Skeletal biology and individual life history of Gombe chimpanzees

ADRIENNE L. ZIHLMAN

University of California, Santa Cruz

MARY ELLEN MORBECK

University of Arizona, Tucson

AND JANE GOODALL

Dar es Salaam, Tanzania

Skeletons of Gombe chimpanzees representing both sexes and ages from infancy to old age are examined in detail by a variety of techniques. The combination of biological and lifetime behavioural data presents an integrated view of individuals which make up a local population. These skeletons reflect species-patterned growth, development and ageing. Furthermore, individual variation is related to lifetime experiences: for example, the impact of nutrition, injury and disease on survival and reproduction in the physical and psychosocial environments. Size, shape and internal structure of bones and teeth record life-history features associated with both primary and secondary life-history characters. These case studies emphasize the role of the individual in the evolutionary process.

Contents

Skeletons, life history and evolution

Skeletons from free-ranging primates are rarely associated with known age, sex, reproductive history and body weight during life. But from Gombe National Park, Tanzania, a series of

individuals has been collected. These individuals are part of a local breeding population of *Pan troglodytes schweinfurthii* and provide an opportunity for close examination of morphological variation relative to other subspecies and species of chimpanzees (Morbeck & Zihlman, 1989). Furthermore, they provide an opportunity to focus on the organism and its life experiences as they relate to survival and reproductive success from the point of view of both the individual and the population.

Population studies of free-ranging, nonhuman primates may be approached using demographic parameters and population dynamics as recorded in life tables (e.g. Altmann *et al.*, 1977; Sade *et al.*, 1977; S. A. Altmann & Altmann, 1979; Dunbar, 1980, 1984, 1987, 1988; J. Altmann, 1980; Sigg *et al.*, 1982; Goodall, 1983, 1986; Hiraiwa-Hasegawa, Hasegawa & Nishida, 1984; J. Altmann, Hausfater & Altmann, 1985; Sade *et al.*, 1985; Rawlins & Kessler, 1986). In another approach, free-ranging primate populations are characterized by their behavioural and ecological features (e.g. Smuts *et al.*, 1987 and references therein) and often are analysed at the subfamily level (e.g. Harvey & Clutton-Brock, 1985). Other studies express statistical patterns of morphological variation in the dentition and skeleton and provide information on size and shape parameters (e.g. Schultz, 1944; Bramblett, 1969; Cheverud, 1982; Cheverud & Buikstra, 1982; DeRousseau & Reichs, 1987). Analysis of disease and trauma adds another dimension to a population profile (e.g. Schultz, 1939, 1944, 1956b; Bramblett, 1967; Buikstra, 1975; Lovell, 1987; DeRousseau, 1988).

These approaches contribute to our understanding of populations. However, features of a particular individual are lost in the abstraction of population characteristics. An individual grows up and survives in the context of a dynamic social, biological and physical environment, and possibly becomes someone's parent and grandparent. Individual life histories—life experiences and reproductive events—unfold within the constraints of an evolved species pattern and determine an adult's genetic contribution to later generations.

'Primary' life-history features—gestation length, ages at weaning, dispersal and first reproduction, and growth and mortality patterns—emphasize the tempo of life stages. They determine the frequency and number of births (and potential costs of reproduction) and, thus, reproductive success (Cole, 1954; Stearns, 1976, 1977; J. Altmann, 1983; Calder, 1984; Harvey & Clutton-Brock, 1985; Harvey & Zammuto, 1985; Stearns & Koella, 1986; Harvey, Martin & Clutton-Brock, 1987; Partridge & Harvey, 1988).

'Secondary' life-history features that promote survival and allow for successful mating and rearing of offspring include the expressed behaviours of the musculo-skeletal and dental systems, (e.g. locomotion, feeding, antipredator strategies) and related social behaviours.

Life-history characters as products of natural selection are evolutionary adaptations and can be 'read' in the skeleton. Bones and teeth also record the interplay of biological and behavioural processes and events, their severity and influence on survival and provide evidence for testing ideas about reproductive success and evolutionary mechanisms.

At the organismal level, differential survival and reproduction of individuals are associated with biology, social behaviour and the effects of environmental interactions *throughout* an individual's lifetime. Reproductive success, that is, the number of surviving offspring with potential for mating and rearing their own offspring, differs among individuals that comprise populations, species and higher taxa. Variation is associated with reproductive life-history variables. These relate to births, migrations and deaths—the demographic variables that affect population size and structure. Factors that contribute to individual variation in both primary and secondary life-history features include energetic relationships (Coelho, 1986; Loudon & Racey, 1987; Laws, 1987) and are important to population dynamics, on-going selection associated with differential survival and

reproduction, and evolutionary change (see also S. A. Altmann & Altmann, 1979; Crews & Moore, 1986; Brown, 1988; Clutton-Brock, 1988a, b; Dunbar, 1988; Lande, 1988).

Variation in timing and frequency of these life events is the basis for evolutionary mechanisms that shift life-history characters through time. This variation and its causes emphasize the important role of the individual in evolution. It is the individual life history placed within this broader demographic-evolutionary framework that can be observed, for example, in the chimpanzees from Gombe National Park.

The Gombe population

Gombe chimpanzees have been a focus of intensive social behavioural study for more than 25 years. They represent a relatively isolated population in rugged terrain bounded on the west by Lake Tanganyika, on the east by mountains, and by human settlements to the north and south. The climate and community ecology have been described (Goodall, 1968, 1986; Clutton-Brock, 1975; Wrangham, 1975). Community structure and interaction between the animals and the environment have been well documented (e.g. Goodall, 1968, 1971, 1983, 1986; McGinnis, 1973; Teleki, 1973; Bygott, 1974; Tutin, 1975; Pusey, 1978; Plooij, 1984). Specific knowledge of some individuals is a result of observations over lifetimes. Individual genealogies and group social interactions cover three generations in some maternal lineages.

Gombe individuals are the product of a range of biological processes patterned by the species' evolutionary history and experiences during life. They sleep, travel, feed, groom, play, mate, but also contract diseases, sustain injuries and have a better or worse start in life. The time and sequence of events affect an individual's development and maturation and, therefore, its role in the population as a breeding adult.

These chimpanzees, as one breeding group in a particular environment, represent a variation on the *Pan troglodytes* theme and, in particular, on *Pan troglodytes schweinfurthii*. The impact of life events on their bones, and on the outcome of reproductive efforts under these environmental circumstances, is put forward, not as representing all chimpanzees, but to document variation in chimpanzees.

Previous analyses of Gombe skeletons show that although Gombe chimpanzees are like other *Pan troglodytes* in cranial and dental dimensions and body proportions, body weight and limb bone dimensions are smaller (Morbeck & Zihlman, 1989). Analyses of bone mineral content and geometry show variation with age (Sumner, Morbeck & Lobick, 1989) as does dental pathology (Kilgore, 1989). Trauma and other skeletal pathologies are common (Jurmain, 1989).

Gombe individuals provide case studies for examining the processes and products of development and factors which influence lifetime reproductive success, including surviving offspring (e.g. Fedigan *et al.*, 1986; Borgerhoff Mulder, 1987, 1988; J. Altmann, Hausfater & Altmann, 1988; Cheney *et al.*, 1988; Chagnon, 1988). This study over generations contributes to understanding evolutionary processes.

Materials and methods

Seven individuals at the core of this study include both sexes and a variety of ages: 10-month-old male 'Gyre'; 8·5-year-old male 'Flint'; c. 19-year-old female 'Gilka'; c. 28-year-old female 'Madam Bee'; c. 43-year-old female 'Flo'; c. 26-year-old male 'Charlie'; and c. 39-year-old male 'Hugo'.

Remains of animals are located by researchers whenever possible, wrapped in plastic and placed in a large

metal container. After decomposition by endemic beetle larvae, bones are collected, washed and stored for later study. In some instances only partial skeletons or isolated skulls can be retrieved, and in some cases the smaller bones are missing.

Information on sex, age and probable or diagnosed cause of death is recorded. Metric data are taken on each individual: cranial volume, craniofacial and dental linear dimensions, postcranial linear and joint surface measurements, bone weights, bone mineral content and cortical area of the humerus and femur. Description and assessment of nonmetric skeletal features include status of tooth eruption, wear and tooth loss, cranial suture closure, epiphyseal closure, and evidence of trauma and other pathologies. Body weights taken when animals were alive are available for several individuals, as is biopsy during life (e.g. 'Gilka') and autopsy after death (e.g. 'Flint').

Quantitative data on cranial volume, standard linear dimensions and joint surface area are collected as described in Morbeck & Zihlman (1988). Since this study considers individuals of all ages, diaphyseal lengths also are included. Bone mineral index (BMI, bone mineral content/width of bone, g/cm^2) on 5 sites on the femur and 1 site on the humerus is assessed using single photon absorptiometry (SPA).[1] Cortical area expressed as a percentage of subperiosteal area (%CA) is assessed by computerized tomography at equivalent sites on the femur and humerus.[2] Standard radiographic techniques using medio-lateral and anterio-posterior views are used on long bones and other elements. Only data relevant to each individual case study are presented here.

Individual case histories

Infant 10-month male ('Gyre')

Skeletal and dental biology

The infant skeleton is nearly complete. The long bones, pelvic and pectoral girdles are present. Some hand and foot bones and most of the vertebrae are missing. The dentition is incomplete. Post-mortem loss of teeth includes the upper left lateral incisor, the upper left deciduous first molar

---

[1] It is unlikely that significant mineral contamination of bones during skeletal cleaning has occurred. Water may enter the metal container. But the combination of using plastic bags to protect cadavers and the relatively short time period (several months) necessary for cleaning suggest that post-mortem mineral contamination prior to bone scanning, if present, is minimal. Soil samples collected from the adjacent hillside above the large metal container are currently being analysed.

