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To the Graduate Council:

I am submitting herewith a dissertation written by Adam David Sylvester entitled "The Decoupling Hypothesis: A new idea for the origin of hominid bipedalism." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Anthropology.

Andrew Kramer, Major Professor

We have read this dissertation and recommend its acceptance:

Lyle Konigsberg, Mohamed Mahfouz, Richard Jantz

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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and recommend its acceptance:

Lyle Konigsberg

Mohamed Mahfouz

Richard Jantz

Acceptance for the Council:

Anne Mayhew
Vice Chancellor and Dean of
Graduate Studies

The Decoupling Hypothesis: A new idea for the origin of hominid bipedalism

A Dissertation
Presented for the
Doctor of Philosophy Degree
The University of Tennessee, Knoxville

Adam David Sylvester
August 2006

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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 hominid 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.

Activity budgets and locomotor and postural behaviors of 18 primate groups, derived from published literature, were used to test a prediction of the Decoupling Hypothesis that bipedalism is a predictable behavior in primates which is correlated with intense demands for shoulder mobility and stability. Time was used as a proxy for estimating conflicting demands for shoulder stability and mobility. Bipedalism, as a proportion of all above-substrate locomotion, was predicted using logistic regression including seven linear variables and four two-way interaction terms. All possible regressions, using R^2 and Mallows' C_p as criterion, and stepwise variable selection procedures were used to determine significant variables.

The model with a relatively high R^2 (0.86) and the lowest Mallows' C_p (-1.62), contained the following predictor variables: shoulder-abduction locomotion

($p < 0.0001$), shoulder-abduction posture ($p = 0.0003$), and an interaction terms, shoulder-abduction locomotion by above-substrate locomotion ($p = 0.011$). The significant interaction term, predicted by the Decoupling Hypothesis, supports the hypothesis and suggests that further consideration is warranted.

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Chapter 1: Introduction

If asked to cite features that distinguish humans from their closest living relative, the chimpanzee, three characteristics come readily to mind: the massive human brain, complex culture and bipedalism (Lovejoy, 1988). It requires only the most casual review of paleoanthropological evidence to reveal that bipedalism precedes the other two by at least a few million years. Thus, it is easily argued that bipedal locomotion is one of the pivotal developments in the course of hominid evolution.

Humans have long ascribed great significance to their bipedalism and erect posture. The earliest recorded ideas attribute human posture to divine design, as a way of empowering humans by providing them with a physical distinction from the rest of the animals. This idea can be traced to the works of Plato, Aristotle, Cicero and Ovid and continued through the Renaissance period (Patrides, 1958). Many Renaissance authors consider erect posture as one of the defining and extraordinary features of humans. John Donne, the English poet (1572-1631), writes in 1624, “Wee attribute but one priviledge and advantage to Mans body, above other moving creatures, that he is not as others, groveling, but of an erect, of an upright form, naturally built, and disposed to contemplation of Heaven” (quoted from Patrides, 1958). Erect posture, as one of human’s distinguishing features, can also be found in the works of John Milton (English author, 1608-1674), Basil the Great (Catholic theologian, 329-379), John Calvin (French reformer, 1509-1564), Peter Lombard

(Italian theologian, 1100-1160), Thomas Adams (English playwright, 1580-1653) as well as a host of other theologians, philosophers and writers (Patrides, 1958). While many attributed great importance to bipedalism, others were not as awed. Walter Charleton (1619-1707), physician to Charles I of England, denied that humans had any “reason to boast a singularity” in their erect posture in view of penguins, the mantis and similar animals (Patrides, 1958).

Long considered by many a conspicuous feature of humans, the importance of bipedalism was appreciated by researchers early in human evolutionary studies (Le Gros Clark, 1955, 1959; Dart, 1925; Darwin, 1871; Engles, 1950; Hooton, 1925; Keith, 1949; Munro, 1893; Smith, 1913; Washburn, 1959; Weidenreich, 1946, 1947). Engels (1876) writes that erect posture was “the decisive step in the transition from ape to man”. Schultz (1951) echoes this sentiment stating that upright posture was the “first major step in man’s evolution.” Washburn considers bipedalism “the basic adaptation for the foundation of the human radiation starting man on his ‘separate evolutionary path’”, although he saw the development of tools as synchronous and synergistic with bipedalism (Washburn 1951, 1959; from Hewes, 1961). Mednick (1955) asserts that “the evolution of bipedal locomotion seems to have preceded other uniquely human attributes. It appears quite probable that our ancestors walked first, and subsequently became large-brained, tool-using humans.” More recently, Lovejoy (1988) writes that the “development of erect walking may have been a crucial initiating event in human evolution.” Wheeler (1992) concurs, stating that habitual

bipedalism “is now widely considered to be the crucial first event in human evolution...”

Scientists now recognize that habitual terrestrial bipedalism was the first uniquely hominid attribute to evolve and that it predisposed hominids to evolve other uniquely human traits (Ward, 2002). So widely accepted is this idea that the question of whether a newly discovered fossil species is a hominid can be appropriately posed as: Was it a biped? Thus, the origin of hominids is both synonymous with, and defined by the origin of bipedalism, making the origin of bipedalism one of the most important questions in paleoanthropology.

As a result of its paramount importance, a great deal of research has been dedicated to the origin of bipedalism. Ward (2002) distinguishes between two separate, although complementary, endeavors. The first, a more functional/biomechanical perspective, is to recognize the earliest bipeds in the fossil record and evaluate their capacity for different locomotor modes. *Australopithecus afarensis*, the main hominid species in the 3.0-4.0 Ma range, is almost universally accepted among anthropologists as having been adapted to terrestrial bipedalism (although see Sarmiento, 1988, 1994, 1998 for the sole dissenting opinion), and the Laetoli footprints are unambiguous evidence of hominid bipedalism between 3.6-3.8 Ma (White and Suwa, 1984). Based on the few and fragmentary remains, the slightly earlier *A. anamensis* appears to have been a biped, pushing hominid antiquity back to approximately 4.2 Ma (Leakey et al. 1995). White et al., (1994) suggest that *Ardipithecus ramidus*, by position of the foramen magnum, may have been bipedal,

although confirmation must wait on more detailed research reports. Two more recently erected species, *Sahelanthropus tchadensis* dated to 6-7 Ma (Brunet et al., 2002) and *Orrorin tugenensis* dated to approximately 6 Ma (Senut et al., 2001) vie for position as the earliest hominid based on dental and post-cranial remains respectively. These species, like *A. ramidus*, will require additional fossils and further analyses to solidify locomotor and taxonomic interpretations.

Not only is it imperative to recognize the first bipeds in the fossil record, it is also essential to evaluate the locomotor capabilities and capacities of early hominids. Much of this research has centered on *A. afarensis* because of its fossil abundance and even more specifically on the specimen AL 288-1 because of its relative completeness. Some suggest *A. afarensis* to have been an obligate terrestrial biped, one that used a bipedalism that was kinematically and kinetically similar to modern humans and possibly even more energetically efficient than the modern form (see Latimer, 1991). Others have interpreted australopithecine anatomy, especially deviations from modern human morphology, as indicating a compromised bipedalism, one less effective than modern human, as well as revealing a significant arboreal component to the locomotor repertoire (Berge, 1994; Jungers, 1991; McHenry, 1995; Susman et al., 1984; Stern, 1999; Stern and Susman 1983). Although debate persists, the question is ever closer to resolution. The emerging picture is one of a hominid that was undoubtedly bipedal, although probably different than modern humans, and not completely detached from the arboreal world.

The second question Ward (2002) identifies is to understand the selective pressure, or suite of pressures, that caused hominid bipedalism to evolve.

Researchers have speculated freely as to the origin of bipedalism, and consequently theories are numerous. A formal and extensive review will follow in the second chapter, but briefly these theories include: increased visual field (Darwin, 1871), males provisioning females (Lovejoy, 1981, 1988), arboreal feeding posture (Hunt, 1996), thermoregulation (Wheeler, 1994), terrestrial locomotor efficiency (Rodman and McHenry, 1980), tool-use (Darwin, 1871; Washburn, 1959), food transport (Hewes, 1961), infant transport in support of a scavenging niche (Sinclair et al., 1986), food acquisition (Wrangham, 1980; Rose, 1976, 1984, 1991; Jolly, 1970), descent from a arboreal biped (Tuttle, 1974, 1981), effective weapon use (Dart, 1953; Darwin, 1871; Kortlandt, 1980), behavioral displays (Livingstone, 1962; Jablonski and Chaplin, 1993), effective digging and throwing (Marzke, 1986), adaptation to an semi-aquatic niche (Hardy, 1960), and a general object transport (Day, 1977). Some researchers have suggested that understanding the origin of bipedalism “might prove resistant to conclusive explanation” (Kramer and Eck, 2000). Kramer and Eck’s (2000) statement, although hopefully premature, highlights clearly the current state of affairs. Despite the diverse hypothesized pressures and the tremendous amount of research, no theory has been met with universal support and, consequently, understanding the origin of bipedalism continues to be an elusive goal for paleoanthropology.

This dissertation is composed of two interconnected goals. The first is to develop a new theory for the origin of bipedalism, referred to here as the Decoupling Hypothesis (DH). To that end, 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 the new hypothesis. The DH posits that hominid bipedalism is an adaptation that split the general primate quadrupedal locomotor body plan into two distinct locomotor modules that evolved independently so that hominids could simultaneously achieve highly effective terrestrial and suspensory behaviors, a combination not accessible to quadrupeds because of trade-off in shoulder stability and mobility.

The second portion of the dissertation is devoted to testing the theory developed in the first stage. One of the predictions of the Decoupling Hypothesis is that bipedalism, as a proportion of all terrestrial and above-branch (together termed above-substrate) behaviors, should be correlated with an interaction between the demands for above-substrate and suspensory behaviors. The null hypothesis is: The proportion of above-substrate locomotion that is performed using bipedalism is predicted only by main effects of locomotor and postural behaviors (or not predictable at all). The alternative hypothesis is: The proportion of above-substrate locomotion that is performed using bipedalism is predicted by interaction effects between above-substrate behaviors and suspensory behaviors. These hypotheses are

tested using locomotor and postural behaviors from 18 published accounts of 10 extant primate (Catarrhini) species. Variable selection procedures and logistic regression are used to determine if interaction variables that include above-substrate and suspensory behaviors emerge as significant predictors of bipedalism.

The dissertation is organized in the following manner. Chapters 2-5 present a review of literature which provides the background necessary to understand the project. Chapter 2 is a review of theories previously proposed for the origin of bipedalism, examining evidence used to support them and identifying problems and shortcomings. Chapter 3 reviews a host of concepts from evolutionary biology that provides the theoretical underpinning for the development of the Decoupling Hypothesis. Chapter 4 examines types of primate locomotor behavior and functional connections with shoulder morphology. Chapter 5 examines the adaptive landscape as well as its employment in developing theories in evolutionary biology. The material and methods are presented in chapter 6 and the results in Chapter 7. In Chapter 8 the ramifications of the results are discussed, additional predictions based on the hypothesis are provided as well as additional avenues for future research. Finally, conclusions are given in Chapter 9.

Chapter 2: Theories for the Origin of Bipedalism

The origin of hominid bipedalism is now universally accepted, among scientists, as synonymous with hominid origins. The Taung fossil, discovered by Dart in 1924, demonstrated that bipedalism preceded brain expansion, although many of Dart's contemporaries did not agree with his taxonomic assessment. It is now known that bipedalism evolved at least two million years prior to the appearance of tools in the archeological record and four million years before the evolution of modern human brain size. As a result, a great deal of research has been dedicated to elucidating the pressures that selected for hominid bipedalism. A multitude of theories have been proposed and a review and critique of many of the theories follows.

Tool-use Theories

Unsurprisingly, Darwin had an early appreciation of the importance of bipedalism and was the first to provide an explanation for the evolution of bipedal hominids from a quadrupedal ancestor. This earliest of theories considered bipedalism as a necessary adaptation, unquestionably superior to quadrupedism, for surviving the savage lifestyle that accompanied a fully terrestrial hominid niche. Darwin (1871) wrote, "If it be an advantage to man to stand firmly on his feet and to have his hands and arms free, of which, from his pre-eminent success in the battle of life, there can be no doubt, then I can see no reason why it should not have been

advantageous to the progenitors of man to have become more and more erect or bipedal.” Darwin (1871) identified several critical selective advantages provided by bipedalism, proposing that a biped “would thus have been better able to defend themselves with stones or clubs, to attack their prey, or otherwise to obtain food.” Darwin (1871) went on to state that “From these causes alone it would have been an advantage to man to become a biped; but for many actions it is indispensable that the arms and whole upper part of the body should be free; and he must for this end stand firmly on his feet.” Further, Darwin (1871) contended that these tasks would have been impossible for a primate that utilized its hands for locomotion because such rough use of the forelimbs would have prevented the refinement of the necessary sensitivity and skill.

Although Darwin may have been the first to consider tools as the key to bipedalism, tools played a critical and central role in many theories for the evolution of bipedalism through most of the 20th century. Dart (1953) contended bipedalism, in short bouts, would have originally evolved to spot enemies or identify distant food resources. Erect posture, however, would have left early hominids vulnerable, and the use of a club for attack or defense would have greatly benefited from the ability to pivot the trunk from a bipedal stance (Dart, 1953). Hooton (1946), clearly under the assumption of prior and at least marginal increases in body and brain sizes, suggested that an increased body size mandated adaptation to the ground, and that unlike the terrestrial gorilla, early hominids made the “supremely intelligent choice” of standing and walking erect. Hooton (1946) asserted that erect posture would have provided

early hominids with increased visual range and freed their hands for weapon and tool use as well as for gathering food.

Washburn (1960) also championed the role of tools in human evolution, contending that tools were the pivotal development which spurred the evolution of all other human traits, including bipedalism. According to Washburn (1960) tools were both cause and effect of bipedalism, and argued that all of hominid evolution must be viewed in the context of the “tool-using” way of life because of the advantages tools provide for digging, pounding, scraping, cutting, as weaponry and for manufacturing wood tools. An early limited bipedalism allowed tools to be carried, thus providing an advantage to the best bipeds, which further encouraged tools use and tool refinement. Washburn also linked tool use to the development of large brains, altricial neonates, intense maternal care, division of labor, pairbonding and reduced canine size. Washburn (1960) supported his position with the associations between tools and hominid fossils, such as the discovery of OH5 (*Australopithecus boisei*) with stone tools.

Washburn was not the last researcher to promote tools as the impetus for bipedalism. Marzke et al. (1988) suggested bipedalism increases the efficiency of tool use for digging and throwing. Kortlandt (1984) proposed that bipedalism evolved to free the hands of early hominids so that they could carry defensive weapons. Subsequent years of paleoanthropological and primate field research, however, have essentially invalidated stone tool based theories. The discovery of fossil hominids that well precede the appearance of stone tools in the archeological

record argues strongly against tools as the seed of humanity. While this does not disprove perishable tool use as an explanation for the origin of bipedalism, it does mean that such tools would have existed for a few million years and remain archaeologically invisible. An additional damaging observation comes from primate research; modern chimpanzees manufacture and utilize tools, carrying some of them for some distance without mandating bipedalism.

Food Acquisition Theories

The primacy of food in evolution is patent; making an evolutionary contribution requires an organism to live until reproducing. Hunt (1998) stressed this point stating that the “hominoid body is a food-getting machine” and starvation is the greatest danger faced by a large-bodied primate. Hewes was an early bipedalism-for-food advocate, offering food transport, specifically scavenged carrion, as a potential activity that would greatly benefit from bipedalism. In Hewes’ (1961) scenario early hominids would have been able to gain access to animal carcasses, but would not have been able to defend them for long periods of time. Ownership would have been important because, lacking sharp teeth and claws, early hominids could not have consumed such a food resource in a timely manner. To maintain ownership and provide adequate time for consumption, the earliest hominids would have been forced to transport such nutrient rich and desirable food resources back to a “home base”. Hewes (1961) went on to suggest that while it is natural for primates to carry objects clutched against the chest or side of the body, it would be reasonable that carrying the

food over the shoulder, on the back, would have developed quickly because it would move the center of gravity backward, thus helping with bipedal walking. Actualistic research used to interpret early hominid archaeological sites indicates that meat did not play a prominent role in diets until later stages of hominid evolution (Selvaggio, 1998). In addition, recent analyses of Sr/Ca ratios of *Australopithecus africanus* from Sterkfontein demonstrate that these early hominids were highly herbivorous (Sponheimer et al., 2005).

The inherent logic of food acquisition as a selective pressure has appealed to several primate researchers. Jolly (1970) suggested, based on gelada baboon observations, that the early hominid niche might have required feeding on small evenly distributed grass seeds. Such an environment would have required a bipedal sitting posture and bipedal shuffling, as is seen in baboons, and then an eventual transition to full bipedal walking. Wrangham (1980) notes, however, that bipedal sitting and shuffling require a bent knee which would not be an effective precursor to bipedal walking which requires a fully extendable knee. Also damaging to Jolly's proposal is Rose's (1976, 1984, 1991) observation that grass seeds do not constitute a major food source of the savannah baboon.

Despite his criticisms, Wrangham (1980) built on Jolly's basic idea, suggesting that feeding from bushes, as chimpanzees do, would elicit a standing bipedal posture. Further, walking short distances bipedally between food resources would eliminate the energy wasted that accompanies transitioning between erect postures and quadrupedal walking. Rose (1976, 1984, 1991), agreeing with

Wrangham, postulated that bipedalism evolved as a terrestrial feeding posture for collecting small food objects from trees and for traveling within densely packed feeding sites.

Foremost among the primate food acquisition models, and currently a leading theory for the origin of bipedalism, is Hunt's (1994, 1998) feeding posture hypothesis which expands on the earlier work of Wrangham, Rose and Jolly. Hunt's hypothesis is based on observational data of wild chimpanzees in Gombe and Mahale where chimpanzees utilize bipedalism both terrestrially and arboreally during foraging and feeding. Whereas Wrangham, Rose and Jolly envisioned terrestrial feeding, Hunt's novel contribution is arboreal feeding as the critical factor, although he does not discount the importance of terrestrial feeding. Hunt (1994, 1998) proposes that bipedalism first evolved as a postural adaptation in conjunction with arm-hanging for effectively gathering small diameter fruits from within diminutive trees. Hunt (1998) also argues that bipedal standing would have freed both hands for food gathering and, following Wrangham's lead, that traveling bipedally between closely spaced food resources would also reduce energetic costs because it eliminates repeated transitions between bipedal postures and quadrupedal locomotion. Hunt (1994, 1998) suggests that an environment entirely of small trees, like those that elicit chimpanzee bipedalism, would select for bipedal postures and eventually locomotion. Hunt (1998) reviews australopithecine locomotor anatomy and dietary reconstructions as additional supporting evidence.

Several researchers have offered support for Hunt's arboreal feeding posture hypothesis. In experimental manipulation of habitat, Videan and McGrew (2002) elicited bipedalism from captive chimpanzees and note that bipedalism is most consistently used to forage and carry food. Stanford (2006) provides wild chimpanzee observation data (Bwindi Impenetrable National Park, Uganda) to support Hunt's hypothesis, reporting an even higher frequency of bipedalism than Hunt (1998). Stanford (2006), however, uses *ad libitum* observations of chimpanzee only in arboreal contexts both of which may bias his results and conclusions.

While Hunt's hypothesis, and by extension those of Wrangham and Rose, is provocative and the frequency of bipedalism as a feeding posture is not contested, there are several problems with the feeding posture hypothesis. First, bipedalism still represents a very small proportion of the chimpanzee locomotor repertoire. Hunt (1998) reported, in 700 hours of chimpanzee observations at Mahale and Gombe, only 97 instances of bipedalism none of which were consecutive. Stanford (2002) reported a much higher 179 bouts of bipedalism in almost 250 hours of observation, but this still averages to only 0.79 bouts per hour, most lasting 5-8 seconds.

The feeding posture hypotheses also require that the bipedal posture provides an enormous energetic savings, large enough to rearrange the entire lower anatomy, which would have been adapted for quadrupedal locomotion. The features that enhance bipedalism are to the detriment of terrestrial quadrupedism. There would have been a point in the course of early hominid evolution, according to Hunt's hypothesis, where hominids would have been standing bipedally to gather fruits and

probably shuffling bipedally, but traveling greater distances quadrupedally just as chimpanzees do today. Thus, two selective pressures would have been acting on the locomotor anatomy, one to rearrange the entire lower anatomy to accommodate bipedal postures (that were probably in part supported by arm-hanging). The second pressure, evident because most primates are quadrupeds, would have acted to retain the ancestral lower anatomy for quadrupedal locomotion. Thus, the selective pressure for energetic savings accrued by standing and shuffling short distances during feeding must have been greater than the selective pressure to retain the quadrupedal anatomy for locomotion. The idea that a body might reflect a posture instead of locomotion is not unfounded. Hunt (1994) connects several features in chimpanzees (e.g. cranial oriented glenoid fossa, dorsally position scapulae) to arm-hanging, an idea supported by Pontzer and Wrangham (2004). In this case however, it is the selective pressure for a dangerous arboreal posture that exceeds that of terrestrial locomotion. It is more difficult to imagine a low energy and relatively safe posture, such as bipedal standing and shuffling, generating a greater selective pressure than a higher energy locomotor behavior.

The feeding posture hypotheses also rest on the energetic savings of “changing gears” between bipedal and quadrupedal behaviors. While it seems clear, from chimpanzee observations, that there is a distance under which a chimpanzee will walk bipedally if already standing bipedally, the reason is not clear. Hunt (1998) cites Wrangham (1980), who states that there is a major energetic cost that

accompanies the bipedal/quadrupedal transition; however, neither researcher offers any data to demonstrate the magnitude of this energy sink.

Finally, the feeding posture hypotheses make certain predictions about the fossil record that have yet to be supported. Hunt contends that bipedalism originally evolved as a postural adaptation and then for locomotion. Hunt (1994, 1998) cites features of *A. afarensis* that he suggests are splendid adaptations to bipedal posture while simply not adequate for effective bipedal locomotion, these include: the extraordinarily wide and short pelvis, small hip joint surfaces, small lumbar vertebrae and lumbosacral articular surfaces. Some australopithecine features, however, are clearly bipedal locomotor adaptations, including the valgus knees and longitudinal and transverse arches of the foot. Thus, it might be expected that the features Hunt links to bipedal posture would precede the features associated with bipedal locomotion in the fossil record. Current fossil evidence does not support such a prediction, but such discriminations may be beyond the resolution of the paleoanthropological record.

