

Bipedalism

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Bipedalism is locomotion on two legs. Among living forms, birds and humans are exclusively bipedal.

Introduction

The first vertebrates to conquer land had four limbs that were derived from the paired pectoral and pelvic fins of their aquatic ancestors. During terrestrial locomotion, such early tetrapods were quadrupedal, using coordinated action of fore- and hindlimbs (as well as undulations of the vertebral column) to support and propel the body. Over their subsequent 400+ million year radiation, most tetrapods retained quadrupedalism. However, some groups evolved bipedalism (bipedality).

Bipedalism has special significance to humans because we ourselves are bipedal. After infancy, we stand and move exclusively with our hindlimbs. Our hands and arms are poorly suited for terrestrial use because they are highly specialized for grasping. Among living forms, birds are also exclusively bipedal. The avian forelimb functions as a wing during flight, leaving the hindlimbs as the sole means of terrestrial movement. Because humans and birds are so specialized for bipedal locomotion, they can be considered 'obligate' or habitual bipeds. Birds and humans differ in many ways, yet they share characteristics related to the common design constraints of obligate bipedalism.

Species that move on the ground using either four or two limbs are 'facultative' bipeds. Like obligate bipedalism, facultative bipedalism has evolved independently multiple times within tetrapods. For example, many lizards are able to run on just their hind legs, but they stand and walk on all four limbs. Marsupials (e.g. kangaroos and wallabies) and several rodent groups (e.g. kangaroo rats and jerboas) have evolved bipedal hopping. Some nonhuman primates, bears and hoofed animals also have bipedal capabilities, but are still usually quadrupeds. As will be discussed, facultative bipedalism is a likely intermediate stage in the evolution from obligate quadrupedalism to obligate bipedalism.

Problems

Interesting questions regarding bipedalism include:

- How do bipeds stand or move?
- Is there more than one way a biped can move?
- How are different forms of bipedalism characterized?

Introductory article

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- How did obligate bipedalism evolve in birds and humans?
- What anatomical and behavioural adaptations do bipeds typically evolve? and
- Why did bipedalism evolve?

We focus on avian and human bipedal locomotion and the evolution of obligate bipedalism. A discussion of gaits and common adaptations is followed by an exploration of ideas about the origins and adaptive significance of bipedalism.

Gaits

Bipeds move their limbs in different ways. Some of these locomotor styles are considered distinct gaits, such as walking, running and hopping. A gait is often used over a specific range of speeds. Like shifting gears in a car, many animals change from walking to running at higher speeds. Similarly, many facultative bipeds transition from four to two legs to achieve higher speeds. Compared to quadrupeds, however, bipeds are much more limited in their number of options. The individual movements of four legs can be combined into many more patterns and therefore gaits than the motions of two legs.

Gait definitions

Understanding the definition and functional significance of each gait requires some basic terminology. Bipeds locomote using cyclical movements of the hindlimbs. One complete cycle is called a stride. Each limb spends a portion of a stride in contact with the ground. During this period, called the stance phase, the limb can support the body and change its forward speed. The stance phase is followed by the swing phase, during which the limb leaves the ground and is brought forward for the next stance phase.

Right and left limbs both undergo one stance phase and one swing phase per stride. However, their relative timing can vary, and interlimb coordination is one feature used to define different modes of bipedalism. In walking and running, for example, the right and left limbs are completely out of synchrony. When the right limb is in

the middle of its stance phase, the left limb is in the middle of its swing phase. Such alternating limb timing is often referred to as ‘striding’. In contrast, both limbs act in synchrony during hopping. The right and left limbs of hoppers have stance and swing phases that occur simultaneously, thereby effectively acting as one single limb. A third alternative is to avoid strict alternation or strict synchronization. Some birds move with some, but not complete, overlap of stance phases. Two different definitions of walking and running gaits are commonly used, based either on footfall patterns or on patterns of energetic fluctuation.

