1

Introduction

MICHIO NAKAMURA

1.1 The chimpanzee

The chimpanzee or the common chimpanzee (Pan troglodytes Blumenbach 1775, Hominidae) is the closest living species to us, humans (Homo sapiens), together with another species of Pan, the bonobo (P. paniscus). The genome-wide nucleotide divergence between chimpanzees and humans is calculated to be only 1.23% (The Chimpanzee Sequencing and Analysis Consortium, 2005). Two species of Pan are more generally called "great apes" together with gorillas (Gorilla spp.) and orangutans (Pongo spp.). "Great ape," in general terminology, usually excludes humans; however, according to recent taxonomy (Groves, 2001), such a category is no longer applicable. In fact, these apes and humans form the family Hominidae and, more specifically, Homo, Pan, and Gorilla (African linage of Hominidae) form the subfamily Homininae, separated from another subfamily Ponginae (i.e. orangutans; Figure 1.1). There are some arguments that the genus Pan should be categorized under Homo as a subgenus (Goodman et al., 1998).

The chimpanzee is currently divided into four subspecies (see also Chapter 46): the western chimpanzee (*P. t. verus*), the Nigeria–Cameroon chimpanzee (*P. t. ellioti*), the central chimpanzee (*P. t. troglodytes*), and the eastern chimpanzee (*P. t. schweinfurthii*). The last subspecies is the subject of our research at Mahale. Chimpanzees range in African tropical forests around the equator from Senegal in the northwest to Tanzania in the southeast (Caldecott and Miles, 2005). The species, as a whole, is considered endangered (Oates *et al.*, 2008).

1.2 Research history of chimpanzees

When chimpanzees were first encountered by the western academic world in the seventeenth century (Tyson, 1699), many scholars were fascinated by their striking anatomical similarities to our own species. In the first half of the twentieth century, several studies were conducted in captivity (Köhler, 1917; Yerkes, 1943), which revealed high cognitive abilities of chimpanzees. After the 1960s, when chimpanzee research began in the wild (Goodall, 1965; Chapter 3), scientists discovered even more amazing similarities in terms of behavior. Chimpanzees share many behavioral patterns with humans, such as tool use, hunting, food sharing, medicinal use of plants, and infanticide. In addition, various behavioral patterns differ among populations and are socially inherited from generation to generation within a group, which resembles human culture (Whiten et al., 1999; Chapter 38). Such findings are important for elucidating human evolution and reconstructing the behavior of early hominids, and have captured the interest of the general public. However, we still have much to learn about chimpanzees because they mature slowly and have long lifespans. Thus, further continuing and painstaking research efforts are essential.

1.3 Long-term study sites

Apart from Mahale, there have been dozens of chimpanzee study sites in Africa. Among them, I briefly introduce some long-term study sites (Figure 1.2) because their names frequently appear in

Mahale Chimpanzees: 50 Years of Research, ed. M. Nakamura, K. Hosaka, N. Itoh and K. Zamma. Published by Cambridge University Press. © Cambridge University Press 2015.

2

Michio Nakamura

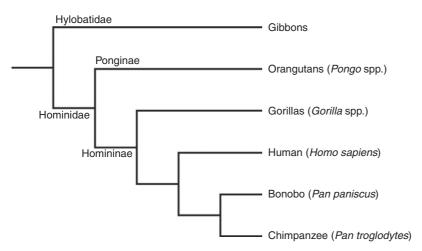


Figure 1.1 Phylogeny of superfamily Hominoidea.

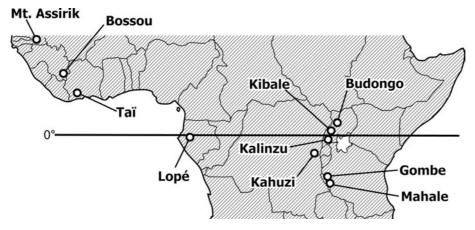


Figure 1.2 Some long-term study sites of chimpanzees.

this volume. Gombe National Park in Tanzania is the oldest and probably most famous chimpanzee research site and is where Jane Goodall started research in 1960 (Wilson, 2012). Several unit-groups have been studied there; among them, the Kasekela group has been the main target of long-term research. Kibale National Park in Uganda is another prominent research site where important findings have emerged (Watts, 2012). There are two study groups at Kibale. One is the Kanyawara group, the studies on which are currently led by Richard Wrangham. Another is the Ngogo group the studies on which are led by David Watts and John