Primate Behavioral Theories

Although food is important for several primate models, not all consider food as the critical factor. Tuttle (1974, 1975, 1981), the main architect of the hylobatian model (Richmond et al., 2001), was one of the first to base a theory for bipedalism on primate observations. Tuttle (1974, 1975, 1981), suggested that hominids evolved from a gibbon-like arboreal ancestor that used bipedalism for above-large-branch

locomotion and as an arboreal feeding posture, as modern gibbons do. Thus, when the proto-hominids came (were forced) to the ground, they were already adapted to arboreal bipedalism and the transition to the terrestrial complement was relatively easy. Tuttle's theory makes specific predictions about the anatomy of the hominid ancestor. The hominid ancestor, according to Tuttle, would have been a small-bodied arboreal climber and biped with the following characteristics: long extensible hindlimbs, intermediate lumbar spine length, relatively low center of gravity, coronally oriented iliac blades, broad thorax, dorsally positioned scapulae, mobile shoulders and wrists, long forelimbs, and long curved fingers (Richmond et al., 2001 p 76). Reconstruction of the last common ancestor strongly suggests that Tuttle's scenario is incorrect (Richmond et al., 2001).

A host of other primate behaviors that elicit bipedalism have also inspired theories. Livingstone (1962) suggested bipedalism as an effective threat display, providing the best male bipeds with greatest reproductive access to females. Tanner (1981) argued sexual display for the origin of bipedalism, while Jablonski and Chaplin (1993) believed that bipedal threats among males reduce within-group physical violence thereby increasing group reproductive success. Bipedalism, however, is used at exceedingly low frequencies for these behavioral displays.

Energetics Theories

Rodman and McHenry (1980) were among the first to suggest an explicit link between energetics and the origin of bipedalism. Rodman and McHenry (1980)

examined the energetic cost of walking for humans and chimpanzees. They predicted the energetic cost of walking at preferred chimpanzee and human speeds using a general quadruped prediction equation that relates body mass and speed to energetic cost. They then compared these predicted values to those observed. Rodman and McHenry (1980) showed that modern humans are more efficient, and chimpanzees are less efficient, than the average quadruped. Rodman and McHenry (1980) used these findings in conjunction with those of Taylor and Rowntree (1973), who found that chimpanzees (and capuchins) are as energetically efficient walking bipedally as quadrupedally, to suggest that bipedalism evolved simply because it offers a more efficient form of terrestrial locomotion and that there is no energetic, and by extension evolutionary, barrier that prevents a quadruped from using bipedalism.

While Rodman and McHenry's basic argument is certainly parsimonious (*i.e.* bipedalism is simply more efficient than quadrupedism and there is no energetic barrier to using bipedalism), it leaves some basic questions unanswered. The first is: If bipedalism is more efficient than quadrupedism why are chimpanzees, or more mammals, not bipeds? Also, why do chimpanzees not use bipedalism more frequently if they are not at a locomotor disadvantage? If Rodman and McHenry are incorrect and there is some energetic evolutionary barrier, then energetic efficiency does not explain bipedalism because selection could not have acted to force a population through an area of lower fitness in order to get to an area of higher fitness (although drift can have this effect). Finally, many of the conclusions are dependent on the chimpanzee data of Taylor and Rowntree (1973) which was collected on two

juveniles, making the data of dubious value. It is also interesting to note that Taylor and Rowntree (1973) indicate earlier that energetics should not be used as an argument for hominid bipedalism because bipedalism does not offer an energetic advantage.

Wheeler (1984; 1985; 1991; 1994) also provided an energy based theory for the origin of bipedalism, one in which bipedalism afforded early hominids with a physiological advantage that reduced heat load and allowed early hominids to forage for food over longer distances at higher temperature while consuming less food and water. Wheeler (1991; 1994) calculated the thermoregulatory advantage of utilizing bipedalism compared to quadrupedalism. This advantage accrues because bipeds present a smaller proportion of their surface area to solar radiation, especially when solar radiation is most intense. Secondly, a bipedal stance moves a greater proportion of the body away from the ground, thus into a cooler microclimate that provides for greater convective heat loss. This would have allowed bipeds to remain in the open savannah for longer periods of time and at higher temperatures, thus extending foraging time. Further, the foraging range is extended because bipeds have a lower energetic cost of locomotion, allowing them to have higher walking speeds without inducing hyperthermia. Critiques of this model include Chaplin et al., (1994), who recalculate the advantage accrued by bipeds, but were unable to find more than a marginal advantage. Also more recent hominid discoveries and paleoenvironmental reconstructions suggest that the savannah was not the likely birthplace of bipedalism (Johanson et al., 1982; Leakey et al., 1995, 2001; WoldeGabriel et al., 1994).

Demographic Theories

Of all the theories for the origin of bipedalism probably no theory has enjoyed such prominence as Lovejoy's (1981, 1988) provisioning hypothesis. Lovejoy's theory examines bipedalism within a host of other uniquely human traits, culminating in a grand theory linking bipedalism with these other characteristics. Lovejoy's (1981, 1988) basic premise is that bipedalism evolved as part of a life history strategy, to resolve a "demographic dilemma." Primates, and especially the large bodied hominoids, are close to the end of K-type demographic strategies. This strategy provides prolonged life spans but also includes longer periods of gestation and infant dependency, delayed sexual maturation, as well as single births. The result is that a chimpanzee must live until she is 21 years in order to have reproduced both herself and her mate (to keep population size stable), in contrast to rhesus macaques which need to live only to 9 years (Lovejoy, 1988).

If reproductive rates are to remain constant as longevity increases, the crude mortality rate must go down. Mortality is a product of both genetic and environmental factors. The risk resulting from environmental factors (predations, accident, parasitism, infection and food supply failure) can be mitigated by social factors (strong social bonds, high levels of intelligence, intense parenting and long periods of learning). There are limits, however, to the effect social cohesion can have on environmentally induced mortality. Lovejoy (1988) pondered the ramifications of a proto-hominid reaching the limits of such strategies. He suggested that selecting a set of highly specialized social strategies would be niche specific and such an

adaptation would limit a hominid's ability to survive in novel environments (mitigate novel mortality risks). In addition, moving to such an extreme end of the K-selected scale might lead a hominoid to a point where a set of parents could barely replace themselves (the demographic dilemma)

As an alternative, Lovejoy (1988) argued that two demographic variables could be altered to improve reproductive success without resorting to highly derived niche specific social behaviors, these are survivorship and interbirth interval. Any behavior that would increase survivorship and/or reduce the interbirth interval would be under strong selective pressure, and Lovejoy (1988) suggested a suite of behavioral changes, of which bipedalism is one, to solve the "demographic dilemma". Lovejoy suggested that bipedalism evolved as a way for males to gather food resources and provision females and their mutual offspring. In this scenario males and females would forage separately; with males traveling great distances away from a core area and females remaining in this core area. Offspring would stay with females during the day, limiting the dangers associated with daily travel and increasing survivorship. Females, however, because of their limited day range would have reduced access to resources and would require supplemental sources of food. Males, foraging great distances from the core area, would be able to collect food resources and would return to provision females and offspring. Males would only be able to carry enough food resources if they were bipeds because of limits to quadrupedal carrying.

The proposed system only works if males and females are pairbonded because it only benefits the provisioning male if he can be certain that he has exclusive reproductive access to the female he is provisioning and that her offspring are his. Thus, in conjunction with bipedalism, Lovejoy envisioned the origin of pairbonding, the nuclear family, continuous sexual receptivity among human females, concealed estrous and secondary sexual characteristics; using present human behavior and anatomy as supporting evidence. Lovejoy (1988) is so convinced of his argument that he declares “The sequential evolution of behavior proposed in this article has a high probability of mirroring actual events during the Miocene.”

One of the major flaws in the provisioning hypothesis is that it predicts that early hominid life strategy (including bipedalism) would have evolved to avoid the demographic dilemma before reaching it. Endnote number 52 from Lovejoy (1988) states “The hominid adaptations proposed in this article are more likely to have been developed to prevent the ‘demographic dilemma.’” This suggests that bipedalism and the suite of accompanying hominid traits evolved before reaching his proposed problem. Thus the adaptation (the effect) would have had to precede the selective pressure (the cause).

Lovejoy also argued the hominids would have had lower survivorship, compared to other hominoids, because of protracted development. Australopithecines, however, do not show the extended development and delayed sexual maturation that would accompany Lovejoy’s scenario. Evidence from australopithecine dental development strongly demonstrates that australopithecines

followed developmental patterns similar to modern chimpanzees (Smith and Tompkins, 1995). In addition, the persistent body size sexual dimorphism in hominids is not consistent with a monogamous primate social structure.

Other Theories

While many of the well-known theories are variations on main themes (food or tools), there are many lesser known theories for the origin of bipedalism that have received little attention in paleoanthropology. Reynolds (1931) suggested that dodging as a defensive mechanism was the impetus for bipedalism. Köhler (1959) noticed that cold or snow-covered ground induces spontaneous bipedalism in his chimpanzees, thus providing a mechanism. Hardy (1960) was among the first to suggest bipedalism as an adaptation to a novel niche, and suggested bipedalism was an adaptation to a semi-aquatic lifestyle. Etkin (1954) discussed bipedalism in the context of a hunting niche although does not explicitly state why bipedalism is necessary. Sinclair et al. (1986) suggested infant transport as a way to increase efficiency of a migratory hominid. In light of current paleoenvironmental reconstructions (Johanson et al., 1982; Leakey et al., 1995, 2001; WoldeGabriel et al., 1994) and current understandings of the early hominid niche (Hunt, 1998), these theories are highly improbable.

Chapter 3: Concepts from Evolutionary Biology

The Character Concept

The field of evolutionary biology is concerned with understanding and reconstructing past biological events, with the remote hope of predicting the future. The complexity of biological life is staggeringly high, making this task difficult at best. An organism's phenotype, which ultimately determines its fitness, can be described by a long list of character values. Such a list, however, would be immense for an adult individual and would need to be further expanded if ontogenetic stages were included. If such a description were required to understand evolution, no progress could be made (Houle, 2001). Genetics fails to offer a better solution because even simple organisms have some 10^4 genes, and while this number is finite, it still prevents realistic progress (Houle, 2001).

As a result, evolutionary biologists are forced to reduce the complexity of a system to the point where they can still sufficiently answer the question at hand without losing crucial information (Houle, 2001). Thus it is desirable to identify only those entities that are important to the process under investigation. Ultimately researchers are searching for those naturally occurring units that play roles in biological processes (Wagner, 2001). Biologists continue to discuss what qualifies as the unit of evolution and phenotypic change, referring to this issue as the character concept (see Wagner ed. volume, 2001). This character problem is an entirely

different one than for cladistic analysis, where a character is simply any feature that can be used to distinguish between two groups of organisms.

Some biological units, such as the cell and the whole organism, are intuitively obvious. The cell is the minimum unit of life because it is capable of self maintenance and reproduction, characteristics shared by organisms, which gives them privileged status as natural units in biology (Wagner and Laubichler, 2001).

Scientific progress requires more than intuition in identifying the units for research, and cannot be restricted to only those that are patently obvious. Wagner (2001) provides a very general definition for these units, calling them “characters” which “can be thought of as a part of an organism that exhibits causal coherence to a well-defined identity and that plays a (causal) role in some biological processes.” Genes and molecules qualify for this definition and the fact that such immense progress has been made in the fields of genetics and molecular biology is testament to the power and importance of defining the units of process (Wagner 2001).

The question for evolutionary biologists is: Are there other units between the cell and the organism (and/or above the organism)? Cuvier suggested that there are no independent units within an organism and that an entire organism could be reliably reconstructed from one of its parts (Schwenk, 2001). Two lines of evidence, however, demonstrate that other levels of integration and process exist, requiring unit identification. First, it is apparent that evolutionary changes in one part of an organism do not mandate changes in all other parts of the organism. Some portions of an organism act and evolve relatively independently, as Lewontin (1984) suggests

“quasi-independently” or as Wagner (1995, 1996, 1999) writes “semi-independently”, despite the fact that characters are spatially and temporally connected within the organism. It is important to note that while all characters are not highly correlated, organisms can also not be atomized to a bag of independent traits. Secondly, there are also processes that exist above the level of the organism. It would not be productive to look for explanations for such phenomena as ecological system invasion resistance (Shea and Chesson, 2002) or demographic history at or below the level of the organism.

Thus, the primary task that must precede research is to define the units relevant to the question at hand. For other sciences this task is relatively straightforward. Physics and chemistry are so rigorous because they define the entities to which their theories apply. Wagner and Laubichler (2001) suggest that character identification must proceed from an ontological prior. While for molecular biology the prior is the cell, for phenotypic evolution the ontological prior is the whole organism (Wagner and Laubichler, 2001). The organism can then be decomposed into functional characters, which is any portion of the organism that plays a central role in a biological process (Wagner and Laubichler, 2001).

Schwenk (2001) offers a slightly different definition, suggesting that “characters are the units of phenotypic evolution that are individuated by a unique set of developmental constraints.” As a result, for Schwenk (2001) characters are irreducible biological features. Schwenk (2001) confers greater functional and evolutionary relevance to complexes of characters which he calls functional units

(following Bock and vonWahlart (1965)). A functional unit consists of a set of characters that are integrated to carry out the same biological role in the natural life of an organism. As a result, the characters of a functional unit are exposed to a specific set of selective pressures (Schwenk, 2001). Schwenk (2001) defines three types of functional units including: structural units, mechanical units and evolutionary stable complexes (ESCs). These types of units are basically measures of complexity. Structural units include the fewest characters and likely appear as a single anatomical structure in the adult. At the other end of the spectrum are the ESCs which include many types of individual characters that function together. ESCs are evolutionarily stable because they are highly integrated units and thus create their own stabilizing selection, especially on short time scales (Schwenk, 2001). At larger time scales, Schwenk (2001) contends that ESCs are highly evolvable because the large number of characters (Schwenk's irreducible characters) involved endows the functional unit with multiple avenues for phenotypic change.

Schwenk's functional units differ in their level of inclusiveness, but all are similar to what Wagner and Laubichler (2001) simply refer to as characters. To maintain simplicity, I will follow Wagner and Laubichler's (2001) lead referring only to characters, but I will include portions of Wagner and Laubichler's and Schwenk's definitions. I will consider a character as any portion of an organism that plays a central role in a biological process and as a result is subjected to a specific set of selective pressures.

Locomotor Modules: A Novel Character

Gatesy and Dial (1996) define a specific character called the locomotor module, which is relevant to this project's attempt to understand the evolution of bipedalism. "Locomotor modules are anatomical subregions of the musculoskeletal system that are highly integrated and act as functional units during locomotion" (Gatesy and Dial, 1996, p.331). Thus in Schwenk's terms, a locomotor module would be considered an ESC consisting of several independent characters which function together in a specific biological process and as a result are subjected to a specific set of selective pressures. Wagner and Laubichler would consider a locomotor module as a single character since all the individual anatomical structures are highly integrated and collectively play a central role in a biological process, locomotion.

Evolutionary Constraints

While it may seem from the apparent diversity of biological life that the possibilities for adaptation are endless, there are widely recognized constraints to evolution. A constraint is any factor that limits the range of realizable phenotypes, a phenomena referred to as the incomplete filling of morphospace (Richardson and Chipman, 2003; Alberch, 1982). Constraints prevent an organism from evolving optimal solutions to all agents of selection simultaneously (Freeman and Herron, 1998).

A number of types of constraints are acknowledged and authors have offered different classification schemes (Gould, 1989; Richardson and Chipman, 2003). Gould (1989) suggests true constraints include only those factors that prevent a given morphology from arising during development, what Richardson and Chipman (2003) call “generative constraints”. Richardson and Chipman (2003) recognize another category they term selective constraints which can be considered internal selective pressures. These are phenotypes that are incompatible with other genetically, developmentally and functionally related traits. To follow is a review of some widely recognized evolutionary constraints.

A primary constraint to evolutionary change is a trade-offs which is “an inescapable compromise between one trait and another” (Freeman and Herron, 1998); essentially a negative correlation between two traits such that an increase in one trait causes a decrease in the other trait. Examples of trade-offs are numerous. The negative correlation between the number and size of female *Begonia involucrata* flowers results because the plant has limited resources to invest in flowers (Schemske and Ågren, 1995). The plant may invest energy in a few large flowers or many smaller ones. Pollinating bees are more attracted to larger flowers; however, a greater number of flowers results in more seeds. Hence there are two selective pressures that cannot both be maximized simultaneously because of limited resources.

Other examples of trade-offs include 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 human children and grandchildren (Hawkes et al., 1998). Life history parameters are heavily influenced by trade-offs in energy allocation. Energy invested in growth and development is no longer available for reproduction. A biomechanical example can be found in the primate shoulder where a trade-off between shoulder mobility and stability occurs because the features that enhance shoulder mobility (curved humeral head, small glenoid, low tubercles and dorsally positioned scapula) are contrary to the features that increase shoulder stability (flat humeral head, large glenoid and laterally positioned scapula) (Larson, 1993). As a result, enhanced shoulder mobility reduces stability, and vice versa.

Another type of evolutionary constraint is limited genetic variability (Freeman and Herron, 1998). The source of phenotypic variability is ultimately genetic variation provided by mutations. Mutations arise from existing genetic material, and hence are limited themselves. Natural selection can only act upon those genotypes and resulting phenotypes (ignoring phenotypic plasticity) that exist. Evolution is thus constrained by the variation in genetic material. Organisms may also be constrained because of the effects of pleiotropy. Mutations in pleiotropic genes may result in a positive change in one trait while also producing devastating effects on a separate trait.

Evolution can also be constrained by the spatial integration of a specific character within several functional units (Freeman and Herron, 1998). The conservancy of the number of cervical vertebrae in mammals provides an example of change constrained by the spatial relationship of characters (Galis, 2001). Because

the vertebrae are physically linked with so many other anatomical structures (nerves, blood vessels, muscles, portions of respiratory and digestive systems), changes in the vertebrae can have consequences on the functioning of numerous systems. Thus the physical proximity of the cervical vertebrae to other structures limits their evolutionary potential (Galis, 2001).

Several authors have argued the importance of developmental constraints in evolution (Gould, 1977; Alberch et al., 1979; Arnold, 1992). Maynard Smith and colleagues (1985) define a developmental constraint as “a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system” (Maynard Smith et al., 1985). Thus, developmental constraints are defined by their timing during ontogeny (Richardson and Chipman, 2003).

Key Innovations and Evolutionary Decouplings

Although evolution is often considered a slow and constant process, it is clear that the rate of evolutionary changes actually varies greatly across space, time and taxa (Simpson, 1944). 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). Galis (2001) identifies four types of key innovations: increased structural complexity, structural duplications, new structures and decouplings.

Structural duplications result from the replication of an original character. The vertebral column and pharyngeal arches are both examples of duplicated structures that provide for diversity in adaptation (Galis, 2001). New structures are those innovations resulting from the development of an entirely novel character which cannot be traced back to a character in the ancestor (Müller and Wagner, 1991; Galis, 2001). Galis (2001) suggests that the hard shells of eggs, as well mollusks and brachiopods, are novel adaptations not traceable to their ancestors. An example of increased structural complexity is the cusps on the molars of mammals which allow for adaptation to different feeding habitats (Hunter et al., 1996; Galis, 2001).

Decouplings are particularly common key innovations that result in the division of a single character into two distinct and independent characters (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 divide single characters into two characters so that neither new character need accommodate multiple functions (or competing selective pressures). The evolution of powered flight in birds involves a decoupling that is pertinent to the origin of hominid 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 hip during bipedal progression (Gatesy and Dial, 1996), the tail of modern birds provides the requisite lift and stability for flight (Peters and Gutmann, 1985) and plays only a minor role in terrestrial locomotion (Gatesy and Dial, 1993). 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 (Figure 3.1). Thus, the function of locomotor decoupling in birds and their ancestors was to redistribute separate locomotor tasks among different appendages so that no limb was forced to accommodate multiple and competing locomotor demands simultaneously.

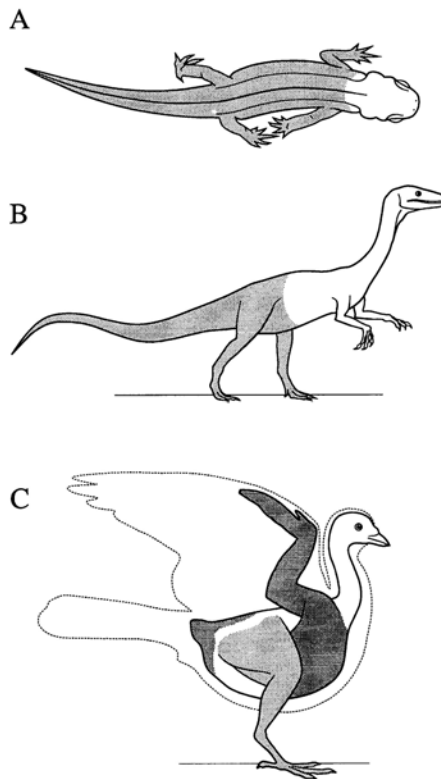


Figure 3.1: Locomotor Decoupling. Reproduced from Gatesy and Dial (1996)
 “Fig. 2. The evolution of locomotor modules and birds. A. In primitive tetrapods the body axis and all four limbs acted as an integrated unit during terrestrial locomotion. This single locomotor module (shading) is still present 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).”

Identifying the characters of evolutionary change is a primary task to any evolutionary analysis. For the evolution of locomotor behaviors, and the phenotypic change that accompanies them, the locomotor module provides the appropriate character for analysis. The general quadrupedal primate body plan consists of a single locomotor module which consists of the forelimbs and hind limbs. Both sets of limbs function cooperatively to carry out the locomotor and postural behaviors required to occupy a specific niche. Early hominids diverged markedly from this pattern. Although it does not appear that the forelimbs of early hominids were relieved of all locomotor function (*i.e.* arboreal locomotion) it is clear that they were no longer involved in weight-bearing during terrestrial locomotion. The early hominid body plan may have consisted of two locomotor modules with the forelimbs adapted to arboreal behaviors and the hindlimbs to terrestrial behaviors. Thus the question of hominid bipedalism is to determine why the forelimb was relieved of its weight-bearing function. To investigate this possibility it is important to determine if there are constraints on the evolvability of the primate shoulder which limit its ability to carry out both arboreal and terrestrial behaviors.

Chapter 4: Primate Shoulder Anatomy and Behavior

Primate Osteological Shoulder Anatomy

Primates are characterized by a number of specialized features related to life in an arboreal habitat, including a relatively mobile shoulder necessary to navigate discontinuous canopy supports (Le Gros Clark, 1959). The importance of shoulder mobility is evident; the primate shoulder 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, there is a great deal of morphological variation among primate shoulders reflecting this group's diverse locomotor and postural behaviors.

