Behavioral, Ecological and Conservation Studies of Chimpanzees and Other Larger Mammals in the Greater Mahale Area

Takuya MATSUMOTO

Abstract

Overall aim of this project is to have better understandings of ecosystem surrounding chimpanzees and other larger mammals at the Mahale Mountains National Park and adjacent areas in Tanzania. This is essential to have knowledge of behaviors and societies of chimpanzees, one of the endangered species and closest living species to us humans, and to have sufficient information for the park management on the wildlife. In order to achieve this overall goal, this project includes various approaches from different disciplines including ecology, behavioral ecology, primatology, anthropology, molecular ecology, etc. and various methods including naturalistic observation, the use of camera traps, collection of meteorological data, phenological data, and DNA samples, and mammalian survey by line transect method.

1. Introduction

The purpose of this Detailed Research Plan is to clarify the aims and details of this project, one of the longterm wildlife research projects conducted in the United Republic of Tanzania. As can be seen in the "Detailed Progress Report of 10 Years" sent at the same time, the project has contributed significantly to the understanding of the ecosystem around the Greater Mahale Area including the Mahale Mountains National Park and the Katavi National Park. In particular, it is worth mentioning that the project has contributed to the accumulation of new knowledge on the ecology and behaviors of wild chimpanzees, an endangered species and the flagship species for nature conservation in the United Republic of Tanzania. More than half a century has passed since this project began in 1965 as Kyoto University Ape Expedition to Africa (KUAPE) (see Nishida, 1990, 2012; Nakamura *et al.*, 2015 for an overview of the research project), and our project has been conducting research under the circumstances with development of new scientific theories, interest, and research methods in the recent decades. We feel it indispensable that we contribute the park management and other Tanzanian institutions by providing scientific knowledge. Such knowledge about the wildlife may be useful for protecting the wildlife and conserving the ecosystem in the Greater Mahale region.

Demographic data on wild chimpanzees and detailed observations of wildlife, as well as ongoing research on meteorological and phenological data, remain the cornerstone of this research project. In addition, the research project plans to develop new research in response to the changing global situation surrounding nature conservation and the remarkable scientific and technological advances.

Firstly, along with economic development, the social conditions surrounding national parks are considered to be very different from those in the past. In addition, the concept of One Health, which aims to protect the health of people, animals and the environment (ecosystem) in an integrated manner and to optimize the balance in a sustainable manner, has been proposed, and the clarification of the relationship between humans and wildlife is becoming even more important. In this project, an anthropological survey of residents living in the vicinity of national parks will be conducted to identify and attempt to solve problems related to the management and maintenance of national parks, while also taking into account what is known about the wildlife in the vicinity.

Secondly, the project will further promote wildlife genome research. With the recent remarkable

development of genome analysis technology, the value of natural samples from Tanzania has increased enormously. Whole genome analysis of individuals is now relatively cheap, and it is becoming easier to give genetic interpretations to the behavioral findings of wild chimpanzees that have been advanced by this project. In addition, as it is now possible to reconstruct sequences even from a small amount of biological material, it should be possible to gain more clarity on the ecology of wild animals that cannot be directly observed. Therefore, the project will continue to investigate the ecology of a wide area and a wider range of wildlife species using a combination of trap cameras and DNA sampling.

Finally, the project will further promote the return of benefits to the United Republic of Tanzania. International cooperation on access to biological resources and benefit sharing, as exemplified by the Nagoya Protocol, has been called for in recent years. This project will further promote wildlife genomics research through closer collaboration and sharing of technology and knowledge with research institutions in the United Republic of Tanzania, particularly in TAWIRI and the University of Dar es Salaam.

We will take maximum cautions to prevent chimpanzee from infections through contact with humans, because chimpanzees are highly susceptible to infection with human-derived viruses. We pledge to take on our responsibility as researchers under a "Joint Statement of the IUCN SSC Wildlife Health Specialist Group and the Primate Specialist Group Section on Great Apes" issued on 15 March, 2020 (see the link at http://www.internationalprimatologicalsociety.org/). In the forest, we will strengthen the health monitoring of individually identified chimpanzees, which we have been conducting for decades. Also, we will continue to enlighten park staff and three private tourism operators on how to prevent transmission of human respiratory viruses to chimpanzees, just as we have done since we overcame a fatal outbreak presumably caused by hMPV in 2006 at Mahale (Hanamura *et al.*, 2015). Up to the present, the cooperation between researchers and ecotourism has been fairly effective, because the park administration has published "chimpanzee viewing regulations" and has disciplined the tourists to observe it (e.g., wearing masks and keeping a 10-m distance from chimpanzees to prevent from droplet infection).

2. Literature review

2.1. Wildlife conservation in and outside of national parks

Conservation is an indispensable issue regarding studies of wildlife (Hosaka & Nakamura, 2015b). Within the national park, tourism on habituated chimpanzees may be a great issue that need to be explored more in detail (Nakamura, 2015c). Local people's involvement is also inevitable for conservation of wildlife. The original inhabitants of the Mahale area, the Tongwe people (Nakamura, 2015d), used to have good indigenous knowledge about wild animals and plants. A study on Tongwe names of mammals (Nakamura *et al.*, 2017) indicated that the local names are almost as fine-grained as the scientific names with some exceptions on smaller mammals.

Within the chimpanzee distribution, the western Tanzania has been a focus of interest, since it is one of the driest habitats for chimpanzees and resembles the habitat of the earliest hominids (Moore, 1996; Ogawa *et al.*, 2007). Since 1994, Japanese research team has conducted an ecological study of wild chimpanzees in the savanna woodland in western Tanzania (Ogawa *et al.*, 2006a; 2006b; 2007; Yoshikawa *et al.*, 2008). The study needs to be connected to wider regions outside the national parks in order to conserve larger mammals that range widely. Kyoto University has a long history of naturalistic studies of chimpanzees in western Tanzania (e.g., Azuma & Toyoshima, 1961–62; Itani, 1979; Izawa, 1970; Kano, 1972; Nishida, 1989). Kano (1972) estimated distribution of chimpanzees in Tanzania. After a few decades, Ogawa *et al.* (1997) found a hitherto undescribed habitat of wild chimpanzees near Kasanga in the southwestern edge of Tanzania. The whole ecosystem including Mahale is also connected to the Katavi National Park to the south and is one of the targets of the Tanzania government to conserve its natural resources. Thus, the Katavi–Mahale Corridor Project (KAMACO) was launched recently. Katavi is one of

the remote parks, which has not been visited by many researchers so far (TANAPA, online). However, the park is rich in wildlife and has one of the largest concentrations of buffalo, elephants, and hippos in Tanzania. It also has giraffes, which are Tanzania's national animal. However, giraffes are facing a "silent extinction" (Vitali *et al.*, 2020). Therefore, understanding the behavior and ecology of giraffes in Katavi National Park could contribute to the conservation of the species and also to a better understanding of the Greater Mahale ecosystem.

Disease outbreaks are one of the key threats to great apes in-situ conservation. Since the spread of some pathogens are mediated by social interactions, it is important to understand how social networks predict the chain of pathogen transmission. For example, using data of social relationship among Mahale M group chimpanzees, Pierron *et al.* (2024) showed that sex and age predict individual centrality, with older males presenting many (degree centrality) and strong (strength centrality) relationships, and thus, males are more central than females within their network, and their centrality determines their probability of getting infected during simulated outbreaks.

Participation of the local community is essential for promoting wildlife conservation. However, human–wildlife conflict sometimes negatively impacts both local livelihoods and conservation efforts (Dickman, 2010; König *et al.*, 2020). Wild animals can sometimes raid crops, damage infrastructure, kill livestock, and cause injuries or deaths of people: such undesired events may lead to negative perceptions of local people against conservation (Bencin *et al.*, 2016; Nyhus, 2016). Therefore, in addition to better understandings of the ecology of the wild animals, it is crucial to understand the local dynamics of human–wildlife conflict through detailed field research for effective conservation.

2.2. Mammalian fauna and microbes

Although studies on fauna and flora of Mahale have been carried out during the early phase of the research (Itani, 1977; Nishida & Uehara, 1981; 1983; Nishida, 1990), the updated information is continually required. Systematic studies on population densities of medium- and large-sized diurnal mammals, which were targets of chimpanzee hunting, have been conducted since 1995 (Uehara & Ihobe, 1998; Uehara, 2003; Itoh *et al.* 2012; Ihobe, 2015a; 2015b).

Most studies of mammalian fauna are conducted in relation to chimpanzee hunting. Chimpanzees of K and M Groups at Mahale were known to eat 17 species of mammals (Uehara *et al.*, 1992; Nakamura, 1997; Hosaka *et al.*, 2001; 2020). Among these 17 species, red colobus (*Procolobus* spp.) were the main hunting target of M group chimpanzees at Mahale after 1980's (Uehara *et al.*, 1992; Hosaka *et al.*, 2001; Hosaka, 2015b; Hosaka *et al.*, 2023), as at Gombe in Tanzania (Stanford *et al.*, 1994), Kibale in Uganda (Mitani & Watts, 1999) and Taï in Ivory Coast (Boesch & Boesch, 1989). Chimpanzee predator–mammalian prey interactions have been investigated at Mahale (Huffman & Kalunde, 1993; Hosaka *et al.*, 2001; 2024a; 2024b; Boesch *et al.*, 2002; Ihobe, 2002), and there is a possibility that chimpanzees at Mahale selected red colobus as the main hunting target because of anti-predatory behavior of red colobus (Ihobe, 2002), as the same reason at Gombe (Stanford, 1995). However, prey selectivity in hunting of Mahale chimpanzees needs to be evaluated in relation to availability of their prey (Nishida & Uehara, 1983; Uehara, 1997). Continuous monitoring on changes of population densities of potential prey mammals such as arboreal primates and small terrestrial ungulates is important to reveal predatory–prey relationships and to investigate chimpanzee hunting behavior in detail.

The fluctuations in population densities of prey mammals hunted by chimpanzees have been reported from Gombe (Stanford, 1995; 1998) and Kibale (Mitani *et al.*, 2000). Ihobe & Uehara (1999) estimated the impact of chimpanzee hunting on population densities of prey mammals based on census data in 1995 and 1996 at Mahale and concluded that predation rates for some species did not exceed population growth rates of the respective species. Long-term data of population changes of potential prey, however, are necessary to evaluate the exact impact of chimpanzee hunting on population densities of them.

Chimpanzees not only hunt small mammals but they are also may be preyed upon by large carnivores such as leopards (*Panthera pardus*) (Nakazawa *et al.*, 2013). Leopards are potential predators of chimpanzees and at the same time they can be competitors of chimpanzees over small mammalian prey (Nakamura *et al.*, 2019). Therefore, it is essential to have better understanding of the basic ecology of the leopards at Mahale. More recently at Mahale, the prey species of leopards (Nakazawa, 2020; 2023) and crowed eagles (Seike, 2022) have been studied in detail.

In addition to such prey species, many other mammalian species have also been recorded in Mahale. To date, at least 70 species from 11 orders of mammals have been documented within the national park (Ihobe, 2015a). These include species adapted to the savannas of Eastern and Southern Africa, as well as species adapted to the forests of Western and Central Africa, including the Congo Basin, making Mahale a biogeographically intriguing area (Itani, 1977).

Related species, such as humans and nonhuman primates, often establish the interspecific relationships as symbiosis or commensalism with many kinds of microbes that live inside and outside of animals (Alberts *et al.*, 2002; Kooriyama & Hasegawa, 2015). The microbes do not innately live in animals but are transmigrated from mothers or from environments. Many kinds of microbes start to migrate to host animals whose immune system are not yet complete at young age. Meanwhile, the animal immune system develops in the first year after birth, during which it selects some microbes establishing immunological tolerance. When humans grow in the low microbe-exposure condition during infancy, they will develop allergies in their later life stages at a high rate (Hamelmann *et al.*, 2008).

