

RESEARCH ARTICLE

Protocol to record and analyze primate leaping in three-dimensional in the wild

Judith Janisch¹  | Jack Kirven^{1,2} | Nicole Schapker^{1,3}  | Lydia C. Myers⁴ | Liza J. Shapiro⁴ | Jesse W. Young¹

¹Department of Anatomy and Neurobiology, Northeast Ohio Medical University, Rootstown, Ohio, USA

²Department of Biology, University of Akron, Akron, Ohio, USA

³School of Biomedical Sciences, Kent State University, Kent, Ohio, USA

⁴Department of Anthropology, University of Texas at Austin, Austin, Texas, USA

Correspondence

Jesse W. Young, Department of Anatomy and Neurobiology, Northeast Ohio Medical University, 4209 State Rte 44, Rootstown, OH USA.
Email: jwyong@neomed.edu

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Abstract

Several studies comparing primate locomotion under lab versus field conditions have shown the importance of implementing both types of studies, as each has their advantages and disadvantages. However, three-dimensional (3D) motion capture of primates has been challenging under natural conditions. In this study, we provide a detailed protocol on how to collect 3D biomechanical data on primate leaping in their natural habitat that can be widely implemented. To record primate locomotion in the dense forest we use modified GoPro Hero Black cameras with zoom lenses that can easily be carried around and set up on tripods. We outline details on how to obtain camera calibrations at greater heights and how to process the collected data using the MATLAB camera calibration app and the motion tracking software DLTdv8a. We further developed a new MATLAB application "WildLeap3D" to generate biomechanical performance metrics from the derived x, y, z coordinates of the leaps. We provide details on how to collect data on support diameter, compliance, and orientation, and combine these with the jumps to study locomotor performance in an ecological context. We successfully reconstructed leaps of wild primates in the 3D space under natural conditions and provided data on four representative leaps. We provide exemplar data on primate velocity and acceleration during a leap and show how our protocol can be used to analyze segmental kinematics. This study will help to make motion capture of freely moving animals more accessible and help further our knowledge about animal locomotion and movement.

KEYWORDS

biomechanics, leaping, motion capture, primate locomotion

1 | INTRODUCTION

Our knowledge of biomechanics, animal behavior, evolution, and ecology has been greatly improved with the introduction of motion capture methods using multiple, high-speed cameras to quantify

animal movement in three-dimensional (3D) space (Demuth et al., 2023). Initial studies were inevitably carried out in laboratory environments, as the cost, fragility, and size of such specialized cameras did not allow their use in harsh field conditions or provide sufficient flexibility for recording in variable environments.

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Additionally, essential parameters for estimating 3D positions from video, such as the focal lengths and principal focal plane points of the cameras (intrinsic parameters) as well as the relative positions of the cameras to each other (extrinsic parameters) had to be obtained by measuring points of known location on a “calibration object” across all camera views to reconstruct 3D global positions of novel objects within the calibrated volume (for a review on camera calibrations, see Hartley and Zisserman [2004]). In the study of biomechanics, multi-camera videography became an essential tool applied under laboratory conditions to study, for example, the mechanics of flight (see Berg & Biewener, 2010; Tobalske et al., 2007), performance during nonsteady locomotion and maneuvering (see Ros et al., 2011; Warrick & Dial, 1998), or human movement and sports science (Fuller et al., 1997; Mündermann et al., 2006). Despite the important insights into many aspects of animal locomotion gained by this research, these previous laboratory-based studies have often focused on single individuals of a selected species under restrained conditions, limiting their interpretative scope.

Over the past decade, researchers have aimed to improve calibration methods and camera systems, such that valid, reliable 3D motion data could be obtained in the field, capturing the kinematics of animal movement in natural environments. One of the most common calibration methods has been direct linear transformation (DLT) (Abdel-Aziz & Karara, 2015), which requires calibration points of known positions to be distributed throughout the volume of interest. Some of the first field studies investigating animal movement used large physical calibration objects at the field site (Clark, 2009; Munk, 2011), which in turn limited the volume that could be calibrated and the corresponding region of interest available for study. To further improve the feasibility of 3D recordings in the field, Theriault et al. (2014) developed openly accessible software using the sparse bundle adjustment (SBA) calibration algorithm (Lourakis & Argyros, 2009) which minimizes the difference between observed and ideal locations of calibration points in each camera view, increasing calibration accuracy and allowing for larger recording areas. Theriault et al. (2014) also provided a workflow for pre-experiment planning of camera placement, in-field calibration protocols and postexperiment camera calibrations for successful 3D recordings of bat and bird flights under natural conditions. Following this, Jackson et al. (2016) then introduced the use of standardized GoPro Hero Black cameras, additional synchronization methods, and a new tool for camera calibrations tracking eastern carpenter bees (*Xylocopa virginica*).

In this study we aimed to supplement existing protocols to track primate leaping under natural conditions, combining the acquired 3D data with additional measurements of the primates' environment. So far, our understanding of primate locomotion and biomechanics as well as primates' evolutionary adaptations to the arboreal environment relies heavily on data from laboratory studies (Granatosky & Young, 2023). Only very few studies have obtained motion capture data of wild primates (Hirasaki et al., 2019; Ostrofsky, 2019). This study faced additional difficulty as the location of primate leaps could not be predicted and cameras could not be prepared or set

up beforehand, complicated by the difficulty of finding good viewpoints for several cameras in a dense forest. Additionally, primates tend to stay high up in the canopy, making zoom lenses and a wide-angle view necessary to capture the entire leap, increasing calibration difficulty.

Despite recent technical advances, recording wild animals' locomotion in the rainforest is still a very challenging task—particularly when their movement is unpredictable. Here, we present a protocol to record wild primates leaping in their natural environment and combine our 3D data set on their locomotor behavior with detailed measurements of the substrate, thus unraveling foundational insights into primate locomotor evolution. Additionally, we provide detailed guidelines on camera calibration to optimize the often-limited opportunities for recordings that can be acquired during fieldwork and possible alternative solutions in case of failure. We want to give an overview for future researchers trying to implement 3D recordings under very challenging conditions, demonstrating an example of success. Our methods can be applied to study any type of animal under challenging conditions, close or at a distance, including birds, lizards, primates, or insects.

2 | MATERIAL AND METHODS

2.1 | Data collection

The behavioral data were collected in Kibale National Park, Uganda between January and March 2022 and Ranomafana National Park and Anja Community Reserve in Madagascar between July and August 2022. We included four leaps of four different primate species to demonstrate the broad application of our method and combine them with environmental measurements of the used substrates.

To obtain valuable data in the wild, primates must be followed through the dense environment of the forest before a spot can be found to set up the individual cameras. To reconstruct the 3D space, a minimum of two cameras is necessary to record the same behavior from different angles, but three cameras are preferred for redundancy. Therefore, it is essential to have a flexible system that can be moved and set up easily and quickly. We used modified GoPro Hero Black 10 with C-mount zoom lenses (Back-Bone) mounted on tripods. These cameras are lightweight, robust, and endure harsh conditions, though they are not waterproof when modified for the attachment of zoom lenses. They also allow the animals to be recorded close or at a distance (depending on the lens used) as well as at different frame rates. Another benefit of newer Go Pros is that they have small screens and one can always monitor the recording in real time. For guidance on which camera models to use depends on the research question, environmental conditions, or model systems—as well as considerations of the timing, financial budgeting, and analytical tools for such studies—see Janisch, Mitoyen, et al. (2021). Here, we will concentrate on the details used to obtain 3D kinematics of primates leaping in the wild.

