Chimpanzee carrying behaviour and the origins of human bipedality

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What selective context led to the origin of human bipedality remains a fundamental question about human evolutionary history, but answers have been hampered by gaps in the fossil record and in our understanding of the behavioural and environmental factors that elicit bipedal locomotion in extant primates, especially our closest living relatives[1-3]. Here, through observations and field experimentation, we show that rare, highly-valued foods and food-related tools increased bipedal locomotion in wild chimpanzees at Bossou, Guinea. Subjects more often carried bipedally items by hand, foot, and mouth, to new locations and in larger amounts when these items were scarce, and carrying capacity was highest

when transporting bipedally. Our results suggest that rare food items, increased resource competition, and enhanced use of the hands to carry and use objects may have acted as selective forces triggering bipedality in the earliest hominins.

Why did our earliest hominin ancestors begin to walk bipedally as their main form of terrestrial travel? One of the oldest unanswered questions about human origins concerns what selective forces triggered the transition to bipedality. This selective regime potentially explains the conditions that first set our ancestors on an evolutionary path separate from that of our closest living relatives, the chimpanzee and the bonobo. As one of the key traits defining the hominin clade[4], Darwin's observation that bipedality may be the primary hominin adaptation[5] remains pertinent today. However, the lack of sufficient fossils and differing interpretations of existing ones have left unresolved the debate regarding what fossils constitute the earliest evidence of habitual bipedality and what forms of locomotion preceded it. Undisputed evidence for habitual bipedality includes the Laetoli footprints at about 3.7 million years ago (Ma) and tibial anatomy of *Australopithecus anamensis* at 4.15Ma[6], and perhaps the pelvic anatomy of *Ardipithecus ramidus* at 4.4Ma[7], femoral anatomy of *Orrorin tugenensis* at c.6Ma[4], or cranial anatomy of *Sahelanthropus tchadensis*[8]. Compelling evidence also shows that this shift in locomotor mode coincided with climatic changes that reduced forested areas, probably forcing the earliest hominins to range in more open settings[9]. While this environmental shift may have played a role in the origins of bipedality and the hominin clade, it remains unknown what selective pressures led the earliest hominins to shift their locomotor repertoire to include a large component of bipedal locomotion[10] relative to the repertoire of the *Pan-Homo* last common ancestor (LCA) that practiced some form of arboreal climbing[11, 13] perhaps combined with knuckle-walking[12]. Insight into these selective pressures requires an understanding of the dynamic interactions among ecological and behavioural factors that motivate an increased level of bipedality within the locomotor repertoire[14]. Here, we report new results showing that wild chimpanzees walk bipedally more often and carry more items in the context of valuable, limited resources, in order to transport them to less-competitive sites.

Many hypotheses have sought to explain the selective advantage that led to the origin of hominin bipedality, including weapon- and tool-use, energetic efficiency, foraging, provisioning, thermoregulation, predator avoidance[2,15,18], carrying items (food, infants, or tools), and placing greater demands on manual manipulation[19,21]. However, these hypotheses cannot be tested adequately with evidence solely from the fossil or archaeological records[12] but require an understanding of the contexts of locomotor behaviour in extant primates.

Many living non-human primates walk on their hind limbs, typically for short distances, but most field studies report postural or arboreal bipedality versus little to no bipedal locomotion on the ground[2,13]. Among wild great apes, bipedality occurs in orangutans (*Pongo pygmaeus*)[13], gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*)[22] and bonobos (*Pan paniscus*)[14], but until now no study has examined how carrying items influences bipedal walking on the ground in wild apes. The single study of chimpanzee bipedal locomotion testing some of the main hypotheses for the origins of habitual bipedality in hominins is from a captive setting[23].

Hewes[20:417] argued that "the environmental stimulus to bipedal locomotion seems to be unmistakably linked to food carrying", such as chimpanzees walking bipedally while carrying papaya or banana. However, in wild chimpanzees, most (80 - 96%) bipedality is postural and occurs during foraging on fruit in short trees[2,24], not while carrying items. If Hewes was right, then bipedal transport of food should be more common terrestrially.

