Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

Woman the Hunter: The Physiological Evidence

Cara Ocobock[1,2] and Sarah Lacy[3]

[1]University of Notre Dame Department of Anthropology, University of Notre Dame Department of Gender Studies, Notre Dame, IN
[2]Eck Institute for Global Health, Institute for Educational Initiatives, University of Notre Dame, Notre Dame, IN
[3] University of Delaware, Department of Anthropology, Newark, DE

Land Acknowledgment

The University of Notre Dame is on the traditional territory of the Haudenosauneega, Miami, Peoria, all of the Bodéwadmik Potawatomi peoples, and particularly the Pokégnek Bodéwadmik/Pokagon Potawatomi.

The University of Delaware occupies lands vital to the web of life for the Lenni Lenape and Nanticoke, who share their ancestry, history, and future in this region.

Running Head: Physiological support for female hunters

Abstract

Myths of "Man the Hunter" and male biological superiority persist in interpretations and reconstructions of human evolution. Although there are uncontroversial average biological differences between females and males, the potential physiological advantages females may possess are less well-known and less well-studied. Here we review and present emerging physiological evidence that females may be better metabolically suited for endurance activities such as running, which could have profound implications for understanding subsistence capabilities and patterns in the past. We discuss the role of estrogen and adiponectin as respective key modulators of glucose and fat metabolism, both of which are critical fuels during long endurance activities. We also discuss how differences in overall body composition, muscle fiber composition, the metabolic cost of load carrying, and self-pacing may provide females with increased endurance capacities. Highlighting these potential advantages provides a physiological framework that compliments existing archaeological (Lacy and Ocobock, this issue) and cultural work reassessing female endurance and hunting capabilities as well as the sexual division of labor. Such a holistic approach is critical to amending our current understanding of hu(wo)man evolution.

INTRODUCTION

"*Popular pictures drawn of the past are too often little more than backward projections of [modern] cultural sex stereotypes onto humans who lived more than a million years ago,*" (Zihlman, 1981, pg. 76). Ideas about the roles female hominins played in our evolutionary past

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

have been based on stereotypes and misconceptions of female physical and intellectual capabilities. Female animals depicted as mere beneficiaries of evolution acting upon males can be traced to Darwin's *Descent of Man*, in which Victorian-era views of human females as passive and submissive were extended to all species (Darwin, 1871). It is not only modern feminists and Marion Petrie who critique his portrait of female passivity; Darwin's supposition faced pushback from his feminist contemporaries such as Antoinette Brown Blackwell and Eliza Burt Gamble (Deutscher, 2004). Despite their criticism, this sexist view seeped into reconstructions of human evolution that would myopically focus on hunting and persist for well over 150 years. Ideas revolving around the importance of hunting and who performed this task were formalized in the 1968 edited volume *Man the Hunter*, based on a 1966 symposium of the same name (Lee and DeVore, 1968). This edited volume presented the idea of a deep sexual division of labor rooted in sex-based (and biased) biological differences. It paints males as dominant and prominent: "Man's life as a hunter supplied all the other ingredients for achieving civilization: the genetic variability, the inventiveness, the systems of vocal communication, the coordination of social life" (Laughlin, 1968, 320). With this quote, it is easy to see exactly what Zihlman was critiquing.

Male hominins were depicted as hunters and providers with the evolution acting upon them as the reason for our uniquely human features. Females were relegated to mothering and gathering—and even more, this was biologically determined:

> Data from the Ainu and other food gatherers imply the possibility of an interpretation of the process of the allocation of hunting to males in the following way: 1) long and active pursuit of larger mammals brought about the differentiation of the activity field into the collecting and hunting fields; 2) the necessity of synchronous exploitation of these spatially separated fields forced the group to split; 3) this splitting and the selection for hunting ability on the basis of physical and psychological differences resulted in the

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

> allocation of hunting to males and collecting to females. (Watanabe, 1968, 74)

> Equally to the point is the lack of challenge or psychological stimulation involved in plant eating. Plants do not run away nor do they turn and attack. They can be approached at any time from any direction, and they do not need to be trapped, speared, clubbed, or pursued on foot until they are exhausted. (Laughlin, 1968, 318)

Implied here is that females did not have the aptitude to hunt or make the necessary hunting implements and were therefore better suited for collecting intellectually unchallenging foods. Furthermore, it was thought that pregnancy, lactation, and childcare would have prevented females from taking part in hunting:

> Most writers agree that hunting is incompatible with pregnancy, carrying infants, and child care, although they are not always agreed as to whether it is the actual physical exertion which hunting demands, the danger it involves, or the long distance travel it engenders, which is most critical to this incompatibility. (Quinn, 1977, 187)

This thinking has not only shaped our reconstructions of the past and become widely accepted as canon within our field, but it has also shaped the direction of current and future work, including who conducts and participates in that research.

These assumptions and stereotypes were challenged by a wave of feminist anthropology kicked off by Reiter's (1975) edited volume *Toward an Anthropology of Women*. This book takes a largely cultural approach to women and discusses the origins of gender inequality, gender identity, and male bias within anthropology, and covers a global array of ethnographies. Notable was the chapter penned by Sally Slocum (1975), "Woman the Gatherer: Male Bias in Anthropology." Slocum criticizes *Man the Hunter* on theoretical grounds, stating, "A theory that leaves out half the human species is unbalanced. The theory of Man the Hunter is not only unbalanced; it leads to the conclusion that the basic human adaptation was the desire of males to

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

hunt and kill" (39). Slocum also contends that human evolution is particularly rife with bias because the data is so scant—with such limited data, it is easy to make data fit the just-so stories rather than more objectively developing hypotheses based on data.

Woman the Gatherer, edited by Frances Dahlberg (1981), highlighted the critical importance of food gathering to human success. This book detailed the high degree of populational variation in sexual division of labor based on ethnographic work among contemporary gatherer-hunters. Throughout this volume, authors contend, and rightly so, that females who gathered food provided the majority of the sustenance among modern and past gatherer-hunter populations.

A primary critique of early feminist anthropological works is the heavy focus on gathering, rather than suggesting females were capable of and did partake in hunting. This has been referred to as a mere repackaging of *Man the Hunter* that perpetuates a deep sexual division of labor rooted in supposed male superiority (Hrdy, 1981). Since hunting as part of the female activity repertoire was not fully incorporated within this edited volume, with the exception of the chapter on the Agta (Estioko-Griffin and Griffin, 1981), we were still left with reconstructions that perpetuate the idea that females were not physically or intellectually suited for hunting. Sarah Hrdy's (1981) *The Woman That Never Evolved*, however, did take direct aim at the stereotype of female passivity and inferiority with substantial evidence from the dizzying array of nonhuman primates. Hrdy lays bare that there is a great deal of diversity in social structure and dominance hierarchies among primates, and it is wrong to assume that because society today is largely patriarchal that our evolutionary past was too.

These feminist works are foundational, and we owe our careers to these trailblazing academics. Their courage, clarity of thought, and reinterpretation of the past set the stage for rethinking our evolutionary origins. Fortunately, feminist anthropology did not stop in the 1980s, and there is now a breadth of work focusing on the role of females in human evolution (Fisher, Garcia, and Chang, 2013; L. Hager, 1997; Hawkes, 2003; Hrdy, 2009; Mattison and Quinlan, 2019; Sear, 2021). However, much of this work relies more on ethnography than biology (notable exceptions include, e.g., Fausto-Sterling, 2012; Tang-Martínez, 2020), which as a field largely still relegates hunting to males and gathering to females, perpetuating supposedly innate sex-based differences.

