NEW APPROACHES

Testing Parallel Laser Image Scaling for Remotely Measuring Body Dimensions on Mantled Howling Monkeys (*Alouatta palliata*)

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Body size is a fundamental variable for many studies in primate biology. However, obtaining body dimensions of wild primates through live capture is difficult and costly, so developing an alternative inexpensive and non-invasive method is crucial. Parallel laser image scaling for remotely measuring body size has been used with some success in marine and terrestrial animals, but only one arboreal primate. We further tested the efficacy of this method on the arboreal mantled howling monkey (*Alouatta palliata*) in La Pacifica, Costa Rica. We calculated interobserver error, as well as the method's repeatability when measuring the same animal on different occasions. We also compared measurements obtained physically through live capture with measurements obtained remotely using parallel laser image scaling. Our results show that the different types of error for the remote technique are minimal and comparable with the error rates observed in physical methods, with the exception of some dimensions that vary depending on the animals' posture. We conclude that parallel laser image scaling can be used to remotely obtain body dimensions if careful consideration is given to factors such as species-specific morphology and postural habits. *Am. J. Primatol.* 77:823–832, 2015.

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INTRODUCTION

Body size is a crucial variable in behavioral ecology, providing data that are imperative to understanding adaptations such as clutch/offspring size, sexual selection, growth, and life history, as well as the intersection between these variables and ecological parameters such as habitat quality and dietary preferences [e.g., Bergeron, 2007; Caillaud et al., 2008; Lourie et al., 2014; Rothman et al., 2008; Wijeyamohan et al., 2012]. In addition, data on body size have significant implications for conservation policy, contributing to our understanding of relationships between habitat quality and alteration with variables such as growth rates and population-level changes in body size over time [e.g., Berger, 2012; Rohner et al., 2011]. Measuring body size in captivity does not provide adequate information to address these questions because, in many species, body size and growth rates can differ considerably from wild conspecifics due to environmental circumstances including provisioning and lack of predator pressure [e.g., Altmann & Alberts, 2005; Leigh, 1994; Smith & Jungers, 1997]. However, measuring body size of wild animals is challenging. Live capture of animals through methods such as traps and darting is costly

and potentially harmful to the animals [e.g., Bosson et al., 2012; Glander, 2013; Pelletier et al., 2004]. Thus, several researchers have developed techniques for remotely and noninvasively estimating body size of wild animals.

DESCRIPTION

Photogrammetric methods, which involve taking measurements of body dimensions from photographs, have been tested in whale sharks [Graham & Roberts, 2007; Jeffreys et al., 2013; Rohner et al., 2011], marine mammals [Durban & Parsons, 2006;

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Ireland et al., 2006; Lourie et al., 2014; Perryman & Lynn, 1993; Perryman and Westlake, 1998; Webster et al., 2010], large terrestrial mammals such as elephants [Lee & Moss, 1995; Morgan & Lee, 2003; Shrader et al., 2006; Wijeyamohan et al., 2012] and artiodactyls [Bergeron, 2007; Berger, 2012; Willisch et al., 2013], terrestrial primates such as baboons [Domb & Pagel, 2001], macaques [Kurita et al., 2012], gorillas [Breuer et al., 2007; Caillaud et al., 2008], and chimpanzees [Deschner et al., 2004; Emery & Whitten, 2003;], as well as one arboreal primate—red colobus monkeys [Rothman et al., 2008]. Several techniques have been developed, and they primarily differ regarding how the scale of the objects in the photograph is determined. Some researchers use scaling poles or an object of known size, including other animals that have been physically measured, in the photograph [e.g., Domb & Pagel, 2001; Deschner et al., 2004; Graham & Roberts, 2007; Ireland et al., 2006; Kurita et al., 2012; Lee & Moss, 1995; Morgan & Lee, 2003; Willisch et al., 2013]. This technique is feasible for terrestrial primates, but not for most arboreal species because the substrates are often difficult to access. Another method of photogrammetry consists of determining the relationship between a pixel and a known unit of measure through a formula calculated using the distance between the photographer and the subject, and the focal length of the camera lens [e.g., Breuer et al., 2007; Berger, 2012; Caillaud et al., 2008; Emery & Whitten, 2003; Perryman & Lynn, 1993; Shrader et al., 2006]. However, as Rothman and colleagues [2008] have noted, distance from a subject can be difficult to accurately obtain in an arboreal environment.