Swing versus stance phase duration

Walking is traditionally distinguished from running by the relative duration of the stance and swing phases of the stride (**Figure 1**). In bipedal walking, each foot spends more than half of the stride in stance. Because the two feet are each on the ground more than half of the stride, there are times when both feet are on the ground simultaneously. Such overlapping of stance phases leads to ‘double support’, which is characteristic of walking. In bipeds, running is traditionally defined as a striding gait lacking double support. During running, each foot spends less than half of the stride on the ground. As a result, there are times when both feet are off the ground simultaneously. Overlapping swing phases create an ‘aerial phase’ as the body leaves the ground and follows a ballistic trajectory until the next stance phase. Hopping is quite similar to running in that it also has an aerial phase. Hoppers simply use both legs for every ground contact, whereas striding runners alternate stance phase legs between aerial phases.

Patterns of energetic fluctuations

More recently, walking and running have been distinguished by their underlying energetic mechanisms, rather than their footfall patterns (**Figure 1**). Walking has been likened to an inverted pendulum, in which the body vaults up and over a relatively stiff stance phase leg. The body of a walking animal is highest at mid-stance, when the body’s gravitational potential energy is at a maximum. The body then falls forward and down, converting gravitational potential energy into kinetic energy as the body increases its forward velocity. This increase in velocity is then used to drive the body upward on the next stance leg. Such an exchange between potential and kinetic energy saves some metabolic energy that would otherwise be used by muscles to elevate and accelerate the body with each step.

Running and hopping, in contrast, are bouncy, spring-like gaits. During ground contact, the stance phase limb of a runner is compressed like the spring in a pogo stick. In contrast to walking, a runner’s body is lowest at mid-stance. As the limb compresses in the first half of stance, elastic strain energy is stored in its tendons and muscles. In the second half of stance, this energy is released as the

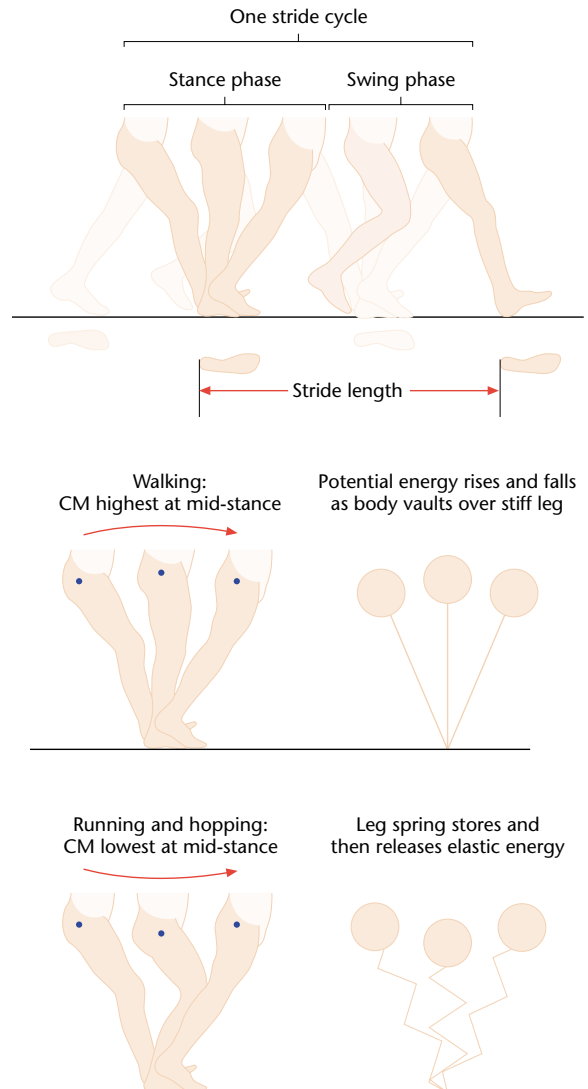


Figure 1 Biomechanics of bipedalism. Top: elements of the stride cycle. Middle: inverted pendulum model of walking. Bottom: spring-like model of running. CM refers to the body’s centre of mass.

stretched musculotendinous springs recoil, propelling the body upward and forward into the air. Kinetic and gravitational potential energy of the body are in phase, not out of phase as in walking. Like a bouncing rubber ball, a runner or hopper conserves metabolic energy by using its hindlimbs like springs, not like stiff struts as in walking. Birds running at intermediate speeds often lack an aerial phase (fitting the former definition of a walk), but are bouncing (fitting the latter definition of a run). This is one of several lines of evidence suggesting that this definition of walking and running is more accurate and meaningful than the previous, simpler definition, although both definitions often work well.