Even recent work examining hunting and persistence hunting continues to develop behavioral reconstructions where females are noticeably absent (see Lieberman and Bramble, 2007; Lombardo and Deaner, 2018; Pickering and Bunn, 2007; Pontzer and Wood, 2022). Baked into these reconstructions is the assumption that males are physically superior to females, and that in addition to physical inferiority, pregnancy and childrearing reduce or eliminate a female's ability to meaningfully contribute to hunting. For example, Lombardo and Deaner (2018) contend that the ability to throw projectiles to ward off predators and eventually hunt prey was a pivotal moment in our evolutionary past and one relegated only to males. They use modern data to demonstrate males have greater throwing speed, distance, and accuracy relative to females; yet, they completely discount the potential for socialization and earlier throwing training among modern males (Fredrickson and Harrison, 2005) and do not mention how hunting-tool technologies such as the atlatl provide a mechanical advantage that can overcome a potential lack of physical strength.

Authors advocating for the value of persistence hunting, with current documented chasing distances of ~17–33 km (Liebenberg, 2006), should consider females in their reconstructions. Where endurance and distance, not speed, are the important factors in hunting, females should not only be included but should, perhaps, be the focus. Speechly and colleagues (1996) found females and males performed similarly during 42 km events, but females outperformed males in running events greater than 90 km. Females were able to maintain a higher running speed throughout and to perform at a higher percentage of their maximal oxygen capacity relative to males (Speechly, Taylor, and Rogers, 1996). Similarly, Bam and colleagues (1997) built a model suggesting females will consistently outperform males in events 65 km or longer. These endurance capabilities could have been hugely beneficial for not only hunting but also bringing kills back to a central location. However, for example, Bramble and Lieberman's (2004) introduction to the persistence hunting hypothesis never mentions sex, so it is not clear whether values given related to human endurance running are averages of both sexes or exclusively male. They describe the *Homo* form in contrast to *Australopithecus* in what could be interpreted to be male or masculine terms, e.g., "tall, narrow body form," "low, wide shoulders," "narrow pelvis" (348) along with masculine figures, as if it were obvious that the endurance runners of human evolution were male, and it need not be explicitly stated. A discussion of sex and female endurance capabilities would actually further their argument if it were acknowledged and included rather than defaulting to males alone.

While there are real, uncontroversial mean biological differences between females and males, the differences that give females an advantage are not only regularly ignored but also understudied. Because of this, science poorly understands female athletic capabilities in terms of strength, endurance, and fatigue. Until this uneven understanding is rectified, our reconstructions of past sexual divisions of labor will be biased and limit the likely broad repertoire of activities females participated in during our evolutionary past.

Our goal here is to present some of the physiological evidence that suggests females are just as, if not more, capable as males at performing arduous physical tasks. Our discussion will focus

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

on the potential athletic-performance-enhancing roles of typical female-associated anatomy, estrogen, adiponectin, recovery, and fatigue. These features, along with greater performance-based research among females, need to be considered if we are to more accurately and inclusively reconstruct our evolutionary past.

SEX, GENDER, AND REPRESENTATION

We believe it is critical to directly address sex, gender, and representation within the realm of exercise physiology research. Sex, like gender, is not a strict binary, and the more work that is done in this area, the more beautifully complicated the picture of biological sex becomes when one takes into account the variety of ways it can be defined: genetics, hormones, gonads, gametes, and secondary sexual characteristics (DuBois and Shattuck-Heidorn, 2021).

Much of our article relies on work conducted within the fields of exercise physiology and sports medicine. Research in these areas tends to rely on a sex binary using female and male descriptors. Therefore, we are constrained in how we can refer to the sex spectrum within this article, and we will use the terms “female” and “male” in order to best represent the research we review. It is also critical to recognize that when making these arguments, we often have to rely on a comparison of the means, which, unfortunately, reinforces the idea of a strict binary. For example, females tend to have higher levels of estrogen and proportionately and absolutely wider hips than males, but these do vary (Dunsworth, 2020). Each of the characteristics discussed here exists on a spectrum with a great deal of interindividual and populational variation. So, while, yes, on average there tend to be differences between females and males, there is overlap for each and every metric, and sometimes considerable overlap. Furthermore, there is more variation within sexes than between (Blackless et al., 2000; Pound and Price, 2013).

Females are woefully underrepresented in exercise physiology and sports medicine studies. A recent study revealed that across sport and exercise science research, only 34% of study participants were female (Cowley et al., 2021), while only 14% of participants in nutritional-supplement research were female (Smith et al., 2022). When one looks in greater detail at the kinds of research conducted, it was found that in studies on athletic performance, only 3% of publications had a female-only participant pool, compared to 63% that were male-only (Brookshire, 2016). This means we know relatively little about female performance, training, nutrition, recovery, and supplementation—and much less about what happens during pregnancy or throughout the menstrual cycle. When research eventually catches up to better represent humanity, this article will likely need heavy revision, which we will welcome.

MUSCULOSKELETAL DIFFERENCES

Anatomical sex-based differences are often used to rationalize deep sexual divisions of labor and implicit male superiority. However, research has largely focused on features that give males an advantage—for example, the typically greater fat-free mass, larger heart, and larger lungs among males—while potential female advantages are ignored. In this section, we will address some of the anatomical differences that may confer an advantage, particularly an endurance advantage, to females.

A typical focus is on pelvic sexual dimorphism and its impact on labor and delivery (Rosenberg and Trevathan, 2002), locomotor biomechanics (Wall-Scheffler and Myers, 2017; Warrener et al., 2015), and the push and pull of these two forces shaping our bipedal locomotion (cf. Dunsworth et al., 2012). The wider female pelvis is associated with the need to carry and birth a highly encephalized fetus, and it has long been thought that this compromised wider pelvis put females at a biomechanical disadvantage resulting in less-efficient bipedal locomotion

(Rosenberg and Trevathan, 2002). However, work using a dynamic rather than static analysis of hip biomechanics and locomotor energetics demonstrated that there may not be any additional metabolic cost associated with wider pelves (Warrener et al., 2015), though more work needs to be done among a greater range of pelvic breadths and for walking and running distances. Furthermore, work conducted by Whitcome and colleagues (2017) demonstrated that females do rotate their hips more than males, but this additional rotation increases their effective limb length, and longer limbs typically confer cheaper, more efficient locomotion. Females may be overcoming any potential disadvantage due to wider pelves by adopting slightly different locomotor biomechanics.

A wider pelvis may even be more energetically efficient for hip-placed load carrying. Wall-Scheffler and Myers (2017) had females and males walk around a gym track with an 11 kg load (toddler manikin) placed on the hip, walking at four different self-selected speeds while collecting biomechanical and energetic data. Despite the load used in these studies being proportionally greater relative to body weight, females had absolutely lower costs, adopted faster self-selected minimum walking speeds, and had greater stride lengths relative to males. Overall, this resulted in 20–35% greater locomotor economy for females, suggesting they may be better able to adapt their locomotion to a hip-placed load than males. Wall-Scheffler conducted a similar study with females and males carrying their own (real) children in various carrying positions in the woods and found that females were more economical than their male counterparts in all conditions (Wall-Scheffler, 2022). It has also been observed ethnographically among circumpolar peoples that females are capable of carrying exceptionally heavy loads (>100 kg) for great distances (Ray, 1884).

