

Using Photogrammetry and Color Scoring to Assess Sexual Dimorphism in Wild Western Gorillas (*Gorilla gorilla*)

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ABSTRACT Investigating sexual dimorphism is important for our understanding of its influence on reproductive strategies including male–male competition, mate choice, and sexual conflict. Measuring physical traits in wild animals can be logistically challenging and disruptive for the animals. Therefore body size and ornament variation in wild primates have rarely been quantified. Gorillas are amongst the most sexually dimorphic and dichromatic primates. Adult males (silverbacks) possess a prominent sagittal crest, a pad of fibrous and fatty tissue on top of the head, have red crest coloration, their saddle appears silver, and they possess a silverline along their stomach. Here we measure levels of sexual dimorphism and within-male variation of body length, head size, and sexual dichromatism in a population of wild western gorillas using photogrammetry. Digital photogrammetry is a useful

and precise method to measure sexual dimorphism in physical traits yielding sexual dimorphism indices (ISD), similar to those derived from traditional measurements of skeletal remains. Silverbacks were on an average 1.23 times longer in body length than adult females. Sexual dimorphism of head size was highest in measures of crest size (max ISD: 60.4) compared with measures of facial height (max ISD: 24.7). The most sexually dimorphic head size measures also showed the highest within-sex variation. We found no clear sex differences in crest coloration but there was large sexual dichromatism with high within-male variation in saddle coloration and silverline size. Further studies should examine if these sexually dimorphic traits are honest signals of competitive ability and confer an advantage in reproductive success. *Am J Phys Anthropol* 134:369–382, 2007. © 2007 Wiley-Liss, Inc.

Dimorphism of sexually selected traits is widespread throughout the animal kingdom, including the order Primates, with males often being larger than females (Alexander et al., 1979; Plavcan and van Schaik, 1997; Weckerly, 1998; Lindenfors et al., 2002) and possessing various conspicuous ornaments (Dixson, 1998). It is a generally accepted concept that the evolution of various sexually dimorphic traits has resulted from competition over mates and/or mate choice, although other mechanisms, such as predation, phylogenetic inertia, diet, and allometric effects have been proposed (Plavcan and van Schaik, 1992, 1997; Lindenfors and Tullberg, 1998; Plavcan, 2001; Gordon, 2006a,b). Secondary sexual traits can act as armaments (weapons) or ornaments affecting female choice or both (Berglund et al., 1996). Traits advertising physical strength (weapons/armaments) are thought to have evolved through intrasexual selection (mainly male–male competition), whereas conspicuous ornaments are thought to be the result of intersexual selection (female choice) (Darwin, 1871; Andersson, 1994). To demonstrate the influence of sexual selection on trait evolution several steps are necessary. First, one must show that there is sexual dimorphism in the trait and that variation between individuals of the same sex exists (Snowdon, 2004). Second one has to demonstrate that this variation is assessed by rivals and/or potential mates and that this has an impact on reproductive success (Plavcan, 2001; Snowdon, 2004). Finally it must be shown that this sexual trait is heritable. The goal of this article is to investigate the first step in western lowland gorillas (*Gorilla gorilla gorilla*).

Many studies have measured sexual dimorphic physical traits in a wide variety of animals and found correlations with trait size and reproductive success (Andersson, 1994). In mammals, for example, larger male elephant seals (*Mirounga angustirostris*) and fallow deer (*Dama dama*) and Soay sheep (*Ovis aries*) males with larger horns have higher success in male–male competition, which provides them increased access to fertile females and higher reproductive success (Le Boeuf, 1974; McElligott et al., 2001; Preston et al., 2003). Similarly, African lions (*Panthera leo*) with darker manes are healthier, have advantages in male–male competition, and are preferred by females (West and Packer, 2002). Although there are detailed descriptions of sexually dimorphic traits in primates (Dixson, 1998; Plavcan,

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2001), variation in body size or ornamentation of male primates has rarely been quantified because it is difficult to measure such traits in free-ranging primates (Pereira et al., 2000; Kappeler, 2002). To our knowledge only one primate study successfully measured male body mass and demonstrated female preference for larger males (squirrel monkeys, *Saimiri oerstedii*) (Boinski, 1987). Hence, very little is understood about the proximate and ultimate mechanisms of female choice for male traits in primates and how these traits influence the outcome of male–male competition (Paul, 2002; Setchell and Kappeler, 2003).

Measuring morphological traits in wild animals, particularly large mammals can be logistically challenging, costly, and occasionally disruptive for the animals (Alibhai et al., 2001; Ancrenaz et al., 2003). Most data on body mass either comes from dead animals or involved animal handling to make measurements, with the exception of some studies that have developed creative, noninvasive methods for live animals (Altmann and Alberts, 1987; Deutsch et al., 1990; Pusey et al., 2005). Noninvasive photogrammetric methods are commonly used to investigate body length of marine mammals (Perryman and Lynn, 1993; Perryman and Westlake, 1998) but have rarely been applied to terrestrial mammals (elephants (*Loxodonta spp.*): (Lee and Moss, 1995; Morgan and Lee, 2003; Shrader et al., 2006), baboons (*Papio spp.*): (Kitchen et al., 2003), and estimates of sexual swellings in chimpanzees (*Pan troglodytes*) (Domb and Pagel, 2001; Emery and Whitten, 2003; Deschner et al., 2004). We here validate and apply digital photogrammetry to quantify within-sex variation and dimorphism in western gorillas.

In addition to size differences, male and female primates often differ in coloration. As with size, there has been little progress made to understand the evolution of colorful visual signals in primates besides conspicuous sexual dichromatism (Hrady and Hartung, 1979; Dixon, 1998; Gerald, 2003). One problem hampering progress in our knowledge of primate coloration lies in methodological difficulties of measuring hair, skin, and plumage patterns of wild animals (Endler, 1990; Gerald et al., 2001; Sumner and Mollon, 2003). Many field studies therefore have relied on subjective measurements by creating categories and/or comparing coloration with graduated color charts.

Gorillas (*Gorilla spp.*) are a logical choice for a study species to examine sexually selected traits because they are the largest and amongst the most sexual dimorphic primate species, with adult males weighting twice as much as females (Leigh and Shea, 1995; Smith and Jungers, 1997). The social system of western gorillas is principally a one-male social unit with intensive male–male competition and mate control (Parnell, 2002a; Stokes et al., 2003; Gatti et al., 2004; Robbins et al., 2004). Although female western gorillas are known to transfer between groups (Stokes et al., 2003), we have little understanding of male traits that are preferred by females and might influence females' group choice (Sicotte, 2001).

Adult male gorillas possess a prominent median sagittal and nuchal/occipital bone crest with large temporal and nuchal muscles attached (Gregory, 1950) and a large pad of skin and connective dense fibrous and fatty tissue on top of the head, which gives the head a mitre like appearance [crown-pad sensu Straus (1942) and Schultz (1969)]. The crown-pad and the underlying bony struc-

tures (hereafter referred as “crest”) are highly variable between individuals (Coolidge, 1929; Gregory, 1950; Schaller, 1963; Dixon, 1981; Parnell, 2002b) and have long been thought to act as ornaments (Schultz, 1969).

Gorillas also show obvious sexual dichromatism. The pelage of the saddle of adult male gorillas is gray to silver in color and in contrast to other body hair, is much shorter (Dixon, 1998). Females do not develop this silver saddle. Western gorilla males also possess a silver-line which runs “from the nape [of the neck], behind the shoulder and ending towards the lower abdomen” (Parnell, 2002b). In addition, both male and female western gorillas may or may not have a red tinge on the crown around the crest area (hereafter referred as crest coloration) (Dixon, 1981). Currently, the degree of sexual dichromatism and individual variation in these pelage patterns has not yet been quantified for gorillas.