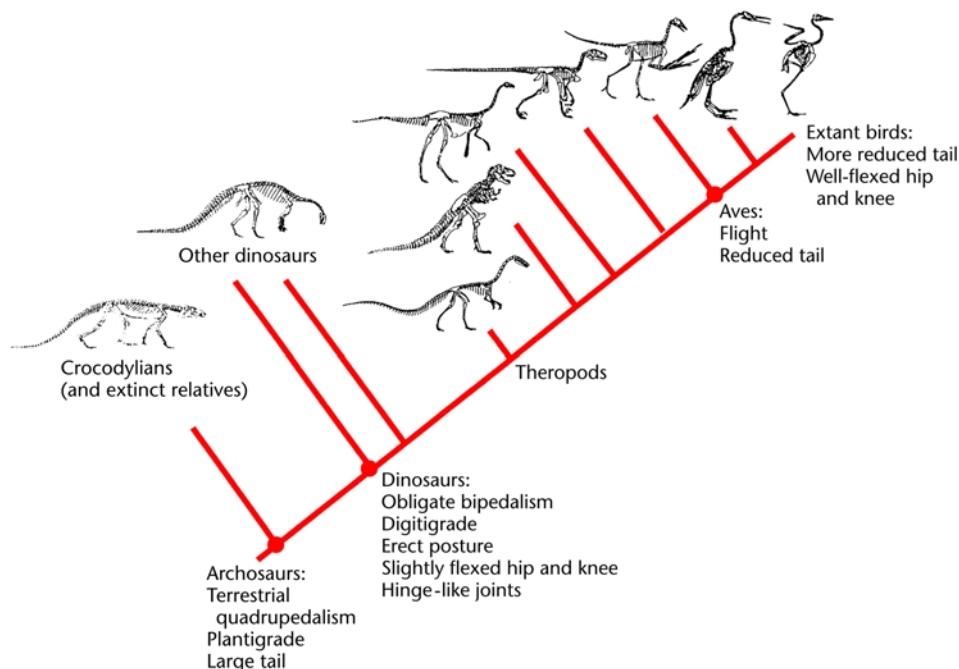


Figure 2 Evolution of bipedalism in archosaurs. Key features are plotted on the phylogeny to reconstruct when they originated. Illustrated skeletons are modified from Carroll RC (1988) *Vertebrate Paleontology and Evolution*. New York: WH Freeman; following Gatesy (1990).

Comparison: birds and humans

Despite many differences in the musculoskeletal design of primate and avian hindlimbs, humans and birds share the energy-saving mechanisms of walking and running outlined above. Other similarities in anatomy and behaviour are also present. For example, humans and birds all have highly adducted limbs, in which the feet are located below the body rather than out to the side as in more sprawling forms. Humans and birds also have relatively large ground contact surfaces. Birds walk on just their toes (digitigrady), but their three main digits tend to be relatively long and widely spread. Humans place their entire five-toed foot on the ground (plantigrady), thereby providing a large base of support. When differences in body size are accounted for, birds and humans use very similar combinations of stride duration and other parameters during locomotion. Such commonalities may be characteristic of obligate bipedalism in general, because they evolved independently in the separate lineages that gave rise to birds and humans.

Birds

In today's world, birds are easily recognized as feathered, flying, endothermic, beaked, bipedal vertebrates. Among

living animals, birds are most closely related to the crocodylians (crocodiles, alligators, caimans, etc.). Crocodylians are all quadrupedal, and appear to offer little to the question of how, when and why birds became bipedal. However, birds and crocodylians are merely the surviving representatives of a much larger group of animals known as archosaurs, the 'ruling reptiles'. Archosaurs include many extinct forms, such as dinosaurs, that provide crucial evidence about the evolutionary history of obligate bipedalism in birds.