Males do tend to have more muscle mass than females, which results in a mean of 40–75% greater strength among males (Bishop, Cureton, and Collins, 1987), and this difference is more apparent in the upper than the lower body (Sale, 1999). However, when controlling for size and muscle mass, there is no difference in strength between females and males (Miller et al., 1993; Bishop, Cureton, and Collins, 1987; Lindle et al., 1997). A female and a male of the same size and body composition will have the same approximate strength capabilities. There are, however, differences in muscle fiber composition. Females tend to have more Type I muscle fibers, while males typically have more Type IIa fibers. Type I are the slow twitch fibers that rely on aerobic metabolism to produce energy more slowly, but they are relatively fatigue-resistant—better for endurance. Type IIa fibers are fast oxidative, while Type IIx are fast glycolytic, and able to produce energy at an intermediate speed, power, and time to fatigue. Type IIx are the fast-twitch fibers that rely on anaerobic metabolism to produce short-lived, powerful bursts of energy—better for power sports (Haizlip, Harrison, and Leinwand, 2015; Miller et al., 1993). When examining muscle fibers from the vastus lateralis, females had 41% Type I, 36% Type IIa, and 23% Type IIx fiber composition, with males at 34%, 46%, and 20%, respectively (Haizlip, Harrison, and Leinwand, 2015). Though there is a high degree of variability from person to person, and even the behavior of different muscle fiber types is subject to change. It was recently reported that female Olympic weightlifters had an exceptionally high number of Type IIa fibers (Serrano et al., 2019), but it is not clear whether that was developed through training or a result of self-selection. Type IIa fibers can also be "trained" to behave more like Type I or Type IIx fibers, and this plasticity introduces a malleable source of variability.

There also appear to be some sex-based differences in how muscle performs. Females appear to have a more effective eccentric contraction (lengthening the muscle) as well as the ability to

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

make the most use of the stretch-shorten cycle. A study by Komi and Bosco (1978) examined sex-based differences in the ability to turn potential energy stored in stretched muscle into kinetic energy during different jump styles. One of these was the counter-movement jump, a jump where one squats down, pauses, and then jumps—creating a stretch in the quadriceps muscles prior to the actual jump. Investigators found that females were able to utilize 90% of the energy created in the stretching phase of this jump, whereas males could only utilize ~50%. Furthermore, females can sustain lifting a higher percentage of their weightlifting maximum for longer than males. For example, at 70%, 60%, and 50% of maximal strength, females were able to perform a mean of 5, 13, and 32 more repetitions, respectively, than males (Maughan et al., 1986; Sale, 1999).

SUBSTRATE METABOLISM

The anatomical differences discussed above are only part of the story behind sex-based physiological differences. For example, females typically have higher levels of estrogen and males typically have higher levels of testosterone. Estrogen is often touted as the female hormone, but like testosterone, estrogen is present and needed in all humans. Estrogen performs a great many functions throughout *all* bodies, which are summarized in Figure 1. The vast array of estrogenic effects may come as a surprise to many, but it should not. It has been hypothesized that estrogen receptors are incredibly ancient, having evolved somewhere between 600 million and 1,200 million years ago, with androgen receptors arriving ~3 million years later, likely from a duplicate copy of the estrogen receptor gene (Thornton, Need, and Crews, 2003).

Critically important to this discussion, however, is the role estrogen plays in substrate metabolism—particularly the metabolism of fatty acids, which can and does influence athletic performance. The ability to utilize stored fatty acids preferentially over glycogen (stored form of glucose) can be beneficial to endurance (Besson et al., 2022; Ikeda, Horie-Inoue, and Inoue, 2019). Fatty acids have more calories per gram (9 kcal/gram) relative to glycogen (4 kcal/gram), and their utilization delays fatigue by preserving glycogen stores, which can be tapped into later during a long bout of endurance exercise. Studies among humans and rodents all indicate that females tend to utilize a greater percentage of fatty acids during endurance activities (Besson et al., 2022). Among humans, females have 70% greater fatty acid oxidation relative to males during exercise (Friedlander et al., 1998).

Greater fatty acid oxidation is likely due to the metabolic effects of estrogen, in particular 17-β-estradiol (E2). From rodent experiments, when E2 is administered to ovariectomized rodents, there is an increase in fatty acid oxidation and an attenuation of glycogen utilization (Nagai et al., 2016). Investigators hypothesize that this is driven by hepatic (rather than skeletal muscle) changes freeing up fatty acids while reducing glycogenolysis. Among humans, when males are given E2, glycogen utilization is significantly decreased, while fatty acid oxidation is significantly increased (Devries et al., 2005).

Female skeletal muscle also contains a greater concentration of fatty acids with ~58 g/kg of intramuscular fat relative to 23 g/kg for males (Tarnopolsky, 2000). This would directly enhance fat oxidation at the source of energy utilization. Females and highly endurance-trained males have a high concentration of E2 receptors on skeletal muscle compared to moderately active men (Wiik et al., 2005). This, in conjunction with greater fatty acid content found in female skeletal muscles, means that an effect of E2 on skeletal muscle during endurance exercise cannot be ruled out. Furthermore, E2 may be responsible for greater insulin sensitivity among females, at least at rest, which means females are better able to maintain stable blood-sugar levels relative to males

(Besson et al., 2022). Greater insulin sensitivity may improve protein sparing by increasing fatty acid storage and utilization, but this has not yet been tested during exercise (Tarnopolsky, 2000).

These potentially hormone-driven differences may provide a cardiometabolic advantage as well. Though females tend to have higher body mass indices and greater body adiposity relative to males, females suffer from cardiometabolic disorders such as type 2 diabetes far less (Smith et al., 2019). One potential reason for this is the distribution of fat between the sexes. Females tend to have greater subcutaneous fat stores, particularly at the hips and thighs, whereas males tend to have greater visceral fat stores. Fat is not an inert tissue; it has important metabolic and endocrine functions (Scheja and Heeren, 2019). Greater visceral fat has been linked to an increase in cardiometabolic disorders, including type 2 diabetes and fatty liver disease, to name a few (Greenberg and Obin, 2006). There is growing evidence that sex hormones are responsible for fat distribution, with estrogen leading to greater subcutaneous adipose depots and testosterone greater visceral fat depots (Bracht et al., 2020).

Females also have higher levels of adiponectin—by as much as 65%. Adiponectin, a lipid-derived hormone, is thought to protect against type 2 diabetes through modulation of glucose and fatty acid oxidation. Over the course of 24 months of endurance training, females started with and maintained higher levels of adiponectin relative to males, suggesting that females are better at fueling endurance exercise with fatty acids as the preferred substrate (Ring-Dimitriou et al., 2006, 2007). The adiponectin-enhanced ability to oxidize fatty acids not only spares glycogen stores for future use but also spares protein breakdown during long-term endurance exercise. When protein (i.e., muscle) is broken down during exercise, there is an increase in urea excretion. Females excrete significantly less urea after a bout of endurance exercise relative to males, even with a standardized diet and exercise-level intensity. Furthermore, it appears that E2 may help modulate this, such that leucine (the key amino acid for muscle growth) breaks down significantly less in females relative to males (Lamont, McCullough, and Kalhan, 2003; Riddell et al., 2003). When males are administered E2, leucine breakdown is attenuated (Hamadeh, Devries, and Tarnopolsky, 2005). Overall, the higher levels of E2 and adiponectin among females means that, relative to males, females burn more fatty acids. Burning fats provides slower, longer energy utilization, which means females are less likely to slow from fatigue over great distances. Furthermore, E2 seems to be rather important for preventing or at least mitigating postexercise muscle damage, which can lead to faster recovery.