Non-invasive photon absorptiometric and computed tomographic scans are obtained from five equivalent diaphyseal sites on the femur (20%, 35%, 50%, 65%, 80% of diaphyseal length) and one site on the humerus (35% diaphyseal length). Bone mineral content, medio-lateral subperiosteal width, and the ratio of bone mineral content to subperiosteal width (Bone Mineral Index, g/cm^2) are assessed from photon absorptiometric techniques (SPA scans). Subperiosteal area and cortical area are calculated from data obtained via computed tomographic (CT) scans.

Bone mineral data are collected using a Lunar Radiation single photon absorptiometer (Iodine 125 source) and Northstar Advantage computer housed in the Department of Anthropology, University of Arizona. Diaphyseal length, scan site locations and medio-lateral and anterio-posterior widths are measured. Bones are wrapped with dialysis tubing filled with water to serve as a tissue equivalent and placed on the photon absorptiometer in a standard position (Sumner, 1984a, b; Sumner et al., 1989). Two to four scans per site are taken in a medio-lateral direction. Data for each scan are corrected for edge placement and results are averaged. Previous work demonstrates a high degree of accuracy and precision using this method (Sumner, 1984a).

Bone Mineral Index estimates bone density. Raw data and values normalized for size (that is, by dividing diaphyseal length) from different sites within an individual as well as among different individuals are compared.

[2] Cross-sectional area values, subperiosteal, medullary and cortical areas, are measured with CT scans using a Siemans Somatom 2 computed tomographic whole-body scanner using 125 kVp, a 2 mm slice thickness, and image reconstruction algorithm 5. Reconstructed images are analysed in digital form using standardized techniques with high degrees of accuracy and precision (Nagurka & Hayes, 1980; Ruff & Hayes, 1982; Sumner et al., 1985, 1989). The ratio of cortical area to subperiosteal area (%CA) is used here. Both raw data and values normalized for size, as with SPA, are used.

(dm1), right and left lower deciduous molars (dm1) and the lower right second deciduous molar, but root cavities are present.

Most of the crucial vault elements are unfused. The frontal bones are fused, but the frontal suture is not obliterated. The frontal, parietal and occipital bones are extremely thin-walled and show little development of muscle attachment areas. There is no visible evidence of disease or trauma in the cranial bones or evidence of bone loss in the orbits. The mandible is small, and like other cranio-facial elements is light in weight. Apparently there was little mineralization of the cranial bones.

The upper and lower deciduous central and lateral incisors appear to have fully erupted. Deciduous canines have not yet erupted, but are visible in the crypt. In the maxilla the first deciduous molars (dm1) appear to have erupted, as they are well above the alveolar margin. The second deciduous molars (dm2) are fully developed at the alveolar margin. Both upper and lower first permanent molars (M1) are visible in the crypt.

Postcranial elements are well developed and lack epiphyses. Long bones and shoulder and hip elements appear small and are light in weight with little evidence of muscular development.

Cranial, dental and skeletal features are compared with a captive sample and data from the literature. Although captive chimpanzees are generally heavier and developmentally advanced compared to free-ranging chimpanzees (Gavan, 1971; Coe *et al.*, 1979; Kraemer *et al.*, 1982; Brizzee & Dunlap, 1986), comparable young free-ranging chimpanzees of known age and sex are rarely available.

Minimal estimate of cranial capacity is 207 cc. Comparative examples (neonate to 10·2 months) range from 128 cc in volume to 287 g in weight. 'Gyre' falls between the 3·8- and 7·6-month-old males in this sample of three. In a larger sample of infant males (1·5–2·5 yrs), 'Gyre' is close to the low end of the range: 228 to 415 cc (average 338 cc (Schultz, 1969; M. E. Morbeck & A. L. Zihlman, unpubl. data)).

TABLE I

Femur in 'Gyre' compared to Gombe infants and captive male infant

Characters of femur[a]	Gombe infants[b]			'Gyre' (10 months)	Captive infant[c] (1 day)
	Infant 1 (stillborn)	Infant 2 (neonate)	Infant 3 (neonate)		
Diaphyseal length (mm)	58·0	46·5	55·5	56·0	59·0
Medio-lateral width at 50% scan site (mm)	7·0 (0·12)	5·0 (0·11)	4·7 (0·08)	6·0 (0·11)	7·0 (0·12)
Bone mineral index at 50% scan site (g/cm^2)	0·412 (0·007)	0·296 (0·006)	0·247 (0·004)	0·141 (0·003)	0·530 (0·009)
Percent cortical area at 50% scan site (%)	87·1 (1·50)	70·6 (1·52)	—	63·9 (1·14)	84·6 (1·43)
Weight (g)	3·2	1·3	1·6	1·4	6·2

[a] For details of techniques and calculation, see **Materials and methods.** Values in parentheses are normalized for size by dividing by diaphyseal length.

[b] Infant 1: mother 'Melissa'; 1969; sex unknown; stillborn; cause of death unknown.

Infant 2: mother 'Patti'; 1978; male; new-born; probable cause of death, inadequate care.

Infant 3: mother 'Gremlin'; 1987; male; new-born; cause of death, either mother's illness and inability to care for him, or presumed pneumonia.

[c] Captive infant: male; cause of death unknown.

In dental eruption, 'Gyre' fits within the range documented for captive chimpanzees. First deciduous molars of captive males erupt at 4·6 months (range 2·6–7·0), second deciduous molars at 9·3 months (range 6·1 to 14·9) (Nissen & Riesen, 1945).

The postcranial skeleton, in contrast to apparently normal brain case growth and tooth eruption, shows minimal growth. Long bone diaphyses are considerably shorter and mid-shaft robusticity is less than measured in captive infant males. 'Gyre' is comparable to neonates in long bone length and in the weight of most bones. BMI and %CA of mid-shaft of the femur are also low (Table I). Radiographs confirm minimal bone density.

Field observations

'Gyre', a male twin, died of respiratory problems (probably pneumonia). Both twins appeared smaller than other new-born chimpanzees from single births at Gombe, and 'Gyre' was the weaker one. Birth weights for captive new-born chimpanzees average between 1·6 and 1·8 kg (Schultz, 1940; Gavan, 1952) and 'Gyre' and his twin 'Gimble' each probably weighed less than these averages.

When they were born in 1977, their mother 'Melissa' was aged approximately 27 and two of her six known offspring were alive. 'Melissa', who retained some neck and shoulder paralysis from contracting polio in 1966, was suffering from respiratory problems (possibly pneumonia) at the time the twins were born. Her illness may have decreased her milk production (Goodall, 1987). 'Gyre' developed a husky cough and died in August, a dry-season month (Goodall, 1983).

At death, 'Gyre' was about the same size and behaved in the same way as a normal three-month-old infant (Goodall, 1987). 'Gimble', the surviving twin, visibly gained weight and immediately accelerated his social and motor development. However, at the age of 11 years, 'Gimble' is still very small for his age compared to other Gombe males and is late in onset of puberty.

Summary

Analyses of the postcranial skeleton suggest that during life there was limited bone growth, and even bone loss. However, brain size and dental development are within the range of variation reported for captive chimpanzees of comparable age. This pattern illustrates the phylogenetically-defined sequence of energy investment in infant growth with early emphasis on neurological development and dentition followed by locomotor development and the skeleton.

'Gyre's' postcranial skeleton reflects a species pattern. But it also shows that in terms of body size and skeletal maturation, he had not grown and developed as a normal chimpanzee infant. Growth and maintenance are competitive when energy sources and activity levels are low in human infants (Bergmann & Bergmann, 1979). The generalized nature of the 'readable' effects of poor nutrition or delayed motor development, however, does not allow assessment of particular kinds of malnutrition or disease in this individual.

Early adolescent 8·5-year male ('Flint')

Skeletal and dental biology

The skeleton is essentially intact. The long bones, vertebral column, ribs, shoulder and hip

girdles and most of the hand and foot bones are present. Most of the epiphyses are partially formed; a few are missing.

The cranial suture lines are fused but distinctly visible except for the obliterated frontal suture. The external bone appears normal.

The dentition is mostly complete but there is post-mortem loss of three teeth: left upper incisor, left deciduous upper molar (dm2) and right upper permanent molar (M2). The maxilla and mandible contain both deciduous and permanent teeth. Deciduous teeth present at death include the canines and the six upper and lower deciduous molars which are well worn. The permanent central and lateral incisors have erupted. The lower permanent lateral incisors have erupted almost directly behind the central incisors and are malpositioned in the mandible. None of the premolars has erupted, but the right lower deciduous molar (dm1) was lost during life and the right lower anterior premolar (P3) is visible in the crypt. Both upper and lower first and second permanent molars (M1 and M2) have erupted.

The long bones have unfused but well-formed epiphyses with the exception of the trochlea of the distal humerus. The scapular epiphyses and the three bones of the innominate are not fused, nor is the iliac crest. The vertebral bodies show little fusion. The first metacarpals are fused, although the epiphyseal line is partly visible. The talus has no fused epiphyses and the calcaneus appears fused except for the small posterior epiphysis. There are no diagnostic external abnormalities of the skeleton.

Body weights of 'Flint' taken during 1972, prior to the illness preceding his death, averaged 15·4 kg. In September 1972 when he died, he weighed 11·8 kg (W. C. McGrew, pers. comm., based on compilation in 1973 of records of 'Flint').

The cranial capacity at 345 cc is within the range (324–420 cc; average 370 cc) reported for an assumed mixed group of 13 Juvenile II chimpanzees (about six years of age according to Schultz's (1969) categories).

Eruption of the permanent teeth, unlike that of the deciduous incisors, is late in 'Flint' compared to captive chimpanzees, but the sequence apparently is the same. Central upper incisors erupted at 7·0 years (84 months: Pusey (1978) based upon first observation; range for captive males, 59–78 months: Nissen & Riesen, 1964). His lateral upper incisors came in at 7·4 years (89 months; range 70–92 months) and his lateral lower incisors at 7·9 years (94·5 months; range 67–83 months). Eruption dates for his premolars and permanent molars were not recorded.

