



A natural history of human tree climbing



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ABSTRACT

Walking and running have dominated the literature on human locomotor evolution at the expense of other behaviors with positive and negative fitness consequences. For example, although modern hunter-gatherers frequently climb trees to obtain important food resources in the canopy, these behaviors are seldom considered within the existing framework of primate positional behavior. As a result, inferences about the arboreal performance capabilities of fossil hominins based on a resemblance to humans may be more complicated than previously assumed. Here we use ethnographic reports of human tree climbing to critically evaluate hypotheses about the performance capabilities of humans in trees compared with other primates. We do so by reviewing the ecological basis of tree climbing behavior among hunter-gatherers and the diversity of human climbing techniques and styles. Results suggest that the biological and adaptive significance of human climbing has been underestimated, and that some humans are surprisingly competent in trees, particularly during vertical climbing and activities in the central core of trees. We conclude that while hominins evolved enhanced terrestrial locomotor performance through time, such shifts may have imposed only minor costs on vertical climbing abilities. The diversity of the locomotor repertoire of modern humans must therefore be taken into account when making form-function inferences during the behavioral reconstruction of fossil hominins.

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Introduction

Committed terrestrial bipedalism is considered a defining feature of the human lineage. This prevailing view underlies the arboreal-terrestrial dichotomous framework that has informed form-function inferences in the fields of comparative primate anatomy and paleoanthropology (Kimbel and Deleuzene, 2009). For example, similarities in ankle and foot traits between humans and some early hominins (e.g., *Australopithecus afarensis*) have led some to reject any significant amount of arboreality for these hominins (Latimer et al., 1987; Latimer and Lovejoy, 1990a, b; Ward et al., 2011). This conclusion rests on the assumption that humans do not climb trees, and if they do, they are clumsy and incompetent (Latimer, 1991). Thus, when a human-like morphology is observed in a fossil hominin, it is assumed to indicate similar incompetence.

This general approach, and the dichotomy upon which it is based, has been criticized as an oversimplification that could lead to the misidentification of particular anatomical features as ‘magic

traits,’ diagnostic of particular behaviors (Susman et al., 1984; Stern and Susman, 1991; Mitchell et al., 2012). This is particularly problematic if the locomotor repertoires of the species that define the comparative framework have not been fully documented. Such data are necessary in order to identify the behaviors that are habitually performed and/or achievable with a given set of morphologies.

Disagreement over the timing and nature of the transition to habitual bipedality has stemmed in part from divergent interpretations of the extent to which a shift toward human-like traits compromised arboreality. Humans who climb trees have received little attention despite being an appropriate model for addressing this issue, as noted by DeSilva (2008).

Hypotheses

This paper reviews human climbing behavior to critically evaluate the hypothesis that hunter-gatherers are capable tree climbers and that the activity has fitness consequences, both in terms of risks and rewards. Although many humans are capable of climbing, we focus mainly on hunter-gatherers because they (by definition) do not completely rely on cultivated foods and thus engage in foraging strategies most relevant to hominin behavioral reconstruction. Consequently, we propose that hunter-gatherers represent the best

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model for exploring the performance capabilities and limits of hominin movement in trees.

Two critical predictions stem from our hypothesis that will determine how human climbing behavior can inform interpretations of the hominin fossil record:

P1. Human climbing can have fitness consequences, both in terms of risk (chance of falling) and reward (high value resources).

P2. Humans can acquire arboreal resources without complete reliance upon technology (e.g., axes, ropes, ladders).

We tested these predictions using a wide body of ethnographic reports focused on tropical savanna and rainforest hunting and gathering populations. For **P1**, in order to understand why humans climb trees and the safety risks associated with this behavior, we reviewed the literature for instances of resource acquisition in trees, and data on mortality, morbidity, and psychological elements of climbing. For **P2**, in order to understand how humans climb trees, we reviewed the literature for instances of climbing behavior where styles and techniques are described in sufficient detail. We purposely searched for extreme and well-documented examples of human tree climbing. Although we do not claim to have compiled an exhaustive list of human climbing behaviors, those presented here represent prominent and thoroughly documented examples of this under-appreciated yet evolutionarily relevant aspect of human locomotion. In an attempt to place human climbing behavior within the existing positional behavior framework for nonhuman primates (e.g., Hunt, 1991), we present, when possible, comparisons between humans and apes regarding frequency, performance variables, and mortality and morbidity associated with vertical climbing. We also consider the ontogeny of and sex differences associated with human climbing behavior.

The results of this study have implications for interpretations of the hominin fossil record. Rejection of the above predictions would conform with the view (but not conclusively demonstrate) that human-like traits in hominins are indicative of negligible climbing behavior (Latimer et al., 1987; Latimer and Lovejoy, 1990a,b; Latimer, 1991). Confirmation of **P1** and rejection of **P2** would indicate that in hominins with human-like traits, tree climbing would have been compromised or necessitated compensatory technologies. The converse case, rejection of **P1** and confirmation of **P2**, is trivial. Confirmation of both predictions would suggest that many hominin traits previously associated with incompetence in trees are not incompatible with substantial amounts of arboreality. These investigations offer context for evaluating the limits of hominin arboreality and performance (Arnold, 1983) in trees, both for species that were primarily terrestrial and those with clear arboreal affinities.

Results

Why humans climb trees

Honey Hunter-gatherers worldwide climb to great heights, mainly for the purpose of collecting honey (see Table 1 in Crane, 1999). Honey is extremely energy-dense (~ 3.0 kcal g^{-1}) and nutritious. It is comprised of up to 95% carbohydrates (Bogdanov et al., 2008) and includes a wide variety of proteins, enzymes, amino acids, minerals, trace elements, vitamins, and polyphenolic compounds (Aparna and Rajalakshmi, 1999; Bogdanov et al., 2008; Alvarez-Suarez et al., 2010). Associated bee brood (larvae and pupae), which are consumed simultaneously, also provide high amounts of protein, fat, and B-vitamins (Finke, 2005). As a result of such high micronutrient diversity, honey has many functional properties desired by humans, such as long

preservation time (Nagai et al., 2006) and antimicrobial (Molan, 1992a,b; Cooper et al., 1999), antiviral, antiparasitory, anti-inflammatory, and antioxidant effects (Bogdanov et al., 2008). Thus, it is perhaps unsurprising that honey is a prized resource among hunter-gatherers (Ichikawa, 1981; O'Dea et al., 1991; Chagnon, 1992; Marlowe and Berbesque, 2009), particularly in rainforests where carbohydrate-rich food resources are scarce (Hart and Hart, 1986; Headland, 1987). For these reasons, honey has been proposed as an important food item in human evolution (Crittenden, 2011; Wrangham, 2011).

It would be difficult to overstate the importance of honey to hunter-gatherers. In Africa, wild honey has both nutritional and sociological significance (Ichikawa, 1981). For example, honey is a seasonally dominant and widely-shared resource for hunter-gatherers in the central Ituri Forest (Democratic Republic of Congo). Honey is the most commonly traded commodity of the Efe (Terashima, 1998), and Mbuti honey consumption reaches 0.83 kg ($\sim 80\%$ of total caloric intake) per person day^{-1} during the three-month honey season (Ichikawa, 1981). For the Mbuti, honey functions as “the lubricant of the social relation” (Ichikawa, 1981: 65). Bailey and Peacock (1988) estimate that honey provides 42.7% of the caloric intake of Efe during the honey season (August). The honey season for the Aka was reported to be between mid-November and mid-June (Bahuchet, 1988), and a separate report for honey collection by middle-aged Aka in the Republic of the Congo found that an average of 1.4 kg per person day^{-1} was harvested between June and October (Kitanishi, 1996). During this time, honey is a staple food for the Aka and eating honey is considered to constitute a ‘true meal’ (Hladik and Bahuchet, 1994). Savanna-woodland populations such as the San (Frisbie, 1971; Yellen and Lee, 1976) and Hadza (Marlowe, 2004) also collect honey extensively. Honey is the most preferred food of the Hadza, accounting for at least 8.0–16.4% of total calories collected (Marlowe, 2004; Marlowe and Berbesque, 2009; Pontzer et al., 2012). These are extraordinary amounts of honey. By comparison, in the USA, Canada, and Australia, the average per capita consumption of honey is between 0.6 kg and 0.8 kg $year^{-1}$, in the European Union annual consumption ranges from 0.3 to 1.8 kg, while in China and Argentina consumption is 0.1–0.2 kg $year^{-1}$ (Bogdanov et al., 2008).