RECOVERY AND DURABILITY

The hormonal differences discussed above also likely impact the muscle recovery process in a way that potentially benefits females. Heat-shock proteins are often considered the stress proteins; they are activated in response to environmental stress and internal cellular damage. Acute exercise can induce cellular damage, which elicits heat-shock protein and inflammatory responses that can further damage cells. A study conducted among rats found that males and ovariectomized females, in order to examine the role of estrogen alone, had two-fold greater heat-shock-protein production after running compared to intact females (Paroo et al., 2002). Human females also have an attenuated creatine kinase response: muscle-damaging creatine kinase leaks out of cells damaged during acute stress (Enns and Tiidus, 2010; Norton et al., 1985; Shumate et al., 1979). These attenuated responses may be regulated by E2 as well, but this has not been thoroughly studied (Bundey, Crawley, and Edward, 1979; Cohen and Morgan, 1976). E2 may also directly impact postexercise damage and inflammation with its antioxidant properties that help stabilize cell membranes—the same membranes that can become degraded during heat and exercise-induced stress and leak creatine kinase (Enns and Tiidus, 2010; Paroo et

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

al., 2002; Stice and Knowlton, 2008). Recent work has demonstrated that estrogen may encourage reperfusion (blood flow) and angiogenesis (blood vessel generation) in skeletal muscle following injury (Sopariwala et al., 2021). This evidence suggests that females incur less cellular damage in response to exercise and, therefore, are faster to recover.

There is a growing body of anthropological evidence that females are more durable than males when it comes to environmental perturbations (Cho et al., 2022; Gray, Straftis, and Anderson, 2021; Ocobock et al., 2020; Stinson, 1985; Waxenbaum and Feiler, 2021). For example, females do not experience the same levels of growth disruption and body-mass loss observed in males during a childhood negative energy balance, and this has been shown both anthropologically (e.g., Bogin, Scheffler, and Hermanussen, 2017) and physiologically (e.g., Cortright, 1999). Though not fully understood, this difference is likely due to a number of factors influenced by estrogen (Cortright, 1999; Tarnopolsky and Cortright, 1999), including greater insulin sensitivity, higher initial body adiposity, regulation of food intake, and ability to more readily metabolize fatty acids (Cortright, 1999)—many of the same reasons that potentially provide females an endurance advantage.

Another aspect of female durability appears to be greater fatigue resistance. Fatigue, though still poorly understood, comes about through poor lactate clearance and through neuromuscular mechanisms (Nuckols, 2019). The neuromuscular mechanisms are bit more well studied and fall into the categories of central and peripheral fatigue. Central fatigue takes place proximal to the motor neuron, while peripheral fatigue happens within the muscle fiber itself (Hunter, 2014). Males reach the point of fatigue faster for both endurance and resistance exercise (Hunter, 2014; Nuckols, 2019). There may also be a potential psychological component; for example, using an analysis of marathon data, it was demonstrated that females were able to maintain a more

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

consistent speed during 10 km races and marathons (Cuk, Nikolaidis, and Knechtle, 2020; Deaner et al., 2016). In a study of the Bolder Boulder 10 k road races over five years, which incorporated more than 190,000 runners, females were 1.96 times and 1.36 times more likely to maintain their pace than males at the halfway point and end of the race, respectively (Deaner et al., 2016). This could be due to the greater fatty acid oxidation (which can delay fatigue), sex-based differences in psychological pacing while covering great distances, or an unknown and unexplored mechanism.

WOMAN THE HUNTER, PAST AND PRESENT

In 1967, the year after the *Man the Hunter* symposium and a year before the edited volume was published, Katherine Switzer ran the Boston Marathon. The official race manager, Jock Semple, chased after Switzer, shouting obscenities, and attempted to physically remove her from the course (Switzer, 2017). Switzer's running crew helped to fend off these attacks so she could continue and finish the race. During her historic run, she reflected on why her participation in this event caused an uproar. At the time, there were no major university athletics programs for females, and the idea that females were not capable of performing rigorous physical activity and that such activity would harm their reproductive capacity was still pervasive. Of course, the irony of these justifications has just been laid bare by the present article: females are better suited for long endurance activities despite science continually trying to pull females out of the evolutionary course of events.

The combination of a wider pelvis, greater proportion of Type I fibers, greater fatty acid oxidation during exercise, increased insulin sensitivity, greater intramuscular fatty acid stores, attenuated cellular damage in response to stress, greater fatigue resistance, and potentially better mental pacing during exercise means that females are well suited for endurance and burdened

Accepted Manuscript
Version of Record at: https://doi.org/10.1111/aman.13915

exercise (Figures 2 and 3). Evidence for impressive female performance can be seen in their domination of ultra-endurance events such as the Montane Spine Race (Brown, 2017). This does not mean that there are not exceptionally strong and powerful females or excellent male endurance athletes—there obviously are. This, however, does mean we cannot and should not rely on the blanket assumption that females are physically inferior to males and incapable of taking part in the same variety of activities.

This is also not just a theoretical contention. Though this evidence is discussed in greater detail in the sister article to this one, there are numerous examples of females hunting and taking part in high levels of physical activity, disproving the idea that females did not hunt in our evolutionary past. However, it does not necessarily address the oft-cited issue of pregnancy, lactation, and childcare interfering with a woman's ability to hunt. It would be easy for one to say a small subset of females remained nonreproductive and took part in hunting. Fortunately, the more modern example of the Agta of the Philippines does address this issue. These people have a wide variety of population and economic structures. For example, the Tasaday Agta rely heavily on plants for sustenance, while the Nanadukan Agta rely on hunting, with both females and males participating in this activity. These female hunters were documented hunting with dogs and bows until the very latest stages of pregnancy and then returned to hunting after a few months postpartum (Estioko-Griffin, 1985; Estioko-Griffin and Griffin, 1981). There are other examples of female hunters among the Inuit (Briggs, 1974), Tiwi (Goodale, 1971), Ojibwa (Landes, 1938), and others.

In fact, it could very well be the supposed burden of pregnancy and childrearing in combination with high degrees of physical activity (hunting, gathering, tool making, etc.) that have shaped the suite of features giving females an endurance advantage over males. A female's total energy expenditure increases throughout pregnancy, with an additional ~500 kcal/day burned in the third trimester. This metabolic cost increases to over ~600 kcal/day throughout lactation (Butte and King, 2005). During this time, females, then and now, would still complete their regular tasks and evade predators (at least in our evolutionary past) in addition to gestating, birthing, feeding, and caring for offspring, and potentially facing resource-limiting and difficult environmental conditions (Natterson-Horowitz, Boddy, and Zimmerman, 2022). In essence, females with offspring take part in an endurance event that spans years, and their bodies both anticipate this and are able to adjust quickly when the hormonal milieu signals its beginning. It should be no surprise females have a greater endurance capacity and durability because the very survival of our species would have depended upon it. Therefore, many pregnancy adaptations in humans are evolutionarily advantageous, not a handicap or a tradeoff, as they are often portrayed.

