Within Arm's Reach: Measuring Forearm Length to Assess Growth Patterns in Captive Bonobos and Chimpanzees

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ABSTRACT

Objectives: Bonobos and chimpanzees are known to differ in various morphological traits, a dichotomy that is sometimes used as an analogy for evolutionary splits during human evolution. The aim of our study was to measure the forearm length of immature and adult bonobos and adult chimpanzees to assess the extent of age–related changes of forearm length in bonobos and sex–dimorphism in bonobos and chimpanzees.

Materials and methods: As a proxy of somatic growth we measured forearm length of captive bonobos and chimpanzees ranging in age from 1 to 55 years. Measures were taken from subjects inserting their arms into a transparent Plexiglas® tube, a novel technique facilitating repeated measures of nonanesthetized apes in captivity.

Results: Measures from adult females (>12 years) showed that bonobos exceed chimpanzees in terms of forearm length and that sexual dimorphism in forearm length is pronounced in chimpanzees, but not in bonobos. Forearm length increased significantly with chronological age in bonobos. Validation tests revealed that the device generates useful data on morphometric dimensions.

Discussion: In most primates, sexual dimorphism in body size is male-biased and the differences in forearm length in chimpanzees follow this trend. Given that males of the two species did not differ in forearm length, the absence/presence of sexual dimorphism of this trait must be due to differences in somatic growth in females. Our novel method offers an alternative to obtain morphometric measures and facilitates longitudinal studies on somatic growth. Am J Phys Anthropol 000:000–000, 2016.   © 2016 Wiley Periodicals, Inc.

There is a long history of morphometric studies in primates and particularly in hominoids. Morphometric measures have provided references for positional behavior and locomotion (Hunt, 1991; Doran, 1993), the intensity of mate competition (Plavcan, 2001), food processing (McGraw and Daegling, 2012), and tool use (Boesch and Boesch, 1993). Morphometry is particularly useful for exploring and comparing stages of somatic growth and development (Roth and Mercer, 2000; Leigh, 2005). Measurements of skeletons from museum collections are a common source for morphometric data (Zihlman and Cramer, 1978; Mitteroecker et al., 2005; Lieberman et al., 2007). While measures of bones provide precise information about size and shape, interpretation of such data is often limited (Morimoto et al., 2011), because of the lack of reliable information on chronological age (Bingham, 1929; Gavan, 1953). Accordingly, the relationship between age and somatic growth is often estimated, making the detection of age-specific developmental stages and its variation within and across species a difficult task (Smith and Boesch, 2011). In addition, the nature of the material excludes the option of longitudinal measures of temporal patterns of growth (Hamada and Udono, 2002), an essential prerequisite for elucidating causal factors of growth and development (Hamada

and Suzuki, 1991). Taking morphometric measures from living apes can be a challenging task, and therefore data are usually collected from captive animals during anesthesia (e.g., Gavan, 1953; Watts, 1993; Schoonaert et al., 2007). However, such interventions are rare due to ethical reasons, preventing the collection of morphometric data on a regular basis.

Recently, photogrammetric techniques have been developed to obtain morphometric measures from wild apes offering a promising alternative to explore body size and shape, growth rates, and developmental
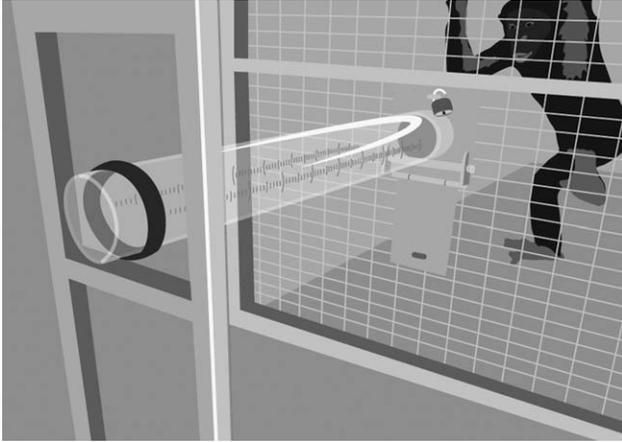
Fig. 1. Schematic picture of the plastic transparent Plexiglas® tube, attached to the fence of an ape enclosure.

features in natural settings (Deschner et al., 2004; Breuer et al., 2007; Rothman et al., 2008). The success of this approach depends often on the technical conditions to obtain high quality pictures and the possibility to place the camera in the correct position (90 degree angle) to the subject, conditions that are not always easy to meet in a natural environment. For example, when taking body size measures of wild Western gorillas, only 20–30% of the pictures met the criteria for taking morphometric data (Breuer et al., 2007).

