

Influence of Male Morphology on Male Mating Status and Behavior During Interunit Encounters in Western Lowland Gorillas

Damien Caillaud,^{1–4*} Florence Levréro,^{3,4} Sylvain Gatti,^{3,4} Nelly Ménard,^{3,4} and Michel Raymond^{1,2}

¹Université de Montpellier 2, France

²CNRS, Institut des Sciences de l'Évolution, place Eugène Bataillon, CC 065, 34095 Montpellier cedex 5, France

³Université de Rennes 1, France

⁴CNRS, Ethologie-Evolution-Ecologie, Station Biologique, 35380 Paimpont, France

KEY WORDS sexual dimorphism; photogrammetry; sexual selection; male–male fight; ritualized displays

ABSTRACT The western lowland gorilla (*Gorilla gorilla gorilla*) is one of the most sexually dimorphic primate species. Mature males are twice the size of females and have grey fur on their backs and a fibrous, adipose crest on their heads. Such traits are likely to have evolved by sexual selection, either because they confer advantages during male–male fights or because females prefer males with more dimorphic traits. We developed photogrammetric methods for distance collection of morphological data from silverback males frequenting the Lokoué forest clearing in Odzala-Kokoua National Park, Republic of the Congo. Body length, head-crest size, musculature development, and extent of the grey color on the back were assessed in 87 nonbreeding and breed-

ing mature males. Behavioral data were also collected during 312 male–male encounters involving 67 mature males in order to estimate their level of aggressiveness. The number of females belonging to a mature male positively correlated with the male crest size, body length, and musculature. Whereas morphological variables did not significantly affect the intensity of male–male encounters, the number of females attending male–male encounters strongly affected the number of agonistic displays by the two males. We discuss the mechanisms through which males with more exaggerated traits could obtain a mating advantage, namely male–male fights or female mate choice. *Am J Phys Anthropol* 135:379–388, 2008. © 2007 Wiley-Liss, Inc.

Sexual dimorphism is extremely variable among primate species. For example, male and female morphology are very similar in lemurs (Kappeler, 1991, 1997), gibbons (Plavcan and van Schaik, 1997), and callitrichids (Goldizen, 1987), whereas male baboons, macaques, and cercopithecines are much larger than females and have longer canines (Plavcan and van Schaik, 1992, 1997). Sexual dimorphism in primates is commonly considered a product of sexual selection (Andersson, 1994). Individuals can increase their fitness relative to conspecifics by either excluding rivals from mating (intrasexual selection) or by increasing their attractiveness (mate choice). The first of these mechanisms has received much attention, mainly through comparative analyses. In particular, dimorphic body size and canine size have been shown to strongly correlate with the intensity of male–male competition (Plavcan and van Schaik, 1992). Mate choice as a cause of primate sexual dimorphism has been less investigated, mainly due to the difficulty of quantifying choice.

While some dimorphic traits such as body size or canine size can be measured in all primate species, certain others are restricted to a few taxa. For example, mature male orangutans (*Pongo sp.*) have cheek flanges, a throat poach, and a long coat of hair (Utami and van Hooft, 2004); male geladas (*Theropithecus gelada*) have a large mane and colorful breast skin (Crook, 1972; Stambach, 1987). Because of the limited distribution of such traits across species, comparative analyses cannot be used to investigate their potential benefit to males. Instead, it is necessary to collect large amounts of mor-

phological data, behavioral data, and reproductive values in wild populations (Arnold and Wade, 1984; Wilkinson et al., 1987; Arnold and Duvall, 1994), which has rarely been accomplished (but see, for example, Lawler et al., 2005).

This intraspecies approach is also fruitful because it allows the dissection of selection mechanisms. For example, estimates of the magnitude of directional, stabilizing, and correlational sexual selection can be obtained by regressing male fitness on male trait values (Lande and Arnold, 1983). Combining these estimates with behavioral observations also reveals proximal mechanisms through which sexually selected traits increase male mating success (Wilkinson et al., 1987).

We examined the intraspecies variability of several dimorphic traits in one of the most size-dimorphic

Grant sponsors: Espèces-Phares program (DG Environnement, UE); Institut Français de la Biodiversité; National Geographic Society; Ministère Français de l'Éducation Nationale et de la Recherche.

*Correspondence to: Damien Caillaud, Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany.
E-mail: damien.caillaud@eva.mpg.de

Received 4 December 2006; accepted 28 September 2007

DOI 10.1002/ajpa.20754

Published online 28 November 2007 in Wiley InterScience (www.interscience.wiley.com).

primates, the western lowland gorilla (*Gorilla gorilla gorilla*). Mature male gorillas are almost twice the size of females (Plavcan and van Schaik, 1997). They are usually called silverbacks because of the grey color of the fur on their back. Their skull is also unlike that of females. In particular, males have a sagittal crest, on which powerful temporal muscles, connected to the mandible, are inserted. This sagittal crest has probably coevolved with the male canines, which are twice as large as female canines (Plavcan and van Schaik, 1997). Male silverbacks also have a fibrous, adipose mass behind their head (Dixon, 1998), which we will refer to as a crest (Fig. 1). Western lowland gorillas live in breeding groups that usually comprise 1–10 adult females, one silverback, and immature gorillas (Magliocca et al., 1999; Parnell, 2002; Gatti et al., 2004). Because of this polygynous mating system, ~40% of mature males live alone (Gatti et al., 2004). Groups are formed when a female joins a young silverback male (Stokes et al., 2003). During the first few years of the male tenure, additional females immigrate and give birth to infants. As the infants grow up and the group gets older, the immigration rate decreases. Secondary transfer of females, female mortality, and subadult natal emigration subsequently decrease the size of the group. Aging males eventually lose their “breeder” status and become solitary again or form nonbreeding groups with immature individuals (Gatti et al., 2004). When a breeding male dies, his group disbands, the other members transferring to several different groups (Stokes et al., 2003).

The habitat of this subspecies includes the tropical rainforests of Gabon, the Republic of the Congo, Cameroon, and the Central African Republic. Gorillas spend most of their time in the dense undergrowth of the forest, a habitat where their observation is generally difficult. However, part of the gorillas’ distribution area is sprinkled with large swampy forest clearings that they regularly visit to feed on mineral-rich herbaceous vegetation (Magliocca and Gautier-Hion, 2002). Gorilla populations visiting several of these clearings have been studied since 1994 (Magliocca et al., 1999; Parnell, 2002; Gatti et al., 2004).