A phylogeny of archosaurs is required to trace the transformation from quadruped to biped on the line leading to extant (= modern, or living) birds. A phylogeny is a hypothesis of the evolutionary relationships between organisms, both living and extinct. By analysing the distribution of morphological features, particularly those in the skeleton, evolutionary biologists can construct hypotheses of archosaur interrelationships and display them using phylogenies. Using such a phylogeny (**Figure 2**), characteristics related to the evolution of bipedalism and locomotion can be surveyed in the clade Archosauria, allowing us to ask important questions. For example, when on the line to extant birds did bipedalism evolve? Is bipedalism a novelty seen only in birds, or did birds inherit bipedalism from their ancestors? Did bipedalism arise more than once in archosaurs? Do bipeds ever return to quadrupedalism?

Based on the phylogeny, the ancestor of all archosaurs was probably a medium-sized quadruped. Where do birds fit into the archosaur family tree? Numerous analyses have resolved that birds evolved from theropod dinosaur ancestors in the Mesozoic era, at least 150 million years ago. Theropods include carnivorous forms such as *Allosaurus*, *Tyrannosaurus* and *Velociraptor*, as well as their avian descendants. The ancestor of all dinosaurs, including the theropods, was probably a small obligate biped. Thus the striding bipedalism seen in living birds is at least 235 million years old. Obligate bipedalism may have evolved in other nondinosaurian archosaurs, although this is controversial. Early members of all dinosaur groups moved on two legs, but at least four lineages reverted back to quadrupedalism. Most armoured dinosaurs, horned dinosaurs and long-necked sauropods were secondarily quadrupedal, having abandoned the bipedal abilities of their ancestors as their lineages attained larger body sizes.

Similarities among birds and their theropod ancestors

Most importantly for this discussion, all theropod dinosaurs were striding, obligate bipeds. Evidence for bipedalism in theropod dinosaurs comes from the interpretation of skeletal remains, as well as from direct evidence of locomotor behaviour: fossil footprints. Extinct theropods had long, digitigrade hindlimbs very similar to those of birds. Their forelimbs were typically much shorter, and bore predatory, grasping hands not suitable for locomotion on the ground. In forms with extreme forelimb reduction, such as *Tyrannosaurus*, habitual quadrupedalism was simply impossible. Additional evidence comes from the structure of the hindlimb joints: they are hingelike, mainly allowing only fore and aft motions (like the human knee), unlike the less constrained joints of crocodylians and other nondinosaurian reptiles.

Fossil trackways attributed to theropods confirm that all theropods were obligate bipeds, because impressions of the hands are almost never found. Left and right footprints alternate, indicating striding rather than hopping gaits. The prints are closely aligned as in other forms with highly adducted limbs. Indeed, the trackways of Mesozoic theropods differ little from those of birds today. Obligate bipedalism did not evolve with the origin of birds or the advent of flight. Rather, birds simply retained this locomotor style from their theropod ancestors.

Differences between birds and their theropod ancestors

Despite strong similarities, extant birds differ from Mesozoic theropods in several important features, suggesting that their limbs were not functionally identical. One such difference is the tail. Birds are unusual in that they

have lost the long, muscular tail characteristic of basal theropods. Such a tail allows the body to balance about the hips as a cantilever. Birds have reduced their tail, which is now mostly composed of feathers. To compensate, their limbs have reoriented to position the knee, rather than the hips, near the centre of mass. Consequently, birds use novel limb movements not present in earlier theropods. The crouched stance and horizontal trunk of birds is quite unlike humans, who have a more upright stance and vertical trunk. Maintaining this crouched stance requires more active muscle relative to the upright stance of humans. Several lines of evidence support the inference that early theropods had a more upright stance than birds do today.

A long tail also appears to have been important for the evolution of bipedalism in archosaurs. The heavy tail (as in crocodylians) locates the centre of mass of the body posteriorly in comparison to a smaller tail (as in birds). The shift from quadrupedalism to locomotion on the hindlimbs is presumably easier if the hindlimbs normally carry a large portion of the body weight. Such a shift occurred in the lineage leading to dinosaurs, and possibly other archosaur groups. Controversy persists over the status of some archosaurs (such as the pterosaurs and ornithosuchids) as obligate striding bipeds, facultative bipeds, hoppers, or obligate quadrupeds.

