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SYMPOSIUM

# Can Sex-Specific Metabolic Rates Provide Insight into Patterns of Metabolic Scaling?

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**Synopsis** Females and males can exhibit striking differences in body size, relative trait size, physiology, and behavior. As a consequence, the sexes can have very different rates of whole-body energy use, or converge on similar rates through different physiological mechanisms. Yet many studies that measure the relationship between metabolic rate and body size only pay attention to a single sex (more often males), or do not distinguish between sexes. We present four reasons why explicit attention to energy-use between the sexes can yield insight into the physiological mechanisms that shape broader patterns of metabolic scaling in nature. First, the sexes often differ considerably in their relative investment in reproduction, which shapes much of life-history and rates of energy use. Second, males and females share a majority of their genome but may experience different selective pressures. Sex-specific energy profiles can reveal how the energetic needs of individuals are met despite the challenge of within-species genetic constraints. Third, sexual selection often pushes growth and behavior to physiological extremes. Exaggerated sexually selected traits are often most prominent in one sex, can comprise up to 50% of body mass, and thus provide opportunities to uncover energetic constraints of trait growth and maintenance. Finally, sex-differences in behavior such as mating-displays, long-distance dispersal, and courtship can lead to drastically different energy allocation among the sexes; the physiology to support this behavior can shape patterns of metabolic scaling. The mechanisms underlying metabolic scaling in females, males, and hermaphroditic animals can provide opportunities to develop testable predictions that enhance our understanding of energetic scaling patterns in nature.

## Introduction

A mouse uses more energy per gram of tissue compared to an elephant (Kleiber 1932, 1947). The finding that larger animals often have a lower metabolic rate per gram of tissue compared to small ones is well documented, yet the reasons underlying this relationship remain an area of active debate (Brown et al. 2004; West and Brown 2005; Glazier 2014a;Harrison 2018; Pettersen et al. 2018; White et al. 2019; Harrison et al. 2022). A mouse and elephant do not just differ in mass, they also differ in their evolutionary history, ecology, and many other aspects of their physiology that also scale with body mass. These differences among species make it difficult to identify the potential causal mechanisms that shape patterns of metabolic scaling (Harrison 2018; Glazier 2022). However, both resting and active metabolic rates can vary considerably even within a single species (Glazier 2005, 2020). A lactating female mouse will consume 4 times as much food as a non-lactating one (Speakman 2008), and a male elephant will double its daily walking speed during the reproductive season, resulting in large increases in daily energy expenditure (Taylor et al. 2020). Animals invest a large proportion of energy in reproduction such as gamete production, mate-searching, sexual displays, ornament maintenance, and offspring care. Yet reproductive investment is not equally distributed among all individuals in a population, it is largely affected by an indi-

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vidual's sex. Many studies acknowledge the importance of the energetic cost of reproduction (Cox and Calsbeek 2010a; Lane et al. 2010; Arnqvist et al. 2017; Shankar et al. 2019; Moffet et al. 2022), yet sex-specific energetic costs are not quantified in most studies of metabolic scaling (but see Thonney et al. 1976; Grafe et al. 1992; Angilletta and Sears 2000; Lane et al. 2010). Our major objective is to highlight the ways that reproductive investment between the sexes shapes energy allocation. We aim to draw attention to the roles that evolutionary history, physiology, and selection play in shaping patterns of metabolic scaling in both males and females.

Different species typically cover a larger range of body sizes than any single species (Glazier 2010). However, different species also exhibit a larger range of lifestyles, have disparate evolutionary histories and inhabit a broader range of environments, thus it becomes difficult to understand the relative roles these variables play in shaping metabolic scaling patterns (Glazier 2005; Harrison 2018). We suspect that a major reason that studies have failed to measure sex-specific metabolic rates is that the scale of differences at intraspecific levels are often assumed to be too small to be affecting interspecific scaling patterns (Glazier 2006, 2020; Konarzewski and Książek 2012). However, studies have shown that ecological variation can lead to intraspecific metabolic rate (MR) variation, and that a quantitative genetic approach to within and across-species variation in MR is an essential tool for understanding the evolution of metabolic rates and scaling (Glazier et al. 2011; Careau and Glazier 2022). Intraspecific studies can therefore allow researchers to uncover physiological, genetic, and selective mechanisms that may play key roles in shaping patterns of metabolic scaling (Bolnick et al. 2011; Burton et al. 2011; Matoo et al. 2019; White et al. 2019).