Lokoué clearing, in Odzala-Kokoua National Park, was visited by a population of ~400 gorillas between 2001 and 2004 (Gatti et al., 2004; Caillaud et al., 2006). Determination of the morphological traits of a large sample of silverbacks frequenting this site, together with behavioral data collected during male–male dyadic encounters, allows two major questions to be addressed. First, how does male morphology correlate with group composition? We tested the hypothesis that males with more developed secondary sexual characteristics gain more females, either because greater strength allows them to “steal” other males’ females during intermale encounters, or because transferring females preferentially choose the males with more developed secondary sexual characteristics. We predicted that the number of adult females per male positively correlates with the male’s dimorphic traits. In mountain gorillas, female transfers occur during interunit encounters (Harcourt, 1978; Sicotte, 2001). Most of these encounters consist of ritualized displays and are rarely accompanied by physical contact (e.g., Schaller, 1963; Harcourt, 1978; Sicotte, 1993; Parnell and Buchanan-Smith, 2001; Levréro, 2005), which may allow stronger males to exclude weaker ones, and at the same time allow females to judge the quality of both males. The second question we

investigated was: do male morphology and the presence of females influence male behavior during encounters? We hypothesized that the main purpose of male–male aggressive behavior is the acquisition of new mates or the protection of current mates, such that the number of females belonging to each male involved in an encounter affects the encounter’s intensity. If male displays serve to establish males’ relative strength, male morphology should also affect the probability that two males engage in a series of displays, and how many displays are made.

MATERIAL AND METHODS

Study site and sample

The Lokoué observation site is a 4-hectare swampy clearing near the Lokoué River, east of Odzala-Kokoua National Park (0°54.38N, 15°10.55E). Large mammals, including buffalos (*Syncerus cafer nanus*), elephants (*Loxodonta africana cyclotis*), antelopes (*Tragelaphus eurycerus*, *T. spekei*), and gorillas (*Gorilla g. gorilla*) frequently visit the clearing to feed on its mineral-rich herbaceous vegetation (Magliocca and Gautier-Hion, 2002; Gatti et al., 2004). Gorillas feed on the whole surface of the clearing. The herbaceous vegetation is available throughout the year. No evidence of contest feeding competition has been recorded at Lokoué.

From April 2001 to March 2004, the clearing was watched 9 h a day for 482 days. Gorillas could be observed on most observation days (94%) until January 2004. Gorillas were reliably individually identified using morphological characteristics such as nose print, body shape, and pelage coloration. From January 2004, visits to the site decreased dramatically due to an Ebola outbreak (Caillaud et al., 2006). None of the behavioral data collected during the latter period were used in this study. The overall data set analyzed here includes 87 silverbacks living either solitarily ($n = 29$), in groups including adult females (breeding groups, $n = 51$), or in groups devoid of adult females (nonbreeding groups, $n = 7$; see Levréro et al., 2006).

Assessment of morphological traits

As direct measurement of traits of a large number of gorillas was impossible, several methods were specifically developed to collect morphological data from a distance.

Body size. A numerical camera (Canon Eos D30), a powerful lens (Canon 600 mm f4 and teleconverter 2 ×), and an infrared telemeter (Bushnell) were used to measure body length. Silverbacks were photographed in a standardized position, with simultaneous recording of the distance between the camera and the gorilla. The real size (in meters) of an object measured on a picture (in pixels) could be calculated as a function of its distance to the telemeter (see details in appendix):

$$\text{size}_m = \frac{(D + b) \times \text{size}_{\text{pix}}}{a}$$

where size_m is the real object size, size_{pix} is the object size on the picture, and D is the distance between the camera and the object. Parameters a and b were estimated empirically, by photographing a 20-cm object at



Fig. 1. The sagittal crest corresponds to the insertion of the temporal muscles. The morphologically visible crest is an adipose tissue deposit situated behind and above the sagittal crest. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

different distances from the camera. Regressing the distance D on $1/\text{size}_{\text{pix}}$ provided estimates of a , b , and the measurement error due to the telemeter precision (± 0.5 m).

This method was successfully used to assess the characteristics of individuals situated between 20 and 140 m from the camera. Silverbacks were photographed standing, as in Figure 2a. The distance between the anterior limit of the shoulders and the posterior limit of the ischium was then measured and corrected for the distance between the individual and the telemeter, as described above. The size of 22 silverbacks was measured using this method.

Crest size. Head profiles (Fig. 2b) were photographed using the numeric camera and the 1200-mm lens. The pictures were subsequently superimposed, and their size was adjusted to maintain a constant distance between the mouth and the supraorbital torus. The outlines of the head profiles were then extracted using Optimas (version 6.2, Media Cybernetics, Silver Spring, MD). As our purpose was to measure the size of only the adipose crest, the outlines were subsequently superimposed as in Figure 2c, and an inferior limit was arbitrarily chosen and delimited; the areas thus obtained were measured using Optimas. The crests of 41 silverbacks were measured using this method.

Grey color of the back fur. Measuring the grey color of the back fur is difficult when using pictures of gorillas