Other changes in limb proportions, joint articulations, muscle attachments, body size and centre of mass position, and neural control of locomotion evolved along the line to extant birds. Thus the overall pattern of locomotion evolved from early bipedal dinosaurs to extant birds. Early theropods and other dinosaurs presumably moved unlike living birds in several ways, such as swinging the thigh (rather than the knee) through a large arc during walking.

Humans

The history of human bipedalism is remarkably short by comparison with birds, but can be studied in much the same way. A phylogeny containing our close living and fossil relatives allows the evolution of bipedalism to be studied (**Figure 3**). We (*Homo sapiens sapiens*) are members of the Hominidae, a group that also includes some extinct nonhuman primates (e.g. the species of *Australopithecus*, *Paranthropus* and *Ardipithecus*) and early humans (e.g. *Homo erectus*), but not gorillas or chimpanzees (the 'great apes'). We are not the only obligate bipeds on the tree; we have several extinct relatives that probably were obligate bipeds. Thus obligate bipedalism is not unique to us; we inherited it from our ancestors. Like birds and other archosaurs, evidence for bipedalism in extinct hominids can be taken from fossil trackways as well as functional anatomy and the use of phylogenies.

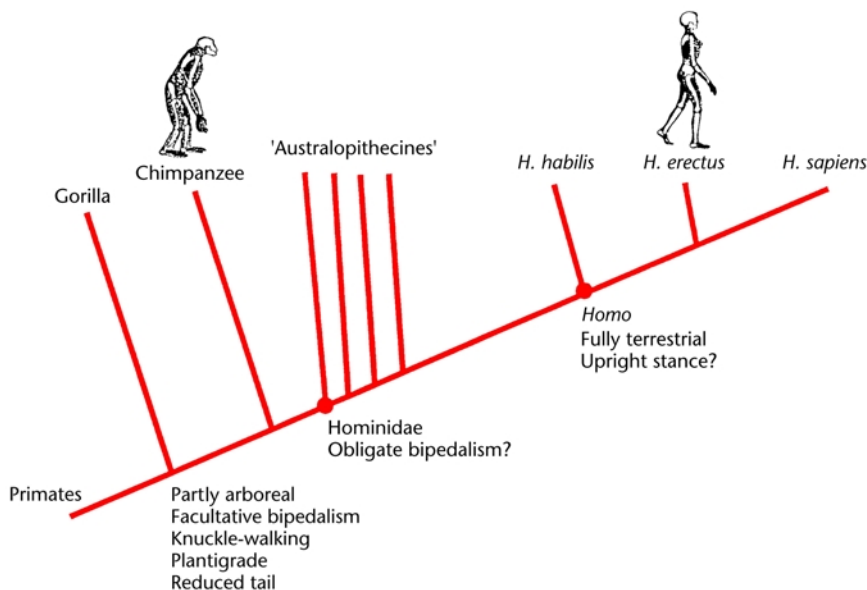


Figure 3 Evolution of bipedalism in hominids. Key features are plotted on the phylogeny to reconstruct when they originated. It is unclear when the most derived features of human bipedalism evolved, but they were clearly present in *Homo erectus* and later hominids. Illustrated skeletons are modified from Norman D (1994) *Prehistoric Life*. New York: Macmillan.

Unfortunately, despite the quite recent acquisition of bipedalism by hominids, the exact point of origin of hominid bipedalism remains murkier than the origin of avian bipedalism. Lack of clear resolution of the interrelationships of hominids is a major obstacle that can be explained by the generally poor fossil record of hominids and their close relatives. Hundreds of fossils of the extinct relatives of birds are well known from complete skeletons (including feathers and other soft tissues), whereas comparatively few hominids are known even from partial skeletons. 'Avian' (or dinosaurian) bipedalism has a 235 + million year, fossil-rich history compared to the known 3.5 million years of hominid bipedalism; it should not surprise us that many mysteries remain.

Evidence for bipedalism in human ancestors

Some confident statements about the evolution of human bipedalism are possible. Facultative bipedalism and plantigrady are ancient features for apes and other primates, and hence were the ancestral conditions from which obligate bipedalism evolved. Most primates carry a disproportionate amount of their weight on their hindlimbs, which facilitates bipedalism. Bipedal hominids existed at least 3.5 million years ago, as shown by a number of bipedal, human-like fossil footprints at Laetoli, Tanzania. The identity of the track makers remains

uncertain. Some think they were *Australopithecus afarensis*, bones of which are known from that area and time period (e.g. the famous 'Lucy' skeleton). An unequivocal identification of the track maker would resolve the latest possible origin of bipedalism in Hominidae.