No better example represents the extreme endurance capacity of females than that of Sophie Power, who participated in the ~168 km Ultra-Trail du Mont-Blanc race while still breastfeeding her three-month-old child. At each aid station, Power would either directly breastfeed or pump milk that would then be handed off to her spouse to give to the child, greatly adding to her metabolic load (Hobson, 2018). Yet, she completed the race three months postpartum. Of course, the importance of paternal investment and alloparenting cannot be ignored. Like Power's spouse ferrying breastmilk to their son or son to the breast, through cooperative breeding, family and peers provide multiple forms of material and moral support (Hrdy, 2009). These alloparents could take over childcare as a mother goes off to hunt, and this activity could easily be added to the grandmother hypothesis (Hawkes, 2003). It is our very social nature that enables females, even when there are children to attend to, to take part in any and every activity males do.

We need to explicitly test these hypotheses regarding female endurance capacities and their relationship to evolution and pregnancy. However, such hypotheses remain untested, and they remain untested because physiological studies focusing solely on females are still lacking. We need to focus research on female physiological capabilities pre-, mid-, and postparous to more accurately describe substrate utilization, biomechanical efficiency, muscle development and recovery, and fatigue resistance. We need to not shy away from including pregnant and breastfeeding study participants. A stronger grasp of female capabilities and changes during pregnancy and motherhood will allow us to develop better evolutionary models. Furthermore, we as researchers have the responsibility to model explanations with clear acknowledgment of the built-in assumptions and then to rigorously test and compare those models using the best available data. In the end, how can we hope to understand the past if we ignore almost half of our present?

Acknowledgments

We would like to thank Dr. Libby Cowgill and Dr. Charles Roseman for their helpful comments on early drafts of this manuscript. Thank you to Dr. Alexandra Niclou and Dr. Barbara Natterson-Horowitz for fruitful conversations. Thank you also to our undergraduate students whose inquiring minds and in-class questions have provided a great deal of inspiration for this article. Finally, we thank the anonymous reviewers for their support and for their excellent suggestions, which have strengthened this manuscript.

REFERENCES CITED

Bam, Jenefer, Timothy D. Noakes, June Juritz, and Steven C. Dennis. 1997. "Could Women Outrun Men in Ultramarathon Races?" *Medicine and Science in Sports and Exercise* 29 (2): 244–47. https://doi.org/10.1097/00005768-199702000-00013.

Besson, Thibault, Robin Macchi, Jeremy Rossi, Cédric Y.M. Morio, Yoko Kunimasa, Caroline Nicol, Fabrice Vercruyssen, and Guillaume Y. Millet. 2022. "Sex Differences in Endurance Running." *Sports Medicine* 52 (6): 1235–57. https://doi.org/10.1007/S40279-022-01651-W.

Bishop, Phillip, Kirk Cureton, and Mitchell Collins. 1987. "Sex Difference in Muscular Strength in Equally-Trained Men and Women." *Ergonomics* 30 (4): 675–87. https://doi.org/10.1080/00140138708969760.

Blackless, Melanie, Anthony Charuvastra, Amanda Derryck, Anne Fausto-Sterling, Karl Lauzanne, and Ellen Lee. 2000. "How Sexually Dimorphic Are We? Review and Synthesis." *American Journal of Human Biology* 12: 151–66. https://doi.org/10.1002/(SICI)1520-6300(200003/04)12:2.

Bogin, Barry, Christiane Scheffler, and Michael Hermanussen. 2017. "Global Effects of Income and Income Inequality on Adult Height and Sexual Dimorphism in Height." *American Journal of Human Biology* 29 (2): e22980. https://doi.org/10.1002/AJHB.22980.

Bracht, John R., Victoria J. Vieira-Potter, Roberta De Souza Santos, Orhan K. Öz, Biff F. Palmer, and Deborah J. Clegg. 2020. "The Role of Estrogens in the Adipose Tissue Milieu." *Annals of the New York Academy of Sciences* 1461 (1): 127–43. https://doi.org/10.1111/NYAS.14281.

Bramble, D. M., & Lieberman, D. E. 2004. "Endurance running and the evolution of Homo." *Nature*, 432: 345-352.

Briggs, J. L. 1974. "Eskimo Women: Makers of Men." In *Many Sisters: Women in Cross Cultural Perspectives*, edited by C. Matthiasson, 262–304. New York: The Free Press.

Brookshire, Bethany. 2016. "Women in Sports Are Often Underrepresented in Science | Science News." Science News, May 25. https://www.sciencenews.org/blog/scicurious/women-sports-are-often-underrepresented-science.

Brown, Meaghen. 2017. "The Longer the Race, the Stronger We Get." *Outside* online, April 11. https://www.outsideonline.com/health/training-performance/longer-race-stronger-we-get/.

Bundey, S., J. M. Crawley, and J. H. Edward. 1979. "Serum Creatine Kinase Levels in Pubertal, Mature, Pregnant, and Postmenopausal Women." *Journal of Medical Genetics* 16:117–21. https://doi.org/10.1136/jmg.16.2.117.

Butte, Nancy F., and Janet C. King. 2005. "Energy Requirements during Pregnancy and Lactation." *Public Health Nutrition* 8 (7A): 1010–27. https://doi.org/10.1079/PHN2005793.

Cho, E. O., L. W. Cowgill, K. M. Middleton, G. E. Blomquist, F. Savoldi, J. Tsoi, and M. Bornstein. 2022. "The Influence of Climate and Population Structure on East Asian Skeletal Morphology." *Journal of Human Evolution* 173: 103268.

Cohen, L., and J. Morgan. 1976. "Diethylstilbestrol Effects on Serum Enzymes and Isozymes in Muscular Dystrophy." *Archives of Neurology* 33 (7): 480–86. https://jamanetwork.com/journals/jamaneurology/article-abstract/574667.

Cortright, R. N. 1999. "Sex Differences on Regulation of Energy Homeostasis, Growth, and Body Composition during Periods of Energy Imbalance: Animal Studies." In *Gender Differences in Metabolism*, edited by M Tarnopolsky, 201–48. New York: CRC Press.

Cowley, Emma S., Alyssa A. Olenick, Kelly L. McNulty, and Emma Z. Ross. 2021. "'Invisible Sportswomen': The Sex Data Gap in Sport and Exercise Science Research." *Women in Sport and Physical Activity Journal* 29 (2): 146–51. https://doi.org/10.1123/WSPAJ.2021-0028.

Cuk, Ivan, P. T. Nikolaidis, and B. Knechtle. 2020. "Sex Differences in Pacing during Half-Marathon and Marathon Race." *Research in Sports Medicine* 28 (1): 111–20. https://doi.org/10.1080/15438627.2019.1593835.

Dahlberg, Frances, ed. 1981. *Woman the Gatherer*. New Haven, CT: Yale University Press.

Darwin, C. 1871. *The Descent of Man*. New York: D. Appleton & Co.

Deaner, Robert O., Vittorio Addona, Rickey E. Carter, Michael J. Joyner, and Sandra K. Hunter. 2016. "Fast Men Slow More than Fast Women in a 10 Kilometer Road Race." *PeerJ* 2016 (7): e2235. https://doi.org/10.7717/PEERJ.2235/SUPP-1.