Maximum long bone lengths are well below the means for other samples of juvenile chimpanzees (A. H. Schultz, unpublished data: Shea, 1982). But each bone length is within the range of variation for broadly comparable age categories: e.g. humerus, 201·3 mm (range 191–242); femur, 197 (range 188–244). In Shea's classification, 'Flint' is a 'Stage 4' male. Although the use of diaphyseal lengths is more appropriate for unossified long bones than that of maximum lengths, overall lengths are used here to conform with these available comparative data.

The long bones are considerably smaller and lighter than those of captive males of similar age (Table II). Femoral BMI and %CA at the mid-shaft scan site are low (Table III) but lie between values for younger and older Gombe and captive juvenile males. Radiographs also show less dense and thinner cortical bone. It is difficult to assess fully the stage of skeletal growth in 'Flint' without more extensive comparative samples of young chimpanzees.

Body weight at 15·4 kg apparently was within range for other Gombe males of similar age (Pusey, 1978), but 'Flint' was much lighter than captive males of similar age (29·8 kg at 7·5–8·5 years for males from Yerkes: Gavan, 1971). However, the shapes of the weight-gain curves are similar even though the captive chimpanzees are heavier and mature earlier (Grether & Yerkes, 1940; Smith, Butler & Pace, 1975; Pusey, 1978).

TABLE II

Long bones in 'Flint' and captive, subadult males

Characters of long bones[a]	Captive males[b]			'Flint' (8·5 years)
	Subadult 1 (3 years)	Subadult 2 (3 years)	Subadult 3 (6–9 years)	
Humerus				
Diaphyseal length	141·0	139·5	210·0	175·0
Midshaft antero-posterior diameter	12·0	13·5	18·5	15·5
Midshaft medio-lateral diameter	10·0	13·5	15·5	15·0
Midshaft circumference	33·5	36·0	53·0	46·0
Weight	16·1	24·8	98·8	40·1
Radius				
Diaphyseal length	128·0	133·0	199·0	169·0
Weight	7·5	10·2	40·2	17·2
Femur				
Diaphyseal length	128·0	127·0	199·0	165·0
Midshaft antero-posterior diameter	10·0	12·1	18·0	15·5
Midshaft medio-lateral diameter	10·0	13·0	18·0	15·5
Midshaft circumference	33·0	39·0	53·5	47·0
Weight	18·0	27·2	119·9	51·0
Tibia				
Diaphyseal length	107·0	118·0	173·0	144·0
Weight	9·4	14·4	61·0	26·6

[a] Linear measurements, mm; clean dry bone weights with variable development of epiphyses, g.
[b] All individuals are *Pan troglodytes*. Subadult 1: male; 3 years; cause of death, euthanized. Subadult 2: male; 3 years; cause of death, euthanized. Subadult 3: male; 6–9 years (based on tooth eruption); cause of death, unknown.

TABLE III

Femur in 'Flint' and captive, subadult males

Characters of femur	Captive males[a]			'Flint' (8·5 years)
	Subadult 1 (3 years)	Subadult 2 (3 years)	Subadult 3 (6–9 years)	
Diaphyseal length (mm)	128·0	127·0	199·0	166·0
Medio-lateral width at 50% scan site (mm)[b]	10·0 (0·08)	13·0 (0·10)	18·0 (0·09)	16·5 (0·01)
Bone mineral index at 50% scan site (g/cm²)	0·443 (0·003)	0·590 (0·003)	1·168 (0·006)	0·709 (0·004)
Percent cortical area at 50% scan site (%)[b]	52·1 (0·41)	—	83·6 (0·42)	55·0 (0·33)

[a] See Table II for information on individuals.
[b] Values in parentheses are normalized for size by dividing by diaphyseal length.

Field observations

Born in 1964 when his mother 'Flo' was aged about 35, 'Flint' was her fourth known offspring. He was weaned at 4·2 years, earlier than other Gombe youngsters (Pusey, 1978), when 'Flo' was in the final stages of another pregnancy. After the infant died when six months old, 'Flint', at 4·6 years, when most young males are becoming independent, continued his dependency on his mother, including suckling, until she died four years later.

After the death of 'Flo', 'Flint' developed chronic diarrhoea, which probably resulted in dehydration. His condition deteriorated rapidly and he died three weeks later. His chronological age was 'early adolescent', but he did not express the anatomical markers nor the hormonally mediated behaviour of adolescence described by Pusey (1978) and Goodall (1986) in Gombe males and by Kraemer *et al.* (1982) in captive males. 'Flint' was autopsied and found to have parasites, gastroenteritis and peritonitis (Goodall, 1983).

Summary

Although eruption of permanent dentition and growth in body size and development were late in 'Flint' compared to captive chimpanzees, they were not exceptionally delayed compared to other Gombe males (Pusey, 1978). But 'Flint's' skeleton none the less indicates growth problems, as shown by the disjuncture of bone and tooth development.

'Flint' was smaller in body size than other free-ranging (not from Gombe) and captive chimpanzees of his age, and bone density seems low. But his cranial capacity is within the range for chimpanzees of similar age. Several factors might have contributed to 'Flint's' possible slow rate of growth: genetics, inadequate nutrition and activity. The generalized nature of small body size, bone-tooth disjuncture, apparently low bone mineral and delayed adolescence does not allow detailed diagnoses of specific causes for observed growth problems. But these factors, in addition to the emotional stress of his mother's death, may have contributed to his own death at the age of 8·5 years.

Young adult 19-year female ('Gilka')

Skeletal and dental biology

The skeleton is intact, with only a few hand and foot bones missing. The skull is complete, and the cranial sutures are fused but mostly distinct: the coronal is clearly visible, the sagittal is visible in its superior portion, the lambdoidal is clearly visible and the temporal line is well defined.

All permanent teeth have erupted. There is an abscess in the upper right central incisor and unusually heavy wear on the upper central and lateral incisors and the lower anterior premolars.

All epiphyses on long bones are fused. The iliac crest is mostly fused but the epiphyseal line is prominent, especially ventrally. The inferior border of the scapula remains unfused.

The most unusual feature of the skeleton is the upper limb asymmetry in linear dimensions, bone weights, joint surfaces, bone mineral content and cortical bone (Morbeck *et al.*, In prep.). The bones of the right upper limb are smaller and lighter than those of the left. The right clavicle is shorter with a noticeably smaller articular facet for the sternum. The right scapula also is smaller and lighter, and the supraspinous and infraspinous fossae are less well developed than those of the left side. In joint surface area, the right humeral head is about 90% that of the left. The humeral

asymmetry in BMI and %CA is also apparent in radiographs which show differences in bone density and cortical thickness in the right and left sides. In addition, they show development of apparent bone reinforcement lines, or bone bars, attributed in humans to variations in growth or the effects of chronic mechanical stress (Kursunoglu *et al.*, 1986).

The hand bones are unusual. Five phalanges show severe erosions; the articular ends are destroyed and two of them show unhealed cloacae in the shifts, diagnostic of osteomyelitis (Jurmain, 1989).

Body weights are available. In 1971 (at menarche, aged about 11 years) 'Gilka' weighed 25 kg; in 1974 when pregnant, 31·5 kg (Pusey, 1978). After her last infant died and her health deteriorated (1977), she weighed 22·5 kg, and 19·5 kg prior to her death in 1979 (Goodall, 1986).

The skeleton shows that 'Gilka' was a small-bodied adult compared to other Gombe females. In cranial capacity (354 cc) but not in tooth size, she is below the Gombe female average. Long bone lengths are shorter than means calculated for other Gombe females. Trunk dimensions, as represented by lengths of clavicle and scapula and ilium breadth, compare favourably with these females. But hip joint surface areas, in particular, are considerably smaller.

In the femur, mid-shaft robusticity is lower than for all other Gombe females, including one individual with shorter maximum and diaphyseal lengths. More importantly, BMI and %CA are also low and only the two very old females exhibit lower values (Sumner *et al.*, 1989) (Table IV).

Field observations

As an infant and young chimpanzee, 'Gilka' was active and apparently healthy. She was weaned when about five years old, during a five-month period when her mother 'Olly' was consorting with

TABLE IV

Femur in Gombe adult females

Characters of femur[a]	Gombe females[b]					
	'Gilka' (19 years)	'Pallas' (27 years)	'Passion' (31 years)	'Melissa' (36 years)	Old female (>40 years)	'Flo' (43 years)
Maximum length (mm)	256·0	258·0	253·0	266·0	284·0	271·0
Diaphyseal length (mm)	220·0	228·0	214·0	227·0	244·0	231·0
Medio-lateral width at 50% scan site (mm)[c]	20·5 (0·09)	22·0 (0·10)	22·0 (0·10)	25·0 (0·10)	25·0 (0·10)	25·0 (0·10)
Bone mineral index at 50% scan site (g/cm²)[c]	0·711 (0·003)	1·002 (0·004)	0·966 (0·005)	1·001 (0·004)	0·532 (0·002)	0·687 (0·003)
Percent cortical area at 50% scan site (%)[c]	46·8 (0·21)	60·7 (0·27)	52·7 (0·25)	—	34·8 (0·14)	42·9 (0·19)
Weight (g)	72·6	101·0	101·9	111·2	91·5	106·1

[a] Values are from clean, dry femora.

[b] 'Gilka': female; estimated age, 19 years; contracted polio at age 7 and experienced partial paralysis of right forearm and hand; cause of death, probably associated with chronic diarrhoea. 'Pallas': female; estimated age, 27 years; cause of death, illness. 'Passion': female; estimated age, 31 years; cause of death, unknown wasting disease. 'Melissa': female; estimated age, 36 years; contracted polio as prime adult, shoulders and neck initially were affected; cause of death, lack of food, old age. Old female: estimated age greater than 40 years; cause of death, unknown. 'Flo': female; estimated age, 43 years; cause of death, old age. Femora are missing in 'Madam Bee', the middle-aged adult discussed in the text.

[c] Values in parentheses are normalized for size by dividing by diaphyseal length.

males (Pusey, 1978). During the 1966 epidemic of a paralytic disease (probably polio) 'Gilka', then seven years old, lost partial use of her right wrist (Goodall, 1983)[1].