Most animals host species-specific symbionts or commensals in their bodies. However, different kinds of animals sometimes share their symbionts/commensals. For example, some nematodes, such as *Strongyloides fuelleborni, Oesophagostomum stephanostomum* or *Ternidens deminutus*, are naturally commensal to nonhuman primates, but sometimes develop cross-infection to humans (Pampiglion & Ricciardi, 1971; 1972; Kagei & Asano, 1980).

2.3. Genetic analysis of chimpanzees and other mammals

Using microsatellite of wild chimpanzees for paternity analysis was first used in 1993 at Bossou, Guinea (Sugiyama *et al.*, 1993). This study showed that non-invasively collected samples could be used for paternity analysis. After this study, some studies using shed hairs or feces for microsatellite typing have been conducted (Morin *et al.*, 1994; Gagneux *et al.*, 1999; Constable *et al.*, 2001; Vigilant *et al.*, 2001). However, the DNA obtained from such samples is typically degraded and of low concentration and so it is necessary to experiment repeatedly in order to get reliable results (Taberlet *et al.*, 1996; Morin *et al.*, 2001). We collected various kinds of non-invasive samples and showed that urine and saliva samples are usable for DNA analyses (Inoue, 2005; 2015; Inoue *et al.*, 2007a; 2007b).

According to some studies on paternity of chimpanzees, there was a positive relationship between male rank and reproductive success (e.g., Boesch *et al.*, 2006), and there was evidence that a high-ranking male mated with his mother and produced an offspring at Gombe, Tanzania (Constable *et al.*, 2001). At the Taï forest (Ivory Coast), incidence of extra-group paternity was 7%. At Mahale, we genetically determined the father of 10 offspring, and highest-ranking males (alpha males) sired five of them and there were no evidence of extra-group paternity and inbreeding between mother and son (Inoue *et al.*, 2008). Several studies have shown that dominant male chimpanzees attain high reproductive success. However, the difference in reproductive success among different alpha males is still unsolved. It is important to compare reproductive success of different alpha males.

Another important aspect of chimpanzees is female-biased dispersal. In mammals, males are typically the dispersing sex (Pusey & Packer, 1987). Thus, the relatedness of male chimpanzees has been assumed to be higher than that of females. However, at Taï and Budongo (Uganda), the average relatedness among males was not significantly higher than that among females (Vigilant *et al.*, 2001; Lukas *et al.*,

2005). At Mahale, the average relatedness among mature males was significantly higher than that among mature females. The existence of an old male and the long tenure of one alpha male may have contributed to this significant difference (Inoue *et al.*, 2008). Although the average relatedness among females is low, some immigrant females may have close relatives. Male chimpanzees clearly prefer to affiliate and cooperate with their maternal brothers in several behavioral contexts (Langergraber *et al.*, 2007). Therefore, it is important to know whether immigrant females have maternal or paternal half-siblings or not.

In order to develop a strategy for conserving wild animals, genetic information is essential. Because it is difficult to observe some mammalian species, fecal census of these animals is the alternative way to estimate their densities. Fecal samples can provide sufficient amount of DNA for analyzing genetic diversities of these animals. By using genetic methods, we can determine their species and genetic characteristic. In addition, we will also extract DNA from bones and hairs when permits are obtained.

2.4. Ecological influences of chimpanzee ranging and behaviors

Chimpanzees are large-brained animals and take a long span before maturity (Fleagle, 1999; Matsumoto & Hayaki, 2015). This has been explained in primate evolutionary context: the evolutionary trend in primates could be explained as a function of enlarged brain sizes and complex social systems and thus need long period for learning (*ibid.*). *Homo sapiens* is the extreme of this trend. Large brain size has been explained in relation to fruit dependent diets that evolved in the common ancestor of apes and humans, because fruits are dispersed in larger area and have much more seasonality compared to leaves, thus need higher cognitive competence (Clutton-Brock & Harvey, 1977). Along with frugivorous diet (Itoh & Nakamura, 2015c), chimpanzees are known for their fluid social system (Itoh & Nakamura, 2015a), called the fission–fusion social system (Hanamura, 2015a) which is also assumed to be related to their frugivorous diet (Nishida, 1968; Goodall, 1986). This latter feature has been studied in socio-ecological paradigm.

The diversity of social systems in primates has been explained by ecological factors in socioecological studies: the diversity of grouping behavior is regarded as a result of balancing costs of competition over resource (foods and mates) and benefits against predation pressure (Kappeler *et al.*, 2003). Chimpanzees who have fission–fusion grouping system are the good subject to test this hypothesis because researchers can compare the same unit-group living within a limited home range (Nakamura *et al.*, 2013; Nakamura 2015b), but changing the actual foraging party sizes in relation to seasonal changes in food availability. The most intensive studies on this hypothesis were done in Kibale, Uganda (Isabirye-Basuta, 1988; Chapman *et al.*, 1995; Wrangham *et al.*, 1996). Wrangham *et al.* (1996) hypothesized that chimpanzees could form larger parties when food is abundant since travel cost imposed by extra companion is reduced. And this hypothesis seemed to finely explain the reason why chimpanzees disperse when fruit availability becomes low in Kibale (*ibid*; Chapman *et al.*, 1995) and also in Mahale (Itoh & Nishida, 2007; Itoh & Muramatsu, 2015).

Compared to intensive focuses on food resources, relatively less is studied about other ecological factors influencing chimpanzees' ranging behaviors. For example, chimpanzees make beds every night and often sleep in proximity with each other. Although there are some studies of nighttime behaviors of chimpanzees at Mahale (Zamma, 2014; Zamma & Ihobe, 2015), there are needs to increase the information of how chimpanzees spend a night.

2.5. Social behaviors and social relationships among chimpanzees

Chimpanzees are highly social animals. They interact socially through various means such as vocalization (Hosaka *et al.*, 2015), grooming (Zamma, 2011; Zamma & Nakamura, 2015), greeting behaviors (Sakamaki, 2011; Sakamaki & Hayaki, 2015), or social play (Shimada, 2013a; 2013b; Shimada & Sueur,

2014; Matsusaka *et al.*, 2015; Shimada *et al.*, 2015). While their social relationships are usually peaceful, there are sometimes antagonistic relationships (Kutsukake & Hosaka, 2015) that may sometimes lead to conspecific killings (Kaburu *et al.*, 2013; Nakamura & Itoh, 2015b) and cannibalism (Nishie & Nakamura, 2018).

Adult males are the most gregarious of all the sex classes and have been studied in detail (e.g., Kaburu & Newton-Fisher, 2015a; 2015b; 2016; Hosaka & Nakamura, 2015a). In addition, more studies recently focus on females (Hanamura, 2015b; Itoh & Nakamura 2015d; Nakamura 2022) and also on immature individuals (Nakamura & Nishida, 2013; Matsumoto *et al.*, 2016; Matsumoto, 2017). Mahale is an ideal study site for the detailed studies on social relationships among individuals because of accumulations of detailed individual information (Hosaka, 2015a; Nakamura, 2015e), demographic data (Nishida *et al.*, 2003; Nakamura 2015a), details of developmental stages (Matsumoto & Hayaki, 2015), and ethograms (Zamma & Matsusaka, 2015). In addition to accumulation of regular behavioral data, sudden and unexpected accidents or events may sometimes highlight chimpanzees' social relationships (e.g., Shimada & Yano, 2023).

2.6. Feeding behaviors and techniques

Chimpanzees are basically ripe fruit eaters (Itoh & Nakamura, 2015b; Itoh *et al.*, 2015), therefore studying fruiting phenology (Itoh & Muramatsu, 2015) is quite important to understand how chimpanzees feeding behaviors are affected by environment. Chimpanzees also affect environment by dispersing fruit seeds through feces (Nakamura & Itoh, 2015a; 2015c; Nakamura *et al.*, 2017). Chimpanzees may choose particular food items by their taste (Hayakawa, 2015), and this topic needs further investigation.

Some food items have physical barriers that require complex techniques to be broken before the food is consumed. A good example is tool-use by the chimpanzees (Nishie, 2011; 2015). In addition, they employ minute manipulations when they eat some difficult-to-process food even without tools. In such cases, laterality of hand uses can often be observed (Marchant, 2015). Feeding behaviors of chimpanzees need to be explored more in detail also with respect to its development (Matsumoto, 2017).

Insectivory (McGrew, 1992; Kiyono, 2015) is another good candidate to explore in relation to chimpanzees feeding. For example, chimpanzees of some groups eat the termite of the genus of *Macrotermes* using fishing tools (Gombe: Goodall, 1986; Lonsdorf *et al.*, 2004; Bossou: Sugiyama & Koman, 1979; Okorobiko: Jones & Sabater Pi, 1969; Goualougo: Sanz *et al.*, 2004; Fongoli: McGrew *et al.*, 2005), whereas chimpanzees of other groups eat other termites species without using tools (Taï: Boesch & Boesch, 1990; Lopé: Tutin *et al.*, 1995; Budongo: Reynolds, 2005). In Mahale, B group chimpanzees use tools to eat *Macrotermes* but very rare in K and M group chimpanzees (McGrew & Collins, 1985; Nishida & Uehara, 1980; Uehara, 1982). It is suggested that the difference of chimpanzees' feeding behavior on termites is based on the difference of termites' distribution (Collins & McGrew, 1987; Uehara, 1982).

Dorylus ants are widespread in chimpanzee habitats but has never been recorded to be eaten by chimpanzees in Lopé (Tutin *et al.*, 1995), Mahale (Nishida, 1973), Kasakati (Suzuki, 1966), and Budongo (Reynolds & Reynolds, 1965). On the other hand, Taï (Boesch & Boesch, 1990), Gombe (McGrew, 1974; Goodall, 1986), and Bossou (Sugiyama, 1995; Humle & Matsuzawa, 2002) chimpanzees are known to feed on these ants by dipping tools.

Camponotus ant-fishing has been observed among the M group chimpanzees at Mahale for more than three decades. Customary *Camponotus* ant-fishing has been recorded for the population of chimpanzees only in Mahale (e.g., Nishida, 1973; Nishida & Hiraiwa, 1982; McGrew, 1992; 2004; Boesch & Tomasello, 1998; Whiten *et al.*, 1999; Nishie, 2011), except for some anecdotal reports from Lopé, Gabon (Tutin & Fernandez, 1992), and Bossou, Guinea (Yamamoto *et al.*, 2008), in spite of the very wide distribution of *Camponotus* spp. in Africa. Pioneering studies of the *Camponotus* ant-fishing of K group chimpanzees at Mahale suggested that juveniles up to 6–8 years of age showed more clumsy techniques

using shorter tools and spent shorter bout-length for *Camponotus* ant-fishing than adults (Nishida, 1973; Nishida & Hiraiwa 1982), and those tendencies are also verified among M group chimpanzees (Nishie, 2011). Thus, the standardization and refinement of ant-fishing behavior seem to develop through ontogeny. However, the developmental process of the behavior has not yet been investigated sufficiently.

Chimpanzees also feed on *Crematogaster* ants but the degree of utilization differs between sites: Lopé chimpanzees do not eat these ants although sympatric gorillas do, and chimpanzees of Gombe, Kahuzi and Dja eat only a small amount of *Crematogaster* ants (Basabose, 2002; Deblauwe & Janssens, 2008; Goodall, 1986). On the other hands, Mahale chimpanzees regularly eat *Crematogaster* ants usually without tools (Nishida & Hiraiwa, 1982; Fuse, 2013; Kiyono, 2015).