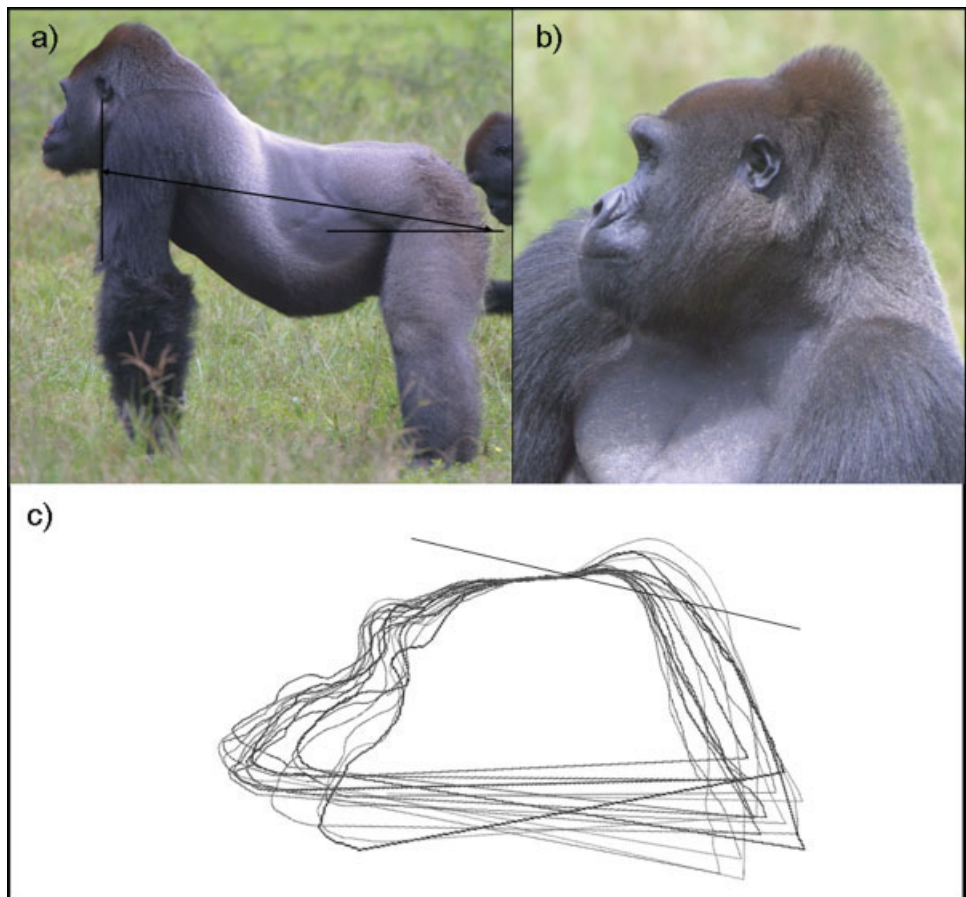


Fig. 2. Measurement of body length and crest size on photographs. (a) Body length was measured as indicated by the arrow. (b) Outlines of the crest were extracted from photographs of head profiles of sitting gorillas. (c) The area above the solid line was used as the measure of crest size. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

due to the fuzziness of the limit of the grey area. Therefore we elected to score individuals with regard to this trait. We sorted all the gorillas and used each individual's rank as its score. As there were many individuals to sort ($N = 57$), we developed an interactive program in Delphi language to assist the scoring procedure. The program presented successively different pairs of photographs of gorilla individuals positioned as in Figure 2a. The dimensions of the photographs were corrected such that the apparent sizes of the gorillas were equal. For each pair of photograph, the program allowed an evaluator to select one of the two corresponding gorillas, according to the criteria of interest. The program, which was based on merge sort, a widely used fusion sorting algorithm (Knuth, 1998), was designed to minimize the number of paired photographs required to obtain a complete scoring of the set.

Musculature development. Musculature development was assessed using the same scoring method described directly above. The volume of the gluteus muscles, which seemed easier to compare between individuals, was chosen as the sorting criterion.

Measurement error

Measurement error for body length can be caused by two main factors: the precision of the telemeter (± 0.5 m) and slight postural variation. We estimated the precision of the telemeter using measurements of the 20-cm object used to estimate parameters a and b . We assessed the overall measurement error using repeated measures with as many males as possible. The mean number of pictures per male averaged 2.2 (range: 1–6). A variance component analysis was performed to compare within-gorilla and between-gorilla contributions to the total variance.

As the head crest is not a stiff anatomic structure, its shape strongly depends on the posture of the silverback. As with body length, we limited the resulting variability by photographing the gorillas in the same standardized posture. The remaining variability, corresponding to measurement error, was estimated using a set of nine gorillas, each photographed on three separate occasions. A hierarchical analysis of variance was performed to compare the within-gorilla and between-gorilla variance components.

The repeatability of the computer-assisted scoring method that we used to quantify musculature and the coloration of the back was estimated by repeating the scoring using four different evaluators, including DC and three nonspecialist evaluators. The Kendall coefficient of concordance W was used to evaluate the agreement between the four score series.

Female group size

The number of adult females belonging to each of the measured males was recorded on the day that morphological measurements were made.

Behavioral data

In mountain gorillas, Sicotte (1993) considers encounters to occur when two units are within 500 m of each other. Within this distance, visual or auditory contact between individuals of the two groups is possible. In forest clearings, visual contact is probably prominent. The

Lokoué clearing is small and roughly circular. The maximum distance between two units is 250 m. Therefore, we defined encounters as the presence of at least two social units in the clearing. Using this same definition, Levréro (2005) found that 73% of 1,092 visits by social units to Lokoué clearing included encounters. Although most of these encounters involved only two units, 39% involved three units or more. In such a case, all interunit behavioral interactions involved only two units. Thus, we chose the simultaneous presence of n units in the clearing as corresponding to $n(n-1)/2$ dyadic encounters.

Data concerning a total of 312 dyadic encounters, involving 67 different silverbacks, were used in this study. For each dyadic encounter, the identity of the two silverbacks involved and the composition of their social unit were noted, and behavioral data were collected. Most behaviors were aggregated in short temporal sequences during which males responded to each other, alternating the running and strutting displays described by Schaller (1963). The data set analyzed here includes all observed running, running accompanied by chest-beating displays, "splash" displays (Parnell and Buchanan-Smith, 2001), and rarely, running accompanied by physical contact. To index the intensity of dyadic encounters, these agonistic displays were summed for each male and each encounter. Encounters including at least one of these displays were categorized as agonistic. Note that following this particular definition, encounters with only stiff postural displays were categorized as nonagonistic.

Statistical analyses

The link between mating status and morphological characteristics was evaluated using generalized linear models (GLMs). The number of females per silverback was modeled using a GLM with Poisson error and a log link function, and breeding status (breeding or nonbreeding) was modeled using a GLM with binomial error and a logit link function. The independent variables of these two models were the four morphological measurements of the mature males and the corresponding quadratic terms. Young, maturing solitary silverbacks are likely to have slightly different morphology than fully mature silverbacks. Therefore, the analyses were performed with and without maturing solitary silverbacks. Goodness of fit of all models was carefully checked.

