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Title: Vertical climbing in free-ranging bonobos: an exploratory study integrating locomotor performance and substrate compliance

Short running title: Vertical climbing in free-ranging bonobos

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Abstract

Objectives: Ecological factors and body size shape animal movement and adaptation. Large primates such as bonobos excel in navigating the demanding substrates of arboreal habitats. However, current approaches lack comprehensive assessment of climbing performance in free-ranging individuals, limiting our understanding of locomotor adaptations. This study aims to explore climbing performance in free-ranging bonobos and how substrate properties affect their behavior.

Methods: We collected data on the climbing performance of habituated bonobos, *Pan paniscus*, in the Bolobo Territory, Democratic Republic of Congo. We analysed 46 climbing bouts (12 ascents, 34 descents) while moving on vertical substrates of varying diameter and compliance levels. This study assessed the average speed, peak acceleration, resting postures, and transitions between climbing and other locomotor modes.

Results: During climbing sequences and transitions, bonobos mitigate speed variations. They also exhibit regular pauses during climbing and show higher speeds during descent in contrast to their ascent. Regarding the influence of substrate properties, bonobos exhibit higher speed when ascending on thin and slightly flexible substrates, while they appear to achieve higher speeds when descending on large and stiff substrates, by using a “fire-pole slide” submodule.

Discussion: Bonobos demonstrate remarkable abilities for negotiating vertical substrates and substrate properties influence their performance. Our results support the idea that bonobos adopt a behavioral strategy that aligns with the notion of minimizing costs. Overall, the adoption of high velocities and the use of low-cost resting postures may reduce muscle fatigue. These aspects could represent important targets of selection to ensure ecological efficiency in bonobos.

Key Words: Evolution, Fieldwork, Hominoid, Locomotion, Mechanical ecology

Introduction

The locomotor apparatus enables animals to move and overcome the physical challenges imposed by their environment. It has been shown that during evolution, key aspects of locomotor performance, such as speed, acceleration and energy efficiency, are driven by ecological factors, and body size plays a critical role as well (Aerts et al., 2000b; Irschick & Garland Jr, 2001; Irschick & Losos, 1999; Preuschoft et al., 1996; Reilly et al., 2007). Animals, particularly primates, that inhabit and forage in arboreal habitats, have developed effective strategies to navigate the discontinuous and compliant substrates found in this demanding environment (Young, 2023). While numerous lab studies have focused on primate gait (i.e., footfall pattern; e.g., Cartmill et al., 2020; Cartmill et al., 2002; Demes et al., 1994; Franz et al., 2005; Higurashi & Kumakura, 2021; Larson & Demes, 2011; Lemelin et al., 2003; Schmitt, 1999; Schmitt et al., 2006; Shapiro & Raichlen, 2005; Young et al., 2016) and field studies have explored the positional repertoire of primates (i.e., postural and locomotor repertoire; e.g., Cant, 1988; Doran, 1992; Hunt, 1992; Morbeck, 1977; Remis, 1998; Rose, 1977; Sarringhaus et al., 2014; Thorpe & Crompton, 2006; Wells & Turnquist, 2001; Workman & Schmitt, 2011), our current approaches commonly miss locomotor performance information in conjunction with environmental structural properties in free-ranging individuals (but see Demes et al., 1995; Dunham et al., 2019; Isler & Thorpe, 2003; McNamara et al., 2019; Neufuss et al., 2018; Thorpe et al., 2009; Thorpe et al., 2007a; Thorpe et al., 2007b; Young et al., 2021). This is also the result of inherent challenges associated with monitoring and observing free-ranging arboreal animals. Consequently, there exists a critical blind spot in our comprehensive assessment of locomotor adaptations in primates, making interpretations of extinct species particularly challenging when it comes to the locomotor repertoire (e.g., Böhme et al., 2019; Böhme et al., 2020; Williams et al., 2020). In this context, the emerging field of “mechanical ecology”, as defined by Bauer et al. (2020) as “the combination of biomechanics and field ecology at the organism level” can provide valuable insights to measure ecologically relevant performance capabilities, with the aim to better understand associations between locomotor apparatus and habitat use (see also D’Août & Vereecke, 2011; Herrel et al., 2006).

Arboreal habitats are challenging because the discontinuity, variability, compliance (i.e., branch flexibility and deflection) and instability of the substrates inherently perturb the basic requirements of legged locomotion, i.e., propulsion, balance and path stability. For instance, the ability to generate mechanical work for propulsion may be reduced, as a substantial part of it is lost in deforming the substrate (Alexander, 1991a; Channon et al., 2011; Coward & Halsey, 2014; Demes et al., 1995; Lejeune et al., 1998), making high-speed movement and acceleration difficult. As a result, the speed of progression and acceleration can hold functional significance in serving as proxies for the effectiveness in negotiating discontinuous and compliant substrates. Acceleration capabilities require proficient propulsive abilities along with effective braking or shock absorbing capacities; note that exhibiting a large body size in such a demanding environment can also shift the selective pressures toward slow and cautious behaviours as observed in orangutans (*Pongo spp.*) thus selecting mobility at the expense of speed abilities (Isler, 2005; Sigmon, 1974; Thorpe et al., 2009; Thorpe et al., 2007a; Zihlman et al., 2011). In this context, it has been shown that vertical climbing poses a notable challenge for great apes, as their body weight acts parallel to the substrate, requiring the exertion of pressure independent of their own body weight to ascend or descend (Cartmill, 1985; Preuschoft, 2002). In a vertical climbing posture, the distribution of body weight on fore- and hindlimbs is biased toward the hindlimbs, thus increasing the risk of toppling backwards. The

gravitational force needs to be overcome via propulsion by the hindlimb when ascending and resisted via braking when descending. This behaviour is also likely to demand a substantial amount of energy during daily activities of great apes (Halsey et al., 2015; Hanna & Schmitt, 2011; Kozma & Pontzer, 2021; Pontzer & Wrangham, 2004). Notably, speed has been suggested to play a crucial role in energy efficiency during climbing (Kozma & Pontzer, 2021).