2.7. Hunting and meat-eating

Chimpanzees are also known as "meat-eating ape" since Goodall (1963) first reported occasional predation in this species. They hunt sympatric mammals, such as monkeys, rodents and small ungulates, and share the procured meat with other individuals. Hunting and meat-eating has been an important topic of long-term study of wild chimpanzees across African habitats: Mahale (Tanzania: Uehara *et al.*, 1992; Hosaka *et al.*, 2001; Hosaka, 2015b; Hosaka *et al.*, 2020), Gombe (Tanzania: Stanford, 1998; Gilby, 2006; Gilby *et al.*, 2006), Taï Forest (Ivory Coast: Boesch & Boesch, 1989; Boesch & Boesch-Achermann, 2000; Gomes & Boesch, 2009), and Kibale (Uganda: Mitani & Watts, 1999; Watts & Mitani, 2002; Gilby & Wrangham, 2007; Gilby *et al.*, 2008).

In all the four long-term study sites, chimpanzees hunt red colobus more frequently than other prey (Uehara, 1997; Hosaka, 2015b). One explanation for this may lie in chimpanzee hunting strategy. Opportunistic capture is typically exploited by a solo hunter that discovers hidden prey, such as squirrels, duikers, and piglets. This tactic is not reliable in terms of efficiency. Hosaka (2015b) insisted that Mahale chimpanzees can kill red colobus only by group hunting. Group hunting seems effective for killing aggressive red colobus, while not effective for killing elusive prey, such as red-tailed monkeys, another abundant forest primate species.

Seasonality has been one of unresolved issues in chimpanzee hunting and meat-eating behavior. With the spread of red colobus hunting by Mahale chimpanzees after the 1990s, group hunting became more concentrated from August to October when the party size of chimpanzees increased. In particular, infant red colobus monkeys seemed to be caught more frequently from July to September compared to other age-group prey (Hosaka *et al.*, 2024a).

The social aspect of hunting and meat-eating is another hot issue to be explored. First, Boesch & Boesch (1989) insisted that chimpanzees of Taï Forest engage in cooperative hunting on red colobus monkeys, which rarely occurs elsewhere. They tried to explain this by a hypothesis that high canopy of primary forests at Taï make hunting forest monkeys costly and cooperation should be the best strategy to compromise costs and benefits of reciprocity in meat-sharing (Boesch et al., 2002). Second, Mitani & Watts (1999) and Watts & Mitani (2002) suggested that the great number of adult male chimpanzees at Ngogo (Kibale Forest, Uganda) and reciprocation for meat-sharing cause group hunts on red colobus more frequently and successfully. However, Gilby et al. (2008) and Gilby & Wrangham (2007) cast a skeptical view from their study at Kanyawara (another site of Kibale). They emphasized the importance of 'impact hunters' (almost the same as 'skillful hunters' in Hosaka et al. (2001)) and insisted that social predation (almost the same as 'group hunting' in Hosaka et al. (2001)) was not simply a function of the additive probability of intrinsic individual hunting rates. Finally, Nishida et al. (1992) suggested that alpha male chimpanzees utilize meat-sharing as a political tactic to form and maintain alliance with other adult males. Hosaka (2015b) suggested that such a tactic may be revealed through the analysis of data on meat-sharing and social relationships accumulated over two decades. At present, there are no published studies demonstrating the effects of adult males' social relationships on hunting and meat-eating behaviors, with

the exception of the finding that male age and alpha status predict annual variation in frequency of successful predation on red colobus (Hosaka *et al.*, 2024b).

The physiological aspect of hunting and meat-eating is a novel issue to be explored. First, Muller and Wrangham (2004a) showed that male testosterone levels increased in the aggressive context of competing for maximally tumescent parous females, not just as a by-product of copulation. While hunting, chimpanzees perform a variety of aggressions, such as barking, charging display, hitting and biting. Thus, it is reasonable to propose a hypothesis that male testosterone levels increase in response to hunting behavior. Furthermore, we can propose a reverse hypothesis that high testosterone levels affect motivation to hunt in chimpanzees. If this is the case, then seasonal or aseasonal fluctuation of testosterone levels may influence chronological change in chimpanzee hunting. Either energetic change due to fruit availability or social change due to male-male relationships may affect testosterone levels in chimpanzees. Second, Muller and Wrangham (2004b) showed that male high dominance rank positively correlated with urinary cortisol excretion in a stable dominance hierarchy. They explained it not by psychological stress but by metabolic stress on the basis of positive correlation between dominance rank and aggression rate in male chimpanzees. If this is the case, then skillful hunters that experience metabolic costs may display higher cortisol levels than predicted from dominance rank. Finally, the relationship between meat intake and reproductive success in female chimpanzees remains unexplored. Hosaka (2015b) stressed that females contributed hunting more than previously reported and that some females may eat as much as adult males. It seems necessary to monitor female reproductive state by analyzing female hormone (estrogen and progesterone) levels, to reveal how meat intake affect reproductive behavior of female chimpanzees (see also Fujita & Inoue, 2015 for review about chimpanzee reproductive strategies).

2.8. Cultural behaviors of chimpanzees

Although culture is an important feature to understand human nature, knowledge about its evolutionary origin is still vague. Chimpanzees are genetically closest species to humans. Thus there has been a hot debate whether chimpanzees have 'cultures' or not (e.g., Boesch & Tomasello, 1998; Byrne *et al.*, 2004; Matsuzawa *et al.*, 2001; McGrew, 1992; 1998; 2004; McGrew & Tutin, 1978; Nakamura & Nishida, 2006; Nakamura & Uehara, 2004; Nishida, 1987; 2003; Nishie & Nakamura, 2015; de Waal, 2001; Whiten *et al.*, 1999; 2001). In such studies of chimpanzee cultures, the stress is usually put on tool use (e.g., McGrew, 1992). Cultural variation in social domains, or social customs, has not been documented fully (Nakamura, 2002; 2010).

Understanding the developmental process of cultural behaviors is important because such behaviors need to be socially learned by individuals who are born to a group. Most, if not all, studies on this topic mention the transmission of some kind of information through non-genetic channels. In other words, cultural behavioral patterns are acquired by some kind of social learning. Comparative psychologists often study this aspect of culture and test whether or not chimpanzees or other nonhuman animals are capable of certain kinds of social learning in well-controlled settings (e.g., Whiten, 1998; Myowa-Yamakoshi & Matsuzawa, 1999). On the other hand, it is relatively difficult to obtain the same kind of knowledge from field studies, and thus field researchers have provided information on behavioral diversities in natural habitats and accumulated information on the general ontogeny of behaviors (Nishida & Hiraiwa, 1982; Boesch, 1991; Matsuzawa, 1994; Inoue-Nakamura & Matsuzawa, 1997; Boesch & Boesch-Achermann, 2000; Lonsdorf *et al.*, 2004). Approaches from both the laboratory and the field are important, but they tend to focus only on the development of tool use. There are no studies conducted on developmental patterns of cultural behaviors outside of tool use.

For example, leaf-clipping behavior, one of the courtship displays, also has been observed for the population of chimpanzees at Mahale for decades (Nishida, 1980). Leaf-clipping occurs mainly in sexual context, but it also occurs in other context such as frustrated contexts and play. Since infant chimpanzees

are sexually immature, it is obvious that their leaf-clipping behaviors are not occurring in sexual contexts, and it is likely that social meaning of this behavior could change in their developmental processes. The developmental process of leaf-clipping behavior will show us how they sexually mature in their social interactions.

2.9. Intergroup relationships

The investigation of wild chimpanzees across neighboring unit-groups (or communities) is related with two scientific interests: the origin of human culture and the evolution of intergroup aggression in chimpanzees and human.

The former topic, the origin of human culture, has recently been one of the hottest topics in biological anthropology (see review in 3.4). Although most examples of behavioral diversity in previous reports are across populations distantly separated (e.g., Whiten *et al.*, 1999), it is also essential to compare the behaviors between neighboring groups. Formerly at Mahale there were two habituated groups, namely K and M groups. However, because the K group is already extinct, we can only compare the K and the M group retrospectively (McGrew *et al.*, 2001; Nakamura & Uehara, 2004) and cannot make direct comparisons. Subtle differences in social customs are expected to be found if we can compare two neighboring groups directly. Thus, in 2005 Sakamaki and Nakamura started the habituation efforts on the Miyako group (Y group) which adjoin the M group to the north (Sakamaki & Nakamura, 2007; Sakamaki *et al.*, 2007).

The latter topic, the evolution of intergroup aggression, is related to the occurrence of fatal attacks during intergroup encounters among chimpanzees (Manson & Wrangham, 1991; Wrangham, 1999; Wilson *et al.*, 2014). There exists dominant–subordinate relationship between unit-groups, and the subordinate generally avoids the dominant (Nishida & Kawanaka, 1972). Male chimpanzees show hostility toward members of neighboring groups. Their territorial behaviors such as territorial defense, border patrols, deep incursions, coalitionary attacks and kills, and border avoidance are relevant to lethal raiding (see Wrangham, 1999; Sakamaki & Nakamura, 2015 for review). The imbalance-of-power hypothesis (Manson & Wrangham, 1991; Wrangham, 1999) suggests two factors for coalitionary kills: one is intergroup hostility, and the other is large power asymmetry between rival parties. It should be noticed that this hypothesis is also significant in the ecological aspect, that is, habitat utilizations in chimpanzees are related not only to ecological factors, such as food availability and distribution, but also to social factors, such as intergroup relationships (Herbinger *et al.*, 2001).

Studies of chimpanzees in Mahale population have mainly focused on two neighboring groups, K and M groups, since 1965 (see Nishida, 1990 for details). After the extinction of K group in the 1980s, only M group has been the habituated group (Nishida *et al.*, 1985; Takahata, 2015). M group has several neighboring unit-groups (Sakamaki & Nakamura, 2015): at least B group to the north, N and/or L group to the south, and probably one unit-group to the east. These neighboring unit-groups are not habituated, and we have no detailed information about them (see Shimada, 2003 about the south groups). In the late 1990s, some other groups began to invade M group's territory probably due to the decrease of its group size (Itoh *et al.*, 1999). Although some members of M group disappeared including most of the high-ranking adult males in 1995 and 1996, the reason for their disappearance is still unknown (Nishida *et al.*, 2003). In the former territory of K group, unhabituated chimpanzees have recently been observed or heard from time to time as well (Uehara, 2002).

An exhaustive list of the behavioral patterns in M and K group was compiled (Nishida *et al.*, 1999). New observations have been added to the list (e.g., Nishida, 2003; Nishida & Wallauer, 2003; Nishida *et al.*, 2003; Zamma & Matsusaka, 2015). The list of food repertory is also available for M and K group (Nishida & Uehara, 1983; Itoh *et al.*, 2015).

2.10. Development of chimpanzees

It is known that mother–infant relationship in primates is indispensable for the growth of immature individuals in terms of nutritional and social needs. Infant chimpanzees need to be nursed by their mothers, and even after they are weaned, they take some foods from their mothers in food sharing. It has also been suggested that immature chimpanzees learn food repertoire and feeding techniques from their mothers through food sharing (Hiraiwa-Hasegawa, 1990a; 1990b; Nishida & Turner, 1996; Silk, 1978; 1979; Ueno & Matsuzawa, 2004). Infant chimpanzees are generally weaned at the age of four or five years (Matsumoto, 2017). They need to be nursed for longer period than most of other primate species. Juvenile chimpanzees gradually become able to travel apart from their mothers and move with other adolescent or adult individuals, but the level of association with mothers continues to be high until adolescence (Hayaki, 1988).

Thus, mother–offspring relationship is thought to be important for immature chimpanzees, and many studies have focused on mother–offspring relationship so far. On the other hand, studies on social interactions between immature chimpanzees and unrelated individuals are still scarce, although immature chimpanzees spend great amount of time in various social interactions with unrelated individuals. Immature chimpanzees often play with unrelated chimpanzees including adult males. They often engage in agonistic interactions and may also show reconciliation and consolation. Greeting behaviors are also observed from childhood. Some mature or immature chimpanzees show great interests in infants, and try to take infants from their mothers to carry, groom or play with. It is plausible to think that immature chimpanzees learn some social skills and information from interacting with other chimpanzees, not only with their mothers.