A primate's ecological niche necessitates travel through specific portions of its environment so that it can benefit fully from resources afforded by that niche. This requires traveling on specific substrates (e.g. the ground, tree branches and trunks) which is accomplished by specific locomotor and postural behaviors. The need to use these behaviors generates selective pressures on shoulder morphology to optimize the efficacy of important behaviors. Two main determinants of joint morphology are mobility and stability. 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 (Hamrick,

1996). A primate's shoulder reflects the need to balance the separate demands for mobility and stability (Larson, 1993).

The link between form and function has been inferred by examining shoulder morphologies and locomotor behaviors across the primate taxa. Several shoulder characteristics are functionally linked to locomotor behaviors, these include: shape of the blade of scapula, size of the supra- and infraspinous fossae, projection of the acromion process and shape of glenoid fossa. Shoulder characteristics of the humerus have also been examined extensively and studied features include: degree of humeral torsion, size and curvature of the articular surface and height of tubercles relative to articular surface.

The Scapula

As a heuristic, the spectrum of primate scapular variation can be summarized by examining its endpoints (see Larson, 1993). At one end are the dedicated quadrupeds which have scapulae that are wide as measured from the glenoid fossa to the vertebral border and short measured from superior to inferior angles. At the other end are the primates that engage in a significant amount of suspensory behaviors. The scapulae of this group are longer in the dimension measured from superior to inferior angles, and narrower measured from the glenoid fossa to vertebral border (Larson, 1993). The shape of the scapula among suspensory primates has been functionally linked to arm-raising behaviors where caudal elongation increases the mechanical advantage of the serratus anterior muscle to assist in scapular rotation

(Larson et al., 1991; Jungers and Stern, 1984; Stern et al., 1980). This is important for suspensory primates to rotate the glenoid fossa superiorly so that it can act as a stable platform for the humerus (Ashton and Oxnard, 1963). The quadrupedal primate scapula resembles that of non-primate mammalian quadrupeds and likely increases the efficacy of quadrupedal behaviors.

The muscles of the rotator cuff (supraspinatus, infraspinatus, teres minor and subscapularis) are thought to have a profound influence on scapular shape and orientation of the scapular spine (Larson, 1993). Especially important are the sizes of the dorsal scapular muscles (supraspinatus, infraspinatus) which determine the size of their respective fossae. Suspensory primates have large supra- and infraspinatus muscles, compared to their exclusively quadrupedal relatives, and this requires wider fossae to accommodate the muscles. Larson and Stern (1986) discovered through EMG studies on chimpanzees that the infraspinatus was consistently active during arm-hanging behaviors, stabilizing the joint against tensile stresses. They also found the supraspinatus to be important, in conjunction with the deltoid, during the early phase of arm-raising behaviors (Larson and Stern, 1986). In humans, arm-raising is performed by the concerted action of the deltoid and supraspinatus to generate a lifting force and the infraspinatus, subscapularis and teres minor which produce a stabilizing downward force (Inman et al., 1944).

During chimpanzee knuckle-walking both the supra- and infraspinatus muscles act as stabilizers of the shoulder against the dorsal displacement of the humerus (shear stress across the joint) (Larson and Stern, 1987). Supporting this

interpretation, it is noted that gorillas have the largest supraspinous fossa, well outside the range of other primates (Larson, 1993), and are the largest and most quadrupedal of the hominoids (presumably having the largest shear stress in the shoulder). In chimpanzees, the subscapularis muscle appears to be related to climbing vertical supports (Larson and Stern, 1986, 1987).

Roberts (1974) examines the functional significance of the shape of the glenoid fossa. The long and narrow glenoid fossa of quadrupeds provides a large range of motion in the parasagittal plane while the cranial lip of the fossa prevents dislocation. Hominoids and atelines have a more oval glenoid which provides for a larger range of motion required by suspensory arboreal behaviors.

The length of the acromion process has also been the subject of functional analyses. The acromion process is very long in suspensory primates, extending beyond the surface of the glenoid fossa while those of quadrupedal primates do not (Ciochon and Corruccini 1977). The long acromion process of suspensory primates is also associated with the presence of a coraco-acromial ligament. Work by Putz et al., (1988) suggests the ligament serves to transmit forces from the acromion to coracoid process. This is necessary because the long acromion process, while improving the lever arm of the deltoid muscle, is subject to greater bending stresses because of its length (Inman et al., 1944).

The final scapular feature that has been considered is the location of the scapula on the thorax. Quadrupedal primates which have narrow (medial-laterally) and deep (dorsal-ventrally) thoracic cages have scapulae that are situated on the

lateral aspect of the thorax such that the glenoid fossa faces ventrally. In the hominoids, the thorax is wide (medial-laterally) and shallow (dorsal-ventrally) and the scapula is positioned on the dorsal aspect such that that glenoid fossa faces laterally. The latter configuration enhances the mobility of the shoulder joint, while sacrificing stability during quadrupedal behaviors. The shoulders of the hominoids must use muscular effort to counteract the shear forces generated during quadrupedalism that act to displace the humeral head dorsally. The ventrally facing glenoid fossa of quadrupedal primates means that the head of the humerus is compressed into the glenoid fossa during locomotion and hence should not require as much muscular effort to maintain joint integrity. This configuration, however, reduces joint mobility.

The Humerus

One of the primary determinants of shoulder function is the size and curvature of the humeral head. Rose (1989) provides a detailed analysis of humeral head morphology for quadrupedal monkeys, hominoids and atelines. Quadrupeds have humeral heads that are generally smaller and flatter and are distinguished by two separate functional regions (Rose, 1989). Proximally the humeral head is flat and narrow providing a more stable configuration when the joint is flexed as during quadrupedal locomotion. When the humerus is extended (e.g. during sitting postures) the glenoid fossa articulates with the more spherical distal region providing greater range of motion. In the hominoids and the atelines, the humeral head is greatly

inflated in size and highly curved (more spherical), providing a great deal of joint mobility (Rose, 1989), but sacrificing inherent joint stability.

In addition to humeral head morphology, the height of the tubercles has been linked with locomotor behaviors. Larson and Stern (1989) suggest that the lower tubercles in suspensory species are an adaptation that increases the mobility of the joint by effectively raising the humeral head. This enhanced mobility comes at the expense of a shortened supraspinatus lever arm and joint integrity must be maintained by increased action of this muscle. Quadrupedal primates, because of lower shoulder mobility requirements, can take advantage of a longer lever arm (higher greater tubercle) that provides a mechanical advantage to the supraspinatus for arm-raising and joint stability.

A final humeral feature that distinguishes the mainly quadrupedal primates from the suspensory ones is humeral torsion (angle between the rotational axis of the elbow and articular surface of humeral head). In contrast to earlier reports that humeral torsion is the result of actual twisting of the humeral head about the shaft (Martin, 1933; Inman et al., 1944; Evans and Krah, 1945), Fleagle and Simons (1982) demonstrated that torsion is the result of the migration of the tubercles. Rose (1989) examines the location of the tubercles and concludes that lateral migration of the lesser tubercles (compared to cercopithecines) results in an appreciable amount of torsion as is seen in *Pongo* and *Ateles*. A greater degree of torsion is achieved if in addition to the lateral migration of the lesser tubercle, the greater tubercle migrates posteriorly, as is seen in the African apes. This greater amount of torsion allows the

humeral head to maintain contact with a laterally facing glenoid while allowing the elbow to flex and extend in a parasagittal plane (Larson, 1988). If the lesser tubercle migrates laterally, while the greater tubercle migrates anteriorly, this results in a greatly inflated articular surface with a low degree of humeral torsion (Rose, 1989). This is the case for gibbons and siamangs and the low torsion results in an elbow that faces laterally. Larson (1988) argues this is important for ricochetal brachiation where the elbow must be able to flex while the humerus is in an extended and adducted position behind the trunk.

The Clavicle

Compared to the humerus and scapula, the clavicle has received very little attention. In general, the suspensory primates have long clavicles, with a high degree of torsion which are positioned such that lateral end is higher than the medial end (Larson, 1993). In contrast, quadrupedal primates have short clavicles, with a small amount of torsion that are horizontally positioned (Larson, 1993).

Summary

Generally, 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 this morphology provides the ability to fully abduct the forelimb thus enhancing suspensory adaptations. Primates

that do not engage in suspensory behaviors, relying almost exclusively on quadrupedism (arboreal and terrestrial), have shoulders distinguished 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 quadrupedalism by adding stability to the joint as well as increasing the lever arm of specific muscles important to this locomotor behavior.

Estimating Selective Pressures on Primate Shoulder Morphology

Understanding the relative effect that different types of locomotor and postural behaviors have on the morphology of a specific species can be a relatively straightforward task. For instance, despite spending most of their time as terrestrial quadrupeds, chimpanzees have shoulders that are clearly adapted to suspensory behaviors. This demonstrates that these behaviors have a relatively greater influence on chimpanzee locomotor anatomy, despite the fact that the selective advantage of this morphology is not yet understood (Pontzer and Wrangham, 2004). The cercopithecines, which do not engage in suspensory behaviors, have shoulders that are relatively stable for the enhancement of quadrupedism.

Estimating the effect of locomotor behaviors on multiple primate species in order to make interspecific comparisons, however, is a staggeringly complex task. Part of the complexity arises because locomotor efficacy is certainly the product of a multitude of factors, each which may contribute differently in various species. For

above-substrate behaviors such as quadrupedalism, which contribute to a demand for shoulder stability, factors likely include (although certainly are not limited to): efficiency (energy consumption), muscle fatigue, day journey, home area, average speed, maximum speed, time spent in activity and the omnipresent body mass. Factors that determine how effective a primate needs to be at suspensory behaviors, which affects the demand for mobility, likely include (but are not limited to): efficiency (energy consumption), muscle fatigue, travel distance, canopy height, stability of support, inherent danger/difficulty (e.g. arm-hanging is likely less demanding than ricochetal brachiation, both of which are less dangerous than quadrupedalism), time spent in activity and body mass.

A third behavioral group, that includes sitting, vertical climbing and lying, does not require abduction of the shoulder nor stability under compression (Hunt et al., 1996). These are behaviors that all primates are capable of and thus are not limited by a specific shoulder morphology. Since these behaviors require neither, mobility to the point of full abduction nor stability under compression, they should have relatively low influence on shoulder morphology.

Many of these factors are available in the literature for some primate species, but most of these variables are not published for a great number of species. Further, almost all of these variables would need to be scaled in order to make them comparable across species boundaries, and the difficulties associated with scaling variables are well known (Jungers, 1985; Schmidt-Nielsen, 1984), especially in the context of locomotor adaptations (Steudel-Numbers and Weaver, 2006). One of the

factors, however, time spent in the activity, is readily available from published literature making it a practical choice. Time is also easily scaled as hours per day, making it comparable across species boundaries. So, for practical reasons, hours per day is used here as a first order approximation of how effective a primate needs to be at different activities.

Some have leveled criticism against employing time engaged in a behavior as a measure of the behavior's effect on morphology (Latimer, 1991) and these criticisms are well founded. It seems reasonable, however, that there should be some basic correlation between the amount of time an animal spends in an activity and how effective it needs to be at that activity. More importantly, the purpose of this study is not to determine which behavior has the greatest influence on morphology within a species (which is relatively well established), but rather to search for patterns of locomotor and postural behaviors that correlate with patterns of bipedalism. So while time might not be able to reveal the absolute magnitude of the effect specific behaviors have on morphology, it should have the ability to reveal patterns between behaviors (if they exist). In allometric terms, this is akin to searching for patterns between shapes after scaling for size. It is well recognized that the addition of other factors may drastically alter or even completely refute the conclusions reached here.

Given that 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. Thus an infinite number of

combinations of mobility and stability demands are possible. Theoretically, if the demands for mobility and stability were known for a specific primate niche, then the shoulder morphology that fulfills and balances these demands could be represented on a bivariate plot. The location of such a point would also define the edges of a large plateau on an adaptive landscape where all morphologies that meet both the demands for mobility and stability have a higher fitness than morphologies which fail to meet either one or both demands (Figure 4.1). The differential fitness results because not all possible morphologies have the same capacity, or equal fitness, for meeting the mobility and stability demands necessary to optimize a specific set of locomotor and postural behaviors.

The morphology of the primate shoulder is largely the product of locomotor and postural behaviors that are required to inhabit a particular niche. Some primate shoulders have a high degree of mobility which enhances suspensory behaviors, while other primate shoulders are more stable which enhances terrestrial and above-branch quadrupedism. Ultimately, shoulder morphology contributes to fitness because the ability to move through the environment is critical to the tasks of getting food, avoiding death and reproducing. Thus, for this project it is important to understand how the morphology of the shoulder influences fitness. The phenotypic adaptive landscape provides a powerful tool to model, explore and understand the relationship between the primate shoulder and fitness for different primate niches.

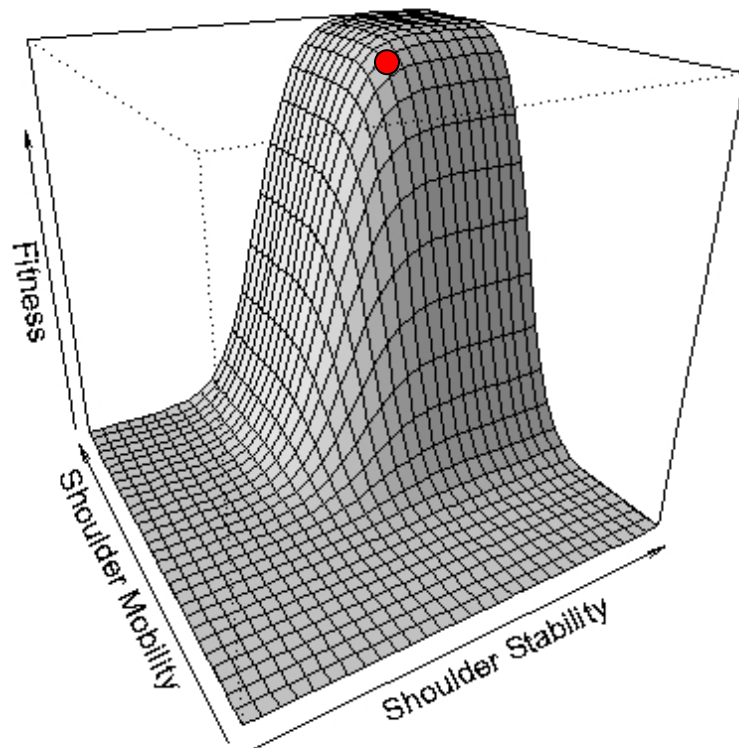


Figure 4.1: Adaptive Landscape for a Set of Exemplar Niche Demands.

Chapter 5: Adaptive Landscapes

The Wrightian Adaptive Landscape

The adaptive landscape was first described by Sewall Wright (1932) as a visual heuristic to accompany his more mathematically demanding models of evolution. Wright's mathematical models are highly dimensional, easily thousands of dimensions, because fitness is affected by a vast number of loci (Wright, 1931). The two-dimensional landscape was meant as a device to intuitively convey the relationship between fitness and genotype that was only possible to model in thousands of dimensions (Skipper, 2004).

Wright envisioned the landscapes as complex and rugged topographies, features that resulted from gene epistasis, and used his landscape to demonstrate his Shifting Balance Theory for evolution. In Wright's Shifting Balance Theory, small sub-populations drift down from a local adaptive peak through maladaptive valleys and climb adjacent peaks. Occasionally, a sub-population may drift to the base of, and then climb, an adjacent peak of higher fitness. The sub-population's improved reproductive success combined with subsequent interbreeding with the main population "pulls" the rest of the population onto the new peak. Wright's landscapes are largely stable and population movement across a landscape indicates changes in a population's allele frequencies.

Although Wright used the landscape to illustrate his evolutionary theory, two main interpretations of the genotype adaptive landscape have emerged (Gavrilets,

1997). In the first, fitness is a function of population allele frequencies and a specific population is represented by a single point on the surface of the landscape. This interpretation is the most common, although it is perhaps misleading (Gavrilets, 1997). Because it relates fitness to allele frequencies, a population concept, this interpretation suggests selection acts at the level of the population and not the individual.

In the second interpretation of Wright's landscape, fitness is a function of genotypes which are characteristic of the individual. Some have argued, however, that Wright's landscape models are inconsistent with this interpretation because individual genotypes are discrete rather than continuous, while Wright's landscapes are clearly continuous (Provine, 1986). Defenders of the genotype interpretation suggest that the landscape is actually a series of discontinuous points that are more easily depicted as a continuous function (Gavrilets, 1997). A population on this interpretation of the landscape is represented by a cloud of points where each individual point corresponds to an individual in the population.

While Wright envisioned a landscape of complex topography, others have reinterpreted Wright's work and have suggested other possibilities. Fisher (1941) argues contra Wright that as the dimensionality of the landscape increases the number of peaks actually decreases (Skipper, 2004). The result is a landscape with a single peak that consisted of a long ridgeline through the multidimensional gene field (Fisher, 1941). More recently, Gavrilets (1997) has criticized both Wright's and Fisher's interpretations, arguing that a better heuristic is a Holey adaptive landscape,

an idea Gavrillets attributes to Dobzhansky (1937). In this view the landscape is flat, but some genotypes result in incompatible gene combinations that have lower fitness and are represented by holes in the landscape. Populations move across the landscape, avoiding the holes, while maintaining the same level of fitness. Speciation occurs when two populations have accumulated enough mutations that they are on opposite sides of a hole (Gavrilets, 1997).

Research on tRNA replication provides an additional interpretation. This work suggests landscapes are best represented by multiple intertwined multidimensional neutral networks (Huynen et al., 1996). A network consists of connected genotypes that differ by a single mutation. In this conception, all genotypes within a single neutral network have the same fitness, but neighboring networks (connected via a mutation link) have different fitness levels (Huynen, 1996).

Phenotypic and Developmental Landscapes

Although Wright used landscapes to visualize the relationship between genes and fitness, the general landscape concept has been employed by other researchers to investigate other aspects of biology. The phenotypic adaptive landscape, an early descendent of Wright's conception, was originally described by Simpson (1944). The phenotypic landscape was proposed to bridge the conceptual gap between micro- and macroevolutionary processes. Microevolution describes the processes leading to phenotypic changes within a single, or closely related, species, while macroevolution

describes those processes that involve the divergence of higher taxa. Simpson (1944) used landscapes to illustrate several critical concepts in evolution, including: phenotypic variation, selection, response to changing environment, speciation, and adaptive radiation (Arnold et al., 2001). 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 change. Unfortunately, despite the fact that Simpson's landscape is over 60 years old, the complaint that microevolutionary changes are unable to account for macroevolutionary processes persists in the evolutionary literature (Arnold et al., 2001).

Rice (1998) develops, what he terms, a phenotypic landscape where some measure of a character phenotype is a function of two relatively undefined variables. Horizontal contours represent individual phenotypes and peaks represent phenotypic extremes. The slope at a given point on a horizontal contour represents the degree of canalization, which is the degree to which adult phenotype is independent of non-genetic factors. Developmental pathways that are highly canalized are represented by low slopes. There are many different pathways (points) to a specific phenotype (horizontal contour), some of which are more canalized (lower slope) than others. If specific adult phenotypes are critical to fitness then selection will drive the population to a position on the landscape that represents the advantaged phenotype as well as the most canalized pathway (Figure 5.1).

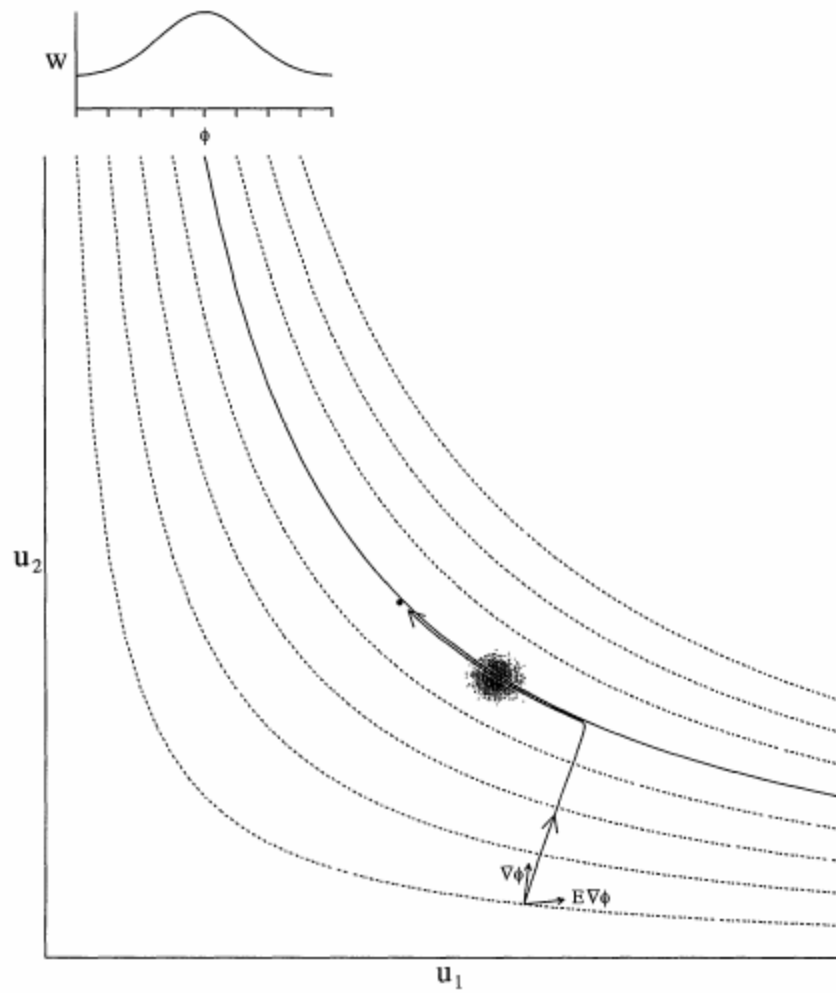


Figure 5.1: Rice's Developmental Landscape. Reproduced from Rice (1998) Figure 3. The optimum phenotype is represented by the solid horizontal contour and the population by the distribution of points. The highly canalized pathway is represented by the greatest slope perpendicular to the contour, and in this figure is represented by the points. Rice defines the axes, u_1 and u_2 , as "underlying factors" that may be either quantitative genetic characters or immediate gene products that influence final phenotype.

Waddington (1957) also used landscapes as a metaphor for developmental canalization, but in a very different way. In Waddington's (1957) landscape, multitudes of genes interact and produce the structure of a specific landscape where surface height was a measure of the developmental potential (Figure 5.2). Development is then viewed as a ball rolling in the valleys of the landscape and different canalized developmental pathways are the specific valleys. This provides a conceptual bridge between genotypes (genes causing the underlying structure), developmental pathways (the valleys) and adult phenotypes (final resting place of the ball).