Deutscher, Penelope. 2004. "The Descent of Man and the Evolution of Woman." *Hypatia* 19 (2): 35–55. https://doi.org/10.1111/J.1527-2001.2004.TB01287.X.

Devries, M. C., M. J. Hamadeh, T.E. Graham, and M.A. Tarnopolsky. 2005. "17-{beta}-Estradiol Supplementation Decreases Glucose Ra and Rd with No Effect on Glycogen

Utilization during Moderate Intensity Exercise in Men." *Journal of Clinical Endocrinology and Metabolism* 90:6218–25. https://doi.org/10.1210/jc.2005-0926.
DuBois, L. Zachary, and Heather Shattuck-Heidorn. 2021. "Challenging the Binary: Gender/Sex and the Bio-Logics of Normalcy." *American Journal of Human Biology* 33 (5): e23623. https://doi.org/10.1002/AJHB.23623.
Dunsworth, H. M. 2020. "Expanding the Evolutionary Explanations for Sex Differences in the Human Skeleton." *Evolutionary Anthropology* 29 (3): 108–16. https://doi.org/10.1002/evan.21834.
Dunsworth, H. M., A. G. Warrener, T. Deacon, P. T. Ellison, and H. Pontzer. 2012. "Metabolic Hypothesis for Human Altriciality." *Proceedings of the National Academy of Sciences* 109 (38): 15212–16. https://doi.org/10.1073/pnas.1205282109.
Enns, D. L., and P. M. Tiidus. 2010. "The Influence of Estrogen on Skeletal Muscle: Sex Matters." *Sports Medicine* 40:41–58.
Estioko-Griffin, A. 1985. "Women as Hunters: The Case of an Eastern Cagayan Agta." In *The Agta of Northeastern Luzon: Recent Studies*, edited by PB Griffin and A Estioko-Griffin, 18–32. Cebu City: San Carlos Publications.
Estioko-Griffin, A., and P. B. Griffin. 1981. "Woman the Hunter: The Agta." In *Woman the Gatherer*, edited by Frances Dahlberg, 121–52. New Haven, CT: Yale University Press.
Fausto-Sterling, Anne. 2012. *Sex/Gender: Biology in a Social World*. *Sex/Gender: Biology in a Social World*. Philadelphia: Routledge.
Fisher, Maryanne., Justin R. Garcia, and Rosemarie Sokol Chang, eds. 2013. *Evolution's Empress: Darwinian Perspectives on the Nature of Women*. New York: Oxford University Press.
Fredrickson, B. L., and K. Harrison. 2005. "Throwing Like a Girl: Self-Objectification Predicts Adolescent Girls' Motor Performance." *Journal of Sport and Social Issues* 29 (1): 79–101. https://doi.org/10.1177/0193723504269878.
Friedlander, Anne L., Gretchen A. Casazza, Michael A. Horning, Melvin J. Huie, Maria Francesca Piacentini, Jeffrey K. Trimmer, and George A. Brooks. 1998. "Training-Induced Alterations of Carbohydrate Metabolism in Women: Women Respond Differently from Men." *Journal of Applied Physiology* 85 (3): 1175–86. https://doi.org/10.1152/JAPPL.1998.85.3.1175.
Goodale, J. C. 1971. *Tiwi Wives: A Study of the Women of Melville Island, North Australia*. Seattle: University of Washington Press.
Gray, Peter B., Alex Straftis, and Kermyt G. Anderson. 2021. "Men and Reproduction." In *The Routledge Handbook of Anthropology and Reproduction*, edited by S Han and C Tomori, 52–67. London: Routledge.
Greenberg, Andrew S., and Martin S. Obin. 2006. "Obesity and the Role of Adipose Tissue in Inflammation and Metabolism." *The American Journal of Clinical Nutrition* 83 (2): 461S–465S. https://doi.org/10.1093/AJCN/83.2.461S.
Hager, L. 1997. *Women in Human Evolution*. Edited by Lori D. Hager. London: Psychology Press.
Haizlip, K. M., B. C. Harrison, and L. A. Leinwand. 2015. "Sex-Based Differences in Skeletal Muscle Kinetics and Fiber-Type Composition." *Physiology* 30 (1): 30. https://doi.org/10.1152/PHYSIOL.00024.2014.
Hamadeh, Mazen J., Michaela C. Devries, and Mark A. Tarnopolsky. 2005. "Estrogen Supplementation Reduces Whole Body Leucine and Carbohydrate Oxidation and Increases

Lipid Oxidation in Men during Endurance Exercise." *The Journal of Clinical Endocrinology & Metabolism* 90 (6): 3592–99. https://doi.org/10.1210/JC.2004-1743.

Hawkes, K. 2003. "Grandmothers and the Evolution of Human Longevity." *American Journal of Human Biology* 15 (3): 380–400. https://doi.org/10.1002/ajhb.10156.

Hobson, Ben. 2018. "British Ultra Runner Sophie Power Defies Breastfeeding." *Runner's World*, September 7. https://www.runnersworld.com/uk/a776387/british-ultra-runner-sophie-power-defies-breastfeeding-stereotypes-with-striking-image/.

Hooven, C. 2021. *T: The Story of Testosterone, the Hormone That Dominates and Divides Us*. New York: Henry Holt and Company.

Hrdy, Sarah Blaffer. 1981. *The Woman That Never Evolved*. Cambridge, MA: Harvard University Press.

Hrdy, Sarah Blaffer. 2009. *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Cambridge, MA: Harvard University Press.

Hunter, S. K. 2014. "Sex Differences in Human Fatigability: Mechanisms and Insight to Physiological Responses." *Acta Physiologica* 210 (4): 768–89. https://doi.org/10.1111/apha.12234.

Ikeda, Kazuhiro, Kuniko Horie-Inoue, and Satoshi Inoue. 2019. "Functions of Estrogen and Estrogen Receptor Signaling on Skeletal Muscle." *The Journal of Steroid Biochemistry and Molecular Biology* 191 (July): 105375. https://doi.org/10.1016/J.JSBMB.2019.105375.

Jordan-Young, R. M., and K. Karkazis. 2019. *Testosterone: An Unauthorized Biography*. Cambridge, MA: Harvard University Press.

Komi, Paavo V., and Carmelo Bosco. 1978. "Utilization of Stored Elastic Energy in Leg Extensor Muscles by Men and Women." *Medicine and Science in Sports* 10 (4): 261–65. https://europepmc.org/article/med/750844.

Lamont, Linda S., Arthur J. McCullough, and Satish C. Kalhan. 2003. "Gender Differences in the Regulation of Amino Acid Metabolism." *Journal of Applied Physiology* 95 (3): 1259–65. https://doi.org/10.1152/JAPPLPHYSIOL.01028.2002.

Landes, R. 1938. *The Ojibwa Woman*. New York: Columbia University Press.

Laughlin, William S. 1968. "Hunting : An Integrating Biobehavior System and Its Evolutionary Importance." In *Man the Hunter*, edited by Richard B. Lee and Irven DeVore, 304–20. Chicago: Aldine Publishing.

Lee, Richard, and Irven DeVore, eds. 1968. *Man the Hunter*. Chicago: Aldine Publishing Company.