Bonobos and chimpanzees are sister species with distinct traits in morphology, behavior, physiology, and life histories (e.g., Barriel, 1997; Boesch et al., 2002; McIntyre et al., 2009; Herrmann et al., 2010; Jaeggi et al., 2010; Behringer et al., 2014), and the dichotomy between the two species is often used as an analogy for evolutionary splits observed within the human evolutionary line (Ponce de León and Zollikofer, 2008). There is information on somatic growth in chimpanzees (*Pan troglodytes*) from both cross–sectional and longitudinal studies (Gavan, 1971; Hamada and Udono, 2002; Hamada et al., 2003). However, to our knowledge, corresponding data sets from living bonobos (*Pan paniscus*) are not available yet. Early studies on bonobos and chimpanzees have highlighted the differences in cranial and postcranial morphology and it was concluded that the morphological traits characterizing bonobos evolved via the process of neoteny (McHenry and Corruccini, 1981). It was thought that the differences in body size and ontogenetic trajectories indicated a heterochronic shift towards paedomorphic features in bonobos (Shea, 1983, 1988). However, when combining information from different data sets, interspecific differences in body size measures seem to be partly explained by the large intraspecific variation in chimpanzees. For example, comparison of postcranial measures revealed that bonobos are taller than Eastern chimpanzees (*Pan troglodytes schweinfurthii*) (Morbeck and Zihlman, 1989), but smaller than Western chimpanzees (*P. t. verus*) (Zihlman et al., 2008). Bonobos were also found to have a shorter arm span length than central chimpanzees (*P. t. troglodytes*) (Coolidge and Shea, 1982). Taken together, while bonobos and chimpanzees differ in their overall morphological appearance, they overlap in many body size measures and the inter-specific variation appears to depend on the chimpanzee subspecies (Zihlman and

Cramer, 1978; Coolidge and Shea, 1982). While the use of morphometric data remains an important source of information, comparing studies on bonobos and chimpanzees, the taxonomy of chimpanzees must be taken into account (Zihlman, 1984).

Here, we use a novel technique to collect cross-sectional data on forearm length that can be applied repeatedly to living captive bonobos and chimpanzees. To our knowledge this is the first data set of body size development in living bonobos. In addition, we assessed the magnitude of sexual dimorphism in forearm length of adult male and female bonobos and chimpanzees, while considering different subspecies of the latter.

MATERIALS AND METHODS

Arm Measure Device

Morphometric measurements from bonobos and chimpanzees were obtained with a device consisting of a transparent Plexiglas® tube that is fixed on a metal frame that can be attached easily to enclosures of zoo facilities (Fig. 1). The tube is 1.40 m long, has a diameter of 12.5 cm, and a metric scale on each side. When taking measurements, the device is attached to a metal plate that is integrated into the wire or bars of the compartment (Fig. 1). Technical information of the device is given in the supplement (Supporting Information Additional File 1).

Ethics Statement

Our method to measure forearm length in apes is a noninvasive method. It was carried out in accordance with NIH published standards and the protocol of data collection was approved by authorities of each zoo. The study was supported by the coordinators of the EAZA Western Chimpanzee EEP and Robust Chimpanzee ESB (Frands Carlsen and Tom de Jongh) as well as by the EEP bonobo coordinators (Jeroen Stevens and Zjef Pereboom). The study was approved by Dr. Fritsche from the Amt für Verbraucherschutz und Veterinärwesen of Switzerland.

Study Subjects

Forearm measures were taken from 29 female and 26 male bonobos and from 23 female and 12 male chimpanzees living in nine different zoos (Supporting Information Table S1). Data were obtained from subjects between 1 and 54 years of age (Supporting Information Table 1). According to studbook information, 15 of the 35 chimpanzees involved in this study belonged to the Western subspecies *P. t. verus*, 16 individuals were subspecies hybrids, and two chimpanzees are *P. t. troglodytes*. In two individuals, the subspecies status has not yet been identified (Supporting Information Table 1) (personal communication, C. Hvilsom and F. Carlsen).

