo et al., 2008; Burness et al., 2010; Eraud et al., 2005). In other cases, reducing energetic investment in immune function may be adaptive and thus the target of selection, rather than a trade-off. Increased immune reactivity and greater immunocompetence, such as that observed in females of many species, may have negative consequences, such as an increased propensity for developing autoimmune disease (Ngo et al., 2014; Zandman-Goddard et al., 2007).

Nonetheless, evidence of trade-offs between systems is found in mammals. Nursing red deer have higher mortality rates than age-matched females without offspring (Clutton-Brock et al., 1983), and changes in maternal foraging and offspring suckling suggest that food-restricted white-tailed deer does (*Odocoileus virginianus*) reduce investment in current offspring to divert limited resources towards their own survival and future reproduction (Therrien et al., 2008). Similar trade-offs between fitness and reproductive effort are evident in mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*), with adults prioritizing their own maintenance and survival and passing on the cost to their offspring (Festa-Bianchet et al., 1998; Festa-Bianchet et al., 2019; Martin and Festa-Bianchet, 2010). Although not a direct test of energetic trade-offs in growing offspring, experimentally increased litter sizes in red squirrels (*Tamiasciurus hudsonicus*) are associated with reduced juvenile growth rate and reduced offspring survival (Humphries and Boutin, 2000). Among primates, shorter inter-birth intervals in wild chimpanzees (*Pan troglodytes schweinfurthii*) are similarly associated with reduced juvenile growth (Emery Thompson et al., 2016). Humphries and Boutin's (2000) experiments did not detect evidence of maternal energetic trade-offs in red squirrels, as maternal survival was not affected by litter size manipulations, but, like Emery Thompson and colleagues' (2016) work on chimpanzees, they suggest constraints on parental investment under an energetic ceiling.

Trade-offs in energy allocation, however, are not always apparent, and animals may exhibit different trade-offs in energy management patterns depending on reproductive status (Tremblay et al., 2022; Welcker et al., 2013), developmental stage (Flack et al., 2020) or resource availability (Glazier, 1999; Lailvaux and Husak, 2017). Among wild baboons, trade-offs between reproduction and female survival were only evident when controlling for variation in age at first live birth, surviving interbirth interval, proportion of offspring surviving to weaning, and reproductive lifespan (McLean et al., 2019). These results underscore the effect of variations in phenotype, with different phenotypes either necessitating or freeing individuals from trade-offs in energy allocation and can be explained by 'quality' or 'big house, big car' hypotheses (e.g. Reznick et al., 2000; van Noordwijk and de Jong, 1986; see Box 3).

**Box 3. 'Big houses, big cars'**

'Quality' and 'big house, big car' hypotheses were first proposed to explain the apparent lack of reproductive 'costs' that would force trade-offs between aspects of life history (van Noordwijk and de Jong, 1986). Though each individual has a maximum energy budget, these individual budgets vary within a population; some individuals simply have larger budgets, providing them with more energy to allocate across domains when environmental resource availability is high (Reznick et al., 2000). As a result, 'big house, big car' hypotheses predict positive correlations between life-history traits mediated by overall access to resources and energy availability (e.g. Beauplet et al., 2006; Hamel et al., 2009; McLean et al., 2019; Olijnyk and Nelson, 2013; van Noordwijk and de Jong, 1986; Weladji et al., 2008). Under this framework, individuals with more energy available to them will exhibit positive correlation between, for example, number of offspring and maternal survival (e.g. Smith, 1981) without requiring the same trade-offs as individuals operating under a more constrained energy budget.

### TEE case study: Primates

The primate order is unique among mammals because its members have some of the longest lifespans and slowest rates of growth and reproduction (Charnov and Berrigan, 1993; Jones, 2011). As a result, patterns of variation between TEE and unique primate traits can help to shed light on the biological significance of variation in TEE. Primate BMRs scale similarly to those of other placentals (Pontzer et al., 2014). Primate TEE, however, is only about 50% of what would be expected for mammals of similar body mass (Fig. 1; Pontzer et al., 2014). This low energy expenditure may necessitate primates' slow pace of life, as the energy that can be allocated to the growth and reproductive events that define life history are governed by energy budgets (Pontzer et al., 2014). Indeed, primate reproductive output and growth rate are similar to those of other eutherians when modeled as a function of TEE (Pontzer et al., 2014). At lower taxonomic levels (e.g. when comparing between genera or species rather than between families), however, the absence of a strong correlation between TEE and the pace of life may be driven by evolved differences in energy allocation to different domains (e.g. reproduction, maintenance, activity; Pontzer et al., 2014). In other words, although overall TEE is not correlated with measures of growth and senescence across Primates, there may be differences in energy allocation to these different domains that are not captured by TEE.