All primate leaps were recorded with 120 frames per second (fps). Once the cameras were placed and began recording (Figure 1), they could not be moved until a calibration had been obtained; otherwise, 3D reconstructions would fail. We had a team of three people, each researcher handling one camera. This allowed for ample flexibility to transport the cameras and quickly set them up when an event of interest occurred.

A critical consideration was ensuring that the camera system could last long enough to finish recording the behavioral events. Along these lines, we found that it was important to have sufficient spare batteries and power banks in case recordings required long hours and overheating or cold temperatures could drain batteries rapidly.

2.2 | Synchronization

Once primate leaps occurred and the animals left the area, we made sure to synchronize the videos before stopping the recordings. To create a set of synchronization events, we either flashed a laser pointer (JLP-RG-S, LightVision Technologies Corp.) on a tree trunk visible to all cameras, or we threw a colorful ball in a space visible to all cameras, treating the apex of the ball's flight as a discrete synchronization event. In cases where we were not able to synchronize the recordings, we searched for a discrete salient event visible in all cameras, such as a primate passing an outstanding branch recognizable in all cameras. For an additional method to align frame numbers to improve synchronization, refer to Section 2.4.

2.3 | Calibration

Following synchronization, we started calibrating the cameras for later 3D reconstructions. First, we carried out intrinsic calibrations for each camera separately to obtain estimates of focal length and lens distortion, followed by extrinsic calibrations to calculate the relative positions of the cameras to each other as well as ground-level calibrations to account for precise positioning relative to horizontal (Jackson et al., 2016). All calibration videos were recorded with 30 fps to optimize storage space. For a review on calibration methods, see Hartley and Zisserman (2004).

2.3.1 | Intrinsic calibrations

In the field, we used a checkerboard attached to a pole that could be extended up to 10 m as primates often moved in the upper canopy (Figure 2). The checkerboard was a pattern provided by the MATLAB camera calibration app (<https://www.mathworks.com/help/vision/ug/using-the-single-camera-calibrator-app.html>) (The MathWorks Inc., 2023), and moved around in front of each camera individually. When filming the checkerboard, not only should the movement cover the entire camera field of view, but the checkerboard should also be tilted, twisted to the left and right, as well as moved towards and away from the camera to obtain the best results. Several other aspects needed to be considered to obtain good intrinsic calibrations when recording primate leaping in the canopy.

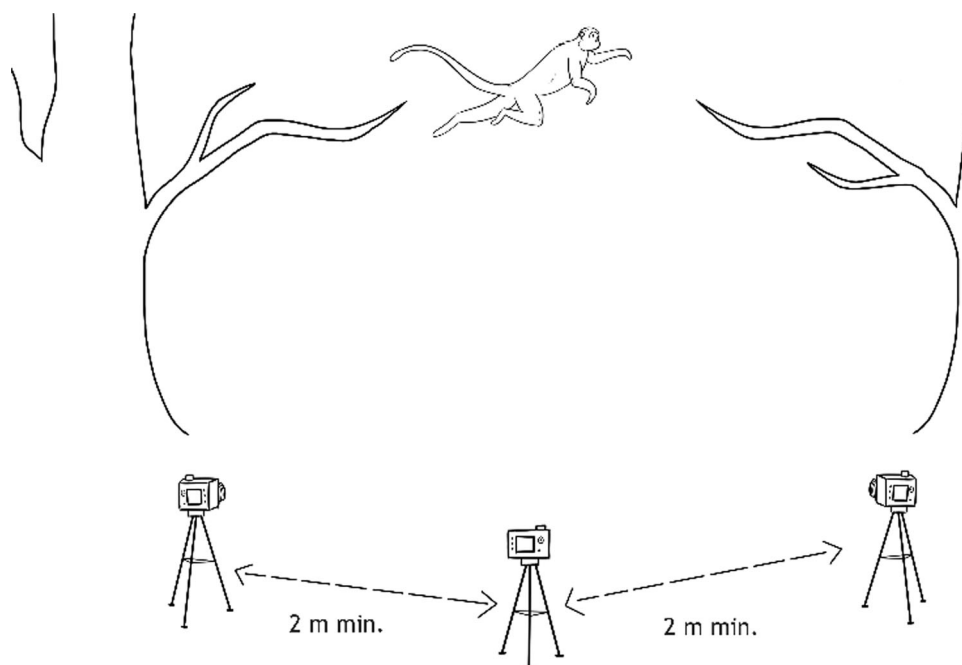


FIGURE 1 Camera set up during recordings of a primate leap. Cameras should be placed at a distance of at least 2 m from each other or more and can be set at different heights. Illustration by Taylor Phelps.



FIGURE 2 Calibration tools. Checkerboard and wand attached to the 10-m pole. For intrinsic calibration the checkerboard faces the cameras; for extrinsic calibrations, we rotated the frame such that only the two wand balls are visible to the cameras.

- First, it was important that the checkerboard was the right size. Something to keep in mind is that with increased zoom the checkerboard might need to be further away from the camera and therefore will cover only a small portion of the camera's field of view, increasing the likelihood of subsequent processing errors to the variable background or bad light conditions. Printing a sufficiently large checkerboard is crucial.
- Second, it was important to be far enough away from the camera for the checkerboard to be in focus. As the focus was often set at a spot higher up in the trees where the primates were leaping, the camera intrinsics had to be recorded from a greater distance to keep the checkerboard in focus but not too far away so that it would not be too small.
- Third, whenever possible the checkerboard should not be covered by excessive shadows or direct reflections of the sun. Tilting the checkerboard just a little could help with the light conditions in case the sun is shining directly at the board. Also considering the material the checkerboard is made of can be crucial (i.e., nonreflective surfaces work best).
- Fourth, the checkerboard should be moved slowly to avoid blurriness and always kept horizontal to the camera, i.e., no rotations. Blurriness and an angled checkerboard make the analysis difficult.

For the analysis of the intrinsic calibration we also used the standard camera calibration app of MATLAB (<https://www.mathworks.com/help/vision/ug/using-the-single-camera-calibrator-app.html>) (The MathWorks Inc., 2023). First, individual frames were cut out from the video using Clip Stride (<http://www.younglaboratory.org/GaitKeeper/Software.html>). The number of frames required for intrinsic calibration can vary depending on the individual situation. As we wanted to make sure to cover enough of the frame and add enough tilts and turns, we aimed for approximately 100 frames. The camera calibration app suggests a minimum of 10–20 frames, but we found that increasing the frame sample resulted in a better outcome, as some frames were rejected or needed to be deleted to obtain a valid

calibration. The video sample was then loaded into the MATLAB camera calibrator app, specifying low distortion for standard frame recordings and high distortion for wide-angle recordings. As the GoPro automatically undistorts frames even in wide angle mode, no fish-eye correction was necessary. For more information on the properties of fisheye and omnidirectional lenses, see Urban et al. (2015) and Scaramuzza (2014). Additionally, the length of the squares of the checkerboard pattern needs to be entered into the program for proper calculations. After calibrating, it's necessary to evaluate the reprojection error and the detected pattern for each camera very carefully. A reprojection error <1 pixel is generally required for an accurate calibration, which was also the case for all our calibrations. Frames where the checkerboard is too far tilted or turned usually give high reprojection errors and should be excluded. In the literature it is stated that the checkerboard should cover about a third of the entire frame. Though this might be possible under laboratory studies, it was often not possible in our study, depending on zoom levels and if we had used a standard or wide-angle filming mode. However, by using enough frames we were able to obtain accurate intrinsic calibrations.