Linear regression was performed to evaluate the correlation between the total number of displays made by the two males in agonistic encounters and the duration of the encounters as well as between the numbers of agonistic displays made by each of the two males. In addition, we investigated the temporal distribution of the agonistic displays. The following exact test was performed to test whether agonistic displays were aggregately distributed. First, interdisplay intervals were calculated for each of the 45 agonistic encounters that included at least two displays. We then computed the proportion of intervals less than or equal to 10 min, the chosen test statistic. Second, for each encounter, the time of occurrence of each display was replaced by values randomly drawn in flat uniform distributions, with zero as the lower limit and the duration of the encounter as the upper limit. The proportion of simulated intervals less than or equal to 10 min was then computed. This operation was repeated 10,000 times in order to obtain a

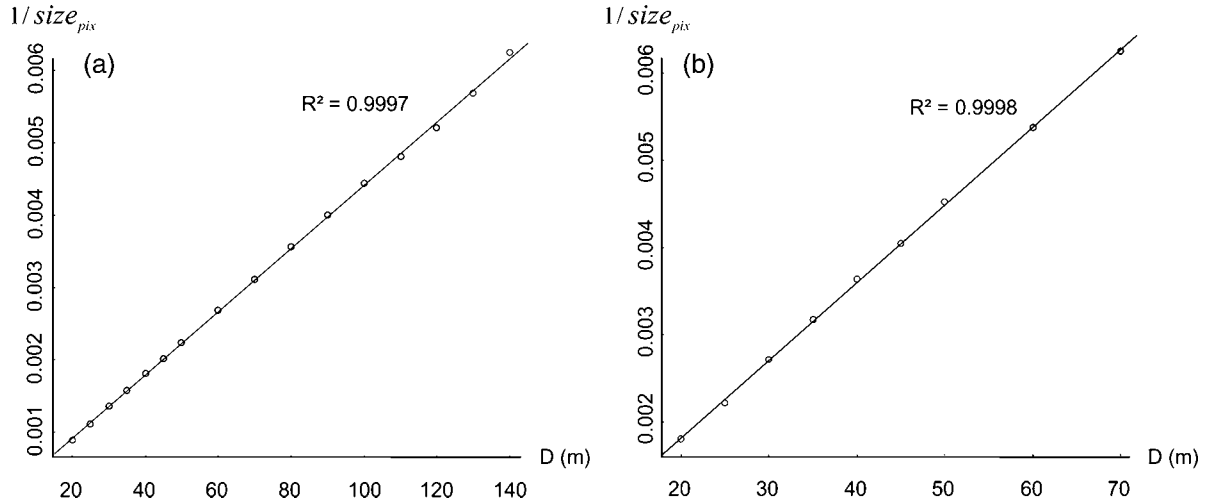


Fig. 3. Regression of $1/\text{size}_{\text{pix}}$ on D . (a) 600 mm f4 lens + teleconverter (doubling the focal distance). (b) 600 mm f4 lens. The linearity is perfect despite the ± 0.5 m precision of the telemeter.

distribution of simulated statistics. Third, the proportion of simulated statistics greater than or equal to the observed test statistic was computed and considered as the P -value of the test.

As keeping or gaining females is the most likely reason for agonistic interactions between silverbacks (Harcourt, 1978; Sicotte, 1993, 2001), the number of females attending the encounters is expected to influence their intensity (Sicotte, 1993; Levréro, 2005). Thus, the more females attending the encounter, the more intense it should be. Alternatively, the greater the difference in the number of females between the two social units involved, the higher the risk of female transfer (Sicotte, 1993). In the latter case, we would expect that the intensity of the encounters would positively correlate with the absolute difference in the number of females between the units. In addition, males with similar morphological trait values can be expected to interact more agonistically than males who are morphologically different (Maynard-Smith, 1982; Riechert, 1998).

Two dependent variables were considered, the type of encounter (agonistic or nonagonistic) and the number of agonistic displays observed, using, respectively, mixed effects GLMs with binomial and Poisson errors. For each dependent variable, two models were constructed. The first model considered five independent variables, i.e., the differences between the interacting males in the four morphological trait values and the total number of females attending the encounter. In the second model, the total number of females was replaced by the absolute difference between the numbers of females in the two interacting social units. The number of infants present during the encounter was also incorporated into these models. Watts (1989) showed that in mountain gorillas, infanticide can occur during interunit encounters. Although no direct evidence of infanticide has been reported among western lowland gorillas, infants often disappear when their mother transfers (Stokes et al., 2003; Gatti, 2005), though this is not systematic (Stokes et al., 2003). If infanticide exists in western lowland gorillas, the number of infants could increase male aggressiveness. Also, if there is a risk of infanticide, females with unweaned infants are not likely to emigrate voluntarily (Sicotte, 1993). To test this last hypoth-

esis, the previous models were also run after replacing female group size with the number of females without infants.

A stepwise AIC-based simplification procedure was applied to each of these models in order to select the most parsimonious one.

Most of the males were involved in several encounters, which led to nonindependence of the encounters. We accounted for the identities of the two males involved by modeling them as random effects. Since the goal of including male identity effects was to model nonindependence of encounters, these variables were maintained, even in simplified models.

All statistical analyses were performed with Splus (version 6.0, Mathsoft, Seattle, WA) and R (version 2.5, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Measurement error

The measurement error resulting from the ± 0.5 m precision of the telemeter was negligible, estimated as 2.5% (Fig. 3). For example, a 20-cm object can be measured at a distance ranging from 20 to 140 m with a precision of ± 5 mm.

The main source of measurement error was variation in the position of the photographed silverbacks. The estimated body length ranged from 78.6 to 99.9 cm (mean 89.4 cm). The interindividual standard deviation was estimated as 4.99 cm, and the intraindividual standard deviation was estimated to be 3.84 cm. As the mean number of photographs per individual was 2.2, the mean measurement precision, defined as half the width of the 95% confidence interval of the intraindividual mean, was equal to $1.96 \times 3.84 / \sqrt{2.2} = 5.07$ cm. This degree of precision is satisfactory for measuring the size of a gorilla standing at a distance of 20–140 m. However, since the intraindividual standard deviation is on the same order as the interindividual standard deviation, the precision may be insufficient to detect small effects in the statistical models we tested.