We tested the hypothesis that bipedal locomotion occurs with greater frequency during carrying in a natural setting with experimentally-controlled conditions. In a natural clearing in Bossou forest ("outdoor laboratory"[25]), we provided chimpanzees with two species of nuts (one locally available, one not) and an assortment of stones suitable for use as hammer or anvil during nut-cracking. The locally unavailable nut (*Coula edulis*) had been presented to Bossou chimpanzees intermittently since 1994, but never for longer than two weeks per year. Therefore, individuals were familiar with the nuts, and most had learned to crack them[26], but they represented a rare resource of unpredictable availability. To test the effect of resource availability on the occurrence and mode of carrying, we compared instances of transport of both nuts and stone tools under three conditions: only naturally available and familiar oil-palm (*Elaeis guineensis*) 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). In all three conditions, we recorded and categorised which items chimpanzees carried, how many they carried at a time, how the objects were held, and what mode of locomotion, quadru-, tri-, or bipedal walking, the carriers used (Fig. 1, see also Supplementary Movie 1).

In 44.5 hr of observation at the outdoor laboratory, we recorded 742 transport events by 11 individuals (mean ± SD number of transports per individual: 67.5 ± 46.5). Two other chimpanzees, a dependent infant and an adult female, never transported items and were never seen to use stone tools. Neither mean party size (total number of individuals in the outdoor laboratory during an experimental session) nor mean session duration differed across the three conditions (Supplementary Table 1), allowing us to compare directly the effects of resource provisioning regimes on behavioural measures related to locomotor and transport events.

Transport rates per individual were three times higher ($F_{2,58}$=5.61, p=0.006) in the HC condition (Fig. 2a) than in the EO and LC conditions (Supplementary Table 2). While most transport overall was done quadrupedally, the frequency of bipedal transports increased by a factor of four in the HC and LC conditions compared to EO ($F_{2,58}$=7.44, p=0.001; Fig. 2b). Thus, the introduction of *Coula* nuts triggered a more dramatic increase in bipedal transports versus quadru- or tripedal carrying; although individual frequencies varied, a chimpanzee on average carried items bipedally once every three hours of observation time (Supplementary Table 3). Moreover, chimpanzees carried more than twice as many items when walking bipedally (11 vs 5 tripedally and 4 quadrupedally; $F_{2,726}=21.73$, $p<0.000$; Fig. 2c, Supplementary Table 4), suggesting that bipedality was being practiced more frequently in order to carry more items. The mean number of items transported per hour doubled during the LC and HC conditions, due to the carriage of large amounts of *Coula* nuts (Fig. 2d), items that by definition were unavailable during the EO condition. When *Coula* nuts were available in greater quantities (LC versus HC), the apes stopped transporting and cracking *Elaeis* nuts, suggesting that they valued *Coula* more highly than the more predictably available *Elaeis*. The introduction of *Coula* also stimulated more varied forms of carrying: chimpanzees used not only hands, but also mouth and feet to transport items and frequently employed more than one body part at a time, thereby increasing the total number of items that could be carried at once (Figs. 1a, 2e, Supplementary Table 5).

The number of individuals present at the time of transports varied across conditions, with HC and LC transports done in the presence of fewer individuals than during EO (Supplementary Table 6). This may reflect the chimpanzees' perception of heightened competition over the more valuable *Coula*. Also, transport bouts occurred sooner after chimpanzee parties arrived at the outdoor laboratory when *Coula* nuts were present (Fig. 2f, although this difference does not reach significance, see Supplementary Table 2), which may signal a need to gather and to transport valuable items quickly.

Chimpanzees in the field experiments carried not only food but also food-related objects such as stone tools when the latter were needed to process the food. For chimpanzees, most food items may not be worth carrying, because gathering is more time-consuming than eating[2]. However, *simultaneously* carrying nuts and tools to another spot may have energetic advantages, particularly when resource competition is strong. Such transports may function to establish temporary “personal space boundaries” (or “exclusion zones”), allowing individuals to consume more and share less, thus representing an effective response to higher levels of group competition.

