

*New Idea***The sexual selection of hominin bipedalism****Michael T. Dale***Michael T. Dale (michaeldale@utexas.edu), Department of Philosophy, The University of Texas at Austin, 2210 Speedway, C3500, Austin, TX, USA 78712***Abstract**

In this article, I advance a novel hypothesis on the evolution of hominin bipedalism. I begin by arguing extensively for how the transition to bipedalism must have been problematic for hominins during the Neogene. Due to this and the fact that no other primate has made the unusual switch to bipedalism, it seems likely that the selection pressure towards bipedalism was unusually strong. With this in mind, I briefly lay out some of the most promising hypotheses on the evolutionary origin of hominin bipedalism and show how most, if not all, fail in the face of the need for an unusually strong selection pressure. For example, some hypotheses maintain that hominins became bipedal so they could use their hands for carrying infants, food, or other valuable objects. But extant apes are able to carry objects in one of their front limbs (while walking with the other three), and thus it does not seem plausible that our hominin ancestors went through the troublesome transition to bipedalism just so they could carry objects a little more efficiently. After I show that past hypotheses are wanting in the face of this challenge, I argue that there is only one selection pressure powerful enough to instigate a strange and problematic evolutionary adaptation like bipedalism, and that is sexual selection. Specifically, from the fact that bipedal locomotion is an important strategy for intimidating others and ascending the dominance hierarchy in extant apes, I argue that *for no particular selective reason* bipedal locomotion became a signal for high fitness (much as a large and intricate tail became a signal for high fitness for peahens), and this led to the trait being continuously reinforced in spite of all its deleterious fitness consequences.

Keywords: bipedalism, evolution, hominin, quadrupedalism, handicap, sexual selection, upright.

Introduction

Why did our hominin ancestors become bipedal? As it is likely that bipedalism preceded the expansion of the brain, language, tool-use, loss of body hair, and many other traits idiosyncratic to *Homo sapiens* (Tuttle 2014), bipedalism is perhaps the first step (!) in the development of modern humanity. While many hypotheses have been put forward, none have made a thoroughly convincing case, and thus this pivotal transition in our evolutionary history remains a mystery.

In this article, I advance a novel hypothesis regarding the evolution of hominin bipedalism. I will begin by discussing what we know about the timeline of the evolution of bipedalism. I will then argue extensively for how the transition to bipedalism must have been problematic for hominins during the Neogene. Due to this and the fact that no other primate has made the unusual switch to bipedalism, it seems likely that the selection pressure towards bipedalism was unusually strong. With this in mind, I will briefly lay out some of the most promising hypotheses on the evolutionary origin of hominin bipedalism and show how most, if not all, fail in the face of the need for an unusually strong selection pressure. Next, I will argue that there is only one selection pressure powerful enough to instigate a strange and problematic evolutionary adaptation like bipedalism, and that is sexual selection. Specifically, I will contend that *for no particular selective reason* bipedal locomotion became a signal for high fitness (much as a large and intricate tail became a signal for high fitness for peahens), and this led to the trait being continuously reinforced in spite of all its deleterious fitness consequences. Indeed, not only does this seem like the most plausible reason that such a troublesome transition occurred, but it also fits well with the fossil record. I end the paper by discussing

some of the interesting consequences this hypothesis has for the evolutionary history of *Homo sapiens*.

Evolutionary Timeline

The earliest uncontroversial evidence of obligate bipedal¹ Homininae is the 3.66 Ma Laetoli (site G) footprints uncovered 45 km south of Olduvai Gorge. These preserved footprint trails are the result of three bipedal hominins walking through volcanic ash (Tuttle 2014: 143). The hominins that made them are considered obligately bipedal because they walked through 27 meters of open habitat without leaving a single handprint.

Moreover, even though there is some contention over whether it was the same creature that left the Laetoli footprints, *Australopithecus afarensis* (Lucy), a hominin that lived between 3.9 and 2.9 Ma, was most likely bipedal (Lovejoy 1988). Interestingly, though, *A. afarensis* also had adaptations for arboreality, such as curved phalanges, and ape-like scapula, a long pisiform bone, and a laterally flared ilium (Tuttle 1981, Green and Alemseged 2012). A plausible interpretation of the evidence is that *A. afarensis* was terrestrially bipedal but still engaged in significant amounts of arboreal activity. However, this is ultimately just speculation. All we can really state is that it is very likely that a terrestrially bipedal hominin existed in east Africa around 3 to 4 Ma.

If we look back further than the mid-Pliocene, the evidence becomes murkier. While there is a compelling case that *Ardipithecus ramidus* (4.4 Ma) was a woodland dwelling hominin capable of bipedalism (Lovejoy 2009, Lovejoy et al. 2009), it is unclear how much bipedal activity *Ar. ramidus* engaged in. For one, its opposable toes (Lovejoy et al. 2009), which seem to be much more adapted to grasping branches, would have made any type bipedal gait primitive and awkward. Indeed, even Lovejoy (2009) (one of the prominent advocates of a bipedal *Ar. ramidus*) admits that upright walking would not have been an energy efficient option for the species. Moreover, its upper pelvis and large femoral shaft also indicate that *Ar. ramidus* spent a significant amount of time in the trees (White et al. 2009, Senut 2012). With all this said, however, it is important to understand that many pivotal aspects of the skeleton of *Ar. ramidus* have yet to be discovered and thus it is difficult to put forward a truly convincing argument either way (Senut 2012, Tuttle 2014: 246).

Going back even further, not enough fossils of *Ardipithecus kadabba* (5.6–5.2 Ma) have been found to make a compelling argument about the locomotion of the species (Stern and Susman 1983, Susman et al. 1984, Stern 2000). Some maintain that that the cranium of *Sahelanthropus tchadensis* (6–7 Ma) hints at bipedality

(Brunet et al. 2002), but many claim that the evidence is unreliable (Pickford 2005, Wolpoff et al. 2002, 2006, Schwartz 2004, Senut 2012). Interestingly, Senut et al. (2001) firmly argue that the femora of *Orrorin tugenensis* (6.1–5.7 Ma) indicate that the species was terrestrially bipedal while the phalanges and humerus imply that it was also arboreal. But again, it is difficult to make such claims convincingly, as only a few bones of *O. tugenensis* have been recovered. Moreover, just because there are signs of bipedality doesn't mean that the species was a terrestrial biped. Perhaps *O. tugenensis* was a bipedal branch walker, similar to *Pongo*.

