ELSEVIER

Locomotor decoupling and the origin of hominin bipedalism

Adam D. Sylvester*

Department of Anthropology, The University of Tennessee, 250 South Stadium Hall, Knoxville, TN 37996, USA

Abstract

Theoretical adaptive landscapes and mathematical representations of key constraints of evolutionary and primate biology are used to propose a new hypothesis for the origin of hominin bipedalism. These constraints suggest that the selective pressure that produced this novel form of locomotion was the need for effective suspensory and terrestrial movement. This testable hypothesis, termed the Decoupling Hypothesis, posits that bipedalism is an adaptation that enables the shoulder to maintain a high degree of mobility, a feature important to suspensory behaviors, in the face of significant demands for a high degree of stability, a feature important for highly effective terrestrial quadrupedism.

© 2006 Elsevier Ltd. All rights reserved.

1. Introduction

Bipedal locomotion is a pivotal development in the course of hominin evolution. Its importance was appreciated early in human evolutionary studies (Dart, 1925; Darwin, 1871) and bipedalism has long been regarded as "the basic adaptation for the foundation of the human radiation starting man on his 'separate evolutionary path'" (Washburn, 1951, 1959; from Hewes, 1961, p. 687). Scientists now recognize that habitual terrestrial bipedalism was the first uniquely hominin attribute to evolve and that it predisposed hominins to evolve other uniquely human traits (Ward, 2002). The question of whether a fossil species is a hominin can be appropriately posed as: was it a biped?

Since Dart's (1925) initial australopithecine discovery, a great deal of research has been dedicated to reconstructing early hominin behaviors. Ward (2002) distinguishes between two separate, although complementary, research questions concerning early hominin locomotion. First, researchers endeavor to reconstruct the daily locomotor behaviors of early hominins and evaluate their relative

capacities for different locomotor adaptations. A great deal of study has been dedicated to this end and, although debate persists, the question is ever closer to resolution (Berge, 1991, 1994; Crompton et al., 1998; Duncan et al., 1994; Jungers, 1988, 1991; Kramer, 1999; Kramer and Eck, 2000; Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990a, b; Lovejoy, 1988; Lovejoy et al., 1973; MacLatchy, 1996; Rak, 1991; Spoor et al., 1994; Stern and Susman, 1983, 1991; Susman et al., 1984).

The second question is to determine the selective pressure that caused hominin bipedalism to evolve. Numerous selective pressures and corresponding scenarios have been put forth to account for the origin of bipedalism. The proposed selective pressures include: provisioning (Lovejoy, 1981), vigilance (Dart, 1925; Darwin, 1871), terrestrial efficiency (Rodman and McHenry, 1980), transporting food (Hewes, 1961), transporting infants (Sinclair et al., 1986), transporting tools (Washburn, 1960), effective tool use (Marzke, 1986), behavioral displays (Jablonski and Chaplin, 1993), seed eating (Jolly, 1970), increased foraging efficiency (Wrangham, 1980), feeding posture (Hunt, 1994), hylobatian model (Tuttle, 1975, 1981) and thermoregulation (Wheeler, 1991a, b). Despite these diverse hypothesized pressures and the tremendous amount of research, no theory has been met

*Tel.: +1 865 974 4408.
E-mail address: asylvest@utk.edu.

with universal support. Consequently, understanding the origin of bipedalism continues to be an elusive goal for paleoanthropology.

The purpose of this paper is to explore a possible increase in fitness resulting from the relaxation of the selective pressure for shoulder stability, which would have accompanied the adoption of bipedalism. I employ adaptive landscapes and mathematical models of well-established concepts from evolutionary biology and apply them to aspects of primate anatomy and behavior. When synthesized, the adaptive landscapes and models produce a series of visually interpretable results that provide the conceptual underpinning for a testable new hypothesis for the origin of bipedalism called the Decoupling Hypothesis (DH). The DH posits that hominin bipedalism is an adaptation that reduces the selective pressure for shoulder stability so that hominins could simultaneously achieve highly effective terrestrial and suspensory behaviors, a combination not accessible to quadrupeds because of a trade-off in shoulder stability and mobility. Negative affects on fitness related to changes in hind limb morphology are not included in the models, but are discussed.

A review of the numerous forms of primate locomotion reveals that most primates, excluding a few notable exceptions, naturally use both the forelimbs and hind limbs simultaneously (Hunt et al., 1996). Since all four limbs act cooperatively during locomotion, the general primate body plan can be considered to consist of a single "locomotor module," a term Gatesy and Dial (1996, p. 331) define as "anatomical subregions of the musculoskeletal system that are highly integrated and act as functional units during locomotion." Humans are similar to other primates in predominantly utilizing a single locomotor module, but have diverged markedly from the quadrupedal pattern. In modern humans, the forelimbs are freed from weight bearing responsibilities, and that entire burden has shifted to the hind limbs. Thus, for primates, quadrupedism represents the primitive state, while bipedalism is the derived one. To understand the origin of hominin bipedalism is to understand the reallocation of weight bearing function during terrestrial locomotor from four limbs to two. Because the forelimb was relieved of its weight bearing function, and the shoulder transmits forces from the forelimb to the body when engaged in locomotion, the shoulder may prove a fruitful place to search for evidence of the selective pressure that caused bipedalism. To begin, pertinent evolutionary concepts and aspects of primate biology will be examined.

2. Adaptive landscapes

The phenotypic adaptive landscape, a descendent of Wright's (1932) adaptive landscapes relating fitness to genotypes, was originally described by Simpson (1944) as an approach to bridge the conceptual gap between micro- and macroevolutionary processes (Arnold et al., 2001).

Simpson (1944) used landscapes to illustrate several critical concepts in evolution, including: phenotypic variation, selection, response to a changing environment, speciation, and adaptive radiation (Arnold et al., 2001). The phenotypic adaptive landscape (referred from here onward as an adaptive landscape) is a two-dimensional surface where each dimension represents the possible character values of a particular continuous trait. Peaks (areas of higher elevation) and valleys (areas of lower elevation) denote phenotypes of higher and lower adaptive fitness, respectively. Since Simpson's description, no tool has been used so successfully and extensively to visualize major concepts in phenotypic evolution (Arnold et al., 2001). These landscapes provide evolutionary biologists with a powerful device to generate and test hypotheses about phenotypic evolution.