The technique of using parallel laser image scaling for photogrammetry involves the use of a device with two laser beams at a fixed distance from each other that are projected onto the animal or nearby surface. Photographs are taken of the animal with the laser points included in the frame. Measurements of the animal are then taken directly from the photographs using the distance between the laser points as a photo scale. Several researchers have used this technique in marine [Durban & Parsons, 2006; Jeffreys et al., 2013; Rohner et al., 2011; Webster et al., 2010], terrestrial [Bergeron, 2007; Lourie et al., 2014; Wijeyamohan et al., 2012], and arboreal environments [Rothman et al., 2008]. Some of the details vary, such as the distance between the lasers and whether the lasers are horizontal or vertical relative to each other, but the principle remains the same. There are several potential sources of error that must be carefully considered during the construction and use of the device [Bergeron, 2007; Durban & Parsons, 2007; Jeffreys et al., 2013; Lourie et al., 2014; Rothman et al., 2008; Rohner et al., 2011; Webster et al., 2010; Wijeyamohan et al., 2012]. The laser beams must be precisely

parallel, such that they are equidistant regardless of the distance between the photographer and the subject. The animal must be in a position in which landmarks are visible and the dimension is not distorted by posture (e.g., laterally flexed spine or splayed hindlimbs). The animal must be in a position relative to the photographer that minimizes error from parallax (e.g., the lateral surface of the animal perpendicular to the photographer's line of sight). In addition, the lasers must be projected on a surface that is perpendicular to the laser beams to minimize parallax distortion of the distance between the laser points. The surface of the projection must be fairly smooth, as an overly bumpy surface can distort the laser points and make their centers difficult to determine.

EXAMPLE

All research reported complied with the protocols approved by the Institutional Animal Care and Use Committees at Duke University (Protocol A130-13-05) and Regis University (Protocol 14-005), and the Animal Care Committee at the University of Waterloo (Protocol 13-10). In addition, all research conformed to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates. All research conducted in this report complied with legal requirements for conducting research in Costa Rica.

In this study we investigated the effectiveness of parallel laser image scaling to measure body dimensions of an arboreal primate, the mantled howling monkey (*Alouatta palliata*). Because arboreal primates are more difficult to remotely measure than terrestrial primates due to their relative inaccessibility, it is thus paramount to develop a suitable method for the arboreal environment. Rothman and colleagues [2008] tested this method on an arboreal primate, the red colobus monkey (*Procolobus rufomitras*), and their results showed minimal error (mean error rate of 1.7%). However, they focused on tail length, and we seek to expand the demonstration of this method to additional body dimensions. Howlers provide some advantages for this method as they are found in social groups and thus several animals can be photographed in a single data collection bout, and they are relatively inactive [Di Fiore et al., 2011] allowing for time to position the camera and lasers. In testing the accuracy of this method, our research determined the degree of three types of error: (i) interobserver error, i.e., the error associated with multiple researchers measuring the same photograph; (ii) repeatability error, i.e., the error across multiple photographs of the same animal; (iii) accuracy error, i.e., the error between measurements obtained physically from live captures and the measurements of the same animal using parallel laser image scaling.

Laser Device Description

We adapted our design from similar devices used by other researchers [e.g., Bergeron, 2007; Durban & Parsons, 2006; Jeffreys et al., 2013; Rothman et al., 2008; Wijeyamohan et al., 2012]. The engineering machine shop at the University of Waterloo constructed the device. Two lasers were mounted horizontally at 4 cm apart in two aluminum barrels which were encased in an aluminum body with PVC struts on either side to provide stability when the device was resting on a flat surface (Fig. 1a). The device was attached to a Canon EOS 7D camera with EFS 55–250 mm zoom lens using a standard tripod bolt. We used green lasers (Apinex, Montreal, model GM-CW02) because of their greater visibility in the canopy as compared with red lasers [Rothman et al., 2008].

We chose to orient the lasers horizontally rather than vertically. In the case of mantled howlers'

typical positional behavior, the lasers are most easily projected onto a branch below the animal, a tree trunk next to the animal, or on the caudal portion of the animal's body. Horizontal orientation is preferable for branches located underneath the animal, and either vertical or horizontal is acceptable for projection onto a tree trunk or the body. We tested this method on tree trunks of various sizes by projecting the lasers onto the trunk and photographing them along with an object of known size. The error was less than 1%—calculated as the difference between the remote measurement and the physical measurement of the object divided by the physical measurement—for tree trunks with diameters as small as 20 cm, so in this study we used tree trunks that were larger than 20 cm in diameter. Furthermore, horizontal placement does not necessitate the use of an inclinometer for the calculation of parallax due to the angle of orientation of the lasers.

