Chapter 16
Long-Term Studies of the Chimpanzees of Gombe National Park, Tanzania

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Abstract The study of chimpanzees at Gombe National Park, which has continued for over 50 years, has yielded many discoveries that would have been impossible without long-term data. The basic data collection procedure has remained constant since the early 1970s, with a team of Tanzanian field assistants conducting all-day focal follows of individual chimpanzees in the Kasekela (1974–present) and Mitumba (1994–present) communities. Field assistants record map location and party composition at 15-min intervals and keep a continuous record of the focal subject's feeding behavior and narrative notes on behavior, including mating, agonistic interactions, tool use, hunting, boundary patrols, and intergroup interactions. Field assistants have also monitored the unhabituated Kalande community since 1999. A relational database developed from these data provides a powerful tool for analyzing long-term patterns. Studies using this database in combination with new technologies have deepened our understanding of chimpanzee pathogens, genetics, hormones, tool use, hunting, meat sharing, social relationships, habitat use, dispersal, life histories, and demography. This chapter focuses on life histories and demography, followed by a section that highlights findings on two topics for which long-term data have proven especially informative: intergroup aggression and disease ecology.

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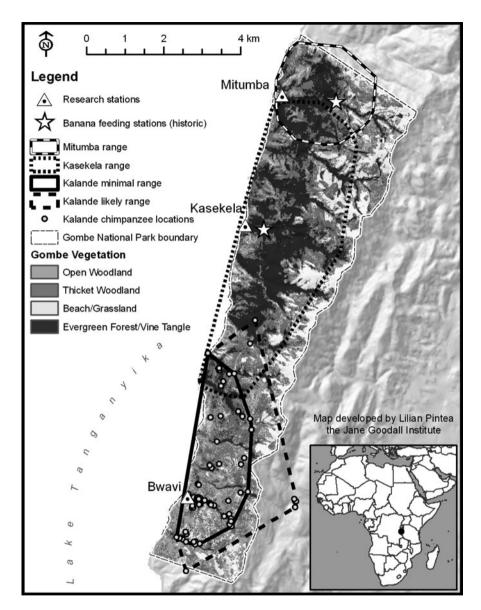e-mail: wilso198@umn.edu

16.1 History and Infrastructure of Gombe Stream Research Centre

Long-term field studies are essential for understanding the lives of our closest relatives, including chimpanzees (*Pan troglodytes*). Jane Goodall began the first such study of chimpanzees at what was then Gombe Stream Game Reserve in 1960. Studies of captive chimpanzees by Wolfgang Köhler (1925) and Robert Yerkes (Yerkes and Yerkes 1929) had provided intriguing insights into chimpanzee cognition, but very little was known about chimpanzees in the wild. Nissen's short study of chimpanzees in French Guinea provided some of the first observations of feeding and social behavior (Nissen 1931). By 1960, technological advances such as jet travel and antimalarial drugs had made tropical field sites more accessible and medically safer for researchers from temperate zone countries, who had begun studying various primate species (e.g., Hanuman langurs (Jay 1962), savannah baboons (DeVore and Hall 1965), and mountain gorillas (Schaller 1963)), including chimpanzees (Kortlandt 1962).
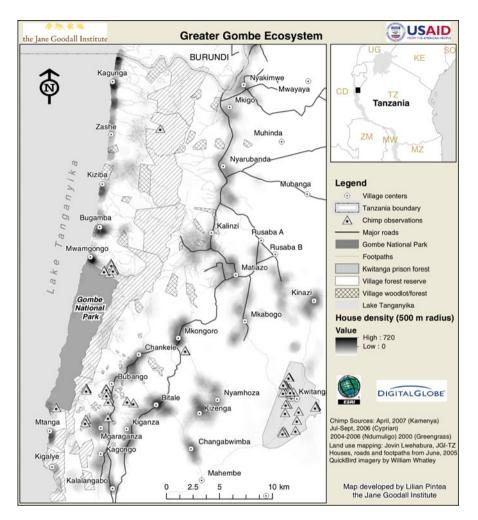
16.1.1 Study Area

Gombe Stream Game Reserve was established in January 1943 (Thomas 1961) and upgraded to national park status in 1968 (Goodall 1986). Gombe National Park constitutes a 2–3.5-km-wide wedge-shaped strip of mountainous terrain rising from an elevation of 766 m along the shore of Lake Tanganyika to peaks ranging from 1,300 to 1,623 m along the crest of the rift escarpment in the east (Pintea et al. 2010; Fig. 16.1). Gombe's southern border is 15 km north of the town of Kigoma. The park extends roughly 14 km along the lake, with villages at its northern and southern ends and less densely settled land to the east (Fig. 16.2).

The park's area of 35.4 km^2 (13.7 square miles) consists of a series of steep ridges and valleys that descend westward to the lake. Roughly half of the 15 major valleys contain year-round streams; other streams flow seasonally. The vegetation varies from evergreen forest in valley bottoms, to thicket, vine tangle and semi-deciduous forest on the lower slopes; open woodland on the upper slopes; and grassland on the highest slopes (Clutton-Brock and Gillett 1979). Moist air from the lake combined with a north–south gradient of decreasing altitude creates a north–south gradient of decreasing rainfall. The north is thus more heavily forested, while the south is drier, with more woodland, and the density of chimpanzee food plants is substantially higher in the northern half of the park (Rudicell et al. 2010). In the 1960s, much of the park burned each year, creating an open habitat with little undergrowth. Fire has been suppressed since 1968, resulting in an increase in shrubs and vines and in overall greenness, especially in the north (Pintea et al. 2010). The increased undergrowth has not only likely improved the amount of food available to chimpanzees (Pintea et al. 2010), but has also reduced visibility and made following chimpanzees more difficult.

Fig. 16.1 Map of Gombe National Park, showing the locations of the research stations and former banana feeding stations, the 2007 ranges of the Mitumba and Kasekela communities, and the minimum and likely ranges of the Kalande community, based on sightings within the park and nest locations found near the park (2002–2009). The vegetation coverage within the park is based on classification from satellite images. The inset shows the location of Gombe within Tanzania. (Map based on Rudicell et al. (2010), Fig. 1, courtesy Lilian Pintea, the Jane Goodall Institute)

Fig. 16.2 Map of the greater Gombe ecosystem, showing Gombe National Park, the recently established village forest reserves, the location of chimpanzee sightings outside the park, and the density of houses, derived from 2005 QuickBird satellite imagery. (Map courtesy Lilian Pintea, the Jane Goodall Institute)

16.1.2 Study Population

Three chimpanzee communities have existed in Gombe throughout the duration of the study: Mitumba in the north, Kasekela[1] in the center, and Kalande in the south. As of January 2010, approximately 101–105 chimpanzees inhabited the park,

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[1] Spelled "Kasakela" in earlier publications; "Kasekela" is the preferred local spelling.

including 25 in Mitumba, 61 in Kasekela, and perhaps 15–19 in Kalande. The Kahama community split from the Kasekela community in the early 1970s but survived only through 1977. Life history details are known for 292 chimpanzees in the Mitumba and Kasekela communities, with less detailed information available for another 40 or so in the Kalande community.

