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International Journal of Primatology
The Official Journal of the International
Primatological Society

ISSN 0164-0291

Int J Primatol
DOI 10.1007/s10764-020-00140-z



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Impressive Arboreal Gap-Crossing Behaviors in Wild Bonobos, *Pan paniscus*

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Received: 6 September 2019 / Accepted: 31 January 2020 / Published online: 11 March 2020
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Abstract

Most primates are arboreal, and the current context of habitat fragmentation makes gap- and road-crossing behaviors more and more common. Great apes may try to avoid behaviors such as arboreal leaping because given their size such behaviors are risky. Here, we report impressive gap-crossing by wild bonobos (*Pan paniscus*) in the Democratic Republic of Congo, induced by human disturbance and habitat fragmentation. We quantify the basic mechanics of leaps and arboreal landing performance in two individuals. The bonobos climbed a tree, 15 m high, and performed pronograde leaps between thin flexible branches, to grasp landing branches *ca.* 4 m further and below their starting point. They reached an instantaneous velocity of about $9 \text{ m} \cdot \text{s}^{-1}$. The bonobos used pendular swinging of landing branches to dissipate the kinetic energy built up during falling, requiring a grip force of about $2.5 \times$ body weight. Moreover, our results show that bonobos might be able to modulate the drag experienced during falling (up to 20% of body weight) by adjusting their posture. Apparently, bonobos evaluate the structural context to perform the best possible leap and balance the risks against the extra energetic costs involved. Further study of locomotor performance is needed to inform conservation planning, owing to the extent of habitat fragmentation due to human activities.

Keywords Fieldwork · Habitat fragmentation · Hominoid · Leaping · Locomotion

Introduction

Many primates travel in trees, because a substantial amount of their food is located in the arboreal niche (Fleagle 2013; Hunt 2016). This habitat implies discontinuity, variability,

Handling Editor: Joanna M. Setchell

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10764-020-00140-z>) contains supplementary material, which is available to authorized users.

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compliance and instability of the substrates. Huge horizontal and vertical gaps are very common between trees. To negotiate such obstacles, primates can climb down to the ground, use tree-swaying behaviors, or leap (Channon *et al.* 2011; Demes *et al.* 1995; Thorpe *et al.* 2007). For instance, orangutans (*Pongo* spp.) practice cautious suspensory behaviors (Thorpe and Crompton 2006; Thorpe *et al.* 2007), while other species perform impressive leaping performances, such as gibbons (*Hylobates* spp., *Symphalangus syndactylus*) and bonobos (*Pan paniscus*; e.g. Fan *et al.* 2013; Fleagle 1976; Scholz *et al.* 2006; Susman *et al.* 1980). Gibbons can leap across gaps exceeding 10 m horizontally when traveling through the forest canopy (Channon *et al.* 2011; Fleagle 1976). Bonobos can also perform impressive jumps in the canopy and from the ground (Scholz *et al.* 2006; Susman *et al.* 1980). Bonobos are the closest living relatives to humans, but their skills greatly exceed human maximal performance. For instance, bonobos can easily perform squat vertical jumps of 0.7 m, while human Parkour practitioners and top-level athletes do not exceed 0.5 m (Grosprêtre and Lepers 2016; Scholz *et al.* 2006).

The various ways of dealing with the arboreal environment obviously require different amounts of energy and the selection of one way over others could be related to energy-saving strategies (Halsey *et al.* 2015; Thorpe *et al.* 2007). The stiffness of the branches, the distance to cross, the number of tree-sways to perform, and the mass of the individuals are all important factors in gap-crossing strategies (Halsey *et al.* 2015). Nevertheless, although large primates could save energy by leaping or using tree-swaying, the risk of injury can override the opportunity to save energy (Halsey *et al.* 2015; Pontzer and Wrangham 2004) and mechanical constraints related to the flexibility of the branches can also limit the locomotor performance, for example (e.g., by reducing power at take-off for leaping; Channon *et al.* 2011). In this context, it is commonly suggested that large primates should avoid the most dangerous locomotor behaviors, such as arboreal leaping (Fleagle and Mittermeier 1980; Halsey *et al.* 2015), unless the benefits outweigh the risks, for example, if they need to escape from a conspecific or predator, or to access a particularly rich food site.