The shape of an adaptive landscape is largely determined by the environment and can consist of single or multiple peaks that correspond to phenotypes with higher fitness for a specific niche. Populations shift across the phenotypic landscapes as selection acts to drive populations to areas of higher fitness. The movement (directional selection) occurs because phenotypes closer to peaks enjoy greater reproductive success than those further away. Stabilizing (a population at the top of a peak) and disruptive (multiple peaks) selection can also be visualized. The shape of the landscape is also susceptible to change resulting in new fitness levels for phenotypes. Change in a landscape reflects variation in environmental/niche conditions and contributing factors may include: climate/ecological changes, colonization of new environments and changing predator/prey relationships (Arnold et al., 2001), although organisms are also dynamic shapers of their own adaptive landscapes (Partridge, 1978). In changing environments, populations will track the moving peak, but rapid peak movement can result in extinction if population change cannot pace environmental change and populations remain in areas of low fitness.

3. Ecological niches, locomotor behaviors and demands on primate shoulders

Primates are characterized by a number of specialized features that are related to life in an arboreal habitat, including a relatively mobile shoulder necessary to navigate discontinuous canopy supports (Clark, 1959). The importance of mobility is evident in primate shoulder morphology which is typified, relative to non-primates, by a globular, highly curved humeral head and a small, relatively flat glenoid fossa (Larson, 1993). While generally more mobile than other mammals, primate shoulders exhibit a great deal of morphological variation, reflecting this group's diverse locomotor and postural behaviors. A primate's shoulder morphology must balance the separate demands for mobility and stability (Larson, 1993). Mobility is defined as the potential range of motion of a joint, while stability is the ability to prevent motion in a

given direction (Hamrick, 1996). Stability can thus refer to the reduction of unwanted passive movements outside normal kinematics and those that disrupt joint integrity.

A primate niche necessitates living and traveling on specific portions of the environment, and as a result, varied substrates (e.g. the ground, tree branches and trunks). These activities are accomplished by locomotor and postural behaviors which generate selective pressures on shoulder morphology. The relationship between shoulder morphology and locomotor behaviors has been examined across primate taxa (see Larson, 1993). Primates adapted to suspensory behaviors have shoulders characterized by large highly curved humeral heads that rise well above the tubercles, relatively small flat glenoid fossae and dorsally positioned scapulae. Analogies in the shoulders of the hominoids and the atelines suggest that this morphology provides the ability to fully abduct the forelimb, thus enhancing suspensory adaptations. Primates that do not engage in suspensory behaviors, relying heavily on quadrupedism (both arboreal and terrestrial), have shoulders distinguish by proximally flattened humeral heads that do not extend above the tubercles, glenoid fossae that are relatively large, and scapulae situated on the lateral aspect of the thorax. These features increase the ability of the shoulder to engage in quadrupedism by adding stability (under compression) to the joint as well as increasing the lever arm of specific muscles. A third set of behaviors, such as sitting and lying (which do not load the shoulder) and vertical climbing (which puts the shoulder under tension) require neither a highly stable shoulder nor one mobile to the point of full abduction. Consequently, these behaviors are likely to have relatively little influence on shoulder morphology. It is interesting to note that while specific morphologies serve to enhance specific locomotor behaviors, it has also been demonstrated that specific loading patterns during growth influence final joint morphology (Duren, 1999; Frost, 1990; Hamrick, 1999; Shefelbine et al., 2002).

The observed morpho-behavioral correlations (Larson, 1993) match the theoretical expectations (Hamrick, 1996) relating morphology with demands for joint mobility and stability. Because the demands for mobility and stability are produced by separate locomotor and postural behaviors, these demands do not have to be correlated. That is, how effective a primate needs to be at one locomotor or postural behavior need not dictate how effective it needs to be at other behaviors, and as a result each unique primate niche will have a unique combination of stability and mobility demands. Thus, an infinite number of combinations of mobility and stability demands are theoretically possible.

4. Trade-off constraints and primate shoulders

While the demands for stability and mobility are independent and the combinations virtually limitless, the actual morphology that a primate shoulder can physically attain is constrained because of a trade-off (negative correlation) between joint stability and mobility. A trade-off is "an inescapable compromise between one trait and another" that makes it "impossible for any population of organisms to evolve optimal solutions to all agents of selection at once" (Freeman and Herron, 1998, p. 297). This type of adaptive constraint is widely recognized in evolutionary biology. Examples of trade-offs include: number and size of female *Begonia involucrata* flowers (Schemske and Ågren, 1995), black and red mating coloration in male threespine stickleback fish (*Gasterosteus aculeatus*) (Hagen et al., 1980; Milinski and Bakker, 1990), current reproduction and future reproduction in birds (Lindén and Møller, 1989), and female investment in children and grandchildren (Hawkes et al., 1998). The trade-off between shoulder mobility and stability occurs because mobile primate shoulders and stable primate shoulder are the extremes of a single phenotypic continuum (Larson, 1993). At one extreme are features that enhance shoulder mobility (curved humeral head, small glenoid, low tubercles and dorsally positioned scapula) while at the opposite extreme are features that increase shoulder stability (proximally flat humeral head, large glenoid and laterally positioned scapula). Thus movement towards one extreme requires movement away from the other extreme. As a result, enhanced shoulder mobility reduces stability, and vice versa.

5. Key innovations and evolutionary decouplings

Accelerations in the rate of evolutionary change of characteristics of an organism are usually called "Key Innovations," especially when they are triggers for diversification (Galis, 2001). Most definitions of key innovations suggest that they increase the number of independent traits and potential versatility of the body plan, opening new character space and allowing for the occupation of more niches (Galis, 2001). Hominin bipedalism appears to be such a key innovation. Four types of key innovations are recognized and include: increased complexity, duplications, new structures and decouplings (Galis, 2001).

Decouplings are particularly common key innovations that result in the division of a single trait into two distinct and relatively independent traits (Galis, 2001; Lauder and Liem, 1989; Schaefer and Lauder, 1986; Vermeij, 1974). Many soft and hard tissue evolutionary novelties are the result of decouplings. Lungs evolved from a pouch in the digestive track and allowed early tetrapods to transition from water to land (Graham, 1997; Johanson, 1970). Muscles are often subdivided into different components, and eventually separated muscles, that have independent lines of action and function (Hildebrand, 1995). Hard tissue decouplings result from modification of bony articulations and can provide greater versatility in function. Cichlid fish decoupled their jaw and cheek bones, increasing mobility and improving predatory capacities

(Galis, 2001). Novel life history stages might also be considered the result of decouplings, as total time between conception and death is divided into more stages with relatively independent developmental purposes (Bogin, 1990). Such physical and behavioral manifestations have underlying genetic causes and correlated genes can become decoupled as selection acts to reduce covariance (Roff, 1997).