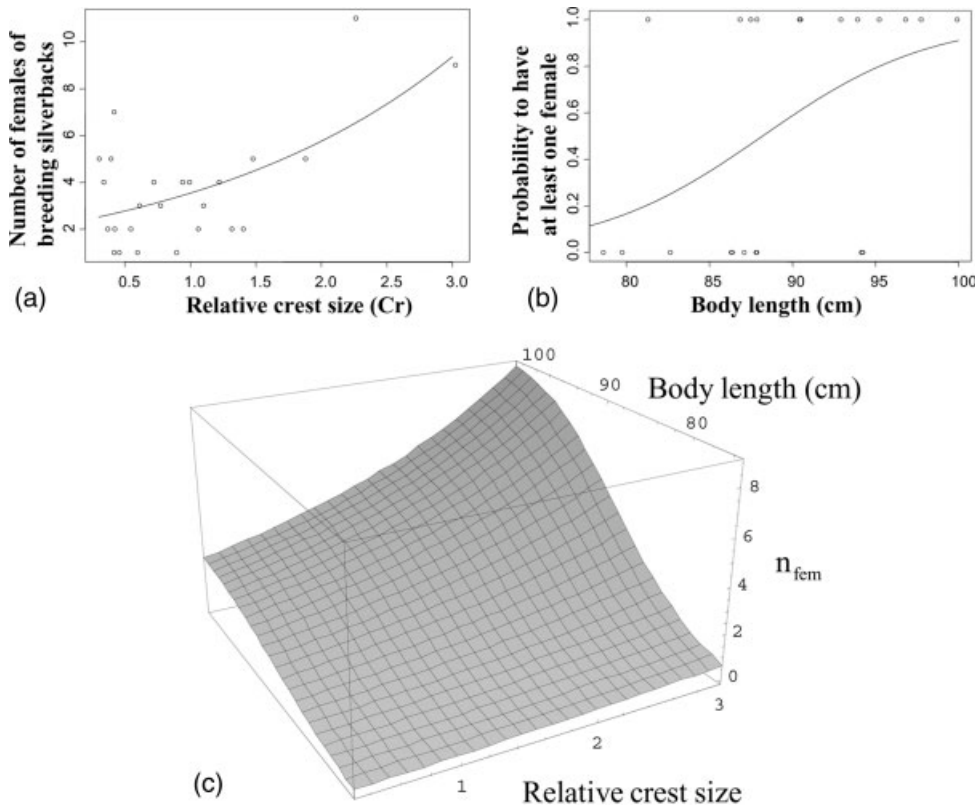


Fig. 4. Male mating status as a function of silverback morphology. (a) and (b) Dots correspond to observed data; the solid lines correspond to the model predictions. (c) 3D plot of the predicted surface.

Analysis of variance of crest size measurements showed that the within-subject component accounted for 23.7% of the total variance, which is satisfactory.

With regard to the scoring method used to quantify musculature and the grey color of the back fur, the Kendall coefficient of concordance was highly significant ($N = 57$, $k = 4$; musculature: $W = 0.77$, $P < 0.01$; grey color: $W = 0.73$, $P < 0.01$). Thus, the computer-assisted ranking method provided reproducible scores. We used the scores obtained by DC in the following analyses.

Correlates of female group size

Among the 59 silverbacks for which morphological data were collected, 34 (58%) lived in breeding groups, 3 lived in nonbreeding groups, and 22 were solitary. Group size averaged 8.1 individuals, with 3.6 adult females.

The initial statistical model containing the four morphological measures as independent variables and the number of adult females per silverback as the independent variable was performed using the complete data set. This model poorly fit the data, with a dispersion coefficient greater than one ($\hat{c} = 3.57$). The presence of nonbreeding silverbacks in the data set was a plausible reason for this high overdispersion. Indeed, excluding nonbreeding silverbacks from the data set led to a much better model, without overdispersion ($\hat{c} = 1.03$). With this model, the number of females belonging to a silverback was best explained by the size of the head crest ($\chi_1^2 = 12.97$, $P < 0.01$; Fig. 4a).

Concerning the binomial GLM used to determine the variables affecting the breeding status of silverbacks, body length was the only variable retained after model

simplification ($N = 19$, $\chi_1^2 = 5.10$, $P = 0.024$; Fig. 4b). Removing the three maturing males from the data set led to a slight increase in the P -value ($N = 16$, $\chi_1^2 = 3.37$, $P = 0.07$), likely due to an increase in Type 2 error. Thus, the size of young males and solitary males does not seem to differ.

The binomial model provided an estimate of the probability that a mature male is a breeding male, while the Poisson model estimated the number of females per breeding male. Thus, the product of these two estimates predicts the number of females owned by any given male. Taking into account the logit and log link functions of the binomial and Poisson models, respectively, leads to:

$$n_{\text{fem}} = \frac{e^{(c \times cr + d)}}{1 + e^{-(a \times \text{length} + b)}}$$

where n_{fem} is the expected number of females, cr is the relative crest size (i.e., the crest size divided by the mean crest size of the sample), length is body length, $a = 0.20$, $b = -17.33$, $c = 0.49$, and $d = 0.78$. The surface corresponding to this equation is represented in Figure 4c. Large crests are only beneficial to males with large bodies.

The lack of significance of musculature development and extent of the grey color on the back could be due to the low sample size used in these models. As these two variables were available for more individuals than were body length and crest size, complementary analyses were performed using musculature development and back color only. The number of females per breeding male was not significantly explained by either variable. However, the probability of a male having at least one

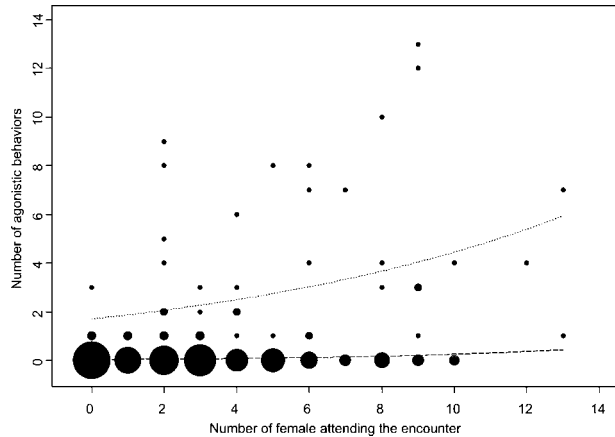


Fig. 5. Intensity of male–male encounters in relation to the number of females present. The surface of the circles is proportional to the number of points superimposed. The higher the number of females attending an encounter, the higher the number of agonistic displays observed. Dashed line: predicted values obtained for all the data (312 dots). Dotted line: predicted values obtained after exclusion of nonagonistic encounters (points with null ordinate).

female appeared to be positively associated with musculature ($\chi^2_1 = 5.28, P = 0.022$).