Mitani. The Ngogo group is an extraordinarily large unit-group containing more than 150 chimpanzees. The Budongo Forest in Uganda is also one of the oldest study sites (Reynolds, 2005). The Sonso group has been the main target there, and habituation has improved since the 1990s. Bossou in Guinea is another long-term study site led by Japanese researchers (Matsuzawa *et al.*, 2011). Although the Bossou group is an isolated small group, studies focusing on various types of tool use have yielded important findings. The Taï Forest in Côte d'Ivoire is a study site led by Christophe Boesch (Boesch and Boesch-Achermann, 2000). Three groups

Introduction

3

(North, South, and Central) have been habituated and inter-unit-group comparisons have produced several outstanding outcomes. Eastern chimpanzees are the target subspecies in Gombe, Kibale, and Budongo, whereas western chimpanzees are the targets in Bossou and Taï. Readers should bear in mind that there are various other chimpanzee study sites (Caldecott and Miles, 2005: 57).

1.4 Introduction to this volume

This volume consists of 50 chapters (or topics). Because each chapter is independent and comprehensive in its topic, readers may begin from any chapter. However, the following chapters are divided into 10 parts with broad affinities among topics. Hereafter, I briefly introduce these parts as a guide map to this volume.

Part I is introductory, giving an overview of the Mahale field site, particularly for readers who are not familiar with it. Chapters in this part provide general information on the field site, research history, chimpanzee distribution at Mahale, and several main individual chimpanzee characters from the study group. Chapter 2 summarizes information such as organizations, abbreviations, and names of places that are used in other chapters.

The initial aim of the Mahale research was to elucidate the social organization of chimpanzees, particularly to look for the origin of the human family. Thus Part II particularly deals with the topics of the chimpanzee society, with chapters introducing the social system, demography, home range, fission–fusion grouping, and intergroup relations. An extraordinary event in the research history, the disappearance of the K-group males and the group extinction in the 1980s, is highlighted in a chapter in this part.

Part III deals with the environment such as climate, flora, and fauna that surrounds Mahale chimpanzees. Long-term monitoring is fundamental in this aspect. Readers can see the decadal changes of climatic parameters, such as temperature and precipitation, vegetation, plant phenology, and relative abundance

of large mammals at Mahale. Some rare but interesting observations of chimpanzees encountering other animals, either alive or dead, during the long-term research are also summarized in a chapter.

Part IV basically focuses on what chimpanzees eat. They are mainly ripe-fruit eaters; however, they also eat various parts of plants and meat from mammals, insects, and others. Chapters in this part deal with several aspects such as the diet, the ways chimpanzees eat, and the taste of chimpanzee foods. Many intact seeds are defecated in chimpanzee feces, and a chapter focuses on studies related to such seeds. Unlike many primate species, a chimpanzee frequently shares foods with others, and a chapter in this part discusses this particular topic.

Part V deals with the life history and health of chimpanzees. A general pattern of physical and social development, aging, diseases, and death are included in this part. Because some chimpanzees live long lives, even more than 50 years, many data provided here are the results of painstaking long-term monitoring of the target chimpanzee group. Particular topics of self-medication and conspecific killing, both of which are amazing findings from wild chimpanzee research, are also summarized in this part.

Various social relationships are discussed in Part VI. Male-male relationships are often conspicuous, and various researchers have depicted intriguing details of these relationships. Female-female and male-female relationships, particularly when females are not in estrus, are relatively less well documented. However, improved habituation of female chimpanzees at Mahale enabled us to realize that females are also an important part of chimpanzee society. The topic of orphanhood and allomothering is also included here.

Particular types of social behaviors are the focus of Part VII. As highly social animals, chimpanzees daily direct various behaviors to group mates, such as intimidation displays, aggression and reconciliation, greeting, grooming, sexual behaviors, courtship displays, and social play. Detailed patterns, frequencies, directions, and other observations of such social behaviors are described in each chapter.