Generally, decouplings serve to distribute individual functions to individual structures so that structures do not need to accommodate multiple functions. The evolution of powered flight in birds involves a decoupling that is pertinent to the origin of hominin bipedalism. Modern birds evolved from bipedal theropod dinosaurs (Gatesy and Middleton, 1997; Gauthier, 1986; Ostrom, 1976). These dinosaurs moved with the hind limbs and tail acting in concert as a single locomotor module (Gatesy and Dial, 1996). While the tail of non-avian theropod dinosaurs was used to counterbalance the front of the body around the

Fig. 1. Reproduced from Gatesy and Dial (1996) "Fig. 2. The evolution of locomotor modules and birds. (A) In primitive tetrapods the body axis and all four limbs acted as an integrated unit during terrestrial locomotion. This single locomotor module (shading) is still present in forms such as salamanders. (B) Basal dinosaurs and theropods were obligate bipeds. The hind limb and tail comprised a single, reduced locomotor module (shading). (C) Birds possess three locomotor modules. During the evolution of birds the forelimb regained locomotor function as a wing. The tail decoupled from the hind limb to specialize in control of the rectrices (flight feathers in the tails of birds). The novel allegiance of the pectoral and caudal modules formed the avian flight apparatus (dark shading). The independent hind limb remains as the remnant of the primitive terrestrial module (shading)."

hip during bipedal progression (Gatesy and Dial, 1996), the tail of modern birds plays only a minor role in terrestrial locomotion (Gatesy and Dial, 1993), but provided the requisite lift and stability for early flight (Peters and Gutmann, 1985). Gatesy and Dial (1996) offer that, during the evolution of avian flight, the hind limbs and tail became decoupled so each could perform, and evolve to meet the specific demands of, different locomotor behaviors (Fig. 1). This decoupling did not result in complete independence of the hind limbs and tail modules as the tail is active during terrestrial locomotion, the hind limbs are active during flight, and both modules are employed for takeoff and landing (Gatesy and Dial, 1993, 1996). Thus, the locomotor decoupling in birds and their ancestors resulted in relatively greater functional independence between the hind limbs and tail as compared to their theropod dinosaur ancestors.

6. Methods

Adaptive landscapes were modeled in the statistical package R (R Development Core Team, 2005) as a bivariate cumulative normal distribution using the pmvnorm function. The x-, y- and z-axes represent the stability and mobility of the shoulder and the shoulder fitness of that combination (or phenotype), respectively. Each varies from zero to one. For the shoulder traits, zero is no capacity and one is maximal capacity for that trait. The shoulder fitness of a phenotype is the cumulative probability at a point on the surface of the landscape, and varies between zero and one, where zero is the lowest possible fitness and one is a perfect match between environment and morphology. Shoulder fitness was modeled using a bivariate cumulative because it provides a landscape where all morphologies that meet the demands for mobility and stability have a higher fitness than all morphologies that fail to meet either one or both demands. The cumulative function provides no negative affect (lower fitness) for morphologies that exceed the demand of the environment, but only marginal increases in shoulder fitness once the environmental demands have been met (i.e. once a relatively high level of fitness has been achieved).

The model requires five parameters: two means, two variances and one covariance. The means were modeled between zero and one, where zero represents no demand for the shoulder trait and one represents the highest demand for a shoulder trait. The fitness peaks for 900 theoretical niches were created by varying both means between zero and one at $0.03\bar{3}$ intervals. The variances were modeled to be equal and were set at a low value (0.01). Increasing the variances results in a flatter adaptive landscape and reduces the fitness differential among phenotypes. The covariance between demands for shoulder mobility and stability was set at zero for all landscapes since, as discussed earlier, the demands for shoulder mobility and stability need not be correlated.
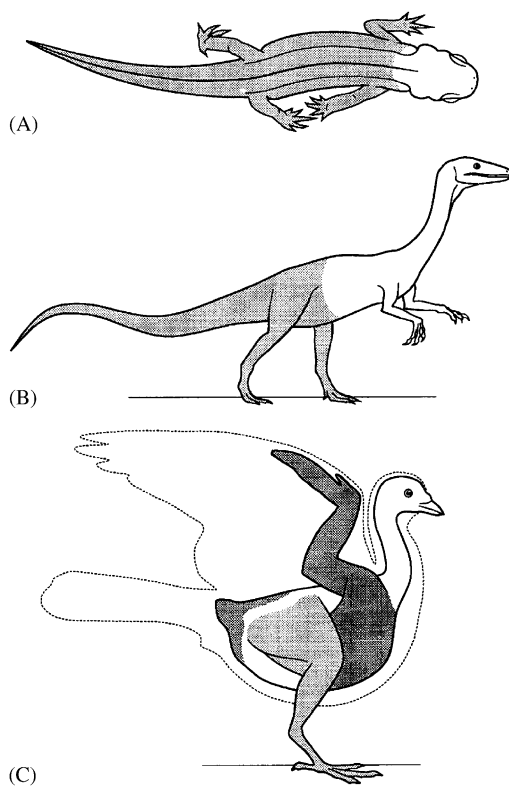
The trade-off between shoulder mobility and stability was modeled as a line across the adaptive landscape. The line represents the physically attainable shoulder morphologies that are part of the theoretical adaptive landscape with highly mobile shoulders towards one end of the line and highly stable shoulders at the other. A hyperbolic model ($y \propto 1/x$) was used to represent the negative correlation between shoulder traits, and provides minimum limits to both traits in order to maintain joint function. Even solid bone provides some mobility because it flexes (Pearson and Lieberman, 2004), and even the most mobile of joints would be stable if compressed so that the force passed through the centers of the joint surfaces. The trade-off line was superimposed upon all 900 theoretical niches. Fig. 2 shows four exemplar landscapes and includes the line of physically attainable shoulder morphologies.

To investigate the effect of the shoulder trade-off on fitness for the modeled niches, the optimize procedure in R (golden search algorithm) was used to search for the maximum shoulder fitness along the trade-off line in each of the 900 modeled niches. The maximum shoulder fitness value for each niche was plotted against the stability and mobility demands for that niche. Then, for each niche that had a maximum shoulder fitness value of less than 0.9, the effect of incorporating bipedalism in each of the lower fitness niches was assessed by reducing the stability demand by increments of 0.002 until the fitness was above 0.9. Bipedalism is modeled as reduction in the demand for shoulder stability because replacing quadrupedism with bipedalism would reduce the demand for shoulder stability. If the maximum fitness for a niche was already above 0.9, then the amount of stability reduction (bipedalism) was set at zero. See Fig. 3 for diagram of methodology.