Bonobos (*Pan paniscus*) are a subject of considerable interest when it comes to deciphering locomotor performance (Aerts et al., 2000a; D'Août et al., 2004; Diogo, 2018; Diogo et al., 2017; Druelle et al., 2020; Druelle et al., 2018; Scholz et al., 2006; Schoonaert et al., 2016; Zihlman & Bolter, 2015; Zihlman & Cramer, 1978). While they exhibit a large body size, averaging around 38-45kg (Druelle et al., 2018), they are semi-terrestrial and their predominant habitat is a forest environment (Doran, 1992; Hashimoto et al., 1998; Hunt, 2020; Pennec et al., 2020; Susman et al., 1980; Terada et al., 2015). They are also characterized by an ability to exhibit relatively fast movements as observed in lesser apes, and in contrast to orangutans (Isler, 2005), and they have been observed performing impressive pronograde leaps between flexible branches (Druelle et al., 2020), hence resolving the mechanical challenges imposed by the arboreal substrates (Demes et al., 1995). Interestingly, the study of the locomotor repertoires of bonobos has yielded conflicting results, i.e., highly arboreal *versus* highly terrestrial, making it challenging to establish a clear connection between their anatomy and behaviour (Hunt, 2020). Nevertheless, bonobos exhibit remarkable abilities in various locomotor modes, including leaping (Druelle et al., 2020; Scholz et al., 2006), climbing (Isler, 2002; Schoonaert et al., 2016) and suspensory modes (Doran, 1992) and are thus likely to be characterized by their versatility. They appear to divide their time between the forest floor (~56%) and the forest canopy (~44%), therefore often ascending and descending between these two habitats (Ramos, 2014). While engaging in arboreal locomotion, they frequently climb, ranging from 9.3% to 39.7% (as detailed in Table 7.1 in Ramos, 2014). The forest canopy where bonobos are living can reach heights of up to 30-50 meters and thus present an important risk if they fall (e.g., Pennec et al., 2016; Susman et al., 1980).

In this context, we conducted an exploratory study on free-ranging bonobos to investigate the locomotor performance of these large primates when climbing vertical substrates of varying diameters and compliance levels, including transitions to, and from, other locomotor modes. Our study aimed to address several hypotheses regarding the behaviour of climbing bonobos. First, we present two hypotheses that revolve around potential strategies aimed at minimizing energetic costs by reducing variations in external mechanical power. Climbing bonobos (during ascent and descent) would maintain a steady speed of progression (Kozma & Pontzer, 2021). Bonobos would avoid prolonged pauses in a vertical clinging posture (a potentially costly posture to maintain) during vertical ascents or descents, while also minimizing speed differentials between consecutive locomotor modes. Second, climbing on flexible substrates has been suggested to present greater challenges compared to climbing on stiff supports, as horizontal forces cannot be effectively applied (Neufuss et al., 2018; Schoonaert et al., 2016). Hence, we expect bonobos to exhibit reduced acceleration peaks when climbing on compliant substrates compared to stiffer ones, and compliant substrates should impose constraints on the speed of progression as well. However, being able to completely encircle the substrate with the hand and foot should provide a better grip as more pressure can be exerted, resulting in smaller substrates providing a better grip (e.g., Toussaint et al., 2020). Note that in natural substrates, branch compliance is expected to be strongly related to its diameter (Dunham et al., 2018; van Casteren et al., 2013). We therefore expect to observe a performance trade-off related to these two substrate properties. By conducting a study on free-ranging bonobos, we

aim to gain valuable insights into the complex relationships between locomotion and the ecological challenges faced by primates in their natural habitats. Our focus is on understanding effective and efficient movements that hold ecological relevance, ultimately shedding light on the evolutionary drivers of the morphology of primates.

Material and Methods

Study site

The study was conducted from May 30 to June 3, 2022, in the Forest Concession of Local Communities of the Mbali River, Bolobo Territory, Democratic Republic of Congo (DRC), a community-based conservation project, led by the Congolese NGO Mbou-Mon-Tour (Narat et al., 2015a). We observed the Manzano community, habituated to human observers (Narat et al., 2015b) and composed by 30 individuals at the time of the study. The level of habituation can be classified as good (i.e., level 3) according to the operational classes proposed by Bertolani and Boesch (2008). This particular long-term study site is known for its fragmented habitat, a forest-savanna mosaic (Pennec et al., 2016).

Data collection

We conducted daytime observations of a bonobo party alongside the local research assistants, from 06:00 to 18:00, resulting in a total observation time of approximately 15 hours. The research protocol was implemented opportunistically, whenever suitable conditions allowed us to capture arboreal locomotor sequences within a wide field of view. A limited number of branches is commonly available between the tree crowns and the ground (Pennec et al., 2016) allowing us to record climbing sequences when bonobos climb up to the canopy or descend to the ground. To record these sequences, we used a digital pocket camcorder (GoPro Hero 8 Black) with a frame rate of 60 Hz and a 4K resolution. All the recorded sequences included autonomous bonobos, capable of independent displacements.

