

## Body Mass in Lowland Gorillas: A Quantitative Analysis

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**ABSTRACT** Body proportions and tissue composition (e.g., relative contributions of muscle, skin, bone, and adipose to total body mass) were determined through dissection of four adult captive lowland gorillas. The relative contribution of bone varies little among the four animals (10.2–13.4%) despite considerable range in body weights (99.5–211 kg). In tissue composition, three animals have on average 37.3% muscle relative to body mass. Maximum estimates of body fat range between 19.4–44%. Differences in age, sex, and life history events partially explain the observed variation in body proportions and tissue composition among the four animals. Although gorillas are considered extremely sexually dimorphic in body weight and canine size, differences in tissue are not as dramatic as body mass differences suggest. This study found sex differences mostly in the upper body; males have relatively heavier forelimbs, including heavier deltoid, trunk-binding, and deep back muscles compared to the younger female. The old, obese female had one half the muscle tissue of the other three animals (16% vs. 37.3%), and twice the body fat (44%); forelimbs and upper body musculature were relatively well-developed to compensate for the restricted hip-joint movement due to arthritis. Data on the variation in tissue composition and body proportions in gorillas provide a basis for comparison with other hominoids, including humans. For example, compared to highly dimorphic orangutans, gorillas have more muscle, less adipose tissue, lighter forelimbs and heavier hindlimbs. Such analyses complement studies of the skeleton and contribute to our understanding of human evolution and adaptation. *Am J Phys Anthropol* 113:61–78, 2000. © 2000 Wiley-Liss, Inc.

With an imposing physical appearance, marked sexual dimorphism, and muscular bodies, gorillas capture the imagination of filmmakers and artists as well as primatologists. Most of our understanding about gorilla anatomy derives from dental and skeletal studies along with information on body weights. Soft tissue of whole animals has been little studied or quantified.

Skeletal studies have focused, for example, on the cranium and face, including cranial capacity and dentition (Krogman, 1931; Gregory, 1949; Groves, 1970; Tobias, 1975; Greene, 1973; Shea, 1985; Aiello and Dean,

1990; Uchida, 1998), and on the trunk, limbs, hands and feet (Schultz, 1930, 1937, 1950; Jungers and Susman, 1984; Jungers, 1985; Inouye, 1994; Taylor, 1992).

The classic Raven Memorial Volume *Anatomy of the Gorilla* (Gregory, 1950), based on a single adult male from Lincoln Park Zoo in Chicago, is unique in describing

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soft tissue from dissection of the entire animal, though it includes little quantitative data. Regional studies that analyze or quantify soft tissue include hands and feet (Straus, 1930; Gregory, 1949; Tuttle, 1969) and the muscular system (Preuschoft, 1963); some information is available on the gastrointestinal system (Chivers and Hladik, 1980).

Body weights are of interest because they serve to characterize gorillas as a species, to assess variation between populations (e.g., lowland, mountain, captive), to establish ratios of brain to body weight, and to provide a yardstick for documenting growth patterns and degree of sex differences (Willoughby, 1978; Leigh, 1994; Leigh and Shea, 1995; Zihlman, 1997).

However, in primate comparisons, body mass is treated as if it were unidimensional, whereas in reality it is multifactorial. Body mass is a composite of different tissues, e.g., muscle, skin, bone, and adipose; the proportions are affected by age, sex, reproductive state, health, access to food, and activity level (Forbes, 1987; Roche et al., 1996; Wang et al., 1999). Body mass does not reflect tissue composition or distribution (Brozek, 1999; Clarys et al., 1999).

In order to directly analyze body mass and its variation in some detail, we dissected four entire captive gorillas. Captive gorillas offer a rare opportunity to directly measure body composition of this taxon. The sample is enhanced by having individuals of known age, sex, and history.

Because body composition relates to every aspect of an individual's growth, survival, and reproduction, the importance of measuring it directly has long been recognized for *Homo sapiens*. Even so, only a total of 51 subjects from a few studies during the past 150 years have been directly assessed because access to entire individuals is extremely limited (Clarys et al., 1999). Our data on gorilla body composition provide some comparative data with humans and other hominoids, and serve as a basis for future study.

The goals of this study on body mass were: to measure directly component tissues and their distribution through the body; to examine variation between individuals and

TABLE 1. Animal sample: captive  
Gorilla gorilla gorilla

| Individual | Age in years | Body weight in kg |
|------------|--------------|-------------------|
| Female A   | 27           | 99.5              |
| Female B   | 38           | 159.1             |
| Male A     | 36           | 172.7             |
| Male B     | 36           | 211.0             |

to explore possible contributing variables; to define a gorilla pattern of tissue composition and body proportions; and to establish a comparative sample with humans and other hominoids. The last is essential for understanding the pattern of human body composition within an evolutionary framework.

## MATERIALS AND METHODS

Gorillas are valuable and rare and live a long time in captivity. Deaths are unpredictable, and few animals are available for complete postmortem study outside zoological gardens or research centers. This research relies on chance events and presents logistical challenges regarding transportation of large specimens, and facilities for freezing and dissecting the animals. However, the potential payoff is considerable because there is so little known about the soft tissue of gorillas; this information is unlikely to be collected from noncaptive animals.

### The animals

Four adult western lowland gorillas (*Gorilla gorilla gorilla*) obtained from zoological parks were frozen after necropsy, and later thawed and dissected immediately after thawing (Table 1). The four animals, two females and two males, were wildborn but grew up in captivity. They were well-fed and cared for and housed with other gorillas, with opportunities for varying degrees of mobility and social interactions.

Information on the life histories of the animals is available, including records on physical and dental health, reproductive histories, and causes of death. Body weights were recorded during life, in some cases over several years, and at necropsy. Three of the four animals had live offspring. The four animals lived long lives in captivity, and were well-muscled at death, a tribute to the

high level of care they received during their lives.

Female A was a healthy and well-muscled animal, with an estimated age of 27 years. At death she weighed 99.5 kg. Female A was housed for most of her life as part of a gorilla social group and had two offspring, both of whom survived to maturity. She died of pneumonia after a brief illness. When necropsied, the thoracic and abdominal viscera were removed; the rib cage and sternum were cut and the cranium was opened to remove the brain. At time of dissection, all the skin was removed and weighed as a unit.

Female B was an old, infirm, and obese individual, with an estimated age of 38 years at death. She weighed 159.1 kg at the time of death. She did not bear offspring and was housed between ages 15–37 with an adult male gorilla. Late in life, she was relatively inactive and had difficulty in moving. Advanced age, arthritis, and the death of her male companion the previous year contributed to her death. At necropsy, the thoracic and abdominal viscera were removed, but the rib cage and cranium were left intact.

Male A was a well-muscled, healthy individual, estimated to be 36 years old at death. He weighed 172.7 kg. He apparently maintained his body weight within a narrow range for many years; 14 years earlier, at age 22, he weighed 170 kg. Male A spent his life as the oldest male in a social group and fathered three offspring. He died within a week of an acute illness. At the time of necropsy, the thoracic and abdominal viscera were removed, but the rib cage and cranium were left intact.