Fig. 1. A schematic of the laser device is shown mounted to a camera; credit Sean Docherty (A); a sample photograph of a howler with laser point (B).

Aluminum can expand and contract due to ambient conditions, so the laser position was adjustable using a set of four small screws per laser. A hex key was used to tighten and loosen the screws. We calibrated the lasers' position by projecting the lasers onto a metal ruler, and adjusting them until the laser beams were 4 cm apart at three distances: 5 m, 10 m, and 20 m. Calibration was performed before, after, and during each photo session. If we found that the distance between the lasers was miscalibrated, all photos taken since the previous calibration session were discarded.

Other potential sources of parallax that could alter the distance between the laser beams include the angle of the surface that the points are projected on, and the angular orientation between the photographer on the ground and the subject in an arboreal environment. We tested the error produced by the first issue by projecting the laser on a board held at various angles tilted away from the observer, and included an object of known size in the photograph as a scale. The distance between the laser points did not increase by more than 2% of 4 cm until the board was more than 15° from perpendicular. We took care during data collection to project the lasers on surfaces, such as tree branches, that were perpendicular to the line-of-sight, but small deviations can be tolerated. The angle between the photographer and the subject was tested by projecting the lasers onto an object of known size that was held at various heights on a three-story building. The resulting error was less than 1% for all angles from horizontal to 60°, and there was no significant increase or decrease in the error with increasing angular position.

Study Sites, Subjects, and Procedure

Hacienda La Pacifica is a privately owned ranch in western Costa Rica (10°28'N, 85°07'W) including disturbed secondary growth in corridors that intersect cleared pasture. It is a lowland tropical dry forest ecozone with deciduous seasonally dry forest [Thompson et al., 2014]. Several generations of adult howlers have been darted, captured, and tagged at this site from 1972 to 2014, and details of the procedure are outlined elsewhere [Glander et al., 1991]. Physical measurements of captured howlers were taken using a measuring tape, and the landmarks are described in Table I. In July 2014, we photographed, using the laser device, 8 known animals from a well-studied group that had been physically measured on multiple occasions (Table II). We used these photographs to determine interobserver error, repeatability, and accuracy comparisons between physical and remote measurements. We also determined interobserver error rates in the physical measurements of animals that were darted on 3 or more occasions since 1972 (Table III) for

comparison to interobserver and repeatability measures using the remote parallel laser image scaling. All the animals included in this analysis were adults at the time measurements were taken.

Analyses of interobserver error and repeatability of the remote laser method were supplemented with data from La Suerte Biological Research Station in northeastern Costa Rica (10°26'N, 83°47'W). The site is a tropical premontane wet forest, including primary forest and advanced secondary growth [Bezanson, 2009]. During May–June 2014, we took 108 usable photographs from two mantled howler social groups, including adults, juveniles, and infants. Because individuals are not known, we could only test interobserver error in most of these photographs. There were, however, two sets of photographs of adult females in which we observed the individual changing positions, and these two sets of 2 and 3 photographs, respectively, were included in the analysis of repeatability (Table II).

Several photographs were taken of each individual in multiple positions at both La Pacifica and La Suerte. We sought out animals that were either walking horizontally across a branch, lying prone with their limbs dangling, or hanging by their tails because these positions allow for several landmarks to be easily located. We also measured the distance between the photographer and the animal using a Nikon ACULON laser rangefinder to ensure that we were within 20 m, as we had calibrated the 4 cm distance between the two laser beams up to 20 m. At the end of each photo session, we reviewed each photograph to determine its suitability. If any researcher detected a problem, the photograph was discarded. Problems included blurriness, bad projection of the lasers (e.g., on leaves or not visible), inability to determine body landmarks, and animals not situated perpendicular to the plane of the photograph.