Anatomical evidence for bipedalism includes modifications of the hip joint and limb muscles that balance the thigh in an upright stance and keep the trunk erect. For example, the ilium (upper bone of the pelvis) supports enlarged gluteal (posterior) muscles that are important for standing and running. Specialized knee and ankle joints place the foot underneath the hip joint. These features provide the ability to balance the body on one foot during upright standing and locomotion. The relatively straight leg minimizes the amount of active muscle needed to balance the body, acting much like a stiff column. The forelimb also lost some specializations for climbing, but gained manipulatory capabilities. Considering this evidence alone, it is clear that *Homo erectus* and other early humans from roughly 2 million years ago were obligate bipeds.

Like early theropods, early hominids probably moved in similar, but slightly different, ways compared to their living descendants. In contrast to the pattern of evolution in theropods, ancestral primates and perhaps some early hominids had a more crouched, less upright stance than their living descendants, who walk and run in an upright stance.

Controversies regarding the origin of human bipedalism

Debate has focused on the functional anatomy of the 'australopithecines' (a diverse assemblage of nonhuman hominids). These hominids have more specializations for bipedalism than their nonhominid relatives do. Thus they had some, although probably not all, derived aspects of human bipedalism. It remains unresolved whether most australopithecines moved bipedally more like chimpanzees (with a crouched stance and shuffling motion) or more like humans (with an upright stance and smoothly striding motion). Some sort of intermediate form of locomotion is also plausible. Australopithecines probably spent less time in the trees than their nonhominid ancestors did, and spent more time on the ground. *Homo* did not evolve until almost 2 million years after the Laetoli hominid left its bipedal footprints.

The origin of bipedalism predates most other major hominid innovations, such as tool use, a highly enlarged brain, larger body size, increased parental care, and more complex language and social organization. Thus bipedalism cannot be seen as a result of those innovations, but could be an important precursor to them. Beyond these statements, little consensus exists. More fossil discoveries will add resolution to this complex debate. The hominid lineage split off from the other apes around 5–7 million years ago. Yet the oldest known hominid, *Ardipithecus ramidus*, is only 4.4 million years old, indicating at least some undiscovered history.

Why Evolve Bipedalism?

Bipedalism is clearly an important part of the lives of birds and humans. Why it evolved is an exciting question with many ramifications. Yet it is a difficult question that may not even be indirectly testable. Teasing apart causation from mere correlation millions of years in the past is no simple task; multiple causes and strong (but noncausal) correlations might exist. Bipedalism is often cited as a 'key innovation' that predisposed the avian and human lineages to achieve the success that they enjoy today (birds have around 10 000 species, whereas humans dominate the globe). Bipedalism is also often cited as a prerequisite for evolving other important adaptations, such as flight in birds or tool use in humans. Although these ideas may be interesting (albeit speculative), they focus on the events

that followed the origin of bipedalism. They have nothing to do with explaining why bipedalism evolved in the first place.

Explanations suggested for evolving bipedalism typically focus on the increased role of the forelimbs in nonlocomotor behaviours such as grasping and carrying food items (or tools). As corollaries, these explanations assume that the forelimbs became unimportant in locomotion as the hindlimbs became dominant. Of course, trade-offs exist; moving on two limbs rather than four may increase food manipulation ability, but decrease speed and/or stability. Other explanations for bipedalism that are falsified by the use of a phylogeny include arboreal climbing, leaping, gliding, or flight (in birds) or increased intelligence (in hominids). Because such traits evolved after obligate bipedalism evolved, they cannot be used to explain its origin.

Many other 'just-so stories' such as social display have been advocated to explain the origins of bipedalism, but are the most difficult to test. Ultimately, the most compelling scenario is that avian and human bipedalism originated in conjunction with increased use of the forelimbs in some nonlocomotor behaviour(s), although additional adaptive factors may have been quite important.

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