Simpson's Phenotypic Adaptive Landscape

The landscape of interest to this project is Simpson's phenotypic adaptive landscape (hereafter referred to simply as an adaptive landscape) which is a function that relates continuous phenotypic traits to fitness, the measure of evolutionary success gauged by fecundity. The elevation of the landscape represents the fitness of specific phenotypes. Peaks (areas of higher elevation) and valleys (areas of lower elevation) denote phenotypes of higher and lower adaptive fitness respectively. The shape of an adaptive landscape is largely, although not exclusively, determined by the environment. Individuals are represented by points on the landscape and populations as clouds of points. Populations shift across the phenotypic landscapes as selection acts to drive populations to areas of higher fitness. Population movement occurs because phenotypes closer to peaks enjoy greater

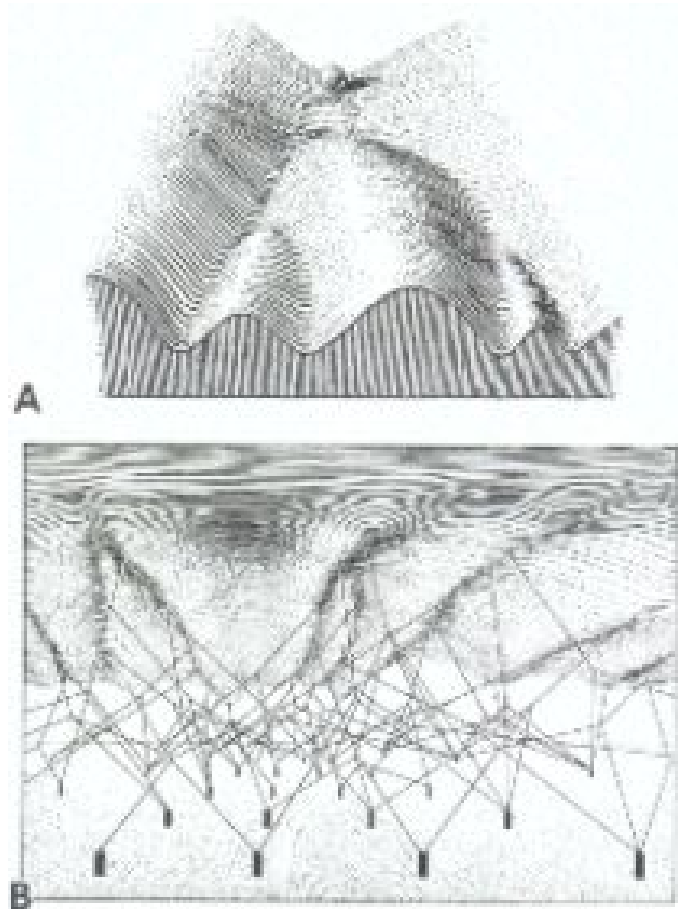


Figure 5.2: Waddington's Developmental Landscape. Reproduced from Arnold et al., (2004) of Waddington (1957). A shows Waddington's developmental landscape where valleys represent developmental pathways. B shows the effects of genes in creating the landscape.

reproductive success than those further away, which shifts the population distribution in subsequent generations towards the peak. Other selective regimes, such as stabilizing and disruptive selection, can also be visualized.

The adaptive landscape is also susceptible to change resulting in new fitness levels for phenotypes. Change in a landscape can reflect 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). 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.

Dimensionality

Any number of dimensions is possible for the phenotypic adaptive landscape. The simplest form of the adaptive landscape is the univariate case, relating a single phenotypic trait to fitness. On one axis, generally the horizontal, are the character values for a specific continuous trait. The other axis, generally the vertical axis, represents levels of fitness. The landscape is a continuous line where fitness is a function of phenotype. Such landscapes can be deceiving because the trait under investigation may be selectively neutral and simply highly correlated with another trait under selection (Arnold et al., 2001). Researchers must be vigilant of this pitfall

in any number of dimensions; however, multivariate approaches provide for some greater level of control (Arnold et al., 2001).

More frequently the adaptive landscape is pursued to investigate two continuous characters. The bivariate landscape fully exploits the power of the concept and is easy to visualize, accounting for its common usage. Two of the axes represent character values and the resulting two-dimensional surface relates these characters to fitness. Three traits can be visualized as a series of nested spheres or ellipses (Philips and Arnold, 1989) although interpretations may not be as intuitive. Higher dimensions are not possible to visualize, but mathematics certainly allows for the extension to numerous character traits. In order to explore the full potential of Simpson's landscape without unnecessary complication, all further discussion will consider the bivariate adaptive landscape.

The Shape of the Adaptive Landscape

The simplest form for an adaptive landscape is the drift landscape (Arnold et al., 2001). This is a flat and level landscape where all phenotypes enjoy the same level of fitness. Because no areas of the landscape have higher fitness, populations move across the landscape in paths best described by Brownian movement (Arnold, 2001). Individual sub-species populations, if not connected by gene flow, are likely to drift independently across the landscape; a theoretical expectation confirmed by tRNA studies (Huynen et al., 1996).

The simplest departure from the drift landscape is a flat landscape that is tilted in either one or both character directions (Arnold, 2001). Populations on such landscapes evolve toward areas of higher fitness. The landscape is prone to changes in its slope as a result of changing niche conditions. Individual populations, derived from the same ancestral population, experiencing different selective regimes (represented by different fluctuations in landscape tilt) will evolve in different directions. Drift is certainly still possible on the directional landscape and can cause movement away from the fitness maximum. The effect of drift on these, or any, landscapes will be more pronounced in small populations.

The curved landscape, described by Lande (1976, 1979), is a landscape generated using a bivariate normal distribution with a single unchanging peak. An attractive feature of this type of landscapes is it provides an optimum solution to niche requirements (Arnold et al., 2001). This allows a population to reach phenotypic stability, where it is still under the influence of selective pressures, but these pressures do not result in phenotypic evolution (movement across the landscape). Drift can cause the population to move down the peak; however, selection will always act to return the population to the top of the peak. If multiple peaks are present, drift can cause the population to move far enough down into a valley that it climbs the adjacent peak.

Population Movement

In a curved adaptive landscape, the optimum is represented by the crest of an adaptive peak. Populations will experience directional selection, movement towards the peak, as well as stabilizing selection, reduced population variance. For a population not yet on top of a peak, the path describing directional selection will be dictated by several factors. One factor that will influence the evolutionary trajectory of a population is the slope of the sides of the peak. Steeply sloped peaks represent of strong directional selection, while a weakly sloping hill corresponds to less intense selective pressures (Lande, 1979). Populations will move more rapidly along lines strong selection, taking the steepest path to the crest. The curvature of the hill, taken as a cross-section parallel to a character axis, will determine the nature of the stabilizing pressure. Highly curved hills represent strong stabilizing pressure, while weak curvature represents weak pressure (Lande and Arnold, 1983). A third aspect of the hill is the orientation (Arnold, 1992). If there is not selection for trait correlation then the two principal axes of the peak are parallel to the character axes. A hill with an upward tilt to its principal axis indicates a selective pressure for positive correlation, while a downward tilt indicates a selective pressure for negative correlation (Figure 5.3).

A population's evolutionary trajectory will also be affected by the variances and covariances of the population traits. In the simplest case, where there is no trait covariance and the trait variances are equal, the population moves up the peak along the path of greatest slope. Deviations from the equalities outlined above will

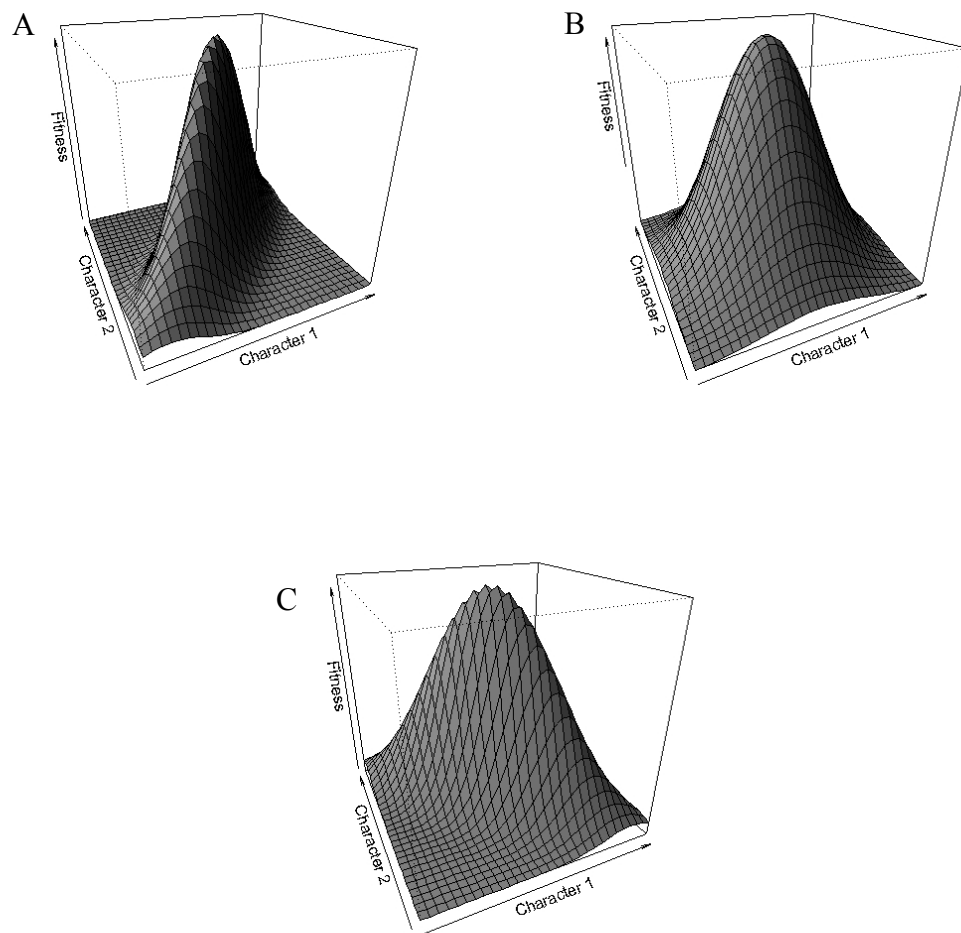


Figure 5.3: Adaptive Landscapes and Hill Orientation. In figure A, the principal axes are aligned with the character axes and so there is no selection for trait correlation. In B the larger principal axis has a positive tilt, indicating selection for positive trait correlation. In figure C the larger principal axis has a negative tilt, indicating selection for negative trait correlation.

contribute to a curved path of ascent. Higher variance in one trait compared to another, in cases of no covariance, will allow evolution to occur more rapidly in the higher variance trait (Lande, 1979, 1980). In the case of trait covariance, it is useful to examine the principal axes of the population (i.e. principal components) (Arnold et al., 2001). If one of the principal components is aligned with one of the axes of the peak, the selection path will be a straight line (Arnold et al., 2001). In the more general case, where neither trait axis is aligned with an axis of the peak, the population will ascend a curved path (Arnold et al., 2001) as depicted in Figure 5.4.

The Changing Adaptive Landscape

One of the most powerful features of the adaptive landscape is that the landscape itself is susceptible to change. In some adaptive landscape models, the location of the peak changes stochastically as a function of time while the shape remains constant (Slatkin and Lande, 1976; Bull, 1987; Lynch and Lande, 1993; Lande and Shannon, 1996). Populations track the location of the optimum as a function of peak deviation (both magnitude and direction), slope gradient and variance/covariance of the population traits and selective pressure. Although these models are instructive in specific case, it seems difficult to connect sporadic peak movement to specific ecological process, although rapid climatic fluctuations provide one possibility (Arnold et al., 2001).

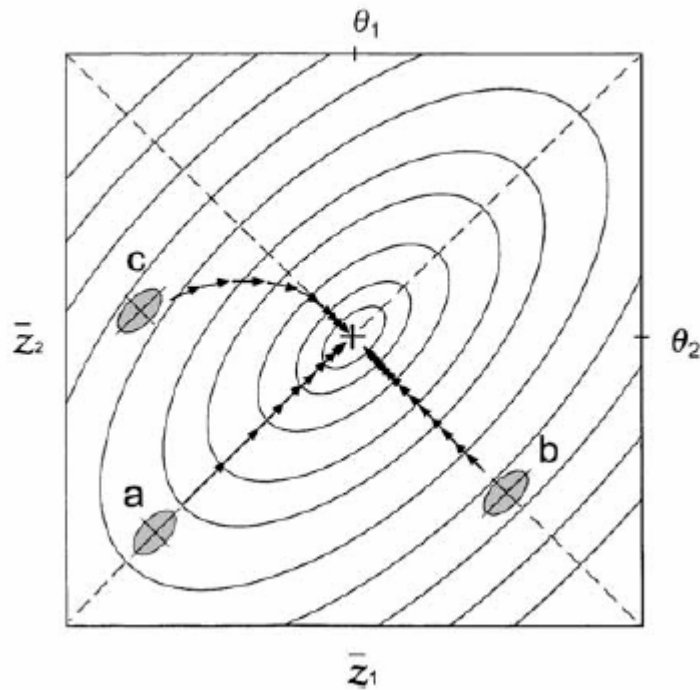


Figure 5.4: Population Movement on an Adaptive Landscape. Reproduced from Arnold et al. (2001) Figure 5. “Evolution on an adaptive landscape depends on the alignment of the axes (principal components) of genetic variation (shaded ellipses) with the axes (principal components) of the adaptive landscape. Evolution follows straight trajectories when major (low left) or minor (lower right) axes are aligned. In general, axes are out of alignment (upper left) and evolution follows a curved trajectory. The small ellipses around each of the population means represent genetic variation around each mean (the eigenvectors and eigenvalues of the G-matrix) and hence are on a different scale of measurement.”

Optima may also experience long term directional change (Charlesworth, 1993; Lynch and Lande, 1993; Lande and Shannon, 1996). This results in long term changes in phenotypes as the population tracks the movement of the peak. Such models are easy to correlate to real ecological variables such as long term trends in climate. This type of model can also be used on smaller time scales to examine the effect of anthropogenic changes to the environment.

Peaks may remain stationary for a long time and then quickly move to a new stable position. This would be the landscape equivalent of Gould and Eldredge's punctuated equilibrium (Arnold et al., 2001). While Gould and Eldredge (1977) envision speciation during periods of rapid evolution, this is not necessarily the case. Rapid peak movement may only result in rapid phenotypic evolution within a lineage (Arnold et al., 2001). Such dramatic and drastic peak shift may be related to invasion of non-native species, cataclysmic climatic events, colonization of novel environment or anthropogenic environmental changes (Arnold et al., 2001).

In all cases of peak movement extinction is a possible outcome if the population cannot keep pace with peak movement. The probability of extinction increases as the distance the peak moves increases (Lande and Shannon, 1996). It is also a function of the steepness of the peak and of the variance/covariance of the population. If the sides of the peak are steep then even small peak movements result in dramatic loss in population fitness, increasing the possibility of extinction. Peaks with less steep sides reduce the chance of population extinction because large peak deviations are required to have drastic effects on population fitness. In addition,

populations are limited in their evolutionary response to a moving peak by their genetic variance/covariance. If the peak moves beyond the population's capacity to evolve, extinction will result (Lynch and Lande, 1993).

Another possibility for peak change, beyond changes in position, is change in the shape of the peak (Arnold et al., 2001). While selection may first act to strengthen positive trait covariance, changing environmental conditions could act to reduce or eliminate trait covariance or even select for negative covariance. New peaks may appear and peaks may bifurcate. Relaxation of stabilizing pressure would result in a peak with lower curvature, while increased stabilizing pressure would result in greater curvature.

Peak bifurcation is an especially interesting possibility and results in two or more peaks which each move in different directions. The original species population may itself divide into smaller groups, each new smaller population tracking a different new peak. This at least would bring about the differentiation of ecological species (Arnold et al., 2001).

Any number of changes in environmental conditions can bring about changes in the shape of an adaptive landscape. Also, adaptive landscapes may change shape as a function of the population. Density-dependent selection can cause an adaptive peak to flatten as the population approaches the peak (Brown and Vincent, 1992; Schluter, 2000). Density-dependent selection is the case when fitness levels of phenotypes are dependent on population composition.

Additional Landscape Features

An interesting potential area of phenotypic landscapes is that of landscape stability. Despite the fact that the evolutionary conservancy of specific features lends great support to long-term stability of adaptive landscapes, this area remains largely unexplored (Arnold et al., 2001). While landscape stability is apparent, its causes remain less clear. There may be basic adaptations, such as the general tetrapod body plan, that are optimum solutions to many niches. Alternatively, feature such as the tetrapod body plan may be the result of pleiotropic genes (such as *Hox* genes). Mutations in these genes could provide novel body plans but could also have deleterious effects on nervous and urogenital systems (Capdevila and Belmonte, 2001).

It must also be remembered that the shape of a landscape is not only the product of environmental and niche conditions. Organisms are dynamic shapers of their own landscapes. Habitat selection is a possible way a population or species contributes to, and potentially controls, the shape and stability of their landscape (Partridge, 1978). Arnold et al., (2001) also suggests that trait interactions that produce ridges and saddles on an adaptive landscape may add to landscape stability.

An additional way in which a population could stabilize their adaptive landscape against change in location and shape is by altering behavioral patterns. Changing environmental conditions can lead to peak movement (changing selective pressure and moving the optimum peak). An organism that utilizes a novel set of

locomotor behaviors to engage the novel environment could maintain the original selective pressures on morphology, resulting in a stable topography.

Another largely unexplored concept in phenotypic adaptive landscapes is that of adaptive plateaus, despite the fact that these have been investigated in the context of Wrightian gene frequency adaptive landscapes. Van Nimwegen et al., (1999) examine the evolution of a population on a “genotype space that contains neutral networks of high, but equal fitness, genotypes”, but the high dimensionality of their problem prevents visualization. Smith et al., (2001) provide graphics of adaptive plateaus in the context of searching for adaptive landscape global optima (Figure 5.5).

Research on RNA is especially instructive for adaptive plateaus and easily understood because phenotypes are derived directly from the genotypes. Huynen et al., (1996) examined the evolution of tRNA molecules using the concept of neutral networks. Networks are sequences of tRNA that are connected by having only a single point mutation. Neutrality exists if networks (a group of connected genotypes) result in the same phenotype (tRNA folding structure). tRNA genotypes change quickly as a population moves within a network, and the original genotype is actually lost while the dominant phenotype (structural folding) goes unchanged. Quick periods of phenotypic evolution occur when populations, evolving within a neutral network of genotypes, move into an area that connects to a different phenotype. If the connected phenotype offers an adaptive advantage (judged by approximation of a predetermined phenotype) the population will transition to the new network. Huynen et al., (1996) also suggest that neutrality is a general characteristic of landscapes that

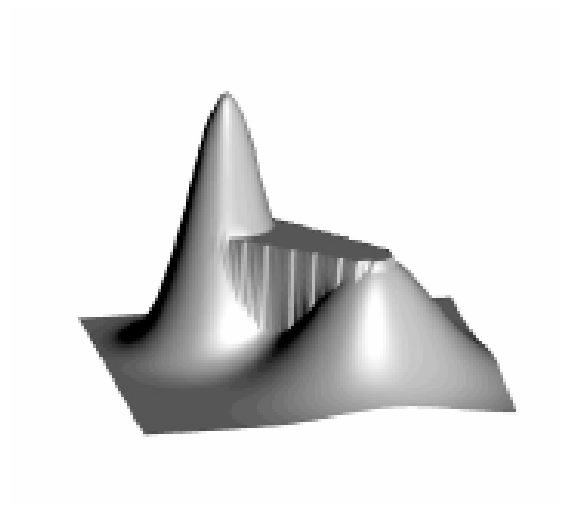


Figure 5.5: Adaptive Plateau: Reproduced from Smith et al. (2001) Figure 2c.

relate phenotypes to fitness. While it is impossible to visualize the highly dimensional neutral networks Huynen and his colleagues describe because of their high dimensionality (4^V where V equals number of base pairs in sequence), it does provide theoretical foundation for two dimensions. In two dimensions, an area of neutrality with high fitness would be represented by a plateau.

The adaptive landscape is a powerful device that has been used in many areas of biological study. It has been used to understand the effect of both genotype and phenotype on fitness as well as to model ontogenetic pathways. For this project, the phenotypic adaptive landscape is the most useful and appropriate device to investigate the interaction of shoulder morphology and the primate niche. In the following chapter the phenotypic adaptive landscape will be adapted to understand the relationship between the morphology of the primate shoulder, which is constrained by the trade-off between mobility and stability, and the demands for mobility and stability, which arise from the need to use specific locomotor and postural behaviors required by a specific niche.

Chapter 6: Adaptive Landscape Modeling

Developing the Decoupling Hypothesis

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 and y axes represent the stability and mobility of the shoulder and the z axis represents the relative fitness of that combination (or phenotype). Each varies from zero to one. For the shoulder traits, zero is no capacity and one is maximal capacity for that trait. The fitness of a phenotype is the point on the surface of the landscape, and varies between zero and one, where zero is lethal and one is scaled to maximum fitness.

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 demands of the environment, but only marginal increases in 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 represent the selective pressures for the theoretical niches. The means were also modeled between zero and one, where zero represents no demand for a shoulder trait and one represents the highest demand for a shoulder trait.

The fitness peaks for nine-hundred theoretical niches were created by varying both means between zero and one at 0.034483 intervals.

The variances were modeled to be equal and were set at 0.01. The variances in this model control the strength of the selective pressure, or the change in fitness for a given change in phenotype. Variances smaller than 0.01 increase the strength of the selective pressure but do not affect the results. Variances lower than 0.01 (Figure 6.1 A-B) were not selected because the resulting landscape is basically a threshold model where any morphology that meets the niche demands has a fitness of 1 and all other morphologies have a fitness of 0. Higher variances decrease the strength of the selective pressure. Increasing the variances results in adaptive landscapes that are increasingly flat, thus reducing the fitness differential among phenotypes (*i.e.*, all phenotypes have the same fitness in a give niche). In Figure 6.1D-E the fitness landscapes do not reach the fitness levels of 0 and 1, and in Figure 6.1F the fitness levels only vary between approximately 0.1 and 0.6. Landscapes with high variances do not allow for shoulder morphologies capable of meeting the demands of the niche and thus were not considered viable for this project.

The covariance between demands for shoulder mobility and stability was set at zero for all landscapes since these demands need not be correlated because they arise from independent locomotor behaviors.

