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Impressive arboreal gap-crossing behaviours in wild bonobos, *Pan paniscus*

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Abstract:	<p>Most primates are arboreal, and the current context of habitat fragmentation makes gap- and road-crossing behaviours more and more common. Great apes may try to avoid behaviours such as arboreal leaping because such behaviours are risky given their size. Here, we report impressive gap-crossing by wild bonobos, <i>Pan paniscus</i>, 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 2 individuals. The bonobos climbed a tree, 15 m high, and performed pronograde leaps between thin flexible branches, to grasp landing branches approximately 4 m further and below their starting point. They reached an instantaneous velocity of about 9 m.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 2.5x 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, due to the extent of habitat fragmentation due to human activities.</p>	

Title: Impressive arboreal gap-crossing behaviours in wild bonobos, *Pan paniscus*

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ABSTRACT

Most primates are arboreal, and the current context of habitat fragmentation makes gap- and road-crossing behaviours more and more common. Great apes may try to avoid behaviours such as arboreal leaping because such behaviours are risky given their size. 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 2 individuals. The bonobos climbed a tree, 15 m high, and performed pronograde leaps between thin flexible branches, to grasp landing branches approximately 4 m further and below their starting point. They reached an instantaneous velocity of about 9 m.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 2.5x 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, due to the extent of habitat fragmentation due to human activities.

KEY WORDS: Fieldwork, Hominoid, Leaping, Locomotion, Habitat fragmentation

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, 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 behaviours, or leap (Channon et al. 2011a; Demes et al. 1995; Thorpe et al. 2007). For instance, orangutans (*Pongo* spp.) practice cautious suspensory behaviours (Thorpe and Crompton 2006; Thorpe et al. 2007), while other species perform impressive leaping performances, such as gibbons (*Hyllobates* 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 travelling through the forest canopy (Channon et al. 2011b; 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. 2011a). In this context, it is commonly suggested that large primates should avoid the most dangerous locomotor behaviours, 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 behaviours in wild bonobos (average body mass is 38kg in females and 42kg 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

Ethical note

All research reported in this manuscript adhered to the legal requirements of the Democratic Republic of Congo and is conformed to the Directive 2010/63/EU.

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. under review).

Data collection

We present the behaviour of 2 bonobo individuals observed 08:30-09:30 on 14 March 2013 in fragmented habitat. A group of bonobos were travelling 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 (5 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 (Figure 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 supplementary material) 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 (Id1) and the second is performed by another adult female carrying an infant ventrally (Id2). The mass of an average female adult is estimated at 38 kg, and the mass of an infant (≈ 1 year old) is about 5 kg (Druelle et al. 2018).

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 centre 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 supplementary material). 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:

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

We approximated the BCoM of Id1 in the recordings as the centre 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 0.4s 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 non-moving 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 m/s. 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 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 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} .

RESULTS

(a) 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 about 5° from the horizontal, suggesting that the leaping force is mainly oriented along the long axis of the branches.

(b) Falling speed and acceleration

The average downwards acceleration is 9.09 m.s⁻² in Id1 and 8.03 m.s⁻² in Id2 (Figure 2). This means that air resistance plays a significant role in these leaping behaviours: 27.4 N in Id1 and 76.4 N in Id2 (estimated from the quadratic equations in Figure 2). Horizontal acceleration is negligible (very close to zero).

(c) 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}/m) 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 (mass x gravity x height) for Id1 and >7 kJ for Id2 (estimating infant mass as >5 kg). Second, we did not observe pumping behaviours, 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. 2011a), 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 x 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 Figure 3 for an overview of the road-crossing 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.

Bonobos regularly use leaping behaviours in their positional repertoire (Doran 1992) and do so more frequently than chimpanzees (*Pan troglodytes*; Doran 1992; Doran 1993). Some morphological features may be related to bonobo's enhanced leaping capacities when compared to 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 behaviours 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. 2011b; 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 behaviours (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, like those we use, can help to assess the distances and the locomotor performance of primates in the wild.