Overall, as the previous paragraphs have illustrated, hominoid fossils from the Late Miocene are few and far between. Notwithstanding the few bones from the species just discussed (which really don't tell us much about locomotion specifics) and some miscellaneous teeth and mandibles (e.g. *Samburupithecus kiptalami*, *Chororapithecus abyssinicus*, and *Nakalipithecus nakayamai*), this time period represents a significant gap in the fossil record, which is unfortunate as it was likely a pivotal period in hominoid evolution.

However, we do know that we most likely evolved from quadrupedal primates that existed during the Middle Miocene. While some middle Miocene primate fossils show evidence of semi-terrestriality (e.g. *Kenyapithecus* and *Equatorrius*), all of them were quadrupedal animals that spent a significant amount of time climbing and maneuvering in trees (Senut 2012). Thus, up until 10 Ma., our ancestors were primarily arboreal, quadrupedal primates. Then, sometime between 10 Ma. and 4 Ma., there was a major transition to bipedalism. Unfortunately, this is about all we can say for sure about the timeline of the evolution of hominin bipedalism, but we can put forward one important (yet tentative) conclusion. Because many of the hominins that existed between 10 and 4 Ma. show adaptations for arboreality, terrestriality, and bipedalism, it is likely that the transition to bipedalism was a very slow, complicated process. Indeed, this makes sense because becoming bipedal is no straightforward matter. As the next section will show in more detail, not only must the physiology of a transitioning biped undergo significant change, but the animal's behavior, diet, and social life must revolutionize, as well. Thus, the transition to bipedality was most likely a gradual, tinkered process that occurred over many millennia.

The Unwelcome Consequences of Bipedalism

Homo sapiens is the only bipedal primate, and there is good reason why all other primates are *not* bipedal. Indeed, the physiology and skeleton of primates are so

¹ An obligately bipedal animal is one that uses bipedalism a primary means of locomotion.

well-adapted to arboreal and terrestrial quadrupedalism that it is surprising that our hominin ancestors were even capable of a transition to bipedalism. To help understand my point, let's begin with the spine. The mammalian spine can of course be traced back to the Osteichthyes (Shubin 2008), but proper terrestrial quadrupedalism didn't begin in the mammalian line until the evolution of amphibians approximately 350 Ma. Over the next few hundred million years, this spine was passed down first to reptiles, then to mammals, and finally to primates. Yet for all this time, it was always used primarily for quadrupedalism, and due to this, it became very well adapted to this type of locomotion.

Essentially, the mammalian spine is built like a cantilever bridge (Krogman 1951, Morgan 1994). It runs horizontally down the back of the animal, with the weight of the body and the internal organs hanging down below it. To support this weight (which is most of the weight of the animal), the spine utilizes two pillars at the front end (the front legs) and two more pillars at the back end (the back legs). With these four supports in place (one at each "corner"), the animal is able to balance the weight between the pillars so that there isn't one aspect of the spine that undergoes too much stress, and it is the center arch of the spine that bears the culmination of the weight. Overall, this is an ideal design for locomotion and weight distribution, and that is why it has been evolutionarily successful for hundreds of millions of years.

When hominins became bipedal, however, all of this changed. Instead of having a central arch, the spine became a vertical, weight-bearing column, and this forced its shape to change into an S-curve, with one curve at the neck region due to the weight of the head, and another curve in the lower trunk. (Interestingly, humans are still born with the ancestral arch in the center; it isn't until they start holding their heads up and walking around in infancy that their spines bend into an S-curve.) To support the pressure of the upper body, the lower vertebrae became larger, but because the mammalian spine was not adapted to the orthograde posture, many problems still ensued.

It is well known that when a person goes to bed, she is slightly shorter than she was when she woke up that morning. This is due to the immense amount of stress that humans put on their spines daily. As they carry themselves bipedally, the weight of the upper body presses down on the spine, while the incessant pounding of walking and running forces pressure back up through the spine. This can result in herniated intervertebral discs, fractured vertebrae, spondylolysis, scoliosis, and kyphosis (Raastad 2015, Walls et al. 2018); and as many people know personally, such painful occurrences are far from uncommon. Indeed, lower back pain is one of the leading causes of disability worldwide (Vos 2012). In the United States, one-half of all working Americans have yearly problems with back pain (with about two-thirds

having some type of back problem at some point in their lives), and about \$50 billion is spent each year to help with such problems (Vallfors 1985, Deyo 2001).

Also consider the fact that a bipedal hominin no longer has four pillars supporting its weight and spine; it only has two. This puts an immense amount of pressure and stress on, first of all, the knees. As a result, knee pain and dysfunction are very common among modern humans. Sprained ligaments, meniscus tears, tendonitis, bursitis, iliotibial band syndrome, Osgood-Schlatter Disease, osteoarthritis, dislocated kneecaps, patellofemoral pain syndrome, and runner's knee are just a few of the problems that come about due to the stress and strain we apply to the complicated architecture of our knees on a daily basis (van der Heijden et al. 2015).

The human foot is similarly problematic. To help dissipate the constant pressure and stress on this mechanism at the end of our pillar, the human foot evolved to have an arch in the center (Latimer 2005). While this was probably the best that natural selection could do with what it was given, this highly unusual design has many risks. If the arch is not pronounced enough (i.e. flat feet), this can lead to significant muscle and ligament pain, as well as fatigue fractures. If it is too pronounced, plantar fasciitis and heel spurs can develop (Beeson 2014). Other foot ailments include hallux valgus, hallux varus, bunions, Achilles tendonitis, arthritis, neuromas, and shin splints (Medline Plus 2018). Overall, it's not surprising that there are such problems, as our feet, which were originally adapted to be two of four centers of support, now need to hold up the entire weight of our bodies and undergo the constant stress of ground contact.