The reduction in shoulder stability was then plotted against the original niche demands for shoulder stability and mobility. The reduction of stability was then divided by the original demand for shoulder stability. This provides the proportion of quadrupedism (original stability demand) that would have to be replaced with bipedalism to raise fitness above 0.9. This proportion was then plotted against the original niche demands for stability and mobility.
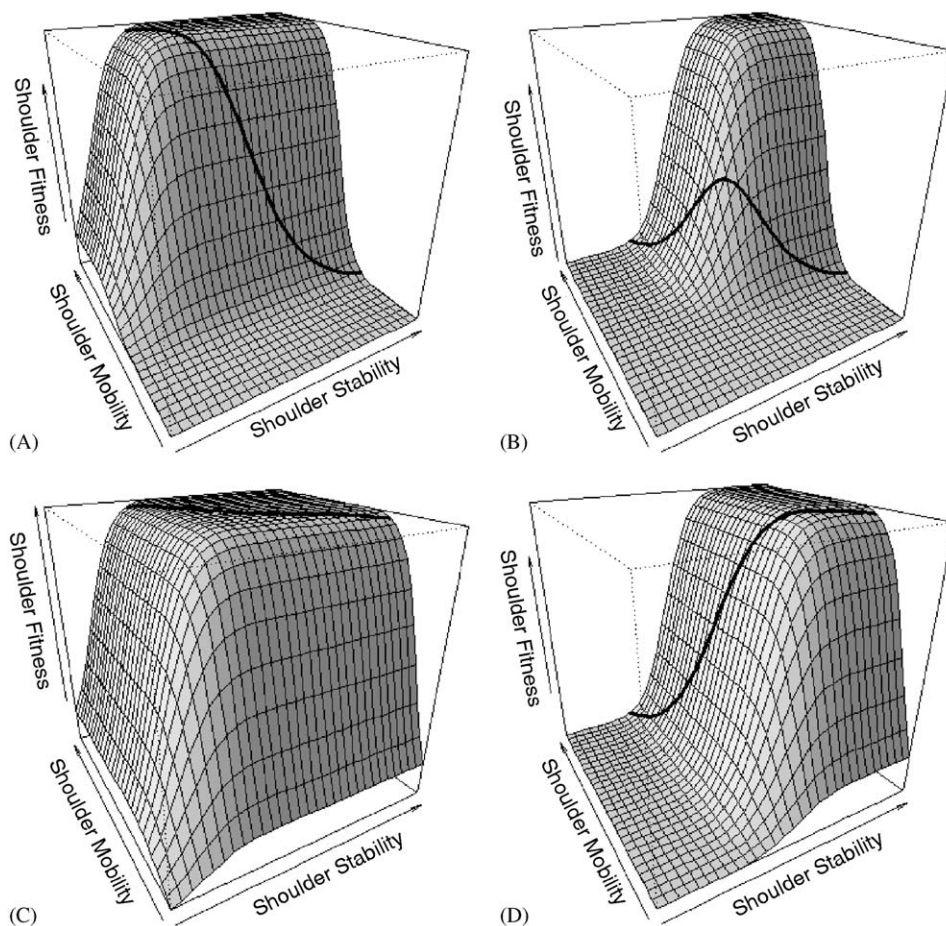

Fig. 2. Adaptive landscapes for four modeled niches that include trade-off line. A–D: Adaptive landscape, that include trade-off line, for niches with demands for: (A) high mobility and low stability ($X_M = 0.5$, $X_S = 0.1$); (B) high mobility and high stability ($X_M = 0.5$, $X_S = 0.5$); (C) low mobility and low stability($X_M = 0.1$, $X_S = 0.1$); and (D) low mobility and high stability ($X_M = 0.1$, $X_S = 0.5$). (X_M = mobility demand, X_S = stability demand). Labeling of vertical axis "shoulder fitness" denotes the contribution of the shoulder to total fitness."
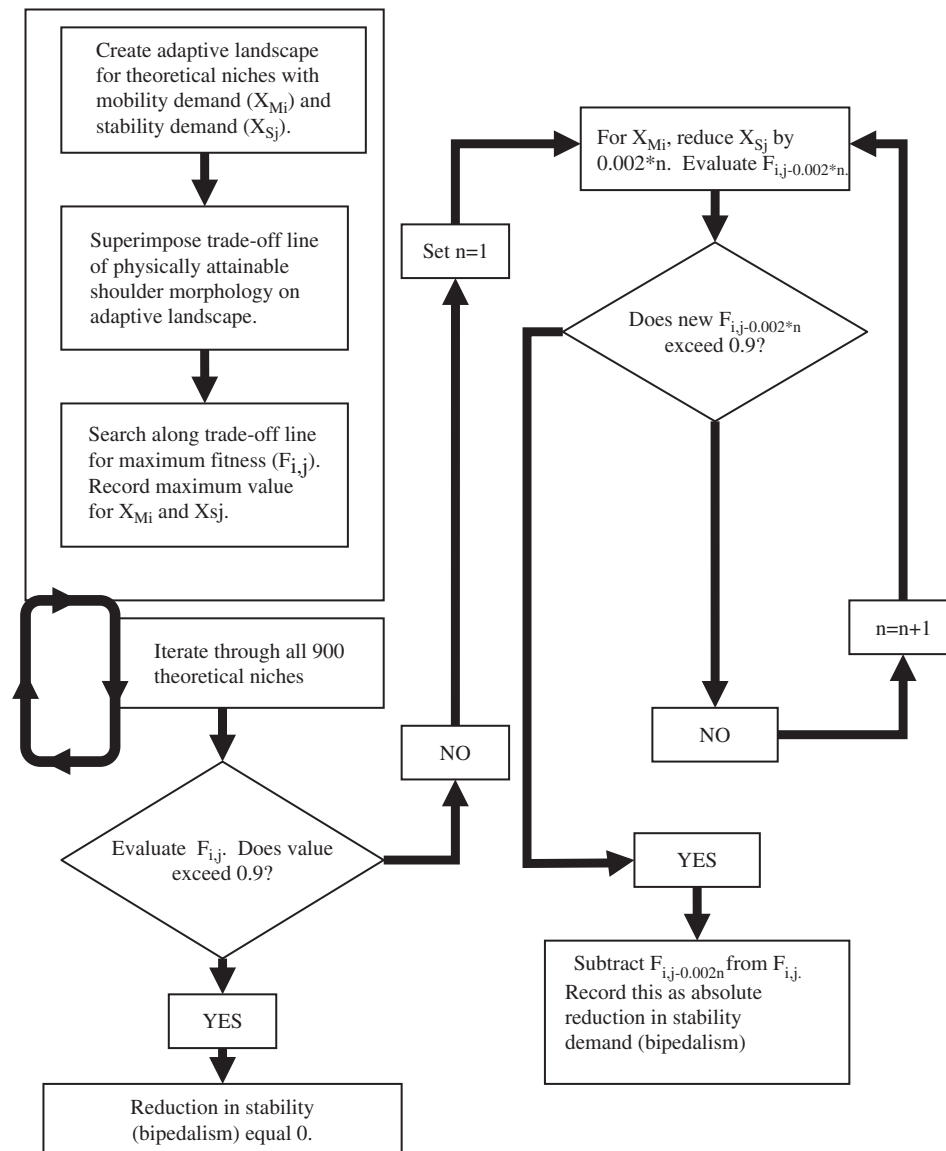
Fig. 3. Flow chart diagramming methodology.