Male B was robust and well-muscled at death. He was estimated to be 36 years old. His weight at death was estimated to be 211 kg, a weight he had maintained for several years. He had been housed in social groups at three zoos and fathered one offspring. He died after a 2-day illness of an aortic aneurism. At necropsy, the thoracic and abdominal viscera and the brain were removed; the neck region, face, and cranium were severely damaged. Prior to the dissection, all the skin was removed and weighed as a unit.

## Dissection methods

The methods used in this study are based on those developed by T.I. Grand for analyzing and comparing tissue composition and distribution in species from several mammalian orders (e.g., Grand, 1977a, b, 1983a, 1992, 1997). Zihlman and colleagues expanded and applied the methods to hominoids (e.g., Zihlman, 1984; Morbeck and Zihlman, 1988; McFarland and Zihlman, 1995; Zihlman and McFarland, 1996; Nichols and Zihlman, 1997). Our approach to body composition directly measures dissectible tissues, as opposed to indirect methods which estimate fat-free weight in living humans and can only approximate absolute amounts of skeletal muscle and bone (Clarys et al., 1999). In addition to tissue composition, our approach also records and analyzes tissue distribution to the limbs.

Ideally, we follow a dissection procedure that uses two complementary methods. On one side, "the segment side," body segments are separated at the relevant joints: upper arm at the shoulder joint; forearm at the elbow joint; hand at the wrist joint; thigh at the hip joint; leg at the knee joint; and foot at the ankle joint (Fig. 1). Muscles crossing the shoulder and elbow joints, and the hip and knee joints, are cut at the attachment sites and weighed with the appropriate segment (Table 2). The hand is severed between the carpals and radius and ulna, and the foot is severed between the tibia/fibula and the top of the talus and calcaneus. On the trunk, the posterior neck and deep back muscles (Table 4) are removed by region: cervical, from atlas to T1; thoracic, from T1 to last rib; lumbar, last rib to top of ilium; and sacral/caudal, the remainder.

Skin, muscle, bone, adipose, and "other" tissues are separated and weighed wet to the nearest gram. Tongue, hyoid, and facial muscles are not included as part of total musculature. "Other" includes tissue that cannot be easily separated or classified in another category, such as connective tissue, nerves, blood vessels, and lymphatic tissue.

Since a completely intact animal is rare because some parts are removed during necropsy, we accommodate to each situation in order to obtain all possible information. For

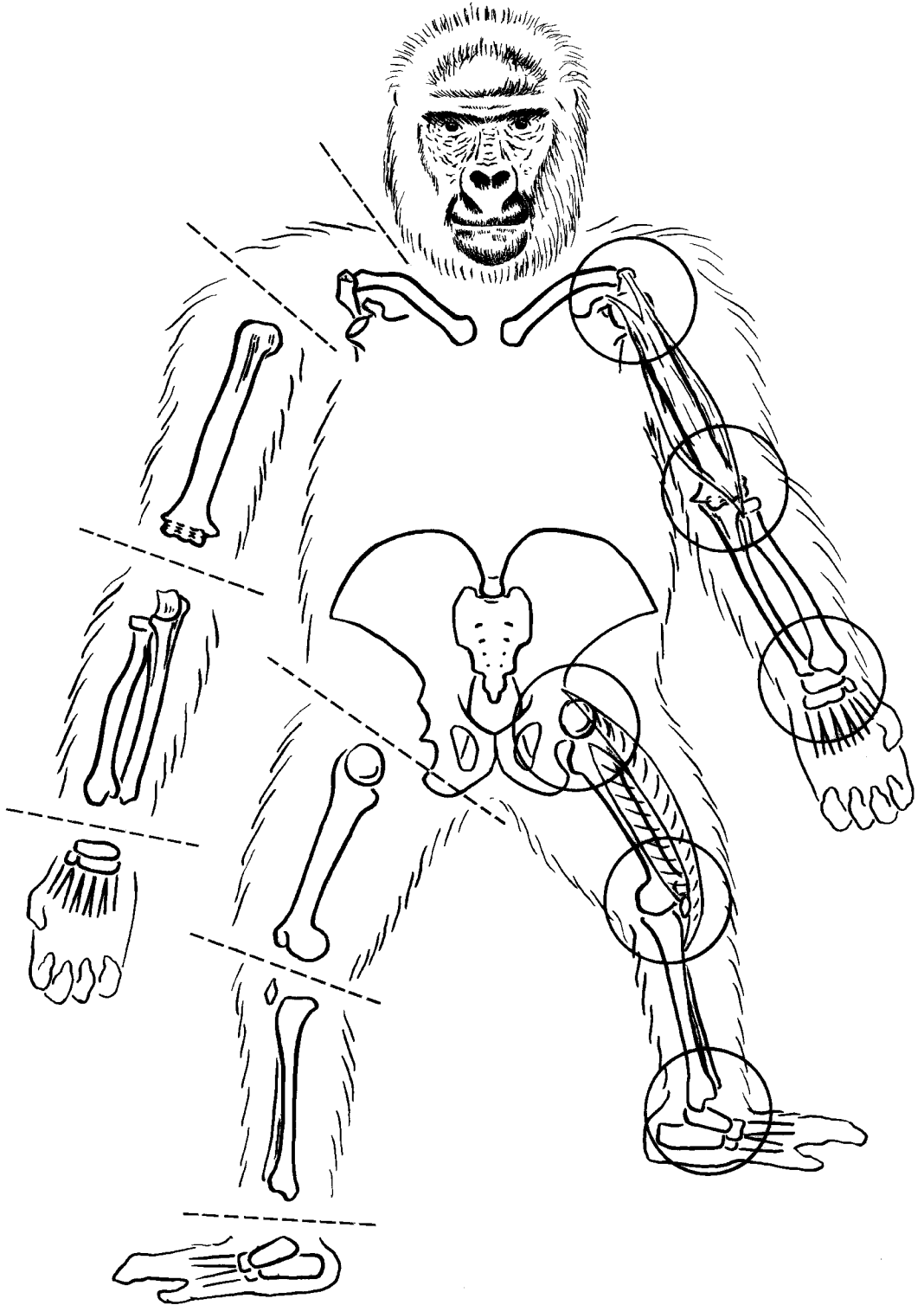


Fig. 1. Dissection methods. Left side, body segments; right side, muscle-by-muscle.

TABLE 2. *Muscles assigned to limbs*

|   |   |   |  |
|---|---|---|--|
| Forelimb  | Arm   | Deltoid                                     |  |
|   |   | Biceps brachii                              |  |
|   |   | Triceps (four parts)                        |  |
|   | Forearm                                       | Brachialis                                  |  |
|   |   | Coracobrachialis                            |  |
|   |   | Extensors                                   |  |
|   |   | Flexors                                     |  |
|   |   | Brachioradialis                             |  |
|   |   | Pronators                                   |  |
|   | Hand  | Supinator                                   |  |
|   |   | Intrinsic muscles                           |  |
|   | Hindlimb                                      | Thigh                                       | Long tendons of forearm, flexors and extensors |
|   |   |   | Quadriceps femoris                             |
| Hamstrings<br>(semitendinosus, semimembranosus, biceps femoris, long and short heads) |   |   |  |
| Leg   |   | Adductors (magnus, longus, brevis, minimus) |  |
|   |   | Pectineus                                   |  |
|   |   | Gracilis                                    |  |
|   |   | Sartorius                                   |  |
|   |   | Gastrocnemius                               |  |
|   |   | Popliteus                                   |  |
|   |   | Soleus                                      |  |
|   |   | Peroneal muscles                            |  |
|   |   | Tibialis anterior                           |  |
|   |   | Deep flexors and extensors                  |  |
| Tibialis posterior  |   |   |  |
| Foot  | Intrinsic muscles                             |   |  |
|   | Long tendons of leg flexors and leg extensors |   |  |

example, total weights of skin are noted for two animals, although the contribution of skin for each segment is not available and is estimated where noted. In the removal of skins in Male A and Male B, we recorded the thickness of the skin and underlying connective tissue at the nuchal midpoint.