Investigation on social relationship of orphans (Nakamura *et al.*, 2014; Nakamura & Hosaka, 2015) may also reveal the importance of relationship between immature and unrelated individuals. In primates, "adoption" is often observed when the mother dies and the infant is left alone (Palthe *et al.*, 1975; Taylor *et al.*, 1978; Uehara & Nyundo, 1983; Gould, 2000; Tanaka, 2004). The foster parent shows some allomothering behaviors, such as carrying the orphan on the back, grooming it, traveling together, sleeping in the same bed at night, and so on.

Play is one of the most frequently observed behaviors among immature chimpanzees (Matsusaka *et al.*, 2015; Shimada, 2013a; 2013b; Shimada & Sueur, 2014; Shimada *et al.*, 2015). Although it is sometimes difficult to detect direct function of play behaviors, it may function as a source of innovation, an opportunity to learn the social environment, or means of physical development.

3. Research Problem

Overall aim of this project is to continue the ongoing long-term studies in order to have better understanding of ecosystem surrounding chimpanzees at the Mahale Mountains National Park and adjacent areas in Tanzania. This is essential to have finer knowledge of behaviors and societies of chimpanzees, one of the endangered species and closest living species to us humans, and to have sufficient information for the park management on the wildlife. In order to achieve this overall goal, this project includes various approaches from different disciplines including ecology, behavioral ecology, primatology, anthropology, molecular ecology, etc.

Specific topics of coming years will be: 1) wildlife conservation in and outside of national parks; 2) mammalian fauna and microbes; 3) genetic analysis of chimpanzees and other mammals; 4) ecological influences of chimpanzee ranging and behaviors; 5) social behaviors and social relationships among chimpanzees; 6) feeding behaviors and techniques; 7) hunting and meat-eating; 8) cultural behaviors of chimpanzees; 9) inter-group relationships; and 10) development of chimpanzees.

4. Objectives and significance of the research

4.1. Wildlife conservation in and outside of national parks

The objectives of this study are 1) to understand the ecological threats of chimpanzees at Mahale National Park and adjacent areas, 2) to show the characteristics of mammalian fauna and vegetations in each study area 3) to grasp a whole conservation status of chimpanzees and other mammals and 4) to elucidate the human–wildlife conflict around the protected areas in western Tanzania. Although the main part of the Japanese team will continue the study of chimpanzees at Mahale, some of us will also investigate woodland areas outside the national park. Some wild animals including chimpanzees live close to human settlement and it will be indispensable to gather information of such chimpanzees and surrounding ecosystem. We will also conduct a behavioral–ecological study of larger mammals, especially giraffes in Katavi National Park, to gain a better understanding of the whole ecosystem in the western Tanzania.

4.2. Mammalian fauna and microbes

The objectives of this research is 1) to improve the knowledge of mammalian fauna; 2) to grasp their densities in relation to the vegetation types; 3) to provide basic availability information on chimpanzee hunting; 4) to stimulate further research on larger mammals the behaviors and ecologies of which are less known compared to chimpanzees; and 5) to understand microbe ecologies and microbe-host relationships at Mahale. Detailed studies on chimpanzees have been conducted in specific areas of the park, leaving the fauna in other regions insufficiently studied. Conducting mammal study over a wider area will be useful for renewing the information of key larger mammals at Mahale in order to have better understandings of ecosystem and aid in the planning and implementation of conservation strategies and activities. Micro-ecology of parasites, bacteria, and viruses are also important for understanding ecosystem of Mahale.

4.3. Genetic analysis of chimpanzees and other mammals

The objectives of this study are 1) to assign paternity of chimpanzees in the M group at Mahale, in particular for clarifying the difference in reproductive success among alpha males; 2) to determine relatedness between female chimpanzees in the M group; 3) to assess the genetic diversity of chimpanzees and other mammalian species of Mahale; and 4) to collect basic genetic information such as DNA barcoding data of mammals at Mahale. The results from this study will provide genetic perspectives to the understanding of ecosystem and conservation plan at Mahale.

4.4. Ecological influences of chimpanzee ranging and behaviors

The objective of this research is to reveal the detailed feeding strategy of chimpanzees when food is abundant and, through this, to reveal the benefits of aggregation. Although many researchers have investigated how chimpanzees change party size according to fruit availability, not much attention has been paid on how chimpanzees utilize food resources when they are abundant. In addition, the grouping pattern is assumed to differ among sites that could not be explained by home range size, unit-group size, or vegetation types (Itoh & Nishida, 2007). In order to make detailed comparison of feeding and grouping strategy among sites, we first need to investigate how food resource is distributed, and how chimpanzees utilize them in different seasons. This should be done not only from the ecological perspective alone but

also from sociological perspective (*i.e.*, how they eat with their companion). Moreover, we have accumulated knowledge that chimpanzees have cultural differences among groups, it can affect the feeding ecology as well. These findings strongly suggest the effective conservation plan may differ from site to site. Thus, the results from this study, we will be able to grasp the basic knowledge required for chimpanzee conservation plan specific to Mahale.

4.5. Social behaviors and social relationships among chimpanzees

The objectives of this research are 1) to advance the knowledge of chimpanzees' complex social relationships within the unit-group; and 2) to investigate the degree of altruism and cooperation among them. Although cooperation is often regarded unique to humans, we expect there will be some rudimentary forms of cooperation among chimpanzees. If this is elucidated, it will be of great advance to understand evolution of sociality in the course of human evolution. The underlying cognitive mechanisms of certain social behaviors of wild chimpanzees are virtually unexplored. Thus, it is also significant to collect finer-grained details of behaviors, e.g., by step-by-step analyses of video images of these behaviors.

4.6. Feeding behaviors and techniques

The objectives of this research are 1) to standardize and refine the information on chimpanzees' feeding behaviors and techniques in relation to developmental process of these techniques within social and ecological environments; 2) to collect preliminary information on insectivory and faunivory by other larger mammals by collecting and analyzing feces; and 3) to grasp the distribution and densities of some potential prey species (insects or mammals) in order to understand the relation between prey and predator animals including chimpanzees.

4.7. Hunting and meat-eating

The objective of this study aims to reveal behavioral and ecological properties in hunting and meat-eating behavior of wild chimpanzees in relation to their social and physiological aspects. The results would be significant because 1) the impact of chimpanzee predation on red colobus and other sympatric mammals will be available and such information would be useful to formulate strategy to conserve fauna at Mahale Mountains National Park; 2) some hot issues of anthropology, such as cooperation, reciprocity and nutritional adaptation, could be discussed with reference to dietary and habitat shift in hominid evolution; and 3) endocrine physiology in the context of hunting and meat-eating may reveal how hunting and meat-eating influence metabolism, reproduction, and society of wild chimpanzees.

4.8. Cultural behaviors of chimpanzees

The objective of this research is to understand the behavioral variation of chimpanzees. Because chimpanzees' behaviors differ even when genetic background is the same, the basic knowledge of behavioral diversity and possible transfer mechanisms of such cultural behaviors are important for understanding chimpanzees' adaptive abilities not directly explained by genetic or ecological differences. The outcomes of this research will obtain interests of tourists who can enjoy the difference of behaviors from other chimpanzee viewing sites such as Gombe. The results also highlight the importance of the conservation of each chimpanzee population.

4.9. Intergroup relationships

The objectives of this research are 1) to advance the habituation of chimpanzees ranging to the neighboring unit-groups of the M group; 2) to grasp their ranging areas, group sizes and compositions; 3) to grasp their food repertories (species and items); 4) to accumulate their behavioral data including cultural variations. The habituation of the new group will be useful for providing another option of chimpanzee viewing to the tourists which will reduce the stress on the M group chimpanzees.

4.10. Development of chimpanzees

The objective of this research is 1) to reveal the developmental process of social relationship between immature and unrelated chimpanzees, such as play, greeting, grooming, and agonistic interactions, 2) to describe the social relationship between orphaned chimpanzees and caregivers, 3) to compare interactions between the mother and offspring, the orphan and caregiver, and immature and unrelated individuals. The results will show the variation and the nature of the life of immature chimpanzees. These pictures will further interest people and may stimulate them to contribute to the conservation of wild chimpanzees including the ecotourism.

5. Hypotheses

5.1. Wildlife conservation in and outside of national parks

This particular study topic is not hypothesis driven, but rather, we will need to collect basic descriptive data on the status of wildlife, ecological threats, and the situation of human–wildlife conflict around the national park. We will also need to have information from various stakeholders, such as tourist camps and local people before we will propose testable hypotheses.

5.2. Mammalian fauna and microbes

Differences in densities of mammalian species will be detected in relation to different vegetation types of the Kasoge area. Because we do not have enough information on detailed ecologies of mammals other than chimpanzees, we first need to conduct preliminary survey before providing concrete hypotheses.

Animals, as well as humans, are normally infected with some parasites in addition to virus and bacteria. The latently infected microbes will sometimes show pathogenesis when the host animal is immunocompromised. In our survey, some pathogens will be detected from both healthy and ill animals. The most important survey is to compare the pathogen between chimpanzees, other animals and humans.

5.3. Genetic analysis of chimpanzees and other mammals

The hypothesis of this study can be summarized as follows: 1) paternity of chimpanzees will be assigned to higher ranking males because the alpha male often monopolize the copulation and male reproductive success will be different according to those tenure as alpha status; 2) although some females will have half-sisters relatedness between female chimpanzees will be lower than that between males because of female

transfer; 3) some loci such as cytochrome b gene in mitochondrial DNA will be sequenced or genotyped in several mammals to assess their genetic diversity at Mahale compared to other populations.

5.4. Ecological influences of chimpanzee ranging and behaviors

The hypothesis of this study all predicts that when feeding competition is weaker, an individual will be meeting variety of other members of the group to widen the chance to collect ecological and/or sociological information at the expense of staying with a specific individual for long time: 1) Ecological information: females' reproductive success depends on the benefits for her dependent offspring (Trivers, 1972). Thus, females with dependents are expected to meet more individuals in feeding context than the other age-sex class; 2) Cultural and sociological information: not only their wide food repertoire, but also the social behaviors are variable, and some are even cultural. Such social information is essential for the survival of infants. Thus, females with dependents and also newly immigrated females are expected to select variety of combination of individuals in social interactions in practice; 3) Ecological and social information: to give dependents the chance to observe both a variety of food repertory and social interactions in practice, but not in the expense of mothers' own feeding time, meeting a large party in a variety of activities may be the most effective strategy.

To estimate chimpanzee populations, information on bed life span is necessary, Zamma and Makelele (2012) have already published on bed life span in Mahale. This year's study conducted by Zamma suggested that bed life span is faster when beds are made between multiple trees. This suggests that, on average, beds may have a faster life span in environments where the distance between trees is shorter and beds are more likely to be made between multiple trees. However, the data from his study is limited, and more data will need to be collected and analyzed in more detail in the future.

Although the following discussion is based on unpublished data, more daybeds have been observed at Mahale when chimpanzees rest during rainy weather than during sunny or cloudy weather (Zamma 2015). The survey this year was conducted during the dry season, and since there were no rainy days, it is inferred that no daybeds were observed. Future surveys should be conducted during the rainy season to detail the frequency of daybed production.

5.5. Social behaviors and social relationships among chimpanzees

Hypotheses of this study would be summarized as follows: 1) Chimpanzees may show some extent of cooperative behaviors; 2) The forms of cooperation may vary between the sexes because chimpanzee males are more closely related with each other than females; 3) Chimpanzees may change such cooperative strategies depending on the relationships with the partner, because they may understand and remember the previous social interactions with each other.