But what makes an item valuable and so worth carrying bipedally? Foods may be worth carrying if they are familiar and exploitable but unpredictable in availability, either because they are absent in the usual home range or because they are exploited by several species with overlapping home ranges. Therefore, more efficient access may be crucial given this unpredictability (i.e. “If I return later, will any of the resource be left?”), or because they are outside the home range’s limits, or are widely dispersed. In wild chimpanzees, these factors combine to increase transport frequency and the number of items carried at a time, in order to optimise time and energy 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, which afford the greatest carrying capacity of any anatomical region available to carry objects.

Evidence from the fossil record supports the hypothesis that selection for manual manipulation was a component of the adaptive regime for the origins of bipedality. Compared with extant great apes, finger length is short relative to other portions of the hand in *Ar. ramidus*[11] and, to a greater extent, *Au. afarensis*[27]. Reduced finger length is key to enhanced manual dexterity as it increases the similarity in lengths between the thumb and fingers, so improving precision grip[28]. Furthermore, *O. tugenensis* has a broad terminal pollical phalanx, associated with enhanced precision grip in higher primates, suggesting that bipedality and enhanced manual dexterity are present in the earliest hominins[29].

Our data support the basic tenets of Hewes’ hypothesis that selection for effective food carrying, perhaps resulting from environmental factors, led to the evolution of bipedal locomotion[19]. We expand Hewes' hypothesis by suggesting ecological contexts in which the transport of valuable items, or of those with unpredictable availability, follows a "carry as much as you can at once" principle and hence promotes bipedal walking. Furthermore, selection for greater manual dexterity may be part of an adaptive complex favouring an increased reliance on walking bipedally, in order to use the hands to transport and manipulate high-valued resources. The unusual and highly flexible adaptations in the foraging behaviour of Bossou chimpanzees, facing a shrinking forested area and ranging in a mosaic distribution of vegetation[30] serves as a proxy scenario to model adaptations to ecological variations.

Bipedality as a key human adaptation may be an evolutionary product of long-lasting competitive strategies that ultimately set our ancestors on an evolutionary path separate from that of our closest living relatives, the chimpanzee and the bonobo. Our results indicate that valuable food items, habitats with increasingly mosaic distributions of vegetation, and higher levels of resource competition may have set the conditions to select for bipedality with greater use of the hands for carrying and manipulation in the earliest ape-like hominins.

Methods Summary

Experiments were done at the long-term chimpanzee field site of Bossou, Republic of Guinea, over two field seasons (Jan 2005; Dec 2008 – Feb 2009). Chimpanzees there customarily use pairs of stones as hammer and anvil to crack open oil-palm (*Elaeis guineensis*) nuts. A natural clearing of about 200m^2 ("outdoor laboratory"[25,26]) in Bossou forest provides the opportunity for the experimental provision of raw materials for nut-cracking (piles of nuts and ~50 stones suitable for use as hammer and anvil). Chimpanzee parties voluntarily visit the outdoor laboratory and use the objects provided. In experimental sessions, we provided both the locally available species of nut (*Elaeis guineensis*) and a species unavailable at Bossou (*Coula edulis*) but cracked by chimpanzees at nearby sites, under three conditions: oil-palm only (7 piles of *Elaeis*), high-competition (7 piles of *Elaeis,* 2 piles of *Coula*) and low-competition (2 piles of *Elaeis,* 7 piles of *Coula*). All experimental sessions were filmed by 2 or 3 digital videocameras. From the video footage, we recorded each instance of chimpanzees transporting items (nuts, stone tools, or both simultaneously), noting the carrying individual, the number and type or identity of the items transported, mode of locomotion (quadrupedal, tripedal, bipedal), body part(s) used for carrying, and identities of other individuals present and engaged in nut-cracking.