To ensure accurate measurements, we calibrated the plane of each recorded sequence immediately after the locomotor activity occurred (Figure 1). We employed an infrared rangefinder equipped with an inclinometer (Solognac, 800 meters) with a precision within a margin of 1 meter. During the calibration process, we identified two specific points on the tree trunk where the bonobos were moving or directly adjacent to the bonobos moving on branches. We measured the distance and angle of these points relatively to the observer, and a photograph was taken using a standard smartphone. Subsequently, we digitized two cross marks directly onto the image to spot the calibrated points. By employing standard trigonometric principles, we calculated the vertical distance, measured in meters, between the two points of interest. This calculation yielded a scaling factor for precise measurements of the recorded sequence. To ensure the reliability of our approach, we applied the identical method to 25 additional (pine) trees in French forest in Provence. Benefiting from convenient access to the tree trunks, we were able to accurately measure the vertical distance using a scale directly on the tree trunk (see supplementary material).

Data analyses

Prior to video digitization, we used the script provided in MATLAB for video stabilization using point feature matching (Lee et al., 2009; Litvin et al., 2003; Matsushita et al., 2005; Tordoff & Murray, 2002) to stabilize our video frames per recorded sequence. In our analysis, the recorded individuals were treated as point-mass models, with their body center of mass

(BCoM) approximated at the hip within each recording. To digitize the positions of the BCoM in each frame, we used the DLTdv7 application developed in MATLAB (Hedrick 2008). These positions were then filtered per sequence using a 4th order zero phase shift low-pass Butterworth filter with a cut-off frequency of 4 Hz (Yu et al., 1999). To establish real-world coordinates, we used the scaling factor calculated for each sequence, which corresponded to the relationship between the measured coordinates in the video and the corresponding distance obtained on the tree climbed by the bonobos using the infrared rangefinder. This provided us with the actual displacements in a x,y plan. This method of tracking the BCoM enabled us to describe the instant-to-instant linear displacement of the focal individual and to calculate the resulting velocity and acceleration (see the custom-made MATLAB script in the supplementary materials).

To analyze each sequence of movement, we delineated the postural and locomotor bouts of the focal individual that occurred in the immediate pre- and post-vertical climbing behaviour. These classifications were based on the standardized description of non-human primates' locomotor and postural modes as provided by Hunt et al. (1996). By analysing the postural and locomotor modes frame-by-frame, we accurately coded the start and end points of each postural and locomotor bout allowing us to segment the sequences based on the temporality of the postural and locomotor events. We used the tracked spatial coordinates of the focal individual (see above) to measure the average speed and peak of acceleration per locomotor mode.

The mechanical properties of the substrates were qualitatively scored based on the videos using a compliance grading system relative to the body mass of the bonobo crossing it. It is inspired from the weight bearing support angle provided in Thorpe et al. (2009) and estimated as follows: unbending referred to substrates where no movement of the substrate was detected as the bonobo moved across it, slight bending indicated a minimal detectable movement of the substrate, while high bending indicated a significant movement of the substrate. In the latter case, the body of the bonobo significantly moves with the substrate. It is worth noting that other quantitative methods have been proposed to measure the compliance of a substrate, but the difficulties associated to keep up following the focal group of bonobos, the distance to them (15 meters minimum) and the complexity of the surrounding forest environment on the ground (e.g., dense Marantaceae; see Figure 1A) did not allow us to setup more complex methods (Dunham et al., 2018; van Casteren et al., 2013). Substrate diameter was scored as follows: a small substrate was defined as one that could be encircled by the hand of the bonobo, whereas a large substrate was defined as one that the bonobo could not encircle with its hand.

Statistical analyses

First, we applied a paired permutation test to determine if bonobos maintain a more consistent speed of progression during climbing bouts compared to the transition from the preceding, or toward the subsequent, locomotor mode (if available). To do so, we measured the speed variation within the climbing bouts by calculating the coefficient of variation of the instantaneous speed. For the transition, we calculated the percentage difference between the average speed of the two locomotor modes (x_1 and x_2) considered as follows: $\frac{x_2 - x_1}{x_1} \times 100$.

Second, we used a chi-squared test to evaluate the association between branch compliance and diameter in the substrates reported. We also evaluated the association between the bouts of vertical ascent and vertical descent with the substrate properties. We applied analyses of variance (ANOVA) to investigate the influence of substrate compliance on the speed of progression and maximal acceleration. Specifically, we tested whether bonobos exhibit

reduced acceleration peaks when ascending and descending on compliant substrates compared to stiffer ones and whether the substrate compliance influences the speed of progression. We log-transformed the dependent variables to satisfy the assumption of the normal distribution (see the custom-made R script in the supplementary materials). We used *paired.perm.test*, *aov* and *chisq.test* functions and all the statistical procedures were performed using R (v.4.0.3, the R Foundation for Statistical Computing). The significance threshold was set at $P < 0.05$.

Ethical note

All research reported in this manuscript complied to the legal requirements of the Democratic Republic of Congo, conformed to Directive 2010/63/EU and the policy statements of the International Primatological Society (code of best practices for field primatology). The authors declare that they have no conflict of interest.

Results

We recorded a total of 46 climbing bouts including 12 occurrences of vertical ascent and 34 occurrences of vertical descent at a distance ranging from 18 to 36 meters. The average speed for vertical ascent is $0.4 \pm 0.3 \text{ m}\cdot\text{s}^{-1}$ (mean \pm SD), while the average speed for vertical descent is $0.8 \pm 0.4 \text{ m}\cdot\text{s}^{-1}$. The highest recorded average speed during vertical ascent is $1.2 \text{ m}\cdot\text{s}^{-1}$ over a distance of 4.3 m, achieved while climbing a small and slightly bending support. The highest recorded average speed during vertical descent is $2.3 \text{ m}\cdot\text{s}^{-1}$ over a distance of 3.7 m, achieved while moving on a large and stiff support. During their climbing behaviors, bonobos frequently stopped their movement (37% of climbing bouts), whether during ascent or descent, before resuming their climbing. The longest climbing bout observed without stopping covered 9.5 m and was performed at an average speed of $0.7 \text{ m}\cdot\text{s}^{-1}$ when descending on a thin substrate exhibiting a slight level of compliance. These pauses serve either to transition to another locomotor mode or to halt their movement before pursuing their climbing behavior. Out of the 46 recorded climbing events, the bonobos switched to another locomotor mode 5 times, while 21 times they transitioned into a postural mode. In the remaining 20 instances, the subsequent movement could not be recorded due to hindrance caused by dense vegetation on the ground. Among the 5 recorded locomotor bouts, 1 involved transitioning to a bipedal walk, 1 to a squat walk, 1 to a leap, and 2 to a bridge. Among the 21 recorded postural bouts, 15 involved the forelimb suspend mode (such as forelimb suspend/cling, sit/forelimb suspend and squat/forelimb suspend), 4 involved sitting, 1 involved sprawling, and 1 involved vertical clinging.