In this article, our goal is to quantify sexual dimorphism and within-sex variation of body length, head size, and coloration within a large population of free-ranging western gorillas at Mbeli Bai, northern Congo. The question we address is whether body size, crest size, and crest and saddle coloration in male gorillas' present individual variation on which sexual selection may occur.

METHODS

Study site and population

Data were collected between February 2004 and January 2006 at Mbeli Bai, a 12.9 ha large swampy forest clearing in the south-west of the Nouabalé-Ndoki National Park, Republic of Congo. The clearing is visited by various large mammal species including western gorillas, which mainly come to feed on aquatic herbaceous vegetation. The gorilla population has been monitored since February 1995 (Parnell, 2002a; Stokes et al., 2003). Observations were made from a 9-m high platform overlooking the clearing providing nearly 100% visibility. During the study period, the clearing was visited by 18 groups of gorillas and 10 solitary adult males. The study subjects could be individually identified by marked features such as the shape of their browridges, coloration, or ear notches (Parnell, 2002b). All adult males investigated in this study had an estimated age of at least 16 years at the start of the study and were therefore considered fully grown (silverbacks). All adult females were fully grown and parous.

Photogrammetry

Photogrammetry has found substantial interest in anthropometry (Tanner and Weiner, 1949; Gavan et al., 1952; Geoghegan, 1953; Martin and Knußmann, 1988) and recently in studies of free-ranging animals with the help of digital cameras (Jaquet, 2006; Shrader et al., 2006). Here digital photos were taken with a Canon EosD10 digital camera (6.5 mio pixel resolution) attached to a Canon EF 600 mm/L4 lens and a 2× extender. The size of an object (o) can be determined by the ratio of the focal length of the lens and the distance from the camera to the object:

$$D/f = o/p;$$

where f is the focal length of the lens, D is the distance from the camera to the object, and p is the size (pixel



Fig. 1. Photo showing landmarks and linear measurements of (A): body length, (B): head size. For description of landmarks and measurements see Table 1. (Photos by Thomas Breuer).

length) of the object in the photo (p). Since we always used the same lens to take photos the only variables that changed for determining body and crest size were the distance to the gorilla and the pixel length in the digital photo. We measured distance to the animal with a Bushnell Yardage Pro 1000 laser range finder with an accuracy of ± 1 m. We used only those photographs for which two consecutive distance measures of the laser range finder gave the same value. Between the two measures, we pointed the laser range finder to a tree of known distance to check its function. We conducted measurements of pixel length in digital photos with the measure tool in Adobe PhotoShop® CS.

Landmarks and measurements

To reduce measurement error, photographs were carefully chosen by the first author based on various quality categories [criteria, such visibility of landmarks, activity (gorillas were not walking or feeding)] were used to estimate the degree of inclination from norma lateralis (tilting from sagittal and frontal plane). After applying these criteria, a total of 138 (average 8.1 ± 3.6 photos per individual, range 3–15) out of 409 silverback ($n = 17$) body length photos and 225 (average 13.2 ± 10.2 photos per individual, range 2–36) out of 1,080 head photos were measured ($n = 17$ silverbacks). We measured body length of 15 different adult parous females from 56 out of 125 photos (average 3.7 ± 2.3 photos per individual, range 1–10) and obtained head measures from 16 out of 29 photos from 11 different females (average 1.45 ± 0.80 photos per individual, range 1–3).

We used rump length instead of the more commonly used crown-rump length as a measure of body length of the gorillas (Fig. 1A). Crown-rump length of immobilized animals is measured when they are in lateral recumbency, but for the free-ranging gorillas it was more accurate to measure rump length because the head of the gorillas in the photo was rarely in a fixed position. Body length was measured along a tangent of the rump as the distance between the most protruding tip of the shoulder (acromion landmark) and the most caudal tip of the buttock (coccygeal or tip of coccyx sensu Schultz (1929).

Ten external measurements were taken to quantify the head size including soft tissues and hair. These measurements represent different parts (e.g. measure B2 includes part of the nuchal crest; see discussion) and are listed in Table 1 and described graphically in Figure

TABLE 1. Description of landmarks (measuring points), measurements, and helplines used for external measurements of a silverback's head as judged from lateral view of a digital photo

| | | Description |
|-------------|-----|----------------------------------------------------------------------------------------------------------|
| Landmark | 1 | Tip of mouth/lower part of upper lip; stomion (sensu Schultz, 1929) |
| | 2 | Anteriorly most protruding point of the browridge in lateral view |
| | 3 | Midpoint of earporus |
| | 4 | Third-way distance from 3 to 2 |
| | 5 | Third-way distance from 2 to 3 |
| | 6 | Intersection of tangent of most sagittal point with line continuing 1 to 2; vertex (sensu Schultz, 1929) |
| Helpline | I | Outer corner of the eye (ectocanthus) Tangent of highest point of the head, orthogonal to 1 to 6 |
| | II | From 2 to 3 |
| | III | From 2 to most posterior protruding point of the head through 3 |
| | IV | From 7 to most posterior protruding point of the head through 3 |
| Measurement | A1 | From 1 to 2 |
| | A2 | From 2 to 6 |
| | B1 | From 1 to 3 |
| | B2 | From 3 to the most posterior protruding point of the head continuing B1 |
| | E1 | From 1 to 4 |
| | E2 | From 4 to most protruding point of the head continuing E1 |
| | F1 | From 1 to 5 |
| | F2 | From 5 to most protruding point of the head continuing F1 |
| | C | Maximal length of orthogonal to III |
| | D | Maximal length of orthogonal to IV |

1B. We used prominent user defined landmarks that were visible from lateral view of the gorilla head and similar to those used in human head measurements (Schultz, 1929; Martin and Knußmann, 1988). All photos used in the analysis were taken and measured by the first author.

TABLE 2. Summary of measurement error: Error associated with the measurement process from the same photo (within photo coefficient of variation (CV)), average value of maximum to minimum difference (average of max-min), and average value of within individual coefficients of variation (average of CV) from different photos of the same individual for body length and 10 different head size measures

| Measurement | Within photo CV [mean (range)] ($n = 138$ for body length; $n = 34$ for head size measures) (%) | Average of max-min (between photo) ($n = 17$ silverbacks, 138 photos for body length; 225 photos of head size) | Average of CV (between photo) ($n = 17$ silverbacks, 138 photos for body length; 225 photos of head size) |
|-------------|--------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------|
| Body length | 0.36 (0.09–1.18) | 0.019 | 0.007 |
| A1 | 1.01 (0.23–2.32) | 0.057 | 0.020 |
| A2 | 1.19 (0.12–2.45) | 0.055 | 0.018 |
| B1 | 0.66 (0.17–1.5) | 0.074 | 0.023 |
| B2 | 1.12 (0.13–2.81) | 0.097 | 0.032 |
| E1 | 0.82 (0.17–1.9) | 0.097 | 0.031 |
| E2 | 0.81 (0–1.72) | 0.103 | 0.032 |
| F1 | 0.78 (0.17–1.39) | 0.099 | 0.030 |
| F2 | 3.44 (0.41–11.02) | 0.347 | 0.090 |
| C | 0.82 (0.2–1.84) | 0.125 | 0.039 |
| D | 1.01 (0.23–2.06) | 0.152 | 0.045 |

See text for details and Table 1 for description of measurements.