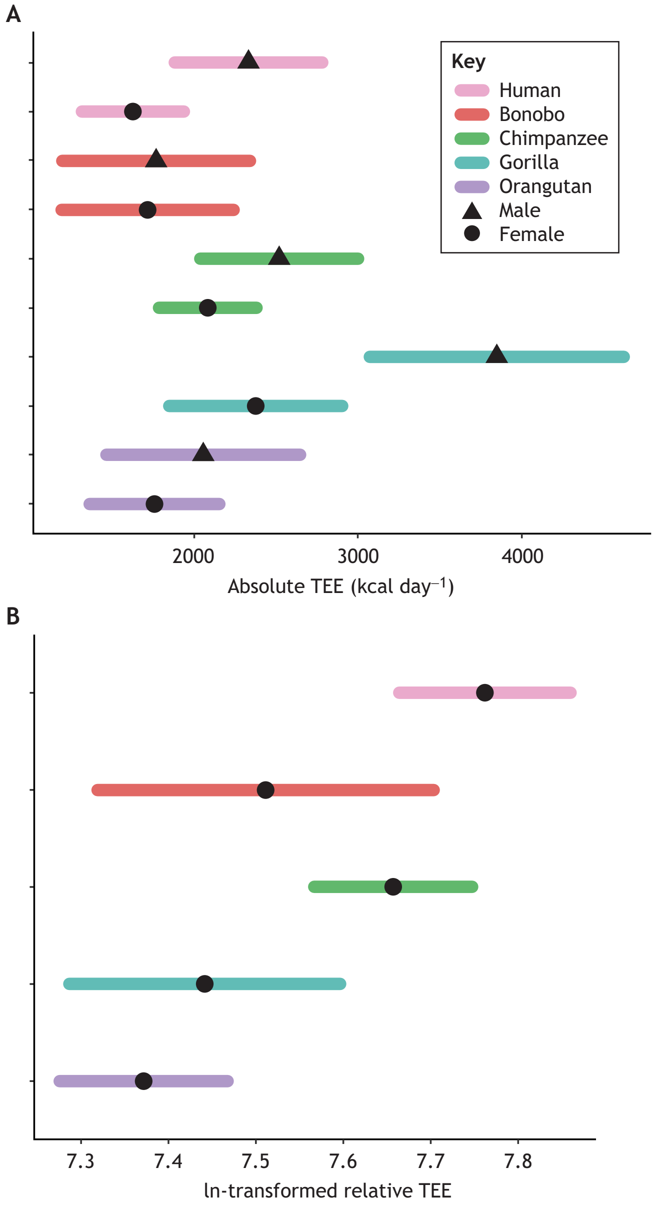

**Fig. 3. Energy expenditure across hominid primates.** Absolute (A) and relative (B) total energy expenditure (kcal day$^{-1}$) across hominoid primates. Relative TEE was estimated at 53 kg lean body mass using equations generated from this paper's dataset (bonobos, chimpanzees, gorillas and orangutans) or Pontzer et al. (2016) (humans). See Supplementary Materials and Methods and Table S1 for methodological details and non-human energy expenditure data.

### Box 4. TEE and human evolution

Human evolution is notable for the development of a hunting and gathering ecology reliant on hard-to-find, hard-to-forage foods, cognitively sophisticated foraging strategies and greater daily physical activity demands than are evident in other apes (Kraft et al., 2021). These ecological changes and their energetic demands appear to have led to metabolic evolution in the hominin lineage. Despite our slow pace of growth and development and long lifespans relative to other hominoids (and our low TEE compared with other mammals), humans do not have low lean mass-adjusted TEE relative to other hominoids (Pontzer et al., 2016; Fig. 3B). Instead, human TEE is greater than that of other hominoids in analyses accounting for body mass and fat percentage (Pontzer et al., 2016). Human BMR is also greater than that of other apes in analyses accounting for body mass, suggesting an evolved increase in mass-specific metabolic rate that is apparent in both basal and total energy expenditure (Pontzer et al., 2016).

Humans' increased metabolic rate relative to that of our closest living relatives (chimpanzees and bonobos) is likely to provide the energy required to fuel our large brain and reproductive output without requiring substantial trade-offs with other domains (Pontzer et al., 2016), while our cultural adaptations and larger fat reserves are likely to provide a buffer against energetic shortfalls (Navarrete et al., 2011). Though human populations do experience trade-offs between domains (e.g. body maintenance and growth or reproduction; Blackwell et al., 2010; Cramer et al., 1983; Dorman et al., 2001; Lee et al., 2019; McDade et al., 2008; Trumble et al., 2016; Urlacher et al., 2018; Zemel, 2017), at the species level, the long lifespans and high lifetime fertility potential of *Homo sapiens* (Bogin and Smith, 1996) makes it unlikely that we have reduced investment in maintenance or lifetime reproductive effort (Emery Thompson and Ellison, 2017) relative to other primate taxa.