7. Results

Fig. 4 depicts the maximum possible fitness for the 900 theoretical niches. The two horizontal axes represent the demands for mobility and stability, and the vertical axis represents the maximum possible fitness along the line of attainable shoulder morphologies. The effect of the trade-off constraint on primate fitness is that there is a large area of the graph, representing many potential niches, where the maximum possible fitness approaches zero. These represent niches that have intense demands for both shoulder stability and mobility. Note that the graph has been rotated so that the area of high shoulder mobility and stability demands is closest to the reader.

Fig. 5 shows the absolute reduction of stability demand (which equals a replacement of quadrupedism with bipedalism) sufficient to raise the maximum level of fitness above 0.9, and Fig. 6 depicts this reduction in shoulder stability (bipedalism) as a proportion of the original demand for stability.

8. Discussion

The results in Fig. 4 show that there are many niches (those that require highly stable and highly mobile shoulders) in which the maximum fitness of any attainable morphology is very low, approaching zero. Thus, niches that require highly effective forms of terrestrial (or above-branch) quadrupedism and suspensory behaviors are unavailable to quadrupedal primates. Many factors probably influence how effective a primate needs to be at locomotor and postural behaviors. Factors affecting quadrupedal efficacy likely include: efficiency (energy consumption), muscle fatigue, body mass, day journey,
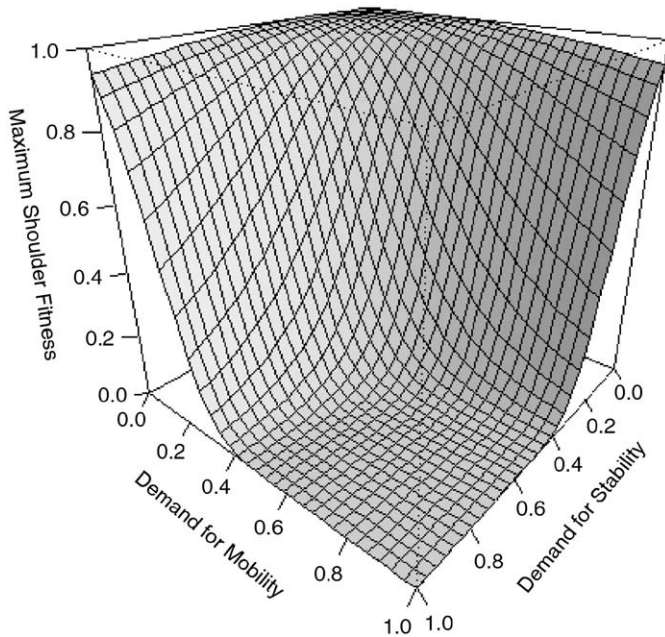
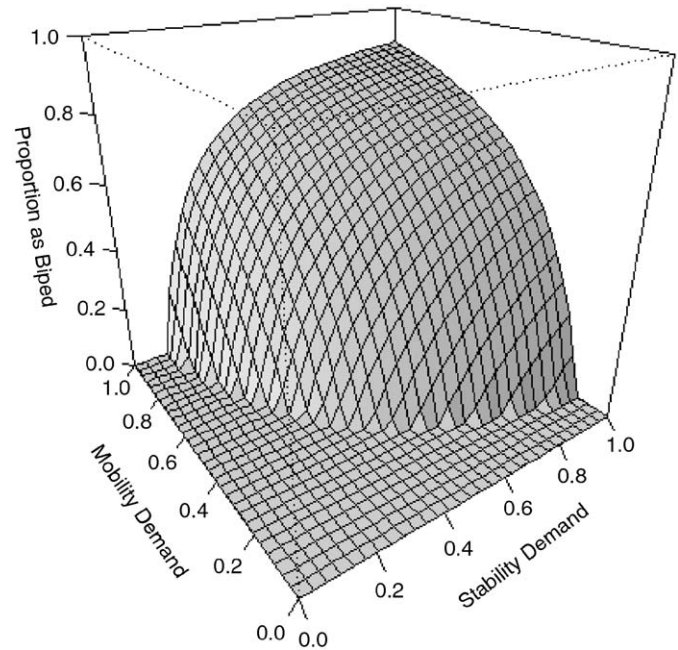Fig. 4. Maximum possible shoulder fitness.

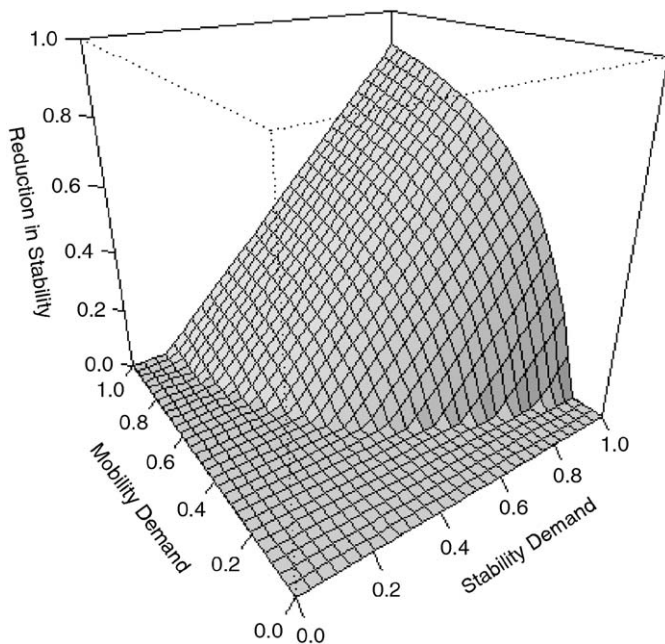Fig. 6. Proportion of terrestrial locomotion performed using bipedalism.