On the other side of the body (Fig. 1), individual muscles are removed at their attachments, and weighed immediately to the nearest tenth of a gram. In this way individual muscles or muscle groups can be compared between animals. For guidance in dissecting the muscles, we closely followed the description in Gregory (1950). Immediately after removing all tissue, we recorded bone weights. In two animals, the rib cage was cut during necropsy, damaging some chest and abdominal muscles. In these cases, individual muscle weights could not be determined, although the remaining muscle was calculated as part of the total body muscle (Fig. 1).

## Analytical methods

We analyze the data in several ways, using known body weights at death or the established weights prior to death. First, we determine the distribution of body mass to each region of the body: 1) forelimb consisting of arm, forearm, and hand segments; 2) hindlimb consisting of thigh, calf, and foot segments; and 3) head and trunk. Muscles were weighed with the designated limb segments, listed in Table 2. Hip musculature, for example, is included in the trunk in the analysis of body proportions. The mass of each of these major body regions divided by total body mass determines the proportion of each relative to total body mass (% TBM).

Second, we determine the percent contribution of individual segments, e.g., the arm, forearm, hand, thigh, leg, and foot, to total body mass (Fig. 1).

Third, we determine the percent contribution to total body mass of each tissue type, e.g., bone, muscle, and skin. For example, to determine total bone in the body, bone weights from each segment (e.g., humerus, radius, ulna, hand bones, femur, patella, tibia, fibula, and foot bones) are added up and doubled and then added to bone from the trunk (scapulas, clavicles, ribs, vertebrae, pelvis). This total amount of bone is then taken as a percentage of total body mass. A similar procedure is followed in determining the total amount of muscle tissue and its percentage of total body mass.

We calculated minimum and maximum estimates of adipose tissue relative to body weight. Because much of the adipose tissue in the trunk is removed along with the organs at necropsy, the minimum possible percentage represents the weight of all the dissected fat relative to the necropsied carcass mass. Maximum percentage, on the other hand, is based upon the difference between the necropsied carcass weight and the animal's weight at death, minus the estimated percent of guts. The actual amount of adipose tissue must fall somewhere between the minimum and maximum estimates.

We use 12% as a minimum estimate for the gastrointestinal tract, a determination based on our direct measurement of an in-

TABLE 3. *Bones assigned to body segments*

|            |         |  |
|------------|---------|--|
| Head/trunk | Head    | Cranium, mandible                              |
|            | Trunk   | Clavicle, scapula<br>Ribs, vertebrae<br>Pelvis |
| Forelimb   | Arm     | Humerus  |
|            | Forearm | Radius, ulna                                   |
|            | Hand    | Carpals,<br>metacarpals,<br>phalanges          |
| Hindlimb   | Thigh   | Femur  |
|            | Leg     | Tibia, fibula, patella                         |
|            | Foot    | Tarsals, metatarsals,<br>phalanges             |
|            |         |  |

tact and completely dissected chimpanzee. A problem in primate anatomical studies is the almost complete lack of information about the morphology and relative weights of the organs and gastrointestinal tract. Some data from Chivers and Hladik (1980) show the similarity in morphology and relative surface area of the gut between chimpanzees and gorillas. We consider the 12% used here to provide a minimum estimate.

In the next analysis, we focus on each tissue type (e.g., bone and muscle) throughout the body. We calculate the weight of all the bone in the body. Then the amount of bone in each body segment is divided by total bone weight. In calculating bone distribution, we include the clavicle, scapula, and pelvis as part of the trunk (Table 3). The long bones go with their respective segments. These calculations indicate the distribution of bone in the body.

To determine muscle distribution, we calculate the total weight of all muscles of the body. The amount of muscle in each segment is then divided by total muscle weight. In determining distribution to the segments, we took a functional, rather than a strictly regional, approach. For example, the muscles acting on the hip joint are calculated with the hindlimb. The trunk muscles attaching on the humerus and acting on the shoulder joint are calculated with forelimb musculature (Table 4). This grouping reflects function in hominoids whose forelimbs are completely independent from, and not bound within, the trunk, in contrast to other quadrupedal mammals. This approach makes it possible for these data to be compared with data from other mammals, primates, and humans (e.g., Grand, 1977a,

1997; Morbeck and Zihlman, 1988; Clarys et al., 1999).

Finally, we analyze the relative mass of individual muscles and muscle groups by calculating each weight relative to total muscle mass. The muscles we compare among the animals are: a) deltoid muscles; b) gluteal muscles (gluteus maximus and tensor fasciae latae; gluteus medius and piriformis; gluteus minimus and scansorius); and c) posterior neck and deep back muscles.

## RESULTS

In this study, our interest is in the gorilla pattern of total body composition, i.e., the proportion of bone, muscle, fat, and other tissues relative to total body mass and their distribution in the body. For this reason, we do not report here on the weights of individual bones and muscles. Skeletal data are the focus of another paper, and weights of individual muscles are considered in a future article that illustrates variation between species, using individual muscle weights.

### Body segments

In distribution of mass to the limbs and trunk and head, the two males and the younger Female A are similar (Fig. 2). Notice that the males are somewhat heavier in the forelimbs (15.0%) and similar in the head/trunk (66.9%, 68.3%) compared to Female A (forelimbs, 13.6%; head/trunk, 68.9%). The older, obese Female B has very light forelimbs (10.5%) and hindlimbs (10.6%) compared to the males and the other female; this low percent in her limbs (21.1%) accounts for the high percent of mass in her head/trunk, at 78.9%. Her disproportionately large trunk is wholly or partially due to large amounts of adipose tissue.

As shown in Figure 3, within the forelimb and hindlimb segments, there is little variation in the relative mass of hands and feet in all four animals (range, 1.5–2.1%). The thighs are relatively heavy (10.2–11.5%) in both males and Female A (Fig. 3B); the arm segments are notably heavier in the two males (Fig. 3A). The older, heavier Female B departs from the pattern in having much lighter

TABLE 4. *Muscles analyzed as % total muscle mass*

|          |  |  |
|----------|--|--|
| Forelimb | Shoulder muscles <sup>1</sup>  | Pectoralis major<br>Latissimus dorsi<br>Teres major and minor<br>Supraspinatus<br>Infraspinatus<br>Subscapularis   |
|          | Arm muscles<br>Forearm muscles<br>Hand muscles<br>Hip muscles <sup>2</sup> | As listed in Table 2<br>As listed in Table 2<br>As listed in Table 2<br>Gluteus maximus (and<br>Tensor fascia latae)<br>Gluteus medius (and<br>Piriformis)<br>Gluteus minimus and<br>Scansorius<br>Gemelli<br>Obturator<br>Iliopsoas |
| Hindlimb | Thigh muscles<br>Leg muscles<br>Foot muscles                               | As listed in Table 2<br>As listed in Table 2<br>As listed in Table 2   |
|          | Trunk  | All remaining muscles:<br>Trunk binding<br>Abdominals<br>Intercostals<br>Neck flexors<br>Deep muscles of the back<br>and neck: splenius capitis<br>and cervicis; erector<br>spinae<br>Mastication                                    |
| Head     |  | Temporalis, masseter,<br>pterygoids  |

<sup>1</sup> Included in this group are those muscles attaching on the humerus and acting on the shoulder joint.