Age Classification

The exact chronological age was known for 53 of the 55 bonobos, and for 32 of the 35 chimpanzees. For the five individuals of unknown age, we used age estimates provided by the studbook. To compare forearm length in bonobos and chimpanzees obtained in this study with published data, we adopted the scheme used by Schoonaert et al. (2007) which considers chimpanzees as adult when older than 12 years of age.

TABLE 1. Comparison of forearm length of bonobos and chimpanzees older than 12 years of age

Species	Sex	N	Age (years)	Forearm length (cm)	SD	CV (%)	Min. (cm)	Max. (cm)
Bonobo	M	13	23.6	31	4.2	13.6	26.3	39.7
	F	13	24	30.9	2.9	9.7	26.8	37.4
Chimpanzee	M	9	25.3	31.5	1.5	4.8	29.2	33.7
	F	22	30	27.5	2.4	8.6	23.5	31.8

Entries refer to species, males (m), and females (f), corresponding sample sizes (N), as well as average age at sampling time (years), the average forearm length, standard deviation (SD), the coefficient of variation (CV%), minimum (Min.) and maximum (Max.) forearm length.

Measuring Forearm Length

Morphometric measurements were taken from digitized images from video recordings of individuals inserting their arms into the tube. Two commercial video camcorders (Sony HDR–CX115EB Full HD Camcorder) were placed on each side of the tube. Video recordings were scanned with the freeware VLC video player and digitized images of inserted arms were taken from the lateral view of the arm. The digitized images were analyzed using the freeware ImageJ (Abràmoff et al., 2004). Pictures were taken when subjects reached out for food placed at the far end of the tube. Apes insert their arms spontaneously. No training, e.g., positive reinforcement training, was necessary, although some individuals were familiar with it. By reaching out for a reward the position of the hand was orthograd and the forearm was pronated. Measurements were based on the constant distance between two marks along the scale of the tube. The distance between two marks (10 cm) provided the reference value for the program to account for deviations of the 90 degree angle between camcorders and forearm (Fig. 2a,b). When the distances between two marks on the screen decreased (<10 cm), this deviation was transposed to the object of measurement. Measurement of forearm length was taken from two anatomical surface landmarks that are clearly visible when arms are seen in lateral view even when subjects had long and dense fur (Fig. 2a,b or in color supporting information Fig. S1a–c): (1) One is located distally at the wrist at the depression between the base of the thumb and distal radius (at roughly the internal position of the scaphoid). (2) The other is proximally at the point of the posterior depression of the lateral group of forearm extensor muscles (e.g., *brachio radialis* and *extensor carpi radialis* muscles) and just lateral to the *cubital fossa* (Fig. 2a,b).

Method Validation

The accuracy and reliability of the method to measure forearms was tested in the following ways: First, we compared measures taken from five different digitized images of the same individual ($N_{bonobo} = 7$; $N_{chimpanzee} = 6$) during the same session. Second, repeated measures were taken from the same digitized images of randomly selected pictures from ten different individuals ($N_{bonobo} = 5$; $N_{chimpanzee} = 5$). Third, interobserver reliability in assessing forearm length was tested with video material of ten different individuals. Fourth, we compared direct measures of forearm length obtained with a tape measure from six chimpanzees that had to be anesthetized for management reasons with measures of the same individuals taken from digitized images. Validation details are given in supplement (Supporting Information Additional File 2).

Statistical Analyses

We used a two-tailed t test to compare forearm length of female chimpanzee subspecies. To compare observer reliability we ran a Spearman's correlation and a paired t test. A paired t test was also run to explore differences between forearm measures with the device and measures taken during anesthesia of the same individuals. To explore sexual dimorphic differences in forearm length in male and female adult bonobos and chimpanzees we ran a two-way ANOVA applied to log transformed forearm length of each sex and species. For subsequent *post hoc* comparison, we used a Tukey's test.