5.6. Feeding behaviors and techniques

There will be a variation of feeding behaviors across individuals in relation to age–sex classes of individuals. For example, younger individuals may not show effective feeding techniques and females may engage more often in insectivory rather than carnivory behaviors. Feeding techniques may differ between adjacent groups of chimpanzees in relation to difference of availability of food species, habitat types and vegetation. However, it is also expected that feeding techniques may differ between groups because of some forms of social transmission.

5.7. Hunting and meat-eating

Hypotheses of this study would be summarized as follows: 1) Chimpanzees may vary their hunting tactics against prey. Specifically, they may adopt 'group hunts' on red colobus and 'opportunistic captures' on other prey including red-tailed monkeys; 2) Tree height and canopy continuity may affect occurrence and success rate of hunting on red colobus; 3) Party size may be the most predictable factor associated with occurrence and success rate of hunting on red colobus; 4) The presence of skillful hunters can increase hunting frequency high above standard levels; 5) Females may contribute about 20 % of prey capture; 6) Both males and females may eat about 30g of mammal meat per day on average; 7) Alpha males assume a social role in controlling meat-sharing sessions; 8) Alpha males preferentially share meat with alliance partners and old individuals; 9) Male testosterone levels increase in response to hunting behavior; 10) High testosterone levels affect motivation to hunt; 11) Skillful hunters that experience metabolic costs may display higher cortisol levels than predicted from dominance rank; 12) Meat intake may affect reproductive behavior of female chimpanzees.

5.8. Cultural behaviors of chimpanzees

Some more behavioral variation of chimpanzees will be detected and described. We hypothesize that more subtle variation that are not explained in relation to ecological and/or genetic differences will be found in domains of social behaviors such as grooming, greeting, courtship, etc. because behavioral patterns in such domains are thought to be only arbitrarily determined with repeated interaction among individuals.

5.9. Intergroup relationships

Some additional behavioral variations will be detected between two neighboring groups. Some of them may be directly caused by the local environmental differences and some may be related to social learning. Chimpanzees of the smaller group will avoid the larger M group when two groups are in proximity or when they hear vocalization of the latter.

5.10. Development of chimpanzees

We address here the developmental process of social behaviors with a focus on interactions between immature and unrelated chimpanzees. There are some possible channels through which immature chimpanzees learn certain behavioral patterns or social skills: they may learn them 1) through interacting with mothers or 2) with unrelated individuals, or 3) from observing mothers' behavior or 4) interactions between unrelated individuals. Important channels for the development can be variable according to the investigated behaviors.

6. Future Plans

6.1. Extensive surveys outside the main study area

Since chimpanzees emit loud calls more frequently while ranging in big parties, it is easier for human observers to find unhabituated chimpanzees in the high fruiting season. The target groups are mainly those groups adjacent to the M group. We intend to follow them thoroughly to habituate them gradually, while

recording their range position by GPS (Global Positioning System) and collecting circumstantial evidences. When direct observation is possible, their behaviors and vocalizations will be record by digital video cameras. Feces and food remains will also be collected for food analysis and for obtaining DNA samples (see above). We will adopt camera trapping survey to monitor ranging behavior of neighboring unit-groups during low fruiting season.

We make census lines in the study area and conduct 1) vegetation surveys to show the ratio of vegetation types, density of plants, and plant phenology, 2) population censuses of habitat mammals, and 3) surveys of chimpanzee beds. Based on these fieldworks and satellite data and GIS, we will compare the environmental characteristics and ecology of chimpanzees and other mammals in Mahale Mountains National Park and adjacent areas around the park.

As for the "bed survey," we need to study the number of daybeds over a longer period of time and analyze factors related to bed lifespan. We plan to continue to accumulate data by conducting a survey similar to the present year's survey.

6.2. Genetic, hormonal, and microbial samplings

Urinary and fecal samples for hormonal analyses will be collected from chimpanzees by the non-invasive techniques (Fujita, 2015). Urine and feces will be collected during daily follows of chimpanzees. Urine and feces should be frozen after collection and maintained at $\leq -20^{\circ}$ C in the solar refrigerator. Alternative methods for storage might be the use of preservatives such as ethanol (urine and feces) or drying with silica gel (feces).

Food wadges, feces, urine and hair from chimpanzees will be collected for DNA extraction. Other materials such as semen (estrous females occasionally drop them from their vulva) and blood (injured individuals occasionally leave them on rocks or fallen leaves) will be non-invasively collected when possible. Carcasses and skeletons of chimpanzees and other mammals will be collected to identify the animal and to investigate causes of deaths and for genetic analyses. Non-invasive DNA samples will be collected also from other chimpanzee groups and other larger mammals. DNA extraction from these samples and analysis of DNA will be conducted in the laboratory of Kyoto University, Japan.

Non-invasive sampling of saliva, urine and feces from various kinds of mammals in order to detect microbes will be made. Trapping of some small mammals (such as bats and rodents) and some birds to collect blood and cerebrospinal fluid under euthanasia with over volume of anesthesia will also be conducted. Sampling from insects for pathogen detection will also be made. The collected microbes will be treated and their DNA or RNA will be analyzed and identified at laboratory in Arusha and in Japan.

6.3. Promotion of joint research

This project has strengthened its links with the University of Dar es Salaam. For example, Shinshu University and the University of Dar es Salaam have an international academic exchange agreement. In addition, project members Takuya Matsumoto, PhD, of Shinshu University, and Fred Chibwana, PhD, of the Department of Zoology and Wildlife Conservation, University of Dar es Salaam, are leading a research project on the wildlife of the United Republic of Tanzania. The documentation of the joint research agreement on wild organisms in the United Republic of Tanzania is being prepared and is being finalized for agreement. We will continue to work with the University of Dar es Salaam, taking into account the "Access to genetic resources and Benefit Sharing (ABS)" under the Convention on Biological Diversity.

6.4. Ecological data sampling

Vegetation, floral and plant phenology will be monitored to compare with utilization of habitat by chimpanzees. Line-transect was set up in 1996 for vegetational survey. To assess the change after the time of this survey will be conducted on this transect again. Phenological monitoring using the above line-transect have been conducted up to now, and the presence of new leaves, flowers and fruits are monitored. This will be continued for assessing food availability and also for assessing global climatic impact on phenological patterns in Mahale. Although about 600 species of plants have collected and identified before (Nishida & Uehara, 1981; Itoh, 2015; Itoh & Nakamura, 2015b), more efforts are needed to collect plant specimens for identification. In light of an expert's estimate, Mahale is expected to have more than 2000 species of vascular plants given its geographical position in the African tropics (Lovett, 1994). Thus, if unidentified plants are found, they will be collected for preparing specimens. The specimen will be sent to herbarium in Tanzania (i.e., Department of Botany, University of Dar es Salaam) for identification.

For the faunal studies, census of diurnal large- and medium-sized animals will be conducted by recording encounters, mainly by sighting, with each animal species within a certain sample width along each route. Fecal census of animals will be made in order to estimate densities of nocturnal animals. Fecal samples will be collected in order to obtain the information of diet and genetic data. For small-sized mammals, camera traps may also be helpful. Efforts will be made to habituate some groups of red-tailed monkeys and red colobus in order to have more details of behavioral adaptations of these primate species. In relation to study of insectivory by mammals, insect specimens will be collected and sent to Department of Zoology, University of Dar es Salaam, Natural History Museum of U.K. and Kyoto University for identification and storage.

6.5. Behavioral observation of wild chimpanzees

For recording the behaviors or habituated M-group chimpanzees, whole-day focal animal sampling or focal group following will be made. We will record various types of behaviors, food items, party types, etc. Targets of the observation will be individuals of various age–sex class depending on the subtopics. We will keep distance of at least 7.5 m from the chimpanzees and always wear face mask in order to minimize the risk of transmitting human diseases. We will also take one-week quarantine period before starting full-day follow of chimpanzees. An audio recorder, still camera, video camera, and field notes may be used to collect data depending on the subtopics. Arbitral collection of food remains, tool materials, or other materials relevant to the subtopics during or after the behavioral observation will be made whenever it is necessary. When collecting these samples, maximum cautions will be paid not to disturb behaviors of chimpanzees.

6.6. Behavioral observation of giraffes

We will record the behavior of giraffes in the Katavi National Park. We will mainly collect data on their feeding behavior, social relationships, and behavioral changes in the presence of humans. We will keep a distance of at least 50 m from the focal animal and collect data in a non-invasive manner.

7. Impacts

The following benefits to Tanzania are expected from our proposed research.

1) Monitoring the habituated M group of chimpanzees, the most precious natural resources of the Mahale National Park

- 2) Estimation of chimpanzee density and gene flow of Greater Mahale ecosystem for better knowledge of wildlife management
- 3) Compilation of checklist of plants, mammals, birds, reptiles and other remarkable animals
- 4) Supply of information that is relevant to wildlife conservation and park management
- 5) Education of Tanzanian students and park rangers
- 6) Supply of information useful for education and contentment of visitors
- 7) Maintenance of observation trails used by scientists, park staff and visitors

8. Bibliography

- Alberts B, Johnson A, Lewis J, Raff M, Roberts K, Walter P 2002. *Molecular Biology of the Cell, Fourth Edition.* Garland Science, New York.
- Azuma S, Toyoshima A 1961–62. Progress report of the survey of chimpanzees in their natural habitat, Kabogo Point Area, Tanganyika. *Primates* 3: 61–70.
- Basabose AK 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *Am J Primatol* 58:1–21.
- Bencin H, Kioko, J, Kiffner, C 2016. Local people's perceptions of wildlife species in two distinct landscapes of Northern Tanzania. *J for Nat Cons* 34: 82–92.
- Boesch C 1991. Teaching among wild chimpanzees. Anim Behav 41: 530-532.
- Boesch C, Boesch H 1989. Hunting behavior of wild chimpanzees in the Taï National Park. *Am J Phys Anthropol* 78: 547–573.
- Boesch C, Boesch H 1990. Tool use and tool making in wild chimpanzees. Folia Primatol 54: 86–99.
- Boesch C, Boesch-Achermann H 2000. The Chimpanzees of the Taï Forest. Oxford University Press, Oxford.
- Boesch C, Kohou G, Nene H, Vigilant L 2006. Male competition and paternity in wild chimpanzees of Taï forest. *Am J Phys Anthropol* 130: 103–115.
- Boesch C, Tomasello M 1998. Chimpanzee and human cultures. Curr Anthropol 39: 591-614.
- Boesch C, Uehara S, Ihobe H 2002. Variations in chimpanzee-red colobus interactions. In: Boesch C, Hohmann G, Marchant LF (eds), *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp. 221–230.
- Byrne RW, Barnard PJ, Davidson I, Janik VM, McGrew WC, Miklosi A, Wiessner P 2004. Understanding culture across species. *Trends Cogn Sci* 8: 341–346.
- Chapman CA, Wrangham RW, Chapman LJ 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiol* 36: 59–70.
- Clutton-Brock TH, Harvey PH 1977. Primates, brains and ecology. J Zool 190: 309-323.
- Collins DA, McGrew WC 1987. Termite fauna related to differences in tool-use between groups of chimpanzees (*Pan troglodytes*). *Primates* 28: 457–471.
- Constable JL, Ashley MV, Goodall J, Pusey AE 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Mol Ecol* 10: 1279–1300.
- Deblauwe I, Janssens GPJ 2008. New insights in insect prey choice by chimpanzees and gorillas in Southeast Cameroon: the role of nutritional value. *Am J Phys Anthropol* 135: 42–55.
- Dickman, A J 2010. Complexities of conflict: The importance of considering social factors for effectively resolving humanwildlife conflict. *Anim Conserv* 13: 458–466.
- Fleagle JG 1999. Primate Adaptation and Evolution. Academic Press, San Diego.
- Fujita S 2015. Field endocrinology. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), Mahale Chimpanzees: 50 Years of Research, Cambridge University Press, Cambridge, UK, pp. 601–611.
- Fujita S, Inoue E 2015. Sexual behavior and mating strategies. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*, Cambridge University Press, Cambridge, UK, pp. 485–495.
- Fuse M 2013. Chimpanzees detect ant-inhabited dead branches and stems: a study of the utilization of plant-ant relationships in the Mahale Mountains, Tanzania. *Primates* 54: 385–397.
- Gagneux P, Boesch C, Woodruff DS 1999. Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Anim Behav* 57: 9–32.
- Gilby IC 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim Behav* 71: 953–963.
- Gilby IC, Eberly LE, Pintea L, Pusey AE 2006. Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii. Anim Behav* 72: 169–180.
- Gilby IC, Eberly LE, Wrangham RW 2008. Economic profitability of social predation among wild chimpanzees: individual variation promotes cooperation. *Anim Behav* 75: 351–360.
- Gilby IC, Wrangham RW 2007. Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behav Ecol Sociobiol* 61: 1771–1779.