Camera calibration and measurement error

Any morphometric method should be concerned about measurement error (or repeatability) and identifying causes of measurement error (Bailey and Byrnes, 1990; Loughheed et al., 1991). The photogrammetric method applied here has several potential sources of error (Tanner and Weiner, 1949; Geoghegan, 1953; Farkas et al., 1980), and we have done our best to control for them (Table 2).

1. There was only very small error associated with the performance of the range finder and no conversion equation was needed. The regression equations for the two validation trials in which the laser range finder was tested against known distance at 50-m intervals between 50 and 450 m under different weather conditions were described by: $y_{\text{real distance}} = 0.9984x + 0.3403$ ($r^2 = 1$). We only used photographs taken between 50–300 m due to inappropriate viewing angle of gorillas less than 50 m from the observation platform. We also excluded photos from a distance greater than 300 m because we faced difficulties in correctly pointing the reticule on the gorilla with increasing distance from the viewing platform.
2. Second, we tested if we could accurately measure the size of a known object (a 62 cm \times 47 cm rectangle) with the range finder and Adobe PhotoShop pixel measurement. Using a 225.9 conversion factor (ruler set to mm and type to pixel in Adobe PhotoShop[®] preferences) from a pixel to a millimeter, we obtained in average 0.09% difference (range 0.03–0.19%) between the real and estimated linear object length.
3. We checked for within-photo measurement variation by remeasuring photos five times without consulting previous results (within photo variation) (Table 2). The average coefficient of variation (CV) from 138 body length photos was of 0.36% (range = 0.09–1.18%). Therefore, we used in our analysis the average of these five body length measures for each photo. For the ten head measures the average CV of repeated measures ($n = 3$ per photo) for 34 photos (two photos each of 17 silverbacks) was 1.16% (range = 0.66–3.44%). Because of this small error and the amount of time it took to measure one photo (~15 min), we decided to restrict our head size analysis to only one measure per photo.
4. To see that two observers can reveal the same results (as a measure of the precision of the measurement done by the first author), we had a second observer repeat the measurements and calculated inter-observer reliability, which showed that there was only minor difference in head size measures (2.1%) and body length (1.1%) between observers. Head size measurements ($n = 10$) between the two observers correlated significantly (average Spearman's rank correlation: $r_s = 0.9437$, range 0.915–0.974, $P < 0.001$, $n = 38$ photos from 19 different silverbacks) as well as body size measurements ($r_s = 0.953$, $P < 0.001$, $n = 17$ silverbacks).
5. Photos with heads being tilted in the sagittal plane might have been more difficult to detect and could have accidentally been included in the analysis, resulting in potentially higher measurement error for some measurements, such as F2, C, or D. Nevertheless we were confident that we were able to detect a 10° inclination (and excluded such photos from analysis) which would have resulted in an error (underestimation) of 1.5% ($1 - \cos \alpha$) (see also (Jaquet, 2006)). Hence, maximum and mean values for all head size measures were highly correlated ($n = 17$ silverbacks, average r_s -values = 0.928, range 0.863–0.998, $n = 10$ correlations). Finally, we controlled for the variation in the measurement from different photos from the same individual, usually at different days or occasions (inter-photo variation). Comparing the results for 17 silverbacks produced on average a CV of 0.69% for body length and 3.6% for head size.

Partitioning the total variance (see Bailey and Byrnes, 1990 for details) showed that only 3.8% of the total variance of body length and 28.7% of head size was explained by the within-gorilla component. From these controls, we felt confident that our methods produced smaller measurement errors than the inter-individual variations in the traits we studied (see results).

Color assessment

We were unable to measure coloration from photos because it was not possible to place white and black standards into the clearing (Gerald et al., 2001). We

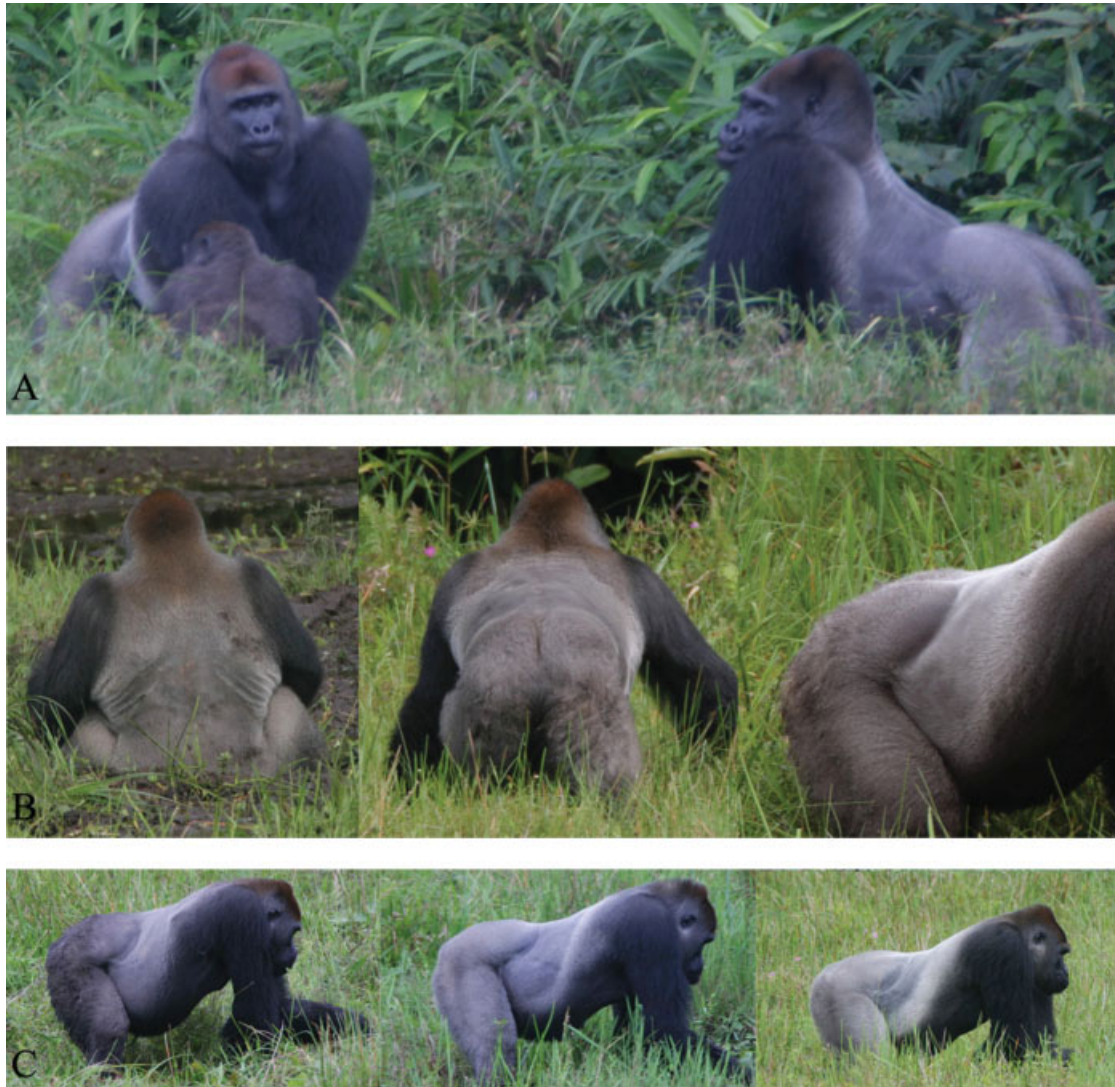


Fig. 2. (A) Photo showing individual differences of red crest coloration of two silverbacks; silverback to the left has a red crest (score 3) and silverback to the right has a dark red crest (score 2), (photo by Vicki Fishlock). (B) Appearance of saddle coloration from different viewing angles and possible scoring of the same silverback photographed under similar light conditions; left: back seated—scoring 3; middle: back quad—scoring 3; right: side—scoring 5. (C) Appearance of silverline: from left to right: absence (Silverback OBI), thin (Silverback ZUL), broad (Silverback SAN). (Photos by Thomas Breuer). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