While this list of maladies is impressive, it is important to make sure that they aren't simply a part of the primate package. That is to say, if extant apes have similar problems, then perhaps it wasn't the transition to bipedalism that caused them. If this were true, then it would cause significant difficulties for my hypothesis, which maintains that the switch to bipedalism was so rife with difficulties that only an extremely strong selective pressure could have caused it. Fortunately, studies addressing this question have been carried out, and the results are very clear: degenerative joint disease is significantly more common in humans than in extant apes such as *Pan troglodytes*, *Pan paniscus*, and *Gorilla gorilla*. Jurmain (2000) found that the prevalence of vertebral osteophytosis (VOP) was 11 to 85 times higher in human bones than in the bones of African apes (e.g. VOP presence in humans from California: 34.1%; VOP presence in a population of chimpanzees: 0.4%). While not quite as dramatic, apophyseal involvement and peripheral osteoarthritis were also significantly higher among humans. Admittedly, not all of these comparisons control for age (some do), and humans usually live longer than African apes, but even with this potential complication, the evidence seems fairly clear. Among the

Gombe chimpanzees that Jane Goodall studied (Jurmain 2000), the rates of peripheral joint osteoarthritis in the left hip, right hip, left knee, and right knee were 0%, 0%, .1%, and 0%, respectively. For a larger population of chimpanzees, those numbers were 1.4%, 2.9%, 2.9%, and 2.9%. In comparison, European Americans had rates of 53.9%, 49.8%, 34.5%, and 17.2%. When age was controlled for, the human numbers were 26.7%, 24.7%, 17.2%, and 14.9%. (Inuit rates were even higher.)

Overall, there have been many studies that support these results (e.g. Bridges 1994, Kilgore 1990, Merbs 1983, Stewart 1966). Bipedalism may of course not be the only causal factor in these dramatically different rates, but seeing as bipedalism is the primary skeletal difference between humans and extant apes, it is quite likely that it is at least the main factor. Indeed, VOP tends to be most prevalent in the segments of our spines with the most curvature (Kilgore 1990, 1998, Jurmain and Kilgore 1995), and of course our spine's newly shaped S-curve is a result of our orthograde posture.

At this point, we are beginning to truly understand the difficulties that resulted from a transition to bipedalism. However, there were more than just skeletal problems. When hominins adopted orthograde bipedal posture, their blood was suddenly being pulled down towards their feet, and this forced the heart, which was now much higher above the ground, to pump blood all the way down to the back legs and then back up. This transition should not be underestimated, and it probably took many millennia for the body to evolve a circulatory system that was capable of such a feat. Even today the system is not perfect, with varicose veins and hemorrhoids occurring often due to the significant amount of blood pressing down on the veins in the lower half of the body.

Now, with all this in mind, consider the fact that modern human skeletons, muscles, and ligaments have had a few million years to adapt to bipedal locomotion. Our early hominin ancestors were not so lucky, as bipedalism was a completely novel trait for them. This means that they didn't have adaptations such as enlarged lower vertebrae or broader iliac bones, and this almost certainly would have meant that the pain and problems we experience today are minor in comparison to those our hominin ancestors dealt with. To take one specific example, when chimpanzees walk bipedally, they do so very awkwardly because the angles of the knee and hip joints don't allow the chimpanzee's body weight and the center of gravity to line up (Lewin 1983). Moreover, chimpanzees cannot extend their legs or lock their knees the way humans can, which means that they rely entirely

on muscle power when walking bipedally. Obviously, such a situation is not very sustainable. (If you think that this may not be so bad, try walking with bent knees for an extended period.) However, this is almost certainly how our hominin ancestors walked when they first started experimenting with bipedalism, and in all likelihood, this awkward phase lasted a substantial period of time.² Indeed, it is incredible to think that they would stick with bipedalism long enough to evolve such adaptations. And those are just two issues! Their feet, their knees, their shins, their hips, their spines, their leg muscles, their abdominal walls; *none* of these structures were adapted to bipedalism, so one can only imagine the constant physiological and skeletal problems our newly orthograde ancestors needed to deal with.³

Overall, though, these internal issues would only have been part of the problem with the transition to bipedalism, and in all likelihood, they were the less significant part. The true drawbacks of such a transition can only be understood by seriously considering the ecology and ethology of our hominin ancestors. First, consider diet. Almost all primates that spend a significant amount of time in the trees do so to have access to the fruits, leaves, gums, flowers, insect galls, and nuts that can be found there. Indeed, for many arboreal primates, these foods are their main source of food and nutrition. In all likelihood, this was also the case for our arboreal primate ancestors, which means that when they made the transition to bipedalism, and lost much of their ability to climb trees, they sacrificed this part of their diet. As one can imagine, making such a significant change in diet is extremely risky for any species, and thus there must have been strong selection pressure against such a switch.

One could argue that this diet change might not have been a sacrifice because hominins had already made a significant change in diet that enabled them to gather food terrestrially, and this led to them simply not needing to spend much time in the trees. However, this is unlikely because the only known major diet transition that hominins went through was the shift to larger amounts of meat-eating, and this shift probably didn't occur until millions of years after the transition to bipedalism (perhaps around 2.5 to 1.8 Ma.) (Wrangham 2009).

A better objection to my view is to point out that as we saw from discussing the fossils in the second section of this paper, the transition from arboreality to bipedalism was a slow, varied process, with many of the intermediate phases possessing adaptations for both arboreality and terrestriality. Which means that when these hominins were becoming slowly more adapted to bipedalism, they

² Looking closely at *A. afarensis*, we see (in comparison to modern humans) extraordinarily wide hips and a short femoral neck, which would have led to extra strain on the gluteals and the femoral neck junction (Jungers 1991, Hunt 1994). We also see a small diameter spine, small joint surfaces beneath the waist, and small sacro-iliac attachments, all of which further indicate that Lucy was a much less efficient walker than a modern human (Jungers 1988, 1991, Hunt 1989, 1990, 1994).

³ Indeed, the Nariokotome boy, a young *Homo erectus*, supposedly suffered from scoliosis (Latimer and Ohman 2001).

still had the abilities to climb trees to gather food. It's just that these abilities were not quite as efficient as they used to be. While this is true, the fact still remains that the transition to bipedalism necessitated an (albeit gradual) shift away from the primary arboreal diet of our ancestors, and thus there must have been a very strong selection pressure behind such a shift.