<sup>2</sup> Included in this group are muscles acting on the hip joint.

thighs, almost half (5.9%) that of the other three animals, not surprising given her much lighter hindlimbs (Fig. 2).

### Tissue composition

As shown in Figure 4, the contribution of bone to total body mass is similar in all four animals, ranging from 10.2–13.4%. The contribution of muscle to body mass is similar in the two males and younger Female A (36.1–38%). The old, obese Female B differs from the others in having only 16% muscle tissue, less than half the muscle calculated for the others.

The proportion of skin is also similar in the four animals. Here the males and the old Female B are similar, but for different reasons. The skin of Female B has more subcutaneous fat, which may contribute to the difference between the two females (13.2% vs. 16.0%). The males, in contrast, have notably thick skin and connective tissue in the nuchal region: 7.5 cm for Male A, and 7.0 cm for Male B.

The maximum possible percentage of adipose stores in the four animals ranged from 19.4–44%. Male A, who maintained a similar body weight for at least 14 years, was estimated at a maximum 19.4% body fat; for Female B, the maximum estimate was 24%, and for Male B, the maximum estimate was 26.6%. The large and obese Female B could have as much as 44% fat, which coincides with the large amount of weight in her head/trunk, and her relatively low muscle mass.

### Bone and muscle distribution in the body

Bone constitutes virtually the same percentage of total body mass in all four animals (Fig. 4), and is distributed similarly to the segments, as shown in Figure 5.

Muscle distribution throughout the body is summarized in Figure 6. There are three different patterns. First, the two males are similar to each other; muscle to the forelimbs and muscle to the hindlimbs are dis-

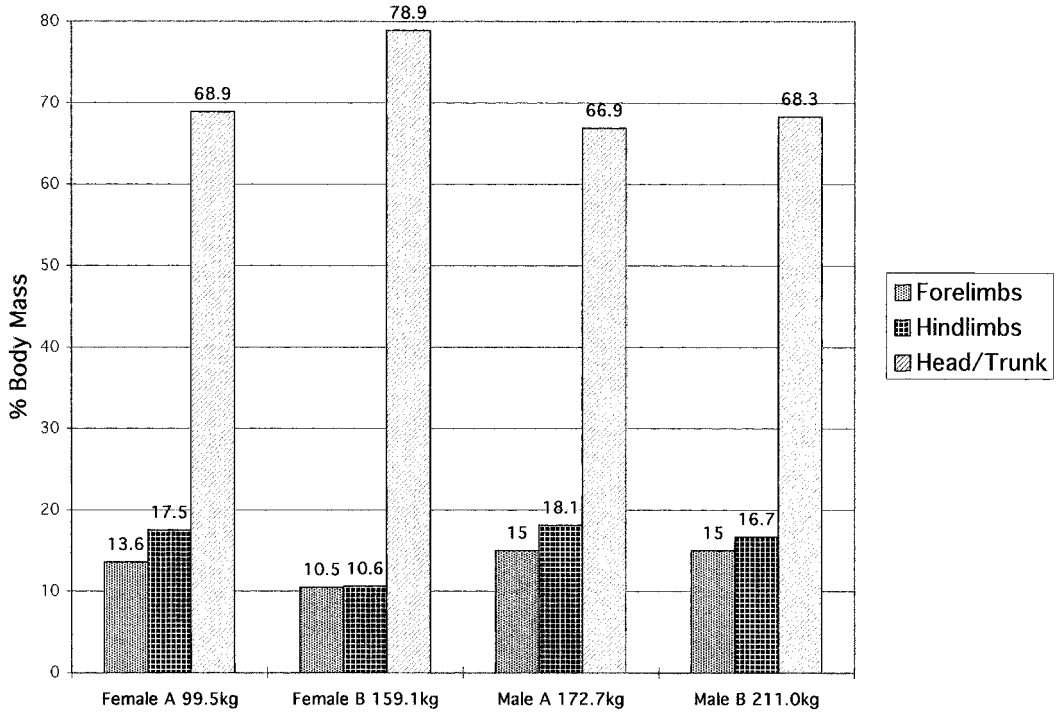


Fig. 2. Body segments as % total body mass.

tributed much the same in both animals. A second pattern in muscle distribution is found in the younger Female A; she has notably less musculature in her forelimbs (32.7% vs. the male average of 36.2%), in contrast to more muscle in the hindlimbs (44.7% vs. the male average of 42.6%). The older Female B has a third pattern; she differs in having much less muscle in her hindlimbs, i.e., 33.3% compared to the other animals (41.8–44.7%), and in having relatively more muscle in her forelimbs, i.e., 39.3% compared to the others (32.7–37%).

#### Individual muscles

To highlight variation and possible function, we examined the contribution of individual muscles or muscle groups to total musculature. We analyzed a) deltoids, b) gluteal muscles, and c) posterior neck and deep back muscles.

Deltoid muscles attach on the clavicle, scapula, and humerus and are massive in gorillas relatively and absolutely. In the males, the right and left deltoid muscles account for 4.2% of total muscle mass in

Male A, and 5.9% in Male B, and contribute significantly to forelimb segment weight. In the females, the deltoids are relatively lighter: 3.2% in Female A, and 3.8% in Female B.

The hindlimb segment (Fig. 3B) and musculature show less variation among the two males and healthy female than does the forelimb. The gluteal muscles comprise a similar percentage of total musculature in all four animals: Male A, 9.5%; Male B, 10.3%; Female A, 9.0%; and Female B, 9.1%.

The posterior neck and deep back muscles (splenius capitis and cervicis, and erector spinae) comprise 5% of total muscle mass in both males and in Female B, and 4.6% in Female A. However, the distribution of these muscles to each region of the back, cervical, thoracic, lumbar, and sacral/caudal differs somewhat among the four animals. The two males have relatively more musculature in the cervical and thoracic regions, related to their massive nuchal region and the function of their large canine teeth. The females have relatively more muscle than do the males in the lumbar and sacral re-