therefore used subjective categories directly from the observation platform of red crest and saddle coloration of the gorillas to assess coloration. We scored color from different viewing angles to see if the appearance of either red crest or saddle coloration changed from the viewing angle. Intensity of the red crest coloration with the head in frontal (front), lateral (side), and posterior (back) view was ranked on a scale from 1 to 4 (1 = black, 2 = dark red, 3 = red, 4 = light red) (see example in Fig. 2A). We scored the brightness of the coloration of the saddle using a scale from 1 to 6 (1 = black, 2 = black to dark grey, 3 = dark grey, 4 = grey, 5 = light grey, 6 = grey to white). Scoring of the saddle was done while the gorilla was (1) standing in quadrupedal position parallel to the observer (side), and from the back while he showed (2) his saddle in seated (seated) and (3) in quadrupedal position (quad) because viewing angle and light reflectance can lead to different color perception (Fig. 2B). We also

scored the size of the silverline (Fig. 2C) as either absent (0), thin (1), or broad (2) from those three viewing angles. We reduced the effect of ambient light condition by limiting our scoring during sunny weather. We only used scorings by one observer because humans can vary in their color vision (Neitz and Jacobs, 1986). However to investigate the reliability of this subjective scoring, we compared results with scorings of a second observer. Scorings of crest coloration were highly correlated between two observers (Spearman's rank correlation: front: $r_S = 0.739$, $n = 33$, $P = 0.001$; side: $r_S = 0.845$, $n = 33$, $P = 0.001$; back: $r_S = 0.58$, $n = 28$, $P = 0.006$). Saddle scorings of silverbacks also were significantly correlated between observers (side: $r_S = 0.682$, $n = 13$, $P = 0.012$) and showed a trend when judged from the back (back seated: $r_S = 0.412$, $n = 9$, $P = 0.092$; back quad: $r_S = 0.432$, $n = 9$, $P = 0.069$). Silverline scoring in the field was highly correlated with scorings from digital photos

done by a judge unfamiliar with the study animals ($r_s = 0.846$, $n = 17$, $P < 0.001$). Crest color categories were consistently assigned by both observers but scorings were more variable in the saddle coloration, possible due to the effect of light reflectance and viewing angle (see results).

Statistics

We describe the degree of sexual dimorphism for each variable by dividing the mean obtained from all males by the mean of all females. We calculate an index of sexual dimorphism (ISD) as [(male mean/female mean) - 1] \times 100 (Lockwood, 1999). Throughout the analysis we report the coefficient of variation (CV) as a measure of variation. We also provide percent difference between maximum and minimum values (max - min). For the comparison of sex differences in the within sex-variation, we log-transformed the data and compared the variances (not the CVs) because absolute variance generally increases naturally with size. We test for difference between sexes with Mann-Whitney U test and for sex differences of within-sex variation using an F -test (Bortz et al., 1990). We conducted multiple testing because we could not combine both sexes into one principal component analysis (PCA) (see results; Appendix Table A1, and Table 3). We only use principal component scores in tests of association with body length or coloration within silverback comparison. We could not compare ISDs of facial and crest height because measurements were highly correlated (Table A1). Therefore we used a two-way ANOVA to analyze the interaction of one crest and one facial height measure ($E1$ and $E2$ because they were most highly loaded in the silverback PCA (Table 3, part A)). We used two-tailed exact nonparametric tests for small sample sizes (Siegel and Castellan, 1988; Mundry and Fischer, 1998). Sample sizes varied because of the lack of suitable photographs for some individuals. Analyses were conducted in SPSS 13. Tests of Spearman Rank correlation were done with the help of a macro in Excel (written by R. Mundry) and either exact ($N \leq 9$) or based on 1,000 permutations.

RESULTS

Principal component analysis of head size measurements

We conducted a principal component analysis (PCA) with Varimax rotation of the ten head size measurements for the silverbacks (to avoid confounding results we did not include females into the PCA; see high correlation values in matrix in Tables A1 and 3) to sort variables and to condense correlated measurements into fewer uncorrelated variables ("principal components," PC's). This procedure was justified as suggested by the large proportion of rather large absolute correlations between the variables and also indicated by the Kaiser-Meyer-Olkin measure of sampling adequacy (0.581) and Bartlett's test of sphericity ($\chi^2 = 258.055$, $df = 45$, $P < 0.001$) (McGregor, 1992). Prior to conducting the PCA, we visually checked data for normality and absence of outliers. From this, we concluded that none of the variables required transformation.

The two PC's of head measurements for silverbacks together explained 84.2% of the variation of the measurements. In comparison, the adult female head was described by three PC's explaining 91.7% of variation.

TABLE 3. Principal component analysis of (A) silverbacks and (B) adult females for 10 head measurements of gorillas with their factor loading of measurements on crest height and facial height

| | Component | | |
|------------------|------------------|-------------------|--------------|
| A: Silverbacks | | | |
| | 1 (Crest height) | 2 (Facial height) | |
| E2 | 0.979 | -0.086 | |
| C | 0.921 | -0.109 | |
| A2 | 0.878 | 0.137 | |
| B2 | 0.879 | -0.235 | |
| F2 | 0.859 | 0.113 | |
| D | 0.821 | -0.183 | |
| E1 | 0.024 | 0.995 | |
| F1 | -0.168 | 0.960 | |
| B1 | 0.164 | 0.918 | |
| A1 | -0.260 | 0.801 | |
| Eigen value | 5.062 | 3.357 | |
| % variance | 48.849 | 35.348 | |
| B: Adult females | | | |
| | 1 | 2 | 3 |
| F1 | 0.974 | -0.092 | 0.057 |
| E1 | 0.929 | 0.338 | -0.132 |
| A1 | 0.852 | -0.403 | 0.227 |
| B1 | 0.780 | 0.542 | -0.259 |
| F2 | -0.016 | 0.937 | 0.012 |
| A2 | 0.102 | 0.895 | 0.233 |
| E2 | -0.010 | 0.856 | 0.501 |
| C | -0.113 | 0.218 | 0.935 |
| B2 | 0.266 | -0.055 | 0.897 |
| D | -0.152 | 0.265 | 0.818 |
| Eigen value | 3.785 | 3.229 | 2.152 |
| % variance | 32.621 | 31.110 | 27.929 |

Bold values indicate correlations of variables with the principal component larger than 0.75.

PC-1 of silverbacks characterized measurements of crest height/neurocranial length (hereafter referred as crest height) and PC-2 was related to facial height (Table 3, part A for silverbacks and Table 3, part B for PCA-results of adult females). PC-2 of silverbacks and PC-1 of adult females both included the same measures (A1, B1, E1, F1), indicating that these measures described facial height in a very similar way for both sexes. In contrast, the crest height component for males could be explained by one component alone, whereas for adult females the remaining six measurements were loaded on two additional components (Table 3). For silverbacks we present the results of head measurements for those four facial height and six crest height measurements separately. We also describe the contribution of the crest to overall length of the head. Therefore for each sex we present the percentage contribution of facial height to overall length for four measurement pairs (A1 + A2, B1 + B2, E1 + E2, F1 + F2).