A further behavioral drawback to bipedalism was a loss of speed and agility (Lovejoy 1988). As can be imagined, primates with four limbs on the ground are able to balance much more effectively, and this almost certainly gives them an edge when it comes to avoiding predators and chasing prey. Moreover, while current speeds of humans and extant apes are comparable, the initial phases of hominin bipedalism must have been awkward and inefficient due to the loss of arboreal and quadrupedal adaptations and the slow gain of bipedal adaptations. Thus, there almost certainly was a significant period of time when hominins were slower and clumsier than they were when they were fully adapted to quadrupedalism. This, of course, was a very dangerous transitional period to go through, which again indicates that there must have been a very strong selection pressure for bipedalism.

Another interesting issue to consider is the fact that bipedal creatures are more vulnerable to injury than quadrupedal creatures. If a bipedal hominin were to break an ankle or a leg, she would be severely injured for many months. Walking, running, hunting, gathering resources, taking care of children, socializing; all of these activities that were very important for survival during the Miocene and Pliocene would suddenly become very difficult for her for an extended period of time. Even spraining an ankle would significantly compromise a bipedal hominin! A quadrupedal hominin, on the other hand, would be significantly less affected by these injuries, as it still has three additional limbs to use.

Previous Hypotheses

With all of this in mind, I now want to move on to some of the most popular hypotheses for why hominin bipedalism evolved. After briefly explaining each hypothesis, I will put forward some significant objections. Of course, there is much more to say about each hypothesis and its objections, and I encourage readers to look into the hypotheses on their own. The main goal right now is to show that because most of the previous hypotheses cannot face up to the challenge of the need of a very strong selection pressure, they are inadequate accounts of the evolution of hominin bipedalism.

Hypothesis 1: When hominins came down from the trees (perhaps due to aridification), they became bipedal so that they could see over the grasses that covered the savannah. This increased viewing distance would have

helped them both avoid predators and gather resources (Dart 1959, Day 1977, 1986, Ravey 1978). *Objections:* If hominins wanted increased viewing distance, they could have simply stood up on their back legs to look over the grass, as many extant apes do. Why would they go through all the difficulties of obligate bipedalism when all they needed was facultative bipedalism? Moreover, none of the extant primate species that live on grasslands, such as the gelada, *Papio* baboon, vervet, and patas monkey, are bipedal.

Hypothesis 2: Hominins became bipedal to free up their hands for tool-use. *Objections:* First of all, hominins probably did not start using (Oldowan) tools until long after they were bipedal (2.6 Ma.) (Tuttle 2015: 226). Moreover, when do we usually use tools? When we are sitting, of course. So why would hominins evolve obligate bipedalism for a skill that they could mostly accomplish while sitting?

Hypothesis 3: Hominins became bipedal because of a cataclysmic flooding event that forced them to adapt to wading through water, which they do by only using their back legs (Morgan 1990, Wrangham et al. 2009). *Objections:* First of all, extant apes are known to actively dislike being in water, probably because they are not adapted to it. Thus, in all likelihood, as the hominins of the late Miocene and early Pliocene had a similar lack of aquatic adaptations, they probably would have done all they could to get out of the flooding areas. If they were unable to do this, they almost certainly would have died off. Indeed, it seems unlikely that they would have been able to survive long enough in this adverse habitat for new bipedal adaptations to evolve.

Hypothesis 4: Hominins became bipedal so they could use their arms to carry food, infants, or other objects (Do Amaral 1996, Hewes 1961, 1964, Lovejoy 1988, De Silva 2009). *Objections:* Extant apes often carry objects quadrupedally by using three limbs to walk and one of their front limbs to carry. Why would hominins go through the immense amount of trouble to evolve obligate bipedalism when they could already carry objects and infants fairly well quadrupedally? Moreover, what new object would hominins need to carry during the late Miocene and early Pliocene? The most likely candidate is meat, but again the evidence indicates that heavy meat eating probably did not begin until the late Pliocene/early Pleistocene (Wrangham 2009).

Hypothesis 5: The transition to bipedalism was a two-step process. First, due to a novel ecological need to ground forage, hominins reoriented their bodies for squatting so that they could use both hands to forage. Then, from this squatting position, they began to stand because they found that they could forage both the ground and

miscellaneous flora from a standing position (Kingdon 2003). *Objections*: Would hominins really completely reorient their bodies to a squatting posture when a quadrupedal posture already does an adequate job? Many extant, quadrupedal apes are able to ground forage, and therefore unless hominins' diet depended *completely* on ground foraging (which seems unlikely), there is little reason to think that there was such a strong selection pressure. Moreover, why would hominins switch from squatting to obligate bipedalism if they could already stand up on their back legs for the short amount of time that they were foraging up high?

The Sexual Selection Hypothesis

While there are often quite a few reasons for why these previous hypotheses are inadequate, there certainly seems to be one underlying factor: none describe a selection pressure strong enough to address the issues brought up in the third section of this paper. That is, none give a fully convincing reason for why hominins would continue to evolve adaptations for bipedalism in the face of all the costs and troubles that would most likely come along with such a transition.

Often, when an animal has bizarre adaptation that seemingly detracts from its fitness, the adaptation is the result of sexual selection. Sexual selection occurs when one sex of a species, for whatever reason, evolves to find a certain trait in the other sex sexually alluring (Darwin 1859). This leads to the genes of the members of the attractor sex with the "best" version of that trait to be selected for, even if evolving the best version of that trait leads to other negative fitness consequences. The classic example of sexual selection is the peacock's tail (Zahavi and Zahavi 1999). It is so large and burdensome that it not only takes away precious energy from other (more important) survival strategies, such as digestion and searching for food, but it also slows it down when running away from predators. However, for whatever reason, female peahens have evolved so that they find the males with the largest and most beautiful tails to be the most sexually alluring, and this leads to larger tails being consistently selected for.

Overall, there are numerous examples of sexual selection in nature. Many mammalian males evolve to have large bony structures emerging from the tops of their heads (e.g. horns and antlers), and even though it is quite energy consuming to grow and carry these structures, males continue to grow them (in ever larger and more complicated arrays) because they are used in intrasexual competition. The bizarre coloring of many birds; the giant horns of male rhinoceros beetles; energy consuming mating dances; the amazingly intricate

structures built by bowerbirds; the spiraling horns of narwhals: all of these phenomena are most likely due to sexual selection, and in every case, even though growing and/or maintaining the traits is deleterious to survival, they continue to be selected for. This is because when one sex (usually the female⁴) develops a taste for a certain trait, males with that trait are selected for (and indirectly so are the females, as the females that are producing the most offspring are the ones attracted to that trait). Then, in the next generation, the males with a better/larger/more intricate version of that trait (and the females with a taste for that better/larger/more intricate trait) are again selected for, and the process continues.