Here, we report impressive gap-crossing behaviors in wild bonobos (average body mass is 38 kg in females and 42 kg in males according to Druelle *et al.* 2018) performing a *pronograde leap* with an extended period of free fall (see Hunt *et al.* 1996). Using basic mechanics, we quantify the pronograde leap and arboreal landing performance and suggest potential capacities to modulate “falling.”

Methods

Study Site

We conducted field observations while following the bonobos in the Manzano community (24 individuals under habituation at that time), Bolobo Territory, Democratic Republic of Congo (Narat *et al.* 2015). This long-term study site is characterized by a fragmented habitat and a forest–savanna mosaic (Pennec *et al.* 2016). A community-based conservation project led by the Congolese NGO Mbou-Mon-Tour started in the area in 2001. There is large spatial overlap between the bonobo’s home range and areas used by humans (Pennec *et al.* *unpubl. data*).

Data Collection

We present the behavior of two bonobo individuals observed at 08:30–09:30 h on March 14, 2013 in fragmented habitat. A group of bonobos were traveling on the ground. The first 12 members of the group crossed a dirt road by quadrupedal running and fast walking. A man then passed by on a bicycle, and the rest of the group (five members) climbed a tree (an energetically demanding locomotor mode) and crossed an impressive horizontal and vertical gap above the track by means of a pronograde leap between flexible branches (Fig. 1). We estimated the take-off height as 15 m. Furthermore, highly flexible branches obviously impede pushing off in a horizontal direction because maximizing power at take-off would create large branch deflection. Thin branches also impede fast running up.

We video recorded the leap made by three individuals (see Electronic Supplementary Material [ESM]) using a handheld digital camcorder (Canon EOS 600D + objective Canon EF 70-300, frame rates: 25 fps) at about 80 m distance. We recorded two of the leaps with the camera fixed and positioned perpendicular to the plane of the leap, making these sequences useful for further analyses. The first leap is performed by a young adult female (ESM Id1) and the second is performed by another adult female carrying an infant ventrally (ESM Id2). The mass of an average female adult is estimated at 38 kg, and the mass of an infant (≈ 1 year old) is *ca.* 5 kg (Druelle *et al.* 2018).

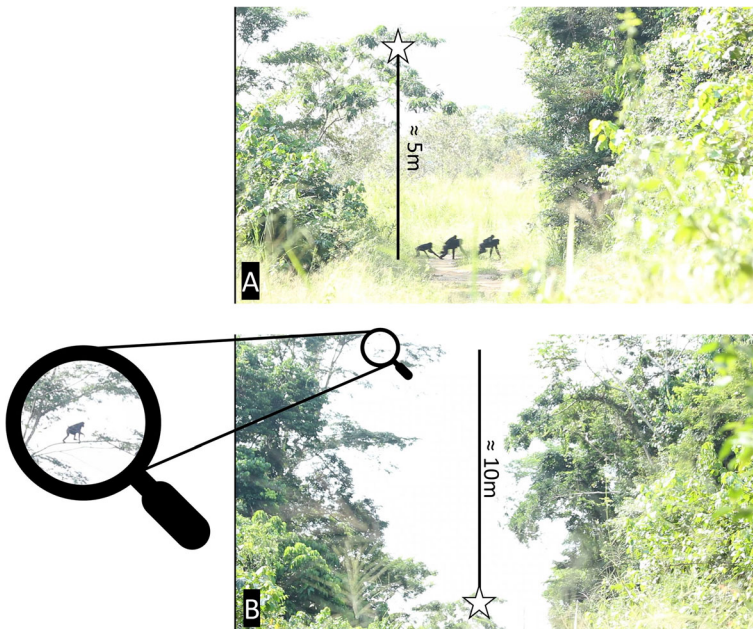


Fig. 1. Context of the pronograde leap observed in bonobos in DR Congo. **(A)** The first part of the group crosses the track on the ground. After the passage of a man on the track, **(B)** the second part of the group climbs up the tree and leaps between flexible branches from the left side to the right. The height of the take-off on the flexible branches has been estimated to be at 15 m above the ground. The stars indicate the same position in both pictures.