1

Michio Nakamura

Behavioral diversity is another important topic in chimpanzee studies that has attained interest relatively recently, and it is specifically introduced in Part VIII. Several subtle but strange behavioral patterns, repertoire of vocal communication, diversity of play, tool and object use, bed making, nocturnal behaviors, and laterality of hand function are introduced in chapters here. The uniqueness of cultural studies at Mahale is also discussed in a chapter.

Part IX introduces works that connect the field and laboratory. Several noninvasive samples are collected in the field and then analysed in the laboratory. Such samples include hormones from feces or urine, skeletons from dead chimpanzees, DNA from feces, hairs, and others, and parasites found in feces. Specialists in endocrinology, morphology, genetics,

and parasitology working on such samples from Mahale contributed to this part, which demonstrates the importance of such samples in addition to direct observations of chimpanzee behaviors.

Finally, in Part X, the relationship between people and chimpanzees is discussed. Particular topics here are tourism at Mahale, the history and culture of the Tongwe people, and conservation efforts by Mahale researchers. A review of anthropological studies on Tongwe people is included here because they are the original residents of Mahale and have supported us as field assistants. Their rich knowledge of nature has contributed to the chimpanzee research at Mahale.

In addition to 50 chapters, the book has several appendices that may be useful for understanding this synthesis of 50 years of research at Mahale.

References

- Boesch, C. and Boesch-Achermann, H. (2000). *The Chimpanzees of the Taï Forest: Behavioral Ecology and Evolution*. Oxford: Oxford University Press.
- Caldecott, J. and Miles, L., ed. (2005). World Atlas of Great Apes and Their Conservation. Berkeley, CA: University of California Press.
- The Chimpanzee Sequencing and Analysis Consortium (2005). Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature*, **437**, 69–87.
- Goodall, J. (1965). Chimpanzees of the Gombe Stream Reserve. In *Primate Behavior*, ed. I. DeVore. New York: Holt, Rinehart and Winston, pp. 425–73.
- Goodman, M., Porter, C. A., Czelusniak, J., *et al.* (1998). Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Molecular Phylogenetics and Evolution*, **9**, 585–98.
- Groves, C. (2001). *Primate Taxonomy*. Washington DC: Smithsonian Institution Press.
- Köhler, W. (1917 [1962]). [*The Mentality of Apes.*] Trans. K. Miya. Tokyo: Iwanami. Japanese translation.
- Matsuzawa, T., Humle, T., and Sugiyama, Y., ed. (2011). *The Chimpanzees of Bossou and Nimba*. Tokyo: Springer.

- Oates, J. F., Tutin, C. E. G., Humle, T., et al. (2008). Pan troglodytes. The IUCN Red List of Threatened Species. Version 2014.2. Available at: www.iucnred list.org. Accessed August 30, 2014.
- Reynolds, V. (2005). The Chimpanzees of the Budongo Forest: Ecology, Behaviour, and Conservation.
 Oxford: Oxford University Press.
- Tyson, E. (1699). *Orang-Outang, Sive Homo sylvestris;* or the Anatomy of a Pygmie. London: T. Bennett and D. Brown
- Watts, D. P. (2012). Long-term research on chimpanzee behavioral ecology in Kibale National Park, Uganda. In *Long-Term Field Studies of Primates*, ed. P. M. Kappeler and D. P. Watts. Heidelberg, Germany: Springer, pp. 313–38.
- Whiten, A., Goodall, J., McGrew, W. C., et al. (1999). Cultures in chimpanzees. *Nature*, **399**, 682–5.
- Wilson, M. L. (2012). Long-term studies of the chimpanzees of Gombe National, Park, Tanzania. In *Long-Term Field Studies of Primates*, ed. P. M. Kappeler and D. P. Watts. Heidelberg, Germany: Springer, pp. 357–84.
- Yerkes, R. M. (1943). *Chimpanzees: A Laboratory Colony*. New Haven, CT: Yale University Press.