Image Analysis

An example of an image of a howler with laser points is shown in Figure 1b. Photographs were downloaded and analyzed on ImageJ 1.44o, designed by the National Institutes of Health, USA, and available online at their website: <http://imagej.nih.gov/ij>. The software has the ability to set the scale of a specified distance. We measured the distance between the two laser projections, and converted the pixel length to 4 cm using this function. We were then able to measure the distances between the anatomical landmarks for each of the body measurements (Table I). We defined the landmarks and practiced measuring distances on a set of photographs not included in the present study [Barrickman & Schreier, 2014]. We measured all of the photographs in this study independently in order to determine interobserver error.

TABLE I. Description of Measurements and Landmarks

Measurement	Description
Glabella to rump (GR) ^a	From most caudal projection of brow in lateral profile to base of tail
Neck to rump (NR) ^a	From bend between skull and vertebral column when cervical spine is extended to base of tail
Body length (BL) ^a	From crown of skull when neck is flexed to base of tail
Distal forelimb (DF)	Straight line from elbow to bend in wrist or proximal edge of palmar surface if visible; for physical measurements, the styloid process on the ulnar side was used as the distal landmark
Distal hindlimb (DH)	Straight line from knee joint to bend in center of ankle joint when viewed laterally; for physical measurements, the lateral malleolus was used as the distal landmark

^aGR and NR were not physically measured. BL was not measured remotely because animals were never positioned correctly. These measurements are included in the analysis to test repeatability and interobserver error only.

Statistical Analysis

To determine interobserver error for the remote measurements, we calculated the percentage error for each individual measurement by subtracting measurer 1's datum from measurer 2's datum, and dividing this difference by measurer 1's datum. We calculated means and standard deviations of error rates for a given measurement (e.g., all the error rates for measurements of the distal forelimb). We created boxplot distributions showing medians, quartiles, and outliers of error rates for each measurement. Pearson's correlation coefficient was also calculated to determine the correlation between the two researchers' datasets (P value of ≤ 0.05 was considered statistically significant). Percentage error was also calculated to determine interobserver error for the physical measurements, calculated by subtracting the minimum value obtained for a given measurement on a specific animal from the maximum value, and dividing the difference by the maximum value. Means and standard deviations of interobserver error rates for measurements (e.g., mean of errors from measurements of distal forelimbs) were compared between remote and physical measurements using Mann–Whitney U rank-sum test (P value of ≤ 0.05 was considered significant; two-tailed). Spearman's rank correlation coefficient

was performed to determine whether error rates were related to the magnitude of the measurement (P value of ≤ 0.05 was considered significant).

Percentage error was used to determine degree of repeatability (i.e., multiple photographs of the same animal in differing positions) and the error rates for accuracy (i.e., the differences between physical and remote methods in measurements of the same animal). We compared means, standard deviations, and boxplots of error distributions for each measurement using each method. Spearman's rank correlation coefficient was performed to determine whether repeatability was related to the magnitude of the measurement (P value of ≤ 0.05 was considered significant).

We also calculated absolute error (i.e., length of error in cm rather than as a percentage) to compare error rates with the sex-specific means and standard deviations of the body dimensions among all the animals our study group.

RESULTS

The distributions of the two trunk measurements demonstrate some sexual dimorphism in the measurements that include the skull (Glabella to Rump, GR, and Body Length, BL; Fig. 2; Table IV).

TABLE II. Sample Composition; All Animals Were Measured Physically and Remotely Except for the Two Adult Females from La Suerte and Zen from La Pacifica, Who Were Measured Remotely Only

Name/Identifier	Site	Sex	Sets of photographs
Talia	La Pacifica	F	2
Zanahoria	La Pacifica	F	2
Fuschia	La Pacifica	F	3
Mimosa	La Pacifica	F	4
Hibiscus	La Pacifica	F	6
AF 1	La Suerte	F	2
AF 2	La Suerte	F	3
Rambo II	La Pacifica	M	2
Zen	La Pacifica	M	3
Aguacate	La Pacifica	M	6

TABLE III. Sample Composition of Animals Used to Determine Error Rate in Physical Measurements. Animals Were Captured and Measured Between 1972 and 2014

Number of occasions animal was captured and physically measured	N (number of animals)
3	26
4	12
5	1
6	6
7	3
8	1
9	1
12	1
Total	51

Physical and remote measurements cannot be directly compared for trunk measurements because the landmarks differed between the two techniques. The distributions of limb measurements also show some sexual dimorphism using both methods (Fig. 3; Table IV). There was considerable overlap in Distal Forelimb (DF) measurements between the physical and remote methods, but not in the Distal Hindlimb (DH) measurements. The remote method consistently resulted in shorter DH measurements than the physical method.