Spatial Calibration of the Recordings

To quantify the performance, we calibrated the video frames in the plane of the leap. We used the path of the body center of mass (BCoM) of Id1 as there is first a brief upwards, then a downwards movement in the free flight part (no contact with the branches) and the vertical velocity equals zero at the apex of the path. We argue that air resistance can be neglected during the first 0.4 s (i.e., 10 recording frames) of the subsequent free fall (see explanations in the [ESM1](#)). This means that the initial vertical accelerating displacement is only governed by gravity. As a result, the vertical BCoM displacement ($Z_{(t)}$) in video coordinates during these first 0.4 s should fit a quadratic equation:

$$Z_{(t)} = at^2 + bt + c$$

where $2a = a$ monotonous acceleration (video-coordinates/s²; equivalent to gravitational acceleration), $b = 0$ because of the zero vertical speed at the apex, and $c =$ the fitted apex position (in video-coordinates). The spatial scaling factor (SSF) for the sequence of Id1 can thus be determined as the following ratio:

$$\text{SSF} = \frac{-9.81}{2a}$$

We approximated the BCoM of Id1 in the recordings as the center of the trunk and digitized it frame by frame (Geogebra 5.0). The premised fit (using SigmaPlot 11) described the displacement over the 0.4-s interval very well ($R^2 > 0.99$), resulting in a highly reliable scaling factor (based on all available data points in the 0.4-s interval) which we used to convert the video data to real-world coordinates. We could not use the same procedure for the Id2-sequence, because the zoom was different and the free fall started with an unknown initial downward speed ($b \neq 0$). Therefore, we used two nonmoving points on the trees to transfer the calibration factor from Id1's sequence to that for Id2.

Leaping Performance

We digitized the positions of BCoM for both sequences throughout the pronograde leap, including the arboreal landing phase, and scaled this to the actual positions (displacements) as described in the previous section. We fitted the BCoM displacement in horizontal and vertical directions to quadratic equations (*cf.* the spatial calibration procedure). We did this for the aerial falling phases when the bonobos had no contact with the trees and the arboreal landing phases, separately. For Id1 the aerial phase started after the calibration period, i.e., when downwards speed exceeds $-3.9 \text{ m} \cdot \text{s}^{-1}$ (*cf.* [ESM1](#)). For Id2 the aerial phase started at a similar downward speed. The first derivatives of these equations provide the instantaneous velocities and we used these to calculate the speed at landing (first branch contact). The second derivatives of these equations (single number = $2a$) represent the mean accelerations of the individual during the phases considered. These accelerations can be used in the equations of motion to determine the mean air resistance on the body and the mean "branch reaction

force” during the landing phase, which is equivalent to the grasping force of the animals onto the branches.

In the vertical direction these equations are:

$$\text{Aerial phase: } ma_V = mg + F_{resV}$$

$$\text{Arboreal landing phase: } ma_V = mg + F_{resV} + F_{brV}$$

In the horizontal direction:

$$\text{Aerial phase: } ma_H = F_{resH}$$

$$\text{Arboreal landing phase: } ma_H = F_{resH} + F_{brH}$$

with m = body mass, $a_{V,H}$ = observed vertical/horizontal acceleration, $F_{resV,H}$ = mean air resistance force, and $F_{brV,H}$ = mean “branch reaction force”. Knowing the respective accelerations, we can calculate F_{res} from the aerial phase. Introducing this in the equation of motion for the arboreal landing phase provides F_{br} .

