

Correspondence

Chimpanzee carrying behaviour and the origins of human bipedality

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Why did our earliest hominin ancestors begin to walk bipedally as their main form of terrestrial travel? The lack of sufficient fossils and differing interpretations of existing ones leave unresolved the debate about what constitutes the earliest evidence of habitual bipedality. Compelling evidence shows that this shift coincided with climatic changes that reduced forested areas, probably forcing the earliest hominins to range in more open settings [1]. While environmental shifts may have prompted the origins of bipedality in the hominin clade, it remains unknown exactly which selective pressures led hominins to modify their postural repertoire to include a larger component of bipedality [2]. Here, we report new experimental results showing that wild chimpanzees walk bipedally more often and carry more items when transporting valuable, unpredictable resources to less-competitive places.

Many hypotheses have sought to elucidate the selective advantage that led to the origin of hominin bipedality [3]. However, these cannot be tested adequately with evidence solely from the fossil or archaeological records [4], but also require an understanding of the contexts of locomotion in extant primates. Occasional bipedality occurs among wild great apes, but no study has examined how carrying influences bipedal walking on the ground in nature.

Hewes [5] argued that bipedal locomotion is unmistakably linked to food carrying; however, most of chimpanzee bipedality (80–96%) is postural, not locomotory, and takes place during fruit foraging in short

trees [6], not while carrying items. We tested for the first time Hewes's 'carrying hypothesis' that bipedal locomotion should occur with greater frequency during carrying.

In a natural clearing in Bossou forest ('outdoor laboratory' [7]), we provided chimpanzees with two species of nuts and stones suitable for use in nut-cracking (see Supplemental Experimental Procedures in the Supplemental Information available with this article online). The locally unavailable coula nut (*Coula edulis*) was a rare resource of unpredictable availability, while the oil palm nut (*Elaeis guineensis*) was naturally available and familiar.

To test the effect of resource availability on the occurrence and mode of carrying, we compared transport of nuts and stone tools under three conditions: Only oil-palm nuts present ('*Elaeis* only' condition; EO); coula nuts present at low availability ('high-competition' condition; HC); and coula nuts present as the majority resource ('low-competition' condition; LC). We noted which items chimpanzees carried, how many items were carried simultaneously, how the objects were held, and what mode of locomotion — quadrupedal, tripedal, or bipedal walking — carriers used (Figure 1 and Supplemental Movie S1).

In 44.5 hours of observation, we recorded 742 transport events by 11 individuals. Transport rates per individual were three times

higher in the HC than in the EO and LC conditions (Supplemental information). When more coula nuts were available, chimpanzees stopped transporting and cracking oil-palm nuts, suggesting that they valued coula more highly than the more predictably available oil-palm. While most transport overall was quadrupedal, the frequency of bipedal transport increased by a factor of four in the HC and LC conditions compared to EO (Supplemental information). Thus, the introduction of prized coula nuts triggered a more dramatic increase in bipedal transports versus quadru- or tripedal carrying. Moreover, chimpanzees carried more than twice as many items when walking bipedally (Supplemental information), suggesting that bipedality was being practised more frequently in order to carry more items. Presence of coula nuts also stimulated more varied forms of carrying: chimpanzees used not only their hands, but also mouths and feet to transport items and frequently employed more than one body part at a time, thereby increasing the number of items that could be carried simultaneously (Figure 1; Supplemental Information).

To complement the field experiments, we studied transport by Bossou chimpanzees in another setting where high-value resources are obtained with unpredictable frequency: crop-raiding. During a 14-month survey, we recorded 112 transport bouts by 12 individuals,