Generally, intrinsic calibrations can be very tricky and tend to fail more easily than extrinsic calibrations (see below). In cases where the calibration does not work there are two alternative methods that can be applied to determine focal length. First, one can carry out intrinsic calibrations in the lab. To do so, a range of possible focal lengths used in the field recordings must be calibrated and a linear regression built to determine interpolation across the possible values. Successfully using this protocol also requires noting all the used focal lengths during recordings in the field to estimate matching intrinsic parameters later. For detailed instructions, see Jackson et al. (2016). Second, one can narrow down the most likely focal length by manipulating the intrinsic values gained from the camera calibration app and increasing/decreasing these values stepwise in EasyWand until the calibration is successful. EasyWand is a MATLAB tool for wand-based camera calibrations (<https://biomech.web.unc.edu/wand-calibration-tools/>) to produce multicamera calibrations (Theriault et al., 2014). To do so, all the intrinsic parameters of each

camera have to be added in this program and can be changed manually in case the original intrinsic calibration was not accurate. For more information, see Section 2.3.3.

2.3.2 | Extrinsic and ground-level calibrations

Extrinsic and ground-level calibrations were usually carried out simultaneously and had to be recorded by all three cameras at the same time. For extrinsic calibrations, we built a wand of known length with two clearly visible colorful ends (Figure 2) that we could attach to our 10-m pole and move around in the space where the primates leapt. It is important to move the wand around to cover the entire space where the locomotion of interest occurred and ensure that both wand ends are visible from all the different camera views. Roughly 100 wand points (i.e., frames of calibration video where both wand ends are visible in all cameras) are needed for good calibrations. Once we had finished filming the wand, we threw a ball to serve as a temporal cue for synchronizing the cameras as well as to indicate vertical z-axis points (i.e., gravity) for ground-level calibration. For the axis points a minimum of 10 tracked points of the ball falling is needed. The tracking of the wand and ball was done using the MATLAB app DLTdv8a (Hedrick, 2008). Before tracking, it is critical to correctly set frame offsets of each camera relative to the other(s), to ensure synchronization. The synchronization of the videos and precise tracking of the points is crucial for a successful calibration.

2.3.3 | Multicamera calibration

Individual calibrations were merged using easyWand (Theriault et al., 2014). As input, the program loads the tracked wand points, additional background points visible to all cameras (if needed for calibration optimization), and the ground-level calibration (axis) points. Axis points should be loaded in with the positive z-direction upward to be aligned with the direction of gravity. Additional input includes the length of the tracked wand (in meters), and image height and width (in our case 1920×1080 pixels). Focal length and principal point values (in pixels) are loaded from the intrinsic calibrations described above. When evaluating multi camera calibration, one should pay attention to the wand endpoints standard deviation, the wand score (estimated wand length standard deviation divided by actual wand length), and the reprojection errors estimated for each camera. Theriault et al. (2014) recommend a wand score ≤ 1.0 for a good calibration. Bad wand points (i.e., tracked points with high reprojection errors) can be excluded to improve the calibration. Following this, if the calibration is still unsuccessful, attempts should be made to improve intrinsic and extrinsic calibrations, as described above. Background points—random points in the background of the video that are easily identifiable in all camera views—can be digitized in addition in DLTdv8a and added into easyWand input to optimize the calibration. They are not necessary but can also contribute to

better calibration if an otherwise insufficient number of wand points is available. For detailed instructions on how to use easyWand, see Theriault et al. (2014) and <https://biomech.web.unc.edu/wand-calibration-tools/>.

2.4 | Primate tracking

Primates were tracked using DLTdv8a. All our data were tracked manually as it seemed more efficient than training an automated model, given the number of videos we had to analyze, and the heterogeneity of the recordings. Recording wild primates leaping in the canopy adds many additional difficulties for automated tracking, including blurriness, a variable background and poor lighting conditions. For an overview of tracking methods please refer to Janisch, Mitoyen, et al. (2021). To start tracking primate leaps, one needs to first associate the leaping videos with the corresponding multicamera calibrations in DLTdv8a. Additionally, the leaping videos must be perfectly synchronized across cameras. For the leaps where we were not able to use a ball or laser for synchronization, (as the primates would not leave the area), we tried to find a discrete event during the leap that was identifiable in all camera perspectives (such as a primate passing a salient feature in the environment). As this method might not be as accurate, we also created a customized program in MATLAB that uses the DLT calibration and tracked primate points during the leaping event (i.e., primate's nose and base of tail) to iteratively identify frame offsets that provide the smallest median error across the camera views (OptimizeOffset2.m). Specifically, with one of the cameras designated as the “master” (i.e., zero offset), the program iteratively applies integral offsets of the other camera(s) relative to the master, where the offsets range from $-n/2$ to $+n/2$, with n equal to the number of frames in the trial. At each offset, the program then calculates the median reprojection errors across all points in all frames for each camera. The combination of offsets that results in the lowest summed median reprojection error across all cameras is chosen as optimal.

Once the cameras are synced, the DLT coefficients from the relevant calibration are imported for final primate digitizing. DLTdv8a provides frame-by-frame feedback on 3D reconstruction accuracy, including placing epipolar lines in videos that have yet to be digitized (i.e., based on the location of a point in one camera, the program indicates a line along which the point should lie in the other camera, provided the calibration is accurate). In total we tracked 16 different points (Supporting Information S1: Table S1) in each 3D jump. We placed markers on the neck of the primate, one on the base of the tail and two more on the trunk, one on the anterior aspect (chest) and one on the posterior aspect (belly button). These points permitted us to fit a polygon around the animal, allowing us to estimate the approximate position of the primate's “center of mass” as the centroid of this shape. Additionally, we placed points on the middle and end of the tail as well as on both hands and feet. Finally, we placed markers on the launching and landing branches, to characterize substrate movement. Primates were tracked during the floating

(ballistic) portion of the leap, as well as during push-off into the leap and during landing, as possible. Additional “dummy” points (i.e., digitized points carrying no spatial information but rather used to indicate the timing of discrete events) were used to indicate the frames in which the primate began the push-off phase of the leap (typically, the start of hindlimb extension), took off from the substrate (first frame in which the primate no longer touched the substrate), touched down on the target substrate, and came to a rest (stopped moving) on the target substrate.

2.5 | Substrate measurements

In addition to the 3D recordings of the primate leaps, we also collected measurements of substrate properties following the protocols outlined in Dunham et al. (2018). We used a forestry-grade rangefinder (TruPulse 360R “missing 3D line setting”, Laser Technology Incorporated) to measure inclination of the launching and landing support relative to gravity, the straight-line distance between the launching and landing supports, the support height above the ground, as well as the horizontal distance from the researcher to the target tree. This final

measurement was used to calculate diameter of the launching and landing supports from digital photographs taken with a Canon EOS 70D equipped with a 55–250-mm zoom lens, noting the focal length used during the photographs (i.e., distance meter method for remote measurement, Galbany et al. [2016] and described in Dunham et al. [2018]). Finally, whenever possible, we also noted tree species of the launching and landing supports, and measured their compliance using a force gauge apparatus, as described by Van Casteren et al. (2013, 2016) and Dunham et al. (2018).

2.6 | WildLeap3D to process 3D position data

A new MATLAB app called WildLeap3D was developed in the process of this study to analyze the 3D reconstructed points of the animals' movement (Figure 3).