Most research has focused on the Kasekela community, which Goodall began studying in 1960. Efforts to habituate the Mitumba community began in 1985. It was originally intended to serve as a focus for tourism, but was subsequently excluded from tourism because of its small size (TANAPA 2005). Several efforts to habituate the Kalande community from 1968 to 1990 proved unsuccessful, but a monitoring program begun in 1999 continues to the present (Rudicell et al. 2010).

16.1.3 Data Collection Methods

Early efforts to observe wild chimpanzees faced challenges common to many other primate studies: chimpanzees use large ranges and generally flee from people. To overcome these challenges, Goodall employed an observational approach that differed greatly from previous attempts to study chimpanzees (e.g., both Nissen (1931) and Kortlandt had tried to watch chimpanzees from blinds), but is now nearly ubiquitous in primate studies. Like Carpenter (1934) had done in his pioneering field study, Goodall approached the animals in plain view, allowing them to become habituated to human presence gradually. Goodall searched for and watched chimpanzees from hilltops and other vantage points, and gradually observed them in more detail as habituation improved. By the end of her fourth month, Goodall had observed chimpanzees eating meat (Goodall 1963) and making and using tools to "fish" for termites (Goodall 1964).

During the 1960s, the study developed from a single researcher recording data *ad libitum* throughout the forest to a large research team focused on systematic collection of behavioral data in the vicinity of a banana provisioning area ("Camp") located near the center of the Kasekela community's range. Goodall began provisioning chimpanzees in 1963 to speed habituation and improve observation and filming conditions. She hired her first research assistant in 1964, and in 1965, she formally established the Gombe Stream Research Centre, which rapidly grew to host a large research team. Researchers kept daily records of chimpanzees seen in camp and of their interactions ("A-record"). Collection of these data continued until banana feeding ended in 2000. Starting in 1967, and then more regularly from 1970, chimpanzees were weighed in camp using a hanging spring balance baited with bananas (Pusey et al. 2005). Robert Hinde developed a check-sheet for recording mother–infant behavior in 1969, forming the basis of data collection that continues to the present. Banana feeding also attracted baboons, and by 1967 Goodall had established a long-term baboon study, which continues today (Ransom 1981; Collins et al. 1984; Packer et al. 1998).

Researchers began to follow chimpanzees away from Camp around 1968, for studies including hunting (Teleki 1973) and sexual behavior (McGinnis 1979). Tragically, in 1968, Ruth Davis fell to her death from a cliff while following chimpanzees in Kahama valley (Goodall 1986). Subsequently, researchers were required to work in teams of at least two for safety, and Goodall began hiring Tanzanian field assistants, starting with Hilali Matama in 1968. Initially, the Tanzanians simply accompanied the foreign students, but their excellent skill at tracking chimpanzees and observing their behavior led to the start of formal training in standardized data collection in 1970. In 1974, Larry Goldman and Donna Anderson began more intensive training of field assistants, introducing the use of check-sheets and reliability tests (Goodall 1986).

Focal follows, necessary for unbiased estimates of behavior rates (Altmann 1974), were first conducted in 1968, as students followed individual chimpanzees through the forest. Richard Wrangham initiated all-day focal sampling that involved following chimpanzees between consecutive night-nesting sites (Wrangham 1977). Focal data were called B-Record to distinguish them from the A-Record data. Field assistants conducted some focal follows in 1973 and have conducted daily all-day focal follows of individuals in the Kasekela community regularly since 1974. Comparable data collection for the Mitumba community began in 1994. Observers record map location, party composition, and female reproductive status at 15-min intervals ("travel and group check-sheets"); continuously record the focal subject's feeding behavior; note all occurrences of mating, agonistic interactions, grooming, and tool use by the focal subject; and take ad libitum narrative notes on other events, including hunting, boundary patrols, and intergroup interactions.

In the early 1970s, Goodall developed an affiliation with Stanford University through David Hamburg. From 1971 to 1975, Goodall was a visiting professor at Stanford. A series of Stanford undergraduates visited Gombe from 1972 to 1975, first receiving training in chimpanzee behavior at the Stanford Outdoor Primate Facility ("Gombe West") before spending 6 months at Gombe. Students also visited Gombe from the Zoology program at the University of Dar es Salaam, where Goodall was a guest lecturer.

The growing and productive international research effort at Gombe, including the partnership with Stanford, abruptly halted in 1975 with the kidnapping of four students by rebels from Zaire (Goodall 1986). All four students were eventually safely returned to their families, but Tanzanian authorities considered the park unsafe for foreign researchers, including Goodall, for many years following the kidnapping. The Tanzanian field assistants took over day-to-day operations at Gombe, which Goodall oversaw from her home base in Dar es Salaam. Thanks to the dedication of the Tanzanian research team, data collection was able to continue at Gombe throughout this time. To raise the funds necessary to continue long-term research, Goodall founded the Jane Goodall Institute in 1977, which continues to fund Gombe research while also expanding into a broader global mission.

In the 1980s, foreign researchers were gradually allowed to return to Gombe for increasing periods. Chris Boehm conducted studies of vocal communication and

behavior (1984–1990) and introduced the use of portable video cameras, which field assistants used to document behavior during B-record observations (Boehm 1989). Anthony Collins, who had studied baboons at Gombe in 1972–1975, returned in 1987 to oversee the baboon project, and since then has also been closely involved in management of the chimpanzee study.

By the 1980s, data accumulating from other sites made comparisons with Gombe possible. The first comparisons were between Gombe and Mahale and focused on diet (Nishida et al. 1983), habitat (Collins and McGrew 1988), and positional behavior (Hunt 1992). In 1990 and 1992, Christophe Boesch visited Gombe to compare hunting behavior at Gombe and Taï Forest, Côte d'Ivoire (Boesch 1994).