In Asia and Australia, honey and bee brood are also integral to the diets of hunter-gatherers. The Asian tropics are home to several honeybee species, including *Apis dorsata*, *A. florea*, *A. cerana*, and the introduced *Apis mellifera*. Honey is collected widely; for instance, by the Jenu Kuruba of southern India (Dempis et al., 2012a,b), the Onge of the Andaman Islands (Dutta et al., 1985), the Batek of Malaysia (Endicott and Endicott, 2008), the Meratus Dayak of Indonesia (Tsing, 2003), the Agta of the Philippines (Griffin and Estioko-Griffin, 1985; Minter, 2010), Australian Aboriginal populations (O'Dea et al., 1991) and the Gurung of Nepal (Valli and Summers, 1988), among others. For some groups, honey is a major and prioritized part of the diet. The Batek of Malaysia are reported to abandon any other work to collect seasonal honey or fruit (Endicott and Endicott, 2008), the former of which makes up $\sim 9\%$ of wild-collected foods by weight. In addition, honey collection is often tied to songs and other important cultural practices (Valli and Summers, 1988; Dempis et al., 2012b). For example, in Malaysia, Skeat and Blagden (1906) documented that marriage nuptials among the Sekai involved three questions, including “are you a good climber?” Only answers in the affirmative led to the next stage of the ceremony.

In South America, the relative importance of honey consumption appears to vary by population and season (Hill et al., 1985). Whereas honey comprises 21.7% of total calories acquired by the Ache (Kaplan and Hill, 1985), it forms a minor (2.3%) component of the Hiwi diet (Hurtado and Hill, 1990). The Ache of Paraguay and



Figure 1. Center illustration: The locomotor and postural behavior of humans in trees (drawing by Annie Putman). (A) A man climbs a palm tree in French Guyana by linking his feet together with a rope (photograph by Serge Bahuchet, reproduced with permission). (B) A Batak man engaged in ambush hunting of a wild pig in the Philippines (photograph by James Eder, reproduced with permission). (C) A Yanomamö man in Venezuela uses two 'A-frame' devices to access the fruit of a peach palm (still frame from the film *Climbing the Peach Palm* (1974) by Timothy Asch and Napoleon Chagnon, reproduced with permission from Documentary Educational Resources). (D) A Biaka man in central Africa extracts honey from a bee nest in the canopy of an ~40 m tree (BBC Motion Gallery Education). (E) An Aka man climbs a large-diameter tree using a vine as a rope harness in the Central African Republic (photograph by Serge Bahuchet, reproduced with permission). (F) A Batek man in Malaysia bridges a gap between trees using small-diameter lianas (photograph by Kirk Endicott, reproduced with permission). (G) In southern India, a Jenu Kuruba man climbs a large-diameter tree in the chinbodn style, by inverting his ankles and hugging the trunk (photograph by Kathryn Demps, reproduced with permission). (H) In Uganda, a Twa man climbs a small-diameter tree in the changwod style in pursuit of honey (photograph by George H. Perry, reproduced with permission). (I) A Batak man in the Philippines climbs a vine by grasping the substrate with his big toes (photograph by James Eder, reproduced with permission). (J) Batek children climbing while engaged in play behavior (photograph by Kirk Endicott, reproduced with permission).

the Yuquí of Bolivia target the honey of native stingless bee species (Hawkes et al., 1982; Stearman, 1991; Stearman et al., 2008) and of introduced stinging bee species, primarily *A. mellifera* (Hawkes et al., 1982; Hill et al., 1984). The Achuar of Upper Amazonia, however, harvest honey only from native stingless bees and the Kayapo of the Brazilian Amazon maintain vast information on native bee species and prefer the honey those species produce (Posey, 1982). As in other geographic regions, in South America honey is a prized resource that often takes priority in foraging decisions (Hawkes et al., 1982; Chagnon, 1992).

The measures of honey consumption reported in the literature are likely underestimates because a large quantity of honey is usually consumed upon collection and is never returned to camp (Terashima, 1998; Marlowe, 2004; Yasuoka, 2006).

Hunting The ability to climb is useful in the pursuit of prey, as a high vantage point can provide a superior position for hunters (Fig. 1B). For example, Efe men spend 4.3% of their time perched in trees, waiting to ambush duikers that are attracted to fallen fruits (Bailey, 1991). In the Philippines, a common hunting technique, termed 'manghaked' by the Agta, involves ambushing prey attracted to heavily fruiting trees (e.g., *Calophyllum* spp.) by shooting them with bows and arrows from above (Griffin and Estioko-Griffin, 1985). While vertical climbing for ambush hunting can be done relatively slowly and cautiously, hunter-gatherers also actively pursue prey in trees. Hunting for birds within tree crowns ('teren' or 'hunting from the treetop') is a favorite activity of Batek children (Lye, 2004). The Batek hunt and ambush prey in the canopy, but the frequent use of blowgun hunting may decrease the necessity of climbing to acquire meat. Batek men shoot blowguns accurately up to 40 m in the canopy when hunting monkeys, birds, bats, and rats (Endicott, 1979).

Likewise, in South America, climbing is employed during blowgun hunting by the Huaorani (Rival, 1993) and in the pursuit of arboreal animals such as monkeys by the Ache (Hill and Hawkes, 1983). The Hadza sometimes climb to steal chicks from mass reproducing bird species and will also occasionally ascend trees to stash meat from successful hunts (Marlowe, 2010).

Other arboreal resources Human climbing behavior is also motivated by fruit, nuts, seeds, rattan (palms of the tribe Calameae), and palm products (Hawkes et al., 1982; Murray et al., 2001; Endicott and Endicott, 2008; Marlowe, 2010). To access prized fruits, in addition to rattan and palm products, the Batek climb to extreme² heights (>50 m; Endicott, 1979). Fruit is especially prominent in the diets of many Asian foragers, and in the case of the Batek it is even more highly valued than honey (Endicott and Endicott, 2008). Such preferences, although anecdotal, are telling given the clear preference for honey among other hunter-gatherers such as the Efe (Ichikawa, 1981) and Hadza (Marlowe and Berbesque, 2009). In terms of caloric importance, fruit also figures prominently in the diet of the Ache (Hawkes et al., 1982). Although the Ache most frequently harvest the fruit of introduced species (i.e., oranges), palm products and other native fruit species form minor components of the diet. The nearby Yanomamö also enjoy fruit found in trees, particularly that of the peach palm (*Bactris gasipaes*) (Fig. 1C; Chagnon, 1992). Like fruit in general, the seeds of baobab trees (*Adansonia digitata*) are preferred less than honey but are central to the diet of the Hadza (Marlowe and Berbesque, 2009). Baobab seeds, which are

² Here we consider 'extreme heights' to be those ≥ 19 m, the height at which the probability of death from falling approaches 100% (Risser et al., 1996).

probably desired for their high protein and fat content (Murray et al., 2001), can sometimes be collected from the ground, but individuals often climb in order to shake and release pods attached to terminal branches (Marlowe, 2010).