It is often thought that the reason why one sex looks for the best version of a trait in the other sex is because that trait signifies high fitness. Indeed, perhaps having the best/biggest/most intricate version of the trait shows that the organism can survive even with needing to have this bizarre, fitness compromising adaptation (i.e. it can survive with this fitness "handicap"), which may be an overall indicator for superior genes (Berglund et al. 1996, Jones and Ratterman 2009, Zahavi 1975). However, this may not be the case. Just because some organisms are selected to evolve a more perfect version of a certain trait doesn't mean that that trait is correlated with superior genes (for example, it could just be an arbitrary "badge" of status (Berglund et al. 1996)—more on this later).

The main takeaway at this point, however, is not why sexual selection occurs; it is that many of the strange, fitness compromising adaptations seen in nature are due to the process of sexual selection. Which is to say, if a trait is continuously selected for, even though it significantly detracts from an organism's fitness, one likely possibility is that the trait is being sexually selected for, and this is my stance on the evolution of hominin bipedalism. In particular, I maintain that the only selection pressure strong enough to overcome all the problems and deleterious fitness consequences that likely resulted from a transition to bipedalism was sexual selection.

Because there is often an emphasis on anchoring the transition to bipedalism on a specific climatic, dietary, or physiological event in our evolutionary history, and it is often unknown why a specific trait became sexually alluring (and thus selected for), sexual selection is rarely (if ever) discussed in the literature on the evolution of hominin bipedalism, and especially not as the starting point of the transition. My hypothesis, however, is not completely novel. It was inspired by some of the ideas put forward in Jablonski and Chaplin (1992), but before I explain what is said in this paper, it is important to understand the basic societal structures of our closest extant relatives. Among *Pan troglodytes*, *Pan paniscus*, and *Gorilla* (as well as among Old and New World

⁴ Females are usually the choosier sex because the reproductive stakes (i.e. the time and energy invested in their offspring) are higher for them than for males.

Monkeys and many other primates), a ranking system is very important to day-to-day group life (Goodall 1971, 1986, 1990, Fossey 1983, de Waal 1982, de Waal and Lanting 1997). Certain members of the group are “ranked” higher than other members, and often the higher-ranking members get more food and mating opportunities. Due to the opportunities at the top, there are often conflicts about rank (more often among males), with many members attempting to ascend the dominance hierarchy and other members attempting to stay in their high-ranking positions.

Now, when certain members want to climb the dominance hierarchy, they attempt to intimidate the higher-ranking members. If the intimidator is successful, the previously higher ranked ape will show submission (which all the other apes will see), and the dominance hierarchy will be adjusted. Interestingly, intimidation displays often consist of running, shrieking, throwing things, hitting, and, most importantly for the topic of this paper, bipedal locomotion. As I have already mentioned, all apes are capable of bipedal locomotion for short distances, and thus it makes sense for members who are trying to climb the dominance hierarchy to stand up on their back legs so that they can look larger and more intimidating.

Jablonski and Chaplin (1992) take this idea and turn it into a hypothesis on the evolution of hominin bipedalism. Specifically, they maintain that as habitats became more desiccated in the late Neogene, competition over increasingly scarce resources escalated, and this resulted in the need for more instances of peaceful resolution of intragroup (and intergroup) violence. Because bipedal display is important in maintaining and enforcing the dominance hierarchy,⁵ and because high ranking members are often the ones attempting to keep peace in the group, Jablonski and Chaplin claim that bipedal display would have become especially important during this time of conflict. That is, high ranking individuals would have been using the strategy more in a time when there was more violence over dwindling resources, and this would have then led for bipedal locomotion to be an all-around more common occurrence.

Overall, this particular hypothesis is unlikely. Many apes and monkeys live in and around dry grasslands, and none have needed to evolve special tendencies to suppress increased competition and violence. Moreover, it is highly unlikely that the selection pressure for bipedal displays for peacekeeping was strong enough to overcome all the difficulties that came along with increased bipedal activity. All apes and monkeys have evolved strategies to help deal with intragroup conflict, so why would hominins choose a strategy that came partnered with so many deleterious fitness consequences?

Even though the hypothesis itself is not promising, it is the inspiration for what I think is a much more promising hypothesis: the sexual selection hypothesis. As Jablonski and Chaplin (1992) point out, short bouts of bipedal locomotion are one aspect of intimidation displays among extant apes, and thus it almost certainly played a similar role in the daily life of our hominin ancestors. For most apes, it is simply one strategy to help ascend the dominance hierarchy (or stay on top of the hierarchy), but according to my hypothesis, it gained particular importance for hominins. Specifically, due to its association with appearing larger and more intimidating, and thus its ability to help individuals help achieve higher ranks, it was “chosen” by one or both sexes as a trait that helped ascertain the fitness of potential mates (because it helped indicate who would likely climb higher in the dominance hierarchy). That is to say, due to the fact that long bouts of bipedal locomotion often did help in dominance conflicts because one could appear larger and more intimidating for a more pronounced period of time, this trait became a signal that potential mates noticed; or, as Berglund et al. (1996) describe it, a status badge. The longer you could walk on two feet, the more likely you could intimidate others and be at the top of the dominance hierarchy, and this is attractive to members of the opposite sex because members at the top of the hierarchy are often in control of the most resources, which leads to their offspring living longer, healthier, and more reproductively fit lives.

Of course, it might not have actually been true that the individuals who were more accomplished bipedal walkers were more capable of ascending the dominance hierarchy. But that didn’t matter, at least in the beginning. All that mattered was that the trait became a *signal* for high reproductive fitness. Then, once it became set in the population, and bipedal walkers were the ones with the most successful matings, it was the offspring of those matings that had the “best” genes, which then led to them being more highly ranked in turn. Moreover, as the desire for the trait became set, having the trait, in and of itself, would have become an intimidating signal of status, which of course helps in conflicts of dominance.