Foreign researchers returned to Gombe in greater numbers in the 1990s, including graduate students (e.g., Charlotte Uhlenbroek) and postdoctoral researchers (e.g., Craig Stanford). Several students started as volunteers habituating the Mitumba community, including Bill Wallauer, who subsequently began a 14-year-long video project to document chimpanzee behavior at Kasekela (Nishida and Wallauer 2003; Wilson et al. 2004; Pusey et al. 2008a). By the 2000s, Gombe once again hosted a regular contingent of graduate students from several universities. Many came from Anne Pusey's laboratory at the University of Minnesota and did work combining analysis of long-term data with new data collection. The 1990s and 2000s saw increased training of Tanzanian scientists, starting with Shadrack Kamenya, who studied red colobus monkeys (Kamenya 1997). In the 2000s, Tanzanian students conducted research for master's (Bakuza 2006; Ndimuligo 2007) and doctoral (Mjungu 2010) degrees.

While behavioral data collection continued using the same methods developed in the early 1970s, new technologies have greatly broadened and deepened our understanding of chimpanzees and their habitat. Advances in molecular technology permitted genetic analyses, including determination of kinship from noninvasively collected samples of hair (Morin et al. 1994) and feces (Constable et al. 2001; Wroblewski et al. 2009). Fecal samples also provided information for hormonal analyses (Emery Thompson et al. 2008), parasites (Gillespie et al. 2010), and virology (Keele et al. 2009). Hand-held video cameras have made possible more detailed analyses of behavior, including termite fishing (Lonsdorf et al. 2004) and meat sharing (Gilby 2006). Laser imaging technology has allowed creation of 3D models for analyzing skeletal materials (Kirchhoff 2010). The entry of demographic, ranging, feeding, and other behavioral data into a relational database has made decades worth of data available for analysis (e.g., Williams et al. 2002, 2004; Gilby et al. 2006; Murray et al. 2007; Wroblewski et al. 2009; Mjungu 2010). On a landscape scale, remote sensing images, from aerial photographs to satellite images, combined with Geographical Information Systems (GIS) software, have enabled the study of changes in habitat and land use in and around Gombe (Pintea et al. 2010). The phenology of key chimpanzee foods is regularly monitored in all three communities, and vegetation plots have been established and sampled throughout the park (Murray et al. 2006; Rudicell et al. 2010). Comparative studies using data from multiple field sites have been conducted on topics including

demography (Hill et al. 2001; Emery Thompson et al. 2007), reproductive ecology (Emery Thompson 2005), and culture (Whiten et al. 1999; Nakamura et al. 2000; Nishida and Wallauer 2003; Schöning et al. 2008).

16.1.4 Infrastructure

Initially, Gombe research infrastructure consisted of a few simple tents, followed by prefabricated metal huts with thatched roofs. In 1971, George Dove helped upgrade the research infrastructure substantially, building breezeblock houses and offices along the lakeshore. The central office block still provides office and laboratory space, and an array of solar panels has provided electricity for lighting, computers, and other purposes, including a freezer for storing laboratory samples, since 2005. A small storage building has been converted into a necropsy laboratory. A herbarium cabinet stores plant samples for identification, and is now located in the JGI office in Kigoma for better protection from humidity. Breezeblock houses provide living quarters for research staff in Kasekela. Simple metal huts house research staff in Mitumba and in the Bwavi station in the Kalande community's range. To reduce risks of disease transmission, garbage pits and latrines are covered, and the entries to staff houses have been enclosed with wire mesh to provide "baboon-proof" outdoor living areas. Because of the rugged terrain, no roads reach the park, and Gombe is thus accessible only by foot or boat. The research center relies on wooden boats, with small ones stationed at Mitumba and Bwavi and larger ones at Kasekela.

16.1.5 Standardization and Management of Long-Term Data

The long-term study has produced many hundreds of thousands of pages of data. Analyzing these by hand is difficult and time consuming, and not really feasible for datasets that span many years, or for complicated analyses. Since 1990, Anne Pusey has worked with Goodall to develop an archive for housing all these datasheets, from which data are extracted and entered into a computer database. The Jane Goodall Institute's Center for Primate Studies operated at the University of Minnesota (1995–2009) and the archive has now moved to Duke University. Pusey has worked with computer scientists, including John Carlis, Shashi Shekhar, and their students, to develop a relational database, which keeps track of demographic data as well as behavioral data from the focal follows, including party composition, map location, and feeding, aggression, mating, and grooming. Data on ranging, party composition, and feeding are entered into the database from the maps and travel and group charts.

Extracting data from the B-record notes takes several steps, because the data are recorded in Swahili and written in a narrative instead of recorded on check-sheets.

(Several attempts have been made to design check-sheets to replace the narrative notes, but given the complexity of the data currently being collected, and the flexibility of the current system for recording both systematic data and descriptions of unusual events, designing check-sheets that are both sufficiently comprehensive and still practical to use in the field has been difficult.) The narrative notes are translated into English, and then entered into a database. Specific datasets such as mating, grooming, and aggression are extracted from the translated narrative notes and entered into tables, which are uploaded into an Access database; this allows efficient analysis of datasets that span many years (e.g., Williams et al. 2004; Gilby et al. 2006; Murray et al. 2006, 2007; Wroblewski et al. 2009; Rudicell et al. 2010). Work in progress includes the development of a searchable video database and computerizing of mother–infant data.

In the 1990s, the field maps used for recording the location of focal chimpanzees were redrawn from aerial photos rectified with the help of Global Positioning System (GPS) measurements. However, GPS signals are often difficult to obtain under heavy tree cover and in steep valley bottoms, so hand-drawn maps are still the main source of information on ranging. Comparison with GPS locations found that hand-drawn maps had a mean error of 133 m (Gilby et al. 2006). To document habitat change in and around the park, Pusey and Pintea have acquired remote sensing datasets, including aerial photographs and a series of satellite images of Gombe and the surrounding area, and have developed a digital elevation model for the park (Pintea et al. 2010).

16.2 Life Histories and Demography

16.2.1 Life Histories

Because chimpanzees can live nearly as long as humans, it has taken many years of study at Gombe and other sites (e.g., Mahale: Nishida et al. 2003; Bossou: Sugiyama 2004) to gain a clear picture of their life histories. During 50 years at Gombe, many individuals have been followed from birth to death. For example, researchers followed Goblin's life, from infancy (Goodall 1971, 1986, 1990), weaning (Pusey 1983), and adolescence (Pusey 1990) through his maturation into a politically savvy alpha male (Goodall 1986; Boehm 1992), followed by his fall from power in a brutal gang attack (Goodall 1992), his coalitionary behavior as a post-prime male (Gilby et al. 2009), and eventual old age and death (Williams et al. 2008; Terio et al. in press). Necropsy revealed that Goblin had suffered from a multinodule infection of the nematode *Oesophagostomum* (Williams et al. 2008; Terio et al. in review). Analysis of Goblin's skeleton found dental problems, including severely worn teeth and abscess drainage points (Kirchhoff 2010), which likely made it difficult for him to feed during the severe dry season of 2004, when he weakened and died.