Sexual dimorphism and within-sex variation in body length

Silverbacks were larger than adult females. They had an average body length of 90 ± 3.3 cm (range 85.3–97.2 cm) and were therefore on average 1.23 times longer (ISD: 22.6) than adult females (average body length: 73.4 ± 0.7 cm; range 72.3–74.8 cm) (Fig. 3; Table 4). There was substantial variation between silverbacks with the largest silverback being 13.9% longer than the smallest silverback (CV = 3.70%). In contrast, females

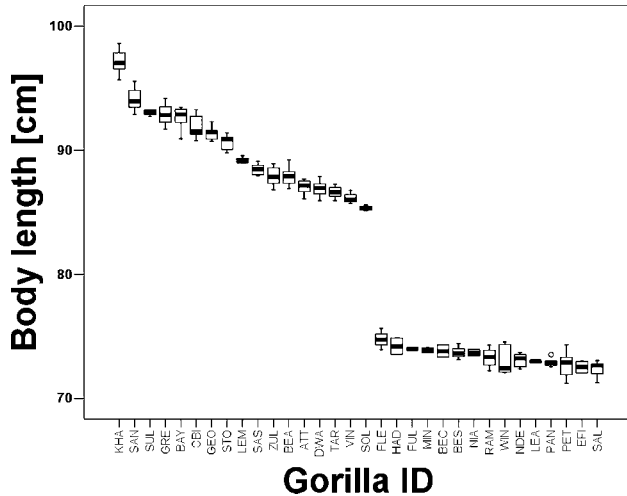


Fig. 3. Box-Whisker-plots showing body length of silverbacks (from KHA-SOL) and adult females (FLE-SAL). Whiskers show minimum and maximum values; boxes show lower and upper quartile, midlines show medians and circle shows one outlier. Individual gorillas are ordered by average body length estimate.

were similar in their body length ($CV = 0.92\%$) with significantly smaller variance (F -test on log-transformed data: $F_{17,15} = 15.79$, $P < 0.001$), and with only 3.3% difference between the largest and the smallest female (Fig. 3).

Sexual dimorphism and within-sex variation in facial and crest height

Sexual dimorphism: A comparison between sexes revealed that all silverbacks were larger than adult females in all measurements. $ISD_{crest\ height}$: 48.9; range 34.8–60.4) were larger than ISD of measures of facial height ($ISD_{facial\ height}$: 21.3; range 17.2–24.7) (Table 4; Figs. 4 and 5). To see if ISD of crest and facial height were different, we conducted a two-way ANOVA with sex and measurement ($E1$ and $E2$) as fixed factors. There was a significant interaction between sex and measurement when testing for between subject effect ($F_{1,52} = 39.945$, $P < 0.001$) demonstrating that ISD of facial height ($E1$) and crest height ($E2$) differ, with crest height being larger (see also Figs. 4 and 5).

Within-sex comparison: There was considerable variation between silverbacks in various measurements (Table 4 for results). Crest height scores had higher CV and max – min between silverbacks than measurements of facial height (except for one case: B2). Variation among females (max – min values) was smaller than that of silverbacks for most crest height measurements but not for facial height measurements.

Another measure of sexual dimorphism is variance dimorphism. A comparison of variation within the sexes revealed that there was no clear variance dimorphism, and variation within females was similar to within silverback variation in facial height (males had higher CV in two out of four measures) and crest height measurements (males had higher CV in four out of six measures) but reaching significance in two measurements of crest height (using F -test) (Table 4).

The percentage that facial height (measures $A1$, $B1$, $E1$, $F1$) contributed to overall length ($A1 + A2$, $B1 + B2$, $E1 - F1$) was always larger in adult females ($A1$, 55.6%;

$B1$, 58.7%; $E1$, 56.2%; $F1$, 63.2%) than for silverbacks ($A1$, 47.8%; $B1$, 56.8%; $E1$, 50.6%; $F1$, 58.9%).

Large head size in some silverbacks may also be a product of large body length, but the PC 's for silverbacks of crest height ($r_S = 0.397$, $n = 16$, $P = 0.125$) and facial height ($r_S = 0.065$, $n = 16$, $P = 0.823$) were not significantly correlated with body length (nor was there a significant correlation of body length with each of the ten head measurements: all $n = 16$, average $r_S = 0.196$; range -0.073 to 0.4, smallest $P = 0.126$).

Selection can act on morphological traits which show high between-individual variation and can lead to large sex differences in those traits. In fact, the largest within-sex variation in head size measures was found in measures with the highest sexual dimorphism. Correspondingly, there was a high correlation of ISD and CV for both silverbacks ($r_S = 0.673$, $n = 10$, no P -values provided due to nonindependence of measures) and adult females ($r_S = 0.830$, $n = 10$ measures, no P -values provided due to nonindependence of measures).

Red crest coloration

Details on color scores are given in Table 5. Silverbacks had a more intensive red crest coloration than adult females when scored from the side and back, but there was no obvious difference when scored from the front (front: $U = 245$, $N_{SB} = 18$, $N_{AF} = 34$, $P = 0.239$; side: $U = 200.5$, $N_{SB} = 18$, $N_{AF} = 34$, $P = 0.042$; back: $U = 129$, $N_{SB} = 18$, $N_{AF} = 34$, $P = 0.001$). Silverbacks had lower CVs compared with adult females (but not significantly) because of a higher percentage of adult females without any red coloration (front: $F_{34,18} = 1.73$, $P = 0.115$; side: $F_{34,18} = 1.13$, $P = 0.409$; back: $F_{34,18} = 1.38$, $P = 0.245$). Crest scorings were highly correlated with each other from different viewing angles (silverbacks: smallest $r_s = 0.9$, all $P < 0.001$; adult females: smallest $r_s = 0.915$, all $P < 0.001$).

Red crest intensity of silverbacks was not significantly correlated with PCA scores of crest height (front: $r_S = -0.319$, $n = 17$, $P = 0.207$; side: $r_S = -0.178$, $n = 17$, $P = 0.49$; back: $r_S = -0.229$, $n = 17$, $P = 0.39$) or with facial height (front: $r_S = 0.096$, $n = 17$, $P = 0.704$; side: $r_S = 0.066$, $n = 17$, $P = 0.78$; back: $r_S = 0.189$, $n = 17$, $P = 0.5$).

Saddle coloration and silverline size

Silverbacks were significantly brighter in saddle coloration than adult females from all three angles (side: $U = 3$, $N_{SB} = 17$, $N_{AF} = 32$, $P < 0.001$; seated: $U = 28.5$, $N_{SB} = 17$, $N_{AF} = 32$, $P < 0.001$; quad: $U = 62.5$, $N_{SB} = 17$, $N_{AF} = 32$, $P < 0.001$). We found no correlation of body length of silverbacks with saddle brightness from the side and from behind in quadrupedal position, but a trend when silverbacks were observed from the back in seated position (side: $r_S = 0.34$, $n = 16$, $P = 0.227$; seated: $r_S = 0.496$, $n = 16$, $P = 0.054$; quad: $r_S = 0.34$, $n = 16$, $P = 0.28$). Adult females that appeared brighter in saddle coloration also had brighter crest coloration (comparison of all viewing angles ($n = 32$): smallest $r_S = 0.433$, largest $P = 0.016$), but this was not the case for silverbacks (comparison of all viewing angles ($n = 17$): largest $r_S = 0.366$, smallest $P = 0.128$).