Protection The need to avoid predators and other dangerous animals is yet another reason to climb trees. Predation is a key factor underlying arboreal nesting in nonhuman primates, explaining why many species choose nest and sleeping sites based on height, visibility, and accessibility to predators (Anderson, 1998; Stewart et al., 2007). Terrestrial ape nests tend to be more common when predation risk is low (Yamagiwa, 2001), perhaps due to the danger of falling and because thermoregulatory balance at night is more easily attainable on the ground relative to the canopy (Samson and Hunt, 2012). Washburn and DeVore (1961) found that the availability of trees was likely a stronger determinant of the spatial dispersion of baboon troops than food and water. The notion that humans and their ancestors would have engaged in tree climbing to afford protection from predators at night has been raised several times (Watanabe, 1971; Tuttle, 1981; Susman et al., 1984; Yamagiwa, 2001), though documentation of analogous behaviors among modern humans is scarce. One example is the Korowai of Papua New Guinea, who construct elaborate treehouses high in the canopy (Henderson and Mornement, 2008). Similarly, Semang populations in southeast Asia have been reported to construct treehouses in order to avoid marauding elephants (Skeat and Blagden, 1906; Evans, 1937; Dunn, 1975). Tree climbing can also protect humans from terrestrial animals, whether predators, prey, or aggressors, that lack the ability to climb. Hill and Hawkes (1983) report that Ache men will quickly climb to avoid charging white-lipped peccaries, while continuing to shoot arrows from above. The possibility that humans have an innate recognition of tree climbing as a means of escaping predators is corroborated by experimental studies in which children recognized the value of tree canopies as refugia from predatory lions (Coss and Moore, 2002).

Summary of 'why humans climb trees'

Human climbing behavior is usually associated with the acquisition of preferred food sources, including those that are rich in protein and carbohydrates. Such foods are thought to be important to survival, particularly within carbohydrate-depleted rainforest environments. Honey most strongly motivates climbing behavior, but hunting, protection, and fruit and seed collection are also important. This association raises the possibility that food acquisition for some hunter-gatherer groups depends on strong tree climbing abilities. Next we review the diversity of positional and locomotor behaviors used by humans as they climb trees.

How humans climb trees

"There are few trees that the Mbuti can not climb."

— Ichikawa, 1981:59.

"I don't think an Efe ever met a tree that he couldn't climb in some way."

— R. Bailey, Personal communication

The technique and style of human tree climbing varies by geographic location, population, and targeted resource (Fig. 1). The great diversity of climbing behavior is itself a testament to the creativity and persistence with which humans approach the unique problem of accessing resources in tree canopies. Climbing occurs

both with and without the assistance of technology. Here we focus primarily on techniques that allow hunter-gatherers to ascend and forage within trees.

Climbing without the assistance of technology Humans are adept at ascending trees without the use of material culture (see Table 1). The languages of habitually-climbing populations have words to describe different climbing styles, illustrating the prominence of these behaviors (Devine, 1985). There are two main styles of unassisted climbing, first described by Skeat and Blagden (1906), then Schebesta (1928), using terms from the Jahai of Malaysia (Table 1). The first, 'changwod', refers to a person applying the plantar surface of his/her feet to a tree or vine and 'walking' upward with the legs and arms advancing alternately (Fig. 1H). This style bears similarities to the 'laybacking' technique used by rock-climbers in which the arms pull and the legs push, generating friction through counter-pressure (Oxlade, 2003). In general, this method is employed with small-diameter substrates that a climber can grasp with his hands (Ichikawa, 1981). Changwod closely resembles the climbing style of chimpanzees (DeSilva, 2009). We have observed changwod climbing by the Baka of Cameroon (T.S.K., Personal observation), the Batek (T.S.K. and V.V.V., Personal observations), and the Twa of Uganda, and found the latter to exhibit extreme dorsiflexion ($>45^\circ$) at the tibiotalar joint during climbing (Venkataraman et al., 2013a). The Batek, who climb trees >50 m tall on a daily basis, utilize this style in combination with others during hunting and in the pursuit of fruit, honey, rattan, and palm products (Endicott, 1979; Endicott and Endicott, 2008):

"To climb thin tree trunks, the climber put his arms around the tree, placed his feet against the trunk, and 'walked' up it. If the trunk was too thick at the base for a climber to fully embrace, he would pull himself up a vine until he could transfer to the lower branches of the tree. Alternatively, he would climb a small tree adjacent to the one he wanted to climb, then get the smaller one swaying so he could reach over and pull himself into the branches of the larger tree"

Endicott and Endicott, 2008:88.

This quote emphasizes the importance of unassisted climbing even in a case where it is not possible to directly climb a resource-bearing tree. One should thus not assume that humans need technology to access honey and other resources that are found high in trees with few surrounding canopy elements.

Table 1
Names and descriptions of unassisted human climbing styles.

Style	Description	Notable joint postures/movements
Changwod ^a (Fig. 1H)	<ul style="list-style-type: none"> With foot placed flat against tree, climber leans back to generate counter-pressure, advancing arms and feet alternately Associated with ascent of small-diameter substrates 	Ankle dorsiflexion, metatarsophalangeal dorsiflexion, shoulder flexion
Chinbodn ^a (‘frog style’; Fig. 1G)	<ul style="list-style-type: none"> Climber ‘hugs’ tree with knees splayed and pulses upward Forelimb and hindlimb generate forces alternately 	Ankle inversion, hip abduction, knee flexion, shoulder flexion
Hallucal grasping (Fig. 1I)	<ul style="list-style-type: none"> Hallux and second toe used to grasp very small substrates (e.g., vines) and propel climber upward 	Hallucal adduction, ankle dorsiflexion, metatarsophalangeal dorsiflexion

^a These are Jahai terms from Peninsular Malaysia (Skeat and Blagden, 1906; Schebesta, 1928). See text for details.

In some cases, climbing is enhanced by grasping a small diameter substrate between the hallux and the second toe (Table 1), as performed by the Mbuti (Ichikawa, 1981), the Batak of the Philippines (Fig. 1I), and the Batek (T.S.K. and V.V.V., Personal observation). Ichikawa (1981) reports that the Mbuti will do this for trees or vines that are less than 2–3 cm in diameter.

The term ‘chinbodn’ (or ‘tinbon’ in Batek) describes another climbing style of the Jahai (Skeat and Blagden, 1906; Schebesta, 1928). For this style, a climber ‘pulses’ up a tree by ‘hugging’ it with his arms and gripping the trunk on either side with the soles of his inverted feet (Table 1; Fig. 1G). Chinbodn style climbing can be used to ascend trees with relatively large diameters compared with changwod style climbing (Fig. 1). The Jenu Kuruba of southern India engage in chinbodn style climbing, which allows them to climb at least 12 m, but probably much higher, on ~60 cm DBH (diameter at breast height) trees with smooth bark, no lower branches, and without technology in pursuit of *A. dorsata* honey (Demps et al., 2012a). In Africa, chinbodn climbing is used in the pursuit of honey by the Mbuti (Turnbull, 1965; Ichikawa, 1981) and Efe (R. Bailey, Personal communication). Finally, the Ache generally climb without the assistance of technology once they have access to the main trunk or branches of a tree. Vertical ascent is achieved by inverting the soles of the feet and ‘hugging’ the tree with the knees pointed straight outwards (K. Hill, Personal communication).

Climbing with the assistance of technology Several technological solutions can reduce the difficulties and dangers of climbing. Here we highlight the technologies that hunter-gatherer populations use to improve access to arboreal resources. One of the foremost problems of unassisted tree climbing using the changwod and chinbodn styles is the difficulty of ascending large-diameter trees, particularly those with smooth bark. Based on theoretical considerations, an unassisted climber’s hands and/or feet must subtend a critical angle to generate frictional forces that counter the pull of gravity on the climber (Cartmill, 1974, 1985). Chimpanzees strongly prefer small-diameter substrates for climbing (DeSilva, 2008). Accordingly, unassisted climbing in humans should be strongly associated with small-diameter trees. Anecdotal reports of climbing humans around the world support this expectation (R. Bailey, Personal communication; Endicott and Endicott, 2008).