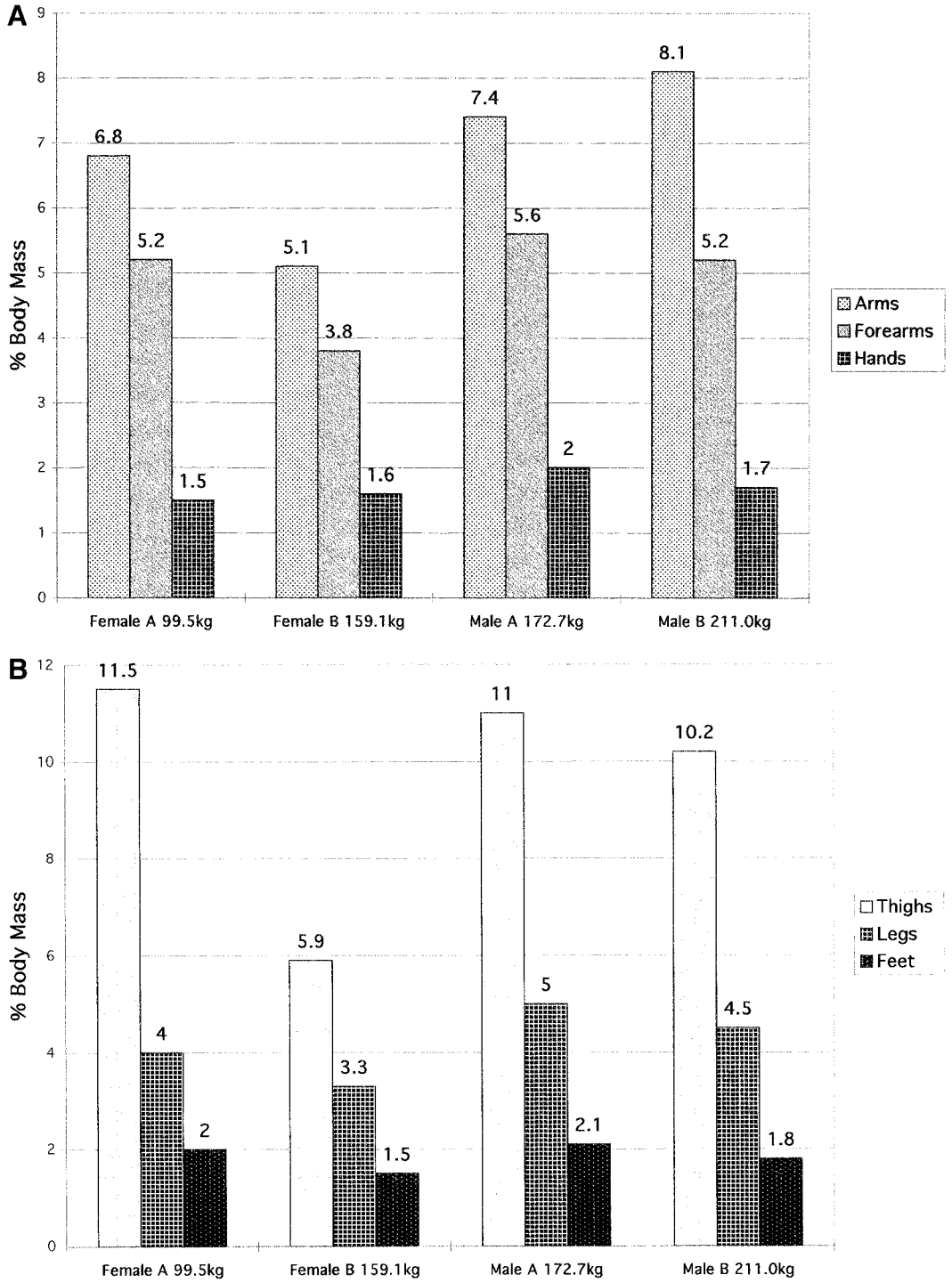


Fig. 3. **A:** Forelimb segments as % total body mass. **B:** Hindlimb segments as % total body mass.

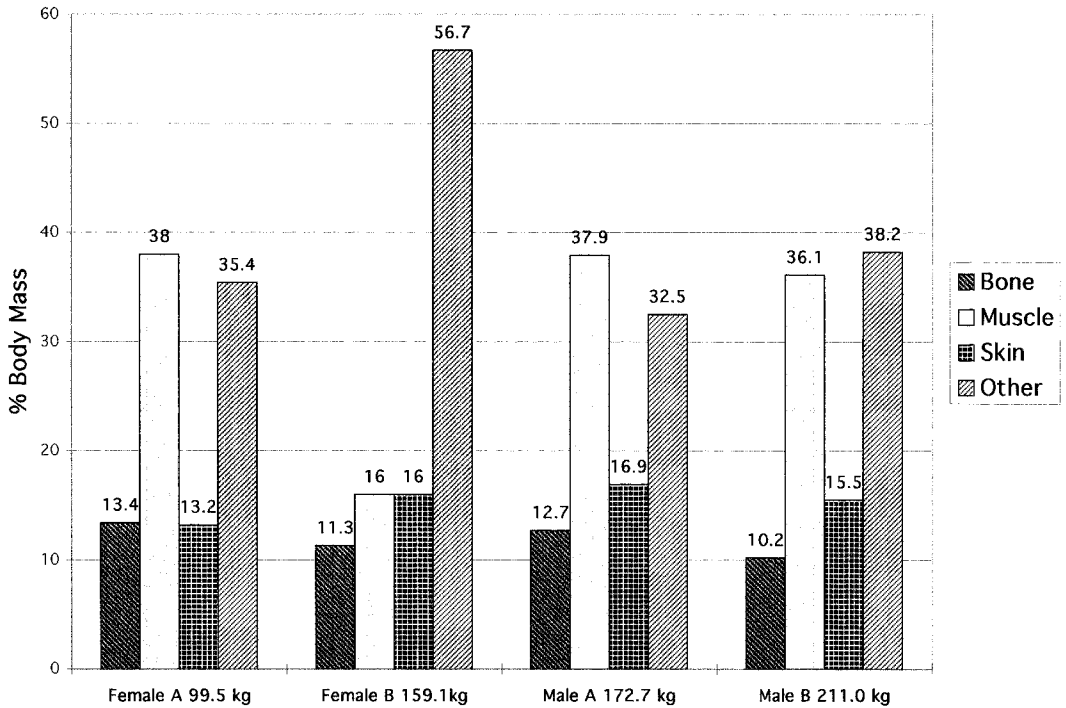


Fig. 4. Tissue composition as % total body mass.

gions, suggesting a more posterior (lower) center of gravity (Fig. 7).

### DISCUSSION

We have made direct measurements of body composition and tissue distribution in gorillas. Although there are few comparable data on nonhuman primates, body composition data from humans have been collected during the past 150 years. Initially, such studies depended upon advances in chemistry, anatomy, and nutrition, and much of the work focused on determining chemical composition of the body (Wang et al., 1999). By 1960, body composition studies were established as a significant area of research within human biology and nutrition (Brozek, 1999). Because living people were the subjects, a variety of indirect methods were employed, e.g., densitometry based on hydrostatic weighing, skinfold thicknesses, and limb circumferences.

The advantage of indirect estimates is that they are noninvasive and can sample widely among populations. Indirect estimates of body composition are more infor-

mative than body weights alone; however, such estimates cannot separate the complex components of fat-free mass, such as skeletal muscle and bone (Clarys et al., 1999). For nonhuman primates, few studies using either direct or indirect methods are available (but see McFarland, 1992 on pig-tailed macaques for an exception).