Variation in TEE is largely determined by lean body mass, but key variations occur across the human life course (Pontzer et al., 2021). Fat-free mass- and fat mass-adjusted TEE peak for both males and females early in life (at around 1 year of age), before declining to relatively stable adult levels at around 20 years. Adult fat mass- and fat-free mass-adjusted TEE remain stable until approximately age 60, at which point they decline (Pontzer et al., 2021).

Primates' slow life history and low TEE may both reflect food availability regimes that predominated during primate evolution. Mammalian species that specialize in abundant and reliable foods typically exhibit a faster pace of life (Sibly and Brown, 2007), but many primates rely on fruits that can be seasonally unpredictable or scarce (Chapman et al., 1999). This can lead to energetic shortfalls (Dewar and Richard, 2007; Knott, 1998; Wright et al., 1999), so the reduced metabolic costs that accompany primates' slow pace of growth and reproduction may be adaptations to inherent irregularity in food resources or periods of food scarcity (Janson and van Schaik, 1993; Jones, 2011). Slow growth is hypothesized to be a way to mitigate starvation risk when competing for scarce resources (Janson and van Schaik, 1993). Consistent with this view, folivorous primates, which rely on a more regular food supply than primarily frugivorous species, tend to have accelerated life histories relative to those of closely related frugivorous taxa (e.g. Conklin-Brittain et al., 1998; van Noordwijk and van Schaik, 2005; Wich et al., 2007). Folivorous gorillas (*Gorilla* spp.), for example, experience accelerated growth rates and an extended early growth spurt compared with humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*) (Leigh, 2001). Comparisons between congeneric populations living in different environments (e.g. Breuer et al., 2008; Yamagiwa et al., 2012) further support the idea that physical maturation schedules are connected to different ecological conditions: although all gorilla populations largely rely on leaves, more frugivorous western gorilla (*G. gorilla gorilla*) populations wean later and undergo slower physical maturation than more folivorous mountain gorillas (*G. gorilla beringei*) (Breuer et al., 2008).

We find some support for an evolutionary link between foraging ecology, social structure and TEE within the hominoid clade (Fig. 3). Orangutans (*Pongo* spp.) exhibit the lowest lean mass-adjusted TEE of any hominoid (Fig. 3B), which may be an evolved strategy to reduce starvation risk in their low productivity, unpredictable southeast Asian forest environments (Hanya et al., 2011; Knott, 1998; van Noordwijk and van Schaik, 2005). Orangutans' highly arboreal and non-gregarious lifestyle may further facilitate their low TEE, as this combination of traits may contribute to low contagious disease transmission among

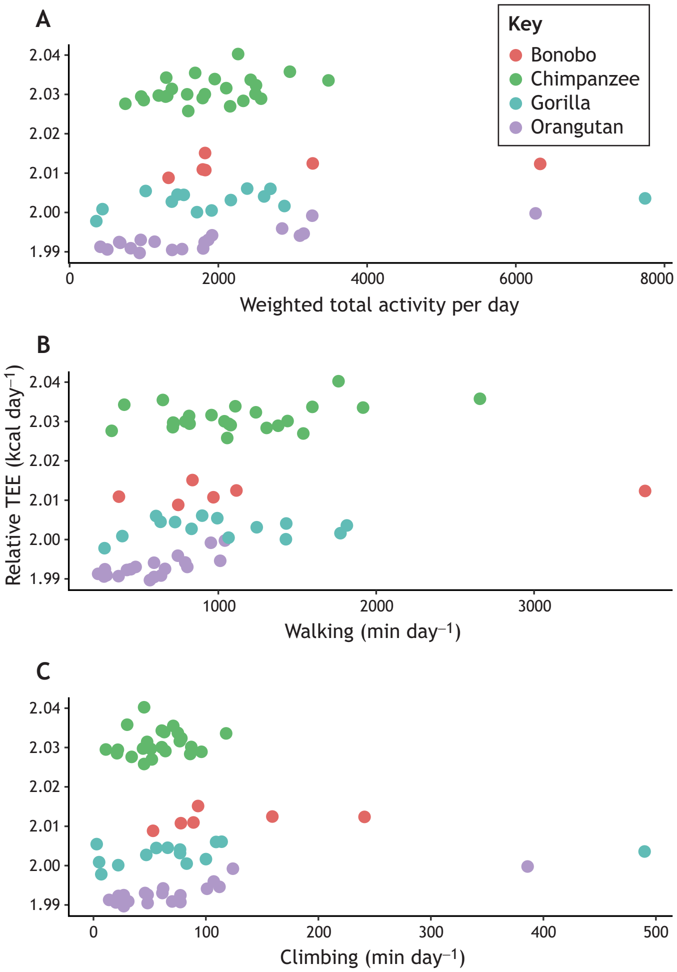

**Fig. 4. Relative TEE as a function of activity across hominoids.** The largest differences in relative TEE are those between taxa, but total daily activity (a weighted metric of time spent walking, climbing and traversing; A) and daily walking duration (B) are positively correlated with TEE when accounting for lean mass, fat mass and species using generalized linear models (total activity: *P*=0.017; walking activity: *P*=0.005). Active climbing duration (C) is not predictive of TEE (*P*=0.11). See Supplementary Materials and Methods and Table S1 for methodological details and data.