Gomes CM, Boesch C 2009. Wild chimpanzees exchange meat for sex on a long-term basis. PLoS One 4: e5116.

- Goodall J 1963. Feeding behaviour of wild chimpanzees: A preliminary report. Symp Zool Soc Lond 10: 39-47.
- Goodall J 1986. The Chimpanzees of Gombe: Patterns of Behavior. Cambridge, Belknap Press of Harvard University Press.
- Gould L 2000. Adoption of a wild orphaned ring-tailed lemur infant by natal group members: adaptive explanations. *Primates* 41: 413–419.
- Hamelmann E, Herz U, Holt P, Host A, Lauener RP, Matricardi PM, Wahn U, Wickman M 2008. New visions for basic research and primary prevention of pediatric allergy: an iPAC summary and future trends. *Pediatr Allergy Immunol Suppl* 19: 4–16.
- Hanamura S 2015a. Fission-fusion grouping. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp. 106–118.
- Hanamura S 2015b. Male–female relationships: Affiliative, interventional, and dominant-subordinate interactions. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 410–420.
- Hanamura S, Kooriyama T, Hosaka K 2015. Diseases and deaths: variety and impact on social life. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 354–371.
- Hayakawa T 2015. Taste of chimpanzee foods. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees:* 50 Years of Research. Cambridge University Press, Cambridge, pp. 246–258.
- Hayaki H 1988. Association partners of young chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates* 29: 147–161.
- Herbinger I, Boesch C, Rothe H 2001. Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Cote d'Ivoire. *Int J Primatol* 22: 143–167.
- Hiraiwa-Hasegawa M 1990a. A note on the ontogeny of feeding. In: Nishida T (ed), *The Chimpanzees of Mahale Mountains*. Tokyo University Press, Tokyo, pp 279–283.
- Hiraiwa-Hasegawa M 1990b. Role of food sharing between mother and infant in the ontogeny of feeding behavior. In: Nishida T (ed), *The Chimpanzees of Mahale Mountains*. Tokyo University Press, Tokyo, pp. 267–275.
- Hosaka K 2022. MWCS under COVID-19 crisis. Pan Afr News 28: 21.
- Hosaka K 2015a. Who's who. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 48–67.
- Hosaka K 2015b. Hunting and food sharing. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50* Years of Research, Cambridge University Press, Cambridge, UK, pp. 274–290.
- Hosaka K, Matsusaka T, Hanamura S 2015. Vocal communication. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 533–543.
- Hosaka K, Nakamura M 2015a. Male-male relationships. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 387–398.
- Hosaka K, Nakamura M 2015b. Conservation and the future. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 679–690.
- Hosaka K, Nishida T, Hamai M, Matsumoto-Oda A, Uehara S 2001. Predation of mammals by the chimpanzees of the Mahale Mountains, Tanzania. In: Galdikas BMF, Briggs NE, Sheeran L, Shapiro G (eds), *All Apes Great and Small, vol. 1: African Apes.* Kluwer, New York.
- Hosaka K, Nakamura M, Takahata Y 2020. Longitudinal changes in the targets of chimpanzee (*Pan troglodytes*) hunts at Mahale Mountains National Park: how and why did they begin to intensively hunt red colobus (*Piliocolobus rufomitratus*) in the 1980s? *Primates* 61: 391–401.
- Hosaka K, Nakamura M, Ihobe H, Takahata Y 2023. Long-term changes in age–sex groups of the captors and developmental stages of the prey in the red colobus hunting behavior by the chimpanzees of Mahale, Tanzania. *Afr Stud Monogr* 43: 28–41.
- Hosaka K, Nakamura M, Ihobe H, Takahata Y 2024a. Seasonal hunting for red colobus monkeys by Mahale chimpanzees. *Pan Afr News* 29: 12–14.
- Hosaka K, Nakamura M, Ihobe H, Takahata Y 2024b. Male chimpanzee age affects red colobus monkey hunting success. *Pan Afr News* 29: 15–16.
- Huffman MA, Kalunde MS 1993. Tool-assisted predation on a squirrel by a female chimpanzee in the Mahale Mountains, Tanzania. *Primates* 34: 93–98.
- Humle T, Matsuzawa T 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am J Primatol* 58: 133–148.
- Ihobe H 2002. Anti-predatory strategies of red colobus against chimpanzee hunting. In: Nishida T, Uehara S, Kawanaka K (eds), *The Chimpanzees at Mahale: Thirty Seven Years of "Panthropology"*. Kyoto University Press, Kyoto, pp. 245–260, in Japanese.
- Ihobe H 2015a. Mammalian fauna. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp. 193–212.
- Ihobe H 2015b. Appendix III. Mammal list. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 740–743.
- Ihobe H, Uehara S 1999. A preliminary report on the impact of chimpanzee hunting on mammal populations at Mahale, Tanzania. *Primate Res* 15: 163–169, in Japanese.

Inoue E 2005. DNA sampling and DNA analysis of chimpanzees at Mahale. Pan Afr News 12: 22-24.

- Inoue E 2015. Genetic studies. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 625–638.
- Inoue E, Inoue-Murayama M, Nishida T, Vigilant L, Takenaka O 2007a. Paternity analysis of wild chimpanzees. DNA Polymorphism 15: 54–58, in Japanese.
- Inoue E, Inoue-Murayama M, Takenaka O, Nishida T 2007b. Wild chimpanzee infant urine and saliva sampled noninvasively usable for DNA analyses. *Primates* 48: 156–159.
- Inoue E, Inoue-Murayama M, Vigilant L, Takenaka O, Nishida T 2008. Relatedness in wild chimpanzees: influence of paternity, male philopatry, and demographic factors. *Am J Phys Anthropol* 137: 256–262.
- Inoue-Nakamura N, Matsuzawa T 1997. Development of stone tool use by wild chimpanzees (*Pan troglodytes*). J Comp Psychol 111: 159–173.
- Isabirye-Basuta G 1988. Food competition among individuals in a free-ranging chimpanzee community in Kibale Forest, Uganda. *Behaviour* 105: 135–147.
- Itani J 1977. Ethnozoology of the Batongwe. In: Itani J, Harako R (eds), *The Natural History of Man*. Yuzan-kaku, Tokyo, pp. 441–537, in Japanese.
- Itani J 1979. Distribution of chimpanzees in an arid area. In: Hamburg DA, McCown ER (eds) *The Great Apes*. Benjamin/Cummings, Menlo Park, pp. 55–71.
- Itoh N 2015. Appendix I. Floral list. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research.* Cambridge University Press, Cambridge, pp. 691–716.
- Itoh N, Muramatsu D 2015. Patterns and trends in fruiting phenology: Some important implications for chimpanzee diet. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 174–194.
- Itoh N, Nakamura M 2015a. Social system: Features and variations. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 71–81.
- Itoh N, Nakamura M 2015b. Mahale flora: Its historical background and long-term changes. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 150–173.
- Itoh N, Nakamura M 2015c. Diet and feeding behavior. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 227–245.
- Itoh N, Nakamura M 2015d. Female–female relationships. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 399–409.
- Itoh N, Nishida T 2007. Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates* 48: 87–96.
- Itoh N, Sakamaki T, Hamisi M, Kitopeni R, Bunengwa M, Matumla M, Athumani K, Mwami M, Bunengwa H 1999. A new record of invasion by an unknown unit group into the center of M group territory. *Pan Afr News* 6: 8–10.
- Itoh N, Nakamura M, Ihobe H, Uehara S, Zamma K, Pintea L, Seimon A, Nishida T 2012. Long-term changes in the social and natural environments surrounding the chimpanzees of the Mahale Mountains National Park. In: The Ecological Impact of Long-Term Changes in Africa's Rift Valley. Plumptre AJ (ed). NOVA Science, New York, pp. 249–277.
- Itoh N, Zamma K, Matsumoto T, Nishie H, Nakamura M 2015. Appendix II. Dietary list. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 717–739.
- Izawa K 1970. Unit-groups of chimpanzees and their nomadism in the savanna woodland. *Primates* 11: 1–46.
- Jones C, Sabater Pi J 1969. Sticks used by chimpanzees in Rio Muni, West Africa. Nature 223: 100–101.Kaburu SS, Inoue S, Newton-Fisher NE 2013. Death of the alpha: Within-community lethal violence among chimpanzees of the Mahale Mountains National Park. Am J Primatol 75: 789–797.
- Kaburu SSK, Newton-Fisher NE 2015a. Trading or coercion? Variation in male mating strategies between two communities of East African chimpanzees. *Behav Ecol Sociobiol* 69: 1039–1052.
- Kaburu SSK, Newton-Fisher NE 2015.b Egalitarian despots: Hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes. Anim Behav* 99: 61–71.
- Kaburu SSK, Newton-Fisher NE 2016. Bystanders, parcelling, and an absence of trust in the grooming interactions of wild male chimpanzees. *Sci Rep* 6: 20634.
- Kaburu SS, Inoue S, Newton-Fisher NE 2013. Death of the alpha: Within-community lethal violence among chimpanzees of the Mahale Mountains National Park. *Am J Primatol* 75: 789–797.
- Kagei N, Asano K 1980. Helminths of animals imported to Japan II: parasitic infection and its problems of imported primates. *Jpn J Trop Med Hygie* 8: 9–12
- Kano T 1972. Distribution and adaptation of the chimpanzee in the open country on the eastern shore of Lake Tanganyika. *Kyoto Univ Afr Stud* 7: 37–129.
- Kappeler PM, Pereira ME, Schaik CP 2003. Primate life histories and socioecology. In: Kappeler PM, Pereira ME (eds), *Primate Life Histories and Socioecology.* The University of Chicago Press, Chicago and London, pp: 1–20.
- Kiyono M 2015. Insect-feeding behavior and insect fauna: With special reference to plant-insect relationships. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 291–309.
- König, HJ, Kiffner C, Kramer-Schadt S, Fürst C, Keuling O, Ford AT 2020. Human–wildlife coexistence in a changing world. *Cons Biol* 34: 786–794.

Kooriyama T, Hasegawa H 2015. Internal parasites. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 639–653.

- Kutsukake N, Hosaka K 2015. Aggression and conflict management. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 448–458.
- Langergraber KE, Mitani JC, Vigilant L 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proc Nat Acad Sci US* 104: 7786–7790.

Lonsdorf EV, Eberly LE, Pusey AE 2004. Sex differences in learning in chimpanzees. Nature 428: 715-716.