To test how forearm length in bonobos varies with chronological age and sex we ran a general linear mixed model (GLMM, Baayen, 2008) using the function lmer provided in the package lme4 (Bates et al., 2013). All tests were run in R (R Core Team, 2015). The response variable "forearm length" was tested by visual inspection of a histogram and was normally distributed. The model included as fixed effects chronological age (continuous variable) and sex as well as a two-way interaction of them. The interaction was included in the model, to account for the possibility that the age-related changes in forearm length were sex–specific as suggested (Leigh and Shea, 1995). As a random effect, we included the facility to control for a possible influence of relevant animal husbandry conditions. Furthermore, we included random slopes of chronological age at sampling time within zoo, to keep type I error rates at the nominal level of 5% (Barr et al., 2013). Chronological age was square root and z-transformed to a mean of zero and a standard deviation of one to achieve comparable estimates (Schielzeth, 2010). All model assumptions were met and model stability was tested by excluding zoos, one at a time that did not indicate any obvious influence of this random effect. We examined Variance Inflation Factors (VIF, Field (2009)) using the function vif of the R-package car (Fox, 2011), to test for the absence of collinearity. Maximum VIF was 1.001 that indicated that collinearity was not an obvious issue.

To establish the significance of the two fixed effects sex and chronological age, and the interaction as a whole (Forstmeier and Schielzeth, 2011), we did a full–null model comparison (excluding the predictor variables and the interactions, but retaining the random effect of zoo as well as the random slopes component) using a likelihood ratio test (Dobson and Barnett (2008), R function 'ANOVA'). Significance for all tests was set at the $P = 0.05$ level.

RESULTS

(A) Validation of the Method

Repeated interobserver measures of the same individual found an average difference for a forearm of 0.5 cm
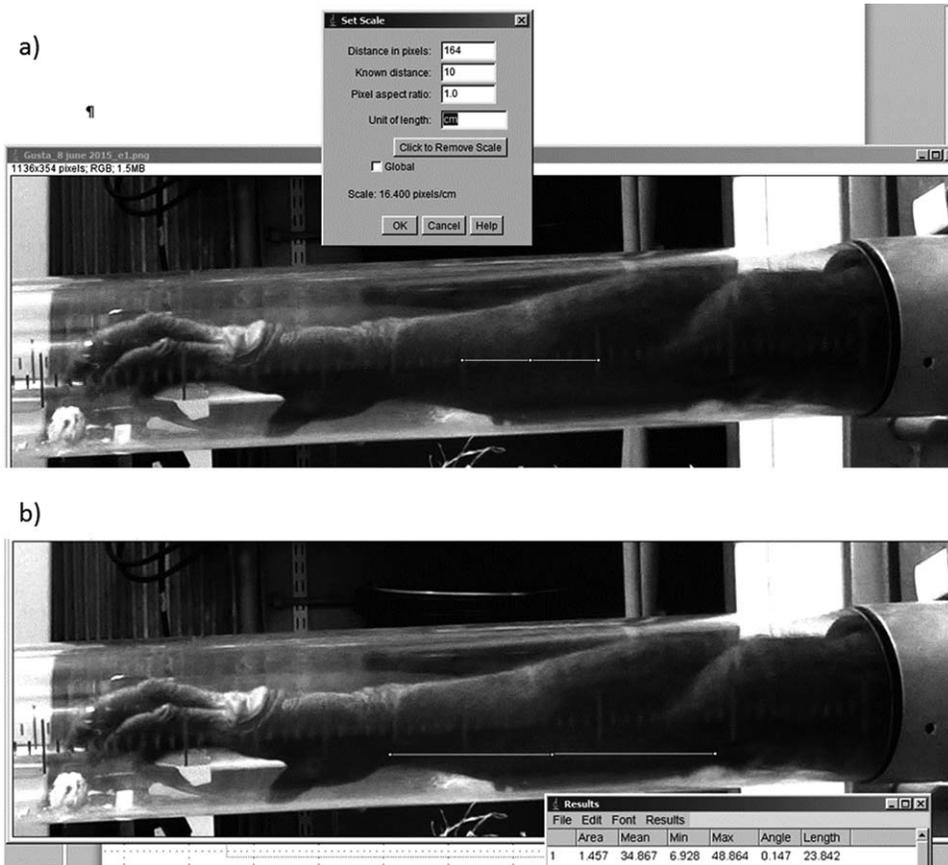
Fig. 2. a, b: Using the freeware ImageJ, we used the scale on the tube to have a referential distance of 10 cm for each picture. Forearm length was taken from two anatomical surface landmarks as descript in the text.
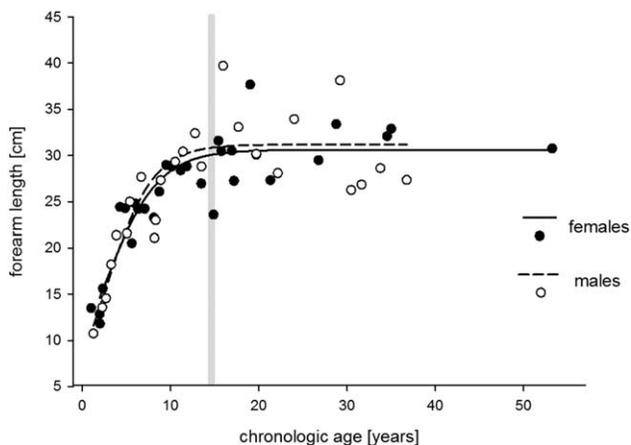