Around ∼95% of animals are gonochoric (come in two separate sexes), and the differential investment in reproduction between the sexes often shapes much of life-history evolution (Stearns 1987; Speakman 2008; Aanen et al. 2016; Lemaître et al. 2020). Males and females differ in gamete size and often differ in body size, lifespan, ecology, growth rates, immunity, and many other physiological traits (Immonen et al. 2018; Hare and Simmons 2019; Xirocostas et al. 2020). These physiological, morphological, and behavioral differences are all implicated in contributing to whole-organism metabolic rates (Thonney et al. 1976; Garland and Else 1987; Glazier 2014b), yet many studies of metabolic scaling patterns typically focus on a single sex or do not explicitly account for sex-differences in metabolic rate (Niven and Scharlemann 2005; Chown et al. 2007; Genoud et al. 2018). For example, in a review of comparative analysis and databases for metabolic rates in mammals, Genoud *et al.* (2018) found (1) many papers on metabolic rates of mammals did not state if tested animals were male or female; (2) sex-specific metabolic rates were rarely given; and (3) the reproductive status of females was often disregarded. Here, we suggest *intersexual scaling*—the relationship between metabolic scaling and body mass between the sexes, provides opportunities to shed light on the causes and consequences of intraspecific scaling patterns.

We begin our discussion by outlining ways in which the sexes differ in their reproductive investments, often a key contributor to metabolic rates. Second, we consider how sex differences in metabolic rates are fundamentally shaped by a shared genome, and the reasons why this presents distinct opportunities for understanding variation in metabolic rates. Third, we discuss how energetic investments are shaped by sex differences in reproduction, which may manifest in sex-specific morphology, behavior, and life-history. We identify testable hypotheses and avenues for future research when examining sex-specific metabolic rates. We argue that the field of metabolic physiology has not adequately acknowledged nor fully capitalized on the opportunities that separate sexes provide in uncovering fundamental processes that shape energy-use in living organisms.

## Reproduction is energetically costly, but these costs are sex-dependent

> "The physiological costs of reproduction are probably the most significant component underlying life-history trade-offs".
> Speakman 2008

Energetic investment in reproduction underlies life-history theory and trade-offs in energy allocation (Stearns 1989). Females are defined by larger gametes and have more than an order of magnitude higher rates of gamete biomass production compared to males (Hayward and Gillooly 2011). Females in many species produce ovarian tissues, and maintaining this tissue and developing offspring can lead to higher mass-specific metabolic rates (Beuchat and Vleck 1990; Angilletta and Sears 2000; Finkler et al. 2014; Ducret et al. 2020), slower growth, and lower survival (Cox and Calsbeek 2010a, 2010b). In many birds, for example, the process of egg formation leads to an increase of ∼22% in metabolic rate (Nilsson and Råberg 2001; Vézina and Williams 2005). The costs of reproduction have been explored from multiple perspectives including hormonal regulation, allocation trade-offs, immune function, stress, and toxicity (Harshman and Zera 2007). The increase in metabolism required to fuel reproduction from pregnancy to offspring provisioning may lead to higher levels of oxidative stress, which can in turn increase cellular damage and rates of senescence (Zera and Harshman 2001; Thometz et al. 2016), but not always (Selman et al. 2012; Speakman and Garratt 2014).

Females in many species carry young for long periods of pregnancy (Avise et al. 2011), supply developing young with food (Nilsson and Råberg 2001; Heeb et al. 2003), and perform a majority of parental care (Martin et al. 2000). In some species, females are in a state of gravidity for a majority of their adult lives (Wellings et al. 1986). The high energetic investment toward offspring in females is often used as justification for why metabolic rate measurements in many species typically focus on males. Gestation and egg production are known to elevate metabolic rates to high levels, yet the qualifiers of basal metabolic rate—a non-reproductive, post-absorptive, individual in its thermal neutral zone—may be impossible to achieve in females for many species (Ricklefs et al. 1996). For example, swamp wallabies *Wallabia bicolor*, are in a state of continuous pregnancy and lactation, with one fetus initiating development as soon as one is weaned (Menzies et al. 2020). In this case, the body and physiology of this species is shaped around constant pregnancy, and a non-reproductive state may not be biologically relevant to understand selection on whole-body metabolic rate.