Key food sources, particularly honey, tend to be located in tall, large-diameter trees, rendering unassisted climbing impossible or necessitating bridging behaviors with the use of nearby vegetation. Humans use technology frequently during the ascent of large trees. The Aka and the Mbuti of Central Africa loop a supporting vine or liana (called ‘nupe’ by the Mbuti) around the trunk of a large tree, whipping it upward as they move between footholds chopped with an axe (Fig. 1E; Turnbull, 1965; Ichikawa, 1981; Bahuchet, 1992). A Biaka man climbing a 40 m tree for honey in this style is captured in detail in a video that conveys the extreme nature of this practice (BBC film: Human Planet: Jungles). A nearly identical technique is also used by many non-hunter-gatherers such as professional palm climbers (Corner, 1966).

Vines are useful for connecting neighboring vegetation. Professional palm climbers connect neighboring tree crowns with rope in order to avoid repeatedly descending and reascending adjacent trees (Hodge, 1963). The ability to bridge gaps with vines, termed ‘plibat’ (‘move over’), is important for the Batek as they navigate canopy gaps and attempt to reach inaccessible tree crowns (Lye, 2004, Fig. 1F). The Batek might face unique problems in this respect, as Southeast Asian forests are notoriously tall, open, and low in liana abundance (Emmons and Gentry, 1983). Gap-bridging by the Batek is described in Endicott and Endicott (2008:90):

“Since most of the hive-bearing trees were too thick to climb directly, people constructed elaborate systems of ‘vine ladders’ out of a very strong species of rattan. From a smaller, climbable tree, they tossed a weighted fishing line over a low limb of the honey tree, attached the rattan vine to the fishing line and pulled the rattan over the limb, and then secured the two ends of the rattan to a smaller tree. They climbed these ladders, which were arranged at about a forty-five degree angle from the vertical, by grasping one vine in each hand and walking up the vines, gripping them between their toes.”

Schebesta (1928) described a third method of climbing by the Semang, termed ‘snriag’, as ‘climbing with the aid of nooses around the feet.’ For this method, the feet are tied together to form a rigid, propulsive lever that provides resistance for a climber to push off of a tree (Fig. 1A). This style is most commonly associated with professional palm climbers (e.g., Corner, 1966). For coconut climbers in India who bind both their feet and hands while climbing, the movements of snriag climbing “...call for flexion, abduction, extension and the lateral rotation of the hip, flexion and extension of the knees, plantar and dorsiflexion at the ankle, inversion at the subtalar joint, and flexion at metatarsophalangeal and interphalangeal joints of the foot...” (George et al., 2012:57). The effects of long-term palm-climbing in this manner can be very harmful and are manifested in lost toes, extreme callouses, and deformed joints (George et al., 2012). Even with the assistance of technology, falls are fairly common, particularly after thirty years of climbing. Bhat and Kumar (2009) have demonstrated an intriguing link between fall rates and the development and subsequent loss of an arched structure in the feet of professional palm climbers.

As noted above, the fruit of the peach palm (*Bactris gasipaes*) is prized by the Yanomamö of the Amazon. Like other species of *Bactris*, the stems of peach palms are covered in long, dense spines that make it difficult, if not impossible, for a human to climb without the assistance of technology. To overcome this defense, the Yanomamö climb up to 75 feet with the aid of a specialized device resembling an ‘A-frame’ (Fig. 1C; Chagnon, 1992). Two ‘A-frames’ are used simultaneously; one is raised while the other serves as a standing platform for the climber.

The Hadza, who live in savannah habitats in Tanzania, climb trees primarily during honey and baobab fruit collection (Marlowe and Berbesque, 2009). Baobab trees tend to have large diameters and are commonly used for nest sites by the seven bee species from which the Hadza harvest honey (Marlowe, 2010). Climbing such large trees, however, requires the aid of technology. Unlike the rainforest populations discussed previously, the Hadza use axes to pierce baobab tree bark and insert wooden pegs from small tree limbs that create a ladder-like structure for access into the tree-crown (Marlowe, 2010). In addition, metal axes are frequently used to open up tree limbs or trunks to access honey (Marlowe, 2010). In the absence of axes, Hadza are still proficient at acquiring honey, either dipping twigs into small holes of the hive and licking them off, or by using rocks that are superficially similar to Acheulean hand axes (Marlowe, 2010). We regard this as a crucial point; vertical ascent and honey acquisition are possible, albeit probably less efficiently, with primitive tools or even in the absence of technology. Indeed, an anonymous reviewer of the present paper noted that Hadza men climb small diameter trees (such as *Acacia* spp.) for honey without the use of axes and that women and children climb small bushy trees to acquire berries.

Finally, trees are sometimes cut down to access desired resources. Chopping down trees to access fruit or honey has been independently documented for the Mbuti (Ichikawa, 2001), Efe (R. Bailey, Personal communication), Aka (Kitanishi, 1996), Baka (T.S.K.,

Personal observation), Batek (Endicott and Endicott, 2008), and Ache (Hill, 2002). However, this practice may be an artifact of modernity and relies heavily on the use of axes or other tools that make it possible to sever the trunks of large diameter trees with hard wood. For instance, Hill (2002:111) reports that even though the Ache commonly cut down trees, “in precontact times, men often climbed trees to extract honey high in the branches using scaffolding or vines to tie themselves in place.” R. Bailey (Personal communication) notes that cutting down trees requires effort and is not always rewarding. He observed Efe men spend two hours cutting down a large beehive-bearing tree, only to find it bereft of honey.

Honey-hunters in Nepal, Tibet, Bhutan and India harvest bee nests found on sheer rock faces (Crane, 1999). This activity is particularly notable for ‘adivasi’ groups living in the Nilgiris of southern India, such as Kurumbas and Irulas, who specialize on the collection of honey from *A. dorsata* and *A. cerana* (Zvelebil, 1979; Thomas et al., 2009; Roy et al., 2011). Collection of honey from rock faces occurs at extreme heights, reportedly up to ~150 m above the ground, but probably much higher (Sharma, 2008). The process is complex and requires at least three men. First, a massive fiber ladder is tied to a tree or rocks at the top of a cliff and is hung over the edge. With one man at the base of the cliff and one at the top, a third man climbs down the ladder to harvest the honey into a basket lowered from above. With smoke from a fire below and sap from a wild plant applied directly to the skin to prevent bee stings, the climber cuts the comb with a knife or long pole (Zvelebil, 1979).

Summary of ‘how humans climb trees’

Humans engage in a wide variety of unassisted and assisted climbing styles. Climbing styles do not appear to be unique to geographic regions but instead occur as responses to substrate size and organization of canopy elements. The changwod and chinbodn styles are the most prominent unassisted climbing methods. Unassisted (and sometimes assisted) climbing is linked with stereotypical joint excursions and positional behaviors (Table 1).

Ontogeny and sex differences in human climbing

Climbing ability and the frequency of climbing varies with age and sex. In many hunter-gatherer populations the development of climbing skill begins at an early age, and is often observed in the play behavior of children (Fig. 1J). In a survey of anthropologists who study seven different hunter-gatherer populations, climbing appeared in the list of play behaviors reported to mimic adult hunting or gathering activities (Gray, 2009). For physically demanding and highly technical skills such as climbing, practice at such an early stage is likely to be advantageous for knowledge acquisition and physical development. Substantial climbing behavior appears in the locomotor repertoire at a very young age in many hunter-gatherers, including the Mbuti (Turnbull, 1961), Pandaram (Morris, 1982), Nayaka (Hewlett and Lamb, 2005), Jenu Kuruba (Demps et al., 2012a,b), Batek (Lye, 2004; Endicott and Endicott, 2008), and Ache (Hill and Hawkes, 1983). The importance of climbing behavior at a young age is exemplified by the Jenu Kuruba, among whom tree climbing begins around age six. Children then accompany adults on honey collecting trips and collect the honey of easily accessible nests for personal consumption (Demps et al., 2012a,b). For the Ache, children actively contribute to hunting expeditions by climbing trees to retrieve arrows or killed game, or to flush prey species in the canopy (Hill and Hawkes, 1983). There may also be a limit to the age at which a person can learn to climb; no Jenu Kuruba men who collect honey learned to climb trees past the age of 26 (Demps et al., 2012b). Given that 26 year-old men are physically fit enough to climb trees, this

observation is consistent with evidence that anatomical (muscular) plasticity reflecting the long-term repetition of a behavior may influence climbing ability (Venkataraman et al., 2013a,b). Climbing ability appears to peak around age 20 years of age, as measured by the climbing height achieved by Jenu Kuruba men during experimental trials (Demps et al., 2012b) and the amount of honey collected per individual. For the Aka, the majority of honey (60%) was collected by middle aged men in amounts of ~1.4 kg per person day⁻¹ (Kitanishi, 1996). Likewise, most Batek climbers tend to be teenage boys and men (Lye, 2004) who appeared to be “the most adept and bravest climbers” (Endicott and Endicott, 2008:135). Despite the physical demands of climbing, a Batek man in his sixties has been documented climbing trees (Lye, 2004).