Our direct measurement of tissue composition adds information on the distribution of tissues to body segments, data not routinely part of direct dissection of body composition in humans. Together, tissue composition and distribution provide the basis for a finer-grained analysis of intraspecific and interspecific variation. The data form the basis for understanding body composition within an evolutionary framework, which necessitates first description, and then comparison. For comparison we use available data on other hominoids (orangutans and humans) to compare with gorillas. Study of interspecific variation in tissue composition and proportions helps establish a gorilla pattern that relates to locomotion, feeding

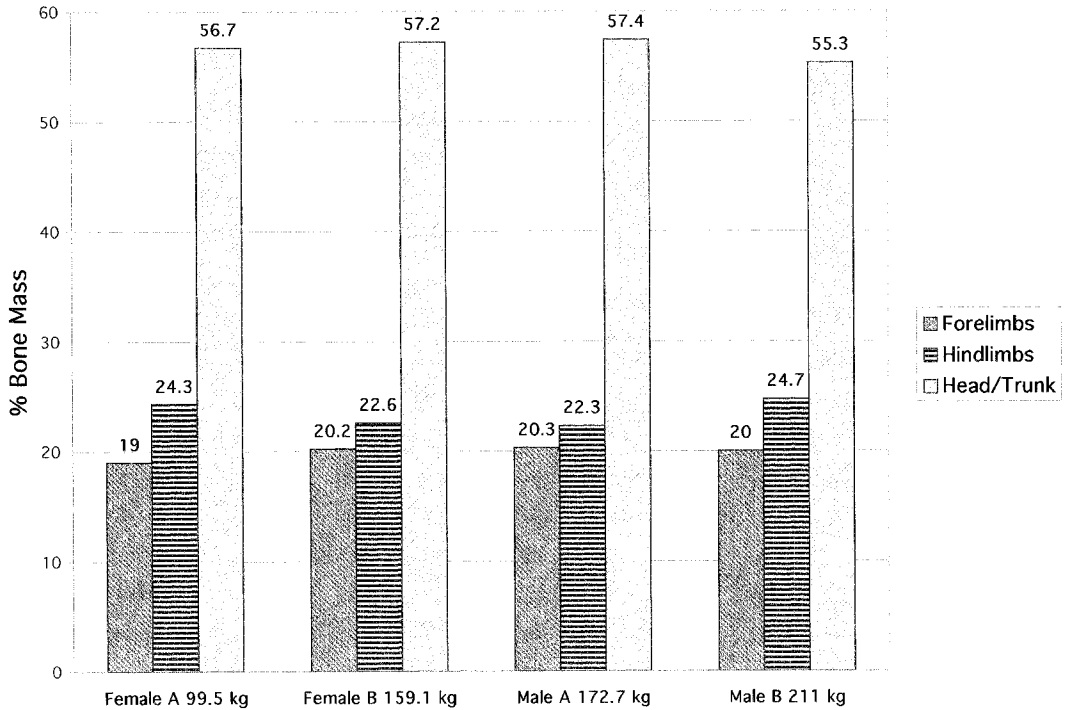


Fig. 5. Bone distribution as % total body mass.

ecology, and reproduction, and is distinct from the pattern of other hominoids.

#### Intraspecific variation

The three healthy animals show a similar pattern of tissue composition and body proportions in spite of a wide range of body weights, i.e., 99.1–211.0 kg. Bone in particular is conservative and shows little variation among the four animals in its contribution to total body mass and in its distribution to body segments. This finding mirrors those of Schultz (1962), later confirmed by Potter (1986), who found that skeletal weight represents a similar proportion of body weight in primates from different families with vastly varying body sizes. Since bone responds to the compressive forces of body mass (Demes and Jungers, 1989), this finding is not unexpected.

Relative amounts of muscle and skin tissue and their distribution show a similar pattern in the three healthy animals. Muscle comprises 36.1–38% of body mass. A greater percentage of muscle is distributed to the hindlimbs than to the forelimbs, par-

alleling the greater overall mass of the hindlimbs. The older, heavier Female B departs significantly from the other three animals.

In the same three animals, the maximum amount of body fat lies within a relatively narrow range (19.4–26.6%). Again, Female B departs significantly, approaching as much as 44% adipose stores. This extensive variation directs attention to conditions under which body fat accumulated in this animal compared to the other three animals. The range in adipose cannot be explained strictly by the condition of captivity, as all are captive animals but are not equally fat. Whatever the contributing factors, adipose tissue comprises a significant component of body mass, and reasons for its variation are of interest. We address this issue further, following a more detailed discussion of Female B.

#### Age and health: Female B's life story.

Female B diverges from the other three animals in a number of measures, and the divergence is instructive. Female B was the oldest of the four animals, weighed signifi-

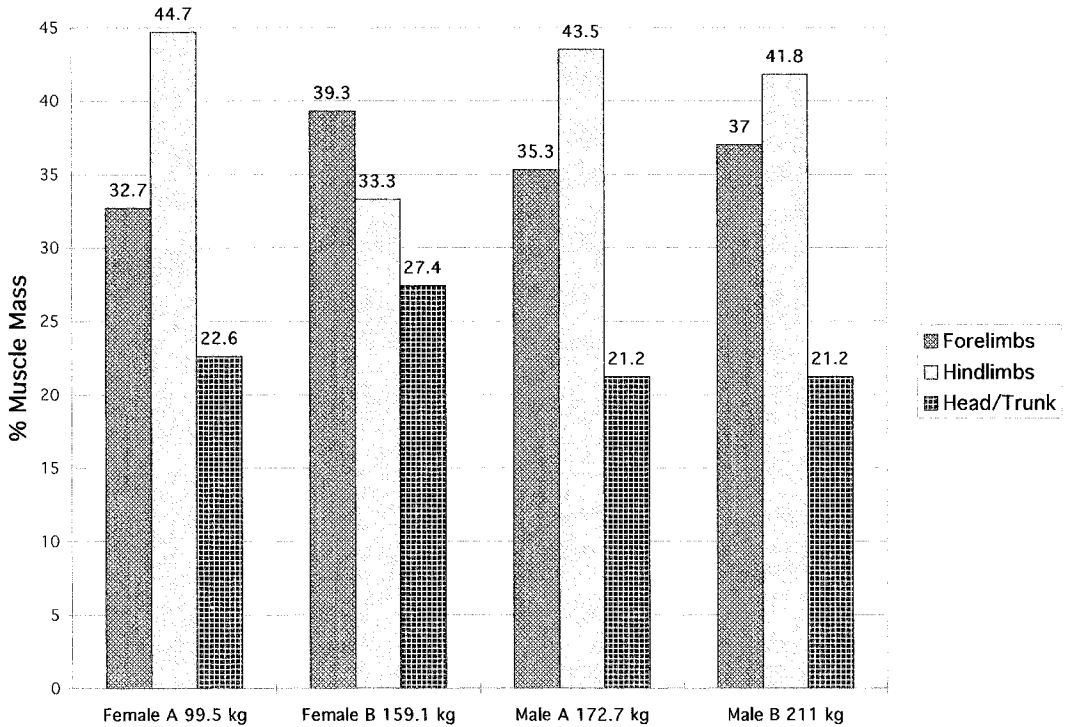


Fig. 6. Muscle distribution as % total body mass.

cantly more than Female A, and had motor difficulties and severe hip arthritis. In body proportions, Female B has much less weight in her forelimbs and hindlimbs (10.5% and 10.6%), and considerably more weight in her trunk and head (78.9% vs. the 68.0% average for the other three animals). Besides extreme adiposity, her muscle mass is less than half that of the other three animals. The forelimbs have greater muscle mass than the hindlimbs (39.3% in forelimbs vs. 33.3% in hindlimbs), unlike the pattern in the other three animals.