The subset of physically attainable shoulder morphologies was modeled as a trade-off line which was then projected onto each adaptive landscape, traversing from

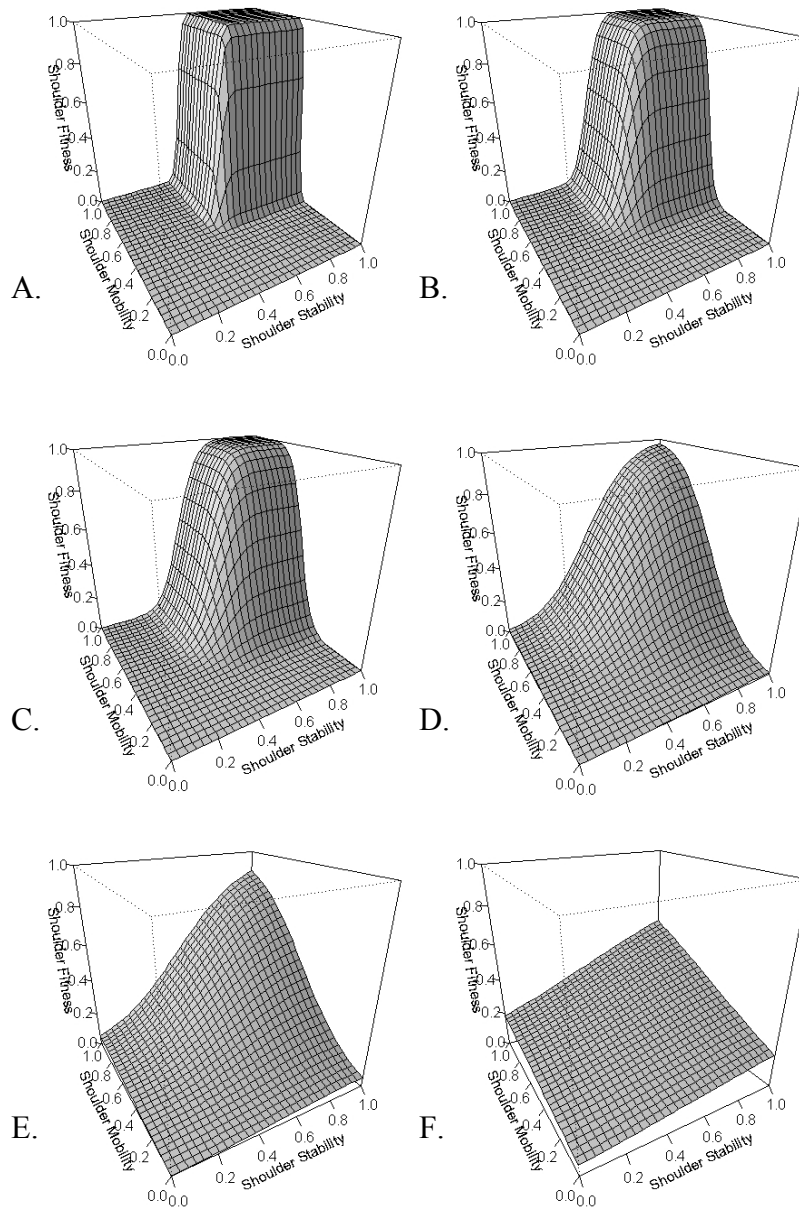


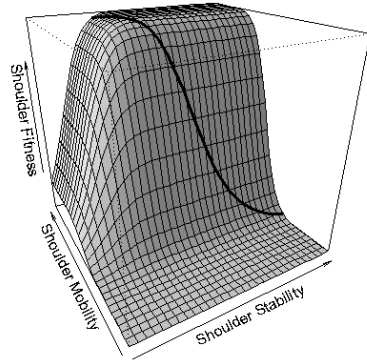
Figure 6.1: Model Variances. For all six landscapes the means are both 0.5. The two variances are equal in each model and are: A = 0.001, B = 0.005, C = 0.01, D = 0.05, E = 0.1, F. 0.5. The variance determines the strength of the selective pressure. In landscape A, the low variance results in what is essentially a threshold model, where most phenotypes have a fitness of either 1 or 0. At the other extreme, model F, the selective pressure is very weak, no potential phenotype reaches a fitness of 1 or 0 and the difference between phenotypic extremes is small.

an area of high stability/low mobility to an area of low stability/high mobility. 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. Minimum limits have the appeal that even a solid piece of bone flexes (some limited mobility) and even a very mobile joint would be stable under compression if load directly through the joint centers. The trade-off line was superimposed upon all 900 theoretical niches. Figure 6.2 shows four exemplar landscapes and includes the trade-off line of attainable shoulder morphologies.

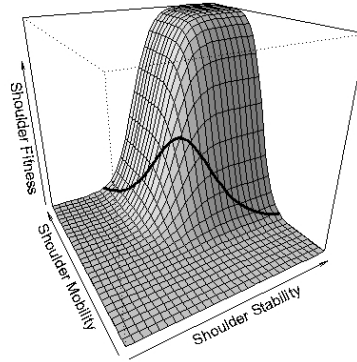
To investigate the effect of the shoulder trade-off on fitness for the modeled niches, the optimize procedure in R (golden search algorithm) was used to search for the maximum fitness along the trade-off line in each of the 900 modeled niches. The maximum fitness values were then plotted as a function of the original stability and mobility demands. Then, for each niche that had a maximum 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 Figure 6.3 for a diagram of the methodology.

The reduction in shoulder stability was then plotted against the original niche demands for shoulder stability and mobility. The reduction in stability was then

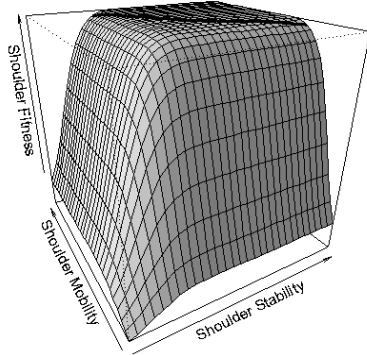
A.



B.



C.



D.

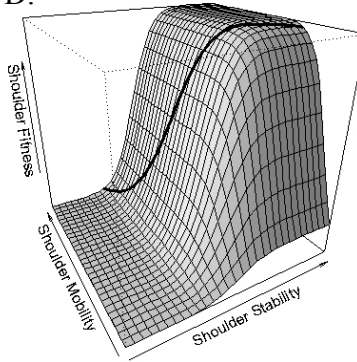


Figure 6.2: Adaptive Landscapes. The adaptive landscapes depicted here, which include the trade-off line, represent niches with demands for: A) High mobility and low stability ($X_M=0.5$, $X_S=0.1$); B) High mobility and high stability ($X_M=0.5$, $X_S=0.5$); C) Low mobility and low stability ($X_M=0.1$, $X_S=0.1$); 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”.

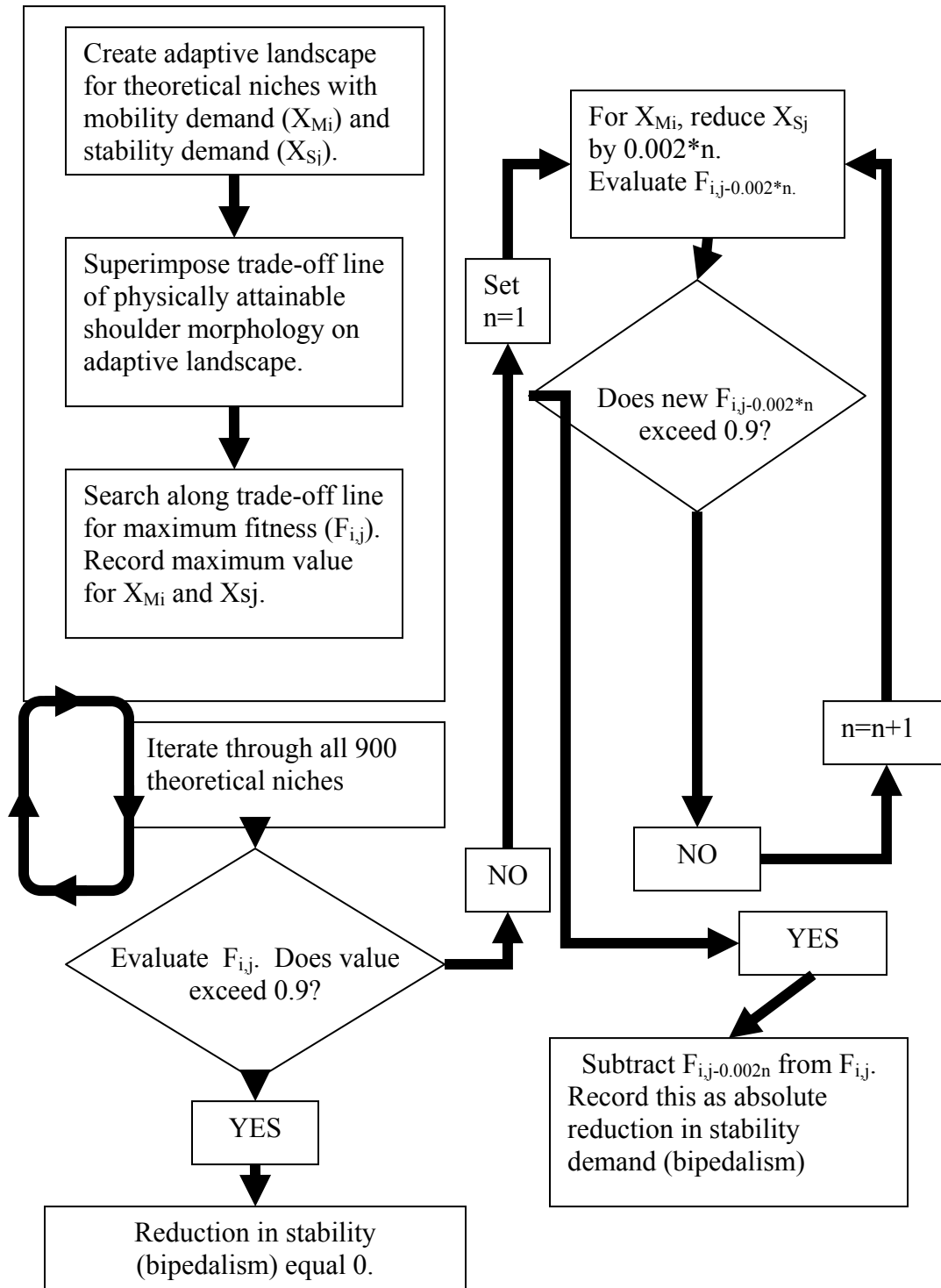


Figure 6.3: Flowchart Diagramming Methodology.

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. All R programs are in Appendix A.

Chapter 7: Materials and Methods

Sample

Daily activity budgets and postural and locomotor behavioral data for 18 primate groups collected from published sources are summarized in Table 7.1. Briefly, these include data for *Pan troglodytes* (Doran, 1996; Doran, 1997; Doran and Hunt, 1994; Hunt, 1989; Hunt, 1992; Matsumoto-Oda, 2002), *Gorilla gorilla* (Doran, 1996; Watts, 1988; Yamagiwa, 1986), *Hylobates agilis* (Gittens 1982; Hunt 1991), *H. pileatus* (Hunt, 1991; Srikosamatara, 1984), *H. lar* (Hunt, 1991; Raemaekers, 1979), *Symphalangus syndactylus* (Hunt, 1991; Leonard and Robertson, 1997), *Pongo pygmaeus* (Cant, 1987; Hunt, 1991; Leonard and Robertson, 1997), *Papio anubis* (Hunt, 1991; Leonard and Robertson, 1997) *Cercocebus albigena* (Gebo and Chapman, 2000; Leonard and Robertson, 1997) and *Colobus guereza* (Gebo and Chapman, 2000; Leonard and Robertson, 1997). Platyrrhine primates were not included in the study because suspensory platyrrhines utilize their tails for suspensory locomotion which almost certainly alters the demands on their shoulders.

All published daily activity budgets included three standard diurnal activity categories: travel, rest and feeding. Occasionally two additional categories were provided: a sleep category and a catch-all “Other” category that generally included activities such as grooming and mating. For the purposes for this study, the published categories were used to divide a day into three more basic activity categories: sleep, posture and locomotion. The percentage of day spent sleeping was used

Table 7.1: Sample of Primate Behavioral Data

Group	Species	Activity Budget	Locomotor and Postural Data
Pan1	<i>Pan troglodytes</i> Mahale (m)	Hunt, 1989	Doran and Hunt, 1994; Doran, 1996
Pan2	<i>Pan troglodytes</i> Mahale (f)	Hunt, 1989	Doran and Hunt, 1994; Doran, 1996
Pan3	<i>Pan troglodytes</i> Mahale (m/f)	Matsumoto-Oda, 2002	Doran and Hunt, 1994; Doran 1996*
Pan4	<i>Pan troglodytes</i> Gombe (m/f)	Hunt, 1989, 1992	Hunt, 1992;
Pan5	<i>Pan troglodytes</i> Tai (m)	Doran, 1997	Doran and Hunt, 1994; Doran, 1996
Pan6	<i>Pan troglodytes</i> Tai (f)	Doran, 1997	Doran and Hunt, 1994; Doran, 1996
Gorilla1	<i>Gorilla gorilla</i> Karisoke (m)	Yamagiwa, 1986	Doran, 1996
Gorilla2	<i>Gorilla gorilla</i> Karisoke (f)	Watts, 1988	Doran, 1996
Hylobates1	<i>Hylobates agilis</i> (m/f)	Gittens, 1982	Hunt, 1991
Hylobates2	<i>Hylobates lar</i> (m/f)	Raemaekers, 1979	Hunt, 1991**
Hylobates3	<i>Hylobates pileatus</i> (m/f)	Srikosamatara, 1984	Hunt, 1991
Symphalangus	<i>Symphalangus syndactylus</i> (m/f)	Leonard and Roberston, 1997	Hunt, 1991
Pongo1	<i>Pongo pygmaeus</i> (f)	Leonard and Robertson, 1997	Cant, 1987
Pongo2	<i>Pongo pygmaeus</i> (m/f)	Leonard and Robertson, 1997	Hunt, 1991
Papio1	<i>Papio anubis</i> (m)	Leonard and Robertson, 1997	Hunt, 1991
Papio2	<i>Papio anubis</i> (f)	Leonard and Robertson, 1997	Hunt, 1991
Cercocebus	<i>Cercocebus algigena</i> (m/f)	Leonard and Robertson, 1997	Gebo and Chapman, 2000
Colobus	<i>Colobus guereza</i> (m/f)	Leonard and Robertson, 1997	Gebo and Chapman, 2000

*Average Pan1 and Pan2; ** Average of Hylobates1 and Hylobates3; m = male; f = female; m/f = mixed sex sample

directly when the category was provided by the author. When a sleep category was not provided, sleeping was assumed to constitute 50 percent of a 24 hour day. This was deemed appropriate because the primates included in the study are diurnal (Fleagle, 1999) and daylight lasts approximately 12 hours in equatorial regions.

The locomotion category created here was equated with the standard travel category. The posture category collapses the standard rest and feeding categories. It is recognized that feeding is not a purely postural activity and may include bouts of travel, however the data used did not make such a distinction and it is necessary to attempt to standardize data when comparing across species (Hunt et al., 1996). This underscores the need for high resolution in primate behavioral data as recommended by Hunt et al. (1996). Data with finer discriminations might alter the conclusions reached here and such data is welcomed should it become available. The catch-all “Other” categories were included in postures since descriptions of these behaviors did not warrant their inclusion in the locomotion category. These data were then used to calculate the number of hours per day spent in sleep, posture and locomotion.

The hours spent in the two daytime categories, posture and locomotion, were further subdivided into more specific posture and locomotor categories using percentages of specific behaviors from the published data. The categories were created to estimate the number of hours per day each primate species used specific groups of behaviors. Three locomotor categories were constructed which were guided by requirements of the stated hypotheses. Descriptions of locomotor behaviors by Hunt et al. (1996) were used to classify specific behaviors into the most

appropriate category. These categories are: 1) above-substrate locomotion (e.g. terrestrial and arboreal quadrupedal walking and running, bipedalism, tripedalism), 2) suspensory locomotion requiring full abduction at the shoulder (e.g. brachiation) and 3) locomotion that is neither above-substrate nor requires abduction (e.g. vertical climbing, below branch quadrupedalism). A fourth category was created, hours of bipedalism, for the purpose of predicting this behavior.

It is worth noting here that bipedal walking and running were included in the first category, along with quadrupedal behaviors, because the purpose is to determine if it is possible to predict bipedalism from other locomotor modes. Bipedalism represents a possible form of locomotion that could be used for above-substrate locomotion. Among primates, above-substrate locomotion is ‘normally’ accomplished by quadrupedalism, a behavior enhanced by joint stability. Grouping bipedalism with quadrupedalism provides an estimate of the total need for moving above-substrate which would ‘normally’ be accomplished by quadrupedalism, a behavior that intensifies the demand for shoulder stability.

Four postural categories were created to subdivide the time spent in the daytime posture category. These categories are based on how the posture affects the shoulder. The categories are: 1) postures that produce compressive forces in the shoulder (e.g. quadrupedal standing), 2) postures that required shoulder abduction (e.g. arm hanging), 3) postures that do not produce compression nor require abduction but that do generate forces across the joint (e.g. clinging, sloth hanging) and 4) postures that do not produce significant forces across the shoulder (e.g. sitting, laying,

bipedal standing). These categories are similar to the locomotor categories except that postures, such as bipedal standing and sitting, are not grouped with behaviors such as quadrupedal standing to form an 'above-substrate' posture category. This was done because postures such as sitting and bipedal standing are not remarkable behaviors among primates that require explanation, since orthograde posture is a common feature among primates.

For the purpose of predicting bipedal locomotion, the hours of bipedal locomotion were scaled by the total number of hours in above-substrate locomotion. Scaling bipedalism in this way provides the proportion of time a primate uses bipedalism, given that the primate is traveling across a substrate that affords the opportunity for bipedalism. This conveys the relative importance of bipedalism as an alternative to quadrupedalism. That is, it discriminates between primates that rarely use bipedalism as part of their above-substrate repertoire from those which frequently use bipedalism as part of their above-substrate repertoire even if both primates use bipedalism the same absolute amount of time.

Analysis

Logistic regression and two variable selection procedures were employed to determine variables that are significant predictors of bipedalism. These procedures were used to test the following hypotheses. The null hypothesis is: The proportion of above-substrate locomotion that is performed using bipedalism is predicted only by main effects of locomotor and postural behaviors. The alternative hypothesis is: The

proportion of above-substrate locomotion that is performed using bipedalism is predicted by interaction effects between above-substrate behaviors and suspensory behaviors.

The proportion of bipedalism was regressed against eleven potential variables. Logistic regression was employed because the proportion of bipedalism is bound between zero and one. An all-possible regressions variable selection procedure was performed using R^2 and Mallows' C_p as criteria for selecting regression equations. The 'best' equation was considered to be the model with the lowest Mallows' C_p and where adding more variables produced only a marginal increase in R^2 . This procedure was used to return the ten best models for each variable number subset. A stepwise variable selection was also carried out with significance set at $\alpha = 0.10$.

The procedures were used to select among seven linear and four interaction predictor variables. The linear variables are those behavior categories outlined earlier and are called: above-substrate locomotion, abducted-shoulder locomotion, non-compressive non-abducting locomotion, shoulder-compressive posture, abducted-shoulder postures, non-compressive non-abducting postures and no-force posture. Interaction variables were selected that directly test the hypotheses presented. Interaction variables that contained linear variables with conflicting shoulder demands were included; these are: above-substrate locomotion*abducted-shoulder locomotion, above-substrate locomotion*abducted-shoulder posture, shoulder-compressive posture*abducted-shoulder locomotion, shoulder-compressive posture*abducted-shoulder posture (Table 7.2). All of the possible two variable

Table 7.2: Variables Included in Regression Analysis

Main Effect Variables	Examples
1. Above-substrate locomotion	Bipedalism, tripedalism, quadrupedism
2. Abducted-shoulder locomotion	Brachiation,
3. Non-compressive non-abducting locomotion	Vertical climbing, below branch quadrupedism
4. Shoulder-compressive posture	Quadrupedal standing
5. Shoulder-abducted posture	Arm-hanging
6. Non-compressive non-abducting posture	Vertical clinging, sloth hanging
7. No force posture	Sitting, laying
Interaction Variables	
8. Interaction between 1 and 2	
9. Interaction between 1 and 5	
10. Interaction between 4 and 2	
11. Interaction between 4 and 5	

interaction terms were not included because the total number of potential variables would have far exceeded the number of observations. Further, Neter et al. (1996) indicate that when using the Mallows' C_p statistic, only important interactions should be included, and useless ones excluded, so that the mean squared error of the total model provides an unbiased estimate of the error variance. The regression models produced by the variable selection procedures were examined to find those models that contained only significant predictor variables.

Finally, a Levene's test was performed on the variances of the predictor model. First the variances were regressed against the means because it is essential to scale variances before comparison if they are positively correlated with the means (Sokal and Rohlf, 1981).

Chapter 8: Results

Adaptive Landscape Modeling

Figure 8.1 depicts the maximum possible fitness for the 900 theoretical niches. The two horizontal axes represent the original demand 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.

Figure 8.2 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, while Figure 8.3 depicts this reduction in shoulder stability (bipedalism) as a proportion of the original demand for stability.

Primate Behavioral Data

Table 8.1 contains the activity budgets (hours in sleep, locomotion and posture) for the 18 primate groups. Table 8.2 provides the hours per day the primate groups engaged in the specific locomotor behaviors and Table 8.3 presents the hours

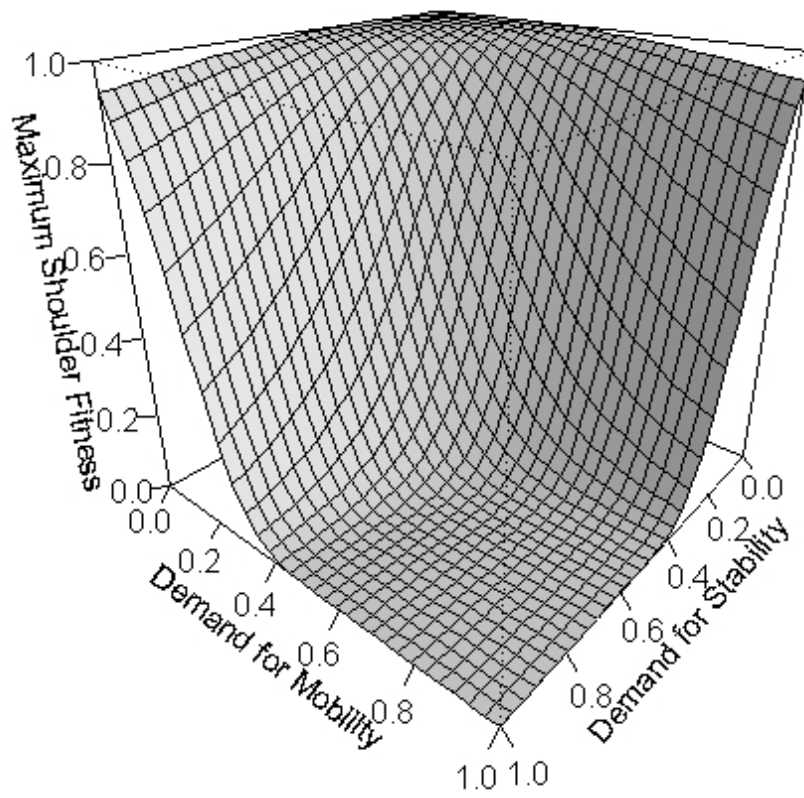


Figure 8.1: Maximum Possible Shoulder Fitness.