The result of the paired permutation test, comparing speed variation within climbing bouts and between consecutive locomotor modes, is not significant (47% and 42% differences, respectively; Paired permutation test=0.51, $P=0.68$). Note that one extreme value can be observed in the 'between locomotor mode' category (see Figure 2) which concerns the transition from a slow climbing bout ($0.2 \text{ m}\cdot\text{s}^{-1}$) to a bipedal walking bout ($0.6 \text{ m}\cdot\text{s}^{-1}$).

We found a significant association between the substrate properties, i.e., substrates of smaller diameter are more compliant, while larger substrates are stiffer ($\chi^2=35.01$, $df=2$, $P < 0.0001$). We found a significant correlation between the direction of the climbing bouts (i.e., ascent and descent) and the compliance of the substrate, but not with the size of the substrate ($\chi^2=6.57$, $df=2$, $P=0.037$; $\chi^2=1.86$, $df=1$, $P=0.17$, respectively; Figure 3). Vertical ascent was primarily performed on stiff substrates and substrates presenting high bending properties were avoided.

Instead, vertical descent was performed on all kinds of substrates with a trend toward substrates presenting slight bending properties, hence being also smaller in size.

There is a significant relationship between the speed of progression and the locomotor mode performed (ANOVA: F value = 37.17, $P < 0.0001$) including a significant interaction with the compliance and the size of the substrates (ANOVA: F value = 12.34, $P < 0.0001$; ANOVA: F value = 11.06, $P = 0.0018$, respectively; Figure 4A,B). Bonobos demonstrated faster speeds when descending during climbing activities, particularly on large and stiff substrates. Conversely, when ascending, they achieved higher speeds on small substrates that exhibit slight bending properties. We found a relationship between peak acceleration and locomotor mode, i.e., bonobos exhibited higher acceleration peaks when descending compared to ascending (ANOVA: F value = 11.28, $P = 0.0017$; Figure 4C,D). However, we did not observe a significant impact of the encountered substrate characteristics (i.e., compliance and diameter), on climbing peak acceleration.

Discussion

Bonobos demonstrate remarkable abilities in ascending and descending arboreal vertical supports. We estimated vertical ascent speeds around $0.4 \pm 0.3 \text{ m}\cdot\text{s}^{-1}$, with a maximum observed speed of $1.2 \text{ m}\cdot\text{s}^{-1}$, and vertical descent speeds around $0.76 \pm 0.4 \text{ m}\cdot\text{s}^{-1}$, with a maximum observed speed of $2.3 \text{ m}\cdot\text{s}^{-1}$. These results contrast with the previous study by Isler (2002) on bonobos in Apenheul Primate Park (Netherlands) where average climbing speeds of $1.17 \pm 0.45 \text{ m}\cdot\text{s}^{-1}$ for females and $0.68 \pm 0.33 \text{ m}\cdot\text{s}^{-1}$ for males during vertical ascent on ropes (4 to 7 meters long) were reported. The discrepancy found between our study and the one of Isler (2002) may stem from various factors, with experience being a notable one as well as substrate properties (as branches *versus* ropes; see below). In the zoo, bonobos are consistently exposed to a relatively restricted environment, leading to heightened familiarity with the encountered substrates. Conversely, free-ranging bonobos, while capable of displaying high-speed movements, including impressive pronograde leaps between flexible branches (Druelle et al., 2020), may tend to exercise more caution when crossing newly encountered substrates.

Minimizing energetic costs

In the present exploratory study, we investigated two hypotheses centered on potential strategies aimed at minimizing energetic costs by mitigating variations in external mechanical power during climbing. Specifically, we hypothesized that bonobos would maintain a steady speed of progression while climbing and minimize speed differentials between climbing and preceding, or subsequent, locomotor modes. We observed that bonobos could perform long, steady climbing bouts of up to 9.5 meters while descending, and 4.3 meters while ascending. Although the speed of progression presents some level of variation (with a coefficient of variation for instantaneous speed of 47%), the range of this variation remains small, providing evidence that bonobos attempt to maintain a steady speed during climbing (see Figure 3). In addition, our results indicated no significant differences in speed differentials between climbing and consecutive locomotor modes, aligning with our hypothesis (see also Aerts et al., 2023). The capacity to self-operate efficient and smooth transitions between locomotor modes might be a target of selection (e.g., Aerts et al., 2023; Biewener & Daley, 2007), and specifically when moving in complex environments. In addition, from a behavioral perspective, we observed that bonobos exhibit regular pauses during climbing bouts, often associated with the fact that they commonly follow each other on the same substrate. However, these pauses were not solely

linked to such interactions, as they were also observed without an obvious social context. These pauses predominantly involved suspensory postures which can be considered as economical postures to maintain given the shoulder adaptations of bonobos (Doran, 1992; Jungers & Susman, 1984). Rare instances of vertical clinging were also observed between two climbing bouts, it is a potentially more costly posture to maintain given the flexed forelimb (Preuschoft, 2004). Interestingly, Kozma and Pontzer (2021) suggested incorporating the postural cost of locomotion into the calculation of climbing's cost of transport, given its importance at slow speed, where the postural cost is likely a significant portion of the overall cost (see also Full & Tullis, 1990). This suggestion aimed to establish a stronger connection to the ecological and evolutionary framework because minimizing climbing postural cost, through higher velocity, could be an important factor for increasing ecological efficiency. While our data do not permit the direct calculation of the cost of transport in bonobos, our observations of free-ranging bonobos show a behavioral strategy that aligns with the notion of minimizing postural costs.