Saddle scorings for silverbacks differed significantly between the three viewing angles (Friedman test: $F = 30.875$, 17 silverbacks, three viewing angles, $P < 0.001$). Scorings were highest when made from the side and larger

TABLE 4. Body length and head size dimorphism and within sex variation in wild western gorillas

| Measurement | ISD | CV _{SB} (%) | CV _{AF} (%) | Max-min SB (%) | Max-min AF (%) | <i>P</i> -values MWU-test (sex difference) | <i>P</i> -values <i>F</i> -test (within-sex variation) |
|-------------|------|----------------------|----------------------|----------------|----------------|--------------------------------------------|--------------------------------------------------------|
| A1 | 17.2 | 5.73 | 4.31 | 23.5 | 12.9 | <0.001 | 0.2005 |
| B1 | 24.7 | 4.18 | 5.70 | 18.1 | 23.9 | <0.001 | 0.1190 |
| E1 | 22.7 | 4.37 | 4.91 | 17.2 | 19.8 | <0.001 | 0.3248 |
| F1 | 20.7 | 5.00 | 4.51 | 19.8 | 15.0 | <0.001 | 0.3777 |
| A2 | 60.4 | 10.74 | 10.58 | 50.0 | 41.5 | <0.001 | 0.5024 |
| B2 | 34.8 | 5.65 | 7.03 | 25.5 | 27.7 | <0.001 | 0.1942 |
| E2 | 53.6 | 7.86 | 8.21 | 34.8 | 26.5 | <0.001 | 0.4234 |
| F2 | 46.3 | 16.64 | 9.85 | 79.8 | 40.4 | <0.001 | 0.0689 |
| C | 48.0 | 7.98 | 7.06 | 37.3 | 26.4 | <0.001 | 0.3964 |
| D | 50.6 | 9.05 | 5.54 | 47.6 | 16.5 | <0.001 | 0.0530 |
| Body length | 22.6 | 3.70 | 0.92 | 13.9 | 3.3 | <0.001 | <0.001 |

SB, silverback; AF, adult female; ISD (index of sexual dimorphism) = [(SB mean/AF mean) - 1] × 100. Test results for sex differences (MWU) and within-sex variation (ln-transformed data) (*F*-test). Significant test results are in bold, trends are shown in italics. A1, B1, E1, F1 are the measurements of facial height and A2, B2, E2, F2, C, D are the measurements of crest height; see text for details and Table 1 for description of measurements.

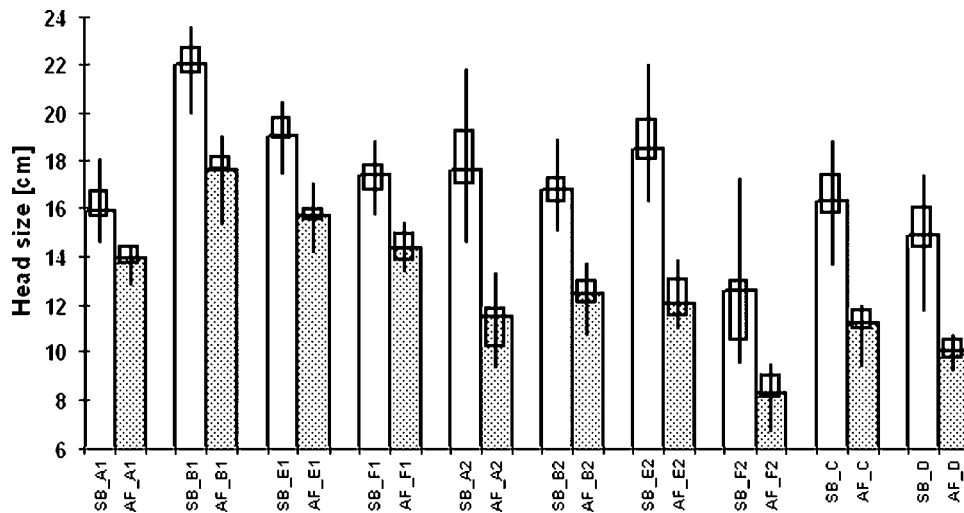


Fig. 4. Median values for head measurements of silverbacks (SB) (blank bars) and adult females (AF) (filled bars) for all 10 head size measurements. Whiskers show minimum and maximum values, boxes show upper and lower quartiles. A1, B1, E1, and F1 are the measures of facial height whereas the other six variables are measures of the crest height (see Table 1 for description of measurements).

when observed from the back in seated compared with quad (Post hoc Wilcoxon test's: side-seated: $T^+ = 153, N = 17, P < 0.001$; quad-side: $T^+ = 153, N = 17, P < 0.001$; quad-seated: $T^+ = 81.5, N = 13$ (four ties), $P = 0.008$).

Females never possessed a silverline. There was high variability of silverline size within adult silverbacks (Fig. 6). Six silverbacks had a very broad silverline whereas for others ($n = 5$) we rarely detected a silverline. Body length did not correlate with silverline scoring (side: $r_s = 0.152, n = 16, P = 0.544$; seated: $r_s = 0.165, n = 16, P = 0.561$; quad: $r_s = 0.137, n = 16, P = 0.616$).

DISCUSSION

Feasibility of digital photogrammetry and application to primatological research

Using different controls we demonstrated that digital photogrammetry shows high repeatability and precision.

The method is easy to implement, precise, and relatively inexpensive, although measurements of head size were very time consuming (~15 min per photo). In our particular case it was possible to obtain photographs from a far distance because of the visibility in the forest clearing (up to 450 m). However, there are limitations to the method. Small objects that are photographed from a far distance might be difficult to measure because of fuzzy images. The distance estimation might be limited due to difficulties of correctly pointing the reticule of the laser range finder on the target. For close range photogrammetry of primates it is important to use more accurate laser range finders together with digital photographs, or alternatively apply stereo-photogrammetry (van Rooij and Videler, 1996; Bräger and Chong, 1999), use scaling poles (Deschner et al., 2004; Ireland et al., 2006), or a laser-pointer mounted to a lens (Durban and Parson, 2006). Applying photogrammetric methods to measure body length differences in similarly sized individuals

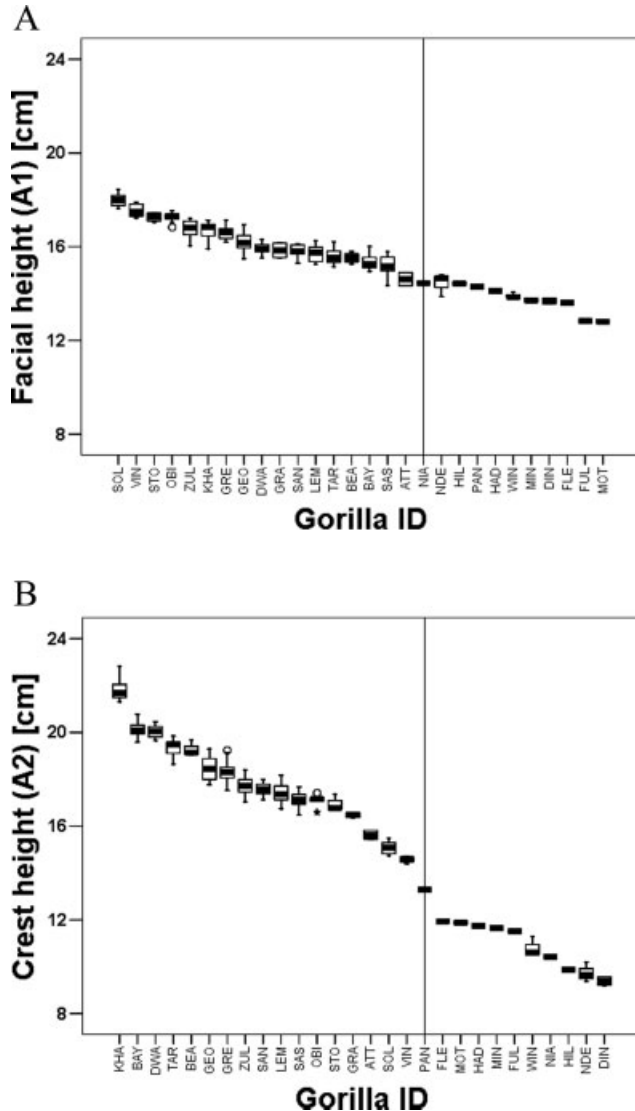


Fig. 5. Box-Whisker-plots showing head size measurements with lowest ISD (Index of sexual dimorphism) for (A) facial height of silverbacks (from SOL-ATT) and adult females (NIA-MOT) and highest ISD for (B) crest height of silverbacks (from KHA-VIN) and adult females (PAN-DIN). Whiskers show minimum and maximum values; boxes show lower and upper quartile, midlines show medians and circles and stars show outliers. Individual gorillas are ordered by average head measure estimate.

might not be an appropriate method because measurement error may become larger than between-individual measurements. Additionally, the feasibility of applying photogrammetry to primate species that are more active and agile than gorillas may prove difficult.