Ethical Note

All research reported in this manuscript adhered to the legal requirements of the Democratic Republic of Congo and conformed to Directive 2010/63/EU. The authors declare that they have no conflict of interest.

Data Availability Datasets supporting the present work are available from the corresponding author upon request.

Results

Negotiating Take-off on Flexible Branches

We estimated the height difference between the take-off and the landing site as 4.3 m for Id1 and 3.8 m for Id2, and the horizontal distance to cross as 3.6 m for Id1 and 4 m for Id2. Therefore, the absolute diagonal distance to cross between the flexible branches was 5.6 m for Id1 and 5.5 m for Id2. We observed that bonobos tried to minimise the deflection of the branches before initiating take-off. Id1 grabbed branches above her with one arm, while Id2 walked slowly on the flexible branches, then took a step back and adopted a static crouched posture. The potential waste of energy in deforming the compliant support seems to be limited in both individuals, and there is no visual recoil of the branches before the contact is lost. Furthermore, the angle of take-off can be visually estimated to be *ca.* 5° from the horizontal, suggesting that the leaping force is oriented mainly along the long axis of the branches.

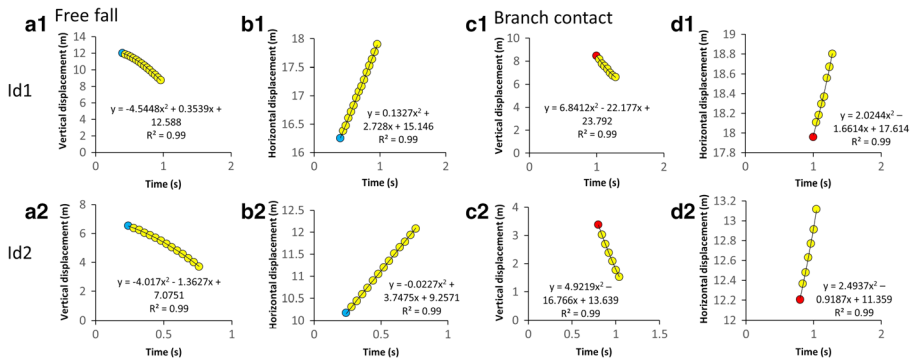


Fig. 2. Instantaneous displacement during the pronograde leap of Id1 and Id2. The graphs represent the freefall period for the vertical (a) and horizontal displacements (b) and the landing period with the flexible branches for the vertical (c) and horizontal displacements (d), including the respective quadratic equation of the fitted regressions. The blue dot indicates the initiation of the freefall including air resistance. The red dot corresponds to the contact with the flexible branches.

Falling Speed and Acceleration

The average downwards acceleration is $9.09 \text{ m} \cdot \text{s}^{-2}$ in Id1 and $8.03 \text{ m} \cdot \text{s}^{-2}$ in Id2 (Fig. 2). This means that air resistance plays a significant role in these leaping behaviors: 27.4 N in Id1 and 76.4 N in Id2 (estimated from the quadratic equations in Fig. 2). Horizontal acceleration is negligible (very close to zero).

Landing on Flexible Branches

We estimated the instantaneous velocity when the bonobos reached the flexible branches of the landing site at $8.89 \text{ m} \cdot \text{s}^{-1}$ for Id1 and $8.34 \text{ m} \cdot \text{s}^{-1}$ for Id2. The related kinetic energies are high ($39.5 \text{ J} \cdot \text{kg}^{-1}$ for Id1 and $34.78 \text{ J} \cdot \text{kg}^{-1}$ for Id2). These energies need to be dissipated during the landing phase and the grasping forces needed largely depend on the overall deceleration during landing. We estimated the mean downwards deceleration during branch contact as $13.68 \text{ m} \cdot \text{s}^{-2}$ in Id1 and $9.84 \text{ m} \cdot \text{s}^{-2}$ in Id2, and the forward acceleration as $4.05 \text{ m} \cdot \text{s}^{-2}$ in Id1 and $4.99 \text{ m} \cdot \text{s}^{-2}$ in Id2. This horizontal acceleration is due to kinetic energy transfer related to the bending of the flexible branches that act as a natural pendulum. In other words, the branch reaction force pulls upwards and forwards because of the pendular swing transfer. The total branch reaction force must be “countered” by grasping. We estimated the total mass-specific grasping force exerted on the branches ($F_{br} \cdot \text{m}^{-1}$) at $26.56 \text{ N} \cdot \text{kg}^{-1}$ for Id1 and $22.91 \text{ N} \cdot \text{kg}^{-1}$ for Id2, equivalent to about 2.5 times body weight. This is high but feasible. Although we observed some differences between the two individuals, both appear to manage the deflection of the branches perfectly.