Climbing is typically a male activity, but women in some populations also climb. At one extreme, only male Aka (Hewlett et al., 1986), Mbuti (Ichikawa, 1981), Jenu Kuruba (Demps et al., 2012a,b), and Andaman Islanders (Radcliffe-Brown, 1922) are known to climb trees for substantial amounts of hunting or gathering. Women may still assist men during honey collection, as for the Aka (Kitanishi, 1996), but it is considered male work and social taboos may be largely responsible for the lack of female climbing, as in the Jenu Kuruba (Demps et al., 2012a,b). Given the safety risks and physical demands required to ascend extremely tall trees by all of these populations, male-biased climbing is perhaps not surprising. In other populations in which climbing is performed more frequently by both sexes, women generally do not climb as often or as high as men do. In the case of the Ache, for example, although both men and women are adept climbers (Hawkes et al., 1982), climbing and honey collection are still mainly male activities (Hurtado et al., 1985). Hurtado et al. (1985:15) emphasized the difference in physical ability of men and women in writing, “Men walk faster than women, run after game, employ bows and arrows, frequently climb trees, and take the honey of stinging bees.” When collecting gingers and rattan fruits, the Agta also forage in mixed-sex groups, but if the tree is particularly tall or lacks vines to facilitate canopy access, males do the climbing (Griffin and Estioko-Griffin, 1985). At the opposite end of the spectrum, men climb most often among the Batek, but women and children are also excellent climbers and climb frequently (Lye, 2004; Endicott and Endicott, 2008). This observation is consistent with the distinct gender-egalitarianism displayed by the Batek (Endicott and Endicott, 2008). Nevertheless, only men undertake very dangerous climbs into the canopy, while women forage in short trees or on low limbs (Endicott and Endicott, 2008). Indeed, Endicott and Endicott (2008) observed that the vast majority of honey was collected by men (87% by weight), men were involved in nine times as many instances of honey collection as women, and women did not collect honey by themselves. Hadza women climb to acquire the easily accessible honey of stingless bees, but men usually climb for honey from stinging bees (Marlowe, 2010). Studies of the Mbuti indicate that only a few select men in villages or bands are excellent climbers (Ichikawa, 1981). These men provision other families with honey and tend to occupy a high social status in the community.

Comparisons of tree climbing performance between humans and great apes

Here we summarize (Table 2) and compare performance variables related to arboreality between humans and great apes. Although Table 2 is not exhaustive and does not present detailed methodological remarks regarding each study cited, it enables general comparisons to be drawn between human and great apes. Given the paucity of data on time spent in trees or climbing for hunter-gatherers, however, the results presented here should be regarded as provisional.

Table 2Climbing performance variables for great apes and humans. All values are for adults and are from wild populations unless otherwise noted. Data for *Homo sapiens* are from select hunter-gatherer populations.

Species	Sex	Mean distance climbed (m/day; ascent only)	Horizontal distance traveled (m/day)	Degree of arboreality (% time spent in trees)	% Climbing (of locomotion, includes ascent and descent)	Climbing speed (m/s)	Climbing mortality (% male deaths)
<i>Homo sapiens</i>	M	80 ^{a,b,*}	9400 ^a , 11400 ^c , 12000 ^d	8.0 ^e	NA	0.21 ^f , 0.27 ^g	1.8 ^h , 6.6 ⁱ
<i>Homo sapiens</i>	F	NA	5000 ^c , 12000 ^d	NA	NA	NA	NA
<i>Gorilla gorilla</i>	M	NA	600 ^j (MG), 2300 ^j (LG)	2.0 ^j (MG), 3.0 ^k (MG), 58.0 ^l (LG)	40 ^{j,m} (MG), 48 ⁿ (LG)	0.70 ^o (LG; captive)	NA
<i>Gorilla gorilla</i>	F	NA	600 ^j (MG)	3.0 ^k (MG), 7.0 ^j (MG), 95.0 ^l (LG)	40 ^{j,m} (MG), 48 ⁿ (LG)	0.70 ^o (LG; captive)	NA
<i>Pan paniscus</i>	M	NA	2000 ^p	94.6 ^q	53 ^{j,m}	0.70 ^o (captive)	NA
<i>Pan paniscus</i>	F	NA	2000 ^p	94.6 ^q	53 ^{j,m}	1.20 ^o (captive)	NA
<i>Pan troglodytes</i>	M	104 ^r	3000 ⁱ , 4900 ⁱ	32.9 ^s , 37.4 ^j , 48.9 ^s	49 ⁱ , 54.2 ^s , 68 ^j , 76.7 ^s	0.50 ^r	4.0 ^u
<i>Pan troglodytes</i>	F	117 ^r	1900 ⁱ , 3000 ⁱ	47.8 ^s , 64.8 ^s , 68.4 ^s	49 ⁱ , 59.8 ^s , 65.6 ^s , 68 ^j	0.50 ^r	4.0 ^u
<i>Pongo pygmaeus</i>	M	77 ^v (captive), 88.3 ^v (range 55.7–121.4)	444 ^v (captive), 712 ^v (range 162–1077), 850 ^w , 868 ^x	90.0 ^y	10 ^z , 26 ^{aa}	NA	NA
<i>Pongo pygmaeus</i>	F	81.5 ^v (range 62–101; captive), 88.3 ^v (range 55.7–121.4)	711 ^w , 712 ^v (range 162–1077), 866 ^x , 891 ^v (captive)	90.0 ^y	10 ^z , 21 ^{ab} , 26 ^{aa}	NA	NA

NA = not available; MG = mountain gorilla; LG = lowland gorilla.

* = See text for details on this estimate.

^a Bailey, 1991.^b Ichikawa, 1981.^c Pontzer et al., 2012.^d Hill and Hurtado, 1996.^e Bailey and Headland, 1991.^f T.S.K. and V.V.V., Unpublished data.^g K. Demps, Unpublished data.^h Headland et al., 2011.ⁱ Hewlett et al., 1986.^j Doran, 1996.^k Tuttle and Watts, 1985.^l Remis, 1999.^m Carlson, 2005.ⁿ Remis, 1995.^o Isler, 2005.^p Kano, 1992.^q White, 1992.^r Pontzer and Wrangham, 2004.^s Doran and Hunt, 1994.^t Hunt, 1991.^u Goodall, 1986.^v Pontzer et al., 2010 (wild data from Singleton et al., 2009 and references therein).^w Galdikas, 1988.^x Campbell-Smith et al., 2011.^y Rodman, 1984.^z Sugardjito, 1982.^{aa} Thorpe and Crompton, 2006.^{ab} Cant, 1987.

The importance of arboreal resources to hunter-gatherers suggests that climbing should be frequent. Indeed, [Endicott \(1979\)](#) reports that Batek men climb tall trees (>50 m) on a daily basis. For !Kung men, the average number of ‘honey days’ per month for males ranged between zero and seven ([Yellen, 1977; Hill et al., 1985](#)), and during the two-month dry season honey extraction occurred during 20% of days. [Bailey and Headland \(1991\)](#) state that Efe men spend up to 8% of time away from camp perched in trees or climbing. By these measures, humans spend less time in trees compared with great apes, with the exception of male gorillas ([Table 2](#)).