Fig. 3. Forearm length of 55 bonobos ($N_{males} = 26$, $N_{females} = 29$) in relation to chronological age at sampling date. The gray bar marks the time when forearm lengths visually reached a plateau in both sexes.

in bonobos and 0.3 cm in chimpanzees. Forearm measurements taken by the second observer correlated significantly with those obtained by the first observer (Spearman's rank correlation: $r_S = 0.9$, $P < 0.001$, $N = 10$ digitized images from ten different individuals), and measurements of both observers were not systematically biased (paired t test: $t = -0.4275$, $df = 9$, $P = 0.6791$).

The average difference between measurements taken with a tape during anesthesia with measurements of the same individuals from the digitized images was not significantly different (average difference: 0.4 cm, $t = 0.3374$, $df = 5$, $P = 0.7495$). Detailed validation results and tables are given in Supporting Information Additional File 2.

(B) Age-Related Variation of Forearm Length in Bonobos

Investigating the relationship of sex and chronological age on forearm length, the comparison between the full model and null model revealed significant effects ($\chi^2 = 10.797$, $df = 3$, $P < 0.01288$). The two–way interaction of sex and chronological age was not significant (Estimate = 0.275, SE = 1.227, z value = 0.224, $P = 0.836$), and therefore was excluded from the model. These results suggest that males and females do not differ in terms of age-related changes of forearm length. In the reduced model, sex and chronological age were run as fixed effects. Sex showed no significant impact on the response variable (Estimate = 0.320, SE = 1.149, z value = 0.278, $P = 0.784$), whereas the chronological age was a significant predictor of forearm length (Estimate = 4.954, SE = 0.784, z-value = 6.319, $P = 0.001$), revealing that forearm length significantly increases with chronological age in bonobos. Forearm length ranged from 10.8 cm in a 1.2-year-old male to 39.7 cm in a 15.9-year-old male. Two curves fitted through the data for males
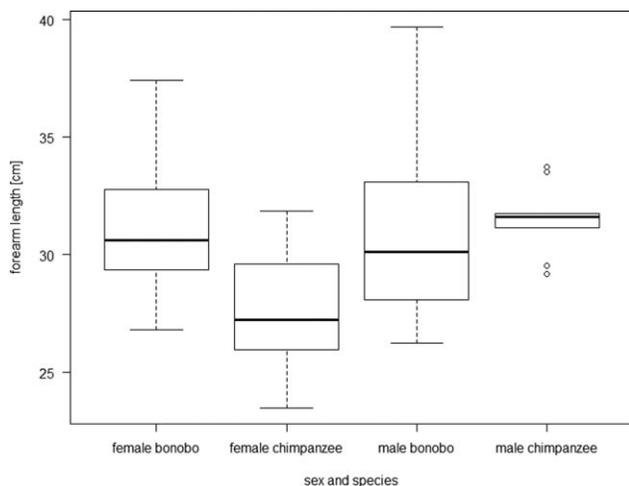
Fig. 4. Average forearm length measures in both sexes of bonobos and chimpanzees (N_{bonobo} = 13 males and 13 females; $N_{\text{chimpanzee}}$ = 9 males and 22 females). Boxes indicate the 25th and 75th percentiles, the whiskers indicate the 10th and 90th percentiles, and the bars indicate the range.

and females, respectively, show a visual increase in arm length until 13–15 years of age (Fig. 3).