Interunit encounters

Most of the 312 encounters were not agonistic. Running, running accompanied by chest beating, and running accompanied by physical contact were observed in 48 encounters, which were therefore classified as agonistic. The number of agonistic displays per agonistic encounter, summed for both males, averaged 3.6 (range: 1–13). The consequences of the agonistic encounters were difficult to estimate directly, as no female transfer between social units was observed in the clearing. The duration of the agonistic encounters did not affect the number of displays observed ($r^2 = -0.003, F_{1,46} = 0.86, P = 0.36$). Unsurprisingly, the number of displays made by each of the two silverbacks in the dyadic encounters were correlated ($r^2 = 0.10, F_{1,46} = 6.13, P = 0.017$). Agonistic displays were aggregately distributed over time (exact test, $P < 0.01$).

Of all the variables tested, only the total number of females (including females with infants) present during the encounter was found to significantly affect the two response variables: the type of encounter and the total number of agonistic displays. The number of females was positively associated with the probability of an agonistic encounter ($N = 312, z = 3.53, P < 0.01$). None of the morphological variables was retained after model simplification. The number of females also strongly correlated with the total number of agonistic displays ($N = 312, z = 2.71, P < 0.01, \text{Fig. 5}$). This relationship was maintained when considering only agonistic encounters ($N = 46, z = 2.59, P < 0.01, \text{Fig. 5}$). None of the other variables was retained after model simplification.

DISCUSSION

Morphological and behavioral data were collected on 87 mature male gorillas of northern Congo, yielding two major findings. First, we found that the number of mates

of silverbacks was differently linked to the four morphological traits assessed. Male reproductive status (non-breeding or breeding) was correlated with their body size and musculature. Interestingly, the number of females of breeding groups appeared to be mainly related to another trait, male crest size. Second, we found that the occurrence and number of male agonistic displays observed during dyadic encounters were not significantly associated with male morphology but were strongly and positively correlated with the total number of females present.

The photogrammetric method developed here appears to be a useful and efficient means for capturing inter-individual morphological variability. The resulting measurement errors were sufficient to reveal several significant correlations with male mating status. However, one can wonder if the nonsignificant effect of the grey color of male fur on mating status or the nonsignificant effect of morphological variables on male behavior is a genuine finding or merely an artifact of high Type 2 error. This is difficult to determine, but if these effects exist, they must be weak. Further studies are needed to replicate our results with a larger sample size that is sufficient to detect small effects.

Both body size and muscle mass of male gorillas are associated with a mating advantage. In most size-dimorphic mammals, the proposed underlying mechanism is usually the ability of larger, strong males to prevent smaller, weaker males from reproducing. However, among western lowland gorillas, no one has observed a solitary challenger taking over a group or two breeding groups fusing after the eviction of a silverback (Robbins et al., 2004). When a silverback dies, the group disbands, which suggests that male–female relationships are more important than female–female relationships in maintaining group cohesion (Stokes, 2004). It is thus probable that if a solitary male took over a group and chased the resident breeding male, he would be unable to coerce the females to remain with him. The only way for a male to switch the allegiance of all the females would be to kill or seriously wound the resident male, which could be too risky. The same pattern is observed in mountain gorillas (Robbins, 2001): single-male groups disband when a silverback dies, and no takeovers have been observed (Watts, 1989; Robbins, 2001). Consequently, the proximal mechanism rendering large male gorillas more fit is likely to be female mate choice and/or forced transfer of females.

The absence of group takeover in gorillas does not eliminate male interest in fighting. Males could use aggression to try to force females to join them. In eastern gorillas, infanticide observed during encounters constitutes such coercion (Watts, 1989; Yamagiwa and Kaheka, 2004). Females losing their infant have been observed to join and mate with the infanticidal male (Watts, 1989), rendering this strategy adaptive.

Encounters provide females with good opportunities to evaluate and compare males. Consistent with this idea, the number of females attending encounters was the only variable significantly affecting the occurrence of agonistic displays. This same effect has been shown in mountain gorillas, a species in which females without infants are known to transfer during encounters (Sicotte, 1993, 2001). Although female mate choice in western gorillas has not been investigated, the main reason for females to choose larger males is probably to gain protection against predators such as leopards (*Panthera pardus*) (Robbins et al., 2004). Larger, stronger males could



Fig. 6. Female gorillas living in captivity (left) and in the wild (right). The adipose crest of the captive female is more developed. Photo on the left courtesy of la Vallée des Singes, France. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

also be more effective at protecting their offspring against infanticide by other males, although no case of infanticide has formally been described in western lowland gorillas, in contrast to eastern gorillas (Fossey, 1984; Watts, 1989; Yamagiwa and Kaheka, 2004). Only indirect evidence of infanticide has been reported so far (Gatti 2005, Stokes et al., 2003). The improved fighting abilities of larger males could also provide females with increased access to limiting feeding resources such as fruit trees. The home ranges of gorilla groups overlap (Bermejo, 2004), and social units frequently meet each other near fruit trees (Tutin, 1996; Bermejo, 2004). Thus, between-groups feeding contest competition is likely to occur; hence male ability to defend resource patches against other males could be important to females.

We found that the effect of body length interacts with that of crest size. The slope of the regression of crest size and number of mates increased with body length. Small males are excluded from reproduction, irrespective of the size of their adipose crest. This suggests that crest size is of secondary importance. As the crest is an adipose structure, it may reflect male health status. The healthier a male is, the more energy he can allocate to adipose tissues. This is supported by the fact that gorillas living in captivity have extremely developed head crests. Surprisingly, even adult females have large crests in captivity (Fig. 6). Males with large crests may therefore be more likely to be healthy and thus provide direct and indirect benefits to females choosing them. Examples of direct benefits could be increased protection against predators and increased survival with a subsequent increase in the duration of paternal investment. Indirect benefits include good genes, which healthy males are more likely to transmit to their offspring (e.g., Kokko et al. 2002). In addition to this mechanism based on mate choice, healthier males could also have increased fighting abilities providing them with an advantage in male–male competition. The two hypotheses are not mutually exclusive and could operate simultaneously.