She subsequently developed a swelling on her nose which eventually spread to her brow ridges and eyes. A biopsy revealed a diagnosis of *Rhinophycomycosis entomophthorae*, a fungus that is common among the people in West Africa but not recorded in Tanzania (Roy & Cameron, 1972). Doses of fanasil and potassium iodine administered in bananas reduced the swelling temporarily (Goodall, 1983).

Her mother, who was low-ranking and not very social, died when 'Gilka' was 8·6 years old. Her brother 'Evered', who was eight years older and her only known surviving relative, was an occasional companion. Her sexual development progressed normally; her first swelling occurred at about 7·5 years, and her first full oestrus when she was between 10 and 11 years old. Between the ages of 12 and 17 'Gilka' had four infants but none survived. 'Gilka' did not cycle after the death of her last infant, 2·5 years before she died.

In 1976 'Gilka' was severely injured during a fight with 'Passion' and 'Pom' when they killed her (last) infant (Goodall, 1986). In 1977 'Passion' attacked 'Gilka' repeatedly and severely bit her hands. Sores developed on the fingers of her right hand, and she walked slowly and often used the back of her hand.

At the end of her life she became increasingly solitary; with a festering hand and perhaps systemic infection, she had difficulty moving quickly. She developed chronic diarrhoea and lost weight. She died in 1979 at the age of 19.

Summary

The dentition and skeleton show that 'Gilka' was among the smallest Gombe adults and that she had experienced poor health and injury during her life. Abnormalities in growth are indicated by the limb bones which are asymmetrical in length, surface area, cortical bone and bone mineral content.

Field data record that 'Gilka' contracted paralytic polio while still growing. Muscle paralysis, reduced muscle force and weight-bearing account for skeletal asymmetry. In addition, differential bone loss and probable remodelling along the shaft of the right humerus and between the right and left sides most likely relate to loading conditions associated with the disease. Unusual wear on the anterior teeth also suggests behaviours to compensate for reduced hand mobility and strength.

Fractures of the hand phalanges, in contrast, show direct evidence of trauma that might have affected locomotor and manipulative abilities during life. These fractures as well as osteomyelitis that probably resulted from the observed sores on her fingers might have severely limited locomotor and manipulative capabilities.

Adult female chimpanzees at Gombe are most social with their offspring. The loss of her mother, followed by the loss of four offspring, must have contributed to poor emotional health and perhaps compounded her physiologically-based illnesses. Her life illustrates the relationship between physical health and psychosocial well-being. Her individual life history provides an example of how profound social-emotional setbacks associated with disease can affect growth, prohibit successful reproduction and shorten life.

[1] Paralytic polio is caused by a virus which attacks the motor units of muscles. Muscle fibres may atrophy, and muscle control is lost. This loss of muscle loading on the bone results in remodelling of bone size and shape.

Middle-aged 28-year female ('Madam Bee')

Skeletal and dental biology

The skeleton is incomplete. The femur, tibia and fibula are missing from both sides. The long bones of the upper limbs, the vertebral column, the pelvic and pectoral girdles and some hand and foot bones are present.

The skull is complete and well preserved. The cranial sutures are fused and mostly obliterated. The permanent dentition is complete and there is moderate to severe wear, especially on the anterior teeth. There is no evidence of caries or abscesses (Kilgore, 1989).

All epiphyses in the postcranial skeleton are fused. The epiphyseal line on the inferior vertebral border of the scapula is faintly evident and is delineated on the ventral border of the ilium. These two epiphyses are the last to fuse in chimpanzees and may do so after all permanent teeth are present (Schultz, 1956a).

Although humeral lengths are similar, there is asymmetry in robusticity and bone quantity. Mid-shaft diameters and circumference, distal joint surface areas, BMI, %CA and bone weight of the left humerus are smaller than corresponding measurements of the right arm. Although the shaft is less robust and distal joint areas are smaller, the left humeral head is larger than the right.

There is evidence of trauma on the right ulna on the distal third of the shaft where a marked callus formed with a fibrous union from an improperly healed fracture. The radiograph reveals that the fracture pseudoarthrosis had been rebroken a few days prior to death. There also is evidence of a well-healed fracture on the right neck of the radius. In addition, two phalanges show possible fractures.

No body weights are available for 'Madam Bee'. Long bone length and joint size suggest that she weighed somewhat less than the average for Gombe females.

Cranial capacity of 399 cc is comparable to that of other Gombe females and is slightly above the average of 385 cc for a larger sample of *Pan troglodytes* females (Cramer, 1977). Forelimb long bones are shorter than the average lengths in other Gombe females. Scapular and innominate linear dimensions are also smaller, as are available shoulder joint surface areas, but not acetabular area.

Field observations

'Madam Bee' was a young adult (estimated year of birth 1947) when she began visiting camp regularly in 1963. In 1966, at the age of about 19, she reappeared in camp after several months' absence with paralysis of the left forelimb. An epidemic of polio had begun in the previous months, and it was presumed that 'Madam Bee' had contracted the disease. Although she retained limited use of her shoulder and a little movement in the fingers of her left hand, she could hold food but not pick it up. When first seen with her paralysed limb, she moved tripedally, her hand held just off the ground (Goodall, 1983). At some later time she damaged her right forearm, and since her left forelimb was paralysed, she relied extensively on the right arm for quadrupedal knuckle-walking, arboreal climbing and feeding.

When her limb became paralysed, she had two daughters; both survived to adulthood. Five years after her illness, in 1971, she gave birth to a female that survived only three months, possibly owing in part to her difficulty in supporting it during travel and feeding. In 1972 she joined the

southern males when they formed the Kahama community (Pusey, 1978). Another offspring was born in 1973 and died of unknown causes later in 1973.

As a member of the southern Kahama group, during 1974 and 1975 'Madam Bee' was attacked and wounded seriously by two or more males from the Kasakela group whenever they encountered her. By September 1975, when observed again, she was in very poor health, walked slowly and displayed several unhealed wounds (Goodall, 1986). In late September four males attacked her and she died five days later.

Summary

The skeleton of 'Madam Bee' is that of a small individual compared to other Gombe adult females. Asymmetry is apparent in the forelimb bones in robusticity and bone mineral content, although not in bone lengths. Field observations document that she first experienced left forelimb paralysis as an adult. The right ulna shows a fracture and pseudoarthrosis; this corresponds with the field observations documenting that she relied on her right forelimb for support and manipulation.

Old 43-year female ('Flo')

Skeletal and dental biology

The skeleton is mostly intact. The skull is complete. The major sutures on the cranium are almost entirely obliterated. All epiphyses in the postcranial skeleton are fused.

During life 'Flo' lost a number of teeth and bone is resorbed: the central and lateral incisors on the maxilla and on the mandible, the lateral incisors, P3, P4, M1 and M2. (The right central incisor is missing but was probably lost post-mortem.) All four canines are present, worn flat to the bone with the pulp cavity exposed. Besides the canines the remaining teeth in the maxilla include P3 through M3 on both sides, all heavily worn. On the mandible, the medial incisors are present and M3. There are four abscesses on the maxilla and five on the mandible (Kilgore, 1989).

'Flo' sustained several fractures. The right clavicle has a deformed lateral acromion; the scapular acromion process may also have been affected by this fracture but it is missing. The right ulna shows a well-healed, slightly displaced fracture on the distal shaft, although it is the same length as the left ulna. The left fifth metacarpal and the right fifth metatarsal show healed fractures (Jurmain, 1989).

The only evidence of joint degeneration is some slight lipping of bone on the distal femur. In particular the vertebral column shows no evidence of degeneration (Jurmain, 1989), and the radiographs show no sign of fractured vertebrae.

Body weights were taken between 1970 and 1972 when 'Flo' was between the ages of 41 and 43, well past her prime. They average 26·4 kg, but range from 22·7 to 35·5 kg (Wrangham & Smuts, 1980). In her prime she no doubt weighed considerably more, perhaps about 40 kg, indicated by her skeletal robusticity.

In cranial capacity (406 cc) 'Flo' is considerably above the mean for Gombe females (375 cc) and other *Pan troglodytes* (Cramer, 1977).

Limb bone linear dimensions are longer than average for Gombe females and for means calculated for the combined pooled sex sample. Trunk dimensions and shoulder and hip joint areas also are large when compared to other Gombe adults.

BMI, %CA and bone weight of her femur are low when compared to other Gombe females (Table IV). BMI measured at mid-shaft of the femur and in the humerus is considerably lower than recorded for younger adult females (with the exception of 'Gilka'). These younger females have shorter limb bones, but their bone mineral values are higher. Computed tomographic cross-sectional area data also exhibit low values in %CA at these femoral and humeral sites (Table IV). Furthermore, the long bones weigh less and radiographs show that they are relatively less dense than observed in prime and middle-aged adult females.

Field observations

It is estimated that 'Flo' was born in about 1929. She was a high-ranking, aggressive female, and by all accounts, attractive to males. In the course of her life, she had five known offspring: three survived to adulthood. The interbirth interval averaged six years for the four older offspring and was less than five years between 'Flint' and her last infant (Goodall, 1986).

When 'Flo' at the age of 35 gave birth to 'Flint', her dentition was heavily worn. Although the skeleton shows healed fractures, no observations of lameness were ever reported. As she aged, 'Flo' became increasingly frail and emaciated and had difficulty in walking and climbing. When unable to climb, she was observed picking through faeces on the ground for food. 'Flo' died aged about 43 during the dry season when food is less available.

Summary

'Flo' was a large adult female, and in many measurements larger than some of the males. The fractures which she sustained in life apparently did not affect her growth or production of offspring. Like other chimpanzee females, she spent most of her adult life either pregnant or lactating. Her long bones show bone loss with age but there is no evidence of joint degeneration. Her extreme tooth loss and wear combined with weight loss might have contributed to nutritional problems, which correlates with decreased physical activity.