Chimpanzees mature more rapidly and grow larger in captivity than in the wild, probably due to the abundance of food and protection from immunological and other stressors. Field data are thus necessary to obtain accurate measures of the timing of life history events in the context of the ecological constraints under which chimpanzee life history evolved. Moreover, life histories vary among sites; the following focuses on what has been learned from Gombe, especially from studies explicitly focused on development (e.g., Pusey 1983, 1990; Plooij 1984; Goodall 1986).

In the wild, chimpanzees grow slowly, being weaned at 50–86 months (Pusey 1983) and not reaching reproductive maturity until around 14–15 years for females and 15–16 years for males (Goodall 1986). At most chimpanzee study sites, the great majority of females transfer into new communities once they reach sexual maturity, whereas males universally stay in their natal communities (Pusey 1979; Stumpf et al. 2009; Nakamura and Nishida 2012). Females presumably disperse from their natal communities to avoid mating with close kin (Pusey 1979). About half of all females born into the Kaselela community, however, have stayed in their natal community (Pusey et al. 1997), perhaps due to limited dispersal opportunities. The proximate factors affecting dispersal and settlement decisions remain unclear, largely because data from neighboring habituated communities are limited. However, at least one Kasakela female that attempted to immigrate into Mitumba was repelled by aggressive attacks by resident females (Pusey et al. 2008a), suggesting that Mitumba is currently crowded, as far as female chimpanzees are concerned.

Once chimpanzees reach reproductive maturity, they focus their efforts on activities associated with reproductive success. Males and females both spend most of their time searching for and eating food, but important sex differences exist in reproductive strategies. Females must establish themselves in suitable areas, often in new communities, that have sufficient food to raise their young, are relatively safe from intercommunity aggression, and have suitable mates (mature, unrelated males). Once established, females spend most of their time gestating, lactating, and otherwise caring for their offspring. For males, the main jobs in life are trying to attain high dominance rank, mating with estrous females, and joining with other males to defend and possibly expand the group territory.

By adulthood, male and female chimpanzees thus lead very different social lives. In general, males are more gregarious, often foraging in large parties, competing for dominance rank, grooming with allies, displaying at opponents, and mating with estrous females (Mitani 2009). Females are generally less gregarious than males (Pepper et al. 1999), perhaps because carrying infants makes mothers more sensitive to the costs of scramble competition associated with larger foraging parties (Wrangham 2000). Wrangham and Smuts (1980) found that Gombe mothers spent more than half of their time alone or with just their families. Females at some other sites, such as Taï and Ngogo, are more gregarious than Gombe females, likely due to greater abundance of food, but are still less gregarious than males (Lehmann and Boesch 2008; Wakefield 2008). When females have fully tumescent sexual swellings, they become more social, traveling with large parties of males or going off on consort with individual males (Goodall 1986).

Besides differing in overall gregariousness, the sexes differ in foraging patterns and range use. Females spend more time foraging for insects such as termites (Pandolfi et al. 2003), whereas males spend more time hunting and eating mammalian prey such as red colobus monkeys (Stanford et al. 1994). Males generally use the community's entire range, patrolling the borders and sometimes making deep incursions into neighboring ranges, whereas females generally use a smaller proportion of the community's total range (Williams et al. 2002). At Gombe, females spend much of their time in smaller "core areas" (Wrangham 1979; Wrangham and Smuts 1980). The extent to which males and females differ in their ranging patterns varies among sites (e.g., Lehmann and Boesch 2008), but evaluating these differences is complicated by the use of different definitions and methods of analysis across sites. At Gombe, female home ranges have been analyzed based on points from all-day follows in which females were "alone" (that is, unaccompanied by adults other than their female relatives) (Williams et al. 2002; Murray et al. 2006), a method not used at other sites. However, analysis of all ranging points indicates that Kanyawara females use different "neighborhoods" within the total range (Wilson 2001; Emery Thompson et al. 2007).

Early observations of these sex differences in space use suggested that the sexes might differ in community membership as well. Wrangham (1979) described three alternative models of chimpanzee social structure, in which females (1) ranged equally over the entire community with males, (2) ranged in smaller core areas but associated only with males of a particular community, or (3) ranged in smaller core areas distributed across the landscape independently of male ranging behavior. Studies at Gombe support the second model (Goodall 1983; Williams et al. 2002), while studies at Taï support the first model (Lehmann and Boesch 2008). In general, though, it appears that each female belongs to a specific community and that community memberships are stable. Exceptions to this rule occur when the number of males in a community declines precipitously, and parous females begin visiting or even transferring to neighboring communities (Nishida et al. 1985; Rudicell et al. 2010).

Both male and female chimpanzees compete for access to key resources. Early studies suggested that chimpanzees had completely egalitarian social relations (e.g., Reynolds and Reynolds 1965). Studies of habituated chimpanzees soon revealed that males compete vigorously for status (Bygott 1979). For females, though, decided agonistic interactions are infrequent and often subtle, leading to early speculations that dominance is not an important aspect of their social relationships (de Waal 1984; Wrangham 1980). Moreover, variation exists among sites; for example, Wakefield (2008) found no evidence for linear female dominance hierarchies at Ngogo. At Gombe, however, both males and females can be assigned dominance ranks based on the outcome of dyadic contests (Murray et al. 2006). At Gombe, higher dominance rank is associated with greater reproductive success for both males and females (Pusey et al. 1997; Constable et al. 2001; Wroblewski et al. 2009; Jones et al. 2010).

Rank appears to affect female reproductive success largely through access to better feeding areas, which in turn allows females to shorten their inter-birth

intervals. In general, female chimpanzees reproduce slowly (Emery Thompson et al. 2007). Kasekela females had a median inter-birth interval of 4.9 years, including intervals where the previous infant died (Jones et al. 2010). High-ranking females at Gombe produce surviving infants at higher rates than low-ranking females and have daughters that mature at younger ages (Pusey et al. 1997). Vegetation plots conducted throughout the Kasekela community's range revealed that high-ranking females had smaller core areas with higher densities of preferred food trees (Murray et al. 2006). Fertility also varies with age (Emery Thompson et al. 2007; Jones et al. 2010), but considerable variation cannot be explained by either rank or age, suggesting that phenotypic quality is an important component of fertility (Jones et al. 2010). Phenotypic quality likely encompasses a broad range of traits, including maternal and other social skills plus immune system function.