Now, it important to understand what I am not putting forward. I am *not* claiming that bipedal locomotion was selected for *because* it improved reproductive fitness. There were many strategies that could improve an individual’s ability to ascend the dominance hierarchy, such as size, arm strength, resilience, endurance, hair length (you look bigger if all of your hair is standing up straight), etc. Thus, it could have been the case that improved versions of all of these traits heightened one’s fitness. The point is that, *for no particular reason*, bipedalism became a trait that signaled high reproductive

⁵ The members on top will often use it to remind the group of their status and intimidate specific members who are thinking about making a move for a top spot.

fitness, just as large antlers did for many mammals and giant, intricate tails did for peacocks.

This is important to understand because it shows why this hypothesis is different than most other evolutionary hypotheses on the transition to hominin bipedalism. Most hypotheses maintain that there was a very specific reason for bipedalism to come about, e.g. there was a change in climate⁶ or there was change in diet or there was a change in predatory activity that caused our hominin ancestors to start walking upright. But my hypothesis does not assert this; instead, it maintains that it was an essentially random occurrence. Bipedalism *just happened* to become a major trait that signaled for “good” genes, and this caused members of the opposite sex to be sexually drawn to that trait.

Of course it couldn't have been *any* trait. The trait did need to be associated with the ability to ascend the dominance hierarchy, but it could have been one of many other traits. The fact that it turned out to be bipedal locomotion does not show that there is anything particularly special about that trait. And indeed, this is common for sexually selected traits. There was no particular reason for antlers to become the signal for high reproductive fitness (besides the fact that it helped win fights with other males, just as bipedal locomotion helped intimidate others in dominance displays); they just happened to become a sexually selected signal. They could have evolved tusks or disproportionately large teeth or strong neck muscles to help withstand strikes to the neck (à la giraffes), but instead many mammals evolved antlers and horns (that are quite different from one species to the next, again emphasizing the particular “taste” of each species).

The case is similar with bower birds and peacocks. As far as we know, there is no particular reason that these odd traits began to be sexually selected for. Indeed, as we see from other types of birds, there are plenty of alternative traits that could have been “chosen” as signals of fitness (note all the strange and interesting dances that males from different species do to entice females). But for whatever reason, the size, shape, and coloring of the tail was what became important for peahens, and this led to that trait being continuously selected for even though it had seriously deleterious fitness consequences. And this is the important point. I have argued throughout this paper that bipedalism was (and still is) such a fitness decreasing adaptation such that only a strong, continuous pressure could have forced it to come about, and the only pressure that fits the bill is sexual selection. So even though it caused so many problems for hominins, the fact that it was a fitness signal continued to reinforce the genes that coded for bipedal locomotion, and this was perpetuated until the species became obligately bipedal.

So far, I haven't been specific about which sex was the allurer and which was the alluree. This is of course speculation, but if extant apes are at all an indicator, it was probably the hominin females that became attracted to the trait of bipedalism among hominin males. In most ape species, it is the males who care most about ascending the dominance hierarchy and who gain the most from such ascension (though of course dominance rank still matters to a certain extent for the females in some species, such as chimpanzees and bonobos). Indeed, usually the alpha of the entire group is the male on top of the male dominance hierarchy (although this is not always the case; see de Waal's discussion of bonobo societies in de Waal 1997). Thus, it is likely that bipedal locomotion became a fitness signal to help females choose which male was the most likely to ascend the dominance hierarchy and keep his spot on top. Indeed, this could be why there are more signs of terrestriality in the fossils of male *Australopithecus afarensis* than in the fossils of the females (Senut 1980, Tardieu 1983, Stern and Susman 1983, Susman et al. 1984, Hunt, 1994).

But if all of this is the case, why are both sexes of *Homo sapiens* bipedal? That is to say, why isn't bipedalism a dimorphic trait, like other traits that are the result of sexual selection, such as the peacock's tail? This, of course, is an excellent question, and because we are in the realm of heavy speculation, we cannot know for sure what the answer is. However, there are some plausible possibilities. First of all, even though I emphasized that dominance hierarchies among extant male apes, there are dominance hierarchies among females, as well (Goodall 1971, 1986, 1990, Fossey 1983, de Waal 1982, de Waal and Lanting 1997). The (reproductive) stakes aren't as high among these hierarchies, but the females on top certainly do garner some benefits due to their status, such as first access to resources and larger and more supportive networks of friends and kin, all of which helps them pass on their genes more effectively than those lower ranked. Thus, as bipedalism became more important for a male's reproductive status, it could have become important for female status, as well. That is, unlike in other dimorphic species, such as peacocks, in which male status is the main factor in reproduction, hierarchical placement could have been important for both hominin sexes, which may have meant that after bipedalism became a signal for high fitness in one sex, it then became important for the other sex. So, if males became bipedal first, it is plausible that after bipedalism became a badge of status in the population, all individuals who benefitted from enhanced status would benefit from bipedal locomotion, and this would include females.

One might wonder why females would need to be bipedal if the desire for the trait existed only in the

⁶ Note that most of the previous hypotheses are, in one way or another, tied to a change in climate, but that there really isn't convincing evidence for a drastic enough change to cause such a strong selection pressure.

females, but this is actually the key to the argument. If the females developed a taste for bipedalism, they would not only be more respectful and submissive to males with this trait, but also other females. Thus, in status competitions among the females, since they already associate bipedalism with more dominant individuals, bipedal locomoting females would have an easier time rising in the hierarchies. And if this were the case, then bipedalism would continue to be selected for not only in the male genotype but also in the female genotype.

This idea makes an interesting point about sexual selection in general. Overall, we have much to learn about sexually selected traits, and for all we know there could be many sexually selected non-dimorphic traits but we haven't discovered them yet because we naturally assume a correlation between sexual selection and dimorphism. But now we have a specific reason to think that in populations in which status hierarchies are important for both sexes, and a status badge is sexually selected for, it is likely that, in time, both sexes will develop the trait because the recognition of dominance applies to both intersexual and intrasexual relations. Thus, we could posit that in species in which there is a significant amount of sexual dimorphism, such as peacocks or rhinoceros beetles, status hierarchies are not an important aspect of female life. However, as extant ape populations suggest (Goodall 1971, 1986, 1990, Fossey 1983, de Waal 1982, de Waal and Lanting 1997), dominance hierarchies were important for the both male and female hominins, and therefore any status badge sexually selected for in one sex will likely develop in the other. And again, males developing bipedalism slightly before the females is what the fossil evidence suggests (Senut 1980, Tardieu 1983, Stern and Susman 1983, Susman et al. 1984, Hunt 1994).