Domesticated rodents provide some of the clearest examples of the energetic demands of reproduction. Lactating mice will more than quadruple food intake when lactating (Speakman 2008). To accommodate milk production, females will increase the size of their digestive tract, liver, and pancreas. Thus, increases in metabolic rate during reproduction may result in part from this remodeling of internal architecture (Speakman 2008). The consequences of lactation in female mammals can be extreme; for instance, female elephant seals, *Mirounga angustirostris*, lose over 40% of their body mass during lactation while provisioning a single pup (Costa et al. 1986), and the energetic demands of pup rearing can be a major contributor to female mortality in sea otters, *Enhydra lutris* (Thometz et al. 2016).

Males in many species bear sexually selected morphological traits such as weapons to compete with rivals over mating opportunities (Emlen 2008), or ornaments used to attract individuals of the opposite sex (Dale et al. 2015; Mccullough et al. 2016). Competition among males can also drive the evolution of post-copulatory traits, which can be highly metabolically costly. Examples include nuptial gifts (Prokop and Okrouhlík 2021), seminal fluid (Dhole and Servedio 2014), and sperm cells (Lüpold et al. 2016). Males of the gift-giving spider, *Pisaura mirabilis*, for example, increase metabolic rates by approximately 37% while holding a nuptial gift (Prokop and Okrouhlík 2021). Spermatophores presented by male bush crickets (Tettigonidae) can account for 20% of male body mass (Wedell 1993), and are used as a metabolic fuel for females (Voigt et al. 2008). Males who produce exaggerated weaponry and post-copulatory traits can also suffer from reduced survival and early reproductive senescence (Van den Beuken et al. 2019). Increased investment in ornaments has been linked to compromised immune function in birds such as barn swallows, *Hirundo rustica* (Saino and Møller 1996) and red jungle fowl, *Gallus gallus* (Ligon et al. 1990). In semelparous Sockeye salmon, *Oncorhynchus nerka*, the estimated cost of reproduction in males was estimated to be around 66% to fuel secondary sexual traits, while the reproductive energetic cost to females was estimated to be around 74% (Hendry and Berg 1999).

In some taxa, reproductive activities that typically evolve in females such as pregnancy are also found in males. These species provide unique opportunities to investigate the conditions that lead to a different type of partitioning of the energetic costs of reproduction (Berglund 2005). For example, in seahorses and pipefish, males internally fertilize their young and have a period of pregnancy (Wilson et al. 2001). Biparental care is found in many fish (Coleman and Jones 2011), and bird species (Safari and Goymann 2021). In an elegant study with sex-changing fish, researchers generated hermaphrodite and male pairs with identical genotypes (Garcia et al. 2016). The study found hermaphrodites invested more energy in gonadal tissue and had relatively higher metabolic rates compared to males, while males invested more in somatic growth. Studies such as these provide exceptional opportunities to examine metabolic shifts not just between species and individuals, but across a range of diverse mating types and within the same individual over time (Aanen et al. 2016).

## Males and females share a genome, which may constrain sex-specific metabolic rates

Studies of intraspecific metabolic scaling typically focus on two types of scaling relationships, the scaling of metabolic rate during growth (ontogenic scaling), or among adults within a population (static scaling). Intraspecific metabolic scaling patterns among the sexes is underappreciated. Both sexes belong to a shared gene pool, which leads to constraints that are absent in interspecific comparisons. Metabolic rate is subject to these within-species constraints (White et al. 2019). This is especially the case because metabolic rates are influenced by multiple genes (i.e., highly polygenic). For example, genetic recombination between generations may prevent the fixation of beneficial combinations of genes which may result in non-optimal and more-shallow scaling relationships with metabolic rate. Recent studies have drawn attention to this quantitative genetics perspective on the scaling of metabolic rate (Careau and Glazier 2022). Here we bring attention to another aspect of the shared genome, intralocus sexual conflict, which should be considered in the study of sex-specific metabolic rates.