Fig. 5. Reduction in stability demand.

home area, average speed, maximum speed and time spent in activity. Factors that determine suspensory efficacy probably include: efficiency (energy consumption), muscle fatigue, body mass, travel distance, canopy height, stability of support, inherent danger/difficulty (e.g. arm-hanging is likely less demanding than ricochetal brachiation), and time spent in activity. One possible niche that would require highly effective terrestrial and suspensory behaviors is one that mandates a highly efficient form of locomotion adapted to relatively long distances of terrestrial travel at

relatively high speeds, punctuated by suspensory forays into the canopy. This niche would be the hominoid equivalent of the baboon niche. The average day journey of *Papio* species (5.4–10.6 km) are long relative to that of *Gorilla gorilla* (0.86 km) and *Pan troglodytes* (2.4–3.6 km), but also include arboreal travel (Fleagle, 1999; Nunn and van Schaik, 2001). While baboons utilize above-branch quadrupedism for arboreal travel, it has been argued that large-bodied hominoids must employ suspensory behaviors to access fruit at the terminal ends of branches (Andrew, 1981).

Changing environmental conditions that reduced the size and/or carrying capacity of the traditional hominoid niche, and increased the proportion of landmass that mandated use of a novel niche, could have forced the proto-hominin population into such a niche to avoid extinction. It is also possible that the proto-hominin could have shifted to occupy a niche that did not require either highly effective suspensory or terrestrial behaviors. A shift to a purely terrestrial niche would have eliminated the use of suspensory behaviors and drastically reduced the demand for shoulder mobility, thus allowing the shoulder to evolve exclusively to meet the demands for shoulder stability and a highly effective quadrupedism. A shift to such a niche, however, would have required a selective pressure for bipedalism different than the one provided here. A shift to a niche that did not require a highly effective form of terrestrial locomotion would have allowed the shoulder to adapt mainly to meet the demand for mobility. This scenario would also require a different explanation for hominin bipedalism than the one envisioned here.

If the proto-hominin were forced into a niche that re-quired highly effective terrestrial and suspensory behaviors,

there would have been a selective pressure to increase population fitness since presumably the population would not be pre-adapted to it. Selection cannot change the requirements for travel through specific parts of the environment to occupy a niche, nor can it remove the trade-off constraint on shoulder morphology. Selection can, however, act to change the locomotor and postural behaviors used to occupy the niche, and as a result, change the demands on the shoulder. Changes in locomotor and postural behaviors that reduce the demand for shoulder mobility or stability could produce the requisite increase in fitness. Morphological changes that increase the efficacy of newly important behaviors would follow. Behaviorally, mobility could be reduced by replacing suspensory behaviors with non-suspensory forms. Suspensory arboreal adaptations are, as discussed earlier, important to hominoids so that they may access fruit on terminal branches and are unlikely to be eliminated (Andrew, 1981).

The alternative to reducing the demand for shoulder mobility is to reduce the demand for shoulder stability. A transition to bipedalism would reduce the demand on the shoulder for stability, allowing the shoulder to adapt mainly for suspensory behaviors. The forelimbs and hind limbs would become increasingly independent with respect to locomotor function. Retaining a highly mobile shoulder must have provided a substantial advantage for early hominins. The advantage would have had to make up for lost arboreal (vertical climbing and suspensory) adaptation in the hind limbs, although such losses may have been small. Pontzer and Wrangham (2004) suggest that vertical climbing represents a small portion of the energy budgets of chimpanzees relative to terrestrial quadrupedism, and arm-hanging without hind limb assistance is frequently used by chimpanzees, comprising approximately 5% of all postures among Mahale and Gombe chimpanzees (Hunt, 1991).

The retention of high mobility in the shoulder (and likely other suspensory adaptations throughout the forelimb and thorax) would have been critical, and of significant advantage, because of dangers that accompany arboreal behaviors. Loss of forelimb suspensory adaptations would result in less effective suspensory behaviors. This could mean not only lower efficiency, but could have also seriously compromised arboreal safety. Serious injury and death may accompany falls from relatively low heights (6 m) (Crites et al., 1998; Steedman, 1989; Urquhart et al., 1991), and a review of average canopy height usage for the African apes demonstrates that even large male gorillas venture as far as 7 m and that chimpanzees regularly travel as high as 20 m (Doran, 1996). Avoiding debilitating injury and/or death represents a significant gain in fitness.

If bipedalism represented only a small proportion of all terrestrial locomotion, it may not have become the dominant form. If bipedalism, however, represented a sufficiently large amount of all terrestrial locomotion then it is expected to become the dominant form. The results in

Figs. 5 and 6 show the absolute and proportional amount of bipedalism (reduction in stability demand) necessary to attain a relatively high fitness level (0.9). Bipedalism, as a proportion of the original demand for stability, exceeds 0.5 for many of the niches in Fig. 6.

The strength of the DH is that it provides several testable predictions about primate behavior and anatomy, the hominin fossil record and the early hominin niche. These predictions include:

(1) Bipedalism is a predictable behavior in primates. Bipedalism, as a proportion of all terrestrial and above-branch behaviors, should be correlated with the interaction between demands for shoulder mobility and stability. Bipedalism should be the dominant form of above-branch and terrestrial behaviors in niches that require highly effective forms of both terrestrial (or above-branch) and suspensory behaviors.
(2) The early hominin body plan should appear to be superiorly/inferiorly split. The upper body should appear adapted to suspensory adaptations and these adaptations should not simply reflect evolutionary lag. The hind limbs should appear adapted to terrestrial locomotion.
(3) The early hominin niche should require highly effective forms of terrestrial and suspensory locomotion. This niche is expected to be different from those occupied by quadrupedal hominoids.
(4) Since loading patterns during development influence joint morphology, primates that require highly mobile shoulders should utilize behaviors during the time of shoulder growth that reduce shoulder forces that would lead to more stable morphologies.
(5) Quadrupedal primates with highly mobile shoulders should have a reduced above-substrate locomotor efficacy. This could include lower efficiency, reduced speed, limited daily journey, or earlier onset of muscle fatigue.
(6) Primates with highly stable shoulders should have a reduced capacity for suspensory behaviors.

9. Conclusion

The results presented here offer paleoanthropology a new testable hypothesis for the origin of hominin bipedalism. The DH posits that bipedalism is the result of a selective pressure that increased the independence of the forelimb and the hind limbs with respect to locomotor function. Bipedalism would have allowed early hominin to occupy niches that mandated highly effective terrestrial and suspensory behaviors which would not have been available to quadrupeds because of the trade-off between shoulder mobility and stability. I submit that exploration of the DH is warranted. Research is currently being planned and conducted to test the proposed hypothesis.