In addition, keeping a relatively constant speed when engaged in a specific locomotor mode and when transitioning between different locomotor modes could also be related to a stability target, i.e., to keep on moving steadily in the desired direction. For instance, in humans and lizards, a stable trajectory of the centre of mass has been shown to be the target during running on uneven terrains (e.g., Druelle et al., 2019; Ernst et al., 2014; Ferris et al., 1999; Kerdok et al., 2002; Müller et al., 2010). A similar trend could be in play during arboreal movements in bonobos when they climb and transition between different locomotor modes, thus increasing dynamic stability despite changes in the amplitude of limb movements. Increasing the stability of the path during climbing, through a limitation of overall speed variations coupled to regular pauses, might also help to reduce muscle fatigue.

In summary, climbing is inherently a costly behavior due to the effort required to move against gravity. Halsey et al. (2017) suggested that vertical climbing is an expensive strategy among great apes, hence arboreal apes should prioritize routes that minimize height changes to conserve energy. However, the results from the present study and previous research do not entirely support this hypothesis (e.g., Druelle et al., 2020; Pontzer & Wrangham, 2004; Susman et al., 1980). Stability might be an essential target of selection since increased stability could potentially reduce additional costs associated with difficult climbs and enhance safety. Comparing the climbing speed of bonobos (both captive and free-ranging) with that of humans reveals that bonobos climb much faster in any condition, with the mean velocity of human rock climbers always lower than $0.2 \text{ m}\cdot\text{s}^{-1}$ (see Kozma & Pontzer, 2021). Although humans are able to climb (Kraft et al., 2014) and can develop specific climbing abilities (Venkataraman et al., 2013), they do so at a much slower pace compared to non-human primates, incurring higher energetic costs and a greater risk of falling (Kozma & Pontzer, 2021). Although we caution that our "simplified" field protocol and our small sample size, as well as the presence of an outlier in the data warrant further investigation for validation, our results support the idea that bonobos increase climbing efficiency by adopting high velocities and employing low-cost resting postures, likely reducing muscle fatigue. These aspects could represent two important targets of selection to ensure ecological efficiency in bonobos. The morphological adaptations observed in their shoulders may be related to climbing velocity and minimizing postural costs (Doran, 1993).

Substrate compliance

We also investigated the influence of substrate properties on climbing behaviors. Our hypothesis was that climbing on thin and flexible substrates would present a greater challenge compared to stiff supports. In other words, stiffer substrates should be easier to climb until the hand and foot can properly encircle the support (e.g., Lammers et al., 2006). Bonobos exhibited higher speeds when descending on large and stiff substrates, with some individuals reaching speeds of up to $2.3 \text{ m}\cdot\text{s}^{-1}$ using a fire-pole slide submode (see Hunt et al., 1996; Susman et al., 1980). Conversely, during ascent, bonobos achieved higher speeds on thin substrates presenting slight bending properties (likely due to their smaller size). This finding supports a trade-off effect, given the relationship between substrate size and compliance in the arboreal environment. The capacity of bonobos to climb faster on slightly compliant substrates corresponds to substrates that they can completely encircle with the hand and foot, thus improving the effectiveness and security of their grip. If the compliance is too high, climbing speed decreases. On the other hand, stiff substrates are commonly larger in size in natural settings, making it difficult for bonobos to fully encircle them during ascent, thereby constraining their climbing speed. Hence substrate size and stiffness play crucial roles in the climbing performance of free-ranging bonobos. To date, no study has tested the influence of substrate compliance on the locomotor performance of hominoids. However, previous authors have suggested that climbing a thin vertical rope is at the extreme of the locomotor capabilities of adult male gorillas (Isler, 2002). It is possible that adult bonobos face similar constraints with large substrates when ascending. Results from studies on marmosets and squirrel monkeys walking quadrupedally on compliant substrates revealed that such challenging substrates had a less pronounced influence on gait parameters in squirrel monkeys compared to marmosets (Schapker et al., 2022; Young et al., 2016). This discrepancy may be related to the strength of their grasping capacities, as squirrel monkeys can apply more effective torques around the substrate compared to marmosets. In future studies, substrate compliance should be an essential factor to consider when investigating climbing and locomotion in primates.

The intrinsic nature of climbing behaviors

Arboreal locomotion is not a continuous scheme implying one locomotor mode that would be repeated for extended periods without interruption, and this is even reinforced in larger primates. Indeed, stop, turns, accelerations, alterations in coordination patterns, and changes in body posture appear to be the norm for effectively negotiating the arboreal environment, thus forming a continuum of movements rather than a combination of different modes (e.g., D'Août et al., 2004; Hunt et al., 1996; Susman et al., 1980; Thorpe & Crompton, 2006). In this context, climbing has been shown to be an essential locomotor capacity as it allows to commute between the canopy and the ground, and thus allows to acquire many sorts of food items. At first glance, vertical climbing might appear like a standardized behavior (but see the diversity of submodes described by Hunt et al., 1996), but previous studies have shown an important variability of the spatio-temporal parameters during the climbing sequence, as well as in kinematics in hominoids (Isler, 2002, 2005; Neufuss et al., 2018; Susman et al., 1980). This observation has led researchers to suggest that versatility, or gait flexibility, was more the norm than the exception in these species. Such a versatility is suggested for bonobos since the first studies about their locomotion (Horn, 1976; Susman et al., 1980) and this has been emphasized again in biomechanical studies focusing on specific locomotor modes (D'Août et al., 2004; Isler, 2002, 2005). Climbing is particularly costly in large animals ($>0.5 \text{ kg}$; Hanna & Schmitt, 2011) and the possibility to use the basic energy-saving mechanisms while walking and running on flat, continuous and rigid substrates (Alexander, 1991b; Cavagna et al., 1977) are unlikely to be applicable (Hanna & Schmitt, 2011). However, behavioral adjustments, such