Determining male reproductive success is challenging in chimpanzees, because females generally mate with multiple males. Goodall initially characterized the chimpanzee mating system as promiscuous (Goodall 1965). While it eventually became clear that high-ranking males tended to monopolize mating with available females, especially during the peri-ovulatory period (or "POP"; Tutin 1979), only with the advent of noninvasive genetic sampling did patterns of paternity become clear (Constable et al. 2001; Wroblewski et al. 2009). As it turned out, high-ranking males do have more offspring at Gombe (Constable et al. 2001; Wroblewski et al. 2009) and elsewhere (e.g., Taï: Boesch et al. 2006; Budongo: Newton-Fisher et al. 2010). However, by competing for access to peri-ovulatory females and by using alternative mating tactics (e.g., consortship) as well as mating with younger, less preferred females, lower-ranking males can achieve higher reproductive success than predicted by the priority-of-access model (Wroblewski et al. 2009).

Like other primates (Charnov and Berrigan 1993), chimpanzees live long lives compared to other mammals their size. Nonetheless, chimpanzees have higher age-specific mortality than human foragers, and appear to senesce more rapidly (Hill et al. 2001). A study compiling data from Gombe and several other sites found that mean life expectancy at birth was below 15 years for both males and females (Hill et al. 2001). The main causes of death were disease and conspecific aggression (Williams et al. 2008). Predation by leopards (Boesch 1991; Furuichi 2000) and lions (Inagaki and Tsukahara 1993) can be important sources of mortality at other sites, and probably were in the past at Gombe, before lions were extirpated and leopards reduced in numbers (Pierce 2009). Chimpanzees are considered "old" by their mid-30s (Goodall 1986), and by their late 30s, they often suffer from ailments of old age such as worn teeth and degenerative joint disease (Morbeck et al. 2002; Kirchhoff 2010). However, because exceptional individuals can live well beyond 50 years, even the 50-year-long Gombe study has not lasted long enough to document the longest chimpanzee lives fully. The oldest chimpanzee in Kasekela, Flo, was initially thought to be 41 ± 5 years old when she died (Goodall 1983). Flo's estimated age was later revised upward to 53 years, based on comparison with other chimpanzees (Williams et al. 2008). The oldest individual currently alive at Gombe, Sparrow, is approximately 52 years, and, with her full coat of hair and generally robust appearance, looks younger than Flo did at the end of her life.

Because Flo was already old in 1960 when the study started, and because Sparrow immigrated into the study community as an adolescent, neither individual's age is known precisely. Despite the longevity of these exceptional individuals, very few chimpanzees at Gombe have lived past 40 years. Among the individuals followed since infancy, the oldest female, Fifi, lived to be 46 years and appeared to be in good health when last seen. The oldest female followed since birth, Gremlin, is now 40 years. Several males are estimated to have lived to 40 years old or just beyond: Evered, Huxley, and McGregor. The oldest male followed since birth, Goblin, died 13 days before he would have turned 40 years.

Like most other mammals, but in contrast to humans, reproductive senescence in chimpanzee follows approximately the same schedule as somatic aging. The interval between births increases with age (Jones et al. 2010), and eventually some very old females may stop cycling altogether (Nishida et al. 2003; Nakamura and Nishida 2012), but females do not typically experience a post-reproductive life phase, or menopause (Emery Thompson et al. 2007).

16.2.2 Population Size

While Gombe is a small park, the park's total chimpanzee population remains uncertain. Estimates of the total population prior to about 2000 rely largely on guesswork. Goodall's estimate for the 1960s was 100–150 chimpanzees (van Lawick-Goodall 1968). Estimates made by extrapolating back from the known and estimated sizes of the Mitumba and Kalande communities yielded a similar range of 120–150 chimpanzees in the 1960s (Pusey et al. 2008b). Estimates of the population since about 2000 are more precise, thanks to the genotyping of fecal samples from the unhabituated Kalande community (Rudicell et al. 2010). Based on detailed demographic data for Mitumba and Kasekela and estimates for Kalande, the minimum population estimate ranged from 91 to 101 chimpanzees (median = 95) from 2000 to 2010, and the maximum estimate ranged from 100 to 109 chimpanzees (median = 103), with no clear upward or downward trend over time.
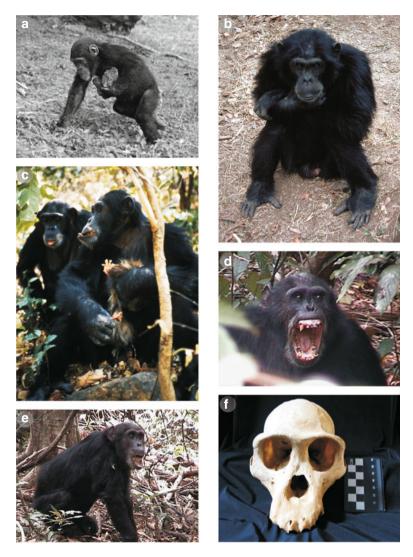
Despite the recent stability of the total population, the sizes of the individual communities have varied considerably. Although research on the Kasekela community began in 1960, it was not until 1966 that all individuals were known, at which time 60 individuals lived in Kasekela. By 1973, Kasekela had divided into two communities: Kasekela, with 40 chimpanzees, and Kahama, with at least 14 (and probably more, given the likelihood that Kahama also included unidentified, unhabituated females). Males from Kasekela killed at least five individuals from Kahama (Goodall 1986). By the end of 1977, the Kahama community no longer existed, as all the males had been killed or disappeared and the surviving females and offspring had rejoined Kasekela or dispersed elsewhere (Goodall 1986). Following a respiratory epidemic in 1987 that killed nine individuals, Kasekela reached its smallest recorded population size, 38, in 1989. Kasekela's

population gradually recovered in the 1990s, and, thanks to immigration, grew rapidly in the 2000s, numbering 61 chimpanzees by the start of 2010.