Female B also differs in individual muscle proportions. Her deltoid muscles comprise 3.8% of total body muscle, more than that of younger, healthier Female A (3.2%), though less than in Male A (4.2%). In relative percentage, her posterior neck and deep back muscles are similar to the other animals (5%), but the distribution differs. She has more muscle in the thoracic region and less in the lumbar region than does Female A, though the two females are similar in cervical and sacral/caudal regions. In the relative

size of gluteal musculature, the two females are similar to each other (9.0% and 9.1%).

The particular life story of Female B helps explain this pattern. She had severe arthritis in her hips that restricted movement. Her advanced age and immobility no doubt contributed to the accumulation of significant body fat and lower relative mass of musculature. From our analysis of muscle proportions, she seems to have compensated for her limited hip-joint mobility by increasing the load on her forelimbs. This shift in locomotor emphasis correlates with the decrease in mass of the hindlimbs, the increase in musculature to the forelimb, the relatively larger deltoid muscles, and the more developed back muscles in the thoracic region.

The body proportions, tissue composition, and tissue distribution reflect her advanced age, restricted joint movement, and considerable body mass. Her great bulk includes the same relative quantity of bone as in the other three animals, but more adipose tissue and much less muscle. The distribution

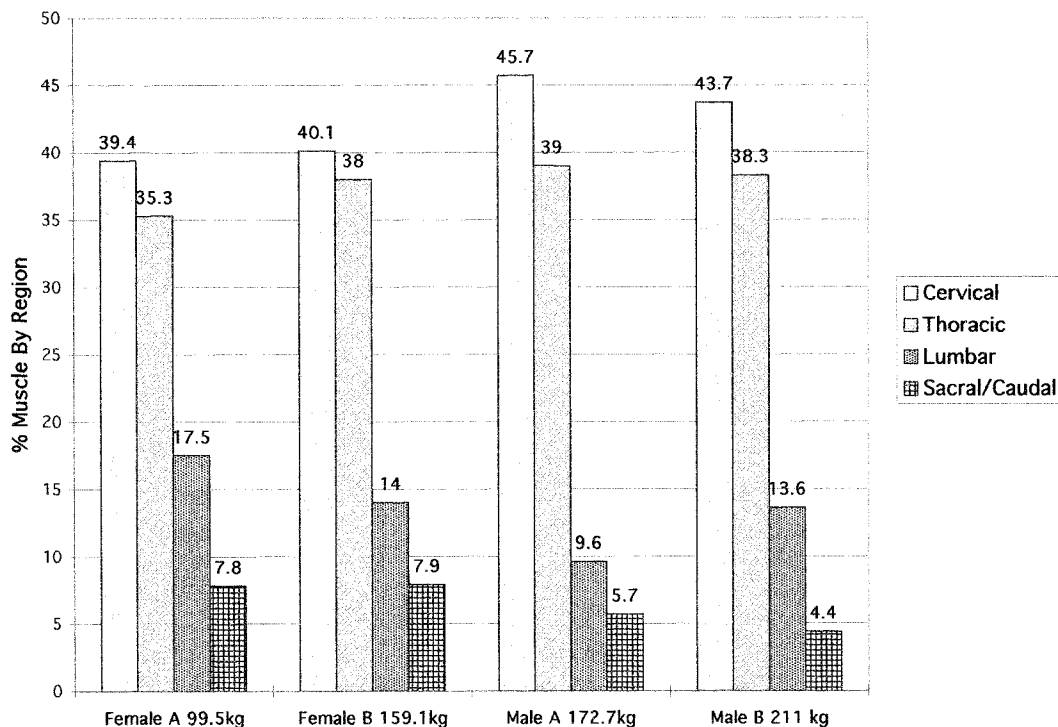


Fig. 7. Regional distribution of posterior neck and deep back muscles: % muscle by region.

of muscle tissue seems to reflect intense use of her upper body in response to locomotor difficulties and disease.

In traditional comparative anatomy, body fat was treated much like packing material for other tissues such as the organs, muscles, and bones. Information on adipose tissue was rarely recorded or discussed. Caroline Pond's pioneering work on mammalian comparative anatomy pointed up the important adaptive function of this tissue, and the necessity of recording it (Pond, 1977, 1984; Pond and Mattacks, 1987). Since then, a few studies have measured body fat and correlated it with activity level and calorie intake (Altmann et al., 1993 on baboons) and with reproductive outcome (McFarland, 1992 on female pig-tailed macaques).

Female B raises the question of the appropriateness of captive animals for anatomical research. There are two studies that provide systematic comparisons of aspects of captive and free-ranging gorilla anatomy. In a study of primate body weights, Leigh (1994) compared gorillas from zoological

gardens and free-ranging gorillas; he reports overlap in the two groups, although captive adult female gorillas appear to be heavier than free-ranging females. Leigh (1994) also points out the problems of weights obtained from free-ranging animals, and Smith and Jungers (1997) discuss in some detail the challenges of establishing accurate body masses in primate species.

A study to investigate variation between captive and free-ranging populations of gorillas focused on skeletal linear dimensions. There was extensive overlap in long bone measurements in the two groups; of the 45 variables tested, the majority were not significantly different (Nichols, 1998, 1999). These studies support the conclusion that captive gorillas are within the range of free-ranging gorillas in terms of body mass and skeletal dimensions.

It is likely that, on average, captive gorillas are heavier and fatter than free-ranging ones. Studies of human and nonhuman primate populations show that access to a rich food source and decreased activity result in

heavier mass and higher body fat. For example, monkeys who are provisioned or can obtain human food remains or crops are demonstrably heavier (Mori, 1979; Strum, 1991; Altmann et al., 1993). Body fat is rarely measured, but Altmann et al. (1993) showed that baboons at Amboseli who ate human food and traveled less were dramatically fatter than their counterparts.

Parallel evidence in humans based on direct measurement of body composition shows that Europeans from the 19th century were lighter in weight and had lower body fat than the 20th century sample, presumably due to changes in diet and activity (Clarys et al., 1999).

Returning to Female B, she shows that, similar to the monkey and human examples, there is a range of body mass and composition among gorillas, a variation that is related to aspects of an individual's life and environmental conditions. The issue is not simply whether animals are captive or free-ranging. Instead, it must be acknowledged that there is a continuum even among free-ranging populations in body mass and fatness, a result of variation in environments. Female B also offers the opportunity to assess the gorilla potential for accumulating body mass and fat. The ability to accumulate body mass, of which a large percentage is fat, may be pronounced in some species, as it appears to be for orangutans, but there is little documentation. Female B is important to establish this potential in gorillas, which may be a significant adaptation for gorillas in the wild. Female B also offers a comparison with aging, inactive humans.

**Sex differences.** Sexual dimorphism is a significant attribute of gorilla anatomy and adaptation. The characterization of sexual dimorphism is based on measurements of canine tooth length and body mass. The female to male body mass ratio in adult lowland gorillas is estimated at 54%, and canine tooth length ratio at 60% (McCown, 1982). In other features, however, such as cranial capacity (measured in volume) and linear lengths of the limb bones, female values are closer to 85% those of males (reviewed in Zihlman, 1997).