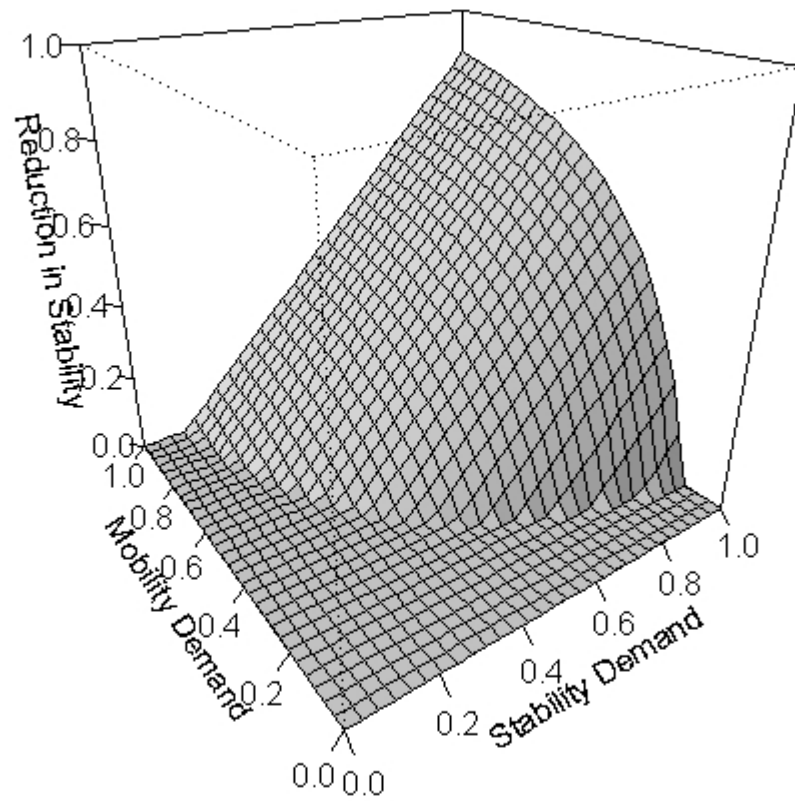


Figure 8.2: Reduction in Stability Demand.

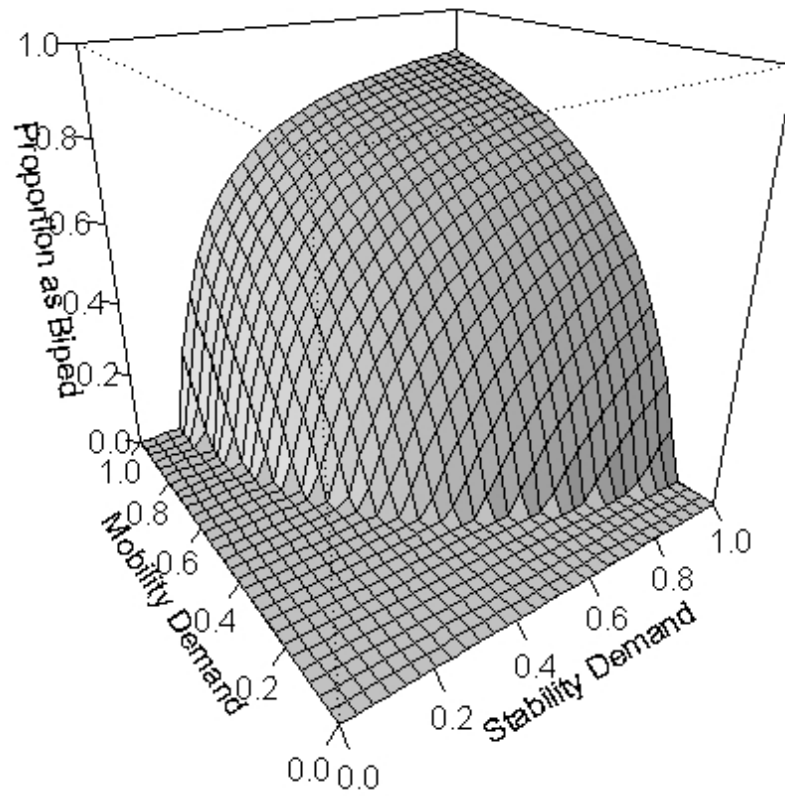


Figure 8.3: Proportion of Terrestrial Locomotion Performed Using Bipedalism.

Table 8.1: Activity Budgets: Hours per Day.

	Loco.	Post.	Sleep
Pan 1	1.37	10.01	12.00
Pan 2	1.32	10.02	12.00
Pan 3	3.42	8.58	12.00
Pan 4	1.63	9.08	12.02
Pan 5	1.44	9.84	12.00
Pan 6	1.44	9.84	12.00
Gorilla 1	0.74	11.27	12.00
Gorilla 2	0.78	11.09	12.00
Hylobates 1	2.74	6.45	15.00
Hylobates 2	2.80	5.80	15.40
Hylobates 3	2.04	6.14	15.79
Syndactylus	2.30	8.10	13.60
Pongo 1	1.36	9.91	12.73
Pong 2	1.21	10.07	12.73
Papio 1	3.62	7.55	12.83
Papio 2	3.24	8.06	12.70
Cercocebus	2.56	9.44	12.00
Colobus	1.95	9.87	12.00

Table 8.2: Hours of Locomotion: Hours per Day.

	Abducted- shoulder	Above- substrate	Other
Pan 1	0.011	1.287	0.070
Pan 2	0.012	1.208	0.102
Pan 3	0.029	3.174	0.219
Pan 4	0.000	1.550	0.082
Pan 5	0.016	1.264	0.160
Pan 6	0.020	1.259	0.157
Gorilla 1	0.000	0.737	0.005
Gorilla 2	0.002	0.757	0.021
Hylobates 1	1.819	0.752	0.173
Hylobates 2	1.434	0.412	0.955
Hylobates 3	1.722	0.196	0.122
Syndactylus	1.840	0.253	0.230
Pongo 1	0.772	0.163	0.426
Pong 2	0.752	0.143	0.119
Papio 1	0.000	3.627	0.025
Papio 2	0.000	3.246	0.023
Cercocebus	0.000	1.630	0.901
Colobus	0.000	1.547	0.294

Table 8.3: Hours of Posture: Hours per Day.

	Abducted- Shoulder	Compressive- shoulder	No compression or abduction	No force
Pan 1	0.24	0.12	0.00	9.63
Pan 2	0.60	0.21	0.00	9.14
Pan 3	0.36	0.14	0.00	8.04
Pan 4	0.50	0.40	0.03	8.22
Pan 5	0.10	0.60	0.00	9.14
Pan 6	0.21	0.55	0.00	9.07
Gorilla 1	0.00	0.87	0.00	10.40
Gorilla 2	0.01	0.59	0.00	10.49
Hylobates 1	2.22	0.00	0.00	4.22
Hylobates 2	2.43	0.00	0.00	3.37
Hylobates 3	2.35	0.00	0.00	3.79
Syndactylus	4.29	0.00	0.00	3.81
Pongo 1	4.16	0.10	0.00	5.05
Pong 2	4.31	1.08	0.00	4.89
Papio 1	0.02	1.49	0.02	6.06
Papio 2	0.02	1.59	0.02	6.46
Cercocebus	0.00	2.80	0.00	6.60
Colobus	0.00	0.39	0.00	9.37

per day spent in the postural categories. Table 8.4 provides the hours per day of bipedalism scaled by the total hours per day of above-substrate locomotion.

The equation that resulted from the stepwise variable selection is provided in Table 8.5. The model includes three predictor variables: abducted-shoulder locomotion ($F = 48.26$, $p < 0.0001$), abducted-shoulder posture ($F = 23.27$, $p = 0.0003$), and an interaction term that contains abducted-shoulder locomotion and above-substrate locomotion ($F = 8.61$, $p = 0.011$).

The all-possible regression procedure which was followed by the search for equations containing only significant predictor variables resulted in eight equations. These include five one-variable models, three two-variable models and one three-variable model. The equations and the t -values and p -values for each of these models are provided in Table 8.6. Of these retained models the ‘best’ model, judged by having the lowest Mallows’ C_p (-1.62) and the highest R^2 (0.86), is the same model arrived at using the stepwise procedure. Again, this model included abducted-shoulder locomotion ($t = 6.95$, $p < 0.0001$), abducted-shoulder posture ($t = -4.82$, $p = 0.0003$) and the interaction between abducted-shoulder locomotion and above-substrate locomotion ($t = -2.94$, $p = 0.011$) as significant variables.

A model that performed nearly as well, having a slightly higher R^2 (0.88) and the second lowest Mallows’ C_p (-0.96), is a four-variable model also included in Table 8.6. This model contained the three variables in the ‘best’ model as well as a fourth variable, the interaction term that contained: abducted-shoulder posture and

Table 8.4: Scaled Hours of Bipedalism.

	Proportion of Bipedalism
Pan 1	0.005
Pan 2	0.002
Pan 3	0.004
Pan 4	0.006
Pan 5	0.014
Pan 6	0.021
Gorilla 1	0.017
Gorilla 2	0.014
Hylobates 1	0.872
Hylobates 2	1.000
Hylobates 3	1.000
Syndactylus	1.000
Pongo 1	0.000
Pong 2	0.000
Papio 1	0.016
Papio 2	0.016
Cercocebus	0.000
Colobus	0.000

Table 8.5: Regression Model from Stepwise Procedure.
 $(y = e^{f(x)} / [1 + e^{f(x)}])$ where $f(x)$ = linear regression

Variables	Regression Estimate	F-value	p-value
Abducted-shoulder locomotion	16.82	48.26	<0.0001
Abducted-shoulder posture	-3.40	23.27	0.0003
Abducted-shoulder locomotion*Above-substrate locomotion	-10.46	8.61	0.0109
Intercept	-4.91	39.98	<0.0001

Table 8.6: Regression Models
 $(y = e^{f(x)} / [1 + e^{f(x)}])$ where $f(x)$ = linear regression.

# of Var	Variables	Regression Estimate	t-value	p-value	R ²	Cp
1	Abducted-shoulder locomotion Intercept	6.75 -6.16	-5.49 5.09	<.0001 0.0001	0.62	8.61
1	Abducted-shoulder locomotion * Above-substrate locomotion Intercept	10.80 -4.90	2.99 -3.58	0.0086 0.0025	0.36	23.92
1	No-force posture Intercept	-1.47 7.45	-2.86 1.93	0.011 0.071	0.34	25.12
1	Compressive-shoulder posture Intercept	-3.84 -0.67	-2.04 -0.38	0.058 0.71	0.21	32.92
1	Abducted-shoulder locomotion * Above-substrate locomotion Intercept	5.55 -5.77	1.97 -2.96	0.067 0.009	0.20	33.59
2	Abducted-shoulder locomotion Abducted-shoulder posture Intercept	11.00 -2.41 -5.22	6.44 -3.17 -5.53	<0.0001 <0.0001 0.0063	0.77	1.53

Table 8.6 Continued.

# of Var	Variables	Regression Estimate	t-value	p-value	R ²	Cp
2	Abducted-shoulder locomotion	7.07	6.29	<0.0001	0.75	3.05
	Abducted-shoulder locomotion*	-11.73	-2.75	<0.0001		
	Compressive-shoulder posture Intercept	-5.71	-5.95	0.015		
2	Abducted-shoulder locomotion	7.02	6.21	<0.0001	0.74	3.23
	Abducted-shoulder posture*	-2.03	-2.70	0.02		
	Compressive-shoulder posture Intercept	-5.64	-5.81	<0.0001		
3	Abducted-shoulder locomotion	16.82	6.95	<0.0001	0.86	-1.62
	Abducted-shoulder posture	-3.40	-4.82	0.0003		
	Abducted-shoulder locomotion* Above-substrate locomotion Intercept	-10.46 -4.91	-2.94 -6.32	0.011 <0.0001		
4	Abducted-shoulder locomotion	18.02	7.43	<0.0001	0.88	-0.96- 0.96
	Abducted-shoulder posture	-3.96	-5.22	0.0002		
	Abducted-shoulder locomotion* Above-substrate locomotion Abducted-shoulder posture* Above-substrate locomotion Intercept	-15.02 3.38 -5.68	-3.37 1.58 -6.42	0.005 0.14 <0.0001		

above-substrate locomotion. This fourth variable, however, is not significant ($t = 1.58, p = 0.1391$).

Because of difficulties in interpreting models with multiple predictors, each of the variables in the ‘best’ model was regressed separately against the proportion of bipedalism to better understand its individual relationship. The equations for these single variable models are provided in Table 8.7 and graphed in Figure 8.4.

Abducted-shoulder locomotion remains the most significant variable ($t = -5.49, p < 0.001$), explaining 62 percent of the total variation in bipedalism ($R^2 = 0.62$).

Abducted-shoulder posture is no longer a significant predictor when used alone ($t = 1.61, p = 0.13$). The interaction between abducted-shoulder locomotion and above-substrate locomotion is the second best single predictor ($t = 2.99, p = 0.009$) explaining over one-third of the variation in bipedalism ($R^2 = 0.36$).

The results from the regression of variable variances on variable means are presented in Table 8.8 and indicate that there is a significant positive correlation between the variable variances and means. This resulted in scaling the variables (\log_{10}) prior to performing the Levene’s test. The results from the Levene’s test are provided in Table 8.9 along with the scaled variances and show that there are significant differences among some of the variable variances. The variance of the shoulder-abducted posture and locomotion are not significantly different from one another, but both are significantly larger than the variance of above-substrate locomotion.

Table 8.7: Single Variables from ‘Best’ Model.
 $(y = e^{f(x)} / [1 + e^{f(x)}])$ where $f(x)$ = linear regression.

Variable	Regression Estimate	R ²	t-value	p-value
Abducted-shoulder locomotion	6.75	0.62	-5.49	<0.0001
Intercept	-6.16		5.09	0.0001
Abducted-shoulder locomotion * Above-substrate locomotion	10.80	0.36	2.99	0.0086
Intercept	-4.90		-3.58	0.0025
Abducted-shoulder posture	1.42	0.14	1.61	0.127
Intercept	-4.73		-2.68	0.017

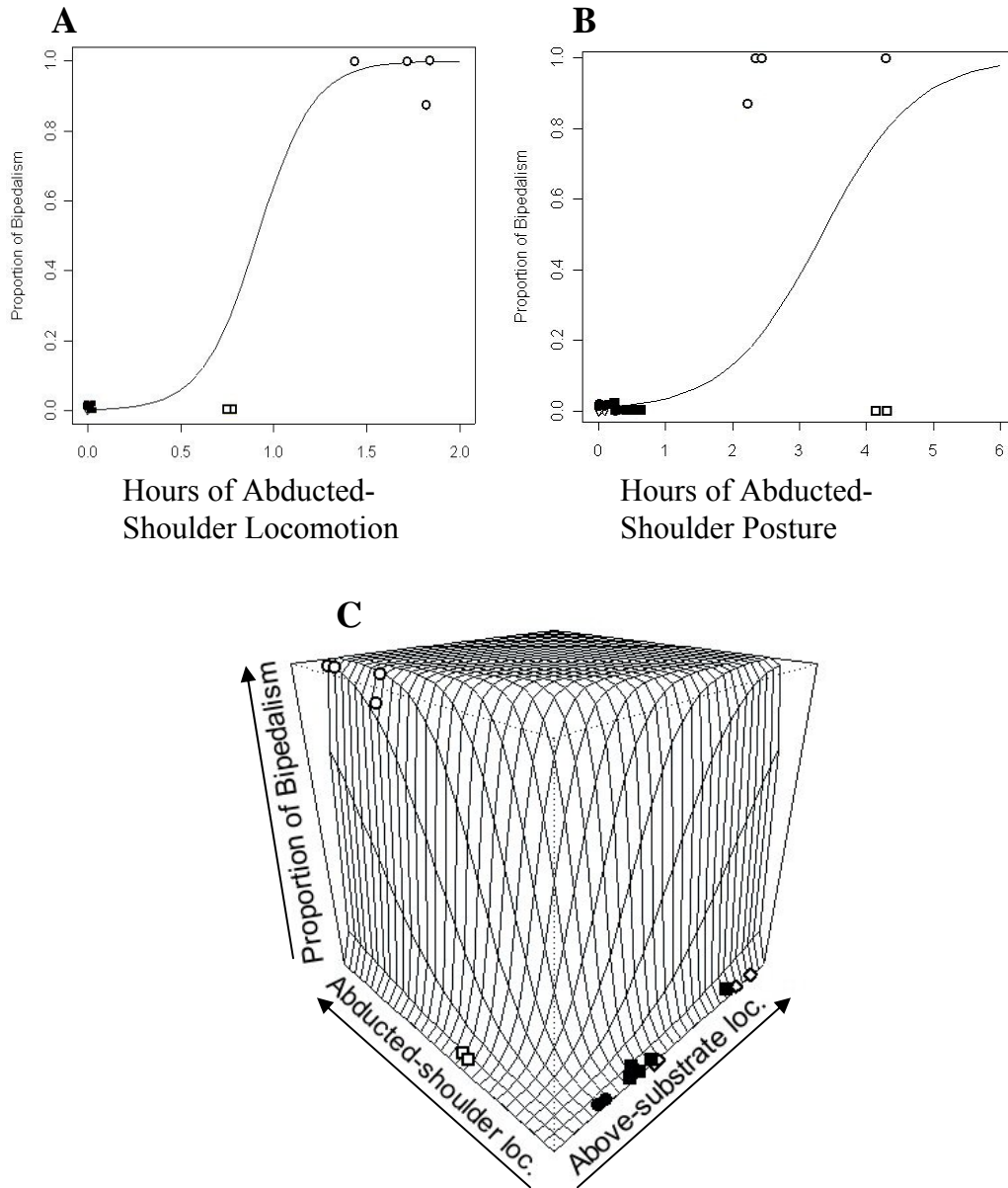


Figure 8.4: Proportion of Bipedalism: Bipedalism plotted against: A) Abducted-shoulder locomotion; B) Abducted-shoulder posture; C) Abducted-shoulder locomotion*Above-substrate locomotion. Open circles = *Hylobates* and *Syndactylus*; Open squares = *Pongo*; Closed circles = *Gorilla*; Closed squares = *Pan*; Open diamonds = Cercopithecoids.

Table 8.8: Regression of Variable Variances on Variable Means.

Variables	Regression Estimate	R²	t-value	p-value
Means	0.261	0.92	7.79	0.0006
Intercept	0.843		0.87	0.42

Table 8.9: Levene's Test for Homogeneity of Variance.

Variables	Scaled Variance	F-value	p-value
Abducted-shoulder locomotion	4.22	2.60	0.12
Abducted-shoulder posture	2.63		
Abducted-shoulder locomotion	4.22	10.62	0.005
Above-substrate locomotion	0.18		
Abducted-shoulder posture	2.63	9.63	0.006
Above-substrate locomotion	0.18		

Chapter 9: Discussion

Adaptive Landscape Modeling

Theoretical niches that require highly stable and highly mobile shoulders carry a dramatic loss in fitness for a quadrupedal primate because a joint cannot be both highly mobile and highly stable. In conjunction with this finding, the known correlations between the demand for mobility and suspensory behaviors, and the demand for stability and quadrupedal behaviors strongly suggest that it would not be possible for a quadrupedal primate to occupy a niche that required highly effective forms of quadrupedism and suspensory behaviors.

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, 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 locomotion 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 (5.4-10.6km) are absolutely long compared to that of *Gorilla gorilla* (0.86km) and *Pan troglodytes* (2.4-3.6km), and if these distances were scaled (possibly by limb length or stride length) the relative distances of *Papio* would likely be even greater (Nunn and van Schaik, 2001). The baboon niche, however, also includes arboreal travel (Fleagle, 1999). 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 (Andrews, 1981).

Changing environmental conditions could have reduced the size and/or carrying capacity of the traditional hominoid niche. A concurrent increase in the size of a novel niche, such as the one outlined above, could have forced the proto-hominid population into such a niche to avoid extinction. While the rate and extent of global cooling and drying during the late Miocene is unresolved, there is evidence of cooler and drier intervals in east Africa between 5-7 Ma (Richmond et al., 2001). In equatorial regions of African this certainly would have fragmented forests, resulting in diverse habitats ranging from dense forests to open grasslands (Richmond et al., 2001).

It is possible that the proto-hominid could have shifted to occupy a niche that did not require either a highly effective suspensory or terrestrial behaviors. A shift to a purely terrestrial niche would have drastically reduced the demand for shoulder mobility (since abduction would no longer be important), thus allowing the shoulder to evolve exclusively to meet the demand for a highly effective quadrupedism. A

shift to such a niche, however, would have required a different selective pressure for bipedalism 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 appears to be the niches occupied by gorillas and chimpanzees. This scenario would also require a different explanation for hominid bipedalism than the one envisioned here.

If the proto-hominid were forced into a niche that required highly effective terrestrial and suspensory behaviors, there would have been selective pressure to increase fitness since the ancestral population would not have necessarily been pre-adapted to such a lifeway. 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 (Andrews, 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 adaptations. The forelimbs and hind limbs would become increasingly independent with respect to weight bearing during above-substrate locomotion. While the single primitive locomotor module of quadrupedal primates is subjected to specific set of selective pressures that acts on both the hind and forelimbs, bipedalism would have changed the selective pressures acting on the forelimbs and hindlimbs. The forelimbs would have adapted mainly to meet the demands of suspensory behaviors and the hindlimbs would have adapted to terrestrial locomotion. Because the fore- and hindlimbs were subjected to separate selective regimes, they are considered separate locomotor modules and hence the primitive single locomotor module was decoupled into two relatively independent modules.