Sexual dimorphism in body length

Our results demonstrated significant sexual dimorphism in body length in adult western gorillas. Within-silverback variation was greater than within-female variation. Body length dimorphism for western gorillas revealed in this study (ISD: 22.6) shows that gorillas are amongst the most sexually dimorphic primates. Similar results were obtained for femoral length dimorphism in

gorillas (ISD: 18.9 [Taylor, 1997]; ISD: 20.9 [Schultz, 1937]). Long bone length in humans and gorillas is significantly correlated with stature or body length [Dupertuis and Hadden, 1951; Wood, 1979; Hens et al., 1998]. Gorillas show substantially higher body length dimorphism than humans (ISD: 8.6), chimpanzees (ISD: 4.9), orangutans (*Pongo spp.*) (ISD: 15.0) (Schultz, 1937), and other primates (*Macaca spp.*: ISD: 10.2–11.5 [Ribeiro Andrade et al., 2004; Schillaci et al., 2007] and *Cercoptes aethiops*: ISD: 10–16 [Turner et al., 1997]). Body length dimorphism was similar to those of baboons (*Papio cynocephalus*) (ISD: 23.0–23.7 [Altmann et al., 1993]) but substantially smaller compared with the most sexually dimorphic primate, the mandrill (*Mandrillus sphinx*) (ISD: 32.6 [Setchell et al., 2001, 2006]).

Body size is an obvious trait indicating fighting ability of males in various primate species (Plavcan and van Schaik, 1997; Plavcan, 2001). Male–male competition in gorillas is intense and can be fatal for silverbacks (Watts, 1989; Robbins, 2003). The body length dimorphism exhibited by western gorillas is consistent with previous comparative investigations, showing that body mass dimorphism in haplorhine primates is greatest in polygynous species, which show highest levels of competition (Clutton-Brock, 1985; Plavcan and van Schaik, 1997; Lindenfors and Tullberg, 1998; Plavcan, 2004).

Sexual dimorphism in head size

For the interpretation of our results of sexual dimorphism and within-male variation of crest height, it is crucial to understand what the different measurements used in this study are representing. Measurement B2 includes the nuchal crest and the nuchal muscles to hold the head in position, which could indicate the overall size of the head. This measure is the least variable among the six crest height measures and shows the lowest ISD value. The other crest measures include parts of the bony sagittal crest and the overlying tissue (muscle and fat deposition) [see also Schultz in (Gregory, 1950)] associated with it and are more comparable with vault or cranial height measures. The smallest sex differences are seen in contributions of facial height component B1 to overall length (B1 + B2), further indicating that both sexes are more similar in this measure (Table 4).

Our results support numerous studies that have confirmed sexual dimorphism of cranial dimensions in gorillas (O'Higgins et al., 1990; Wood et al., 1991; O'Higgins and Dryden, 1993; Uchida, 1996; Lockwood, 1999; Schaefer et al., 2004). These studies have also shown that there is a high variability of dimorphism among the dimensions studied. Here we could demonstrate that measures that revealed the highest ISD also showed the highest within-sex-variation. Facial height dimorphism reported here (ISD: 21.3) is similar to findings of other studies (ISD: 19.9 (Lockwood, 1999; Schaefer et al., 2004); ISD: ~20 (Schaefer et al., 2004)), but slightly larger compared with mandibular size dimorphism (ISD: 18.3 (Taylor, 2006)). Interestingly facial height dimorphism revealed in our study is very similar to our estimate of body length dimorphism and could indicate isometric scaling, although within silverbacks there was no influence of body length on facial height and cranial height measures.

Crest height dimorphism measured here was substantially greater than facial height dimorphism and body length dimorphism. Sagittal crests are believed to de-

TABLE 5. Between sex comparison of (A) crest coloration ranking as scored from different viewing angles (front, side, and back) and (B) saddle coloration as scored from the side, and the back in seated and quadrupedal (quad) position

| Sex | Viewing angle | Sample size | Mean value | Standard deviation | Maximum | Minimum |
|----------------------|---------------|-------------|------------|--------------------|---------|---------|
| A: Crest coloration | | | | | | |
| Male | Front | 18 | 2.7604 | 0.6089 | 3.800 | 2.0000 |
| Female | Front | 34 | 2.4975 | 0.8011 | 4.000 | 1.0000 |
| Male | Side | 18 | 2.8294 | 0.7290 | 4.000 | 2.0000 |
| Female | Side | 34 | 2.3326 | 0.7735 | 3.830 | 1.0000 |
| Male | Back | 18 | 2.6830 | 0.6755 | 3.900 | 2.0000 |
| Female | Back | 34 | 1.8723 | 0.7926 | 3.670 | 1.0000 |
| B: Saddle coloration | | | | | | |
| Male | Side | 17 | 4.1171 | 0.9180 | 5.5000 | 2.7300 |
| Female | Side | 32 | 1.6078 | 0.5466 | 3.0000 | 1.0000 |
| Male | Back seated | 17 | 2.2057 | 0.3807 | 2.9000 | 1.5000 |
| Female | Back seated | 32 | 1.2759 | 0.3896 | 2.0000 | 1.0000 |
| Male | Back quad | 17 | 1.9902 | 0.3377 | 2.5600 | 1.5000 |
| Female | Back quad | 32 | 1.2379 | 0.3801 | 2.1700 | 1.0000 |

Higher values indicate brighter coloration, see text for color codes.

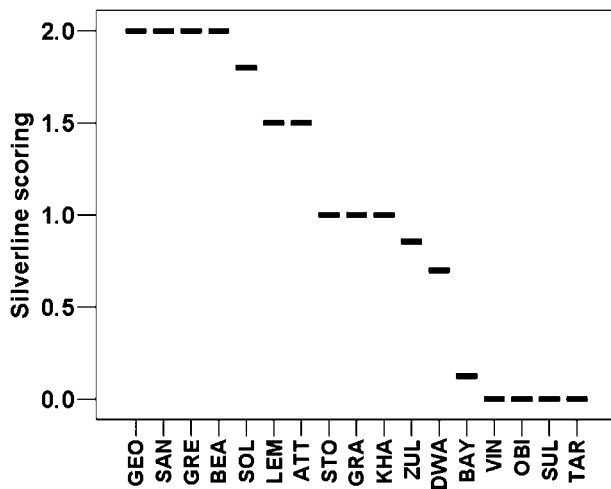


Fig. 6. Average silverline scorings of silverbacks when observed from the side.

velop to increase surface area for the attachment of the connective tissue of the temporal muscles (Ashton and Zuckermann, 1956; Robinson, 1958; Wolpoff, 1974; but see (Sakka, 1985)). In particular, measurements which include muscle attachment areas have been shown to reveal the highest degree of sexual dimorphism (Plavcan, 2002). In those species in which males show clearly developed sagittal and nuchal crests (orangutans, gorilla), dimorphism is particularly high in these and other related dimensions (e.g. zygomatic arches) with substantial within-male variation (Sakka, 1985; Uchida, 1996; Hens, 2002). Findings of high variation and significant degree of dimorphism in these measures are not surprising given the influence of muscle activity on bone morphology (O’Higgins et al., 2001). Earlier craniometric studies have demonstrated high variance dimorphism (Coolidge, 1929; Sakka, 1985; Albrecht et al., 2003; Stumpf et al., 2003), but we found only little evidence for variance dimorphism in crest height.