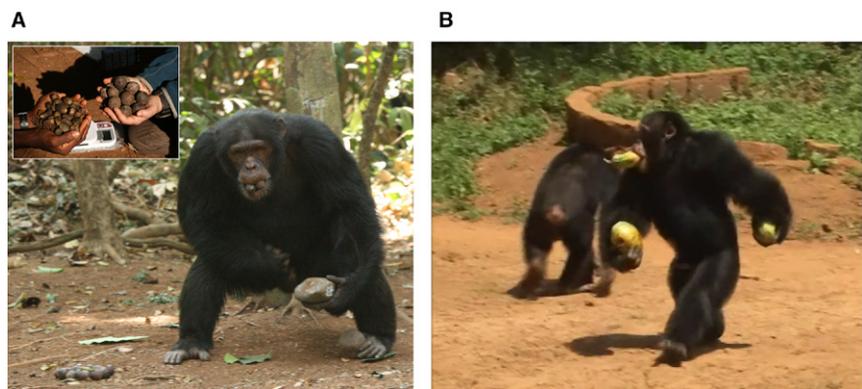


Figure 1. Bipedal transport of items by wild chimpanzees.

(A) Adult male carries both anvil and hammer stones (anvil in left hand, hammer in left foot) and *Coula edulis* nuts (in mouth and right hand) during an experimental nut-cracking session, before depositing items and starting to crack nuts. Inset shows two species of nuts presented at outdoor laboratory (left: *Elaeis guineensis*, right: *Coula edulis*) (see also Supplemental Movie S1). (B) Adult male carries three papayas (one in each hand and one in mouth) during crop-raiding (see also Supplemental Movie S2).

involving eight different cultivars. Over a third (35%) of transports included bipedal strides, and the number of items carried in these bouts was significantly higher than in bouts involving only quadrupedal or tripedal locomotion (Supplemental information). Correspondingly, chimpanzees more often used both hands and mouth during bipedal transport (Supplemental information).

Chimpanzees carried food-items and food-related objects (tools), when the latter were needed to process the food. Simultaneously carrying nuts and tools to another location may have energetic advantages — such transports may help individuals to establish temporary ‘personal space boundaries’, or ‘exclusion zones’, allowing them to consume more and share less, especially at higher levels of group competition.

But what makes an item valuable and worth carrying bipedally? Foods may be worth carrying if they are unpredictable in availability. More efficient access to resources may be crucial given this uncertainty (i.e., ‘If I return later, will any resource be left?’). For Bossou’s chimpanzees, these factors combine to increase transport frequency and the number of items carried at a time, apparently in order to optimise time and energy intake through reduced competition. The potential benefit of ‘first come, first served’ access to resources may lead to using extra parts of the body as ‘containers’, shifting to bipedal locomotion to free the hands, affording greater carrying capacity.

Our data support Hewes’ hypothesis [5] that selection for effective food carrying, perhaps resulting from environmental uncertainty, led to the evolution of bipedality. We expand this by predicting ecological contexts in which the transport of valuable items of unpredictable availability follows a ‘carry as much as you can at once’ principle and hence promotes bipedal walking. Our data also reveal sex differences in carrying, with males transporting more often — including a higher proportion of bipedal transports under more intense competition — and carrying more items per bout than females (Supplemental

information). Furthermore, Bossou’s habitat matches predictions of the ‘variability selection’ hypothesis, in which the emergence of novel adaptations results from increases in environmental variability, and adaptive changes are due to ecological uncertainty [8]. Flexible adaptations in the foraging behaviour of Bossou’s chimpanzees, facing a shrinking forested area and ranging in a mosaic distribution of vegetation [9], serve as a proxy scenario to model hominin adaptations to ecological variations.

For chimpanzees, whose activity budgets comprise little overall daily locomotion [10], such carrying of valuable items could act as a strong selection pressure. The energetic intake resulting from resource monopolizing through short bipedal bouts of carrying may eventually select for a gradual anatomical change. We predict that if the environment of early hominins provided similar high-value, unpredictable resources at a greater frequency than seen in most of today’s chimpanzees, this could reward higher frequencies and/or longer distances of bipedal bouts of carriage, creating a selection pressure for more economical bipedality.

Bipedality as the key human adaptation may be an evolutionary product of persisting competitive strategies that ultimately set our ancestors on a separate evolutionary path. Increased energy intake through the monopolization of valuable, unpredictable resources under greater levels of competition may have set the conditions that selected for bipedality in the earliest ape-like hominins.

Supplemental Information

Supplemental Information includes experimental procedures, two figures and two movies and can be found with this article online at doi: 10.1016/j.cub.2012.01.052.

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