Discussion

We quantify leaping basic mechanics in free-ranging bonobos in the context of forest fragmentation and route decision. First, the bonobos climbed from the ground, which

already requiring work of approximately 6 kJ ($\text{mass} \times \text{gravity} \times \text{height}$) for Id1 and >7 KJ for Id2 (estimating infant mass as >5 kg). Second, we did not observe pumping behaviors; hence the propulsive forces of branch recoil were not used (Demes *et al.* 1995; Fleagle 1976). The minimization of branch deflection has also been experimentally tested and observed in gibbons (Channon *et al.* 2011), suggesting no use of the energy storage capability of the flexible substrate at take-off. Third, the difference in F_{res} for the two similar individuals suggest that the bonobos use postural strategies to influence their surface area during the pronograde leap, therefore controlling their momentum to some extent, as observed in lemurs (see also Dunbar 1988). The fact that Id2 was carrying an infant may be related to important postural modulation, resulting in lower total acceleration and a lower velocity at landing. Arboreal locomotion is inherently energetically demanding and risky (Halsey *et al.* 2015; Pontzer and Wrangham 2004; Thorpe *et al.* 2007), but our study suggests that the perception of danger (e.g., road \times human presence) is a fundamental factor in whether to move on the ground or in the trees. The bonobos studied could correctly evaluate the situation to perform optimal leaps (see Fig. 3 for an overview of the road-crossing context; [ESM Context](#)). Crossing a considerable horizontal distance as such when the forward propulsive capacities are limited (running up and pushing of thin flexible branches are limited) requires climbing higher. The question remains whether they are able to perform such optimal leaps in every situation encountered.