Another important way in which bipedalism differs from many others sexually selected dimorphic traits is that it is such a major aspect of human life. What would human life be like if one sex were bipedal and the other quadrupedal? Such a significant difference seems like it would cause problems in how the two sexes relate to each other. Indeed, they would almost seem like two different species! Thus, perhaps once the males began to locomote bipedally for significant periods of time, this forced the females to adopt a similar stature. Another possibility is that the genes for locomotion were carried over to female sex for no particular adaptive reason, much the same as human male nipples. That is, perhaps it just became more selectively efficient for the trait for bipedalism to be instilled in the entire population, instead of just one sex, and this led to the genes coding for the trait to become common in both males and females. (Admittedly, the male nipple may not be the best comparison example because a nipple is significantly less costly than a transition to bipedalism, but this doesn't mean that a similar process couldn't account for both traits.) Finally,

it could have been the case that as bipedalism became more important for male fitness and status, it became viewed as an overall important aspect in day to day life. Individuals may have wanted to mimic the most powerful individuals in the community, and this could have led to a general increase in that type of locomotion.

Importantly, the sexual selection hypothesis fits well with the (admittedly incomplete) fossil record. As discussed, most hypotheses put forward a story that centers around a relatively quick transition. For example, due to a sudden and specific climate change, hominins now had to adapt to a new savannah-like habitat, or a new swampy habitat. But these quick-transition hypotheses don't fit well with the fossil evidence discussed near the beginning of this paper. In particular, the evidence indicated that the transition was a slow, drawn out process, with many different hominin species having adaptations for arboreality, quadrupedalism, and bipedalism. Thus, it seems unlikely that there was some specific event that forced hominins to change locomotive abilities in a relatively short period of time.

Instead, the evidence indicates that the transition came about as a result of a strong, consistent, yet drawn out selective pressure that acted on hominins over many millennia, and this is exactly what the sexual selection hypothesis posits. When bipedal locomotion became a signal for high fitness, individuals desired to have mates with that trait, but it wasn't as if there was some dramatic change to bipedal locomotion. If an individual could walk bipedally for an extended period of time, then that trait raised the individual's fitness. However, this was only one trait among many, and thus the difference in fitness was probably only minor, at least at first. Thus, while the selection pressure was consistent (because the trait *continued* to be a signal for high fitness), it didn't quickly lead to obligate bipedalism. But as generations of hominins continued to evolve, the genes that enabled individuals to walk bipedally for even longer periods of time were continually selected for. This then led to the skeleton and muscles being forced to slowly adapt to this new, bizarre type of locomotion that they were not structurally prepared for. However, because it had already become a signal for high fitness, there was no stopping the unrelenting power of sexual selection, i.e. there was no way to stop individuals from being sexually attracted to this trait because this attraction was already set in the genetic code.

According to the sexual selection hypothesis, this process continued for many thousands, and perhaps millions, of years until hominins eventually became obligately bipedal. And it's at this point that they could be actively compared to the peacock. We find it strange to see an animal invest so much of its energy in a large, intricate tail that will, for the most part, only hurt its chances of survival (how much easier would it be for the peacock to avoid and outrun predators without its

massive, handicapping tail?) (Zahavi and Zahavi 1999). What I'm suggesting is that we look at hominin bipedal locomotion in the same way. As I already pointed out, bipedal locomotion has serious, deleterious fitness consequences in almost every sphere of hominin life. Thus, it was by all means a bizarre adaptation that we were probably better off without in terms of survival. But because there was no stopping the strong and consistent selective power of sexual selection, we ended up as the strange creatures we are today, walking around on our back legs and still dealing with the pains and problems that predictably come along with a bipedally adapted primate physiology.

Conclusion

In this article, I have argued that hominin bipedalism came about through a process of sexual selection because that is the only type of selection that could overcome all the deleterious fitness consequences that almost certainly resulted from such a transition. I also laid out a specific evolutionary story of how bipedalism was sexually selected for. But if my hypothesis is correct, this has interesting consequences for the evolutionary history of *Homo sapiens*. First, it means that the reason why we walk bipedally and all of our closest ape relatives walk quadrupedally is simply chance. Indeed, it could have been another lineage that "chose" bipedalism as a fitness signal, and our ancestors could have just as easily stayed quadrupedal and/or arboreal. In the end, though, it is important to remember that because there was no particular reason for this selection pressure to occur, the emergence of a bipedal fitness signal is, in general, an extremely unlikely event. Which is to say, if we "rewound the tape of history" (Gould 1989), there is every reason to believe that none of the ape lineages would have become bipedal.

Another interesting consequence of this hypothesis comes from stepping back and looking at our evolutionary history as a whole. As I mentioned in the beginning, the fossil evidence indicates that bipedal locomotion was the first major development towards modern humanity. Only after bipedalism did brain expansion, tool-use, language, and loss of body hair occur. So what does this mean? One intriguing possibility is that once hominins became bipedal, and their hands were free, they started using them for other purposes, such as tool-use and object manipulation. This could have then resulted in brain expansion, due to the new and complicated possibilities that emerged from using their hands in novel ways. Of course this specific turn of events is quite speculative. What's important to realize, though, is if bipedalism was the catalyst for all the modern adaptations of *Homo sapiens*, then that means that we are who we are only because of a random bout of sexual selection.

Acknowledgements

I thank Sahotra Sarkar for all of his very helpful guidance, comments, and advice. I also thank Michael Wilson, Chris Kirk, Liza Shapiro, Jerry Samet, Kevin Hunt, William Edgecomb, and Blair Baron for their feedback and support.

Referees

Michael L. Wilson – wilso198@umn.edu
University of Minnesota

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Response to Referee

I am very grateful to Michael Wilson (2018) for his insightful response to my article. Indeed, his challenging points not only do much to develop the debate, but they also occasionally reveal novel, and potentially fruitful, avenues of research related to the hypothesis. For example, Wilson mentions the sexually alluring nature of tall(er) men in modern culture. Could this be a byproduct (or an extension) of the original attraction to bipedal males? That is, could a taller man (or woman) be interpreted by our genes to be “more bipedal”? And what about gait itself? Intriguingly, men find it sexually alluring when women swing their hips while women find the strutting of broad-shouldered men to be attractive (Morrison et al. 2018, Swami et al. 2007). Could strutting, broad shoulders, and swinging hips be related to our attraction to bipedal ability? Finally, what about dancing? We seem to be attracted to good dance partners; could this be related to their ability to maneuver well on two feet? Of course, contemporary research in evolutionary psychology continues to be controversial, and we should be very aware of the possibility that modern sexual attractiveness could have emerged from a multitude of factors, some of which may be relatively recent. However, it remains a plausible hypothesis that if

bipedalism was originally a sexually selected trait, then other traits that were related to (or at the very least confused with) bipedal locomotion also became sexually attractive.