Analyses of interobserver error using the remote parallel laser method showed an average percentage of error across all measurements of 3.62% with a standard deviation of 2.90%. The mean interobserver error rates and correlation coefficients in remote measurements varied depending on the measurement (Fig. 4). Analyses of physical measurements taken at La Pacifica revealed higher levels of interobserver error than the remote method (mean = 7.08%; SD = 4.81%; Fig. 5). The results of the Mann-Whitney U rank-sum test revealed significant differences between the interobserver error rates of trunk length measurements, with physical measurements resulting in higher error rates (mean error rate for body length = 6.13%) than remote measurements (mean error rates for GR = 2.75% and NR

= 2.74%) (Mann-Whitney U rank-sum of trunk length error rate v. GR error rate: $U = -438$, d.f. = 47, $P < 0.0001$, two-tailed; trunk length v. NR: $U = -430$, d.f. = 47, $P < 0.0001$, two-tailed). There were no significant differences between interobserver error rates for limb measurements across the remote and physical measurements (mean error rate physical measurement of DF = 4.25%, mean error rate for remote measurement = 3.52%, Mann-Whitney U rank-sum: $U = -2.5$, d.f. = 4, $P = 0.6$, two-tailed; mean error rate of physical measurement of DH = 5.79%, mean for remote measurement = 4.16%, Mann-Whitney U rank-sum: $U = -7.0$, d.f. = 6, $P = 0.28$, two-tailed).

Measurements of a smaller magnitude (i.e., limbs) resulted in a greater percentage of interobserver error than trunk measurements using both the physical and remote methods. The error rates from both the remote and physical methods were combined to test for relationships with the magnitude of measurement, and the non-parametric Spearman's rank correlation was significant ($\rho = -0.57$, $N = 14$, $P = 0.03$, two-tailed). However, the absolute error was smaller in the case of smaller measurements. Using the remote method, the average error in the trunk length measurements (GR and NR) was 1.2 cm, DF was 0.75 cm, and DH was 0.56 cm. As with the remote method, the absolute error using the physical method was higher among the greater measurements (e.g., absolute error of body length was 3.4 cm as compared to 0.7 cm in the hindlimb and 0.4 cm in the pollex).

The results of tests of repeatability, or multiple measurements of the same individual taken from different photographs in varying positions, reveal that error varied depending on the measurement (Fig. 6). The measurements of trunk length had lower error rates (GR mean = 6%; NR mean = 5.4%) than the limb measurements (DF mean = 8.4%; DH mean = 18%). Thus, hindlimb measurements had a particularly low repeatability. Absolute rates showed an average error of 3.1 cm for GR, 2.1 cm for NR, 1.4 cm for DF, and 2.6 cm for DH. Spearman's rank

Fig. 2. Distribution of trunk measurements taken physically (BL) and remotely (GR and NR). Sample sizes are indicated in parentheses. Open boxes denote females and shaded boxes denote males. BL = body length; GR = glabella to rump; NR = neck to rump.

TABLE IV. Comparison of Measurement Means and Standard Deviations with Error Rates; All Values Are in cm

Measurement ^a	Male Mean, Standard Deviation ^a	Female Mean, Standard Deviation ^a	Mean Interobserver Error (physical)	Mean Interobserver Error (remote)	Mean Repeatability Error	Mean Error Physical v. Remote
BL	49.43, 2.73	44.79, 2.45	3.44	b	b	b
GR	52.70, 4.25	50.30, 3.29	b	1.39	3.08	b
NR	40.24, 4.91	39.68, 1.83	b	1.06	2.15	b
DF	17.57, 1.09	15.82, 1.57	0.62	0.76	1.37	1.01
DH	14.01, 1.54	13.57, 1.59	0.65	0.56	2.57	1.86

^aThe means and standard deviations provided in this table are from measurements taken using the remote method with the exception of BL, which is from physical measurements. Details regarding sample size are provided in the text and Tables II and III.

^bThese error rates were not calculated for this study. See text for details.

correlation test showed no significant relationship between the degree of repeatability error and the magnitude of the measurement ($\rho = -0.80$, $N = 5$, $P = 0.20$, two-tailed). However, the sample size (i.e., number of measurements) was small, and it is difficult to determine whether a correlation exists without a larger sample.