WildLeap3D takes as input the saved MATLAB data (.mat) file from the digitized DLTdv8a project. Calibrated 3D point data are loaded from this file, and then fit to a quintic smoothing spline function (MATLAB function “spaps”), allowing us to mitigate digitizing error and interpolate feature positions for frames where the marker

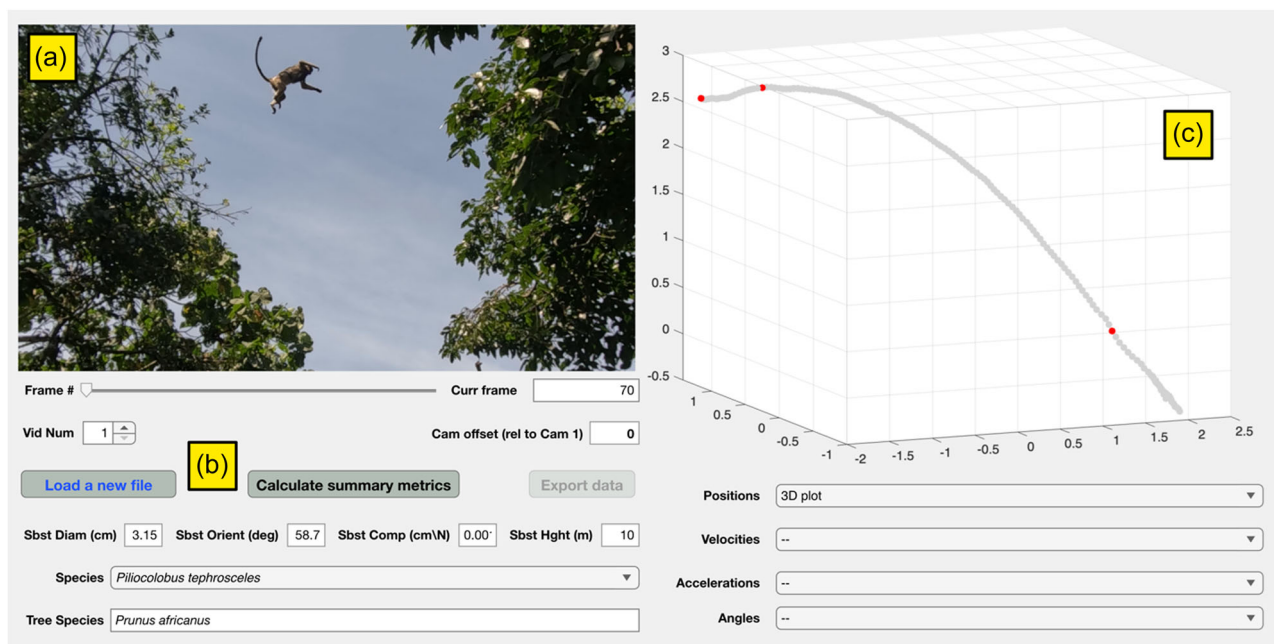


FIGURE 3 Graphical user interface (GUI) of the WildLeap3D MATLAB app. (a) The synchronized videos of the leaping event are loaded into the window on the top left of the GUI. The user can navigate through the video using the Frame Slider or by typing specific frame numbers into the Current Frame control box. Typing “takeoff” or “landing” into the Current Frame control box will navigate to those frames, as identified during the digitizing process. (b) Buttons in this region of the GUI will load a new DLTdv8a analysis file, calculate summary metrics about the leap (see text for details), or export data once summary metrics have been calculated. Text boxes and dropdown menus in this region can be used to record metadata about the leap being analyzed. Note that the primate species must be chosen from the dropdown list to include the correct body mass for later analyses. (c) The instantaneous x, y, z position, velocity, and acceleration of the primate “center of mass” (i.e., centroid, see text for details) and the launching and landing substrates can be plotted in the window on the right side of the GUI. Dropdown menus below the plot are used to select among these options. The exemplar plot shown in the figure shows the x-y-z position of the primate center of mass during the leap. Red points are used to indicate the timing of salient events (i.e., start of push-off, take-off, and landing). This plot is one of the options under the “Positions” drop down menu. Summary metrics describing leap kinematics are also displayed here after the user pushes the “Calculate summary metrics” button.

was not visible across gaps of ≤ 100 ms (Walker, 1998). Instantaneous velocities and accelerations were calculated as the first and second derivatives of smoothed x , y , and z trajectories, respectively (MATLAB function “fnder”). The linear kinematics of the primate's “center of mass” (i.e., centroid) were then calculated as the frame-by-frame mean of the positions, velocities, and accelerations of the nose, base of tail, and trunk points, as described in the “Primate tracking” section above. Kinematic data are then used to calculate a set of summary metrics describing the biomechanics of each leap (Supporting Information S1: Table S2). Following Janisch, Perinot, et al. (2021) we projected each 3D leap trajectory onto the 2D plane described by the positive z -axis and the horizontal line defined by the start and end positions of the primate's center of mass during the ballistic phase of leap. These rotated x - y data permitted us to characterize changes in position, velocity, and acceleration that were colinear with the predominant direction of the leap, and therefore likely exerted the most significant contributions to performance.

3 | RESULTS

We present four successfully reconstructed 3D leaps of four different species of primates (Table 1). The jumps range from short leaps (*Eulemur rufifrons*), vertical leaping (*Lemur catta*) to crossing large gaps at greater heights (*Propithecus edwardsi* and *Ptilocolobus tephrosceles*). We confirmed the leap distance estimated from WildLeap3D by comparing it to the distance between the launching and landing support measured using the Rangefinder. Discrepancies between the estimated and measured leap distances ranged from 17 to 55 cm

(9.8% up to 49% of measured leap distance), with an average of 43 cm (25% of measured leap distance). Some of this discrepancy could be explained by the researchers not being able to measure the distance between exact take-off and landing branches of the leap due to the cluttered environment. Measured take-off velocities ranged from 1.36 m/s for the shortest leap of 0.51 m—requiring an average force of 44% body weight during push-off, up to 4.11 m/s in the longest leap of 5.05 m—requiring an average push-off force of 272% body weight. Substrate displacement at take-off varied depending on diameter and tree species and ranged from 0.6 cm up to 5.6 cm. Landing velocities ranged from 1.1 m/s for the shortest leap, producing an average landing force of up 16% body weight, up to 7.8 m/s with an average landing force of 174% body weight. Branch displacement at landing was greatest (85 cm) for the longest jump of 5.05 m (Table 1). Exemplar linear and angular kinematics of the *Ptilocolobus tephrosceles* leap are plotted in Figures 4 and 5, respectively.

4 | DISCUSSION

Using the flexible motion capture protocol outlined here, we successfully characterized the 3D biomechanics of leaping from high-speed videos of several different species of wild primates leaping in the canopy. Though particularly focused on detailed guidelines to record wild primates in 3D, this protocol can also be applied to 3D motion capture of any other animal model and environment. We provide detailed information on postprocessing the recordings to obtain successful camera calibrations and alternative solutions in case of failure. Video calibrations were done with

TABLE 1 Measured and calculated variables of the four leaps and split into variables related to species, substrate, take-off, performance, and landing.