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 Figure 8.2 and 8.3 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 Figure 8.3.

The strength of the DH is that it provides several testable predictions about primate behavior and anatomy, the hominid fossil record and the early hominid niche. The hypotheses 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 behavior in niches that require highly effective forms of terrestrial (or above-branch) locomotion in association with efficient suspensory behaviors.
- 2) The early hominid 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 hominid niche should require highly effective forms of terrestrial and suspensory locomotion. This niche is expected to be different from that 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) 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.

Primate Behavioral Data

The results of the analyses indicate that rejection of the null hypothesis is warranted and that the alternative hypothesis, which proposes that interactions between behaviors that create conflicting demands for mobility and stability are significant predictors of bipedalism, is tentatively accepted. The interaction term indicates a positive correlation between conflicting shoulder demands and bipedalism. The DH does not predict, however, that the linear variables (abducted-shoulder locomotion and posture) would be the most significant predictors, instead anticipating that these variables would be part of interaction terms that would include a behavior that selects for joint stability. While it is encouraging that the interaction between above-substrate locomotion and abducted-shoulder locomotion is the second most significant single predictor variable and that the interaction between abducted-shoulder posture and above-substrate locomotion appears as a variable in the four-variable model, it is necessary to seek an explanation for lower predictive power of the interaction terms.

One possible reason for the lower significance of the interaction terms, compared to the linear variables, is that it is an artifact of the sample. If an interaction term were actually the most significant predictor variable, but because of the sample utilized one of the variables included in the interaction had a low variance (i.e. is relatively constant) then the most significant predictor is expected to be the variable from the interaction with the higher variance. Thus if the sample utilized in this study, were relatively homogenous with respect to above-substrate locomotion

compared to the suspensory behaviors, then the suspensory behaviors would be expected to become the most significant behaviors. To explore this possibility the variables that were part of the ‘best’ model, abducted-shoulder locomotion, abducted-shoulder posture and above-substrate locomotion, were compared for equality of variance. These results demonstrate that of the three variables from the ‘best’ model, above-substrate locomotion has the lowest variance while the abducted-shoulder locomotion has a significantly higher variance. Abducted-shoulder postures have a variance that is significantly different than abducted-shoulder locomotion but is significantly greater from above-substrate locomotion. This suggests that if additional primates that expanded the range of hours of above-substrate locomotion were included in the sample then the interaction variable might become the most significant predictor of bipedalism. Early hominids, with a greater reliance on terrestrial locomotion, might represent such a primate.

The Fossil Record and Paleoecology

The results of this study provide initial support for the DH and indicate that it should be explored further as a potential explanation for the origin of bipedalism. Any theory for the origin of bipedalism, however, must be also compatible with the fossil record. The DH makes specific predictions about the nature of the early hominid niche and provides expectations about the morphology of the earliest hominids. The DH anticipates that the earliest hominid would appear split with respect to the locomotor capacities of the forelimbs and hindlimbs. The hindlimbs

should appear to have adapted mainly to terrestrial locomotion while the forelimbs should have conformed to the demands of arboreal suspensory behaviors. The current fossil record suggests that post-cranial anatomy of pre-*Homo erectus* (*ergaster*) is relatively stable and that these hominids retain a large number of arboreal features in the trunk and forelimbs (Wood and Collard, 1999). In addition, it is virtually undeniable that the hindlimbs of these hominids had adapted mainly for terrestrial bipedal progression (although see Sarmiento, 1994, 1998).

The arboreal features of the upper body of *Australopithecus afarensis*, the best represented early hominid, are well known (for a list see McHenry, 1995). Some of the features, such as cone-shaped torso, cranially oriented glenoid fossa and chimpanzee-like brachial index have been directly linked to suspensory behaviors (Hunt, 1991, 1998). *A. anamensis* appears to have also retained many primitive forelimb features, perhaps even more than *A. afarensis* (Ward et al., 2001). The difficulty, as Ward (2002) points out, is in the interpretation of these features. Do they represent features preserved because of adaptive significance as some propose or simply primitive features that are evolutionary retentions? If the maintenance of primitive features in the forelimbs of the earliest hominid can be linked to selection for arboreal (suspensory) behaviors then this would provide support for the hypothesis presented here. If the primitive features can be demonstrated to be evolutionary lag and that arboreal contexts did not provide important resources and were without adaptive significance for early hominids, then the DH would be without merit.

It is clear that the hindlimbs had undergone a major reorganization to accommodate the demands of terrestrial bipedal progression. As with the features of the forelimbs, however, deviations from modern human anatomy in the hindlimbs of early hominids have multiple interpretations. Some suggest early hominids were well adapted (possibly obligated) to a terrestrial lifestyle and practiced bipedalism that was energetically and kinematically similar to modern humans (see Latimer, 1991). This interpretation is compatible with the DH as long as bipedalism did not confine the hominid to the ground.

Others have interpreted the evidence as revealing a compromised bipedalism, one not yet on par with modern humans (Berge, 1994; Jungers, 1991; Susman et al., 1984; Stern, 1999; Stern and Susman 1983). Early hominid bipedalism need not have been as effective as modern human bipedalism to remain consistent with the DH as long as early hominids were capable of meeting niche requirements for above-substrate locomotion and that the amount of above-substrate locomotion was sufficient to generate a large demand for shoulder stability. Modern chimpanzees and gorilla retain a mobile shoulder despite being largely terrestrial quadrupeds (Doran and Hunt, 1994), thus it might be expected that the early hominid niche mandated a more effective terrestrial locomotion than modern African apes. As noted earlier, the average day journey for *G. gorilla* (0.86km) and *P. troglodytes* (2.4-3.6km) is relatively small compared with that of *Papio hamadryas* (10.6km) and *Papio anubis* (5.9km) (Nunn and van Schaik, 2001). In addition, there is some indication that chimpanzees forfeit terrestrial efficiency (Taylor and Rowntree, 1973) and speed

(Hunt, 1989) in order to retain suspensory adaptation (Pontzer and Wrangham, 2004). A need to increase the importance of these variables, or others not imagined, could increase the demand for shoulder stability.

The earliest forms of bipedalism might have been less effective relative to terrestrial quadrupedalism since a normally quadrupedal primate may not be equally capable of bipedalism (although see Taylor and Rowntree, 1973). The fitness gain bipedalism provided the early hominids by retaining the mobile shoulder for suspensory behaviors would have had to offset this early cost of a less effective terrestrial locomotion until a more effective bipedalism evolved. It is difficult to imagine that the early hominids would have existed in a low adaptive area for very long. The transition from quadrupedalism to bipedalism is hence expected to have been swift.

The increase in fitness for suspensory behaviors by retaining shoulder mobility also needs to have compensated for any loss in other arboreal behaviors resulting from the hindlimbs becoming adapted to terrestrial bipedalism. Pontzer and Wrangham (2004) suggest that vertical climbing represents a small portion of the energy budgets of chimpanzees relative to terrestrial quadrupedalism. A decrease in hind limb vertical climbing efficiency may have only a marginal influence on overall energy cost of early hominids. Additionally, modern human groups climb trees without the suite of hind limb adaptations associated with arboreal behaviors (Chagnon, 1997; Descola, 1986) and some humans are capable of exceptional feats of climbing (Sylvester, pers. comm.). While many features suggest that the hindlimbs

were still partially adapted to arboreality (Berge and Ponge, 1983; Jungers and Stern, 1983; Stern, 1999; Stern and Susman, 1983) it seems unlikely that the hindlimbs could have been as effective for suspensory postures and locomotion as the hindlimbs of a modern ape. The hindlimbs, however, are not necessary to accomplish suspensory behaviors. Arm-hanging without assistance from the hindlimbs is frequently used by chimpanzees, comprising approximately 5% of all postures among Mahale and Gombe chimpanzees (Hunt, 1991).

The fitness gain generated by retaining suspensory adaptations in the shoulder must have been able to counterbalance any loss engendered by an ineffective early bipedalism and diminished arboreal capacities of the hindlimbs. The retention of high mobility in the shoulder (and likely other suspensory adaptations throughout the forelimb and thorax) is critical because of dangers that accompany arboreal behaviors. Loss of forelimb suspensory adaptations would result in less effective suspensory behaviors. This could mean only lower efficiency, but could have also seriously compromise arboreal safety. Serious injury and death may accompany falls from relatively low heights (6m) (Crites et al., 1998; Steedman, 1989; Urquhart et al., 1991) and a review of average canopy height usage for the African apes demonstrate that even large male gorillas venture as far as seven meters and that chimpanzees regularly travel as high as 20 meters (Doran, 1996). Avoiding debilitating injury and/or death represents a significant gain in fitness, one possibly large enough to compensate for losses in the other behaviors.

Finally for the DH to remain a viable explanation, the hominid niche must have required greater demands for above-substrate locomotion while maintaining relatively significant demands for suspensory behaviors. Classical savannah models, more recent data indicating closed woodland habitats (WoldeGabriel et al., 1994), and unstable environments (Potts, 1999) have all been envisioned as the selective environments for hominid evolution. All of these, however, are consistent with the DH, since terrestrial and arboreal locomotion could remain important in any of these contexts. The critical factor is not the environment *per se*, but rather it is the niche within the environment that is available to the proto-hominid which is important. A niche that requires highly effective terrestrial and suspensory adaptations is conceivable in any environment assuming it has some trees available for suspensory behaviors. It is easiest to envision such a niche in an environment of open grassland dotted with groups of trees. Such a niche could also be possible within a closed forest if the proto-hominid populations were marginalized to arboreal resources that had very low spatial density.

Hunt's (1998) review of the australopithecine dental evidence provides a clearer picture of the early niche, although mainly limited to *A. afarensis* and later hominids. Hunt (1998) concludes, based on the intersection of several lines of cranio-dental evidence, that the australopithecine diet consisted mainly of small-diameter, fibrous fruits with a lesser emphasis placed on leaves. *A. anamensis* is reported to have dental characteristics similar to *A. afarensis*, including molar enamel thickness (Leakey et al., 1995) which may betray a similar diet. The thinner enamel

of *Ardipithecus ramidus* (White et al., 1994) may indicate a substantially different diet or possibly the evolutionary conservatism of teeth which had yet to change to meet a dietary shift.

If the earliest bipeds did concentrate on small high-fibrous fruits this could have generated the large demands for above-substrate and suspensory behaviors. Despite higher nutrition content per volume, fruit is known to have a lower spatial density (and hence lower nutritional spatial density) compared to leaves, compelling larger home ranges among frugivores compared to folivores (Clutton-Brock and Harvey, 1977; Milton and May, 1976; Nunn and Barton, 2000). Fruits that are highly fibrous present a lower nutritional content per volume (than lower fiber fruits), therefore reducing the nutritional spatial density even further. Focusing on small high-fibrous fruit could have demanded greater terrestrial travel than that seen in modern apes, while maintaining the need to suspend from arboreal supports. Chimpanzees prefer traveling terrestrially between arboreal resources despite the cost associated with ascending and descending trees (Pontzer and Wrangham, 2004) (possibly because of dangers associated with traveling on terminal branches). If early hominids followed a similar behavior pattern, then the early hominid niche would have mandated relatively long bouts of terrestrial travel, punctuated by forays into the canopy. Such a niche, and travel it required, could have generated the intense demands for joint stability and mobility that cannot be accommodated by a single articulation.

Chapter 10: Conclusions

The results presented here offer paleoanthropology a new testable hypothesis for the origin of hominid 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 hominids to occupy niches that mandate highly effective terrestrial and suspensory behaviors that would not be available to quadrupeds because of the tradeoff between shoulder mobility and stability.

The preliminary test of the DH conducted here provides provisional support of the hypothesis. Additional factors will need to be incorporated in order to more accurately test the DH and such efforts may significantly alter the conclusions reached here. This project provides only the most preliminary tests of the DH performed solely to determine if further investigation is justified. At this point, using the data analyzed here, it is submitted that further exploration of the Decoupling Hypothesis is appropriate and justified.

Work Cited

- Alberch P. 1982. Developmental constraints in evolutionary processes. In Evolution and development. Bonner JT editor. Berlin:Springer-Verlag. p 313-332.
- 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 SJ. 1992. Constraints on phenotypic evolution. Am Nat. 140:S85-S107.
- 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.
- Ashton EH, Oxnard CE. 1963. The musculature of the primate shoulder. Trans. Zool. Soc. Lond. 29:553-650.
- Berge C. 1991. Quelle est la signification fonctionnelle du pelvis très large d'*Australopithecus afarensis* (AL 288-1)? In: Senut B, Coppens Y editors. Origine(s) de la bipédie chez les Hominidés. Paris: CNRS. p 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.
- Berge C, Ponge J-F. 1983. Les caractéristiques du bassin des australopithèques: sont-elles à une bipédie de type humain? Bull Mem Soc Anthropol Paris 10:335-354.
- Bogin, B., 1990. The evolution of human childhood. Bioscience 40, 16-25.
- Bock WJ, vonWahlart G. 1965. Adaptation and the form-function complex. Evolution 19: 269-299.
- Brown JS, Vincent TL. 1992. Organization of predator-prey communities as an evolutionary game. Evolution 46: 1269-1283.
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Ahounta D, et al. "A new hominid from the upper Miocene of Chad, central Africa". Nature, 418:145-51, 2002.
- Bull JJ. 1987. Evolution of phenotypic variance. Evolution 41:303-315.
- Cant JGH. 1987. Positional Behaviors of Female Bornean Orangutans. Am J Primatol 12:71-90.

- Capdevila J, Belmonte JCI. 2001. Perspectives on the Evolutionary Origin of Tetrapod Limbs. In GP Wagner editor. The Character Concept in Evolutionary Biology. Academic Press: New York. p531-558
- Chagnon NA. 1997. Yanamamo. Fort Worth: Harcourt Brace.
- Chaplin G, Jablonski NG, Cable NT. 1994. Physiology, thermoregulation and bipedalism. J. Hum. Evol. 27:497-510.
- Charlesworth B. 1993. Directional selection and the evolution of sex and recombination. Genet. Res. 61: 205-224.
- Ciochon RL, Corruccini RS. 1977. The coraco-acromial ligament and projection index in man and other anthropoid primates. J. Anat. 124:627-632.
- Le Gros Clark WE. 1955. The fossil evidence for human evolution. Chicago, University of Chicago Press.
- Le Gros Clark WE. 1959. The Antecedents of Man, Edinburgh University Press, Edinburgh.
- Clutton-Brock TH, Harvey PH. 1977. Primate ecology and social organization. J Zool 183:1-39.
- Crites BM, Moorman CT III, Hardaker WT Jr. 1998. Spine injuries associated with falls from hunting tree stands. J South Orthop Assoc 7:241-245.
- Crompton RH, Li Y, Wang W, Günter MM, 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 RA. 1925. *Australopithecus africanus*: The Man-Ape of South Africa. Nature 115:195-199.
- Dart RA. 1953. The predatory trantsisiton from ape to man. International Anthropological and Linguistic Review 1: 201-219.
- Darwin C. 1871. *The Descent of Man*. New York: New York University Press.
- Day MH. 1977. Locomotor adaptations in man. Biol. Hum. Affairs. 421:149-151.
- Dobzhansky TH. 1937. Genetics and the Origin of Species. Columbia University Press.

- Doran DM, Hunt KD. 1994. Comparative Locomotor Behavior of Chimpanzee and Bonobos. In: Wrangham RW, McGrew WC, de Waal FMB, Heltne PG, editors. Chimpanzee Cultures. Cambridge: Harvard University Press. p 93-108.
- Doran DM. 1996. Comparative positional behavior of the African apes. In: McGrew MC, Marchant LP, Nishida T, editors. Great Ape Societies. Cambridge: Cambridge University Press. p 213-224.
- Doran DM. 1997. Influence of seasonality on the activity patterns, feeding behavior, ranging and group patterns in Tai chimpanzees. *Int J Primatol* 18:183-206.
- Descola P. 1986. In the Society of Nature: a native ecology in Amazonia. Cambridge: Cambridge University Press.
- Duncan AS, Kappelman J, Shapiro LJ. 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.
- Engles F. 1950 (1876). The part play by labor in the transition from ape to man. New York, International Publishers
- Etkin W. 1954. Social behavior and the evolution of man's faculties. *American Naturalist* 88:129-142.
- Evans FG, Krahle VE. 1945. The torsion of the humerus. A phylogenetic survey from fish to man. *Am. J. Anat.* 76:303-367.
- Fisher RA. 1941. Average Excess and the Average Effect of a Gene Substitution. *Annals of Eugenics* 11:53-56.
- Fleagle JG. 1999. Primate adaptation and evolution. San Diego: Academic Press.
- Fleagle JG, Simons EL. 1982. The humerus of *Aegyptopithecus zeuxis*: A primitive anthropoid. *Am. J. Phys. Anthropol.* 59:175-193.
- 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. *Memoirs of the California Academy of Sciences* 8, 1-55.
- Gavrilets S. 1997. Evolution and Speciation on Holey Adaptive Landscapes. *Trends in Ecology and Evolution* 12:307-312.
- Gebo DL, Chapman CA. 2000. Locomotor behaviors in Ugandan monkeys. In: Whitehead PF, Jolly CJ, editors. *Old World Monkeys*. Cambridge: Cambridge University Press. p 480-495.
- Gittens SP. 1982. Feeding and Ranging in the Agile Gibbon. *Folia Primatol* 38:39-71.
- Gould SJ. 1989. A developmental constraint in Cerion, with comments on the definition and interpretation of constraint in evolution. *Evolution* 43:516-539.
- Gould SJ. 1977. *Ontogeny and phylogeny*. Harvard University Press, Cambridge, Mass.
- Gould SJ, Eldredge N. 1997. Punctuated equilibria: the temp and mode of evolution reconsidered. *Paleobiol.* 3:115-151.
- 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 strepsirrhine primates. *J. Morphol.* 230, 113-127.

- Hamrick, M.W., 1999. A chondral modeling theory revisited. *J. Theor. Biol.* 201, 201-208.
- Hardy AC. 1960. Was man more aquatic in the past?. *New Scientist* 7:642-645.
- 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. *Proceedings of the National Academy of Science* 95, 1336-1339.
- Hewes GW. 1961. Food Transport and the Origin of Hominid Bipedalism. *Am Anthropol* 63:687-710.
- Hildebrand, M., 1995. *Analysis of Vertebrate Structure*, John Wiley and Sons, Inc, New York.
- Hooton EA. 1925. The asymmetrical character of human evolution. *Am. J. Phys. Anthropol.* 8:125-141.
- Hooton EA. 1946. *Up from the Ape*. New York, Macmillan.
- Houle D. 2001. Characters as the Units of Evolutionary Change. In GP Wagner editor. *The Character Concept in Evolutionary Biology*. Academic Press, New York p 109-140.
- Hunt KD. 1989. Positional behavior in *Pan troglodytes* at the Mahale Mountains and Gombe National Parks, Tanzania. Ph.D Dissertation. University of Michigan: Ann Arbor.
- Hunt KD. 1991. Positional behavior in the Hominoidea. *Int J Primatol* 12:95-118.
- Hunt KD. 1992. Positional behavior in *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *Am J Phys Anthropol* 87:83-105.
- Hunt KD. 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.

- Hunt KD. 1998. Ecological morphology of *Australopithecus afarensis*: traveling terrestrially, eating arboreally. In: Strasser E, Fleagle JG, McHenry HM, Rosenberger A, editors. *Primate Locomotion: Recent Advances*. New York: Plenum. p 397-418.
- Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. *Primates* 37: 363–387.
- Hunter J, Jernvall JP, Forteliu M. 1996. The hypocone as a key innovation in mammalian evolution. *Proc. Nat. Acad. Sci USA* 92:10718-10722.
- Huynen MA, Stadler PF, Fontana W. 1996. Smoothness within Ruggedness: The Role of Neutrality in Adaptation. *Proc Nat. Acad. Sci. USA* 93:397-401.
- Inman VT, Saunders JB deCM, Abbott LC. 1944. Observations on the function of the shoulder joint. *J. Bone Joint Surg.* 26:1-30.
- 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.
- Johanson D, Taieb M, Coppens Y. 1982 (a). Pliocene Hominids From the Hadar Formation, Ethiopia (1973-1977): Stratigraphic, Chronologic, and Paleoenvironmental Contexts, With Notes on Hominid Morphology and Systematics. *American Journal of Physical Anthropology.* 57:373-402.
- Jolly, C.J., 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5, 1-26.
- Jungers WL. 1985. *Size and Scaling in Primate Biology*. New York: Plenum Press.
- 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.

- Jungers WL, Stern JT. 1983. Body proportions, skeletal allometry and locomotion in the Hadar hominids: a reply to Wolpoff. *J Hum Evol* 43:195-215.
- Keith A. 1949. A new theory of human evolution. New York, Philosophical Library.
- Köhler W. 1959. The mentality of apes. New York, Vintage Books.
- Kramer PA. 1999. Modeling the locomotor energetics of extinct hominids. *J Exp Biol* 202:2807-2818.
- Kramer PA, Eck GG. 2000. Locomotor energetics and leg length in hominid bipedality. *J Hum Evol* 38:651-666.
- Kortlandt A. 1980. How Might Early Hominids have Defended Themselves Against Large Predators and Food Competitors?. *J Hum. Evol.* 9:79-112.
- Lande R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30: 314-334.
- Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain-body size allometry. *Evolution* 33: 402-416.
- Lande R. 1980. Microevolution in relation to macroevolution. *Paleobiol.* 6_233-238.
- Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210-1226.
- Lande R, Shannon S. 1996. The role of genetic variation in adaptation and population persistence in changing environments. *Evolution* 50:434-437.
- Larson S. 1988. Subscapularis function in gibbons and chimpanzees: Implications for interpretation of humeral head torsion in hominoids. *Am. J. Phys. Anthrop.* 76:449-462.
- 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.
- Larson S, Stern JT. 1986. EMG of scapulohumeral muscles in the chimpanzee during reaching and "arboreal" locomotion. *Am. J. Anat.* 176:171-190.
- Larson S, Stern JT. 1987. EMG of chimpanzee shoulder muscles during knuckle-walking: Problems of terrestrial locomotion in a suspensory adapted primate. *J. Zool. Lond.* 212:629-655.