members of the taxon (van Noordwijk et al., 2018) and limit exposure to soil-dwelling parasites (Foitová et al., 2009). Although links between the potential for disease exposure, immune costs and TEE have not been explicitly tested in hominoids, and links between group size and parasite infection were not found in red colobus (*Piliocolobus rufomitratus*; Chapman et al., 2009), female primates with more sexual partners (and thus more encounters with males) have higher white blood cell counts (Nunn et al., 2000), and lymphocyte concentrations are higher in populations that are likely to be exposed to higher rates of environmental parasitism (Semple et al., 2002). Additional work is needed to test hypotheses that a lower risk of disease is linked to reduced immune response costs and thus lower TEE across primates.

TEE in other taxa, however, shows mixed support for links between energy budgets and foraging ecology. Among African hominoids, gorillas have lower TEE despite being mostly folivorous and having faster life histories than either chimpanzees or bonobos (*Pan paniscus*), which are both largely frugivorous (Leigh, 2001; Pontzer et al., 2016). Chimpanzees and bonobos also carry the least body fat of any hominoid (Pontzer et al., 2016; Zihlman and Bolter, 2015), which challenges the idea that irregularities in food supply, such as those experienced by frugivorous species, necessarily select for increases in adipose tissue energy stores (Simmen and Rasamimanana, 2018). More work is needed to test hypotheses linking foraging ecology and environmental pressures to TEE and physiological adaptations such as adiposity across primates (see Box 4 for a case study of the relationship between TEE, foraging ecology and adiposity in humans).

As noted above, habitual TEE in humans and other primates appears to be independent of habitual physical activity levels. Although TEE can (and does) increase over short time scales in response to sudden changes in physical activity, TEE is not correlated with physical activity levels in observational (Dugas et al., 2011; Ebersole et al., 2008; Pontzer et al., 2012, 2018) and exercise intervention (Riou et al., 2015; Thomas et al., 2012) studies. Observed TEE is also similar in captive versus wild primates (Pontzer et al., 2014). Interestingly, among a sample of captive hominoid primates, lean mass- and fat mass-adjusted TEE appears to be positively correlated with observed physical activity in some species (Fig. 4), but most differences in adjusted TEE fall along taxonomic lines. Additional TEE and experimental activity data in primates of different activity levels are needed to tease out the effects of higher activity levels on primate energy expenditure and to test whether taxa approach a metabolic ceiling beyond which energy expenditure is unsustainable.

## Future directions and conclusions

Energy is central to every aspect of organismal ecology and physiology, and TEE is a critical measure for a wide swath of research in experimental biology. Broad patterns of variation in TEE and its components have emerged over the past four decades, but the range of species with TEE measures remains relatively small, particularly in comparison to BMR. Expanding the taxonomic breadth of TEE measures would be beneficial to further test relationships between energy budgets, ecology and the selective pressures that shape energy throughput.

As the taxonomic breadth of TEE data in free-living individuals expands, additional hypotheses about the limits of energy expenditure across species and variation in physiological adaptations to different environments can be tested. Little is known, for example, about TEE in fish, amphibians or most invertebrates, for which high rates of water turnover and small body size make the DLW method difficult to employ. Other methods, such as accelerometry that has been calibrated against metabolic rates using respirometry (Lear et al., 2017; Wright et al., 2014), will be needed to explore TEE in these groups. It would be particularly interesting to explore whether energy budgets are constrained in these taxa in the same way that they appear to be in humans and other mammalian species.

Variation in TEE within species also remains poorly understood. For humans, which have the largest datasets for TEE of any species, the best statistical models incorporating body size and composition (i.e. lean and fat mass), age, sex and physical activity explain only ∼60–70% of the variance in TEE among adults (Pontzer et al., 2021). Investigations of the hormonal, genetic and epigenetic mechanisms that proximally drive interspecific and intraspecific variations in energy expenditure will shed light on the plasticity and flexibility of total energy budgets. Given that energy budgets are sensitive to temperature and food availability, advancing our understanding of animal energy budgets will become increasingly important as animals adjust to the changing and increasingly variable environments that accompany global climate change. As energy is the currency of life, future studies of energy expenditure will continue to inform our understanding of species' biological and evolutionary success.

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