Prime 26-year male ('Charlie')

Skeletal and dental biology

The skeleton is complete. The cranial sutures are fused but still visible. The temporal lines are faint and do not form prominent ridges. There is a puncture hole on the superior right browbridge that extends into the right frontal sinus. Its size and shape reflect that of a canine tip.

The maxillary and mandibular dentition are all present. Most teeth show only slight wear, although the lingual surfaces of the central incisors show moderate wear (Kilgore, 1989). The right lower M3 appears to have been broken or cracked. This apparently led to deformation of the protoconid and hypoconid but the tooth apparently was fully functional. In addition, this tooth exhibits the only carious lesion on an occlusal surface of Gombe chimpanzee dentition (Kilgore, 1989).

All epiphyses are fused although there is a visible epiphyseal line on the ventral iliac surface. Most of the skeleton appears to be normal. Porotic lesions on the distal joint surface of the right distal tibia and a small area on the calcaneus are evident; this may indicate a possible fungal infection (Jurmain, 1989).

TABLE V

Femur in Gombe adult males

Characters of femur[a]	Gombe males[b]	
	'Mac Dee' (15 years)	'Charlie' (26 years)
Maximum length (mm)	267·0	260·5
Diaphyseal length (mm)	223·0	220·0
Medio-lateral width at 50% scan site (mm)[c]	24·0 (0·11)	22·0 (0·10)
Bone mineral index at 50% scan site (g/cm²)[c]	1·134 (0·005)	1·188 (0·005)
Percent cortical area at 50% scan site (%)[c]	65·8 (0·30)	72·8 (0·33)
Weight (g)	158·0	152·0

[a] Values are from clean, dry femora.

[b] 'Mac Dee': male; estimated age 15 years; contracted polio and lost use of forelimbs; cause of death, shot for humane reasons. 'Charlie': male; healthy adult; estimated age, 26 years; cause of death, circumstantial evidence of attack by other male chimpanzees. Femora are missing in 'Hugo', the older adult male discussed in the text.

[c] Values in parentheses are normalized for size by dividing by diaphyseal length.

'Charlie' was small in overall body size compared to other adults. He probably weighed about 40 kg (Wrangham & Smuts, 1980), but body weights during life are not available.

Cranial capacity at 408 cc is similar to other Gombe adult males and is close to the mean (404 cc) of a larger sample of male *Pan troglodytes* (Cramer, 1977).

On the other hand, all long bones, the clavicle and the innominate are shorter than those of a combined-sex sample of other Gombe adults. Shoulder and hip joint surface areas also are smaller. However, scapular length, a partial measure of upper trunk breadth, approximates that of other Gombe adults. And iliac breadth, which reflects lower trunk width, is greater than the mean for other Gombe adults.

BMI, %CA and bone weight of the femur show lower values than those obtained for captive adult males (Table V). Femoral mid-shaft BMI and %CA exhibit higher values than in a young Gombe adult male, but bone length, mid-shaft diameter and bone weight are lower.

Field observations

'Charlie', a male in his prime, estimated to have been born in 1951, first visited camp as an adolescent in 1963. 'Charlie' seemed unusually fearless and had a very supportive relationship with 'Hugh', who may have been his older brother (Goodall, 1986). 'Charlie' and 'Hugh' formed the nucleus of the developing Kahama subgroup where 'Charlie' became alpha male.

'Hugh' disappeared at the end of 1972. Over a three-year period (1972 to 1975), three males of the Kahama community were attacked by Kasakela males. In May 1977 'Charlie' was found dead three days after the sounds of fighting had been heard, near a place where Kasakela males had been

seen (Goodall, 1983). His death very probably was a result of extensive wounds on the head and neck, arms and hands, rump, scrotum, legs and feet.

Summary

At the time of his death, 'Charlie' was in prime condition. He was a somewhat stocky chimpanzee with short and dense limb bones and had few pathologies and no fractures. The puncture in his skull could have been made by a chimpanzee canine, and might have been inflicted during the fight that resulted in his death.

Old 39-year male ('Hugo')

Skeletal and dental biology

The skeleton is relatively complete, but both femora and the left innominate are absent. The cranial sutures are mostly obliterated. There are prominent nuchal ridges on the lateral parts of the nuchal line, but the temporal lines are faint.

Most teeth were lost during life: on the left maxilla, the incisors, canine and P3; on the right, central and lateral incisors and P3 and P4. On the mandible, P4 through M3 are missing on both sides and P3 also is missing on the left. Where teeth are missing, marked bone resorption indicates that the losses were not recent. The upper left canine appears to have been lost post-mortem. The other three canines are present and heavily worn. On the surface of the remaining molars, tooth wear is advanced and little enamel exists. Moreover, six abscesses are present, three in the maxilla and three in the mandible (Kilgore, 1989).

All epiphyses are fused including that of the iliac crest. The spinal column shows some degenerative changes in the small apophyseal joint surfaces in six places (Jurmain, 1989). However, the vertebral bodies are uninvolved. There is no evidence of degeneration in the remaining joints.

During his life, 'Hugo' sustained a minimum of eight fractures (Jurmain, 1989). On the cranium, the right zygomatic has a fracture with some medial displacement. Two left adjacent ribs (possibly 12 and 13) exhibit well-healed fractures on the shaft and were probably the result of a single injury. The spinous process of the fifth cervical vertebra was fractured and did not re-unite. A radiograph confirms a healed fracture of the right fifth metacarpal which is slightly shorter than the left.

The right foot sustained a major injury, with a compression fracture of the calcaneus, characteristic of jumping or falling hard on the foot. There is considerable remodelling of the sub-talar joint surface to accommodate the fractured calcaneus. Two foot phalanges are also fractured and show angular deformities. These three fractures might have been incurred in the same event.

Six body weights are available for 'Hugo' during 1970–73 (age 34–37) with an average of 39·1 kg (range: 35·9 to 44·5 kg (Wrangham, 1975)). His weight dropped to 28 kg just prior to his death (Goodall, 1983).

Cranial capacity is 408 cc, about average for other male *Pan troglodytes* (Cramer, 1977).

'Hugo's' average body weight is similar to the adult male mean, but his skeleton is large for a Gombe chimpanzee. All limb bone lengths, trunk dimensions and shoulder and hip joint surface areas are greater than those averages in the combined sex sample of Gombe adults; only the radius approximates the comparative mean.

The femora are missing. However, BMI, using both raw values and normalized data for size for the 35% scan site in the humerus, is lower than those of other Gombe males but higher than those of most Gombe females. BMI is considerably lower than is observed in captive males and females.

Field observations

'Hugo' at about 39 years old (estimated year of birth 1936) was one of the three very old males at Gombe when he died in 1975. When first encountered, he was high-ranking with pronounced leadership qualities; he was quick to threaten others but was also quick to reassure.

In the early 1960s, 'Hugo' came into camp limping. The chimpanzees that accompanied him moved slowly to accommodate his impaired gait. He was with an oestrous female and may have fallen or jumped from a tree while fighting or chasing a competing male. After a few months, the limp was less noticeable and subsequently his gait seemed normal.

Toward the end of his life, his teeth were well worn or lost. He became increasingly frail and emaciated during his last two years of life. Like 'Flo', he had difficulty in moving during his final months. Essentially he died of old age, the immediate cause being presumed pneumonia contracted during the wet season (Goodall, 1983).

Summary

'Hugo' was high-ranking in his prime, overcame injury and lived to an old age of about 40 years. His skeleton was large, and body weights recorded late in his life well after his prime were average for Gombe adult males. Prior to his death his weight declined sharply. Extreme tooth loss and wear affected his ability to chew properly and difficulty in climbing and travelling may also have affected his nutritional intake. Although some joint degeneration had occurred, deterioration was minimal and, as with 'Flo', muscle loss might have accounted for locomotor and, possibly, feeding difficulties.

As an adult, 'Hugo' suffered a major trauma to his ankle joint. The observed limp probably occurred as a result of the crushed calcaneus and perhaps fractured toe phalanges. Other fractures may have occurred at this time. The healing process was effective in terms of expressed locomotion, and 'Hugo' showed no lameness several months after the injury.

Discussion

The synthesis of skeletal data with field observations gives a picture of what it takes for Gombe chimpanzees to survive at each stage of the life cycle in order to achieve maturity, mate and rear offspring. Life experiences can affect survival, health and reproductive potential at any time. Individuals known from infancy or childhood, for example, illustrate both short- and long-term consequences of malnutrition, disease, injury and emotional trauma. For males, without genetic studies, reproductive potential can be observed but not confirmed. Females, however, followed through adulthood to old age, yield data on factors that promote lifetime reproductive success.

Early life: consequences for development and survival

The early months or years of life are documented for three individuals: 'Gyre', 'Flint' and 'Gilka'. Different combinations of circumstances of birth, family and life events led to early death.

'Gyre' as a twin had a poor start in life. The competition for limited nutritional resources probably compromised prenatal and early postnatal skeletal growth, as well as development of the brain and immune systems (Chandra, 1975; McCormick, 1985; Martorell & Gonzalez-Cossio, 1987).

Mother's age and health affect birth weight and milk production. A mother's personality, social relationships and treatment of her offspring also may affect reproductive outcome and have a long-term influence on offspring. When the twins were born, mother 'Melissa' was in poor health. When 'Flint' was born, the advanced age and heavily worn teeth of his mother 'Flo' probably diminished her ability to obtain sufficient calories and a nutritious diet. In turn, her milk production might have been inadequate for 'Flint's' proper bone growth and development. 'Olly', the mother of 'Gilka', was low-ranking and led a solitary life, factors that influenced 'Gilka's' later social interactions.

Juvenile: striving for independence—weaning and puberty

Body size and development at various stages of life directly affect survival and later reproductive outcome. The pattern of developmental events, i.e. age at weaning, age at maturity, age at dispersal and first reproduction, as well as the pattern of growth in different body regions, is species-specific. Social and other factors can influence the timing of these events in individuals. Each of the three young chimpanzees discussed was small for its age. The skeletons suggest and field observations confirm that they had slow rates of growth and, in 'Gyre' and 'Flint', slow maturation.