- Larson S, Stern JT. 1989. The role of supraspinatus in the quadrupedal locomotion of vervets (*Cercopithecus aethiops*): Implications for interpretation of humeral morphology. *Am. J. Phys. Anthrop.* 79:369-377.
- Larson S, Stern JT, Jungers WL. 1991. EMG of serratus anterior and trapezius in the chimpanzee: Scapular rotation revisited. *Am. J. Phys. Anthrop.* 85:71-84.
- Latimer, B., 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality, in: Senut, B., Coppens, Y. (Eds.), *Origine(s) de la bipédie chez les Hominidés*, CNRS, Paris, pp. 169-176.
- 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, 1215-133.
- 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*, John Wiley and Sons, Ltd., New York: Dahlem Conference, pp. 63-278.
- Leakey MG, Feibel CS, McDougall I, Walker A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565-571.
- Leakey MG, Spoor F, Brown FH, Gathogo PN, Kiarie C, Leakey LN, McDougall I. 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410:433-440.
- Leonard WR, Robertson ML. 1997. Comparative Primate Energetics and Hominid Evolution. *Am J Phys Anthropol* 102:265-281.
- Lewontin R. 1984. Adaptation. In *Conceptual Issues In Evolutionary Biology* E Sober editor. p 234-251. MIT Press, Cambridge, Mass.

- Lindén, M., Møller, A.P., 1989. Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.* 4, 367-371.
- Livingstone FB. 1962. Reconstructing man's Pliocene pongid ancestor. *Am. Anthropol* 64:301-305.
- 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.
- Lynch M, Lande R. 1993. Evolution and extinction in response to environmental change. *Biotic Interactions and Global Change*. P Kareiva, JG Kingsolver and RB Huey editors. Sinauer, Sunderland, MA p 234-250.
- MacLachy, L.M., 1996. Another look at the australopithecine hip. *J. Hum. Evol.* 31, 455-476.
- Martin CP. 1933. Cause of torsion of the humerus and the notch on the anterior edge of the glenoid cavity of the scapula. *J. Anat.* 67:573-582.
- 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.
- Matsumoto-Oda A. 2002. Behavioral Seasonality in Mahale Chimpanzees. *Primates* 43:103-117.
- Maynard Smith J, Burian R, Kauffman SA, Alberch P, Campbell J, Goodwin BC, Lande R, Raup D, Wolpert L. 1985. Developmental constraints and evolution. *Q Rev Biol* 60:265-287.
- McHenry HM. 1995. Tempo and Mode in Human Evolution. In: Walter M, Fitch F, Ayala J, editors. *Tempo and mode in evolution: genetic and paleontology 50 years after Simpson*. Washington DC: National Academy Press.
- Mednick LW. 1955. The evolution of the human ilium. *Am J Phys Anthropol* 13:203-216.
- Milinski, M., Bakker, T.C.M., 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* 344, 330-333.

- Milton K, May ML. 1976. Body weight, diet and home range area in primates. *Nature* 259:459-462.
- Müller GB, Wagner GP. 1991. Novelty in evolution: restructuring the concept. *Annu. Rev. Ecol. Syst.* 22:229-256.
- Munro R. 1893. Address to Section H (Anthropology), British Association for the Advancement of Science: 885-95.
- Neter J, Kutner MH, Nachtsheim CJ, Wasserman W. *Applied Linear Statistical Models*. New York: McGraw-Hill.
- Nunn CL, Barton RA. 2000. Allometric Slopes and Independent Contrasts: A Comparative Test of Kleiber's Law in Primate Ranging Patterns. *Am Nat* 156:519-533.
- Nunn CL, van Schaik CP. 2001. A comparative approach to reconstructing the socioecology of extinct primates. In: Plavcan JM, Jungers WL, Kay RF, van Schaik CP, editors. New York: Plenum. p 159-216.
- Ostrom, J.H., 1976. *Archaeopteryx* and the origin of bird. *Biological Journal of the Linnean Society of London* 8, 91-182.
- Partridge L. 1978. Habitat selection. In *Behavioral Ecology* JR Krebs NB Davies editors. P 351-376. Blackwell Scientific, Oxford, England.
- Patrides CA. 1958. Renaissance Ideas on Man's Upright Form. *Journal of the History of Ideas* 19(2):256-258.
- 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* Conference, Eichstätt 1984, Freunde des Jura-Museums Eichstätt, Eichstätt, pp. 233-242.
- Philips PC, Arnold SJ. 1989. Visualizing multivariate selection. *Evolution* 43:1209-1222.
- Pontzer H, Wrangham RW. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *J Hum Evol* 46:317-335.
- Potts R. 1999. Variability selection in hominid evolution. *Evol Anthropol* 7: 81-96.

- Provine WB. 1986. Sewall Wright and Evolutionary Biology. Chicago: University of Chicago Press.
- Putz R, Liebermann J, Reichelt A. 1988. Funktion des Ligamentum coracocromiale. Acta Anat. 131:140-145.
- 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>.
- Raemaekers J. 1979. Ecology of sympatric gibbons. Folia Primatol 31:227-245.
- Rak Y. 1991. Lucy's pelvis anatomy: its role in bipedal gait. J Hum Evol 20:283-290.
- Reynolds E. 1931. The evolution of the human pelvis in relation to the mechanics of erect posture. Papers of the Peabody Museum of American Archaeology and Ethnology 11:255-334.
- Rice SH. 1998. The Evolution of Canalization and the Breaking of Von Baer's Laws: Modeling the Evolution of Development with Epistasis. Evolution 52:647-656.
- Richardson MK, Chipman AD. 2003. Developmental Constraints in a Comparative Framework: A Test Case Using Variation in Phalanx Number During Amniote Evolution. Journal of Experimental Zoology 296B:8-22.
- Richmond, B.G., D.R. Begun, D.S. Strait. 2001. The origin of human bipedalism: the knuckle-walking hypothesis revisited. Yearbook of Physical Anthropology 44: 70-105.
- Roberts D. 1974. Structure and function of the primate scapula. In FA Jenkins (ed.): Primate Locomotion. New York: Academic Press p 171-200.
- Rodman PS, McHenry HM. 1980. Bioenergetics and the origin of hominid bipedalism. Am J Phys Anthropol 52:103-6.
- Roff, D.A., 1997. Evolutionary Quantitative Genetics, Chapman and Hall, New York, pp. 165-195.
- Rose MD. 1976. Bipedal behaviour of olive baboons *Papio anubis* and its relevance to understanding the evolution of human bipedalism. Am J Phys Anthropol 44: 247-261.

- Rose MD. 1984. Food acquisition and the evolution of positional behaviour: the case of bipedalism. In: Chivers DH, Wood BA, Bilsborough B, editors. Food acquisition and processing in primates. New York: Plenum. p 509-524.
- Rose MD. 1989. New postcranial specimens of catarrhines from the Middle Miocene Chinji Formation, Pakistan: Descriptions and a discussion of proximal humeral functional morphology in anthropoids. *J Hum Evol* 18:131-162.
- Rose 1991. MD. The process of bipedalization in hominids. In: Coppens Y, Sentu B, editors: Origine(s) de la bipédie chez les Hominidés. Paris. Centre National de la Recherche Scientifique. P 37-48.
- Sarmiento EE. 1988. Anatomy of the hominoid wrist joint: its evolutionary and functional implications. *Int J Primatol* 9:281-345.
- Sarmiento EE. 1994. Terrestrial traits in the hands and feet of gorillas. *Am Mus Nov* 3091:1-56.
- Sarmiento EE. 1998. Generalized quadrupeds, committed bipeds and the shift to open habitats: an evolutionary model of hominid divergence. *Am Mus Nov* 3250:1-78.
- Schaefer, S.A., Lauder, G.V., 1986. Testing historical hypotheses of morphological change: biomechanical decoupling in loricarioid catfishes. *Evolution* 50, 1661-1675.
- Schemske, D.W., Ågren, J., 1995. Deceit pollination and selection in female flower size in *Begonia involucre*: an experimental approach. *Evolution* 49, 207-214.
- Schluter D. 2000. The Ecology of Adaptive Radiation. Oxford University Press, Oxford England.
- Schmidt-Nielsen K. 1984. Scaling: Why Is Animal Size so Important?. Cambridge. Cambridge University Press.
- Schultz H. 1951. The specializations of man and his place among the catarrhine Primates. *Cold Spring Harbor Symposia on Quantitative Biology* 15:37-53.
- Schwenk K. 2001. Functional Units and Their Evolution. In Wagner GP editor: The Character Concept in Evolutionary Biology p 165-198. Academic Press New York.

- Selvaggio MM. 1998. Evidence for a Three-Stage Sequence of Hominid and Carnivore Involvement with Long Bones at FLK Zinjanthropus, Olduvai George, Tanzania. *Journal of Archaeological Science* 25:191-202.
- Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya) *C R Aca Sci [Iia]* 332:137-144.
- Shea K, Chesson P. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17:170-176.
- Shelfelbine, 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*, New York, Columbia University Press.
- Sinclair A, Leakey RE, Norton-Griffiths MD. 1986. Migration and hominid bipedalism. *Nature* 324:307-308.
- Skipper RA. 2004. The Heuristic Role of Sewall Wright's 1932 Adaptive Landscape Diagram. *Philosophy of Science* 71:1176-1188.
- Slatkin M, Lande R. 1976. Niche width in a fluctuating environment – density independent model. *Am. Nat.* 110:31-35.
- Smith GE. 1913. *The evolution of man*. Smithsonian Report for 1912:553-572. Washington, C.C., Smithsonian Institution.
- Smith BH, Tompkins RL. 1995. Toward a life history of the Hominidae. *Annual Review of Anthropology* 24:257-279.
- Smith T, Husbands P, Layzell P, O'Shea M. 2001. Fitness Landscapes and Evolvability. *Evolutionary Computation* 10(1):1-34.
- Sokal RR, Rohlf FJ. 1981. *Biometry*. San Francisco: W.H. Freeman and Company. p 419-422.
- Spoor F, Wood B, Zonneveld F. 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. *Nature* 369:645-648.
- Sponheimer, M., Lee-Thorp, J., de Ruiter, D., Codron, D., Codron, J., Baugh, A. & Thackeray, F. 2005. Hominins, Sedges, and Termites: New Carbon Isotope Data from the Sterkfontein Valley and Kruger National Park. *Journal of Human Evolution* 48, 301-312.

- Srikosamatara S. 1984. Ecology of Pileated Gibbon in South East Thailand. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The Lesser Apes: Evolutionary and Behavioural Biology. Edinburgh: Edinburgh University Press. p 242-257.
- Stanford CB. 2006. Arboreal Bipedalism in Wild Chimpanzees: Implications for the Evolution of Hominid Posture and Locomotion. *Am J Phys Anthropol* 129:225-231.
- Steedman DJ. 1989. Severity of free-fall injury. *Injury (British Journal of Accident Surgery)*. 20:259-61.
- Stern JT. 1999. The cost of bent-knee, bent-hip bipedal gait: a reply to Crompton et al. *J Hum Evol* 36:567-570.
- Stern JT, Wells JP, Jungers WL, Vangor AK. 1980. An electromyographic study of serratus anterior in Atelines and *Alouatta*: Implications for hominoid evolution. *Am J Phys Anthropol* 52:323-334.
- Stern JT, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. *Am J Phys Anthropol* 60:279-317.
- Stern JT, Susman RL. 1991. "Total morphological pattern" versus the "magic trait:" conflicting approaches to the study of early hominid bipedalism. In: Senut B, Coppens Y editors. *Origine(s) de la bipédie chez les Hominidés*. Paris: CNRS. p 99-112.
- Steudel-Numbers K, Weaver TD. 2006. Froude Number Corrections in Anthropological Studies. *Am J Phys Anthropol* (In Press).
- Susman RL, Stern JT, Jungers WL. 1984. Arboreality and bipedality in the Hadar hominids. *Folia Primatol* 43:113-156.
- Tanner NM. 1981. *On Becoming Human*. Cambridge University Press: Cambridge.
- Taylor CR, Rowntree VJ. 1973. Running on two or on four legs: Which consumes more energy? *Science* 179:186-187.
- Tuttle RH. 1974. Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. *Curr Anthropol* 15:389-398.
- Tuttle RH. 1975. Parallelism, brachiation, and hominoid phylogeny, In *Phylogeny of the Primates: a Multidisciplinary Approach*. (W. P. Luckett and F. S. Szalay, eds.), 447-480, Plenum, New York.

- Tuttle RH. 1981. Evolution of hominid bipedalism and prehensile capabilities. Phil. Trans. Royal Society, London, B 291: 89-94.
- Urquhart CK, Hawkins ML, Howdieshell TR, Mansberger AR Jr. 1991. Deer stands: a significant cause of injury and mortality. South Med J 84:686-688.
- van Nimwegen E, Crutchfield JP, Huynen M. 1999. Neutral Evolution of Mutational Robustness. Proc Nat Acad Sci USA 96:9716-9720
- Vermeij, G.J., 1974. Adaptation, versatility, and evolution. Syst. Zool. 22, 466-477.
- Videan EN, McGrew WC. 2002. Bipedality in chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*): Testing hypotheses on the evolution of bipedalism. Am J Phys Anthropol 118:184-190.
- Waddington CH. 1957. The Strategy of the Genes. MacMillan, New York.
- Wagner GP. 1995. The biological role of homologues: a building block hypothesis. N Jb Geol Paläont Abh 195:279-288
- Wagner GP. 1996. Homologues, natural kinds and the evolution of modularity. Am Zool 36:36-43.
- Wagner GP. 1999. A research programme for testing the biological homology concept. In Homology Bock GR Cardew G editors p 125-140. Wiley, Chinchester.
- Wagner GP. 2001a. The Character Concept in Evolutionary Biology. Academic Press, New York.
- Wagner GP. 2001b. Historical Roots Of The Character Concept. In Wagner GP editor The Character Concept in Evolutionary Biology. Academic Press, New York. P13-36.
- Wagner GP, Laubichler MD. 2001. Character Identification: The Role of the Organism. P 141-164. In Wagner GP editor The Character Concept in Evolutionary Biology. Academic Press, New York.
- Ward CV. 2002. Interpreting the Posture and Locomotion of *Australopithecus afarensis*: Where Do We Stand? Am J Phys Anthropol 45:185-215.
- Ward CV, Leakey MD, Walker A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. J Hum Evol 36:69-95.

- Washburn SL. 1951. The analysis of primate evolution with particular reference to the origin of man. Cold Spring Harbor Symposia on Quantitative Biology 15: 67-77.
- Washburn SL. 1959. Speculations on the interrelations of the history of tools and biological evolution. Hum Biol 31:21-31.
- Washburn SL. 1960. Tools and human evolution. Sci Am 203:63-75.
- Watts DP. 1988. Environmental influences on mountain gorilla time budgets. Am J Primat 15:195-211.
- Weidenreich F. 1946. Generic, specific, and subspecific characters in human evolution. Am J Phys Anthropol 4:413-432.
- Weidenreich F. 1947. The trend of human evolution. Evolution 1:221-236.
- Wheeler, P.E. (1984). The evolution of bipedality and loss of functional body hair in hominids. Journal of Human Evolution 13, 91-98.
- Wheeler PE. 1985. The loss of functional body hair in man: the influence of thermal environment, body form and bipedality. Journal of Human Evolution 14, 23-28.
- Wheeler PE. 1991. The influence of bipedalism on the energy and water budgets of early hominids. J Hum Evol 21:117-136.
- Wheeler, P.E. (1992) The influence of the loss of functional body hair on the energy and water budgets of early hominids. Journal of Human Evolution 23, 379-388.
- Wheeler, P.E. (1994). The thermoregulatory advantages of heat storage and shade-seeking behaviour to hominids in equatorial savannah environments. Journal of Human Evolution 26, 339-350.
- White, T. D., and Suwa, G. (1987) Hominid footprints at Laetoli: facts and interpretations. Am J Phys Anthropol 72: 485-514.
- White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominids from Aramis, Ethiopia. Nature 371:306-312.
- WoldeGabriel G, White TD, Suwa G, Renne P, de Heinzelin J, Hart WK, Helken G . 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. Nature 371:330-333.

- Wood B, Collard M. 1999. The Changing Face of Genus *Homo*. *Evol Anthropol* 8:195-207.
- Wrangham RW. 1980. Bipedal locomotion as a feeding adaptation in Gelada baboons, and its implications for hominid evolution. *J Hum Evol* 9:329-331.
- Wright S. 1931. Evolution in Mendelian population. *Genetics* 16:97-159.
- Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proc VI Inter. Congr. Genet.* 1, 356-366.
- Yamagiwa A. 1986. Activity rhythm and the ranging of a solitary male mountain gorilla. *Primates* 27:273-282.

Appendix A

Adaptive Landscape Program

```
function (mean=c(.5,.5))
{
  library(mvtnorm)
  x <- seq(0, 1, length= 30)
  y <- seq(0, 1, length= 30)
  z<-matrix(rep(0,30*30),nc=30)
  for(i in 1:30){
    for(j in 1:30){
      R<-matrix(c(.01,0,0,.01),nc=2)
      # Below line is cumulative bivariate
      z[i,j]<-pmvnorm(lower=rep(-
Inf,2),upper=c(x[i],y[j]),mean=mean,sigma=R)
    }
  }

  op <- par(bg = "white")
  persp(x,y,z, theta = -30, phi=25, col="white", xlab = "Shoulder
Stability",
ylab = "Shoulder Mobility", zlab = "Shoulder Fitness", shade=.4)->
pmat

x2 <- seq(.3, 1, length = 30)
y2 <- .3/(x2)
z2<-0
for(i in 1:30){
  z2[i] <- pmvnorm(lower=rep(-
Inf,2),upper=c(x2[i],y2[i]),mean=mean,sigma=R)
}
lines(trans3d(x2,y2,z2, pm=pmat), col="black", lwd=3)
trans3d <- function(x,y,z, pmat) {
  tr <- cbind(x,y,z,1) %*% pmat
  list(x = tr[,1]/tr[,4], y= tr[,2]/tr[,4])
}
}
```


Maximum Fitness Program

```
function ()
{
  library(mvtnorm)
  x <- seq(0, 1, length= 30)
  y <- seq(0, 1, length= 30)
  z<-0
  g<-matrix(rep(0,900),nc=30)

  for(i in 1:30){
    for(j in i:30){
      R<-matrix(c(.01,0,0,.01),nc=2)
      # Below line is cumulative bivariate
      z<- function(p) pmvnorm(lower=rep(-
Inf,2),upper=c(p,.3/p),mean=c(x[i],y[j]),sigma=R)
      sto<-optimize(z, c(0,1), maximum=TRUE)
      sto<-sto$objective[1]

      g[i,j]<-sto
      g[j,i]<-sto
    }
  }
  op <- par(bg = "white")
  persp(x,y,g, theta = 130, phi=25, col="lightblue", xlab = "Above
Substrate Locomotion",
ylab = "Supensory Locomotion", zlab = "Probability of Bipedalism",
shade=.8)-> pmat

  return(x)
}
```

Stability Reduction Program

```
function (n=10)
{
  library(mvtnorm)
  b<-matrix(rep(seq(0,1,length=30),30),nc=30)
  c<-t(b)
  x <- seq(0, 1, length= n)
  y <- seq(0, 1, length= 30)
  f <- seq(0, 1, length= 30)
  z<-0
  g<-matrix(rep(0,90),nc=3)
  a<-matrix(rep(0,900),nc=30)
  q<-matrix(rep(0,900),nc=30)

  for(j in 1:30){
    for(i in 1:n){
      R<-matrix(c(.01,0,0,.01),nc=2)
      # Below line is cumulative bivariate
      z<- function(p) pmvnorm(lower=rep(-
Inf,2),upper=c(p,.3/p),mean=c(x[n+1-i],y[j]),sigma=R)
      sto<-optimize(z, c(0,1.2), maximum=TRUE)
      sto<-sto$objective[1]
      if (sto>=.9){break}}
      g[j,2]<-x[n+1-i]
      #g[31-j]<-(.3/(x[n-i]))
      g[j,1]<-y[j]
      g[j,3]<-sto
    }
  }

  for(j in 1:30){
    for(i in 1:30){

      a[j,i]<-b[j,i]-g[i,2]
      if(a[j,i]<=0) (q[j,i]=0) else (q[j,i]<-a[j,i])
    }
  }

  op <- par(bg = "white")
  persp(f,y,q, theta = -35, phi=25, col="white", zlim=c(0,1), xlab =
"Stability Demand",
ylab = "Mobility Demand", zlab = "Reduction in Stability", shade=.4,
ticktype="detailed")-> pmat

  return(q)
}
```

Bipedalism Proportion Program

```

function (n=10)
{
  library(mvtnorm)
  b<-matrix(rep(seq(0,1,length=30),30),nc=30)
  c<-t(b)
  x <- seq(0, 1, length= n)
  y <- seq(0, 1, length= 30)
  f <- seq(0, 1, length= 30)
  z<-0
  g<-matrix(rep(0,90),nc=3)
  a<-matrix(rep(0,900),nc=30)
  q<-matrix(rep(0,900),nc=30)
  w<-matrix(rep(0,900),nc=30)
  l<-matrix(rep(0,900),nc=30)

  for(j in 1:30){
    for(i in 1:n){
      R<-matrix(c(.01,0,0,.01),nc=2)
      # Below line is cumulative bivariate
      z<- function(p) pmvnorm(lower=rep(-
Inf,2),upper=c(p,.3/p),mean=c(x[n+1-i],y[j]),sigma=R)
      sto<-optimize(z, c(0,1.2), maximum=TRUE)
      sto<-sto$objective[1]
      if (sto>=.9){break}}
      g[j,2]<-x[n+1-i]
      #g[31-j]<-(.3/(x[n-i]))
      g[j,1]<-y[j]
      g[j,3]<-sto
    }
  }
  for(j in 2:30){
    for(i in 1:30){

      a[j,i]<-b[j,i]-g[i,2]
      w[j,i]<-a[j,i]/f[j]
      if(w[j,i]<=0) (q[j,i]=0) else (q[j,i]<-a[j,i])
    }
  }
  for(j in 2:30){
    for(i in 2:30){

      if(w[j,i]<=0.5) (l[j,i]=0) else (l[j,i]<-w[j,i])
    }
  }
  op <- par(bg = "white")
  persp(f,y,l, theta = -35, phi=25, col="white", zlim=c(0,1), xlab =
"Stability Demand",
ylab = "Mobility Demand", zlab = "Bipedalism (Proportion)",
shade=.4)-> pmat

  return(l)
}

```

Vita

Adam David Sylvester was born in Teaneck, New Jersey on October 17, 1974. He attended elementary school through high school in Teaneck, graduating from high school in 1992. He started as a freshman at The University of Tennessee in the fall of 1992, and graduated with a Bachelor of Science in zoology in the spring of 1996. After realizing his interest in human evolution, he began coursework in anthropology in the fall of 1997 and was accepted to the graduate program in anthropology at the University of Tennessee for the fall of 1998. He received a Master of Arts degree in the summer of 2001 and a Doctor of Philosophy in the summer of 2006. He hopes to continue teaching and conducting research in a university setting.