In order to evaluate whether humans climb similar distances to apes during a day, we estimated climbing distance based on information from [Ichikawa \(1981\)](#) and [Bailey \(1991\)](#). [Ichikawa \(1981\)](#) found that during the honey season, an Mbuti group exploited on average 3.75 honeybee hives day⁻¹, and sometimes up to ten. He further notes that individuals climb a maximum of four trees per day ([Ichikawa, 1981](#)). Assuming that honey in the Ituri is located at an average height of 19.1 m ([Bailey, 1991](#)), this translates to ~200 m of vertical climbing per group day⁻¹ and ~80 m per person day⁻¹ for the most able climbers. This per capita value is exceeded by the mean climbing value for wild chimpanzees and orangutans by a factor of 1.3–1.5 and 1.1, respectively. It is important to note that this value for humans is for the honey season when climbing behavior is extreme, but climbing also occurs during other seasons and for a variety of resources. Because the energetic cost of climbing depends on distance climbed ([Pontzer et al., 2011](#)) and climbing efficiency is similar across a wide range of body masses ([Hanna et al., 2008; Hanna and Schmidt, 2011](#)), humans and great apes should expend similar absolute amounts of energy on vertical climbing.

Speed is a common locomotor performance measure used by biologists (e.g., [Autumn et al., 2006](#)). Based on most ethnographic reports, humans tend to move cautiously within trees. Consistent with these reports, human vertical climbing is relatively slow compared with that of the great apes ([Table 2](#)), although data are limited. We recorded human climbing by Twa hunter-gatherers in Uganda and found that men climbed at an average of 0.21 m s⁻¹ (S.D. = 0.06 m s⁻¹, max = 0.35 m s⁻¹, n = 43; ascent only; T.S.K. and V.V.V., Unpublished data). The Jenu Kuruba, climbed at similar speeds (mean = 0.27 m s⁻¹, S.D. = 0.13; max = 0.71; ascent and descent; K. Demps, Unpublished data) during trials on trees with ~60 cm DBHs. By comparison, chimpanzees and bonobos climb at an average of 0.5 m s⁻¹, and gorillas climb slightly faster at an average of 0.7 m s⁻¹ ([Pontzer and Wrangham, 2004; Isler, 2005](#); ascent only).

Humans are sometimes capable of moving adeptly in trees. [Lye \(2004\)](#) notes that Batek children can move quickly through the canopy and also describes arm-swinging from branch to branch by the Batek (this movement is termed ‘tabing’ in the Batek language; [Lye, 2004](#)). Hunting and ambushing within the canopy ([Hill and Hawkes, 1983](#)) are also presumably accompanied by rapid movement. That humans generally move slowly but have the capability to move rapidly in canopies is important in the context of fitness benefits. On a similar note, [Thorpe and Crompton \(2009\)](#) state that although orangutans are considered slow and cautious arborealists, they can also move rapidly if necessary (i.e., to escape from aggressive conspecifics during feeding competition).

In terms of location, humans tend to forage near the central core of trees. There are few reports of humans foraging near the terminal branches of trees. When food is located on the terminal branches, knives are used to cut branches at their base ([Endicott and Endicott, 2008; Marlowe, 2010](#)).

Costs of climbing trees: mortality, morbidity, and psychological considerations

“Honey of *Apis mellifera* is removed from nests high in trees, which are hard to locate and to access. Climbing the tree requires great skill and a well worked out strategy. After all this, there may or may not be a large amount of honey to be had. In short, honey is a tremendously rich resource, but taking it from African killer bees while dangling from a vine 120 feet off the ground with a basket of burning leaves in one hand and an axe in the other means that it is also very costly and risky”

Laden, 1992:197

The heights attained by hunter-gatherers in forest canopies are extreme. Efe men climb on average 19.1 m to acquire honey, and as high as 51.8 m ([Bailey, 1991](#)). Batek men climb 50 m trees on a daily basis ([Endicott, 1979](#)). Even minor excursions into forest canopies can be dangerous. Data on falling (from industrialized populations) show that the chance of death is 44.4%, 56.2%, 77.8%, and 100.0% from falls of 12.0 m, 15.6 m, and 19.2 m, and >19.2 m, respectively ([Risser et al., 1996](#)). By any measure, tree climbing is an extremely dangerous behavior, especially among the towering canopies of tropical rainforests. The heights at which honey is harvested in rainforests in Asia and Africa are congruent with a high risk of death in the event of a fall ([Fig. 2](#)). It is interesting to note that human foragers may in fact climb to greater heights on average than some great apes, particularly during honey acquisition. Chimpanzees at Mahale and Gombe spend most of their time below 20 m, while male chimps at Tai spend about half their time above 20 m ([Doran and Hunt, 1994](#)). For bonobos, the modal height was 31–35 m

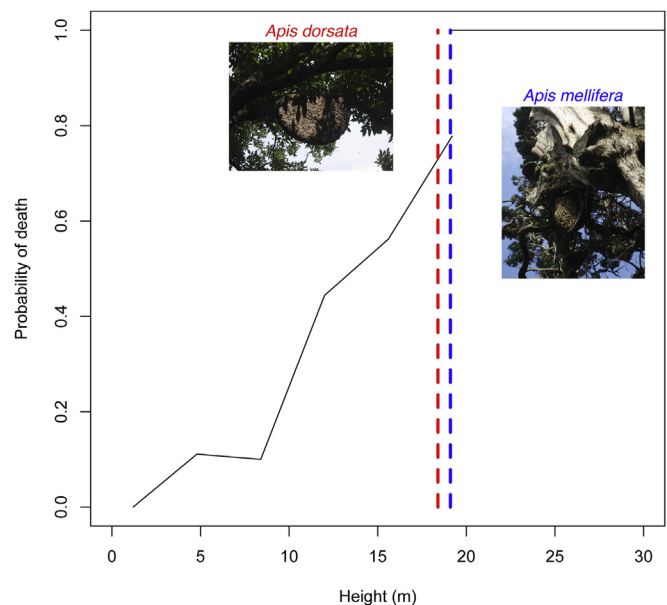


Figure 2. The probability of death due to falling as a function of height (solid black line, data from [Risser et al., 1996](#)). The average height of *Apis dorsata* nests in Thailand (18.4 ± 4.3 m red dashed line, data from [Seeley et al., 1982](#)) and the average height climbed by the Efe to collect honey (mainly *Apis mellifera*) in the Democratic Republic of Congo (19.1 ± 9.7 m, blue dashed line, data are from [Bailey, 1991](#)). Climbing to mean heights necessary for the collection of honey in both Africa and Asia is extremely dangerous. Photo of *A. mellifera* by Sailko, retrieved from the Wikimedia Commons under the Creative Commons Attribution-Share Alike 3.0 Unported license. Photo of *A. dorsata* by Sean Hoyland, retrieved from the Wikimedia Commons. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(White, 1992). The average height in trees of lowland gorillas at Bai Hokou is >20 m, while at Karisoke mountain gorillas are on average found at tree heights of <7 m heights (Watts, 1984, 1990; Remis, 1994, 1995; Doran, 1996). For orangutans, 66% of locomotion took place below 20 m (Thorpe and Crompton, 2005). However, Thorpe and Crompton (2009) also state that 16/21 (76%) of orangutans treated at a veterinary field station in Borneo had fallen from heights >20 m, and possibly as high as 50 m (Kehoe and Chan, 1986).

Hewlett et al. (1986) found that 6.6% of deaths among middle-aged and young men of the Baka in the Central African Republic were due to climbing accidents. Death due to falls from trees appears to be rarer among Southeast Asian foragers; over 40 years, 1.8% (~4/400) of Agta men died from tree-falls (Headland et al., 2011). One long-term Batek researcher (K. Endicott, Personal communication) heard of one man dying from a tree-fall in a thirty-year period. Another researcher reported two deaths among the Temiar and Batek within a short time in the 1970s, both while climbing for honey (G. Benjamin, Personal communication). Few comparable data are available for woodland-savanna hunter-gatherers, though 21 cases of injuries due to falls from trees were reported for the Hadza out of a sample of 491 individuals (Bennet et al., 1973). Some comparable data are available for nonhuman primates. In Gombe, Tanzania, 4% of chimpanzee deaths over a two-year period resulted from falls from trees (Goodall, 1986). Teleki (1973) also directly observed a chimpanzee death due to falling. As noted above, risk of death from falling for orangutans could also be serious but, to our knowledge, no mortality statistics are available.