- Lovett JC 1994. Zambezian regional centre of endemism: CPD site AF33 Mahale-Karobwa Hills, Tanzania. In: Davis SD, Heywood VH, Hamilton AC (eds), Centres of Plant Diversity, A Guide and Strategy for their Conservation. WWF-IUCN-ODA.
- Lukas D, Reynolds V, Boesch C, Vigilant L 2005. To what extent does living in a group mean living mean living with kin? *Molecul Ecol* 14: 2181–2196.
- Manson JH, Wrangham RW 1991. Intergroup aggression in chimpanzees and humans. Curr Anthropol 32: 369-390.
- Marchant LF 2015. Laterality of hand function. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees:* 50 Years of Research. Cambridge University Press, Cambridge, pp. 556–567.
- Matsumoto T 2017. Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania: Implications for nutritional independence long before cessation of nipple contact. *Am J Phys Anthropol* 163: 356–366.
- Matsumoto T, Hayaki H 2015. Development and growth: With special reference to mother-infant relationships. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 313–325.
- Matsumoto T, Itoh N, Inoue S, Nakamura M 2016. An observation of a severely disabled infant chimpanzee in the wild and her interactions with her mother. *Primates* 57: 3–7.
- Matsusaka T 2014. The Evolution of Laughter in Chimpanzees and Humans. *The 6th International Symposium: The Culture* of Laughter in Japan: Tradition and Present. Kansai University Japan-EU Research Center Report 5(5):39–44.
- Matsusaka T 2014. [Why do humans laugh: From the perspective of ethology.] Warai-gaku Kenkyu 21: 5-18, in Japanese.
- Matsusaka T, Shimada M, Nakamura M 2015. Diversity of play. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp. 544–555.
- Matsuzawa T 1994. Field experiments of use of stone tools in the wild. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds), *Chimpanzee Cultures*. Cambridge, Mass. Harvard University Press, pp 351–370.
- Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G 2001. Emergence of culture in wild chimpanzees: education by master-apprenticeship. In: Matsuzawa T (ed), *Primate Origins of Human Cognition and Behavior*. Tokyo Springer, pp 557–574.
- McGrew WC 1974. Tool use by wild chimpanzees in feeding upon driver ants. J Hum Evol 3: 501-508.
- McGrew WC 1992. Chimpanzee Material Culture: Implications for Human Evolution. Cambridge University Press, Cambridge.
- McGrew WC 1998. Culture in nonhuman primates? Annu Rev Anthropol 27: 301-328.
- McGrew WC 2004. The Cultured Chimpanzee: Reflections on Cultural Primatology. Cambridge Univ. Press, Cambridge.
- McGrew WC, Collins DA 1985. Tool use by wild chimpanzees (*Pan troglodytes*) to obtain termites (*Macrotermes herus*) in the Mahale Mountains, Tanzania. *Am J Primatol* 9: 47–62.
- McGrew WC, Marchant LF, Scott SE, Tutin CEG 2001. Intergroup differences in a social custom of wild chimpanzees: the grooming hand-clasp of the Mahale Mountains. *Curr Anthropol* 42: 148–153.
- McGrew WC, Pruetz JD, Fulton SJ 2005. Chimpanzees use tools to harvest social insects at Fongoli, Senegal. *Folia Primatol* 76: 222–226.
- McGrew WC, Tutin CEG 1978. Evidence for a social custom in wild chimpanzees? Man 13: 234-251.
- Mitani JC, Struhsaker TT, Lwanga JS 2000. Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: implications for conservation and census methods. *Int J Primatol* 21: 269–286.
- Mitani JC, Watts DP 1999. Demographic influences on the hunting bahavior of chimpanzees. *Am J Phys Anthropol* 109: 439–454.
- Moore J 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew WC, Marchant LF, Nishida T (eds), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 275–292.
- Morin PA, Chambers KE, Boesch C, Vigilant L 2001. Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Molecul Ecol* 10: 1835–1844.
- Morin PA, Wallis J, Moore JJ, Woodruff DS 1994. Paternity exclusion in a community of wild chimpanzees using hypervariable simple sequence repeats. *Molecul Ecol* 3: 469–477.
- Muller MN, Wrangham RW 2004a. Dominance, aggression and testosterone in wild chimpanzees: a test of the 'challenge hypothesis'. *Anim Behav* 67: 113–123.
- Muller MN, Wrangham RW 2004b. Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 55: 332–340.
- Myowa-Yamakoshi M, Matsuzawa T 1999. Factors influencing imitation of manipulatory actions in chimpanzees (*Pan* troglodytes). J Comp Psychol 113: 128–136.
- Nakamura M 1997. First observed case of chimpanzee predation on yellow baboons (*Papio cynocephalus*) at the Mahale Mountains National Park. *Pan Afr News* 4: 9–11.

- Nakamura M 2002. Grooming-hand-clasp in Mahale M group chimpanzees: implication for culture in social behaviors. In: Boesch C, Hohmann G, Marchant LF (eds), *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp 71–83.
- Nakamura M 2010. Ubiquity of culture and possible social inheritance of sociality among wild chimpanzees. In: *The Mind of the Chimpanzee: Ecological and Experimental Perspectives*, Lonsdorf EV, Ross SR, Matsuzawa T (eds), University of Chicago Press, pp.156–167.
- Nakamura M 2015a. Demography of the M group. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 82–93.
- Nakamura M 2015b. Home range. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 94–105.
- Nakamura M 2015c. Current status of tourism. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees:* 50 Years of Research. Cambridge University Press, Cambridge, pp. 657–667.
- Nakamura M 2015d. Culture and subsistence ecology of the Tongwe, and their significance in chimpanzee research. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 668–678.
- Nakamura M 2015e. Appendix VI. List of abbreviations used for Mahale chimpanzees' names. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 753–761.
- Nakamura M 2022. Greetings among female chimpanzees in Mahale, Tanzania. Am J Primatol, e23417.
- Nakamura M, Hosaka K 2015. Orphans and allomothering. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 421–432.
- Nakamura M, Itoh N 2015a. Seeds from feces: Implications for seed dispersal and fecal analyses. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 259–273.
- Nakamura M, Itoh N 2015b. Conspecific killings. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp.372–383.
- Nakamura M, Itoh N 2015c. Larger chimpanzee-dispersed seeds are elongated at Mahale, Tanzania: Possible consequence of plant-disperser interaction? *J Trop Ecol* 31: 183–186.
- Nakamura M, Nishida T 2006. Subtle behavioral variation in wild chimpanzees, with special reference to Imanishi's concept of *kaluchua*. *Primates* 47: 35–42.
- Nakamura M, Nishida T 2013. Ontogeny of a social custom in wild chimpanzees: Age changes in grooming hand-clasp at Mahale. *Am J Primatol* 75: 186–196.
- Nakamura M, Uehara S 2004. Proximate factors of different types of grooming hand-clasp in Mahele chimpanzees: implications for chimpanzee social customs. *Curr Anthropol* 45: 108–114.
- Nakamura M, Corp N, Fujimoto M, Fujita S, Hanamura S, Hayaki H, Hosaka K, Huffman MA, Inaba A, Inoue E, Itoh N, Kutsukake N, Kiyono-Fuse M, Kooriyama T, Marchant LF, Matsumoto-Oda A, Matsusaka T, McGrew WC, Mitani JC, Nishie H, Norikoshi K, Sakamaki T, Shimada M, Turner LA, Wakibara JV, Zamma K 2013. Ranging behavior of Mahale chimpanzees: a 16 year study. *Primates* 54: 171–182.
- Nakamura M, Hayaki H, Hosaka K, Itoh N, Zamma K 2014. Orphaned male chimpanzees die young even after weaning. *Am J Phys Anthropol* 153: 139–143.
- Nakamura M, Hosaka K, Takahata Y 2015. Research history. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 21–32.
- Nakamura M, Hosaka K, Itoh N, Matsumoto T, Matsusaka T, Nakazawa N, Nishie H, Sakamaki T, Shimada M, Takahata Y, Yamagami M, Zamma K 2019. Wild chimpanzees deprived a leopard of its kill: Implications for the origin of hominin confrontational scavenging. J Hum Evol 131: 129–138.
- Nakamura M, Nakazawa N, Nyundo BR, Itoh N 2017. Tongwe names of mammals: Special reference to mammals inhabiting the Kasoje Area, Mahale Mountains, western Tanzania. *Afr Stud Monogr* 38: 221–242.
- Nakamura M, Sakamaki T, Zamma K 2017. What volume of seeds can a chimpanzee carry in its body? Primates 58: 13–17.
- Nakazawa N 2020. Primates are an important food resource for leopards (*Panthera pardus*) in Mahale, Tanzania. Afr J Ecol 58: 399–408.
- Nakazawa N 2023. Overlap of activity patterns between leopards and their potential prey species in Mahale Mountains National Park, Tanzania. *J Zool* 319: 188–199.
- Nakazawa N, Hanamura S, Inoue E, Nakatsukasa M, Nakamura M 2013. A leopard ate a chimpanzee: The first evidence from East Africa. *J Hum Evol* 65: 334–337.
- Nishida T 1968. The social group of wild chimpanzees in the Mahali Mountains. Primates 9: 167-224.
- Nishida T 1973. The ant-gathering behavior by the use of tools among wild chimpanzees of the Mahali Mountains. *J Human Evol* 2:357–370.
- Nishida T 1980. The leaf-clipping display: a newly-discovered expressive gesture in wild chimpanzees. J Human Evol 9: 117–128.
- Nishida T 1987. Local traditions and cultural transmission. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds), *Primate Societies*. University of Chicago Press, Chicago, pp 462–474.
- Nishida T 1989. A note on the chimpanzee ecology of the Ugalla area, Tanzania. Primates 30: 129-138.
- Nishida T 1990. A quarter century of research in the Mahale Mountains: An overview. In: Nishida T (ed) The Chimpanzees of

the Mahale Mountains. Univ. of Tokyo Press, Tokyo, pp 3-35.