When attempting to explain correlations between traits and mating status, it is impossible to rule out the possibility that the trait of interest is not itself under selection but is simply correlated with another trait that influences mating status. Increasing the number of traits measured usually limits—but does not totally prevent—misinterpretation. In iteroparous species, age is such a trait (e.g., elephant seal: Leboeuf and Reiter, 1988; redlip blenny: Cote and Hunte, 1993). The western lowland gorilla is an iteroparous, long-lived species, and the number of females owned by a male probably varies according to his age (Parnell, 2002). Theoretical works have shown that, in the absence of male investment, female preference for males of a given age class can be an evolutionary stable strategy if: 1) male survival depends on their genetic quality, 2) the cost of choosiness is low, 3) the mutation rate generates sufficient variability in viability among males for the choosiness to be advantageous, and 4) adult males do not have greater survival than juveniles (Kokko and Lindstrom, 1996; Beck and Powell, 2000). The latter condition is not fulfilled in the case of gorillas. Therefore, the perceived age of a male by a female is unlikely to provide a sufficient genetic benefit to females for selection to operate in this way. However, females choosing younger males may obtain direct benefits such as a decreased probability that the male will die, and subsequently, that the group will disband. Of the four morphological traits assessed here, all but body size are potentially age dependent in mature males. Only a long-term study can enable investigation of whether and how silverback morphology varies with age. This would allow determination of the age at which selection pressure on the different traits is the strongest (Kokko and Lindstrom, 1996; Coltman et al., 2002). During the 3 years of the present study, no visible change was observed in most of the silverback males. Although the transformation of blackbacks into silverbacks appeared to be spectacularly rapid, lasting less than 1 year, no subsequent morphological change was detected.

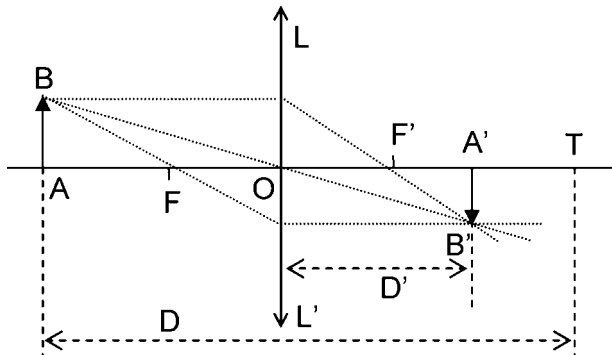
CONCLUSION

The present study reveals that dimorphic traits are linked to male mating status in western lowland gorillas. To our knowledge, this is the first study to investigate the variability of male morphology in this species. Males with a developed musculature, large body size, and large adipose crest have more females. In the absence of take-over in this species, female mate choice appears a potentially important contributor to the evolution of sexual dimorphism, although male–male competition needs to be further investigated. In addition, the extent to which male size and musculature are related to offspring survival against predator attack needs exploration, as does the link between crest size and health status.

ACKNOWLEDGMENTS

The authors thank A. Gautier-Hion, A. Alvergne, S. Tancredi, and A. Courtiol for useful discussions, M. Douadi for her help in Odzala, V. Durand for her assistance with the bibliography, the ECOFAC program for its support in the field, and two anonymous referees for their useful comments on the manuscript. We also thank “La Vallée des Singes” for providing us pictures of captive gorillas. We are particularly grateful to R. Andembo, J.-B. Lépalé, J.-F. Ndong, J.-P. Ayo, W. Opingo, V. Bossi, J.-P. Opingo, J. Millot-Keurinck, and P. Montuir for their help in the Gabon and Congo. This is publication ISEM 2007-106.

APPENDIX: MEASUREMENT OF DISTANT OBJECTS WITH A CAMERA AND TELEMETER



Let AB be the photographed object and A'B' be the corresponding image. The straight line (AO) is the optic axis of the converging lens (LL'). The position of the image is defined by the three light rays (dotted lines) crossing F, O, and F'. The points F and F' are the foci of the lens, and FO = FO' = f is the focal length of the lens. The length of the image is given by

$$\begin{cases} \frac{AB}{A'B'} = \frac{f}{OA' - f} \\ \frac{AO}{OA'} = \frac{AB}{A'B'} \end{cases}$$

which gives

$$A'B' = \frac{A'B' \times AO}{f} \times AB$$

$$\Leftrightarrow A'B' = \frac{AB \times f}{AO - f} \tag{1}$$

The telemeter is in T, at a distance D from the object and D' from the optical center. Eq. (1) can then be written as follows:

$$A'B' = \frac{AB \times f}{D - D' - f}$$

which is equivalent to the expression $size_m = \frac{(D+b) \times size_{pix}}{a}$ presented in the main text.