as those observed in the present study, may offer ways to reduce muscular work and limit the overall costs. In the context of the explosive task of vertical climbing, adopting certain behavioral strategies, including climbing up at high velocity for short periods, taking regular pauses using an economic posture, and limiting acceleration and deceleration of the centre of mass during climbing bouts, could prove beneficial. Although spatio-temporal parameters and kinematics can be related to morphology in some respects, the domain in which natural selection occurs during locomotion may be more strongly related to other factors, such as energy conservation, balance control, path stability, and manoeuvrability (e.g., Aerts et al., 2000b; Arnold 1983; Reilly et al., 2007). The observed versatility in gaits among hominoids may represent contextual and instantaneous adjustments in response to the encountered substrate, aimed at ensuring better path stability and overall efficiency.

Limits and perspectives

Overall, our study shows that a simple field protocol as the one proposed here can bring valuable insights into the climbing abilities of free-ranging primates (see also Schmitt, 2011). Our findings shed light on the climbing strategies employed by bonobos and how substrate properties affect their climbing performance. However, further investigations with a larger sample size and more detailed substrate analyses are needed to enhance our understanding of the complex interplay between locomotor performance and habitat use in this species. Also, including ontogenetic variations would greatly enhance our understanding of how bonobos develop their locomotor performance over time (Doran, 1992). Studies as the one presented here contributes to a better understanding of the complex interplay between mechanical factors and ecology, thus contributing to the development of the mechanical ecology approach (Bauer et al., 2020). Note that given the opportunistic nature of our exploratory protocol, the distribution of substrates used does not reflect the full range of substrates utilized by bonobos. Furthermore, as previously reported by other studies (Doran, 1992; Susman et al., 1980), closely tracking bonobos on the ground proves to be exceptionally challenging due to the dense environment and their rapid progression on the ground. Given the good level of habituation (level 3 here, according to the definitions provided by Bertolani & Boesch, 2008) of the population studied here, we could readily observe their descent from the trees, but capturing their ascent from the ground to the canopy remained very difficult. Despite our efforts, we consistently arrived too late to witness their climbing from ground to canopy. This inherent limitation significantly restricts our ability to assess their capacity to climb up over longer distances. Although a full habituation (level 4) should allow to solve this challenge, security and sanitary risks of monitoring great apes must be considered when addressing this objective (Kühl, 2008). Integrating the primate's interaction with the environmental structure in biomechanical studies is promising for future research. Capturing the performance of free-ranging bonobos is a unique opportunity to understand the diversity of their capacities and to frame their locomotor versatility into a more accurate evolutionary context.

Data availability statement

The complete dataset from the current study is accessible through the following public link on CNRS My CoRe: <https://mycore.core-cloud.net/index.php/s/BqqnE5qtq7gPK2P>

If you encounter any issues when trying to access the dataset, please reach out to the study's corresponding author for assistance.

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Authors declare no competing interests.