Species variables	Substrate variables	Take-off variables	Leaping performance	Landing variables	Angles ($\bar{x}$)
Species: <i>Propithecus edwardsi</i> Body mass: 5.68 kg	Diameter: 6.35 cm Orientation: 36.5° Height: 8.67 m Compliance: NA	Velocity: 3.58 m/s $\bar{x}$ Force (in BW): 1.5 Substrate displacement: 5.6 cm	Total distance: 1.62 m Straight line distance: 1.46 m Δ Height: 0.92 m	Landing velocity: 1.58 m/s $\bar{x}$ Force (in BW): 0.91 Branch displacement: 0 cm	Angle of attack: 154° Tail-trunk: 160.4° Mid-tail: 140.4°
Species: <i>Eulemur rufifrons</i> Body mass: 2.22 kg	Diameter: 2.78 cm Orientation: 33.1° Height: 3.47 m Compliance: 0.00268	Velocity: 1.36 m/s $\bar{x}$ Force (in BW): 0.44 Substrate displacement: 0.64 cm	Total distance: 0.51 m Straight line distance: 0.51 m Δ Height: 0.5 m	Landing velocity: 1.11 m/s $\bar{x}$ Force (in BW): 0.16 Branch displacement: 0.7 cm	Angle of attack: 156° Tail-trunk: 130.61° Mid-tail: 135.1°
Species: <i>Lemur catta</i> Body mass: 2.21 kg	Diameter: 8.03 cm Orientation: 72.2° Height: 1.46 m Compliance: 0.00066	Velocity: 1.62 m/s $\bar{x}$ Force (in BW): 0.71 Substrate displacement: 0.6 cm	Total distance: 1.08 m Straight line distance: 0.93 m Δ Height: -0.51 m	Landing velocity: 2.83 m/s $\bar{x}$ Force (in BW): 1.37 Branch displacement: 0 cm	Angle of attack: 121° Tail-trunk: 110° Mid-tail: 143.6°
Species: <i>Ptilocolobus tephrosceles</i> Body mass: 8.37 kg	Diameter: 3.15 cm Orientation: 58.7° Height: 10 m Compliance: 0.00164	Velocity: 4.11 m/s $\bar{x}$ Force (in BW): 2.72 Substrate displacement: 3.4 cm	Total distance: 5.05 m Straight line distance: 4.6 m Δ Height: -2.32 m	Landing velocity: 7.8 m/s $\bar{x}$ Force (in BW): 1.74 Branch displacement: 85 cm	Angle of attack: 131° Tail-trunk: 119.5° Mid-tail: 141.1°

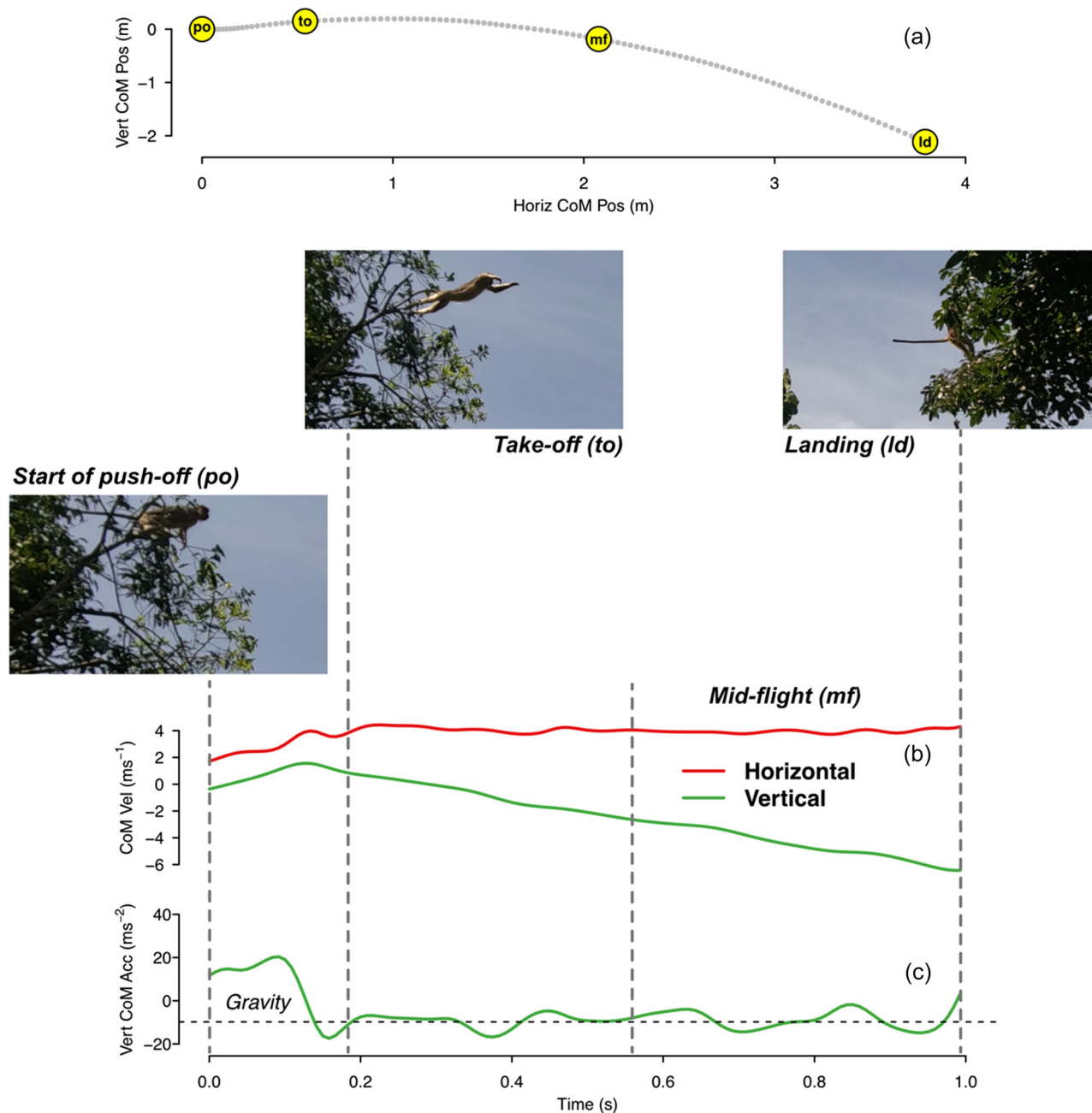


FIGURE 4 Linear kinematics of the estimated trunk center of mass during an exemplar arboreal leap of *Ptilocolobus tephrosceles* (see Table 1 for summary data on this leap). (a) x-y position of the estimated trunk center of mass during the leap, projected onto the plane defined by the global z-axis (i.e., gravity) and the horizontal vector between the positions of the estimated trunk center of mass at the start and end of the leap (see text for details). Yellow circles indicate critical events during the leap: start of push-off (po), take-off from the launching substrate (to), mid-flight during the ballistic phase of the leap (mf) and landing on the target substrate (ld). (b) Instantaneous horizontal and vertical velocities of the estimated trunk center of mass during the leap. Note that the monkey accelerates into the leap during the push-off phase and is able to maintain a fairly constant horizontal velocity during the ballistic phase. In contrast, vertical velocity declines throughout the ballistic phase of the leap, under the influence of gravity. (c) Instantaneous vertical acceleration of the estimated trunk center of mass during the leap. Note strong positive vertical acceleration during the push-off phase of the leap that quickly becomes negative during the ballistic phase, under the free-fall influence of gravity. Gravitational acceleration (i.e., -9.81 ms^{-2}) is indicated by the horizontal dashed line. The video frames above panels b and c correspond to the time points indicated in yellow in panel a.