(C) Comparison of Forearm Length in Adult Bonobos and Adult Chimpanzees

Adult female chimpanzees (N = 22) had an average forearm length of 27.5 cm (SD = 2.4 cm) and adult males chimpanzees (N = 9) had an average forearm length of 31.5 cm (SD = 1.5 cm). The CV was larger in measurements taken from females than in those from males (CV$_{\text{males}}$ 4.8% versus CV$_{\text{females}}$ 8.6%) (Table 1).

Considering taxonomic status of chimpanzees, forearm length of female chimpanzees ranged from 28.2 cm (SD = 1.9 cm) in *P. t. verus* (N = 11), to 27.5 cm (SD = 2.8 cm) in hybrids (N = 11). A comparison of forearm length did not indicate taxonomic differences (T = 0.7537, df = 17.53, P = 0.4611).

In female bonobos older than 12 years (N = 13) average forearm length was 30.9 cm (SD = 3.0 cm). In males of the corresponding age class (N = 13) average forearm length was 31.0 cm (SD = 4.2 cm). Forearm length of males was more variable than in females (CV$_{\text{males}}$ 13.5% versus CV$_{\text{females}}$ 9.7%) (Table 1).

The two species differed in terms of the intraspecific sex difference in forearm length [$F(3,53)$ = 7.4184, $P < 0.001$] (Fig. 4).

A posthoc pairwise comparison of forearm length of female and male bonobos and chimpanzees revealed that female chimpanzees had significantly shorter forearms than female bonobos (Tukey's test, P = 0.0053), male bonobos (Tukey's test, P = 0.0055), and male chimpanzees (Tukey's test, P = 0.0033). All other forearm length comparisons were not significantly different.

DISCUSSION

Forearm measurements were obtained from 90 bonobos and chimpanzees representing a wide chronological age range (1–54 years) living in multiple zoos (N = 9). The novel device used in our study offers an alternative technique for morphometric measures of captive apestes

and has the potential to facilitate longitudinal studies on somatic growth.

In our study, a comparison of average forearm lengths of females, aged 12 years and older, showed that female bonobo forearm length exceeded that of female chimpanzees. Furthermore, we found that there was no significant difference in our data set of forearm length between females of *P. t. verus* and hybrid females. However, the subspecies status of central and eastern chimpanzees is a matter of debate. For example, the genetic differences between *P. t. troglodytes* and *P. t. schweinfurthii* have been questioned, making the differentiation between subspecies uncertain (Fünfstück et al., 2015). Moreover, there is also evidence for population differences within chimpanzee subspecies. For example, while the average humerus length of *P. t. schweinfurthii* was found to be 30.1 cm, the corresponding value of chimpanzees from Gombe is 27.0 cm (Morbeck and Zihlman, 1989). On the other hand, *P. t. schweinfurthii* from Kibale National Park in Uganda and *P. t. verus* from Taï National Park are very similar in terms of humerus length (Carlson et al., 2011). In wild populations, variation in the size of body segments has been explained by environmental differences (Carlson et al., 2008, 2011). However, it seems unlikely that the shorter forearm length in female chimpanzees found in our study could be driven by subspecies status or environmental traits. In male chimpanzees, the sample size for each subspecies was too small to test differences in forearm length between them. Individual body mass data at the time of forearm measures are not available for chimpanzees or for bonobos.