Morbidity due to climbing is also costly. Injury due to falling is relatively common among primates, and falling is thought to be the greatest cause of long bone trauma in the order (Lovell, 1990; Jurmain, 1997; Carter et al., 2008). In a thorough study of primate morbidity, Jarrell (2011) found evidence of long bone trauma consistent with falling in 13.3% of 1672 individuals sampled from 22 taxonomic groups ranging from prosimians to apes. Jurmain (1997) found that 21.7%, 17.7% and 13.3% of chimpanzee, lowland gorilla, and bonobo skeletons, respectively, showed evidence of postcranial trauma consistent with falls from trees. In addition, Goodall (1986) directly observed 51 cases of chimpanzees falling from trees, 25.5% of which were from heights exceeding 10 m, and two of which resulted in death. In Kakamega Forest, Kenya, von Hippel (1998) observed three nonlethal falls to the ground by black and white colobus monkeys from heights of 13 m, 17 m, and 28 m, with one individual breaking its tail.

Modern humans also suffer injuries due to falling from trees, but data on long-bone trauma due to falling in hunter-gatherers are sparse. In locations where palm and other fruits are routinely harvested for food and fermented drinks, injuries due to falls can comprise a large proportion of overall injuries in a population and are thus a major occupational hazard. In Ilorin, Nigeria, falls from kola-nut and palm trees accounted for 23% of hospital admissions from 1999 to 2000 (Solagberu et al., 2002). In Papua New Guinea, injuries due to falls from trees accounted for 41% of trauma observed at a single rural hospital, and at least 28 people from a surrounding village died from falls over a four year period (Barss et al., 1984). Accidental falls from heights can also result in dangerous injuries to the spine, legs, arms, and internal organs (Solagberu et al., 2002). Barss et al. (1984) note that falling from a mature coconut palm tree is equivalent to a fall from a 10-story building and generates velocities comparable with those encountered in motor vehicle crashes. Falls from unbranched trees are particularly dangerous because there is little opportunity to arrest the fall (Barss et al., 1984).

Some falls are due to the fright of encountering snakes at height (Barss et al., 1984). The concern of encountering snakes in tropical rainforest canopies may also be a serious one for rainforest foragers. Mortality due to snakes among Amazonian, African, and Southeast Asian hunting and gathering populations can be nontrivial (Headland and Greene, 2011).

Psychology of climbing

“Confidence with heights, dexterity, and all-round physicality are definitely prerequisites for all kinds of climbing.”

Lye, 2004:139

The physical ability to climb tall trees safely and efficiently is preceded by the psychological will to undertake this dangerous task. In addition, effective climbing requires a participant to overcome the fear of falling while moving within the canopy and performing technically complex tasks (such as honey collecting). This point is demonstrated in a documentary film in which an expert Biaka climber in the Central African Republic explains, “When climbing big trees you have to empty your heart of fear...if you have fear, you will fall...many friends have died doing this” (BBC Human Planet).

The framework of evolved navigation theory predicts that humans should generally overestimate heights in order to avoid exceedingly costly navigation (Jackson and Cormack, 2007). Fear associated with exaggerated perception should function to reduce the likelihood of undertaking a dangerous climb if potential costs outweigh expected benefits. Indeed, there is evidence that both men and women systematically overestimate heights, and that distance overestimation is positively correlated with fear of heights (Stefanucci and Proffitt, 2009).

Several psychological factors may contribute to observed sex and age differences in hunter-gatherer climbing behavior. First, males exhibit generally greater risk-taking tendencies in comparison with females (Byrnes et al., 1999). Second, adolescents tend to exhibit greater risk-taking tendencies in comparison with adults (Steinberg, 2007). The available evidence suggests that these general trends hold when specifically examined in relation to fear of heights. For example, Fredrikson et al. (1996) found that women and older individuals exhibited significantly more intense fear of heights compared with men and younger individuals, respectively. Bourdan et al. (1988) also reported a higher prevalence of fear of heights in women than men. The sex- and age-specific climbing behavior of hunter-gatherers follows general trends of risk-taking behaviors in humans. As such, it is not surprising that young men collect the most honey and undertake the majority of climbing behavior in foraging populations worldwide. Although children often climb to much lesser heights than adults, elevated risk-taking in children may also contribute to the development of climbing skills at a young age during key periods of developmental plasticity.

Discussion

Data from the ethnographic literature suggest that hunter-gatherers are capable tree climbers, that the activity has positive and negative fitness consequences, and that in many cases climbing is performed without reliance on technology. Climbing by hunter-gatherers is usually associated with food acquisition, particularly honey and fruit, and it is performed in a kinematically distinct fashion that bears some similarities to that of chimpanzees (Venkataraman et al., 2013a). The manner in which humans vertically climb and move within trees compared with chimpanzees is

consistent with anatomical differences between these species. It thus stands to reason that functional inferences of climbing performance in hominins would benefit from a consideration of how humans move within trees. Yet studies on the nature and timing of the transition to terrestrial bipedalism in hominins seldom take human arboreal behavior into account. A conspicuous exception is Darwin, who wrote that for some modern humans "...the foot has not altogether lost its prehensile power, as shown by their manner of climbing trees, and of using them in other ways" (Darwin, 1874:58).

Difficulties associated with foraging in the terminal branches of trees can be attributed to the reduced grasping ability of human hands and feet. Some have argued that the loss of a grasping hallux in hominins would result in catastrophic falls, thus making it a definitive marker of terrestriality (Latimer and Lovejoy, 1990a; Latimer, 1991; but see; Susman et al., 1984; Stern and Susman, 1991). While the advantage of a grasping hallux within trees is obvious, it is virtually unknown to what extent (and in what respects) performance in trees is compromised by climbing and clambering with an adducted hallux, an arched foot, and no mid-tarsal break. Unlike apes, hunter-gatherers do not frequently grasp with their feet while in trees and seldom forage in terminal branches. By inference, fine-branch foraging would have been similarly difficult for most non-tool bearing hominins. Despite these limitations of the hindlimb, humans are nevertheless capable of ascending trees and performing fitness-enhancing behaviors associated with food acquisition.

Currently, too few data on human climbing behavior exist to allow rigorous systematic comparisons with other primates. This has complicated attempts to assess the evolutionary significance of human climbing behavior and its implications for the interpretation of fossil hominins. Our review suggests that compared with great apes, hunter-gatherers are less arboreal (with the exception of mountain gorillas), climb more slowly by a factor of 1.9–5.7, and ascend fewer meters per day by a factor of 1.1–1.5 (Table 2). While it is not surprising that humans do not surpass great apes in terms of performance variables, our results indicate that humans are surprisingly capable in trees. In particular, the similarity in distance climbed per day is striking. When placed within the context of daily ranging distance, however, the proportion of energetic expenditure due to climbing may be low for humans, compared with great apes (Pontzer and Wrangham, 2004), due to large day ranges by humans (Table 2). If so, safety risks could represent the primary cost of climbing, rather than energetic expenditure. Indeed, humans experience mortality due to falls from trees at roughly equivalent rates (chimpanzee comparison only) (Table 2). Given the wide body of (largely anecdotal) literature on frequent and proficient climbing behavior reviewed here, the sparse quantitative data in Table 2 probably represent severe underestimates of human climbing abilities and frequencies. As such, interpretations based on the available literature are necessarily provisional and would benefit from additional quantitative data on human climbing behavior.

Is human climbing adaptively significant?