Gestation in *Pan* is about 5·5% of the total growth period (average 232 days) (Krogman, 1969). In primates, including humans, the *in utero* environment is most important for brain growth and dental formation, whereas early bone development is influenced postnatally by nourishment through lactation and by loading conditions associated with movement. Enamel formation of incisors and postcanine teeth occurs earlier than bone growth of the jaws which hold the teeth. The brain grows rapidly postnatally and reaches its adult size in four to five years. The first permanent molars erupt in about three years when the brain has almost reached its adult size. All permanent teeth have erupted before epiphyseal fusion of the long bones is complete (Schultz, 1956a; Kerley, 1966; Watts, 1986).

Limb bone growth and muscle development are emphasized later in the growth sequence. Body weight peaks in early adulthood (Gavan, 1953). The sequence of growth and development observed at Gombe is similar to that of humans and other primates—brain growth first, with tooth formation and dental eruption, followed by musculo-skeletal development, sexual maturity and finally total body weight reaching adult size (Holliday, 1978; Grand, 1983; Brizzee & Dunlap, 1986).

Brain growth and tooth development in 'Gyre' proceeded at the expense of limb bone growth. Brain size for his age seems 'on track' but bone weights show little mineralization. The teeth present at death are those expected for a 10-month-old chimpanzee. But limb bone lengths, %CA and BMI are less than those of new-born Gombe chimpanzees. Skeletal growth exhibits more plasticity and illustrates a 'decoupling' of skeletal and dental features.

'Flint', at a later developmental stage, also shows a decoupling of growth rates. Like 'Gyre', his cranial capacity apparently was within the range for juveniles. Although deciduous tooth eruption was similar to that observed for other chimpanzees, his permanent tooth eruption and mandibular growth were slow.

Tooth development is controlled by genetic fields and environmental conditions; each is relatively independent of jaw development, and sometimes they are not congruent (Krogman, 1972; Ortner & Putschar, 1981). This clearly was the case for 'Flint'. Biological stages of growth and thus size of jaws and teeth must develop together, since the jaw accommodates larger permanent teeth. Anterior tooth crowding in 'Flint' illustrates a disjuncture of two different components of the skeletal-dental system and indicates abnormal growth.

Field data collected during 'Flint's' life also confirm retardation in onset of puberty and physical growth at the time of his death. 'Flint' had not yet undergone the spurt in weight gain and testes development associated with puberty. Normally, the testes descend at birth but may remain undescended in sickly juvenile chimpanzees (Wislocki, 1933). When 'Flint' died, his scrotum was small. One testicle remained undescended; the other had not grown, which suggests abnormal sequence or timing of sexual development.

'Flint's' slow rate of growth and immaturity at death might have been influenced by several variables: unknown genetic factors, mother's advanced age and possible poor health affecting his prenatal development and her milk production, and his own limited feeding and travelling activities (see also Nissen & Riesen, 1949). Because of dependency on his mother 'Flo', who was then old and did not range widely, he seldom left her. Such restricted ranging might have affected his diet adversely. His muscular activity might have been reduced, both because he travelled less and because he did not take part in the fighting and chasing involved in establishing peer relationships. His 'retarded' growth and development reflect individual variation but may also indicate a trend towards slower growth rates in this local population.

From the perspective of reproductive outcome, 'Gyre', 'Flint' and 'Gilka' each were unsuccessful. 'Gyre' and 'Flint' died before reaching maturity. Although 'Gilka' gave birth to several infants, none survived.

Adulthood and reproduction: nutrition, disease, injury

Emphasis on survival in infant and juvenile life stages shifts to an emphasis on mating and promoting survival of offspring in adulthood. As with all mammals, chimpanzee females are the 'primary investors' in offspring through feeding, protecting and socializing. Energetics related to long gestation and milk production, which are essential for growth of a large and complex brain, are added to the energetic requirements of a mother's own feeding and locomotion. Furthermore, in these chimpanzees, the mother's social investment involves recognizing the infant's readiness for learning new behaviours, promoting independence while passing on social and survival skills and continuing social interactions throughout life (Goodall, 1967; Van de Rijt-Plooij & Plooij, 1987). A mother must be healthy and vigorous to withstand insults from the environment in the form of disease and injury. And her social network and status also contribute to her own and to her infant's well-being. Similarly, reproductive success for males requires surviving to reproductive age, maintaining themselves and establishing relationships in the community.

Timing and nature of disease

Diseases, including respiratory infections, malnutrition and parasites (Goodall, 1983, 1986), and the time in an individual's life when they occur have an impact on potential lifetime reproductive success. Similarly, the timing and duration of minor or major injuries during the entire course of life affect well-being, survival and success in reproduction and rearing offspring.

'Gilka' contracted polio as a growing seven-year-old; it partially paralysed her right wrist and affected the growth of her forelimb, as indicated by asymmetry in bone lengths, joint sizes, bone mineral content and cortical area. Besides polio, she had a fungal infection which affected her vision; she also lost her mother before she was nine years old. These physical problems, combined with the absence of a family social network, contributed to her low-ranking social status and poor emotional well-being. Her health deteriorated after the death of her fourth offspring and led to termination of her reproductive capability and early death at the age of 19.

In contrast, 'Madam Bee' contracted polio as an adult, and it almost totally paralysed one forelimb. At the time, she had two surviving offspring. Since bone growth was complete with fused epiphyses, bone remodelling in response to muscle paralysis and altered loading conditions is reflected in differential shaft robusticity, BMI and %CA and bone weights. Her paralysed arm was useless for securing and supporting an infant, and the other was needed for walking and climbing. Although the two infants born after she contracted polio might have been healthy at birth, they probably died from inadequate maternal care.

'Gilka' and 'Madam Bee' each suffered from the impact of disease; its timing affected their lifetime reproductive success. In the case of 'Gilka', disease occurred prior to maturity; she did not reproduce successfully. 'Madam Bee' contracted polio following the birth and rearing of two offspring beyond infancy, and one daughter had two offspring.

Timing and nature of injuries

Traumatic injuries, especially broken long bones, apparently occur frequently in free-ranging primate populations (Schultz, 1944; Bramblett, 1967; Buikstra, 1975; Lovell, 1987) and may be fatal, especially when they occur in adults (Bulstrode, King & Roper, 1986). Several of the Gombe individuals show evidence of healed, partly healed or recent fractures. The ages at which such injuries occur and their nature directly affect survival and the quality of later life and, therefore, reproductive opportunities and the survival of offspring.

'Madam Bee' fractured her right ulna in the limb not paralysed by polio, and it did not heal properly. The injury, combined with the polio, further hindered her ability to move and to support her infants. 'Flo's' fractures healed well and had not interfered with her mating and rearing of offspring.

Two adult males, 'Hugo' and 'Charlie', experienced severe trauma and the outcome differed dramatically. 'Hugo', after suffering a serious stress fracture during middle-age, continued to live into old age; apparently the injury did not prohibit reproductive opportunities or shorten life. 'Charlie', in contrast, died as a result of severe injuries. His reproductive potential, therefore, was terminated through intergroup conflict, even though skeletal and dental analyses confirm his prime condition.

When injury and disease, including malnutrition as already discussed for 'Gyre' and 'Flint', occur during growth, they may have permanent effects in adulthood (e.g. 'Gilka'). Debilitating injuries or diseases at different times during an individual's reproductive span may also affect future mating opportunities or survival of offspring (e.g. 'Charlie', 'Madam Bee'). It may also happen that injuries have little impact on reproductive success (e.g. 'Flo', 'Hugo').

Life span: reproductive life span, ageing and death

From an evolutionary perspective, it is the length of the reproductive life span and the numbers

of offspring that are significant, rather than total life span. Gombe male chimpanzees reach puberty at about nine years of age but are not socially mature until about 15 (Goodall, 1986). Therefore it is difficult to determine from field observations the length of male reproductive life. Gombe females reach sexual maturity (menarche) at about 11 years of age, with the birth of the first offspring at about 13 years of age (Tutin, 1980). The ovarian cycle of females may cease before death (e.g. 'Flo').

Interbirth interval is about five years, and infant mortality is highest for the first and last infants. Given this interbirth interval and age at first reproduction, the maximum number of offspring for females is five or six, but perhaps in reality is closer to four or five.

Life span in captive chimpanzees is considerably longer than in free-ranging populations (Washburn, 1981) and may exceed 50 years (King et al., 1988). Many Gombe chimpanzees have lived to over 40 years of age (Goodall, 1983, 1986), as have Mahale chimpanzees (Hiraiwa-Hasegawa et al., 1984). Reproductive life span for females, then, is about 27 years, from 13 to 40 years.

Physical and social changes in Gombe chimpanzees associated with ageing are recorded in the dentition and skeleton, and in field observations. The ageing process in primates, including humans (Weiss, 1981; Cutler, 1981; Washburn, 1981; Borkan, Hults & Mayer, 1982), may be similar to that of other mammals. For example, tooth deterioration can lead to death. In old individuals the most obvious age changes are severe tooth wear, tooth loss and absorption of supporting bone, caries and several abscesses. Such dental pathologies increase with old age. The percentage of caries, abscesses and bone resorption is 2·5–3·5 times greater in old chimpanzees than in prime adults (Schultz, 1939, 1956a).

As they aged, 'Hugo' and 'Flo' lost body weight, musculature and apparently bone mineral. They had difficulties during quadrupedal travel and climbing which affected their feeding and social interactions. 'Hugo', for example, no longer went on patrols with other males. 'Flo' spent more time on the ground. Locomotor problems were probably due to loss of muscle mass and tone rather than to problems in their joints since the vertebral column and major limb joints do not show arthritic lesions.

Gombe chimpanzees, as other primates, are especially susceptible to respiratory diseases, including pneumonia and influenza. Although not clearly defined in bones, such diseases often are the direct cause of death for both young and elderly Gombe chimpanzees. Respiratory illnesses leading to death strike more frequently during the rainy season (Goodall, 1983).