Intra-locus sexual conflict (IASC) arises when selection pressures for a trait in one sex displaces the other sex from their phenotypic optima (Pennell and Morrow 2013). Males and females can differ in a number of life history aspects: the production of gametes, parental care, mate attraction, courtship, or direct competition for reproductive resources (Garlovsky et al. 2022). These differences can favor divergent metabolic rates between sexes, resulting in a genetic "tug-of-war." Critically, if selection is particularly strong in one sex, it can favor genes that shift metabolic rate to a non-adaptive level when expressed in the opposite sex. Intralocus sexual conflict is a direct result of a shared genome between the sexes. An important implication is that when there is strongly divergent selection between sexually dimorphic traits, neither sex may express their optimal phenotype. IASC can be cryptic and difficult to study, but can be measured by comparing the fitness of parents and their offspring of the opposite sex. If metabolic rates differ between sexes in a species, one strategy could be to measure the fitness of individuals with extreme metabolic rates, and compare the fitness of their offspring of the opposite sex. For example, females may have overall higher metabolic rates than males. Under the effects of IASC, we should expect to see that females with the highest metabolic rates have male offspring with higher metabolic rates but lower fitness than the male offspring of average or lower metabolic rate mothers.

In addition to considering the effects of metabolic rate in isolation, IASC may also affect population-wide scaling relationships with body mass. To our knowledge there has been little consideration as to how selection on the scaling of one sex could affect the relationship in the opposite sex (Boratyński and Koteja 2010; Boratyński et al. 2010; Videlier et al. 2019, 2021). How does the relative fitness of individuals with extreme metabolic rates for their body size relate to fitness of their female versus male offspring? How does selection on metabolic slope of one sex affect the slope of the opposite sex? Lab-based selection regimes that artificially select for more extreme metabolic slopes in a single sex while observing the fitness effects in the opposite sex may be a powerful way to study these types of questions. For example, a recent study found a positive correlation between standard metabolic rate and daily locomotion in male *Drosophila melanogaster*, suggesting pleiotropic effects of selection on locomotion to metabolic rate. However, because genetic variation was mostly shared between males and females, this sets the stage for intralocus conflict (Videlier et al. 2021).

IASC is just one example of how the comparison of metabolic rates across sexes must be treated differently than those across species. The fundamental nature of a shared gene pool creates unique considerations and challenges to understanding the evolution of metabolic rates. Ultimately, taxon-wide patterns of metabolic rate originate with natural selection on individuals. Elucidating the evolution of metabolic rates therefore requires deep consideration of how genetic architecture constrains and facilitates this complex trait.

## Exaggerated sexually selected traits provide a window into intraspecies energy allocation

Sexual selection is a type of social selection where trait evolution is shaped not only by the abiotic environment but also by competition with conspecifics for mating opportunities. This competition not only pushes different traits beyond shared optima, but sometimes to physiological extremes (Emlen 2008). For example, the claws of male fiddler crabs (Allen and Levinton 2007), the jaws of male harvestmen (Painting et al. 2015), or the elongated heads of male giraffe weevils (Somjee et al. 2021) are used in competition for mates; these weapons can account for up to 50% of total body mass in some species (Figs. 1 and 2). These enlarged traits are often not present in females and suggest extreme sex differences in energy allocation to growth and maintenance (Allen and Levinton 2007; Tullis and Straube 2017; Dinh 2022). Large sexually selected weapons are known to contribute to resting metabolic rate in some species (Basolo and Alcaraz 2003; Bywater et al. 2014; Somjee et al. 2018), while these costs are not detectable in other species (Fig. 3; Askew 2014; Thavarajah et al. 2016; Somjee 2021; Somjee et al. 2021). Traits that account for this large proportion of body mass have consequences for metabolic machinery used in locomotion (Basolo and Alcaraz 2003; Bywater et al. 2018; Martin 2019), may limit feeding abilities (Valiela et al. 1974), increase behavioral costs of maintenance such as cleaning (McCullough et al. 2020), and affect thermoregulation (Darnell and Munguia 2011). Thus, examining how these structures contribute to metabolic energy expenditure (Somjee et al. 2021; Dinh 2022), or the physiological mechanisms and adaptations that different species have used to reduce or compensate for energetic costs (Balmford et al. 1994; Thavarajah et al. 2016), provide

