



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, antiparasitoid, 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 (Dempsey 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; Dempsey 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

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