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Figures

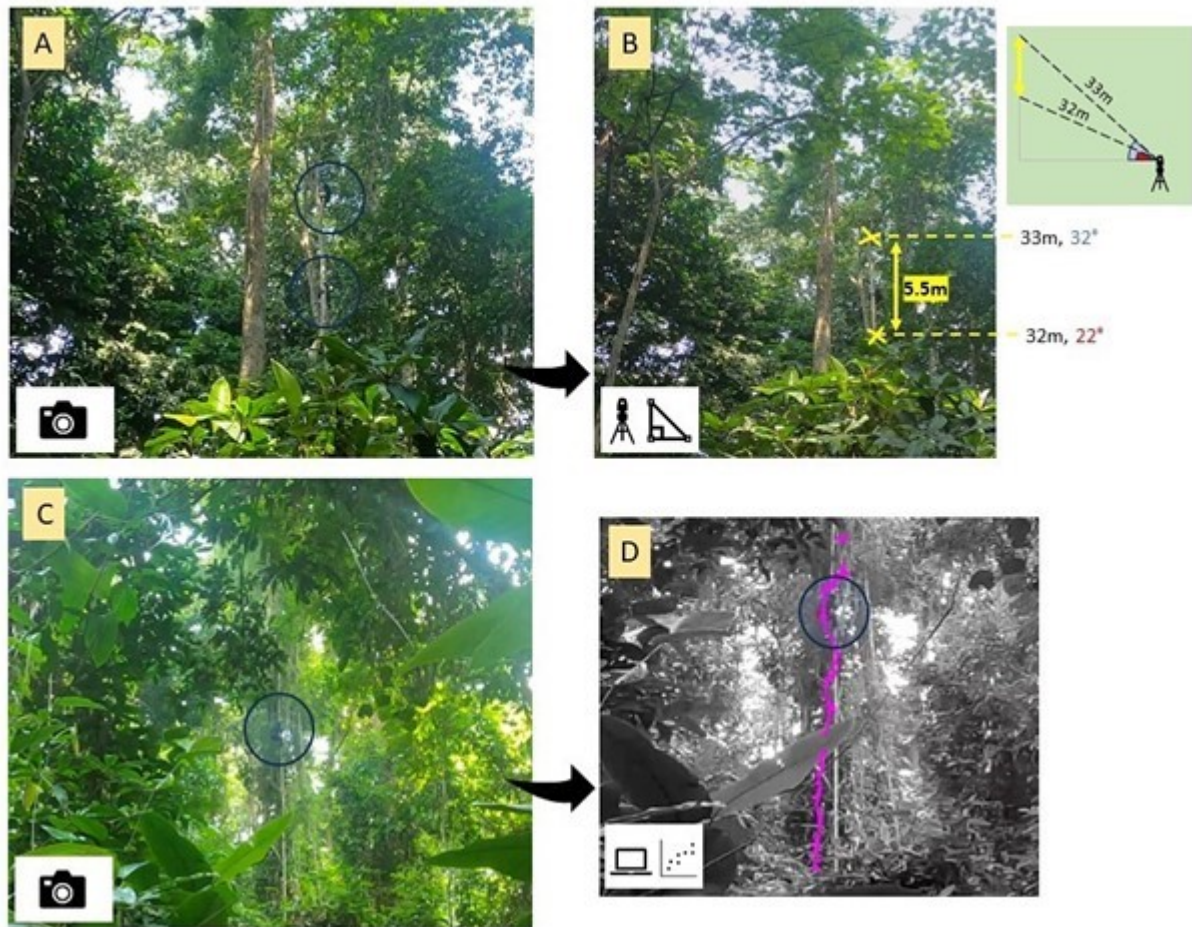


Figure 1. Workflow of the measurement protocol with two examples. (A) Recording of the climbing sequence in a large field of view. The two bonobo individuals (within the two circles) are moving on a large and stiff vertical substrate; (B) calibration of the sequence using the infrared rangefinder and trigonometric principles; (C) Recording of the climbing sequence in a large field of view. The targeted individual is moving on a small vertical substrate that presents slight bending properties; (D) Digitization of the hip joint during the recorded sequence. The video frames were stabilized before digitization and this process removes the color of the video.

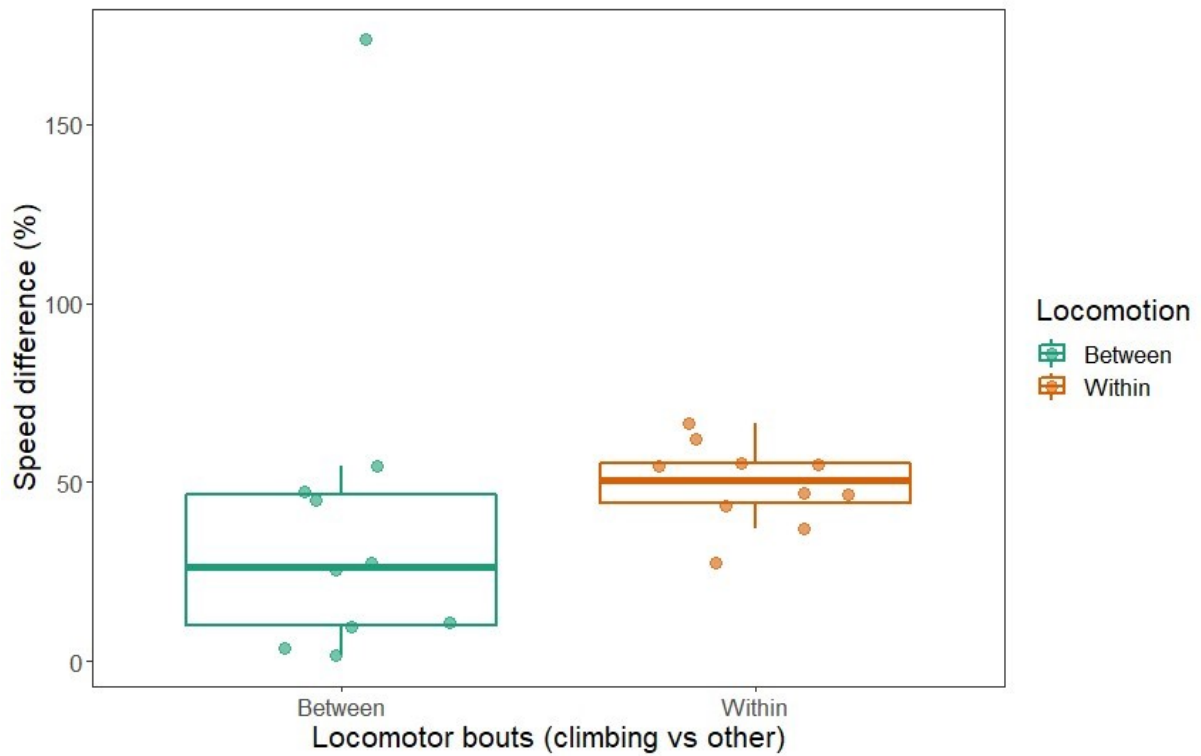


Figure 2. Speed differences between consecutive locomotor bouts including a climbing behavior (i.e., a locomotor mode toward a climbing bout, and a climbing bout toward another locomotor mode; calculated as the percentage difference between the average speed of the two locomotor modes considered) and within climbing bouts (coefficient of variation of the instantaneous speed).