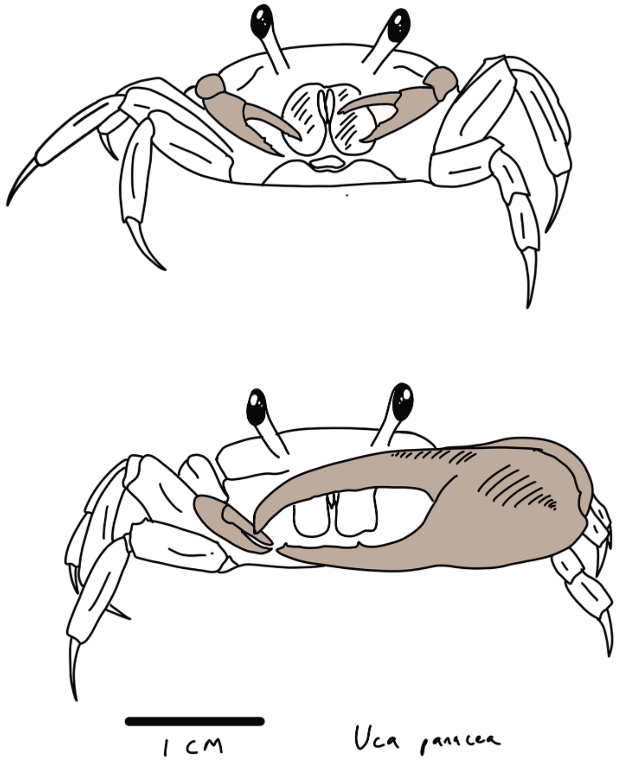

**Fig. 1** A fiddler crab, *Uca panacea*, female (top) and male (bottom) with claws highlighted. Sexually dimorphic traits can shape whole-organism physiology and energetics. Fiddler crabs provide an example of an extreme sexually selected trait. Males invest in enlarged claws that are used as signals to attract females (Perez and Backwell 2019), and as weapons used in male-male competition for mating opportunities (Dennenmoser and Christy 2013). These claws can account for up to 50% of body mass, contribute to metabolic rates (Bywater et al. 2014), incur behaviorally costly cleaning (McCullough et al. 2020), require enlarged legs to support their mass (Bywater et al. 2018) and likely affect temperature regulation (Darnell et al. 2015). Many animals have sexually dimorphic traits, and extreme traits such as the fiddler crab claw provide avenues to understand the mechanisms underlying the production and maintenance of these structures (Somjee 2021).

opportunities to understand the mechanisms underlying metabolic scaling (Somjee 2021).

Growth can comprise 30–50% of daily energy needs and the energetic cost of growth can differ considerably between the sexes (Rennie et al. 2008; Tidière et al. 2020). However, both the growth rates and the energetic requirements of growth often vary by sex (Teather and Weatherhead 1988). Sexual selection can drive the evolution of extreme growth in specific traits (Emlen 2008). The growth of antlers in cervids occurs annually during a relatively short period, leading to one of the fastest growing structures in all vertebrates (Moen et al. 1999; Price et al. 2005). For example, male elk, among the largest of the cervids, cannot get sufficient minerals from their environment to grow their antlers. To fuel antler growth, calcium and phosphorus are leeched from the skeleton and deposited into these structures every year (Moen et al. 1999). In all species of cervids (with one exception), these annual antler-growth costs are borne exclusively in males (Lemaître et al. 2014). Female cervids, on the other hand, bear the cost of producing and caring for offspring which likely impose very different selection pressures on their energetic allocation compared to males (Loe et al. 2019). However, relatively few studies have quantified the energetic costs of sexually selected trait growth and maintenance from an energetics perspective (Hendry and Berg 1999; Bywater et al. 2018; Somjee et al. 2018; Ducret et al. 2020), providing an opportunity for future studies.

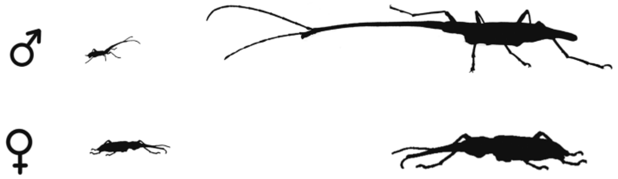

**Fig. 2** Males of the New Zealand giraffe weevil, *Lasiorhynchus barbicornis*, have an extreme range of sizes. The largest males are over 30 times heavier than the smallest males, which is the largest documented adult size range in any beetle species (Somjee et al. 2021). Sexual selection drives the evolution of extreme differences in body size within non-growing adults of a single species, providing opportunities to examine how individuals of the same species respond to size-specific challenges. In this case, males bear disproportionately large sexually selected weapons used in competition for mating opportunities, while females do not bear these large weapons. The morphological differences in males and females of this species are so extreme that they were initially identified as separate species. However, despite extreme differences in body shape and relative trait investment, both males and females have similar hypometric scaling of metabolic rate with body size (Somjee et al. 2021).