A long life span is characteristic of large-bodied, large-brained mammals (Eisenberg, 1981). The potential for a long life, and possible long reproductive span, may be species-specific. Causes of death may reflect genetic factors and ecological conditions as well as components of individual life history at previous stages.

Summary

Events recorded in bones and teeth combined with information from long-term behavioural field studies illustrate the connections between biology and life experiences and characterize individual life history and its variation within a local population. Data from these two sources indicate the effects of nutrition, disease and injury on health and well-being, the extent of reproductive productivity and life-span, and the causes and circumstances of death. They demonstrate the interrelationship of the factors which determine whether an individual will succeed in contributing genes to the next generation. Both success and failure are illustrated by the individual Gombe chimpanzees described.

REFERENCES

Altmann, J. (1980). *Baboon mothers and infants*. Cambridge, Mass.: Harvard University Press.

Altmann, J. (1983). Costs of reproduction in baboons (*Papio cynocephalus*). In *Behavioral energetics: the cost of survival in vertebrates*: 67–88. Aspey, W. P. & Lustick, S. I. (Eds). Columbus, Ohio: Ohio State University Press.

Altmann, J., Altmann, S. A., Hausfater, G. & McCuskey, S.A. (1977). Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. *Primates* **18**: 315–330.

Altmann, J., Hausfater, G. & Altmann, S. A. (1985). Demography of Amboseli baboons, 1963–1983. *Am. J. Primatol.* **8**: 113–125.

Altmann, J., Hausfater, G. & Altmann, S. A. (1988). Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. In *Reproductive success: studies of individual variation in contrasting breeding systems*: 403–418. Clutton-Brock, T. H. (Ed.). Chicago: Chicago University Press.

Altmann, S. A. & Altmann, J. (1979). Demographic constraints on behaviour and social organization. In *Primate ecology and human origins*: 47–63. Bernstein, I. R. & Smith, E. O. (Eds). New York: Garland Press.

Bergmann, R. L. & Bergmann, K. E. (1979). In *Human growth* 3. *Neurobiology and nutrition*: 331–360. Falkner, F. & Tanner, J. M. (Eds). New York: Plenum Press.

Borgerhoff Mulder, M. (1987). Resources and reproductive success in women with an example from the Kipsigis of Kenya. *J. Zool., Lond.* **213**: 489–505.

Borgerhoff Mulder, M. (1988). Reproductive success in three Kipsigis cohorts. In *Reproductive success: studies of individual variation in contrasting breeding systems*: 419–435. Clutton-Brock, T. H. (Ed.). Chicago: Chicago University Press.

Borkan, G. A., Hults, D. E. & Mayer, P. J. (1982). Physical anthropological approaches to aging. *Yb. phys. Anthrop.* **25**: 181–202.

Bramblett, C. (1967). Pathology in the Darajani baboon. *Am. J. phys. Anthrop.* (N.S.) **26**: 331–340.

Bramblett, C. (1969). Non-metric skeletal age changes in the Darajani baboon. *Am. J. phys. Anthrop.* (N.S.) **30**: 161–172.

Brizzee, K. R. & Dunlap, W. P. (1986). Growth. In *Comparative primate biology* 3. *Reproduction and development*: 363–413. Dukelow, W. R. & Erwin, J. (Eds). New York: Alan R. Liss.

Brown, D. (1988). Components of lifetime reproductive success. In *Reproductive success: studies of individual variation in contrasting breeding systems*: 439–453. Clutton-Brock, T. H. (Ed.). Chicago: Chicago University Press.

Buikstra, J. E. (1975). Healed fracture in *Macaca mulatta*: age, sex and symmetry. *Folia primatol.* **23**: 140–148.

Bulstrode, C., King, J. & Roper, B. (1986). What happens to wild animals with broken bones? *Lancet* **1986(i)**: 29–31.

Bygott, J. D. (1974). *Agonistic behaviour and dominance in wild chimpanzees*. PhD Diss., Cambridge University.

Calder, W. A., III (1984). *Size, function, and life history*. Cambridge, Mass. & London: Harvard University Press.

Chagnon, N. A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science, N. Y.* **239**: 985–992.

Chandra, R. K. (1975). Fetal malnutrition and postnatal immunocompetence. *Am. J. Dis. Child.* **129**: 450–454.

Cheney, D. L., Seyfarth, R. M., Andelman, S. J. & Lee, P. (1988). Reproductive success in vervet monkeys. In *Reproductive success: studies of individual variation in contrasting breeding systems*: 384–402. Clutton-Brock, T. H. (Ed.). Chicago: Chicago University Press.

Cheverud, J. M. (1982). Relationships among ontogenetic, static, and evolutionary allometry. *Am. J. phys. Anthrop.* (N.S.) **59**: 139–149.

Cheverud, J. M. & Buikstra, J. E. (1982). Quantitative genetics of skeletal nonmetric traits in the rhesus macaques on Cayo Santiago. III. Relative heritability of skeletal nonmetric and metric traits. *Am. J. phys. Anthrop.* (N.S.) **59**: 151–155.

Clutton-Brock, T. H. (1975). Feeding behaviour of red colobus and black and white colobus in East Africa. *Folia primatol.* **23**: 165–207.

Clutton-Brock, T. H. (1988*a*). Reproductive success. In *Reproductive success: studies of individual variation in contrasting breeding systems*: 472–485. Chicago: Chicago University Press.

Clutton-Brock, T. H. (Ed.) (1988*b*). *Reproductive success: studies of individual variation in contrasting breeding systems*. Chicago: Chicago University Press.

Coe, C. L., Connolly, A. C., Kraemer, H. C. & Levine, S. (1979). Reproductive development and behavior of captive female chimpanzees. *Primates* **20:** 571–582.

Coelho, A. M., Jr (1986). Time and energy budgets. In *Comparative primate biology* **2A.** *Behavior, conservation, and ecology*: 141–166. Mitchell, G. & Erwin, J. (Eds). New York: Alan R. Liss.

Cole, L. C. (1954). The population consequences of life history phenomena. *Q. Rev. Biol.* **29:** 103–137.

Cramer, D. L. (1977). Craniofacial morphology of *Pan paniscus*. A morphometric and evolutionary appraisal. *Contr. Primatol.* **10:** 1–64.

Crews, D. & Moore, M. C. (1986). Evolution of mechanisms controlling mating behavior. *Science, N.Y.* **231:** 121–125.

Cutler, R. G. (1981). Life-span extension. In *Aging: biology and behavior*: 31–76. McGaugh, J. L. & Kiesler, S. B. (Eds). New York: Academic Press.

DeRousseau, C. J. (1988). Osteoarthritis in rhesus monkeys and gibbons. A locomotor model of joint degeneration. *Contr. Primatol.* **25:** 1–145.

DeRousseau, C. J. & Reichs, K. J. (1987). Ontogenetic plasticity in nonhuman primates. 1. Secular trends in the Cayo Santiago macaques. *Am. J. phys. Anthrop.* **73:** 279–287.

Dunbar, R. I. M. (1980). Demographic and life history variables of a population of gelada baboons (*Theropithecus gelada*). *J. Anim. Ecol.* **49:** 485–506.

Dunbar, R. I. M. (1984). *Reproductive decisions. An economic analysis of gelada baboon social strategies*. Princeton: Princeton University Press.

Dunbar, R. I. M. (1987). Demography and reproduction. In *Primate societies*: 240–249. Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). Chicago & London: Chicago University Press.

Dunbar, R. I. M. (1988). *Primate social systems*. London & Sydney: Croom Helm.

Eisenberg, J. F. (1981). *The mammalian radiations. An analysis of trends in evolution, adaptation, and behaviour*. Chicago: Chicago University Press.

Fedigan, L. M., Fedigan, L., Gouzoules, S., Gouzoules, H. & Koyama, N. (1986). Lifetime reproductive success in female Japanese macaques. *Folia primatol.* **47:** 143–157.

Gavan, J. A. (1952). Birth order and birth weight in the chimpanzee. *Am. J. phys. Anthrop.* (N.S.) **10:** 23–30.

Gavan, J. A. (1953). Growth and development of the chimpanzee: a longitudinal and comparative study. *Hum. Biol.* **25:** 93–143.

Gavan, J. A. (1971). Longitudinal, postnatal growth in chimpanzee. In *The chimpanzee* **4.** *Behavior, growth, and pathology of chimpanzees*: 46–102. Bourne, G. H. (Ed.). Basel: Karger.

Goodall, J. van Lawick (1967). Mother-offspring relationships in free-ranging chimpanzees. In *Primate ethology*: 287–346. Morris, D. (Ed.). London: Weidenfeld & Nicolson.

Goodall, J. van Lawick (1968). *The behavior of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr.* **1**(3): 161–311.

Goodall, J. van Lawick (1971). *In the shadow of man*. London: Collins.

Goodall, J. (1983). Population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. *Z. Tierpsychol.* **61:** 1–60.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, Mass. & London: Cambridge University Press.

Goodall, J. (1987). *Newsletter of the Jane Goodall Institute, Spring 1987*. Tucson, Arizona: The Jane Goodall Institute.

Grand, T. I. (1983). The anatomy of growth and its relation to locomotor capacity in *Macaca*. *Spec. Publs Am. Soc. Mammal.* No. 7: 5–23.

Grether, W. F. & Yerkes, R. M. (1940). Weight norms and relations for chimpanzees. *Am. J. phys. Anthrop.* **27:** 181–197.

Harvey, P. H. & Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution, Lawrence, Kans.* **39:** 559–581.

Harvey, P. H., Martin, R. D. & Clutton-Brock, T. H. (1987). Life histories in comparative perspective. In *Primate societies*: 181–196. Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds). Chicago & London: Chicago University Press.

Harvey, P. H. & Zammuto, R. M. (1985). Patterns of mortality and age at first reproduction in natural populations of mammals. *Nature, Lond.* **315:** 319–320.