While the adult males of the two species did not differ in forearm length, other studies found that adult bonobos had shorter total arm length (average 55.7 cm) than chimpanzees (average 57.1 cm) (Coolidge and Shea, 1982). It should be noted that these data (Coolidge and Shea, 1982) refer to pooled measures presumably of females and males of *P. t. troglodytes*, and that the exact chronological age of specimens was unknown, making interpretation of the data difficult. Another possibility is that the differences in total arm length reflect relative species differences in the upper limb proportions. However, based on humerus and radius lengths from bonobos and different chimpanzee subspecies for combined sex samples, the proportions of these two segments are 1.07 (humerus divided by radius) in *P. t. verus*, *P. t. troglodytes*, and bonobos. Only *P. t. schweinfurthii* and a subset of measurements from the Gombe chimpanzees have a proportion of 1.09 (Morbeck and Zihlman, 1989). In future studies, it would be beneficial to relate absolute values of forearm measures to relative body mass.

Most anthropoid primates display sexual dimorphism in body size, with males being larger than females (Plavcan, 2001). In our study, we found sexual dimorphism in forearm length of chimpanzees (with males having significantly longer forearms than females), but not in bonobos. The significant difference between forearm lengths in chimpanzees is in line with the results of other studies (Schoonaert et al., 2007) which found that male chimpanzees had longer forearms than females. Bonobos show a lower level of sexual dimorphism in the skull and in the face (Cramer, 1977) as well as in body mass, and no significant sex difference in the humerus or radius length was detected (Cramer and Zihlman, 1978). Therefore, the finding that female and male adult bonobos are similar in terms of forearm length is in line

with measures of bones (Cramer and Zihlman, 1978). Our study found that bonobos of both sexes show a visual increase in arm length until 13–15 years of age, a result that is consistent with previous work on weight (Leigh and Shea, 1995). Information on somatic growth from captive chimpanzees revealed a high growth velocity until ten years of age and a steady decline thereafter (Hamada and Udono, 2002; Hamada et al., 2003). Leigh and Shea (1995) found sex differences in terms of the temporal weight growth patterns of bonobos, a finding that was not confirmed in our study. The nature of material used for morphometrics, or constraints from sample size or individual growth patterns (Hamada et al., 2003) may explain such differences, highlighting the importance for larger data sets, and—most importantly—longitudinal growth profiles.

Measurements of forearm length taken from adult chimpanzees in this study correspond well with direct measures obtained in previous studies (Gavan, 1971; Schoonaert et al., 2007). While these data come from captive chimpanzees, variation exists with respect to housing and living conditions and the method of obtaining morphometric measures. For morphometric studies it is crucial to test the reliability of the technique and the error of measurement (Bailey and Byrnes, 1990), because a large measurement error in a variable data set can result in a type II statistical error (Lougheed et al., 1991). Comparison of forearm lengths measured directly on anesthetized individuals with those obtained with our novel method found an average error of 0.4 cm. The same average error was found in multiple forearms measured from the same digitized image.

Given the low technical effort, the high motivation of subjects to participate, and the precision of measurements, the specific value of the method is its utility for longitudinal studies on somatic growth and development in captive apes. Comparison of measures of body size and body weight between captive individuals and those living in natural environments demonstrate consistent differences in growth rate (O'Regan and Kitchener, 2005) with a clear bias towards faster rates in captive animals (Altmann and Alberts, 1987). However, because the effects of captive settings are similar, comparison of data from different species may still be useful for detecting interspecific variation. Another argument supporting the use of data from captive animals is that for many species, large sample sizes are difficult to obtain, a limitation that precludes quantitative testing (Martin and Harvey, 1985). Finally, in wild populations members of the migrating sex disappear from study groups constraining the assignment of morphologic measures to chronological age in this sex. Thus, despite the consistent discrepancy in somatic development between wild and captive animals, morphometric measurements can be compared to other parameters of development such as physiological markers, reproductive performance, and cognitive development. Given that similar devices have been used in field studies (Tanaka et al., 2008; Mannu and Ottoni, 2009), the method may also be applicable to wild primate species.

CONCLUSION

The forearm length of captive bonobos shows a significant increase with age. Results from adult females (>12 years) revealed that bonobos exceed chimpanzees in terms of forearm length. Comparison of adult forearm length between the sexes revealed significant sexual dimorphism in chimpanzees but not in bonobos. Given that males of the two sister species did not differ, the results indicate that the absence/presence of sexual dimorphism is due to differences in somatic growth by females. Our novel method facilitates the detection of sudden shifts in somatic growth and longitudinal studies on captive apes.

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