For extant organisms, the term adaptive significance has been used to describe traits or behaviors that affect fitness. Some have analogized human climbing behavior with sleeping or lying down. These behaviors are thought to be adaptively insignificant because the anatomies associated with the activity are not linked with differential reproduction and survival (Latimer, 1991; Ward, 2002). Yet human climbing differs from sleeping and lying down in three fundamental ways, all of which pertain to fitness. First, climbing involves the acquisition of key food resources. Second, climbing to great heights is dangerous. Third, the climbing techniques practiced

by hunter-gatherers are stereotypical and thus rely on specific anatomical traits (Table 1).

According to this framework, the mortality rates and fitness benefits associated with human tree climbing would suggest a history of selection for behavioral and anatomical adaptations. In particular, the stereotypical changwod and chinbodn styles of climbing, which necessitate extreme dorsiflexion and inversion in the ankle, are predicted to be associated with skeletal signals in the distal tibia and/or talus that permit/reflect these movements (Lovejoy et al., 1999). A recent study of climbing rainforest hunter-gatherers revealed no such skeletal signals (Venkataraman et al., 2013b) but found instead that dorsiflexion could be facilitated by phenotypic plasticity of muscle architecture (Venkataraman et al., 2013a). While this may facilitate force production during climbing, increased fiber lengths in the gastrocnemius muscle may simultaneously compromise walking efficiency for climbers because muscles with longer fibers use more energy than muscles with shorter fibers to generate the same force per unit time (Roberts et al., 1998; Pontzer et al., 2011). This is suggestive of a tradeoff in a trait that affects both climbing and walking performance. Similarly, the presence of a midtarsal break in humans (Bates et al., 2013; Crompton et al., 2010; DeSilva, 2010; DeSilva and Gill, 2013) could benefit tree-climbing abilities at the expense of walking.

Morbidity from falls is also likely to have fitness consequences, as incurring injuries in a pathogen- and predator-rich environment has substantial costs. Trauma in the postcranial skeleton due to falling is relatively high among nonhuman primates (Jarrell, 2011). In primate studies, associations between fitness, behavior, and morbidity frequently underlie adaptive hypotheses. However, the relationship between morbidity, morphology, and behavior is not clear and could be complicated by numerous factors. Jarrell (2011) predicted that degree of arboreality would be correlated with postcranial trauma in long bones among primates due to falls from trees. However, degree of arboreality and fracture frequencies for primates were unrelated (Jarrell, 2011). A non-primate example could prove instructive to explain this result. Porcupines present a case in which morphological adaptations for tree climbing and observed arboreal behaviors diverge to a striking degree.³ For example, Roze (2009) provides evidence of North American porcupines (*Erethizon dorsatum*) falling from trees, sometimes fatally, and hypothesizes that falls may be particularly problematic in this species because porcupines have relatively high mass, their foods are often located on fine branches far from the trunk, and frequently-climbed tree species have brittle branches. Roze's (2009) analysis of 37 North American porcupine skeletons found that 35.1% had evidence of healed fractures likely due to falling from trees. By comparison, a control sample of ground-dwelling woodchucks and raccoons (which sometimes climb trees but do not forage among fine branches) evinced fall-related trauma at rates of 6.7 and 10.3%, respectively (Roze, 2009). Elevated values among the porcupines can thus be attributed to these animals foraging among fine branches despite not being particularly suited for doing so. This example illustrates how foraging behavior could mediate the association between locomotor adaptation, diet, and morbidity.

The above considerations have implications for inferring tree climbing abilities and frequencies in fossil hominins. For example, DeSilva (2008) hypothesizes that if hominins were climbing, they should evince high rates of morbidity. The paucity of observed

³ An anonymous reviewer of this paper called attention to the extreme case of goats climbing trees with agility (El Aich et al., 2007). An Internet search of the phrase 'goats in trees' illustrates this point. Similar animals, such as sheep, do not appear to be equally capable in trees.

postcranial trauma among hominin skeletons was then taken to indicate low or negligible climbing frequency. We suggest that the case of porcupines (as contrasted with woodchucks and raccoons) and the human model provide an alternative explanation for low hominin morbidity rates. Hominins with bipedally adapted ankles and feet could have avoided falls by foraging within the central core of trees, as modern hunter-gatherers do. These considerations suggest that arboreality, at least with reference to hominins, would be more usefully defined with respect to a modern human model that emphasizes vertical climbing behavior and foraging location within tree crowns, rather than the presence or absence of the grasping behaviors that characterize the quadrupedal arborealism of other primates.

Inference for fossil hominins

Because soft-tissue does not preserve in the fossil record, studies on skeletal features (e.g., phalangeal curvature (Richmond, 1998) or scapular morphology (Green et al., 2012)) that permit/reflect (Lovejoy et al., 1999) tree climbing abilities among hunter-gatherers would be informative for inferring climbing signals in the hominin fossil record. Morphologies that compensate for the disadvantages of bearing a bipedally adapted hindlimb (Ward, 2002; DeSilva, 2008) could also be prominent among climbing humans. Examination of climbing related trauma among modern humans, especially hunter-gatherers, may be a promising avenue for interpreting postcranial trauma (or lack thereof) in fossil hominins that are likely to have climbed in a fashion similar to modern humans (Venkataraman et al., 2013a). Additionally, anatomies associated with one form of locomotion do not necessarily compromise different forms of locomotion. For example, the capacity to dorsiflex at the metatarsophalangeal joint, which is used during toe-off while walking and is interpreted as evidence of poor climbing abilities in *Australopithecus afarensis* (Latimer and Lovejoy, 1990b), may actually be co-opted to reduce the overturning moment while climbing (illustrated in Fig. 1H; Cartmill, 1974; Autumn et al., 2006).

Our conclusions do not imply that habitually-climbing hunter-gatherers are specifically 'adapted' for climbing behavior, although aspects of the human pygmy phenotype such as small body size and derived skeletal proportions might be beneficial for climbing relative to walking (Venkataraman et al., 2013a). In fact, there is strong evidence that the economy of terrestrial bipedalism has been steadily refined throughout the hominin lineage (Steudel, 1994; Bramble and Lieberman, 2004; Steudel-Numbers and Tilkens, 2004; Jungers, 2009; Pontzer, 2012). Yet derived human-like traits do not definitely discount arboreal resource acquisition via vertical climbing, and such a shift toward enhanced terrestrial locomotor performance in the hominin fossil record does not alone constitute positive evidence for a proportional reduction in arboreal behaviors. Instead, we argue that a change in climbing style and foraging location in the canopy may have accompanied shifts toward terrestrial locomotion and could, in turn, have imposed a unique set of selection pressures.

The implications of this study extend beyond locomotor ecology. As noted before, vertical climbing behavior in humans is closely linked to food acquisition. In this regard, it resembles nonhuman primate vertical climbing behavior (e.g., Fleagle, 1976). In Africa, rainforest and savanna foragers climb to acquire honey, baobab, meat, and fruit, among other things. Because it is unquestionable that these resources also existed during the Plio-Pleistocene, we suggest that hominin climbing behavior, if and when it occurred, could have occurred in pursuit of similar food resources as that of modern hunter-gatherers. It is crucial to avoid, however, the 'tyranny of ethnography' (Wobst, 1978) by suggesting that modern

hunter-gatherer behavior is the only guide to past behavior. Instead, as proposed by others (Tuttle, 1981; Susman et al., 1984), the climbing behavior of hominins might have centered on the ascent of sleeping trees at night and/or predator evasion, in addition to the pursuit of resources entirely different from those acquired by modern people. In addition, many elements of human climbing behavior cannot be easily extended to hominins. For example, sex differences in climbing ability and frequency for humans are more or less inverted compared with those of the great apes (Table 2), and numerous cultural and psychological factors figure into human climbing decisions. It remains a matter of speculation how and when these elements of climbing behavior arose in the human lineage. The primary lesson from considering a modern human model as a basis for reconstructing hominin locomotor behavior is that humans can be capable climbers and acquire large quantities of arboreal resources despite anatomy that indicates otherwise. The human model therefore presents a necessary conceptual framework for exploring the performance capabilities of hominins in arboreal settings.

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