The size of the Mitumba community has been documented only since 1985. Goodall (1986) estimated that Mitumba contained 50 individuals in the 1970s and early 1980s. During this time, the Mitumba successfully defended its boundaries against the Kasekela community, and even expanded its range at the expense of Kasekela in the early 1980s, suggesting that it was similar in size to Kasekela (which contained 51–58 individuals in 1978–1983). However, records from the first years of direct observation indicate that probably at least 20 individuals, but no more than 31, were alive in 1985 (Mjungu 2010). We do not know whether Mitumba's population declined in the early 1980s, whether some individuals were not recorded at that time, or if the pre-habituation estimates of the community's size were too high. However, by the mid-1990s, the chimpanzees were sufficiently well habituated, and observations sufficiently frequent, that all individuals were likely identified. A respiratory epidemic in 1996 caused Mitumba's population to drop from 25 to 20 (Mjungu 2010). The community's population declined to a minimum of 19 at the start of 1999, followed by a gradual recovery to 25 individuals at the start of 2010 (Mjungu 2010; Rudicell et al. 2010). Despite the overall increase, the number of adult males decreased from five in 1994 to only two from 2005 on (Mjungu 2010). The number of adult males in Mitumba may yet recover, though. The community has six males aged 8–13 years, suggesting that the Mitumba males might yet again pose a significant challenge to the Kasekela males in adulthood.

In 1969, Gale identified more than 20 individuals in the Kalande community and estimated that it totaled at least 40 (Rudicell et al. 2010) and might have been substantially larger. By the late 1990s, though, Kalande chimpanzees rarely met Kasekela chimpanzees, suggesting that Kalande had declined substantially. Estimates based on sightings, molecular genetics, and likely migration patterns indicate that Kalande contained 19–43 individuals in 1998, but declined to only 15–19 by the start of 2010, with a particularly severe loss in 2002 (Rudicell et al. 2010). During this time, Kalande had an unusually high prevalence of the virus SIVcpz, which is known to increase mortality in chimpanzees (Keele et al. 2009), suggesting that at least some of the decline resulted from the impact of SIVcpz infection (Rudicell et al. 2010).

As recently as the 1970s, forest and woodland habitat outside the park likely connected Gombe to other chimpanzee populations (Pintea et al. 2010). Intergroup encounters observed in 1975 to the extreme east of Kasekela's range suggest that an "Eastern" or "Rift" community might have persisted to the east of the park (Goodall et al. 1979), though those encounters might have simply involved individuals from Kalande moving north along the eastern margin of their rivals' range (Goodall 1986). By the late 1990s, however, rapid deforestation had turned Gombe into a largely isolated island of chimpanzee habitat (Pintea et al. 2010). Nonetheless, an unknown number of chimpanzees survive in forest fragments outside the park, including a small population (perhaps 15 weaned individuals) in Kwitanga Forest

Fig. 16.3 Goblin through the ages (**a**) juvenile in ~1969, (**b**) as a young adolescent in ~1972, (**c**) as alpha male in 1985, presiding over a red colobus carcass, (**d**) as an old male with severely worn teeth in 2003, (**e**) shortly before his death in August 2004, and (**f**) his skull in the Gombe skeleton collection. Photos ©David Bygott (**a**, **b**), ©Chris Boehm (**c**), ©Michael Wilson (**d**, **e**), and ©Claire Kirchhoff (**f**)

(Ndimuligo 2007), which may be close enough for chimpanzees to travel between there and Gombe. Chimpanzee nests have also been found near Zashe village, in the hills along the rift escarpment to the north of Gombe, near the border with Burundi (Fig. 16.3).

16.3   Research Highlights

16.3.1   Intergroup Dynamics

One topic for which Gombe is especially well known and that is relevant to many aspects of the long-term study is intercommunity dynamics. Only long-term data provide information needed to understand the consequences of interactions between communities. As Goodall noted (1986:3), "Had my colleagues and I stopped after a mere 10 years, we should have had a very different picture of the Gombe chimpanzees than we do today. We would have observed many similarities in their behavior and ours, but we would have been left with the impression that chimpanzees were far more peaceable than humans".

Because chimpanzees live in fission–fusion societies, many years were required just to determine the boundaries of social groups at Gombe. Goodall initially supposed that the entire chimpanzee population interacted freely and peacefully (Goodall 1965). Reynolds formed a similar impression of "loose unstable groupings and apparent lack of group social organization" at Budongo (Reynolds and Reynolds 1965:422). In contrast, Itani and Suzuki (1967) inferred that chimpanzees lived in stable "large-sized groups." In 1965, Nishida began research in the Mahale Mountains, 150 km south of Gombe, with the specific goal of understanding the social organization of wild chimpanzees (Nishida 1979; Nakamura and Nishida 2012). By 1968, Nishida had inferred that chimpanzees lived in socially bounded fission–fusion societies. Observations at Gombe, and eventually other sites, confirmed that chimpanzees indeed live in socially bounded, mutually hostile groups called "communities" (Goodall et al. 1979).

Once observers began to follow Kasekela chimpanzees away from the feeding station in the late 1960s, they witnessed encounters with neighboring communities (Goodall et al. 1979). Around the same time, the Kasekela community began to fission. By 1970, two subgroups could be discerned. Six adult males, an adolescent male, and three adult females began avoiding the northern part of the range and spending more time in the south, while 8 adult males and 11 adult females occupied the north and avoided the south. The chimpanzees that ranged to the south were called the Kahama community, while those that stayed in the north retained the name Kasekela. Besides the three habituated females that became part of the Kahama community, an unknown number of unhabituated females also probably associated with the Kahama males (Goodall 1983). By 1973, the two communities were clearly distinct, and threatened each other when they met – with only occasional friendly contacts among some of the older males giving any hint that the two communities had once been one (Goodall 1983, 1986).

The first observed intercommunity violence involved the killing of the infant of an unfamiliar female in 1971 (Bygott 1972). In 1973, observers following three males from the Kahama community found a freshly dead adult female, possibly a Kalande female killed by Kahama males (Wrangham 1975). Observers then witnessed a series of attacks from 1974 to 1977, during which Kasekela males

fatally wounded four adult males and an adult female from Kahama; the freshly killed body of a fifth male was also found (Goodall 1986). By the end of 1977, all of Kahama's males had died or disappeared, and the remaining females either returned to Kasekela or joined other communities. Intercommunity infanticides continued, with two in 1975 and one in 1979 (Goodall 1986). These attacks took place to the south of Kasekela's range, indicating that the infants' mothers were either unhabituated members of the Kahama community, or members of the Kalande community.