Acknowledgments

References

Andrew, P., 1981. Species diversity and diet in monkeys and apes during the Miocene. In: Coichon, R.L., Fleagle, J.G. (Eds.), Primate Evolution and Human Origins. Aldine Press, New York, pp. 1–23.

Arnold, S.J., Pfrender, M.E., Jones, A.G., 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. Genetic 112–113, 9–32.

Berge, C., 1991. Quelle est la signification fonctionnelle du pelvis trés large d'*Australopithecus afarensis* (AL 288-1)? In: Senut, B., Coppens, Y. (Eds.), Origine(s) de la bipédie chez les Hominidés. CNRS, Paris, pp. 113–120.

Berge, C., 1994. How did the australopithecines walk? A biomechanical study of the hip and thigh of *Australopithecus afarensis*. J. Hum. Evol. 26, 259–273.

Bogin, B., 1990. The evolution of human childhood. Bioscience 40, 16–25.

Clark, W.E.LeGros, 1959. The Antecedents of Man. Edinburgh University Press, Edinburgh.

Crites, B.M., Moorman III, C.T., Hardaker Jr., W.T., 1998. Spine injuries associated with falls from hunting tree stands. J. South Orthop. Assoc. 7, 241–245.

Crompton, R.H., Li, Y., Wang, W., Günter, M.M., Savage, R., 1998. The mechanical effectiveness of erect and "bent-hip, bent-knee" bipedal walking in *Australopithecus afarensis*. J. Hum. Evol. 35, 55–74.

Dart, R.A., 1925. *Australopithecus africanus*: the man-ape of South Africa. Nature 115, 195–199.

Darwin, C., 1871. The Descent of Man. New York University Press, New York.

Doran, D.M., 1996. Comparative positional behavior of the African apes. In: McGrew, M.C., Marchant, L.P., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, pp. 213–224.

Duncan, A.S., Kappelman, J., Shapiro, L.J., 1994. Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. Am. J. Phys. Anthropol. 93, 67–82.

Duren, D.L., 1999. Developmental determinants of femoral morphology. M.A. Thesis, Kent State University, Kent, OH.

Fleagle, J.G., 1999. Primate Adaptation and Evolution. Academic Press, San Diego.

Freeman, S., Herron, J.C., 1998. Evolutionary Analysis. Prentice Hall, Upper Saddle River, NJ.

Frost, H.M., 1990. Skeletal structure adaptations to mechanical usage (SATMU): redefining Wolff's law: the remodeling problem. Anat. Rec. 226, 403–413.

Galis, F., 2001. Key innovations and radiations. In: Wagner, G. (Ed.), The Character Concept in Evolutionary Biology. Academic Press, London, pp. 581–605.

Gatesy, S.M., Dial, K.P., 1993. Tail muscle activity patterns in walking and flying pigeons (*Columba livia*). J. Exp. Biol. 176, 55–76.

Gatesy, S.M., Dial, K.P., 1996. Locomotor modules and the evolution of avian flight. Evolution 50, 331–340.

Gatesy, S.M., Middleton, K.M., 1997. Bipedalism, flight, and the evolution of Theropod Locomotor diversity. J. Vertebr. Paleontol. 17, 308–329.

Gauthier, J., 1986. Saurischian monophyly and the origin of birds. Mem. Calif. Acad. Sci. 8, 1–55.

Graham, J.B., 1997. Air-Breathing Fishes: Evolution, Diversity, and Adaptation. Academic Press, San Diego.

Hagen, D.W., Moodie, G.E.E., Moodie, P.F., 1980. Polymorphism for breeding colors in *Gasterosteus aculeatus*. II. Reproductive success as a result of convergence for threat display. Evolution 34, 1050–1059.

Hamrick, M., 1996. Articular size and curvature as determinants of carpal joint mobility and stability in stresirhine primates. J. Morphol. 230, 113–127.

Hamrick, M.W., 1999. A chondral modeling theory revisited. J. Theor. Biol. 201, 201–208.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., Alvarez, H., Charnov, E.L., 1998. Grandmothering, menopause, and the evolution of human life histories. Proc. Natl Acad. Sci. 95, 1336–1339.

Hewes, G.W., 1961. Food transport and the origin of hominid bipedalism. Am. Anthropol. 63, 687–710.

Hildebrand, M., 1995. Anaylsis of Vertebrate Structure. Wiley, New York.

Hunt, K.D., 1991. Positional behavior in the Hominoidea. Int. J. Primatol. 12, 95–118.

Hunt, K.D., 1994. The evolution of human bipedality: ecology and functional morphology. J Hum. Evol. 26, 183–202.

Hunt, K.D., Cant, J.G.H., Gebo, D.L., Rose, M.D., Walker, S.E., Youlatos, D., 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37, 363–387.

Jablonski, N.G., Chaplin, G., 1993. Origin of habitual terrestrial bipedalism in the ancestor of the Hominidae. J. Hum. Evol. 24, 259–280.

Johanson, K., 1970. Air breathing in fishes. In: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology. Academic Press, London, pp. 361–411.

Jolly, C.J., 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5, 1–26.

Jungers, W.L., 1988. Relative joint size and hominoid locomotor adaptations with implications for the evolution of hominid bipedalism. J. Hum. Evol. 17, 247–265.

Jungers, W.L., 1991. A pygmy perspective on body size and shape in *Australopithecus afarensis* (A.L. 288-1, "Lucy"). In: Senut, B., Coppens, Y. (Eds.), Origine(s) de la bipédie chez les Hominidés. CNRS, Paris, pp. 215–224.

Kramer, P.A., 1999. Modeling the locomotor energetics of extinct hominids. J. Exp. Biol. 202, 2807–2818.

Kramer, P.A., Eck, G.G., 2000. Locomotor energetics and leg length in hominid bipedality. J. Hum. Evol. 38, 651–666.

Larson, S., 1993. Functional morphology of the shoulder in primates. In: Gebo, D.L. (Ed.), Postcranial Adaptations in Nonhuman Primates. Northern Illinois University Press, Dekalb, IL, pp. 45–69.

Latimer, B., Lovejoy, C.O., 1989. The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. Am. J. Phys. Anthropol. 78, 369–386.

Latimer, B., Lovejoy, C.O., 1990a. Metatarsophalangeal joint in *Australopithecus afarensis*. Am. J. Phys. Anthropol. 83, 13–24.