Further investigations are needed to determine which proximate factors promote the development of crests in gorillas and if crest size (and its associated muscles)

directly reveals weapon performance (bite force) (Lappin et al., 2006) and/or signals other physical abilities, such as whole-organism performance (Lailvaux et al., 2005).

Sexual dichromatism in gorillas

We did not find sexual dichromatism in red crest coloration in western gorillas when color was judged from the front, but males have brighter red coloration than females when observed from the side and the back. Red crest coloration does not seem to change over the lifespan of a gorilla, as it is already present in immature individuals (Breuer, unpublished data), and is therefore unlikely to be indicating condition (Hill and McGraw, 2006). However it is possible that there are genotypic differences in condition. Additionally those females with brighter crest also had brighter saddle coloration.

In contrast, there are age and sex differences in the saddle coloration and silverline size. Clearly the silver saddle coloration is a sign of adulthood for male gorillas (Dixson, 1981; Schultz, 1969). However, it is not more intensive in color in very old silverbacks (Breuer, unpublished data), indicating that it reaches its greatest intensity at a certain stage at maturation. The saddle hair of the blackbacks first becomes shorter and appears red-brownish (Gatti et al., 2004; Breuer, personal observation). The saddle becomes silver when males are clearly larger than females. The silverline develops at a later stage but not in all silverbacks. Saddle brightness and silverline size seem to be fixed and do not change once an individual is fully adult (Breuer, personal observation). These color traits are therefore not likely to be a status- or condition-dependant signal, although they may correlate with reproductive success. Body posture had a significant influence on the appearance of saddle brightness, as has been suggested by Parnell (2002b) (see also Taylor et al., 2000).

Further studies are needed to investigate the behavioral context in which these dichromatic traits are used/displayed and to confirm previous suggestions that the red crest coloration in gorillas could help to highlight the sagittal crest and if the saddle coloration could also amplify the size of the arms (Parnell, 2002b).

CONCLUSIONS

Given the difficulties of obtaining noninvasive measures of morphological traits in wild primates, we applied digital photogrammetry and subjective color assessment in a large population of adult wild western gorillas at Mbeli Bai, northern Congo. The photogrammetric method proved to be a useful and a precise method to measure sexual dimorphism and within-male variation in body length and head size yielding degrees of sexual dimorphism similar to what is known from osteometric studies. Adult males showed particularly large high within-sex variation in measures of crest height, a highly sexual dimorphic trait that has long been thought to have evolved through sexual selection. In addition, we assessed sexual dimorphism using subjective color scorings made from an observation platform overlooking the forest clearing. Using color categories, we showed that adult male gorillas (silverbacks) were relatively similar to adult females in their red crest coloration, but showed clear sexual dichromatism in their saddle coloration. Silverbacks showed high within-male variation in saddle coloration and in the size of their silverline. Given this substantial within-male variation, we suggest that sexual selection may act on these dimorphic traits in gorillas and further

studies are needed to investigate if these dimorphic traits confer an advantage in reproductive success.

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APPENDIX 1. Correlation matrix of silverbacks and females combined (A), silverbacks (B), and adult females (C)

| A: Correlation matrix of silverbacks and adult females combined | | | | | | | | | | |
|-----------------------------------------------------------------|----|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| | A1 | A2 | B1 | B2 | C | D | E1 | E2 | F1 | F2 |
| A1 | 1 | 0.671 | 0.870 | 0.738 | 0.736 | 0.730 | 0.918 | 0.705 | 0.959 | 0.525 |
| A2 | | 1 | 0.885 | 0.920 | 0.937 | 0.907 | 0.860 | 0.978 | 0.792 | 0.912 |
| B1 | | | 1 | 0.828 | 0.835 | 0.828 | 0.989 | 0.876 | 0.948 | 0.780 |
| B2 | | | | 1 | 0.970 | 0.949 | 0.822 | 0.964 | 0.795 | 0.832 |
| C | | | | | 1 | 0.989 | 0.820 | 0.979 | 0.782 | 0.846 |
| D | | | | | | 1 | 0.805 | 0.961 | 0.762 | 0.831 |
| E1 | | | | | | | 1 | 0.850 | 0.982 | 0.739 |
| E2 | | | | | | | | 1 | 0.790 | 0.892 |
| F1 | | | | | | | | | 1 | 0.647 |
| F2 | | | | | | | | | | 1 |
| B: Correlation matrix of silverbacks | | | | | | | | | | |
| | A1 | A2 | B1 | B2 | C | D | E1 | E2 | F1 | F2 |
| A1 | 1 | -0.298 | 0.550 | -0.311 | -0.160 | -0.160 | 0.747 | -0.336 | 0.877 | -0.284 |
| A2 | | 1 | 0.309 | 0.654 | 0.688 | 0.519 | 0.190 | 0.881 | -0.038 | 0.821 |
| B1 | | | 1 | -0.144 | -0.013 | -0.077 | 0.932 | 0.079 | 0.785 | 0.309 |
| B2 | | | | 1 | 0.836 | 0.744 | -0.228 | 0.891 | -0.322 | 0.701 |
| C | | | | | 1 | 0.958 | -0.114 | 0.903 | -0.228 | 0.640 |
| D | | | | | | 1 | -0.199 | 0.781 | -0.291 | 0.530 |
| E1 | | | | | | | 1 | -0.058 | 0.944 | 0.154 |
| E2 | | | | | | | | 1 | -0.242 | 0.790 |
| F1 | | | | | | | | | 1 | -0.087 |
| F2 | | | | | | | | | | 1 |
| C: Correlation matrix of adult females | | | | | | | | | | |
| | A1 | A2 | B1 | B2 | C | D | E1 | E2 | F1 | F2 |
| A1 | 1 | -0.288 | 0.409 | 0.385 | 0.025 | 0.043 | 0.627 | -0.248 | 0.849 | -0.339 |
| A2 | | 1 | 0.481 | 0.264 | 0.427 | 0.263 | 0.359 | 0.896 | 0.056 | 0.728 |
| B1 | | | 1 | -0.081 | -0.215 | -0.145 | 0.940 | 0.328 | 0.667 | 0.489 |
| B2 | | | | 1 | 0.766 | 0.560 | 0.105 | 0.411 | 0.334 | -0.091 |
| C | | | | | 1 | 0.790 | -0.150 | 0.660 | -0.070 | 0.187 |
| D | | | | | | 1 | -0.154 | 0.610 | -0.166 | 0.376 |
| E1 | | | | | | | 1 | 0.210 | 0.862 | 0.305 |
| E2 | | | | | | | | 1 | -0.062 | 0.783 |
| F1 | | | | | | | | | 1 | -0.106 |
| F2 | | | | | | | | | | 1 |

Significant results are highlighted in bold.

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