Table 1. Examples of maximum leaping distances recorded in primates

Species	Leaping distance (m)	Type of measure ¹	Mean body mass (kg) ²	Context	Method	Study
<i>Semnopithecus priam</i>	19.8	Linear	16.8	On a transmission tower	Estimated from tower height	Anecdotic report in National Geographic ³
<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 ⁴	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 et al. 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 et al. 2011b
<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 et al. 1980
<i>P. paniscus</i>	8	Horizontal	45	Natural environment	Visual estimation	Susman et al. 1980

¹Distances are estimated horizontally, vertically (drop), or linearly (i.e. the absolute linear distance), between the take-off and the landing site

²Values are given for males and are from Fleagle (2013)

³<https://www.nationalgeographic.com/animals/2018/08/langur-monkey-jump-tower-india-news/>

⁴Estimate of the length of the gap crossed by the animal

While the recorded behaviours involved adults, a young bonobo spent 30 mins 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 behaviours (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 behaviours is more important to adults than to juveniles. This behaviour presumably requires both learning and morphological maturation to be effective, due

to 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 (anatomo-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 behaviours (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 socio-cultural 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 peri-urban areas (Lindshield 2016). To 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 behaviours and their consequences in fragmented habitats.

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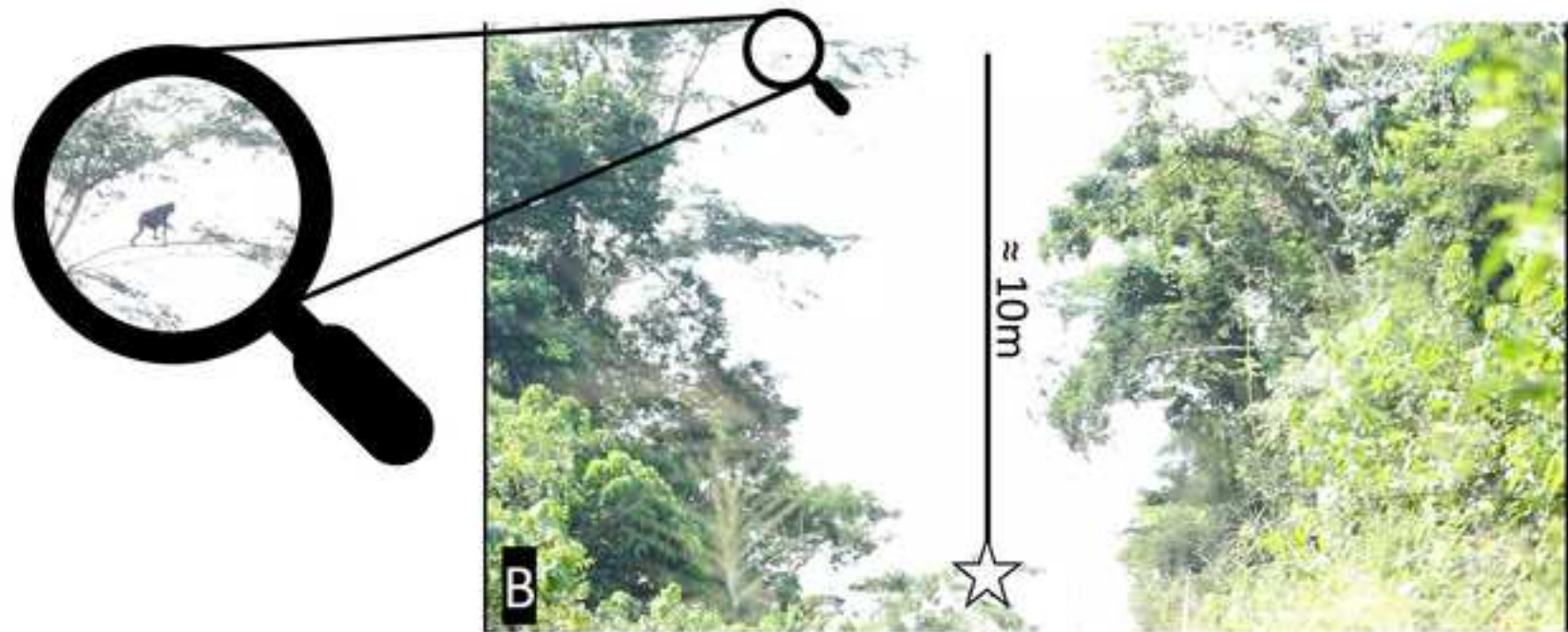
FIGURE LEGENDS