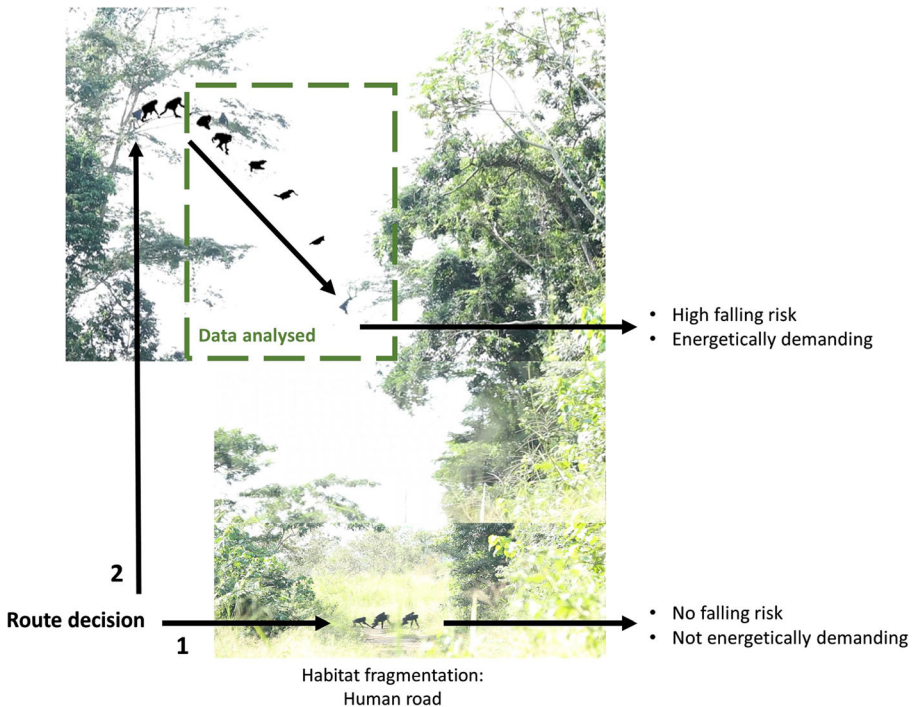


Fig. 3. Reconstruction (using three pictures) of the road-crossing context studied in free-ranging bonobos. This includes both routes, i.e., moving on the ground (1) and using pronograde leap between flexible branches (2). The illustration framed with the green dashed line shows six different frames of an adult female carrying an infant ventrally (Id2) performing the leap.

Bonobos regularly use leaping behaviors in their positional repertoire (Doran 1992) and do so more frequently than chimpanzees (*Pan troglodytes*: Doran 1992, 1993). Some morphological features may be related to bonobos' enhanced leaping capacities when compared to those of chimpanzees. For instance, their slightly smaller size, their elongated trunk, their smaller girth, and the subtle differences toward longer leg may improve leaping performance (Coolidge and Shea 1982; Druelle et al. 2018; Shea 1984; Zihlman and Cramer 1978). However, studies comparing the morphology of bonobos and chimpanzees are generally limited by small sample sizes and the extent of any differences remains unclear (see Druelle et al. 2018 for an overview), making a straightforward interpretation of leaping adaptation in bonobo difficult.

Bonobos are the heaviest primate for which such impressive leaping behaviors have been reported. Other, lighter, primates perform remarkable leaps in the trees (Table 1). Although the leaping performance of primates has been studied in controlled captive environments (e.g., Channon et al. 2010; Channon et al. 2011; Demes et al. 1999; Demes et al. 1995), it is difficult to evaluate the maximum locomotor performance of these species in these contexts. Reports from field studies allow us to assess the maximum locomotor performance of primates in their natural habitat. However, given the infrequent nature of these behaviors (primates do not use their maximum performance every day) and the difficulty of measuring the distances animals cover in the trees (commonly estimated by eye; Table 1), any information of this kind is very valuable for our understanding of primate locomotor evolution. Methods based on basic mechanics, such as those we use, can help to assess the distances and the locomotor performance of primates in the wild.

While the recorded behaviors involved adults, a young bonobo spent 30 min on the flexible branches before leaping (we did not video-record this leap). The young bonobo missed the landing branches and fell to the ground. We noticed no obvious injury as a result of the fall. However, in gibbons, infant deaths have been reported in the context of gap-crossing behaviors (Das et al. 2009). Furthermore, a fall such as the one we observed in the juvenile bonobo could be fatal for an adult because of the larger impact forces. Hence, successful gap-crossing behaviors are more important to adults than to juveniles. This behavior presumably requires both learning and morphological maturation to be effective, because of the work and control of momentum required. Adult bonobos may be able to modulate their fall by changing their posture, while the young individuals still need to learn to do this, as in orangutans (Chappell et al. 2015).

Beyond the interest of these observations for biological (anatomy-functional) studies (e.g., Doran 1993; Druelle et al. 2018; O'Neill et al. 2017; Scholz et al. 2006), the locomotor performances of wild primates are of interest because of the importance of habitat fragmentation due to human activities. The current fragmentation of primate habitats is likely to increase gap-crossing and associated risky behaviors (Junker et al. 2012), and a better understanding of how primates cope with habitat fragmentation is a fundamental topic of research for conservation purposes. Beyond the loss of habitat connectivity, forest fragmentation may increase the risk of falling because attempts to cross gaps can fail. Natural canopy bridges are effective to decrease the consequences of habitat fragmentation (Das et al. 2009). Depending on the sociocultural context and the species targeted, it is also possible to associate artificial rope bridges with natural canopy bridges, for example in neotropical primates living in periurban areas (Lindshield 2016). To