LITERATURE CITED

Andersson M. 1994. Sexual selection. Chichester: Princeton University Press.
 Arnold SJ, Duvall D. 1994. Animal mating systems—a synthesis based on selection theory. *Am Nat* 143:317–348.
 Arnold SJ, Wade MJ. 1984. On the measurement of natural and sexual selection—theory. *Evolution* 38:709–719.
 Beck CW, Powell LA. 2000. Evolution of female mate choice based on male age: are older males better mates? *Evol Ecol Res* 2:107–118.
 Bermejo M. 2004. Home-range use and intergroup encounters in western gorillas (*Gorilla g. gorilla*) at Lossi Forest, North Congo. *Am J Primatol* 64:223–232.
 Caillaud D, Levrero F, Cristescu R, Gatti S, Dewas M, Douadi M, Gautier-Hion A, Raymond M, Menard N. 2006. Gorilla susceptibility to Ebola virus: the cost of sociality. *Curr Biol* 16:R489–R491.
 Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C. 2002. Age-dependent sexual selection in bighorn rams. *Proc R Soc Lond B Biol Sci* 269:165–172.
 Cote IM, Hunte W. 1993. Female redlip blennies prefer older males. *Anim Behav* 46:203–205.
 Crook JH. 1972. Sexual selection, dimorphism, and social organization in the primates. In: Campbell B, editor. *Sexual selection and the descent of man 1871–1971*. Chicago: Aldine. p 231–281.
 Dixon AF. 1998. Primate sexuality: comparative studies of the prosimians, monkeys, apes, and human beings. Oxford: Oxford University Press.
 Fossey D. 1984. Infanticide in mountain gorillas with comparative notes on chimpanzees. In: Hausfater G, Hrdy SB, editors. *Infanticide*. New York: Aldine. p 217–235.
 Gatti S. 2005. Structure, dynamique et génétique d'une population de gorilles de plaine de l'ouest (*Gorilla gorilla gorilla*) au nord de la République du Congo [Ph.D. thesis]. Rennes: University of Rennes 1. 278 p.
 Gatti S, Levrero F, Ménard N, Gautier-Hion A. 2004. Population and group structure of western lowland gorillas (*Gorilla gorilla gorilla*) at Lokoue, Republic of Congo. *Am J Primatol* 63:111–123.
 Goldizen AW. 1987. Facultative polyandry and the role of infant-carrying in wild saddle-back tamarins (*Saguinus fuscicollis*). *Behav Ecol Sociobiol* 20:99–109.
 Harcourt AH. 1978. Strategies of emigration and transfer by primates, with particular reference to gorillas. *Z Tierpsychol* 48:401–420.
 Kappeler PM. 1991. Patterns of sexual dimorphism in body-weight among prosimian primates. *Folia Primatol* 57:132–146.
 Kappeler PM. 1997. Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. *Behav Ecol Sociobiol* 41:115–127.
 Knuth DE. 1998. *Sorting by merging. The art of computer programming*, 2nd ed. Reading, Massachusetts: Addison-Wesley. p 158–168.
 Kokko H, Brooks R, McNamara JM, Houston AI. 2002. The sexual selection continuum. *Proc R Soc Lond B Biol Sci* 269: 1331–1340.
 Kokko H, Lindstrom J. 1996. Evolution of female preference for old mates. *Proc R Soc Lond B Biol Sci* 263:1533–1538.
 Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.

- Lawler RR, Richard AF, Riley MA. 2005. Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *J Hum Evol* 48:259–277.
- Leboeuf BJ, Reiter J. 1988. Lifetime reproductive success in elephant seals. In: Clutton-Brock TH, editor. *Reproductive success*. Chicago: Chicago University Press. p 344–362.
- Levréro F. 2005. Structure d'une population de gorilles (*Gorilla g. gorilla*) visitant une clairière forestière- nature et rôle des rencontres intergroupes dans sa dynamique [Ph.D. thesis]. Rennes: University of Rennes 1. 278 p.
- Levréro F, Gatti S, Ménard N, Petit E, Caillaud D, Gautier-Hion A. 2006. Living in nonbreeding groups: an alternative strategy for maturing gorillas. *Am J Primatol* 68:275–291.
- Magliocca F, Gautier-Hion A. 2002. Mineral content as a basis for food selection by western lowland gorillas in a forest clearing. *Am J Primatol* 57:67–77.
- Magliocca F, Querouil S, Gautier-Hion A. 1999. Population structure and group composition of western lowland gorillas in north-western Republic of Congo. *Am J Primatol* 48:1–14.
- Maynard-Smith J. 1982. *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- Parnell RJ. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *Am J Primatol* 56:193–206.
- Parnell RJ, Buchanan-Smith HM. 2001. Animal behaviour—an unusual social display by gorillas. *Nature* 412:294.
- Plavcan JM, van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. *Am J Phys Anthropol* 87:461–477.
- Plavcan JM, van Schaik CP. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *Am J Phys Anthropol* 103:37–68.
- Riechert SE. 1998. Game theory and animal conflict. In: Dugatkin LA, Reeve HK, editors. *Game theory and animal behaviour*. Oxford: Oxford University Press. p 64–93.
- Robbins MM. 2001. Variation in the social system of mountain gorillas: the male perspective. In: Robbins MM, Sicotte P, Stewart KJ, editors. *Mountain gorillas: three decades of research at Karisoke*. Cambridge: Cambridge University Press. p 29–57.
- Robbins MM, Bermejo M, Cipolletta C, Magliocca F, Parnell RJ, Stokes E. 2004. Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*). *Am J Primatol* 64:145–159.
- Schaller GB. 1963. *The mountain gorilla: ecology and behaviour*. Chicago: University of Chicago Press.
- Sicotte P. 1993. Intergroup encounters and female transfer in mountain gorillas—influence of group composition on male-behavior. *Am J Primatol* 30:21–36.
- Sicotte P. 2001. Female mate choice in mountain gorillas. In: Robbins MM, Sicotte P, Stewart KJ, editors. *Mountain gorillas: three decades of research at Karisoke*. Cambridge: Cambridge University Press. p 59–87.
- Stammbach E. 1987. Desert, forest and montane baboons: multi-level societies. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: Chicago University Press. p 112–120.
- Stokes EJ. 2004. Within-group social relationships among females and adult males in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Am J Primatol* 64:233–246.
- Stokes EJ, Parnell RJ, Olejniczak C. 2003. Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behav Ecol Sociobiol* 54:329–339.
- Tutin CG. 1996. Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In: McGrew WC, Marchant LF, Nishida T, editors. *Great apes societies*. Cambridge: Cambridge University Press. p 58–70.
- Utami SS, van Hooff JARAM. 2004. Alternative male reproduction strategies: male bimaturism in orangutans. In: Kappeler PM, van Schaik CP, editors. *Sexual selection in primates: new and comparative perspectives*. Cambridge: Cambridge University Press. p 196–207.
- Watts DP. 1989. Infanticide in mountain gorillas—new cases and a reconsideration of the evidence. *Ethology* 81:1–18.
- Wilkinson GS, Clutton-Brock TH, Grafen A, Harvey PH, Howard RD, Linsenmair KE, Poethke HJ, Reyer HU, Sutherland WJ, van Noordwick AJ, Wade MJ, Wirtz P. 1987. The empirical study of sexual selection. In: Andersson MB, Bradbury JW, editors. *Sexual selection: testing the alternatives*. Chichester: Wiley Press. p 234–246.
- Yamagiwa J, Kaheka J. 2004. First observations of infanticides by a silverback in Kahuzi-Biega. *Gorilla J* 29:6–9.