## Sex-specific behavior alters metabolic rates

The scaling of metabolic rate with mass is dependent on activity (Glazier 2005, 2008). For instance, metabolic rates are expected to scale with mass with a slope close to 0.67 when driven by surface area related processes (e.g., heat loss or water flux), while volume related processes (e.g., activity and torpor) generate slopes closer to one (Glazier 2005; metabolic levels boundary hypothesis). Males and females often differ markedly in their activity level leading to potential differences in the scaling of metabolic rate with body size. Examples include acoustic calling in male insects, frogs, and birds where metabolic rates can be an order of magnitude above resting (Ryan 1988; Kotiaho et al. 1998; Gillooly and Ophir 2010; Stoddard and Salazar 2011), and visual mating displays in male birds (Barske et al. 2013; Ligon et al. 2018). The sexes also often differ in body composition and daily activity patterns, which are im-

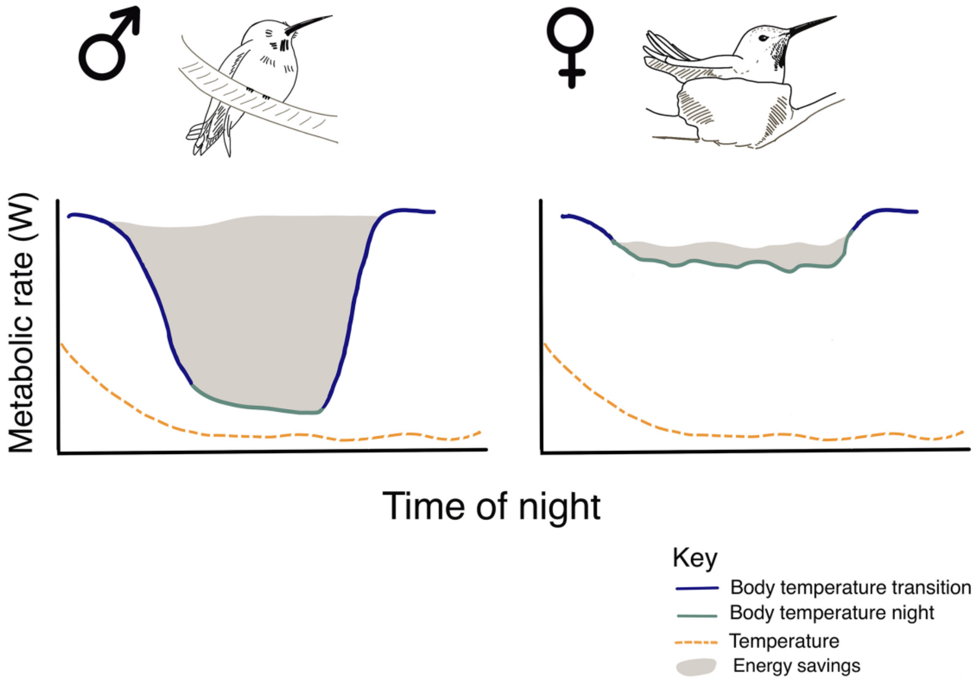

**Fig. 3** In hummingbirds, females take on all the parental care. This involves foraging, thermoregulatory costs, nestbuilding costs and potentially increased chances of predation because nesting birds may be easier targets. Females also tend to avoid using torpor at night while they are in the nest (Vleck 1981; Calder 1971, Smith et al. 1974, Eberts et al. unpublished). In contrast, male hummingbirds perform most of the mating displays, often invest in colorful or elaborate plumage, and often expend energy and time to maintain territories that females do not. Though it has not been explicitly studied, the contribution of all these costs to daily energy expenditure might be similar for both sexes even though the mechanisms by which those costs arise can be drastically different.

plicated in shaping metabolic scaling with body size. Males in many species have higher investment in locomotion or mobility which often results in selection for reduced body size (Rivas and Burghardt 2001) and increased investment in appendages and locomotor muscles (Murphy 2007; Kelly et al. 2008).