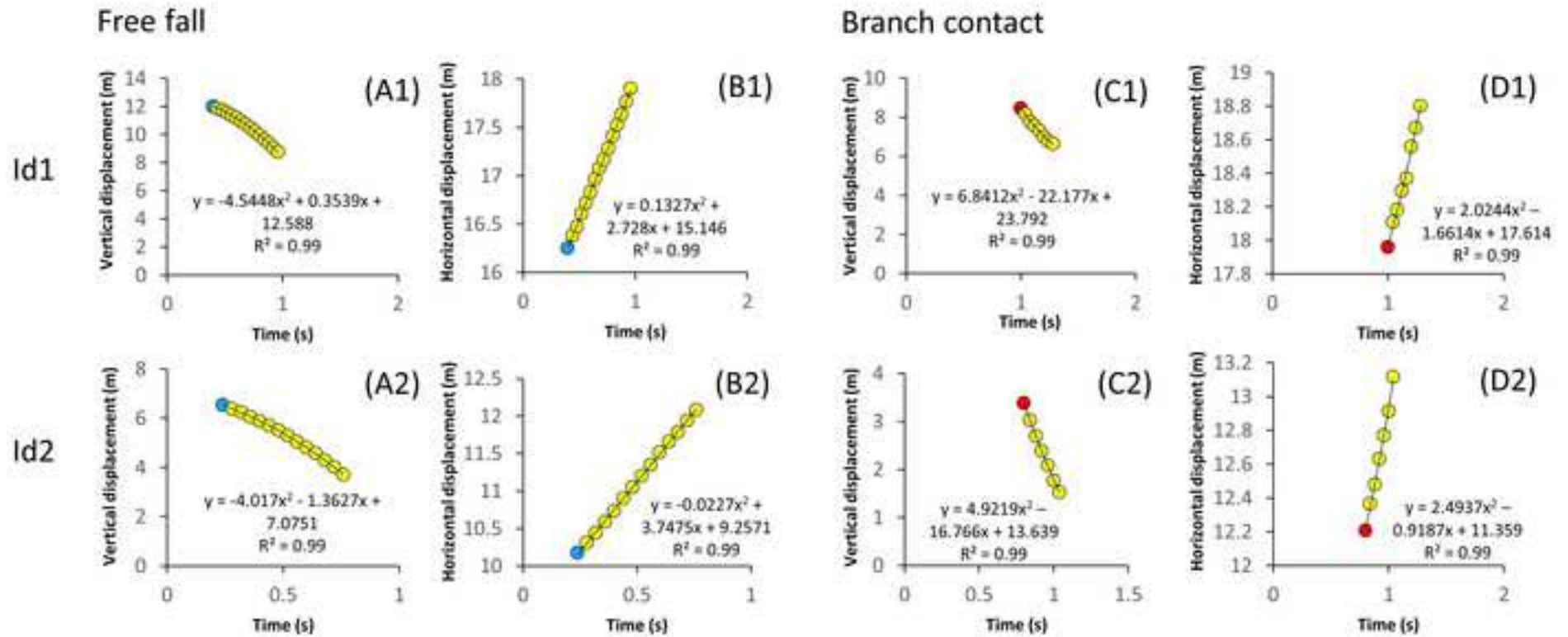
Figure 1. Context of the pronograde leap observed in bonobos in DR Congo. (A) The first part of the group crosses the track on the ground. After the passage of a man on the track, (B) the second part of the group climbs up the tree and leaps between flexible branches from the left side to the right.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