Liebenberg, Louis. 2006. "Persistence Hunting by Modern Hunter-Gatherers." *Current Anthropology* 47 (6): 1017–25. https://doi.org/10.1086/508695/ASSET/IMAGES/LARGE/FG2.JPEG.

Lieberman, Daniel E., and Dennis M. Bramble. 2007. "The Evolution of Marathon Running." *Sports Medicine* 37 (4): 288–90. https://doi.org/10.2165/00007256-200737040-00004.

Lindle, R. S., E. J. Metter, N. A. Lynch, J. L. Fleg, J. L. Fozard, J. Tobin, T. A. Roy, and B. F. Hurley. 1997. "Age and Gender Comparisons of Muscle Strength in 654 Women and Men Aged 20–93 Yr." *Journal of Applied Physiology* 83 (5): 1581–87. https://doi.org/10.1152/JAPPL.1997.83.5.1581.

Lombardo, Michael P., and Robert O. Deaner. 2018. "On the Evolution of the Sex Differences in Throwing: Throwing Is a Male Adaptation in Humans." *Quarterly Review of Biology* 93 (2): 91–119. https://doi.org/10.1086/698225/.

Manolagas, S. C., and S. Kousteni. 2001. "Perspective: Nonreproductive Sites of Action of

Reproductive Hormones." *Endocrinology* 142 (6): 2200–2204. https://academic.oup.com/endo/article-abstract/142/6/2200/2988898.

Mattison, S. M., and R. J. Quinlan. 2019. "The Expendable Male Hypothesis." *Philosophical Transactions of the Royal Society B* 374 (1780): 20180080. https://doi.org/10.1098/rstb.2018.0080.

Maughan, R. J., M. Harmon, J. B. Leiper, D. Sale, and A. Delman. 1986. "Endurance Capacity of Untrained Males and Females in Isometric and Dynamic Muscular Contractions." *European Journal of Applied Physiology and Occupational Physiology* 55 (4): 395–400. https://doi.org/10.1007/BF00422739.

Miller, A. E. J., J. D. MacDougall, M. A. Tarnopolsky, and D. G. Sale. 1993. "Gender Differences in Strength and Muscle Fiber Characteristics." *European Journal of Applied Physiology and Occupational Physiology* 66 (3): 254–62. https://doi.org/10.1007/BF00235103.

Nagai, Saki, Kazuhiro Ikeda, Kuniko Horie-Inoue, Sachiko Shiba, Saya Nagasawa, Satoru Takeda, and Satoshi Inoue. 2016. "Estrogen Modulates Exercise Endurance along with Mitochondrial Uncoupling Protein 3 Downregulation in Skeletal Muscle of Female Mice." *Biochemical and Biophysical Research Communications* 480 (4): 758–64. https://doi.org/10.1016/J.BBRC.2016.10.129.

Natterson-Horowitz, B., A. M. Boddy, and D. Zimmerman. 2022. "Female Health across the Tree of Life: Insights at the Intersection of Women's Health, One Health and Planetary Health." *PNAS Nexus* 1 (2): pgac044.

Norton, J. P., P. M. Clarkson, J. E. Graves, P. Litchfield, and J. Kirwan. 1985. "Serum Creatine Kinase Activity and Body Composition in Males and Females." *Human Biology* 57:591–98.

Nuckols, Greg. 2019. "The Effects of Biological Sex on Fatigue during and Recovery from Resistance Exercise." Master's Thesis: University of North Carolina at Chapel Hill.

Ocobock, Cara, Päivi Soppela, Minna T. Turunen, Ville Stenbäck, and Karl-Heinz Herzig. 2020. "Elevated Resting Metabolic Rates among Female, but Not Male, Reindeer Herders from Sub-Arctic Finland." *American Journal of Human Biology* 32 (6): e23432.

Paroo, Zain, James V. Haist, Morris Karmazyn, and Earl G. Noble. 2002. "Exercise Improves Postischemic Cardiac Function in Males but Not Females: Consequences of a Novel Sex-Specific Heat Shock Protein 70 Response." *Circulation Research* 90 (8): 911–17. https://doi.org/10.1161/01.RES.0000016963.43856.B1.

Pickering, Travis Rayne, and Henry T. Bunn. 2007. "The Endurance Running Hypothesis and Hunting and Scavenging in Savanna-Woodlands." *Journal of Human Evolution* 53:434–38. https://doi.org/10.1016/j.jhevol.2007.01.012.

Pontzer, H., and B. Wood. 2022. "What Do Living and Recent Hunter-Gatherers Tell Us." In *American Association of Biological Anthropology*, 146. Denver.

Pound, Nicholas, and Michael E. Price. 2013. "Human Sex Differences: Distributions Overlap but the Tails Sometimes Tell a Tale." *Psychological Inquiry* 24 (3): 224–30. https://doi.org/10.1080/1047840X.2013.817297.

Quinn, N. 1977. "Anthropological Studies on Women's Status." *Annual Review of Anthropology* 6:181–225.

Ray, P. H. 1884. "Ethnographical Sketches of the Natives of Point Barrow." *Report of the International Polar Expedition to Point Barrow, Alaska, in Response to the Resolution of the House of Representatives*.

Reiter, Rayna, ed. 1975. *Toward an Anthropology of Women*. New York: Monthly Review Press.

Riddell, Michael C., Sara L. Partington, Nicole Stupka, David Armstrong, Courtney Rennie, and Mark A. Tarnopolsky. 2003. "Substrate Utilization during Exercise Performed with and Without Glucose Ingestion in Female and Male Endurance-Trained Athletes." *International Journal of Sport Nutrition and Exercise Metabolism* 13 (4): 407–21. https://doi.org/10.1123/IJSNEM.13.4.407.

Ring-Dimitriou, Susanne, Bernhard Paulweber, Serge P. Duvillard, Monika Stadlmann, Linda M. LeMura, Josef Lang, and Erich Müller. 2006. "The Effect of Physical Activity and Physical Fitness on Plasma Adiponectin in Adults with Predisposition to Metabolic Syndrome." *European Journal of Applied Physiology* 98 (5): 472–81. https://doi.org/10.1007/S00421-006-0291-9/FIGURES/2.

Ring-Dimitriou, Susanne, Serge P. Duvillard, Bernhard Paulweber, Monika Stadlmann, Linda M. LeMura, Kayla Peak, and Erich Mueller. 2007. "Nine Months Aerobic Fitness Induced Changes on Blood Lipids and Lipoproteins in Untrained Subjects versus Controls." *European Journal of Applied Physiology* 99 (3): 291–99. https://doi.org/10.1007/S00421-006-0347-X/FIGURES/1.

Rosenberg, Karen, and Wenda Trevathan. 2002. "Birth, Obstetrics and Human Evolution." *BJOG: An International Journal of Obstetrics and Gynaecology* 109 (11): 1199–206. https://doi.org/10.1046/j.1471-0528.2002.00010.x.

Sale, D. G. 1999. "Neuromuscular Function." In *Gender Differences in Metabolism*, edited by M Tarnopolsky, 61–85. New York: CRC Press.

Sapolsky, R. M. 1998. *The Trouble with Testosterone: And Other Essays on the Biology of the Human Predicament*. New York: Simon and Schuster.