MATLAB programs but there are open-source programs to achieve the same results, for example, Argus (<http://argus.web.unc.edu>). We further developed a new MATLAB-based app called "WildLeap3D" for analysis of the derived x, y, z coordinates which we provide in the

data repository. Primate jumps are described as parabolic motion as they jump ballistically between tree crowns. These data allow us to calculate the total (curvilinear) distance traversed by the primates and obtain precise estimates of primate center of mass velocity,

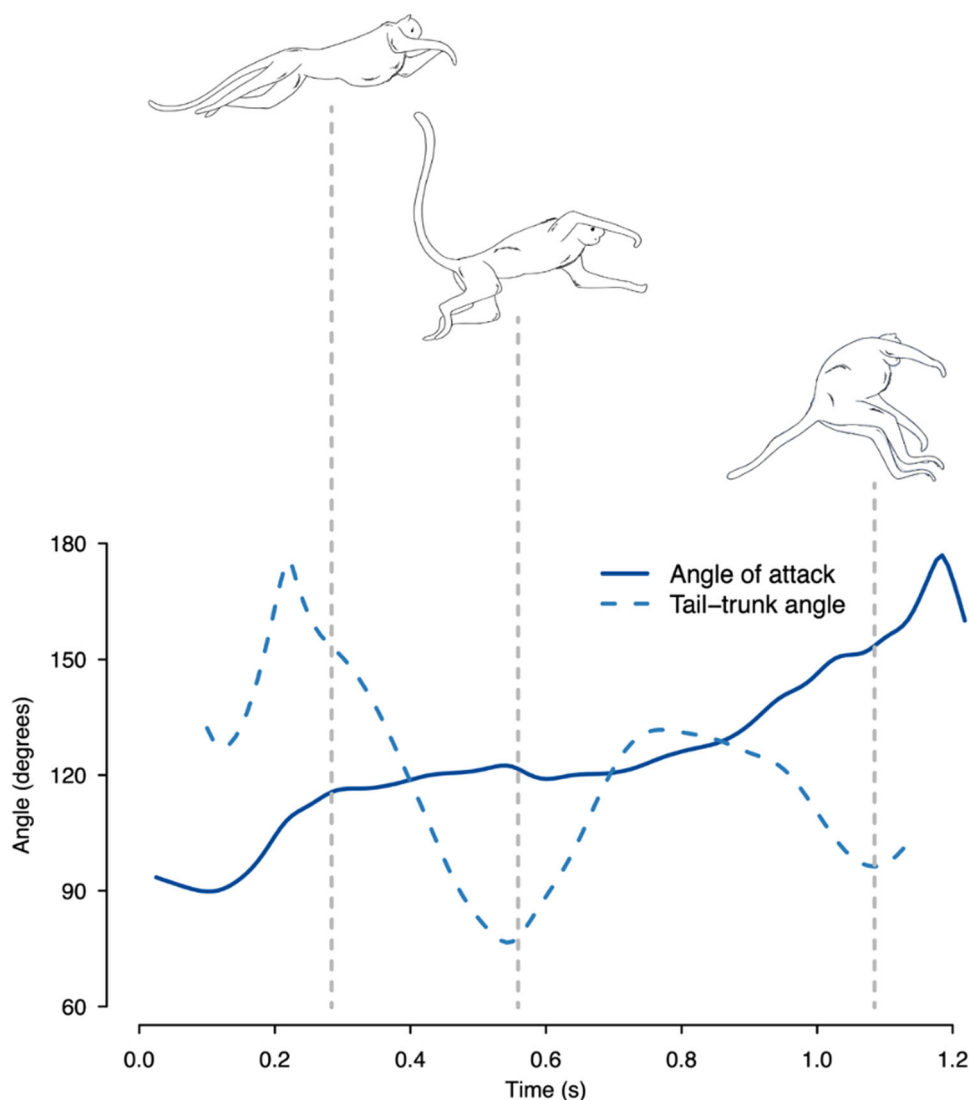


FIGURE 5 Angular kinematics during an exemplar arboreal leap of *Ptilocolobus tephrosceles* (see Table 1 for summary data on this leap). Angle of attack quantifies the craniocaudal axis of the monkey relative to gravity (90° = horizontal/pronograde trunk; 180° = vertical/orthograde trunk). Tail-trunk angle quantifies the deviation of the tail base-to-tip vector relative to the monkey's craniocaudal axis (90° = dorsally extended, perpendicular to trunk axis; 180° = neutral posture, parallel with trunk axis). The monkey begins the ballistic phase of the leap with trunk oriented perpendicular to gravity (angle of attack near 180°). By strongly extending the tail during the first half of the ballistic phase (tail-trunk angle $\leq 90^\circ$), the monkey is able to use the conservation of angular momentum to reorient the trunk to a more upright position (angle of attack near 90°), ensuring a foot-down position at the moment of landing (angle of attack near 90°). Illustrations by Taylor Phelps.

acceleration, or force (for more details, see Table 1 and Figures 4 and 5). Additionally, we included the possibility to add metadata measures of the substrate such as diameter, compliance, or orientation in the "WildLeap3D" app to facilitate further biomechanical analysis of leaping performance.

Though several studies have examined the biomechanics of leaping in captive or semi-captive primates (see Bobbert et al., 2014; Channon et al., 2010, 2011, 2012; Demes et al., 1995, 1999, 2005; Legreneur et al., 2011), and a few studies have examined wild primate leaping biomechanics (Dunbar 1988; Blanchard & Crompton, 2011; Blanchard et al., 2014; Crompton et al., 1993; Demes et al., 1996; Warren & Crompton, 1998), to our knowledge this is the first study

investigating the 3D kinematics of primate leaping in the wild. Previous studies on primate locomotion have found discrepancies between findings of the lab versus field studies. For example, Shapiro et al. (2011) directly compared quadrupedal kinematics of *Saimiri boliviensis* in field and laboratory settings. They found that instead of fine-tuning limb phases to different types of substrates as seen in the lab, animals used a variety of gait types across all branch sizes and orientations under natural conditions. Therefore, it is important to address kinematic questions in an ecologically relevant context (see also Stevens et al., 2011).

Several lab-based studies have also successfully characterized the 3D kinematics of captive and semi-captive primates (see,

Demes, 2011; Isler, 2005; Malinzak et al., 2012; Polk, 2002; Shapiro et al., 2016), in situ 3D motion capture of wild species is still underrepresented as it comes with its challenges. Such difficulties include a lack of control over the animals' direction of movement, variable lighting conditions, and no availability of a uniform background. All these factors influence the outcome of high-resolution recordings (Janisch, Perinot, et al., 2021; Janisch, Mitoyen, et al., 2021; Mitoyen et al., 2021; Uhlmann et al., 2017). However, it is hardly possible to recreate the complex 3D arboreal environment of a rainforest in the lab; therefore, in situ studies are incredibly valuable. Two-dimensional video recordings do not allow straightforward analysis of the movements of most arboreal animals given that their movements from moment to moment are decidedly nonplanar. Two-dimensional recording is unable to capture precise measurements of movements that occur on a parallel plane to the image plane of the recording camera. An additional benefit of studying kinematics in the wild is that recording wild groups of primates or other animals can allow for greater sample sizes and include species that are unlikely to be accessible for lab-based research (Janisch et al., 2024). This in turn provides possibilities for phylogenetic comparative studies which are often not possible under laboratory conditions due to limited numbers of individuals, species or space availability to house the animals (Stevens & Carlson, 2008; Vereecke & D'Août, 2011).

Finally, our system offers several logistical benefits for working in remote field sites. The equipment is easy to move around, even in a dense forest. Interchangeable batteries can be powered by power banks and lenses can be changed effortlessly depending on the model species. The system is easy to assemble at a low cost without sacrificing image resolution and, therefore, data fidelity.

5 | CONCLUSIONS

Despite the manifold recording devices and techniques, recording free-ranging animals with unpredictable movement patterns in 3D is still quite challenging. Arboreal primate locomotion is particularly challenging as wild primates typically live in dense forests and move very high up in the canopy. We hope the equipment and protocol described here make motion capture of wild animals more accessible, facilitating these important studies.