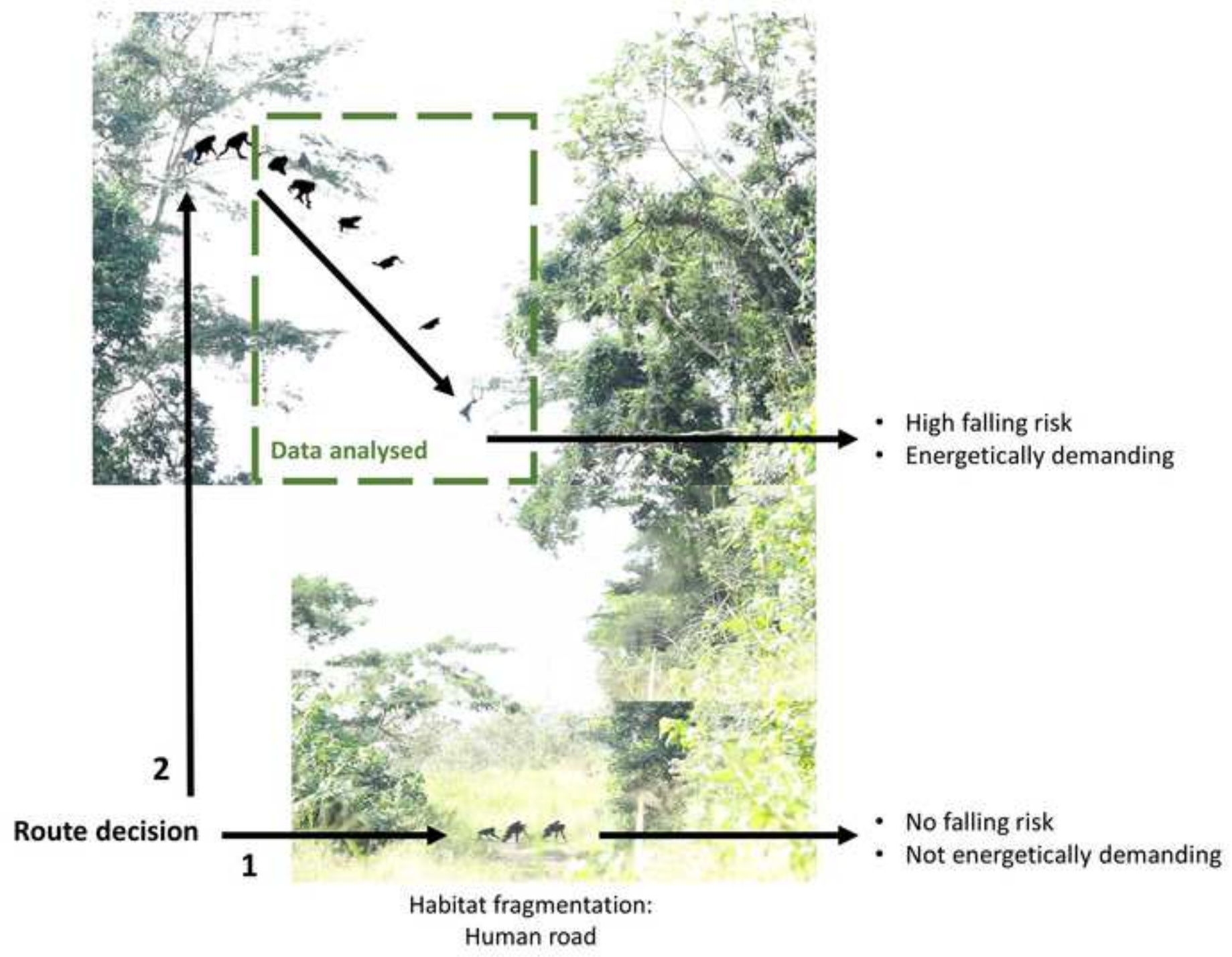
Figure 2. Instantaneous displacement during the pronograde leap of Id1 and Id2. The graphs represent the freefall period for the vertical (A) and horizontal displacements (B) and the landing period with the

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.

Figure 3. Reconstruction (using 3 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 8 different frames of an adult female carrying an infant ventrally (Id2) performing the leap.









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