Transport was defined as the movement of object(s) from their original position during a session, or, subsequently, the movement of object(s) from the endpoint of a previous transport. A bout was considered to be terrestrial bipedal locomotion when the individual took two or more steps using the legs without the arms touching the ground between the start of the first and the end of the second step. Tripedal and quadrupedal bouts followed the same criteria, with the addition of one or both of the arms touching the ground, respectively.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Figure Legends

Figure 1. Bipedal transport of items by a wild chimpanzee. An adult male carries both anvil and hammer stones (anvil in his left hand, hammer in his left foot) as well as *Coula edulis* nuts (in his mouth and right hand) during an experimental nut-cracking session, before depositing the items and starting to crack nuts. Inset shows the two species of nuts presented at the outdoor laboratory (left: *Elaeis guineensis*, right: *Coula edulis*).

Figure 2. Transport of items by wild chimpanzees under three experimental conditions of resource availability. Rates were calculated for each experimental session as bouts of transport of tools or nuts per hour of observation per individual present. Error bars are standard errors of the mean. **a,** Overall transport rates. **b,** Rates of bipedal transport. **c,** Number of items carried per bout of transport, when moving quadru-, tri- or bipedally. **d,** Number of items of different kinds transported per hour per individual. **e,** Proportion of transports involving more than one body part (any combination of hands, feet, and mouth). **f,** Minutes elapsed since the start of an experimental session at the time of the first transport bout. For all pairwise comparisons, * : $p < 0.05$, ** : $p < 0.01$, *** : $p < 0.001$, *ns*: $p > 0.05$.

Methods

Study site. Experiments were done at the long-term chimpanzee field site of Bossou, Republic of Guinea, over two field seasons (Jan 2005; Dec 2008 – Feb 2009). The forest of Bossou (5-7 km^2 core area) harbours one chimpanzee population (*Pan troglodytes verus*). Between 1976 and 2003, the size of the group ranged from 16-22 individuals; however, due to a respiratory disease outbreak in late 2003, the number of chimpanzees declined and remained at 13 during the study-period.

Bossou chimpanzees customarily use pairs of stones as hammer and anvil to crack open oil-palm (*Elaeis guineensis*) nuts. A natural clearing of about $200m^2$ ("outdoor laboratory"[25,26]) in Bossou forest has been used since 1988 for the intensive study of chimpanzee stone tool technology and the ontogeny of nut-cracking behaviour. Here, experimenters provide raw materials for nut-cracking (piles of nuts and an assortment of ~50 stones suitable for use as hammer and anvil) and observe chimpanzees' interactions with these objects from close range[26]. Chimpanzee parties voluntarily visit the outdoor laboratory and use the objects provided about once or twice a day during regular ranging activities.

Experimental procedure and data collection. In our experimental sessions, we provided both the locally available species of nut (*Elaeis guineensis*) and a species unavailable at Bossou (*Coula edulis*) but cracked by chimpanzees at nearby sites. In any given session, resources were made available under one of three conditions: oil-palm only (7 piles of *Elaeis*), high-competition (7 piles of *Elaeis* and 2 piles of *Coula*) and low-competition (2 piles of *Elaeis* and 7 piles of *Coula*). Piles of different nuts were approximately the same size, but contained different numbers of nuts due to *Coula* being larger (one pile of *Elaeis* = ~70 nuts; one pile of *Coula* = ~20 nuts). The same set of ~50 stone tools was available throughout all sessions. Sessions began when the first chimpanzee of a visiting party entered the outdoor laboratory and ended when the last of the party exited. All experimental sessions were filmed by at least two digital video cameras.

From the video footage, we recorded each instance of chimpanzees transporting items (nuts, stone tools, or both simultaneously), noting the carrying individual, number and identity of the items transported, mode of locomotion (quadrupedal, tripedal, or bipedal), body part(s) used for carrying (hand, foot, or mouth), timing of the event relative to the start of the experimental session, and identities of other individuals present and engaged in nut-cracking.

Transport was defined as the movement of object(s) from their original position during a session, or, subsequently, the movement of object(s) from the endpoint of a previous transport. A bout was considered to be terrestrial bipedal locomotion when the individual took two or more steps using the legs without the arms touching the ground between the start of the first and the end of the second step. Tripedal and quadrupedal bouts followed the same criteria, with the addition of one or both of the arms touching the ground, respectively.