Scheja, Ludger, and Joerg Heeren. 2019. "The Endocrine Function of Adipose Tissues in Health and Cardiometabolic Disease." *Nature Reviews Endocrinology* 15 (9): 507–24. https://doi.org/10.1038/s41574-01-0230-6.

Schulster, M., A. M. Bernie, and R. Ramasamy. 2016. "The Role of Estradiol in Male Reproductive Function." *Asian Journal of Andrology* 18 (3): 435. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4854098/.

Sear, Rebecca. 2021. "The Male Breadwinner Nuclear Family Is Not the 'Traditional' Human Family, and Promotion of This Myth May Have Adverse Health Consequences." *Philosophical Transactions of the Royal Society B: Biological Sciences* 376 (1827): 20200020. https://doi.org/10.1098/RSTB.2020.0020.

Serrano, Nathan, Lauren M. Colenso-Semple, Kara K. Lazauskus, Jeremy W. Siu, James R. Bagley, Robert G. Lockie, Pablo B. Costa, and Andrew J. Galpin. 2019. "Extraordinary Fast-Twitch Fiber Abundance in Elite Weightlifters." *PLOS ONE* 14 (3): e0207975. https://doi.org/10.1371/JOURNAL.PONE.0207975.

Shumate, J. B., M.H. Brooke, J. E. Carroll, and J. E. Davis. 1979. "Increased Serum Creatine Kinase after Exercise: A Sex-linked Phenomenon." *Neurology* 29 (6): 902–20. https://n.neurology.org/content/29/6/902.short.

Slocum, Sally. 1975. "Woman the Gatherer: Male Bias in Anthropology." In *Toward and Anthropology of Women*, edited by Rayna Reiter, 36–50. New York: Monthly Review Press.

Smith, Ella S., Alannah K. A. Mckay, Megan Kuikman, Kathryn E. Ackerman, Rachel Harris, Kirsty J. Elliott-Sale, Trent Stellingwerff, and Louise M. Burke. 2022. "Auditing the Representation of Female Versus Male Athletes in Sports Science and Sports Medicine Research: Evidence-Based Performance Supplements." *Nutrients*14 (5): 953.

https://doi.org/10.3390/NU14050953.
Smith, Gordon I., Bettina Mittendorfer, and Samuel Klein. 2019. "Metabolically Healthy Obesity: Facts and Fantasies." *Journal of Clinical Investigation* 129 (10): 3978-3989. https://doi.org/10.1172/JCI129186.
Sopariwala, D. H, N. Likhite, G. Pei, F. Haroon, L. Lin, V. Yadav, Z. Zhao, and V. A. Narkar. 2021. "Estrogen-related Receptor α Is Involved in Angiogenesis and Skeletal Muscle Revascularization in Hindlimb Ischemia." *The FASEB Journal* 35 (5): e21480.
Speechly, D. P., S. R. Taylor, and G. G. Rogers. 1996. "Differences in Ultra-Endurance Exercise in Performance-Matched Male and Female Runners." *Medicine and Science in Sports and Exercise* 28 (3): 359–65. https://europepmc.org/article/med/8776224.
Stice, James P., and Anne A. Knowlton. 2008. "Estrogen, NFκB, and the Heat Shock Response." *Molecular Medicine* 14 (7): 517–27. https://doi.org/10.2119/2008-00026.STICE.
Stinson, Sara. 1985. "Sex Differences in Environmental Sensitivity during Growth and Development." *American Journal of Physical Anthropology* 28 (6 S): 123–47. https://doi.org/10.1002/AJPA.1330280507.
Switzer, Katherine. 2017. *Marathon Woman: Running the Race to Revolutionize Women's Sports*. Boston: Da Capo Press.
Tang-Martínez, Z. 2020. "The History and Impact of Women in Animal Behaviour and the ABS: A North American Perspective." *Animal Behaviour* 164:251–60. https://www.sciencedirect.com/science/article/pii/S0003347219304130.
Tarnopolsky, Mark A. 2000. "Gender Differences in Substrate Metabolism During Endurance Exercise." *Canadian Journal of Applied Physiology* 25 (4): 312–27. https://doi.org/10.1139/H00-024.
Tarnopolsky, Mark, and R. N. Cortright. 1999. "Hormonal Differences between Males and Females." In *Gender Differences in Metabolism*, edited by M Tarnopolsky, 15–35. New York: CRC Press.
Thornton, Joseph W., Eleanor Need, and David Crews. 2003. "Resurrecting the Ancestral Steroid Receptor: Ancient Origin of Estrogen Signaling." *Science* 301 (5640): 1714–17. https://doi.org/10.1126/SCIENCE.1086185.
Wall-Scheffler, Cara M. 2022. "Women Carry for Less: Body Size, Pelvis Width, Loading Position and Energetics." *Evolutionary Human Sciences* 4:e36.
Wall-Scheffler, Cara M., and Marcella J. Myers. 2017. "The Biomechanical and Energetic Advantages of a Mediolaterally Wide Pelvis in Women." *The Anatomical Record* 300 (4): 764–75. https://doi.org/10.1002/AR.23553.
Warrener, Anna G., Kristi L. Lewton, Herman Pontzer, and Daniel E. Lieberman. 2015. "A Wider Pelvis Does Not Increase Locomotor Cost in Humans, with Implications for the Evolution of Childbirth." *PLOS ONE* 10 (3): e0118903. https://doi.org/10.1371/journal.pone.0118903.
Watanabe, Hitoshi. 1968. "Subsistence and Ecology of Northern Food Gatherers with Special Reference to the Ainu." In *Man the Hunter*, edited by Richard Lee and Irven DeVore, 69–77. Chicago: Aldine Publishing Company.
Waxenbaum, Erin B., and Maria E. Feiler. 2021. "Influence of Climatic Stress on Nonmetric Sexually Dimorphic Features of the Skull and Pelvis." *American Journal of Human Biology* 33 (6): e23559. https://doi.org/10.1002/AJHB.23559.
Whitcome, K. K., E.E. Miller, and J. L. Burns 2017. "Pelvic rotation effect on human stride length: Releasing the constraint of obstetric selection." *The Anatomical Record* 300 (4):

752-763.
Wiik, A., T. Gustafsson, M. Esbjörnsson, O. Johansson, M. Ekman, C. J. Sundberg, and E. Jansson. 2005. "Expression of Oestrogen Receptor α and β Is Higher in Skeletal Muscle of Highly Endurance-Trained than of Moderately Active Men." *Acta Physiologica Scandinavica* 184 (2): 105–12. https://doi.org/10.1111/J.1365-201X.2005.01433.X.
Zihlman, Adrienne. 1981. "Women as Shapers of Human Adaptation." In *Woman the Gatherer*, edited by Frances Dahlberg, 75–120. New Haven, CT: Yale University Press.

Figure Captions

Figure 1: This is a diagram providing a summary of the many functions estrogen performs throughout the body for both females and males (Tarnopolsky, 2000; Manolagas and Kousteni, 2001; Schulster, Bernie, and Ramasamy, 2016).

Figure 2: This is a diagram providing a summary of the anatomical, physiological, and psychological features that confer an endurance performance advantage to females. Citations are provided in text along with greater details about these features.

Figure 3: This is a diagram providing a summary of the anatomical, physiological, and psychological features that confer strength performance advantage to males (Manolagas and Kousteni, 2001; Jordan-Young and Karkazis, 2019; Hooven, 2021; Sapolsky, 1998).