Hiraiwa-Hasegawa, M., Hasegawa, T. & Nishida, T. (1984). Demographic study of a large-sized unit-group of chimpanzees in the Mahale Mountains, Tanzania: a preliminary report. *Primates* **25:** 401–413.

Holliday, M. A. (1978). Body composition and energy needs during growth. In *Human growth 2. Postnatal growth*: 117–138. Falkner, F. & Tanner, J. M. (Eds). New York: Plenum Press.

Jurmain, R. (1989). Trauma, degenerative disease, and other pathologies among Gombe chimpanzees. *Am. J. phys. Anthrop.* (N.S.) **80**: 229–237.

Kerley, E. R. (1966). Skeletal age changes in the chimpanzee. *Tulane Stud. Zool.* **13**: 71–82.

Kilgore, L. (1989). Dental pathologies in ten free-ranging chimpanzees from Gombe National Park, Tanzania. *Am. J. phys. Anthrop.* (N.S.) **80**: 219–227.

King, F. A., Yarbrough, C. J., Anderson, D. C., Gordon, T. P. & Gould, K. G. (1988). Primates. *Science, N. Y.* **240**: 1475–1482.

Kraemer, H. C., Horvat, J. R., Doering, C. & McGinnis, P. R. (1982). Male chimpanzee development focusing on adolescence: integration of behavioral with physiological changes. *Primates* **23**(3): 393–405.

Krogman, W. M. (1969). Growth changes in skull, face, jaws, and teeth of the chimpanzee. In *The chimpanzee 1. Anatomy, behavior, and diseases of chimpanzees*: 104–164. Bourne, G. H. (Ed.). Basel: Karger.

Krogman, W. (1972). *Child growth*. Ann Arbor: University of Michigan Press.

Kursunoglu, S., Pate, D., Resnick, D., Haghighi, P., Tyson, R. & Pitt, M. (1986). Bone reinforcement lines in chronic adult osteopenia: a hypothesis. *Radiology* **158**(2): 409–415.

Lande, R. (1988). Genetics and demography in biological conservation. *Science, N. Y.* **241**: 1455–1460.

Laws, R. M. (1987). Introduction. Historical perspective. *Symp. zool. Soc. Lond.* No. 57: 1–6.

Loudon, A. S. I. & Racey, P. A. (Eds) (1987). *Reproductive energetics in mammals. (Symp. zool. Soc. Lond.* No. 57).

Lovell, N. C. (1987). *Skeletal pathology of wild-shot pongids: implications for human evolution*. PhD Diss., Cornell Univ.

Martorell, R. & Gonzalez-Cossio, T. (1987). Maternal nutrition and birth weight. *Yb. phys. Anthrop.* **30**: 195–220.

McCormick, M. C. (1985). The contribution of low birth weight to infant mortality and childhood morbidity. *New Engl. J. Med.* **312**: 82–90.

McGinnis, P. R. (1973). *Patterns of sexual behaviour in a community of free-living chimpanzees*. PhD Diss., University of Cambridge.

Morbeck, M. E. & Zihlman, A. L. (1988). Body composition and limb proportions. In *Orang-utan biology*: 285–297. Schwartz, J. H. (Ed.). New York: Oxford University Press.

Morbeck, M. E. & Zihlman, A. L. (1989). Body size and proportions in chimpanzees, with special reference to *Pan troglodytes*, Gombe National Park Tanzania. *Primates* **30**(3): 369–382.

Nagurka, M. L. & Hayes, W. C. (1980). An interactive graphics package for calculating cross-sectional properties of complex shapes. *J. Biomech.* **13**: 59–64.

Nissen, H. W. & Riesen, A. H. (1945). The deciduous dentition of chimpanzee. *Growth* **9**: 265–274.

Nissen, H. W. & Riesen, A. H. (1949). Retardation in onset of ossification in chimpanzee related to various environmental and physiological factors. *Anat. Rec.* **105**: 665–675.

Nissen, H. W. & Riesen, A. H. (1964). The eruption of the permanent dentition of chimpanzees. *Am. J. phys. Anthrop.* (N.S.) **22**: 285–294.

Ortner, D. J. & Putschar, W. G. J. (1981). *Identification of pathological conditions in human skeletal remains*. Washington D.C.: Smithsonian Institution Press.

Partridge, L. & Harvey, P. H. (1988). Ecological context of life history evolution. *Science, N. Y.* **241**: 1449–1455.

Plooij, F. X. (1984). *The behavioral development of free-living chimpanzee babies and infants*. Norwood, New Jersey: Ablex Publ. Corp.

Pusey, A. (1978). *The physical and social development of wild adolescent chimpanzees (Pan troglodytes schweinfurthii)*. Unpubl. Diss., Stanford University, California.

Rawlins, R. G. & Kessler, M. J. (1986). Demography of the free-ranging Cayo Santiago macaques (1976–1983). In *The Cayo Santiago macaques. History, behavior and biology*: 46–72. Rawlins, R. G. & Kessler, M. J. (Eds). Albany: State University of New York Press.

Roy, A. D. & Cameron, H. M. (1972). Rhinophycomycosis entomophthorae occurring in a chimpanzee in the wild in East Africa. *Am. J. trop. Med. Hyg.* **21**: 234–237.

Ruff, C. B. & Hayes, W. C. (1982). Subperiosteal expansion and cortical remodelling of the human femur and tibia with aging. *Science, N. Y.* **217**: 945–948.

Sade, D. S., Cushing, K., Cushing, P., Dunaif, J., Figueroa, A., Kaplan, J. R., Lauer, C., Rhodes, D. & Schneider, J. (1977). Population dynamics in relation to social structure on Cayo Santiago. *Yb. phys. Anthrop.* **20**: 253–262.

Sade, D. S., Chepko-Sade, B. D., Schneider, J. M., Roberts, S. S. & Richtsmeier, J. T. (1985). *Basic demographic observations on free-ranging rhesus monkeys*. New Haven, CT.: Human Relations Area Files.

Schultz, A. H. (1939). Notes on diseases and healed fractures of wild apes. *Bull. Hist. Med.* **7**: 571–582.

Schultz, A. H. (1940). Growth and development of the chimpanzee. *Contr. Embryol.* **28:** 1-63.

Schultz, A. H. (1944). Age changes and variability in gibbons. *Am. J. phys. Anthrop.* (N.S.) **2:** 1-129.

Schultz, A. H. (1956a). Postembryonic age changes. *Primatologia* **1:** 887-964.

Schultz, A. H. (1956b). The occurrence and frequency of pathological and teratological conditions and of twinning among non-human primates. *Primatologia* **1:** 965-1014.

Schultz, A. H. (1969). The skeleton of the chimpanzee. In *The chimpanzee 1. Anatomy, behavior, and diseases of chimpanzees:* 50-103. Bourne, G. H. (Ed.). Basel: Karger.

Shea, B. T. (1982). *Growth and size allometry in the African Pongidae: cranial and postcranial analyses.* PhD diss., Duke University, Durham, N.C.

Sigg, H., Stolba, A., Abegglen, J. J. & Dasser, V. (1982). Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. *Primates* **23:** 473-487.

Smith, A. H., Butler, T. M. & Pace, N. (1975). Weight growth in colony-reared chimpanzees. *Folia primatol.* **24:** 29-59.

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (Eds) (1987). *Primate societies.* Chicago & London: Chicago University Press.

Stearns, S. C. (1976). Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51:** 3-47.

Stearns, S. C. (1977). The evolution of life-history traits: a critique of the theory and a review of the data. *A. Rev. Ecol. Syst.* **8:** 145-171.

Stearns, S. C. & Koella, J. C. (1986). The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution, Lawrence, Kans.* **40:** 893-913.

Sumner, D. R. (1984a). *Size, shape and bone mineral content of the human femur in growth and aging.* PhD Diss., University of Arizona, Tucson.

Sumner, D. R. (1984b). Postembryonic dimensional allometry of the human femur. *Am. J. phys. Anthrop.* (N.S.) **64:** 69-74.

Sumner, D. R., Mockbee, B., Morse, K., Cram, T. & Pitt, M. (1985). Computed tomography and automated image analysis of prehistoric femora. *Am. J. phys. Anthrop.* (N.S.) **68:** 225-232.

Sumner, D. R., Morbeck, M. E. & Lobick, J. (1989). Apparent age-related bone loss among female Gombe chimpanzees. *Am. J. phys. Anthrop.* **79:** 225-234.

Teleki, G. (1973). *The predatory behavior of wild chimpanzees.* Lewisburg, Pa.: Bucknell University Press.

Tutin, C. E. G. (1975). *Sexual behaviour and mating patterns in a community of wild chimpanzees.* PhD Diss., University of Edinburgh.

Tutin, C. E. G. (1980). Reproductive behaviour of wild chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fert.* (Suppl.). **28:** 43-57.

Van de Rijt-Plooij, H. H. C. & Plooij, F. X. (1987). Growing independence, conflict and learning in mother-infant relations in free-ranging chimpanzees. *Behaviour* **101:** 1-86.

Washburn, S. L. (1981). Longevity in primates. In *Aging: biology and behavior:* 11-29. McGaugh, J. L. & Kiesler, S. B. (Eds). New York: Academic Press.

Watts, E. S. (1986). Skeletal development. In *Comparative primate biology 3. Reproduction and development:* 415-439. Dukelow, W. R. & Erwin, J. (Eds). New York: Alan R. Liss.

Weiss, K. M. (1981). Evolutionary perspectives on human aging. In *Other ways of growing old:* 25-58. Amoss, P. T. & Harrell, S. (Eds). Stanford, Calif.: Stanford University Press.

Wislocki, G. B. (1933). Observations on the descent of the testes in the macaque and in the chimpanzee. *Anat. Rec.* **57:** 133-148.

Wrangham, R. W. (1975). *The behavioural ecology of chimpanzees in Gombe National Park, Tanzania.* PhD Diss., University of Cambridge.

Wrangham, R. W. & Smuts, B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fert.* (Suppl.) **28:** 13-31.