Turning now to Wilson's more critical comments, he first discusses how I overlook some the benefits of bipedal locomotion, such as travel efficiency, object carrying, tool use, and weapon wielding. However, he agrees with me that it is unlikely that any of these were the original cause of obligate bipedal locomotion, and instead were probably downstream effects. What he does not agree about are the advantages of bipedalism during foraging. Indeed, he claims that bipedalism would have been so beneficial to particular types of foraging (e.g. shallow water and small tree foraging) that it is there that we can find the strong selection pressure that I was looking for, as opposed to in the more arbitrary power of sexual selection.

Why is foraging a more promising hypothesis than sexual selection? First, he points out that natural selection primarily equips organisms with the ability to feed itself effectively, and only secondarily with abilities to charm mates. While this is ultimately an empirical question, it seems likely that the realities of selection are much more complicated than Wilson suggests. Indeed, instead of natural selection first equipping an organism with one (more primary) capability before another (more secondary) capability, it is more likely that these abilities are wrapped up in each other in a complicated relationship of energy efficiency and developmental tradeoffs. True, foraging and eating are important capabilities that are fundamental for an organism's survival, but survival is only important to selection insofar as an organism is able to pass on genes. And of course the *only* way this occurs is through attracting mates. Thus, it is most likely the case that *sometimes*—depending on the specifics of the organism, its evolutionary history, and its developmental constraints—feeding is more important than mate attraction but at other times mate attraction is the more primary focus. And importantly, this is what we often see. As mentioned in the article, peacocks would almost certainly be able to forage and digest their foods more efficiently and effectively if they invested the energy required to develop and maintain their enormous, costly tails into feeding capabilities, but in this case it seems that mate attraction was the more important investment.

However, for the sake of argument, I'll grant Wilson this point. Let's say that it *is* the case that the ability to feed is more primary and fundamental than the ability to attract mates. Does this lead to the idea that foraging is a more likely cause of the evolution of hominin bipedalism than sexual selection? I would argue that it doesn't and, in fact, lends further support to the sexual selection hypothesis. Recall the section of my article that discusses the diet transition that our hominin ancestors went through when they came down from the trees. Instead of

eating the fruits, leaves, gums, flowers, insect galls, and nuts found in the trees, our ancestors then had to focus on ground foraging and even hunting, which would not only have been significantly more difficult—as there is less food to be found on the ground floor—but also more dangerous. So what exactly would the foraging-focused cause be that led to our ancestors revolutionizing their diet for a less reliable and more dangerous menu? Wilson mentions small tree foraging and shallow water wading, but he doesn't give us any hint for why we should, first of all, believe that such foraging techniques couldn't be accomplished by facultative bipedalism and, second of all, accept that the benefits of such specific types of foraging were so strong that they forced a revolutionary transition that was deleterious for so many other aspects of daily life. Which is all to say, if feeding was so fundamental, why didn't we just stay in the trees?

Now that we have considered the positive case that Wilson gives for his alternative explanation, let's turn to the negative case he puts forward against the sexual selection hypothesis. One interesting assertion Wilson makes is that in modern humans, both females and males are equally bipedal, and if the Laetoli footprints are any indication, the same was the case for our hominin ancestors 3.66 Ma. Overall, I agree that the equally bipedal status of modern humans is a legitimate objection to my hypothesis, and that is why I spend significant time addressing it in my article (and will not spend more time addressing it here). However, the claim that the Laetoli footprints support the idea that our ancestors during that time were also equally bipedal is straightforwardly false. All the footprints tell us is that three bipedal creatures walked through the volcanic ash without leaving a single handprint (Tuttle 2014: 143), and of course this tells us nothing about the genders or ages of the individuals who left the footprints. However, as I mentioned in the article, there is *specific, skeletal evidence* that *Australopithecus afarensis* males were more terrestrial than females (Senut 1980, Tardieu 1983, Stern and Susman 1983, Susman et al. 1984, Hunt, 1994), which lends support to the idea that males and females were in fact not equally bipedal in ancestral populations.

Next, Wilson states that my understanding of bipedalism as an arbitrary fitness badge is confused because I am conflating its use in mate attraction with its (possible) use in rival competition. In response, I'll admit to a certain amount of conflation, but I believe there is good reason for such conflation. Recall my explanation of how bipedalism began among our hominin ancestors. First, there were males using different strategies to intimidate each other for higher ranking status (and thus more reproductive rights), and one of these strategies was bipedal locomotion. Thus, my hypothesis posits that the original reason that bipedalism was sexually selected for was for its use in status competition, just as antlers, horns, and tusks were. The reason that it is arbitrary is because

it could have been the case that a different trait—one that was also used in status competition, such as arm strength, hair length, or speed—was singled out to become a badge of status in and of itself. Thus, bipedalism is just as arbitrary as any of the other traits related to intra-sexual competition that Wilson mentions. But here is the important point, and one that I believe Wilson misunderstands in his response. Once one of these traits is “chosen” by the selector sex, it is no longer only a trait helpful in intra-sexual competition; it is also a symbol of status in and of itself. Large antlers, canine teeth, bipedalism: all of these became associated with more dominant male standing and, in effect—often without the need to engage in any intra-sexual competition whatsoever—led to more reproductive success.

Finally, I agree with Wilson that a broader comparative perspective can only help. However, there’s something interesting and potentially revealing about all of the animal species he mentions. In particular, each species adopts (either facultative or obligate) bipedalism for very specific and obvious reasons. Bears and gerenuks become bipedal to feed; Jesus lizards, kangaroo rats, and spring hares to avoid predators; pangolins to dig; and birds to fly. For humans, however, there is no specific and obvious reason, and that lends further credence to the idea that the more random and arbitrary process of sexual selection provides perhaps the most compelling explanation yet.

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