AUTHOR CONTRIBUTIONS

Judith Janisch and Jesse W. Young conceived the ideas and designed methodology; Judith Janisch, Nicole Schapker, and Lydia C. Myers collected the data; Judith Janisch, Jesse W. Young, and Jack Kirven analyzed the data; Judith Janisch and Jesse W. Young led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The "WildLeap3D" app and OptimizeOffset2 function are publicly accessible at <https://doi.org/10.5281/zenodo.10728502>. All other data supporting this study are included within the article.

ORCID

Judith Janisch  <http://orcid.org/0000-0003-3300-6292>

Nicole Schapker  <http://orcid.org/0000-0001-9138-5433>

REFERENCES

- Abdel-Aziz, Y. I., & Karara, H. M. (2015). Direct linear transformation from comparator coordinates into object space coordinates in close-range photogrammetry. *Photogrammetric Engineering and Remote Sensing*, 81(2), 103–107.
- Berg, A. M., & Biewener, A. A. (2010). Wing and body kinematics of takeoff and landing flight in the pigeon (*Columba livia*). *Journal of Experimental Biology*, 213, 1651–1658. <https://doi.org/10.1242/jeb.038109>
- Blanchard, M. L., & Crompton, R. H. (2011). Field study methods for primate locomotor ecology and biomechanics. In K. D'Août, & E. E. Vereecke (Eds.), *Primate locomotion: Linking field and laboratory research* (pp. 183–199). Springer.
- Blanchard, M. L., Furnell, S., Sellers, W. I., & Crompton, R. H. (2014). Locomotor flexibility in *Leopoldus* explained by habitat and biomechanics. *American Journal of Physical Anthropology*, 156, 58–66. <https://doi.org/10.1002/ajpa.22627>
- Bobbert, M. F., Plas, R. L., Weide, G., Clairbois, H. E., Hofman, S. O., Jaspers, R. T., & Philippens, I. H. (2014). Mechanical output in jumps of marmosets (*Callithrix jacchus*). *The Journal of Experimental Biology*, 217, 482–488. <https://doi.org/10.1242/jeb.089177>
- Van Casteren, A., Sellers, W. I., Thorpe, S. K. S., Coward, S., Crompton, R. H., & Ennos, A. R. (2013). Factors affecting the compliance and sway properties of tree branches used by the Sumatran orangutan (*Pongo abelii*). *PLoS One*, 8, e67877. <https://doi.org/10.1371/journal.pone.0067877>
- Van Casteren, A., Venkataraman, V., Ennos, A. R., & Lucas, P. W. (2016). Novel developments in field mechanics. *Journal of Human Evolution*, 98, 5–17. <https://doi.org/10.1016/j.jhevol.2016.03.003>
- Channon, A. J., Crompton, R. H., Günther, M. M., D'Août, K., & Vereecke, E. E. (2010). The biomechanics of leaping in gibbons. *American Journal of Physical Anthropology*, 143, 403–416. <https://doi.org/10.1002/ajpa.21329>
- Channon, A. J., Günther, M. M., Crompton, R. H., D'Août, K., Preuschoft, H., & Vereecke, E. E. (2011). The effect of substrate compliance on the biomechanics of gibbon leaps. *Journal of Experimental Biology*, 214, 687–696. <https://doi.org/10.1242/jeb.046797>