Table 1 Examples of maximum leaping distances recorded in primates

Species	Leaping distance (m)	Type of measure ^a	Mean body mass (kg) ^b	Context	Method	Study
<i>Semnopithecus priam</i>	19.8	Linear	16.8	On a transmission tower	Estimated from tower height	Anecdotic report in <i>National Geographic</i> ^c
<i>S. entellus</i>	12.2	Linear	14.3	Natural environment	Visual estimation	Ripley (1967)
<i>Macaca fuscata</i>	4	Horizontal	11	Natural environment	Visual estimation	Chatani (2003)
<i>M. fascicularis</i>	6	Gap crossed ^d	5.4	Natural environment	Visual estimation	Cannon and Leighton (1994)
<i>Colobus guereza</i>	10	Linear	9.53	Natural environment	Visual estimation	Mittermeier and Fleagle (1976)
<i>Colobus guereza</i>	15	Vertical	9.53	Natural environment	Visual estimation	Mittermeier and Fleagle (1976)
<i>Ateles geoffroyi</i>	10	Linear	7.8	Natural environment	Visual estimation	Mittermeier and Fleagle (1976)
<i>Cebus capucinus</i>	2.95	Horizontal	3.7	Natural environment	Visual estimation based on body lengths	Gebo (1992)
<i>Alouatta palliata</i>	2.69	Horizontal	7.2	Natural environment	Visual estimation based on body lengths	Gebo (1992)
<i>Propithecus diadema</i>	7	Linear	6.05	Natural environment	Visual estimation	Blanchard (2007)
<i>Nomascus leucogenys</i>	4	Horizontal	5.8	Captivity	Personal observation	Channon, Crompton, Günther, D'Aout, and Vereecke (2010)
<i>Symphalangus syndactylus</i>	20	Vertical	11.9	Natural environment	Visual estimation	Fleagle (1976)
<i>S. syndactylus</i>	10	Horizontal	11.9	Natural environment	Visual estimation	Fleagle (1976)
<i>Hylobates lar</i>	5.2	Linear	5.9	Captivity	Measured (laser)	Channon, Usherwood <i>et al.</i> (2011)
<i>Pan paniscus</i>	5.6	Linear	45	Natural environment	Free fall method	This study
<i>P. paniscus</i>	10	Linear	45	Natural environment	Visual estimation	Susman <i>et al.</i> (1980)
<i>P. paniscus</i>	8	Horizontal	45	Natural environment	Visual estimation	Susman <i>et al.</i> (1980)

^a Distances are estimated horizontally, vertically (drop), or linearly (i.e., the absolute linear distance), between the take-off and the landing site.

^b Values are given for males and are from Fleagle (2013).

^c <https://www.nationalgeographic.com/animals/2018/08/langur-monkey-jump-tower-india-news/>

^d Estimate of the length of the gap crossed by the animal.

reach this objective, it is critical to raise awareness in local people and stakeholders, for example, to encourage the maintenance of natural canopy bridges near agricultural fields or along logging roads. A better understanding of the locomotor performance of young and adult individuals should be included and considered in conservation strategies, to limit risky behaviors and their consequences in fragmented habitats.

Acknowledgments We thank Mbou-Mon-Tour staff and especially our field assistants Osa Otsiu Epany and Mozungo Ngofuna. We thank French NGO Bonobo ECO and the Eco-anthropology unit of the CNRS for financial support. We thank the two referees for their constructive and detailed comments on the first version of the manuscript. We are very grateful to the editor-in-chief of the *International Journal of Primatology*, Joanna M. Setchell, who revised the manuscript and improved the English.

Author Contributions VN conceived the initial part of the study and the methodology; VN and JCBN acquired funding and conducted fieldwork; FD and PA analyzed the data; and FD wrote the original draft. PA and VN reviewed the manuscript and JCBN provided editorial advice.

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