Goodall describes the extermination of the Kahama community as "The Four Year War" (Goodall and Berman 1999). While the rate of killings appears to have been particularly high during the 1970s, it also seems that chimpanzee communities are never fully at peace. In the late 1970s, having vanquished the Kahama community, the Kasekela chimpanzees experienced hostile encounters with their powerful neighbors to the north and south. By 1983, outside males were making deep incursions into the heart of Kasekela's range (Goodall 1986). Several otherwise healthy adult males disappeared, suggesting they might have been killed (*ibid.*), but no intergroup killings were directly observed in the 1980s. This may be at least partly due to the reduced number of observation hours per year compared to that in the preceding and following decades, resulting in fewer follows to border areas where intercommunity interactions are most likely. The intercommunity encounters that were observed were hostile, and severe attacks on females from neighboring communities were seen (Williams et al. 2004).

By the early 1990s, the Kasekela community had begun recovering in population size and range size. In March 1993, the Kasekela chimpanzees killed Rejea, an infant from the Mitumba community (Wilson et al. 2004). By the late 1990s, the expansion of the Kasekela range accelerated, largely at the expense of the Kalande community, which apparently started a steep population decline (Rudicell et al. 2010). On deep incursions into Kalande's range in 1998, Kasekela males attacked two infants, killing one, and severely attacked and likely killed an adolescent male (Wilson et al. 2004). During the 2000s, the Kasekela community maintained a large range, and intercommunity violence continued intermittently. Kasekela males likely killed a Mitumba male, Rusambo, in 2002 (Wilson et al. 2004), and killed a Mitumba infant, Andromeda, in 2005 (Wrangham et al. 2006). In turn, Mitumba males killed Patti, an adult female from Kasekela (Wrangham et al. 2006; Williams et al. 2008).

Intergroup aggression has been a major source of mortality at Gombe (Williams et al. 2008). Intergroup killings have also been reported for all of the other long-term study sites, including Mahale, Kanyawara, Ngogo, and Budongo (summarized in Wrangham et al. 2006; Mitani et al. 2010), and Taï (Boesch et al. 2008). Killings have also occurred at some sites where studies have less time depth, such as Kalinzu (Hashimoto and Furuichi 2005) and Petit Loango (Boesch et al. 2007). Overall, the evidence strongly suggests that intercommunity killing is a species-typical behavior.

16.3.1.1   Causes of Intergroup Aggression

Studies at Gombe and elsewhere have helped to clarify the causes of intercommu-
nity aggression. Males apparently benefit from defending and expanding territories
by excluding rival males; by increasing the amount of food available for self, mates,
and offspring; and by making territories more attractive to potential immigrants
(Wilson and Wrangham 2003; Mitani et al. 2010). Females benefit from male
territorial defense and expansion due to improved safety and improved food
resources (Williams et al. 2004).

Male chimpanzees are hostile to foreign males, and genetic evidence supports
the view that males are generally successful at preventing outside males from
mating with their females. At Gombe, all infants tested in the Kasekela community
had fathers from within their own community (Constable et al. 2001; Wroblewski
et al. 2009). Paternity tests of Mitumba chimpanzees have likewise found no
evidence of extra-community paternity (Wroblewski unpublished data). One
female from the Kalande community apparently has an infant fathered by a
Kasekela male (Rudicell et al. 2010). This conception might have occurred during
a prolonged visit by that female to the Kasekela community (*ibid*.). No extra-group
paternities have been reported for Budongo (Reynolds 2005), though extra-group
paternity accounted for 7–11% of offspring born into communities at Taï (Vigilant
et al. 2001; Boesch et al. 2006).

Several lines of evidence support the view that chimpanzees benefit by increas-
ing the size of their territories. Analysis of 33 years of body mass data found that
individuals in Kasekela were heavier when territory size was larger and population
density was lower (Pusey et al. 2005). Analysis of 18 years of data for Kasekela
found that females reproduced more quickly, individuals traveled in larger parties,
and males encountered receptive females more often when the territory size was
larger (Williams et al. 2004). Females dispersing from the declining Kalande
community settled more often in the larger Kasekela territory than in the smaller
Mitumba territory (Rudicell et al. 2010).

The quality of a territory may depend on other factors besides size, including food
abundance and the density of competitors. When the number of adult males in
Kalande was reduced to one, parous females began to visit the Kasekela community,
and at least one emigrated permanently (Rudicell et al. 2010). This resembles the
mass transfer of mothers from Mahale's K-group following the reduction of the
community to a single adult male (Nishida et al. 1985) and suggests that females
base their residence decisions on having enough males in the community to provide
some or all of the following benefits: defense of food resources, protection from
intercommunity aggression, and providing sufficient mating partners. Investigations
are currently under way to determine how food abundance and distribution affect the
timing and location of intergroup encounters (Wilson et al. 2010).

Overall, the causes of intergroup aggression in chimpanzees are similar to those
of many other group territorial species (Crofoot and Wrangham 2010). In most such
species, though, intergroup conflict is rarely fatal. In contrast, among chimpanzees,

humans, some social carnivores, and several social insects, intergroup conflict can account for a substantial portion of adult mortality. Manson and Wrangham (1991; cf. Wrangham 1999) argued that among mammals, fatal fighting is most likely in species with fission–fusion social systems, coalitionary bonds, and inter-group hostility, which together create opportunities for killing rivals at relatively low cost to the attackers (Manson and Wrangham 1991). Killing rivals, rather than merely chasing them off, benefits the killers by reducing the coalitionary strength of their opponents (Wrangham 1999). This "imbalance of power hypothesis," based on observations at Gombe, where the attackers generally greatly outnumbered the victims (Goodall 1986), has been supported by evidence from other sites, including the Kanyawara and Ngogo communities in Kibale National Park (Watts 2012). Playback experiments found that Kanyawara males were more likely to approach a simulated intruder the greater their numerical superiority (Wilson et al. 2001). Kanyawara males visited borders more often when in parties with more males (Wilson et al. 2007), and Ngogo males conducted boundary patrols more often when with many males (Mitani and Watts 2005).

16.3.2   Disease Ecology

Disease is the major cause of death for chimpanzees at Gombe (Williams et al. 2008), as at other sites (e.g., Mahale: Nishida et al. 2003 and Taï: Boesch and Boesch-Achermann 2000). Many deaths have occurred during epidemics, which included suspected polio, respiratory infections, and mange (Goodall 1986; Lonsdorf et al. 2006; Williams et al. 2008). Because chimpanzees and humans are so closely related, they share many of the same diseases. Molecular evidence indicates that at least some of the infections suffered by chimpanzees at research and tourism sites originate from humans (Köndgen et al. 2008). Humans may also contract diseases originating in chimpanzees (Wolfe et al. 1998). Understanding disease ecology is thus important for several reasons, such as guiding conservation management decisions, ensuring the health of people visiting and working in primate conservation areas, and understanding the origins and natural history of diseases that affect humans.