PART I H

History and overview



7

Overview of the field site: Mahale Mountains and their surroundings

MICHIO NAKAMURA AND NORIKO ITOH

2.1 General introduction to the Mahale Mountains National Park

This chapter introduces the locale of the studies described in this volume, the Mahale Mountains National Park (MMNP), and some other places relevant to Mahale research. The name "Mahali" was used instead of "Mahale" in some early literature. Mahale became a national park on June 14, 1985 (Government Notice No. 262, 1985; Nishida, 1985) after 20 years of research; the main historical introduction is given in Chapter 3. Here, we will first briefly introduce the location, access, geographic features, and the names of some relevant places in and around the park. Then, we will introduce the Kasoje area, which is the main site for our chimpanzee research, in detail. Further information on the Mahale study site can be found in several publications, which give outlines of the site both in English (Nishida, 1990; Itoh et al., 2012a; Nakamura and Nishida, 2012) and Japanese (Nakamura et al., 1999; Itoh et al., 2012b).

MMNP (6°15′S, 29°55′E) is located at the southernmost part of the Kigoma Region, which is at the western end of the United Republic of Tanzania, East Africa (Figure 2.1). Being remote from Dar es Salaam, the economic capital of Tanzania, the population of the Kigoma Region used to be relatively low compared with other regions in Tanzania, at approximately 470 000 based on statistics from 1967 (Anonymous, 1998). However, the population had more than tripled to 1 674 047 by 2002 (Anonymous, 2005a) and had increased to 2 127 930 by 2012 (Anonymous, 2013). Now, the Kigoma Region is the seventh largest region in

Tanzania. There are a large number of refugees from neighboring areas such as Burundi and the Democratic Republic of Congo staying in Western Tanzania, mostly in the Kigoma and adjacent Rukuwa Regions. In the year 2000, the number of refugees exceeded 700 000 (Anonymous, 2005b) but recently decreased to approximately 100 000 in 2012 (Anonymous, 2012). Chimpanzees in Tanzania are mostly found in the Kigoma Region, which also includes the world-famous Gombe National Park that was home to Jane Goodall's study of chimpanzees (Goodall, 1986).

Mahale is on the eastern shore of Lake Tanganyika (Figure 2.2), which is the second deepest lake in the world and a part of the Great Rift Valley. Thus, the Mahale Park includes not only inland areas but also a 1.6 km wide strip of coastal waters. The park covers an area of approximately 1600 km² (Figure 2.3), which is more than 30 times larger than the Gombe National Park. As indicated by its name, the park is penetrated by the chain of Mahale Mountains that roughly runs from the northwest to the southeast of the park; thus, the park is mostly hilly. The park's highest peak is Mt. Nkungwe (2462 m above sea level; Figure 2.4), which is also the highest peak on the eastern shore of Lake Tanganyika.

2.2 Access to Mahale

Access to Mahale has not been easy compared with other chimpanzee research sites, mainly because Mahale remains unreachable by car. When Toshisada Nishida began research at Mahale in 1965 (see Chapter 3), he had to take a train from Dar es Salaam

Mahale Chimpanzees: 50 Years of Research, ed. M. Nakamura, K. Hosaka, N. Itoh and K. Zamma. Published by Cambridge University Press. © Cambridge University Press 2015.

8

Michio Nakamura and Noriko Itoh

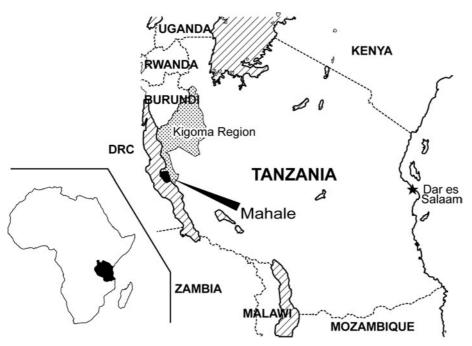


Figure 2.1 Locations of the Kigoma Region and Mahale Mountains National Park in Tanzania.



Figure 2.2 Lake Tanganyika viewed from the Mahale Mountains' main ridge. ${}^{\circ}$ M. Nakamura.