Only measurements of DF and DH were comparable between the physical and remote methods. For other physical measurements, remote measurements were not possible because either landmarks could not be reliably located in the photographs, as was the case for proximal limbs, or the animals did not naturally assume the proper position for measurements such as body length. The results showed differing distributions of error depending on the measurement (Fig. 7). The DF measurements had an average error of 6.3%, resulting in an absolute error of 1.0 cm. The DH measurement had a considerably higher average error of 13.1%, resulting in an absolute error of 1.9 cm.

A comparison between measurement distributions and absolute errors (i.e., length of error in cm)

Fig. 3. Distribution of limb measurements taken physically and remotely (DF = distal forelimb, and DH = distal hindlimb). Measurements of females are indicated by white boxes and males by shaded boxes. Physical measurements are denoted by "p" following the measurement code and do not have speckled pattern in the boxes, and remote measurements are denoted by "r" and have speckled pattern in the boxes. Sample sizes are indicated in parentheses.

showed that the error was less than the standard deviation of sex-specific distributions in most cases except DH (Table IV). These results indicate that the natural variation in most body dimensions of the population exceeded the error variation of both physical and remote methods.

COMPARISON AND CRITIQUE

The interobserver error rates using the remote parallel laser image scaling are lower than those of the physical method, and significantly lower in the case of trunk measurements. The difference between the interobserver rates could be because two observers measured animals using the remote method during a single field season, whereas several researchers performed physical measurements over several field seasons from 1972 to 2014. Waite and Mellish [2009] emphasize that interobserver error rates in physical measurements are rarely compared with error rates in photogrammetry. In their study comparing these two measurement methods in sea lions, they found no significant differences between interobserver rates [Waite & Mellish, 2009]. However, to be comparable to multiple occasions of live capture and measurement, the repeatability (multiple photographs of the same individual) of the

Fig. 4. Interobserver error percentages using the remote method. The first value in parentheses is the sample size (i.e., number of times the measurement was taken by each observer; multiple animals are included), followed by the Pearson's correlation coefficient. GR = glabella to rump; NR = neck to rump; DF = distal forelimb; DH = distal hindlimb.

Fig. 5. Interobserver error percentages using the physical method, separated by measurement. The sample size, in terms of number of animals that were measured on multiple occasions, was 51 animals for all measurements except for distal hindlimb (4 animals) and distal forelimb (6 animals). See text and Table III for details regarding sample composition.

remote method must be considered. The repeatability error rates in our study are similar to the interobserver error rates for physical measurements of trunk measurements, but the repeatability error rates for limb measurements are higher using the remote method. This result is likely explained by the greater variability of limb position as compared with trunk position. The howlers' limbs were not always precisely perpendicular to the camera's line-of-sight. We eliminated many of the photographs with this problem before the image analysis stage, but some degree of error was difficult to avoid in field conditions as the animals are rarely in an ideal position for the measurement of certain body dimensions. Specifically, we noted that the animals' hindlimbs were often splayed when resting in a prone

Fig. 6. Distribution of repeatability error, i.e., measurements from multiple photographs of the same individual in different positions. Sample sizes are as follows: GR consists of 2 individuals measured twice and 2 individual measured 3 times; NR consists of 3 individuals measured twice and 1 individual measured 3 times; DF consists of 5 individuals measured twice; DH consists of 3 individuals measured twice, 2 individuals measured 3 times, and 2 individuals measured four times. GR = nglabella to rump; NR = neck to rump; DF = distal forelimb; DH = distal hindlimb.

Fig. 7. Distribution of error between measurements of same animals using physical and remote methods. The sample size is 7 animals for each measurement. DF = distal forelimb; DH = distal hindlimb.

position on a horizontal branch with the limbs hanging down, a common resting posture in howlers.