Various health data have been collected over the course of the study (Lonsdorf et al. 2006). Since March 2004, Lonsdorf and colleagues have been collecting systematic health data on the Kasekela and Mitumba chimpanzees (Lonsdorf et al. 2006; Travis et al. 2008). For each regular B-record follow, observers visually assess the health of the focal subject and collect a fecal sample for parasitological analysis. Gillespie and colleagues (2010) found that parasite prevalence was higher at Mitumba than Kasekela, perhaps due to the proximity of the Mitumba chimpanzees to the densely populated village of Mwamgongo. The health monitoring project has also provided tools and training to improve the recovery of samples and information during necropsies, which has proven invaluable in investigating the impact of another infection at Gombe: SIVcpz.

Current evidence indicates that HIV-1, the cause of the global AIDS pandemic, originated in the transmission of SIVcpz from chimpanzees to humans (Hahn et al. 2000). The strains of SIVcpz most closely related to HIV-1 occur in west-central Africa (Keele et al. 2006). Related strains of SIVcpz occur in the eastern Congo basin, but the virus is distributed unevenly and has not been detected in Uganda or Mahale (ibid.). Gombe is thus the only site with habituated chimpanzees at which some of the chimpanzees are naturally infected with SIVcpz (Santiago et al. 2002; Keele et al. 2006). SIVcpz infection was initially thought to be harmless (Silvestri 2008). However, detailed demographic data have revealed that it increases the mortality risk of infected chimpanzees by 10–16 times, and analysis of tissues collected from necropsies revealed that infected chimpanzees suffered AIDS-like damage to immune system tissues (Keele et al. 2009). Implications of this discovery for the future of Gombe's chimpanzees are sobering. The Kalande community, which has a much higher prevalence of the virus than Mitumba or Kasekela, has suffered a dramatic decline that may at be due at least partly to SIVcpz infection (Rudicell et al. 2010). Population models indicate that infected populations are likely to decline. Nonetheless, in small populations like Gombe, the virus may go extinct before the host population does. Moreover, factors such as immigration may help prevent population decline.

16.4   Discussion and Conclusions

In five decades of long-term research at Gombe, researchers have learned a great deal about the behavior and life histories of wild chimpanzees. While some striking behaviors such as tool use and hunting were observed early, only in the second decade of study did the outlines of chimpanzee social structure began to emerge, including group territorial defense, lethal aggression, and female transfer. The importance of female dominance rank was not clear until the study's fourth decade. Direct measures of male reproductive success were not obtained until the study's fifth decade, and we are still learning how female settlement patterns and ecology affect reproductive success. While many complete life histories have now been documented, the study has still not exceeded the lifespan of the longest lived chimpanzees. Gombe is small, but we are only now getting accurate estimates of the total chimpanzee population, and only two of the park's three communities are fully habituated. A wealth of data has been accumulated on intercommunity dynamics, yet we are just starting to understand what influences frequencies of intercommunity conflict. An integrated, multidisciplinary effort has begun to address disease, the major source of mortality, yet much work is needed to reduce the risk of disease transfer from humans to chimpanzees. Moreover, Gombe has unexpectedly emerged as a key site in the study of a virus that was unknown in 1960, but which has since claimed the lives of millions of people around the world. The presence of SIVcpz in Gombe presents both a fascinating opportunity for research and a challenging threat to the population.

Meanwhile, other field studies across Africa have broadened our understanding of chimpanzees and have confirmed that many patterns of behavior observed at Gombe are species typical. These studies have also found important differences among chimpanzee societies, revealing a diversity of social customs and raising questions about the extent to which behavioral differences depend on genetic differences, ecology, or social learning.

Many questions remain, even within a specific topic, such as aggression. For example: Will the Kasekela males kill the remaining Mitumba and Kalande males? If they eliminate their rivals, will they control a single super community, or will the community fission? Instead, if the adolescent males of Mitumba survive into adulthood, will they take back territory from Kasekela?

In the coming decades, molecular analyses of noninvasively collected samples will no doubt continue to yield new ways of detecting and analyzing viruses, parasites, genes, hormones, and more. The analysis of entire genomes will become practical. Molecular studies will continue to complement behavioral work in important ways, helping to confirm the identities of individuals as they move among communities and identifying likely maternal and paternal relationships, even among unhabituated chimpanzees (Rudicell et al. 2010). Yet however much technology advances, the core of the research must remain the individual chimpanzees, with their distinctive personalities and sometimes unexpected behavior. The more we learn about these individuals and their relationships, the more potential there is to ask interesting questions, including many that we have not yet thought of.

One of the most pressing questions is whether chimpanzees will survive in the wild. As human populations grow and forests become fragmented by logging and conversion to agriculture, many chimpanzee populations face a future similar to Gombe: living in ecological islands, surrounded by people, and heavily impacted by human activities and climate change (see also Jolly 2012). Gombe provides a field laboratory for promoting the survival of chimpanzees across Africa. Current efforts seek to address two major threats: disease risk, and habitat loss and subsequent population isolation. The health monitoring project is collecting baseline data essential for assessing chimpanzee health. Efforts have been made to improve sanitation around human settlements and minimize contact between chimpanzees and humans, including researchers, park staff, and tourists. Improvements in sanitation and enforcement of existing rules are still needed. The Jane Goodall Institute has been working with local villages to establish an interconnected network of village forest reserves around Gombe (Fig. 16.2). These could provide benefits both to villagers, in terms of protected watersheds, reduced erosion, and better conservation of forest products, and to chimpanzees, by providing a buffer and by enabling them to move more easily between Gombe and other remnant populations in the area (Pintea et al. 2010). If chimpanzees begin moving through these forest reserves, efforts will be needed to maintain local good will and prevent poaching.

Despite many threats, the Gombe chimpanzee population has remained stable over the past 10 years, giving some hope that it will survive well into the future.

Moreover, the government of Tanzania continues to demonstrate that it regards Gombe as one of the nation's natural treasures. In 2010, President Kikwete announced that the Tanzanian government would nominate Gombe for consideration as a World Heritage Site. Moreover, plans are underway to extend the park boundaries 1.5 km into the lake to protect freshwater species, resulting in a total park area of over 56 km^2 (Kayanda 2010). Gombe will need continued national and international support to ensure that its chimpanzees continue to survive, and that we will continue to learn from them.

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