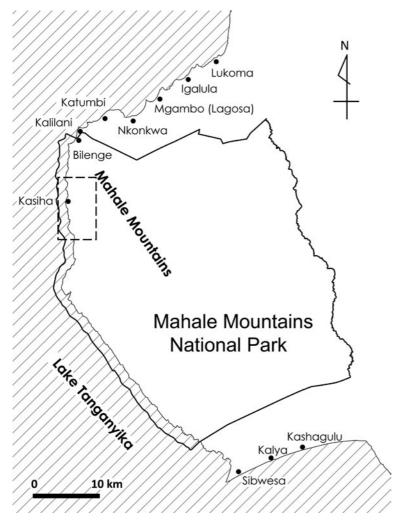


Figure 2.3 Park boundary of the Mahale Mountains National Park. The boundary shown here is tentative because several existing maps show different boundaries. The boundary is currently displayed on-site by signboards and beacons or, in some places, by 20 m wide belts cleared of vegetation (to prevent invasion of fire). However, no existing maps concur with this boundary in practice. In Government Notice No.262 (1985), which should have defined the boundary of the park, a description regarding the southwestern boundary is lacking, and there are obvious errors in the description of the southern boundary. The boundaries shown here are based on Koichiro Zamma's surveys on the locations of signboards, beacons, and the 20 m wide belts devoid of vegetation. The area with a dashed rectangle is shown in Figure 2.7.

to Kigoma, which took 3 days and 2 nights, a steam ship named Liemba from Kigoma to Mgambo for 12 h, and finally a small boat from Mgambo to Mahale for approximately 3 h (for which he had to wait for 4 or 5 days). When he wanted to go out from Mahale, he used a sailboat or a rowboat (Nishida, 1989). Today,

regular flights from Dar es Salaam to Kigoma are available (6 days a week in 2013), but the schedule is often subject to change. The road from Dar es Salaam to Kigoma has recently been significantly improved; thus, it is also possible to reach Kigoma by bus or car in 2 to 3 days.

10

Michio Nakamura and Noriko Itoh

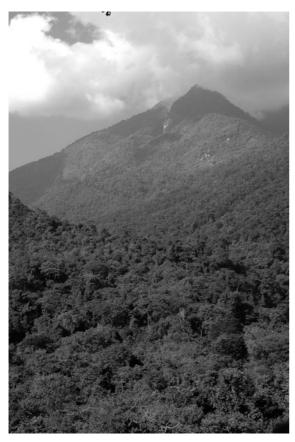


Figure 2.4 Mt. Nkungwe, the highest peak in Mahale.

M. Nakamura.

All research supplies have to be brought from Dar es Salaam or abroad and sent by parcels to Kigoma, or bought at a local market in Kigoma. These supplies then have to be brought from Kigoma to Mahale via Lake Tanganyika. There are two ways to travel from Kigoma to Mahale. If one uses public transportation, steamships are available once or twice a week from Kigoma to Mgambo (Lagosa), a nearby fishing village to the north of Mahale. It usually takes approximately 8 h to travel from Kigoma to Mgambo, but the schedule is notoriously changeable because of the kinds of cargo carried by the steamships. Boarding a steamship at the Kigoma Port can be a bit chaotic as many porters rush to assist with the baggage, but the trip is usually very comfortable and relaxing once on board in a

first-class cabin. After several stops, the steamship reaches Mgambo, where one disembarks to a small boat, often owned by the National Park; this takes tourists to the park station in another 2 to 3 h. Another option for the trip from Kigoma to Mahale is to arrange for a private boat with an outboard engine. The National Park and the research team have their own boats, and several hotels and tour companies at Kigoma own boats that can be chartered by tourists. A boat trip from Kigoma to Mahale takes approximately 10-12 h on a wooden boat and 6-8 h on a fiber boat. Traveling on a smaller boat can sometimes be tough compared with a steamship because the waters can be rough and passengers may get wet and feel cold; thus, a rain suit should be worn.

Most tourists, who do not have to go to Kigoma to buy supplies, now fly directly to the Mahale airstrip (Figure 2.5) on shared chartered flights from Arusha, the second largest city in Tanzania. While this is the easiest way to travel, it is also the most expensive one.

2.3 Organizations and abbreviations

This section introduces some organizations working at or relating to Mahale. Abbreviations mentioned here will be used throughout the book.

2.3.1 Mahale Mountains Chimpanzee Research Project (MMCRP)

This is a project run by a group of researchers conducting research on chimpanzees and other wildlife. The main members originated from KUAPE (see below). They were Jun'ichiro Itani's former students at Kyoto University or Toshisada Nishida's former students at the University of Tokyo or Kyoto University, among others. Nishida had taken a leading role in the project for decades, but the four editors of this volume took on joint executive roles after his death. The members of MMCRP have a project