Latimer, B., Lovejoy, C.O., 1990b. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. Am. J. Phys. Anthropol. 82, 125–133.

Latimer, B., Ohman, J.C., Lovejoy, C.O., 1987. Talocrural joint in African hominoids: implications for *Australopithecus afarensis*. Am. J. Phys. Anthropol. 74, 155–175.

Lauder, G.V., Liem, K.F., 1989. The role of historical factors in the evolution of complex organismal functions. In: Wake, D.B., Roth, G. (Eds.), Complex Organismal Functions: Integration and Evolution in Vertebrates. Wiley, New York: Dahlem Conference, pp. 63–278.

Lindén, M., Møller, A.P., 1989. Cost of reproduction and covariation of life history traits in birds. Trends Ecol. Evol. 4, 367–371.

Lovejoy, C.O., 1981. The origin of man. Science 211, 341–350.

Lovejoy, C.O., 1988. Evolution of human walking. Sci. Am. 259, 118–125.

Lovejoy, C.O., Hieple, K.G., Burstein, A.H., 1973. The gait of Australopithecus. Am. J. Phys. Anthropol. 38, 757–780.

MacLatchy, L.M., 1996. Another look at the australopithecine hip. J. Hum. Evol. 31, 455–476.

Marzke, M.W., 1986. Tool use and the evolution of hominid hands and bipedality. In: Else, J.G., Lee, P.C. (Eds.), Primate Evolution. Cambridge University Press, Cambridge, pp. 203–209.

Milinski, M., Bakker, T.C.M., 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. Nature 344, 330–333.

Nunn, C.L., van Schaik, C.P., 2001. A comparative approach to reconstructing the socioecology of extinct primates. In: Plavcan, J.M., Jungers, W.L., Kay, R.F., van Schaik, C.P. (Eds.), Plenusm, New York, pp. 159–216.

Ostrom, J.H., 1976. *Archaeopteryx* and the origin of bird. Biol. J. Linn. Soc. London 8, 91–182.

Partridge, L., 1978. Habitat selection. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioral Ecology. Blackwell Scientific, Oxford England, pp. 351–376.

Pearson, O.M., Lieberman, D.E., 2004. The aging of Wolff's "law": Ontongeny and responses to mechanical loading cortical bone. Yearb. Phys. Anthropol. 47, 63–99.

Peters, D.S., Gutmann, W.F., 1985. Construction and functional preconditions for the transition to powered flight in vertebrates. In: Hecht, M.K., Ostrom, J.H., Viohl, G., Wellnhofer, P. (Eds.), The Beginnings of Birds, Proceedings of the International *Archaeopteryx* Confernece, Eichstätt 1984, Freunde des Jura-Museums Eichstätt, Eichstätt, pp. 233–242.

Pontzer, H., Wrangham, R.W., 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. J. Hum. Evol. 46, 317–335.

R Development Core Team, 2005. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Rak, Y., 1991. Lucy's pelvis anatomy: its role in bipedal gait. J. Hum. Evol. 20, 283–290.

Rodman, P.S., McHenry, H.M., 1980. Bioenergetics and the origin of hominid bipedalism. Am. J. Phys. Anthropol. 52, 103–106.

Roff, D.A., 1997. Evolutionary Quantitative Genetics. Chapman and Hall, New York (pp. 165–195).

Schaefer, S.A., Lauder, G.V., 1986. Testing historical hypotheses of morphological change: biomechanical decoupling in loricarioid cat-fishes. Evolution 50, 1661–1675.

Schemske, D.W., Ågren, J., 1995. Deceit pollination and selection in female flower size in *Begonia involucrate*: an experimental approach. Evolution 49, 207–214.

Shefelbine, S.J., Tardieu, C., Carter, D.R., 2002. Development of the Femoral Bicondylar Angle in Hominid Bipedalism. Bone 30, 765–770.

Simpson, G.G., 1944. Tempo and Mode in Evolution. Columbia University Press, New York.

Sinclair, A., Leakey, R.E., Norton-Griffiths, M.D., 1986. Migration and hominid bipedalism. Nature 324, 307–308.

Spoor, F., Wood, B., Zonneveld, F., 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. Nature 369, 645–648.

Steedman, D.J., 1989. Severity of free-fall injury. Injury (Br. J. Accident Surg.) 20, 259–261.

Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. Am. J. Phys. Anthropol. 60, 279–317.

Stern, J.T., Susman, R.L., 1991. "Total morphological pattern" versus the "magic trait:" conflicting approaches to the study of early hominid bipedalism. In: Senut, B., Coppens, Y. (Eds.), Origine(s) de la bipédie chez les Hominidés. CNRS, Paris, pp. 99–112.

Susman, R.L., Stern, J.T., Jungers, W.L., 1984. Arboreality and bipedality in the Hadar hominids. Folia Primatol. 43, 113–156.

Tuttle, R.H., 1975. Parallelism, brachiation, and hominoid phylogeny. In: Luckett, W.P., Szalay, F.S. (Eds.), Phylogeny of the Primates: A Multidisciplinary Approach. Plenum, New York, pp. 447–480.

Tuttle, R.H., 1981. Evolution of hominid bipedalism and prehensile capabilities. Phil. Trans. R. Soc., London, B 291, 89–94.

Urquhart, C.K., Hawkins, M.L., Howdieshell, T.R., Mansberger Jr., A.R., 1991. Deer stands: a significant cause of injury and mortality. South Med. J. 84, 686–688.

Vermeij, G.J., 1974. Adaptation, versatility, and evolution. Syst. Zool. 22, 466–477.

Ward, C.V., 2002. Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? Am. J. Phys. Anthropol. 45, 185–215.

Washburn, S.L., 1951. The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harbor Symp. Quant. Biol. 15, 67–77.

Washburn, S.L., 1959. Speculations on the interrelations of the history of tools and biological evolution. Hum. Biol. 31, 21–31.

Washburn, S.L., 1960. Tools and human evolution. Sci. Am. 203, 63–75.

Wheeler, P.E., 1991a. The thermoregulatory advantages of hominid bipedalism in open equatorial environments, body form and bipedality. J. Hum. Evol. 14, 23–28.

Wheeler, P.E., 1991b. The influence of bipedalism on the energy and water budgets of early hominids. J. Hum. Evol. 21, 117–136.

Wrangham, R.W., 1980. Bipedal locomotion as a feeding adaptation in Gelada baboons, and its implications for hominid evolution. J. Hum. Evol. 9, 329–331.

Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. Proc VI Int. Congr. Genet. 1, 356–366.