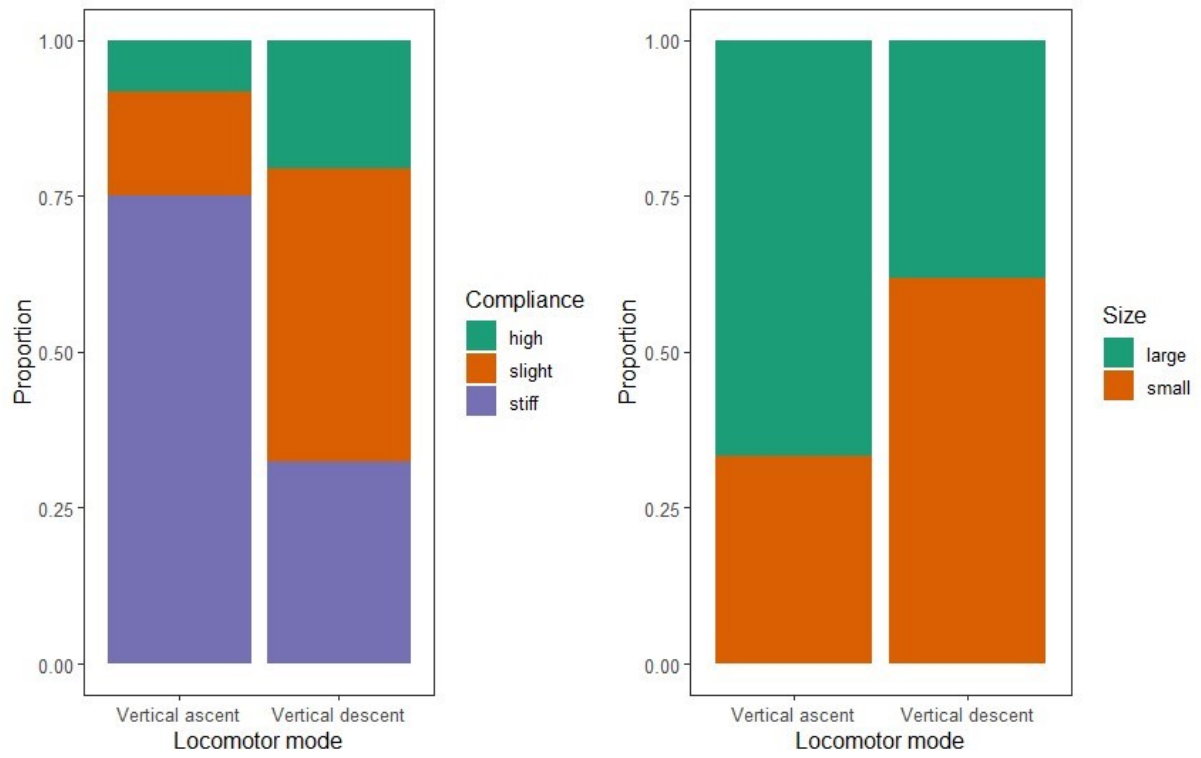


Figure 3. Distribution of the substrate properties observed among the climbing bouts recorded: vertical ascent, N=12; vertical descent N=34.

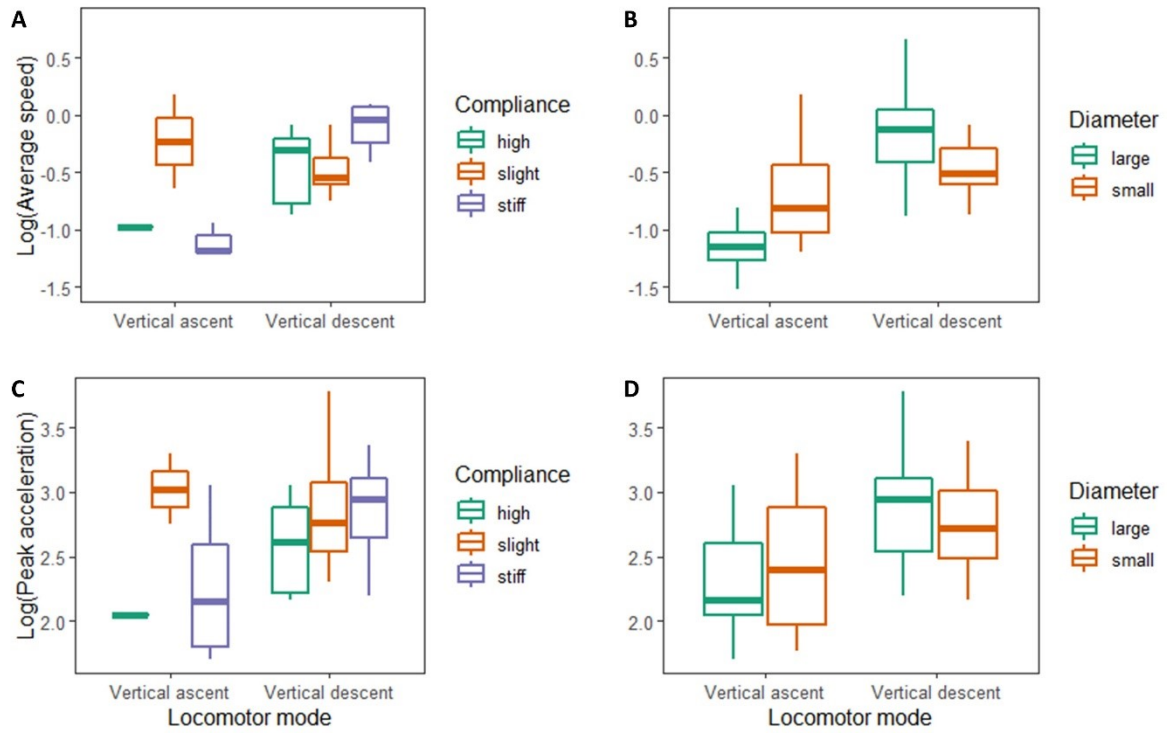


Figure 4. Speed differences during vertical ascents and descents across multiple vertical substrates presenting different properties: compliance (A) and size (B). Differences in peak acceleration during vertical ascents and descents across substrates presenting different properties: compliance (C) and size (D).