Although our findings on three animals must be considered preliminary, they add the dimension of soft tissue to the discussion of sex differences. Beginning with the two males, who differ in body weight by almost 40 kg, they are comparable in relative mass in the limbs (forelimbs, 15.0%; hindlimbs, 18.1%, 16.7%), and in proportions of muscle, skin, and bone. Within the limbs, the segments of the two males (e.g., arm, forearm, hand; thigh, leg, foot) are also similar in relative mass. The males differ primarily in the estimated maximum amount of body fat: 19.4% (Male A) compared to 26.6% (Male B).

Comparison of the two males with the younger Female A shows similarities and differences. For example, the three animals are similar in three dimensions: in the relative contribution of bone and muscle to total body mass; in the relative heaviness of the thighs (11.5% in Female A vs. the 10.6% male average); and in the relative amount of gluteal musculature (9.0% in Female A vs. the 9.9% male average).

However, the upper body region shows pronounced sex differences. The males' forelimbs are heavier (13.6% of total body mass in Female A vs. 15.0% in the males). This correlates with the fact that the forelimbs of the males have more muscle (36.1% male average vs. 32.7% in Female A), a difference that is at least partly due to the males' massive deltoid muscles (3.2% of total body muscle in Female A vs. the 5.0% male average). Furthermore, males have noticeably heavier cervical and thoracic muscles and very thick subcutaneous tissues in the nuchal region, which contribute to a massive neck.

The sex differences in gorillas in tissue distribution perhaps reflect a primate pattern of sex differences, but which is more exaggerated. For example, Schultz (1956) documented that males have a larger chest circumference than females in many species of anthropoid primates, even when body weights are similar. Supporting Schultz (1956), Galloway et al. (1996) documented sex differences in the vertebrae of Gombe chimpanzees.

Even though body weights in gorillas are markedly different in the two sexes, they

are remarkably similar in tissue distribution, especially in relative proportions of muscle and bone, although with some differences in the upper body. In other words, differences in tissue are not as dramatic as body weight differences might suggest.

### Interspecific variation

A goal of this research is to place tissue composition and distribution data in a comparative, evolutionary framework. A few data from studies on captive apes and on humans are available for comparison. We review information on the other large-bodied, sexually dimorphic ape, the orangutans (*Pongo pygmaeus*) ( $n = 2$ ) (Morbeck and Zihlman, 1988), and *Homo sapiens* ( $n = 51$ ) (compiled by Clarys et al., 1999).

**Orangutans.** Like gorillas, orangutans show marked sexual dimorphism in body mass and linear measurements. In tissue composition, gorillas and orangutans are relatively comparable in amounts of bone and skin. The striking difference in the two species is in the relative proportions of muscle and body fat. Healthy gorillas in our sample have on average 37.3% muscle, which exceeds that of the female orangutan (27%) and that of the male (35%). In the "other" category of tissue, which includes body fat, organs, and the gastrointestinal tract, gorillas at 35.4% are lower than orangutans at 42.7%, suggesting a greater amount of body fat or a heavier gastrointestinal tract in orangutans.

In body proportions, gorillas have lighter forelimbs than orangutans. In the hindlimbs, female and male gorillas are comparable (17.5% of total body mass vs. 17.3%), whereas the female and male orangutan differ markedly from each other in their hindlimb proportions (17.8% vs. 12.0%).

These comparisons suggest correlations between the different behavioral ecology of the two species. Lowland gorillas consume foliage, fruit, and insects, feed and sleep in trees or on the ground, and travel exclusively on the ground (Tutin et al., 1991; Remis, 1997a). They live in relatively cohesive groups, usually with several adult males, adult females, and young (Tutin, 1996; Remis, 1997b). Although there are dif-

ferences in foraging and locomotion in female and male gorillas, they do not appear to be marked.

Orangutans, in contrast, are highly arboreal and eat fruit, and adults are relatively solitary while foraging (Galdikas, 1984, 1985, 1988). Females and males differ in their arboreal travel, diet and foraging, social interactions, and caretaking of offspring (Sujardito, 1982; Cant, 1987). Relative proportions of muscle or body fat probably relate to a balance between locomotion and the ability to store fat.

Muscle and adipose tissue seem to be the most labile tissues. Observed distributions suggest that orangutans have more body fat and less muscle compared to gorillas. Free-ranging orangutans have a documented ability to put on body fat when food is abundant, and they lose fat when food is scarce (Knott, 1997, 1998). Free-ranging lowland gorillas may have a similar though less marked ability to accumulate fat during times of abundant fruit (Remis, personal communication). The varying proportions of these tissues apparently accommodate locomotion, food scarcity, and reproductive function.

The differences between females and males in the two species do not bear a simple correlation with body weight. Gorilla males have more mass in their upper body and forelimbs than do females, but a similar amount of muscle. In orangutans, males also have heavier upper bodies, notably heavier forelimbs, lighter hindlimbs, and more muscle than do females.

***Homo sapiens.*** Clarys et al. (1999) summarized the available data on direct measurement of tissue composition based on 51 individuals (20 females, 31 males) compiled over a 150-year period. The individuals had known body weights, and absolute weights recorded for skin, muscle, bone, and adipose tissue. The subjects ranged in age from 16–94 years; the average age for men was 56.6 years (SD 21.5), and for women, 75.5 years (SD 15.4). Body weights ranged from 38.5–97.2 kg in men, and from 32–75.4 kg in women. Muscle relative to body weight averaged 39.4% (SD 5.4%) in men; in women, 28.8% (SD 6%). Adipose tissue averaged

19.4% in men and 35.3% in women. For men, the standard deviation was 9.6%, and in women, 11.8%. The older age of the female subjects probably contributed to the higher amount of adipose tissue, and lower muscle mass.

The data on gorillas, orangutans, and humans suggest that hominoids have the ability to accumulate body mass, of which a significant proportion is fat. Further analysis of body composition in hominoids can refine the species comparisons and so more fully connect body composition and distribution to adaptation and evolutionary history.

### CONCLUSIONS

The results of our dissection of four adult lowland gorillas add to our knowledge of gorilla biology through analysis of body composition and proportions. These methods, in combination with information from the behavioral ecology of free-ranging animals, offer a quantitative way to assess function and adaptation within a species and to compile data for comparison with other hominoids. This anatomical approach analyzes the major soft tissues along with bone, and supplements studies on the skeleton. The emphasis on whole animals reveals patterns of variation due to age, sex, and life history.

Studies on captive gorillas and other primates are a source of important biological and behavioral information not easily obtained from wild primates, e.g., body weights (Leigh, 1994), growth and development (e.g., Schultz, 1927, 1942; Beynon et al., 1991; Leigh and Shea, 1995; Grand, 1983b, 1992), muscle function (e.g., Tuttle and Basmajian, 1974; Larson and Stern, 1987), reproduction (e.g., Nadler, 1975; Meder, 1986), and communication, (e.g., Tanner and Byrne, 1999). The addition of anatomical data as discussed here enlarges our view of gorilla variation and adaptation.

Body composition and distribution of mass, like all aspects of anatomy, are a product of evolutionary history and relate to locomotion, diet and foraging, and reproduction. In the divergence of hominoids, each species developed a slightly different pattern. To more fully understand the transition of humans to a bipedal locomotor sys-

tem and modified reproductive pattern, we need to understand the anatomical changes that go beyond bony features.

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