- Nishida T 2003. Individuality and flexibility of cultural behavior patterns in chimpanzees. In: de Waal FB, Tyack PL (eds), *Animal Social Complexity: Intelligence, Culture, and Individualized Societies*. Harvard University Press, Cambridge, pp 392–413.
- Nishida T 2012. Chimpanzees of the Lakeshore: Natural History and Culture at Mahale. Cambridge University Press, Cambridge.
- Nishida T, Corp N, Hamai M, Hasegawa T, Hiraiwa-Hasegawa M, Hosaka K, Hunt KD, Itoh N, Kawanaka K, Matsumoto-Oda A, Mitani JC, Nakamura M, Norikoshi K, Sakamaki T, Tuner L, Uehara S, Zamma K 2003. Demography, female life history and reproductive profiles among the chimpanzees of Mahale. *Am J Primatol* 59: 99–121.
- Nishida T, Hasegawa T, Hayaki H, Takahata Y, Uehara S 1992. Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM (eds), *Topics in Primatology, Vol. 1: Human Origins*, University of Tokyo Press, Tokyo, pp.159–174.
- Nishida T, Hiraiwa M 1982. Natural history of a tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. *J Human Evol* 11: 73–99.
- Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y 1985. Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. Z Tierpsychol 67: 284–301.
- Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M 1999. Ethogram and ethnography of Mahale chimpanzees. *Anthropol Sci* 107: 141–188.
- Nishida T, Kawanaka K 1972. Inter-unit-group relationships among wild chimpanzees of the Mahali Mountains. *Kyoto Univ* Afr Stud 7: 131–169.
- Nishida T, Turner LA 1996. Food transfer between mother and infant chimpanzees of the Mahale Mountains National Park, Tanzania. *Int J Primatol* 17: 947–968.
- Nishida T, Uehara S 1980. Chimpanzees, tools, and termites: Another example from Tanzania. Curr Anthropol 21: 671-672.
- Nishida T, Uehara S 1981. Kitongwe names of plants: A preliminary listing. *Afr Stud Monogr* 1: 109–131.
- Nishida T, Uehara S 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): Long-term record from the Mahale Mountains, Tanzania. *Afr Stud Monogr* 3: 109–130.
- Nishida T, Wallauer W 2003. Leaf-pile pulling: an unusual play pattern in wild chimpanzees. Am J Primatol 60: 167–173.
- Nishie H 2011. Natural history of Camponotus ant-fishing by the M group chimpanzees at the Mahale Mountains National Park, Tanzania. Primates 52: 329–342.
- Nishie H 2015. Use of tools and other objects. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees:* 50 Years of Research. Cambridge University Press, Cambridge, pp. 568–582.
- Nishie H, Nakamura M 2015. Culture. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 521–532.
- Nishie H, Nakamura M 2018. A newborn infant chimpanzee snatched and cannibalized immediately after birth: Implications for "maternity leave" in wild chimpanzees. *Am J Phys Anthropol* 165: 194–199.
- Nyhus PJ 2016. Human-wildlife conflict and coexistence. Annu Rev Env Res 41: 143-171.
- Ogawa H, Idani G, Moore J, Pintea L, Hernandez-Aguilar A 2007. Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. *Int J Primatol* 28: 1397–1412.
- Ogawa H, Kanamori M, Mukeni SH 1997. The discovery of chimpanzees in the Lwazi River area, Tanzania: A new southern distribution limit. *Pan Afr News* 4: 1–3.
- Ogawa H, Moore J, Kamenya S 2006a. Chimpanzees in the Ntakata and Kakungu areas, Tanzania. *Primate Conserv* 21: 97–101.
- Ogawa H, Sakamaki T, Idani G 2006b. The influence of Congolese Refugees on chimpanzees in the Lilanshimba area, Tanzania. *Pan Afr News* 13: 21–22.
- Palthe TVW, van Hoof JARAM 1975. A case of the adoption of an infant chimpanzee by a suckling foster chimpanzees. *Primates* 16: 231–234.
- Pampiglion S, Ricciardi ML 1971. The presence of *Strongyloidesfalleborni* von Linstow, 1905, in man in Central and East Africa. *Parassitologia* 13: 257–269.
- Pampiglion S, Ricciardi ML 1972. Experimental infection with human strain *Strongyloidesfulleborni* in man. *Lancet* 7752: 663–665.
- Pierron M, Sueur C, Shimada M, MacIntosh AJJ, Romano V 2024. Epidemiological consequences of individual centrality on wild chimpanzees. *Am J Primatol* e23682.
- Pusey AE, Packer C 1987. Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds), *Primate Societies*. University of Chicago Press, Chicago, pp 250–266.
- Reynolds V 2005. The Chimpanzees of the Budongo Forest: Ecology, Behaviour, and Conservation. Oxford University Press, Oxford.
- Reynolds V, Reynolds F 1965. Chimpanzees of the Budongo Forest. In: De Vore I (ed), *Primate Behavior*. New York Holt, Rinehart and Winston. pp 368–424.
- Sakamaki T 2011 Submissive pant-grunt greeting of female chimpanzees in Mahale Mountains National Park, Tanzania. *Afr Stud Monogr* 32: 25–41.
- Sakamaki T, Hayaki H 2015. Greetings and dominance. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 459–471.
- Sakamaki T, Nakamura M 2007. Preliminary survey of unhabituated chimpanzees in the Mahale Mountains National Park,

Tanzania: Behavioral diversity across neighboring unit-groups and intergroup relationships. In: *Formation of a Strategic Base for Biodiversity Studies*. The 21st Century COE Program of Kyoto University, pp 278–280.

- Sakamaki T, Nakamura M 2015. Intergroup relationships. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 128–139.
- Sakamaki T, Nakamura M, Nishida T 2007. Evidence of cultural differences in diet between two neighboring unit groups of chimpanzees in Mahale Mountains National Park, Tanzania. *Pan Afr News* 14: 3–5.
- Sanz C, Morgan D, Gulick S 2004. New insights into chimpanzees, tools, and termites from the Congo basin. *Am Nat* 164: 567–581.
- Seike T 2022. Frequent predation on primates by crowned eagles (*Stephanoaetus coronatus*) in Mahale Mountains National Park, Tanzania. *Primates* 63: 327–333.
- Shimada M 2003. A note on the southern neighboring groups of M group. Pan Afr News 10: 11-14.
- Shimada M 2013a. Dynamics of the temporal structures of playing clusters and cliques among wild chimpanzees in Mahale Mountains National Park. *Primates* 54: 245–257.
- Shimada M 2013b. Wild chimpanzees can perform social grooming and social play behaviors simultaneously. *Primates* 54: 315–317.
- Shimada M, Sueur C 2014. The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania. *Am J Primatol* 76: 1025–1036.
- Shimada M, Matsusaka T, Hayaki H 2015. Social play: History of the studies at Mahale and a new perspective. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 496–509.
- Shimada M, Yano W 2023. Behavioral responses of wild chimpanzees toward a juvenile that suddenly lost its animacy due to a fall accident. *Sci Rep* 13: 16661.
- Silk JB 1978. Patterns of food sharing among mother and infant chimpanzees at Gombe National Park, Tanzania. *Folia Primatol* 29: 129–141.
- Silk JB 1979. Feeding, fotaging, and food sharing behavior of immature chimpanzees. Folia Primatol 31:123-142.
- Stanford CB 1995. The influence of chimpanzee predation of group size and anti-predator behaviour in red colobus monkeys. *Anim Behav* 49: 577–587.
- Stanford CB 1998. Chimpanzee and Red Colobus: The Ecology of Predator and Prey. Harvard University Press, Cambridge.
- Stanford CB, Wallis J, Matama H, Goodall J 1994. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *Am J Phys Anthropol* 94: 213–228.
- Sugiyama Y 1995. Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates* 36:193–205.
- Sugiyama Y, Kawamoto S, Takenaka O, Kumazaki K, Miwa N 1993. Paternity discrimination and inter-group relationships of chimpanzees at Bossou. *Primates* 34: 545–552.
- Sugiyama Y, Koman J 1979. Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. *Primates* 20: 513–524.
- Suzuki A 1966. On the insect-eating habits among wild chimpanzees living in the savanna woodland of western Tanzania. *Primates* 7: 481–487.
- Taberlet P, Griffin S, Goossens B, Questiau S, Manceau V, Escaravage N, Waits LP, Bouvet J 1996. Reliable genotyping of samples with very low DNA quantities using PCR. *Nucl Acids Res* 24: 3189–3194.
- Takahata Y 2015. Disappearance of K group male chimpanzees: Re-examination of group extinction. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 119–127.
- Tanaka I 2004. Non-offspring nursing by a nulliparous pregnant female just before first parturition in free-ranging Japanese macaques. *Primates* 45: 205–206.
- Tanzania National Parks online. https://www.tanzaniaparks.go.tz/ accessed on 16th Oct, 2024.
- Taylar H, Teas J, Riche T, Southwick C 1978. Social interactions between adult male and infant rhesus monkeys in Nepal. *Primates* 19: 343–351.
- Trivers RL 1972. Parental investment and sexual selection. In: Bernard Campbell (ed), *Sexual Selection and the Descent of Man 1871–1971*. Aldine Publishing Company, Chicago, pp 136–179.
- Tutin CEG, Fernandez M. 1992. Insect-eating by sympatric lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *Am J Primatol* 28: 29–40.
- Tutin CEG, Ham R, Wrogemann D 1995. Tool-use by chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *Primates* 36:181–192.
- Uehara S 1982. Seasonal change in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). Folia Primatol 37: 44–76.
- Uehara S 1997. Predation on mammals by the chimpanzee (Pan troglodytes). Primates 38: 193-214.
- Uehara S 2002. Evidence of the leaf-clipping behavior by chimpanzee of an habituated group at Mahale. *Pan Afr News* 9: 3–4.
- Uehara S 2003. Population densities of diurnal mammals sympatric with the chimpanzees of the Mahale Mountains, Tanzania: Comparison between the census data of 1996 and 2000. *Afr Stud Monogr* 24: 169–179.
- Uehara S, Ihobe H 1998. Distribution and abundance of diurnal mammals, especially monkeys, at Kasoje, Mahale Mountains, Tanzania. *Anthropol Sci* 106: 349–369.

- Uehara S, Nishida T, Hamai M, Hasegawa T, Hayaki H, Huffman MA, Kawanaka K, Kobayashi S, Mitani JC, Takahata Y, Takasaki H, Tsukahara T 1992. Characteristics of predation by the chimpanzees in the Mahale Mountains National Park, Tanzania. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM (eds), *Topics in Primatology, Vol. 1: Human Origins.* Univ. of Tokyo Press, Tokyo, pp 143–158.
- Uehara S, Nyundo R 1983. One observed case of temporary adoption of an infant by unrelated nulliparous females among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates* 24: 456–466.
- Ueno A, Matsuzawa T 2004. Food transfer between chimpanzee mothers and their infants. Primates 45: 231-239.
- Vigilant L, Hofreiter M, Siedel H, Boesch C 2001. Paternity and relatedness in wild chimpanzee communities. *Proc Nat Acad Sci US* 98: 12890–12895.
- Vitali F, Kariuki EK, Mijele D, Kaitho T, Faustini M, Preziosi R, Gakuya F, Ravasio G 2020. Etorphine-azaperone immobilisation for translocation of free-ranging Masai giraffes (*Giraffa camelopardalis tippelskirchi*): A pilot study. *Animals* 10:322.
- de Waal F 2001. The Ape and the Sushi Master: Cultural Reflections of a Primatologist. Basic Books, New York.
- Watts DP, Mitani JC 2002. Hunting Behavior of Chimpanzees at Ngogo, Kibale National Park, Uganda. Int J Primatol 23: 1–28.
- Whiten A 1998. Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). J Comp Psychol 112: 270–281.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C 1999. Cultures in chimpanzees. *Nature* 399: 682–685.
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C 2001. Charting cultural variation in chimpanzees. *Behaviour* 138: 1481–1516.
- Wilson ML *et al.* (30 authors) 2014. Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. *Nature* **513**:414–417.
- Wrangham RW 1999. Evolution of coalitionary killing. Yearb Phys Anthropol 42: 1-30.
- Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew WC, Marchant LF, Nishida T (eds), Great Ape Societies. Cambridge University Press, Cambridge, pp 45–57.
- Yamamoto S, Yamakoshi G, Humle T, Matsuzawa T 2008. Invention and modification of a new tool use behavior: ant-fishing in trees by a wild chimpanzee (*Pan troglodytes verus*) at Bossou, Guinea. *Am J Primatol* 70: 699–702.
- Yoshikawa M, Ogawa H, Sakamaki T, Idani G 2008. Population density of chimpanzees in Tanzania. Pan Africa News 15: 17–20.
- Zamma K 2011 Frequency of removal movements during social versus self-grooming among wild chimpanzees. *Primates* 52: 323–328.
- Zamma K 2014. What makes wild chimpanzees wake up at night? Primates 55: 51-57.
- Zamma K 2015. [Techniques for video recording of primate in the wild.] In: Bundo D, Kawase I, Murao S (eds), [*Visual Practice in Fieldwork*], Kokon-Shoin, Tokyo, pp 68–77, in Japanese.
- Zamma K, Ihobe H 2015. Bed making and nocturnal behavior. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 583–598.
- Zamma K, Matsusaka T 2015. Ethograms and the diversity of behaviors. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 510–517.
- Zamma K Makelele M 2012. Comparison of the longevity of chimpanzee beds between two areas in the Mahale Mountains National Park Tanzania. *Pan Afr News* 19: 25–28.
- Zamma K, Nakamura M 2015. Grooming: Its hygienic and social aspects. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds), *Mahale Chimpanzees: 50 Years of Research*. Cambridge University Press, Cambridge, pp. 472–484.

9. Research Periods and Regimen

- 1) Ten years from November 2024 to October 2034.
- At least one researcher should be expected to stay at the Kansyana Research Camp to record climatic data, monitor reproductive state of chimpanzees, take demographic data and recover corpses of chimpanzees, if available, as the minimum routine work.
- 3) Maximum numbers of researchers observing Mahale M group chimpanzees simultaneously should be 6 including assistants (i.e., 3 researcher-tracker pairs).