Males may also be selected for relatively larger body sizes or muscles used in male-male competition and sexual signaling. Examples include the extreme large body sizes of male elephant seals relative to females, *M. angustirostris* (Le Boeuf 1974), the sexually dimorphic muscles of golden-collared manikins, *Manacus vitellinus,* used for "wing-snapping" displays (Barske et al. 2013; Shogren et al. 2022), the hypertrophied muscles in the arms of male gorillas, *Gorilla gorilla* (Zihlman et al. 2011), and large flight muscles of male eastern kingbirds, *Tyrannus tyrannus,* used in aerobatic flight displays (Murphy 2007). Sex differences in energy use between males and females have been found in sexually dimorphic fish (Rennie et al. 2008; Methling et al. 2020), and sexual selection likely drives dimorphism and the scaling of resting metabolic rates in different populations of Anolis lizards (Curlis et al. 2021). Sex-specific covariances have been found between morphology, behavior, and metabolic rate in Carabid ground beetles (Yarwood et al. 2021).

Sex differences in the scaling of metabolic rates have reported in salamanders (Ryan and Hopkins 2000), moths (Strauss and Reinhold 2010), humans (Sandboge et al. 2012; Jagim et al. 2018), and birds (Schmidt et al. 2012; Stuber et al. 2015). In the sexually dimorphic fish, *Gambusia affinis,* virgin females and males had similar scaling coefficients of routine metabolic rates with body size, while pregnant females had a steeper scaling coefficient. The authors used a model to reveal that sex-specific differences in metabolic scaling can result in reduced population-level energy demand under realistic population sex-ratio scenarios (Moffet et al. 2022). In many cases, males and females differ in mass, activity or morphology and yet converge on similar scaling of metabolic rate (Tomlinson and Menz 2015; Somjee et al. 2021). An open question to explore in future studies is to what extent males and females of the same species are constrained to similar metabolic scaling patterns because of their largely shared genome and physiology.

The differences in activity levels suggest that the scaling of metabolic rate may differ considerably between males and females (Videlier et al. 2019). For example, if females were to spend the majority of their daily energy on thermoregulation and digestion, the metabolic levels boundary hypothesis would predict allometric slopes would be closer to 0.67, while if the males were to spend most of their daily energy on flying and on mating displays, their allometric slope would be closer to 1. A promising avenue to examine this prediction is in small mammals and birds, where females cannot exploit the energy saving of torpor because of embryo development and brooding (Speakman 2008; Fig. 2), and as a result, daily energetic costs of thermoregulation can be very different among the sexes (Vleck 1981; Shankar et al. 2019). While energetically costly activity has been implicated as a factor shaping resting metabolic rates (Reinhold 1999; Glazier 2009; Mathot and Dingemanse 2015), the role that the differences in activity between the sexes plays in shaping metabolic rates has received little attention.

## Conclusions and suggestions for future research

Investment in reproduction is a major contributor to an organism's rate of energy expenditure. However, relatively little attention has been paid to the role sex-specific mechanisms play in shaping scaling patterns of metabolic rate. We have suggested four avenues for future research that will deepen our understanding of the processes that shape the diversity of metabolic scaling patterns both within and across species.

(1) Males and females often experience very different energetic costs as a consequence of different investments in reproduction. We suggest studies that explicitly examine males and female energetic investment to reproduction, with time- and activity-corrected estimates of energetic investment. Using energy as a currency for reproductive investment may allow us to uncover general physiological mechanisms that shape metabolic scaling relationships.
(2) Males and females share a genome yet can have different adaptive optima for mass-specific metabolic rates. Thus, the specific selection pressures that act on the sexes may constrain energetically costly behavior or physiology in one or both sexes. Artificial selection experiments on metabolic rates in males and females would be valuable to uncover how a shared genome may shape or constrain the scaling of metabolic rates.
(3) The sexes often face different ecological challenges, both biotic (e.g., predation and parasitism) and abiotic (e.g., temperature and food limitation). Identifying these sex-specific adaptations to different challenges can help us develop a deeper mechanistic understanding of how energetic processes may shape sex-specific life-history evolution (Glazier 2022).
(4) In many species males and females differ in body size, relative trait size, and behavior. Measuring the scaling of sex specific metabolic rates may be especially important because levels of sexual dimorphism increase with increasing body size in many taxa (Rensches rule), but many studies average metabolic rates in a species. Sex differences in metabolic scaling, body composition, and energy budgets may allow us to better understand systematic differences in body-size and selective pressures that shape energy allocation.

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## Conflicts of interest

The authors do not have conflicts of interest to declare.

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