The repeatability error rates in this study are higher than those found by some other researchers who tested methods of photogrammetry. For instance, Bergeron [2007] found a particularly low mean repeatability error of 3.1% when measuring the annuli of ibex using parallel laser image scaling. In contrast, our mean repeatability error rate ranged from 5.4% (2.1 cm) for NR to 18% (2.6 cm) for DH measurements. Other studies, however, found a mean absolute repeatability error that is similar to or greater than our results. Caillaud and colleagues [2008] remotely measured gorillas, determining scale through a calculation involving distance from object and focal lens length. Their mean repeatability error was 5.07 cm for body length (percentage not provided; approximately 5% given a mean body length of 89.4 cm). Durban and Parsons [2006] found similar repeatability error rates to the present study when they remotely measured dorsal fin size in killer whales using parallel laser image scaling. Error in females averaged 9% (6 cm), whereas error in males averaged 16% (23 cm). They attribute their error rates to several factors, primarily the parallax from orientation of photographer above the whale and fins that were not positioned perpendicular to the surface of water [i.e., tilted towards the photographer; Durban & Parsons, 2006]. These factors also affected our study. In an arboreal environment, there is parallax as the photographer is always below the animal. In addition, postural issues were present in our study, as noted above—limbs were rarely precisely perpendicular to the camera's line-of-sight. The distal hindlimbs, exhibiting the highest mean repeatability error, were particularly problematic because of the postural variation. Because live capture is often not possible, many studies validated their remote measurements by using objects of known size such as boards rather than study animals, and obtained low error rates [e.g., Jeffreys

et al., 2013; Perryman & Lynn, 1993; Wijeyamohan et al., 2012]. However, animals have complex morphologies and tests for accuracy on the actual study subjects, as in our study, is ideal. Rothman and colleagues [2008] demonstrated the efficacy of parallel laser image scaling in measuring tail length in red colobus monkeys, with a low mean error rate of 1.7% (1.1 cm) as compared to physical measurements. Physically and remotely obtained measurements of ibex annuli also had low error rates; Bergeron's [2007] results showed a mean error rate of 3.9% (0.2 cm), while Willis and colleagues' [2013] results showed that 88% of the annuli were within 0.75 cm of one another. We were able to directly compare physical and remote measurements of the limbs, and our mean error rates were higher than previous studies though the absolute error rates were comparable to the measurements of red colobus tails (6.3% or 1.0 cm and 13.1% or 1.9 cm for the DF and DH, respectively). As with previous analyses of error rates detailed above, the distal hindlimbs were particularly problematic, likely the result of the howlers' postural behavior. For some body dimensions such as distal hindlimbs in howlers, it is difficult to replicate measurements with small degrees of error because of the animals' positional behavior. Tail length in colobus and horn annuli in ibex are easier to replicate than trunk or limb length because the tails and horns are not as variable in position during the animals' normal behavior as the trunk and limbs. However, body dimensions such as trunk and limb length are more pertinent than tail length to many aspects of primate biology, such as sexual dimorphism or growth and development. Thus, determining a reliable method for remotely measuring these dimensions is paramount, especially as live capture and measurement is prohibitively expensive and potentially dangerous. As long as a given measurement can be repeated on the same individual at different times and different locations (assuming the animal is an adult), they are reliable indicators and provide valuable data. After completing the analyses reported above, we re-examined our photographs using stricter criteria regarding consistency of posture, and eliminated several photographs. We did not have a large enough sample for analysis, but we were able to reduce the repeatability error to less than 3% in three individuals for which we had multiple photographs.

In line with previous studies, the results of this study reveal both the benefits and limitations of remotely obtained measurements. For some measurements, we found high error rates, primarily due to three factors. First, the limbs of howlers are smaller than the dimensions used in other studies, such as body length in gorillas or tail length in red colobus monkeys. Our results revealed a strong correlation between the magnitude of the measurement and the degree of error, so the measurement of smaller

species can be difficult. Second, landmarks and appropriate postures can be difficult to obtain for some body dimensions, as we noted for distal hindlimbs. Thus, the postural habits of the species must be carefully considered before a reasonable assessment of possible measurements can be made. Finally, using remote measurements in an arboreal environment versus a terrestrial environment adds another potential source of error—the parallax in body position created by the angle of the line-of-sight is often inevitable because the photographer must be below the animal. Thus, researchers should consider remotely measuring animals on only lower substrates.

Despite the limitations, parallel laser image scaling has substantial advantages. Live capture is costly and invasive, and remote techniques are relatively inexpensive and non-invasive. In addition, error from parallel laser image scaling is less than the variation in body dimensions in howlers (as indicated by the standard deviation), demonstrating that the measurements are a reliable biological signal. With careful consideration of factors such as species-specific morphology and postural habits, remote measurements can be obtained that are as reliable as physical measurements. With time, patience, luck, and strict adherence to postural criteria, researchers can obtain body size dimensions non-invasively in wild arboreal populations.

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