- Channon, A. J., Usherwood, J. R., Crompton, R. H., Günther, M. M., & Vereecke, E. E. (2012). The extraordinary athletic performance of leaping gibbons. *Biology Letters*, 8, 46–49. <https://doi.org/10.1098/rsbl.2011.0574>
- Clark, C. J. (2009). Courtship dives of Anna's hummingbird offer insights into flight performance limits. *Proceedings Biological sciences*, 276, 3047–3052. <https://doi.org/10.1098/rspb.2009.0508>
- Crompton, R. H., Sellers, W. I., & Gunther, M. M. (1993). Energetic efficiency and ecology as selective factors in the saltatory adaptation of prosimian primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 254, 41–45. <https://doi.org/10.1098/rspb.1993.0124>
- Demes, B. (2011). Three-dimensional kinematics of capuchin monkey bipedalism. *American Journal of Physical Anthropology*, 145(1), 147–155. <https://doi.org/10.1002/ajpa.21484>
- Demes, B., Fleagle, J. G., & Jungers, W. L. (1999). Takeoff and landing forces of leaping strepsirrhine primates. *Journal of Human Evolution*, 37, 279–292. <https://doi.org/10.1006/jhev.1999.0311>
- Demes, B., Franz, T. M., & Carlson, K. J. (2005). External forces on the limbs of jumping lemurs at takeoff and landing. *American Journal of Physical Anthropology*, 128, 348–358. <https://doi.org/10.1002/ajpa.20043>
- Demes, B., Jungers, W. L., Fleagle, J. G., Wunderlich, R. E., Richmond, B. G., & Lemelin, P. (1996). Body size and leaping kinematics in Malagasy vertical clingers and leapers. *Journal of Human Evolution*, 31, 367–388. <https://doi.org/10.1006/jhev.1996.0066>
- Demes, B., Jungers, W. L., Gross, T. S., & Fleagle, J. G. (1995). Kinetics of leaping primates: Influence of substrate orientation and compliance. *American Journal of Physical Anthropology*, 96, 419–429. <https://doi.org/10.1002/ajpa.1330960407>
- Demuth, O. E., Herbst, E., Polet, D. T., Wiseman, A. L. A., & Hutchinson, J. R. (2023). Modern three-dimensional digital methods for studying locomotor biomechanics in tetrapods. *Journal of Experimental Biology*, 226(Suppl. 1), jeb245132. <https://doi.org/10.1242/jeb.245132>
- Dunham, N. T., McNamara, A., Shapiro, L., Hieronymus, T., & Young, J. W. (2018). A user's guide for the quantitative analysis of substrate characteristics and locomotor kinematics in free-ranging primates. *American Journal of Physical Anthropology*, 167(3), 569–584. <https://doi.org/10.1002/ajpa.23686>
- Fuller, J., Liu, L. J., Murphy, M. C., & Mann, R. W. (1997). A comparison of lower-extremity skeletal kinematics measured using skin-and pin-mounted markers. *Human Movement Science*, 16(2–3), 219–242. [https://doi.org/10.1016/S0167-9457\(96\)00053-X](https://doi.org/10.1016/S0167-9457(96)00053-X)
- Galbany, J., Stoinski, T. S., Abavandimwe, D., Breuer, T., Rutkowski, W., Batista, N. V., Ndagijimana, F., & McFarlin, S. C. (2016). Validation of two independent photogrammetric techniques for determining body measurements of gorillas. *American Journal of Primatology*, 78(4), 418–431. <https://doi.org/10.1002/ajp.22511>
- Granatosky, M. C., & Young, J. W. (2023). Primate locomotion: A comparative and developmental perspective. In C. S. Larsen (Ed.), *A Companion to Biological Anthropology* (pp. 587–602). <https://doi.org/10.1002/9781119828075.ch35>
- Hartley, R. S., & Zisserman, A. (2004). *Multiple view geometry in computer vision* (2nd ed.). Cambridge University Press.
- Hedrick, T. L. (2008). Software techniques for two-and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration & Biomimetics*, 3(3), 034001. <https://doi.org/10.1088/1748-3182/3/3/034001>
- Hirasaki, E., Malaivijitnond, S., & Hamada, Y. (2019). Locomotor kinematics of two semi-wild macaque species (*Macaca assamensis* and *Macaca arctoides*) in Thailand. *Folia Primatologica*, 90(3), 162–178.
- Isler, K. (2005). 3D-kinematics of vertical climbing in hominoids. *American Journal of Physical Anthropology*, 126(1), 66–81. <https://doi.org/10.1002/ajpa.10419>
- Jackson, B. E., Evangelista, D. J., Ray, D. D., & Hedrick, T. L. (2016). 3D for the people: Multi-camera motion capture in the field with consumer-grade cameras and open-source software. *Biology Open*, 5(9), 1334–1342. <https://doi.org/10.1242/bio.018713>
- Janisch, J., McNamara, A., Myers, L. C., Schapker, N., Dunham, N. T., Phelps, T., Mundry, R., Hieronymus, T., Shapiro, L. J., & Young, J. W. (2024). Ecological and phylogenetic influences on limb joint kinematics in wild primates. *Zoological Journal of the Linnean Society*. zlae004. <https://doi.org/10.1093/zoolinnean/zlae004>
- Janisch, J., Mitoyen, C., Perinot, E., Spezie, G., Fusani, L., & Quigley, C. (2021). Video recording and analysis of avian movements and behavior: Insights from courtship case studies. *Integrative and Comparative Biology*, 61(4), 1378–1393. <https://doi.org/10.1093/icb/icab095>
- Janisch, J., Perinot, E., Fusani, L., & Quigley, C. (2021). Deciphering choreographies of elaborate courtship displays of golden-collared manakins using markerless motion capture. *Ethology*, 127(7), 550–562. <https://doi.org/10.1111/eth.13161>
- Legreneur, P., Monteil, K. M., Pellé, E., Montuelle, S., & Bels, V. (2011). Submaximal leaping in the grey mouse lemur. *Zoology*, 114, 247–254. <https://doi.org/10.1016/j.zool.2011.03.004>
- Lourakis, M. I., & Argyros, A. A. (2009). SBA: A software package for generic sparse bundle adjustment. *ACM Transactions on Mathematical Software (TOMS)*, 36(1), 1–30.
- Malinzak, M. D., Kay, R. F., & Hullar, T. E. (2012). Locomotor head movements and semicircular canal morphology in primates. *Proceedings of the National Academy of Sciences*, 109(44), 17914–17919. <https://doi.org/10.1073/pnas.12061391>
- Mitoyen, C., Quigley, C., Boehly, T., & Fusani, L. (2021). Female behaviour is differentially associated with specific components of multimodal courtship in ring doves. *Animal Behaviour*, 173, 21–39. <https://doi.org/10.1016/j.anbehav.2020.12.014>
- Mündermann, L., Corazza, S., & Andriacchi, T. P. (2006). The evolution of methods for the capture of human movement leading to markerless motion capture for biomechanical applications. *Journal of Neuroengineering and Rehabilitation*, 3(1), 6. <https://doi.org/10.1186/1743-0003-3-6>
- Munk, J. D. (2011). *The Descent of Ant*. PhD thesis. University of California.
- Ostrowsky, K. R. (2019). Using behavioral and kinematic methods to characterize arboreal behavior of Bwindi Mountain Gorillas (Doctoral dissertation, The George Washington University).
- Polk, J. D. (2002). Adaptive and phylogenetic influences on musculoskeletal design in cercopithecine primates. *Journal of Experimental Biology*, 205(21), 3399–3412. <https://doi.org/10.1242/jeb.205.21.3399>
- Ros, I. G., Bassman, L. C., Badger, M. A., Pierson, A. N., & Biewener, A. A. (2011). Pigeons steer like helicopters and generate down- and upstroke lift during low-speed turns. *Proceedings of the National Academy of Sciences*, 108, 19990–19995. <https://doi.org/10.1073/pnas.1107519108>
- Scaramuzza, D. (2014). *Ocamcalib: Omnidirectional camera calibration toolbox for matlab*. <http://robotics.ethz.ch/~scaramuzza/DavideScaramuzzafiles/Research/OcamCalibTutorial.htm>
- Shapiro, L. J., Chadwell, B. A., & Young, J. W. (2016). Tail kinematics during asymmetrical gaits in mouse lemurs (*Microcebus murinus*). *American Journal of Physical Anthropology*, 159(Supplement S62), 288–289.
- Shapiro, L. J., Young, J. W., & Souther, A. (2011). Quadrupedal locomotion of *Saimiri boliviensis*: A comparison of field and laboratory-based kinematic data. In *Primate locomotion: Linking field and laboratory research* (pp. 335–356). Springer.
- Stevens, N. J., & Carlson, K. J. (2008). Bridging gaps between experimental and naturalistic approaches in the study of primate behavior.

- International Journal of Primatology*, 29, 1395–1399. <https://doi.org/10.1007/s10764-008-9310-5>
- Stevens, N. J., Ratsimbazafy, J. H., & Ralainasolo, F. (2011). Linking field and laboratory approaches for studying primate locomotor responses to support orientation. In K. D'août & E. E. Vereecke (Eds.), *Primate locomotion: Linking field and laboratory research* (pp. 311–333). Springer.
- The MathWorks Inc. (2023). Computer vision toolbox version: 23.2 (R2023b), *The MathWorks Inc.* Natick. <https://www.mathworks.com/help/vision/ug/using-the-single-camera-calibrator-app.html>
- Theriault, D. H., Fuller, N. W., Jackson, B. E., Bluhm, E., Evangelista, D., Wu, Z., Betke, M., & Hedrick, T. L. (2014). A protocol and calibration method for accurate multi-camera field videography. *The Journal of Experimental Biology*, 217(11), 1843–1848. <https://doi.org/10.1242/jeb.100529>
- Tobalske, B. W., Warrick, D. R., Clark, C. J., Powers, D. R., Hedrick, T. L., Hyder, G. A., & Biewener, A. A. (2007). Three-dimensional kinematics of hummingbird flight. *Journal of Experimental Biology*, 210, 2368–2382. <https://doi.org/10.1242/jeb.005686>
- Uhlmann, V., Ramdya, P., Delgado-Gonzalo, R., Benton, R., & Unser, M. (2017). FlyLimbTracker: An active contour-based approach for leg segment tracking in unmarked, freely behaving drosophila. *PLoS One*, 12(4), e0173433. <https://doi.org/10.1371/journal.pone.0173433>
- Urban, S., Leitloff, J., & Hinz, S. (2015). Improved wide-angle, fisheye and omnidirectional camera calibration. *ISPRS Journal of Photogrammetry and Remote Sensing*, 108, 72–79. <https://doi.org/10.1016/j.isprsjprs.2015.06.005>
- Vereecke, E. E., & D'Août, K. (2011). Introduction. Primate locomotion: Toward a synergy of laboratory and field research. In K. D'Août & E. E. Vereecke (Eds.), *Primate locomotion: Linking field and laboratory research* (pp. 1–6). Springer.
- Walker, J. A. (1998). Estimating velocities and accelerations of animal locomotion: A simulation experiment comparing numerical differentiation algorithms. *Journal of Experimental Biology*, 201(7), 981–995. <https://doi.org/10.1242/jeb.201.7.981>
- Warren, R. D., & Crompton, R. H. (1998). Diet, body size and the energy costs of locomotion in saltatory primates. *Folia Primatologica*, 69, 86–100.
- Warrick, D. R., & Dial, K. P. (1998). Kinematic, aerodynamic and anatomical mechanisms in the slow, maneuvering flight of pigeons. *Journal of Experimental Biology*, 201(5), 655–672. <https://doi.org/10.1242/jeb.201.5.655>

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