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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

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Abstract We analyzed the long-term changes in the age–sex of chimpanzee captors and the developmental stages (estimated by body size) of the colobus prey. We also analyzed whether any specific male chimpanzees disproportionately contributed to the red colobus hunting over time. The data were obtained from a 46-year observation at Mahale Mountains National Park, Tanzania. In the early stages of this long-term study, only mature and adolescent male chimpanzees hunted red colobus, and these hunts were mostly single-kill episodes. But over time, mature and adolescent female chimpanzees began to participate in red colobus hunts as well, and the number of multiple-kill episodes increased. The developmental stages of the red colobus taken as prey also diversified over time. In particular, the rate of infant prey increased, which suggests that chimpanzees may have developed hunting tactics to counter the antipredator tactics of female colobus that have dependent offspring. Thus, the spread of red colobus hunting appears to have increased the diversity of the age–sex classes of chimpanzees acting as hunters and the range of developmental stages of red colobus taken as prey. No consistent tendency was observed that specific male chimpanzees contributed in red colobus hunting more than others continuously over the years. Nevertheless, male chimpanzees tended to kill the red colobus more frequently when they had the alpha status.

Keywords: Chimpanzee; Hunting tactics; Long-term change; Mahale; Red colobus.

Introduction

As the chimpanzee (*Pan troglodytes*) is one of the most closely related species with humans, understanding their hunting behaviors may be useful in considering the evolution of human hunting. One of basic information of hunting is what kind of animals are frequently hunted and how. The red colobus (*Piliocolobus* spp., the species may differ by study site) generally appear to be the preferred prey of chimpanzees in the field sites where these two species are sympatric, although the intensity and frequency of red colobus hunting varies among populations (Boesch 1994; Uehara 1997; Newton-Fisher 2015).

On the other hand, such preferences for specific prey species sometimes changed over the course of a long-term study (e.g., Stanford et al. 1994; Watts & Mitani 2015; Hobaiter et al. 2017). At Mahale Mountains National Park, Tanzania, Hosaka et al. (2020) reported

an example of long-term changes in chimpanzee preferences regarding prey species. From the 1960s to 1970s, Mahale chimpanzees rarely hunted red colobus and opportunistically harvested a wide range of sympatric mammals, including blue duikers (*Cephalophus monticola*) and bushbucks (*Tragelaphus scriptus*). However, beginning in the 1980s, the chimpanzees in this area began to target red colobus, which reached about 80% of all chimpanzee prey from 1990 to 1995.

As noted above, Hosaka et al. (2020) identified and discussed general aspects of long-term changes in hunting by the Mahale chimpanzees. However, because they showed overall trend of hunting, they did not focus on the chronological changes regarding each target species. Given the current importance of a single prey species, the red colobus, it may be interesting to see the propagation of hunting of this prey species by a chimpanzee group. Here, we report the process of how red colobus hunting spread among the chimpanzees of M group by focusing on the long-term changes of age–sex classes of chimpanzee captors and the developmental stages of the red colobus prey extracted from the dataset used by Hosaka et al. (2020) (see Table 1).

In addition, several previous studies are examining the presence of skillful hunters as factors influencing hunting frequency (Taï: Boesch & Boesch 1989; Gombe: Stanford et al. 1994; Mahale: Hosaka et al. 2001). In particular, Gilby et al. (2008, 2013, 2015) referred to males with these characteristics as "impact hunters" that act as "catalysts" to initiate group hunts involving other chimpanzees. Thus, it is necessary to analyze not only the ages and sexes of the hunters but also whether there were such specific individuals who consistently contributed to colobus captures over a period of years.

Methods

I. Study site and subjects

The study subjects were the wild chimpanzees of the Kajabala (K) and the Mimikire (M) groups of the Mahale Mountains, Western Tanzania, where long-term observations have been ongoing since 1965 [for research history and habitats, see Nakamura et al. (2015)]. In both groups, the chimpanzees were individually identified. In this study, their age–sex classes were categorized following those defined by Hiraiwa-Hasegawa et al. (1984): mature males (≥16 years), mature females (≥15 years), adolescent males (8–15 years), adolescent females (8–14 years), juveniles (5–7 years), and infants (0–4 years). Among the immigrant females, ages were estimated at first observation by comparison with females of known ages based on the body size, face color, genital swelling, etc. (Nakamura et al. 2015).

Red colobus is an arboreal and folivorous primate species. They form multi-male and multi-female groups of about 30 individuals at Mahale (Ihobe 2015). In the 1970s, local people were forced to relocate due to Tanzanian government policy, and then reforestation progressed (Itoh 2015). The red colobus population may have increased within the range of M group (Hosaka 2002), although no systematic census of the red colobus was carried out before the 1990s. In 1995 and 1996, the population densities of the red colobus were estimated to be 99–126 individuals/km^2 in the forest area and 27.4–29 individuals/km^2 in the woodland area (Uehara & Ihobe 1998). Since the exact age of red colobus is not known, the red colobus prey was divided into several developmental stages, adults, adolescents, juveniles, and infants based on body size assessment on a visual basis.

Mahale chimpanzees were also observed to hunt mammals and birds other than red

Table 1 Source of publications and databases used in this study

Publications	Database referenced for this study*	Dates of hunting observation	Months	Observation methods	Observers**
Nishida et al. 1979	—	Dec 12, 1966–Jan 4, 1976	65	Ad lib. observations at the feeding station or in the forest	TN, SU, RN, KK, HI
Norikoshi 1983	—	Jun 2, 1976–Oct 28, 1977	26	Ad lib. observations	KN
Kawanaka 1982	—	May 10, 1978–Jan 29, 1979	15	Ad lib. observations	KK, AK, IK, MoS, SM
Takahata et al. 1984*	YT's DB (1979–1984)	Aug 13, 1979–Dec 23, 1981	35	Focal and ad lib. observations	YT, TN, TH, MH, HH, HT, RN, SM
Uehara et al. 1992*	SU's DB (1983–1990)	Sep 19, 1983–Jan 15, 1990	51	Focal and ad lib. observations	SU, TN, MiH, TH, HH, MAH, KK, SaK, JM, YT, HT, TT
Hosaka et al. 2001*	KH's DB (1991–1994)	Aug 16, 1991–Mar 4, 1992, Apr 4, 1993–Feb 3, 1994	18	KH's focal and ad lib. observations (1,589.9 and 535.3 h). Gathering information from other researchers and research assistants during KH's fieldwork	KH, TN, MB, RK, MiH, MiN, RN, KK, AM
	TN's DB (1991–1995)	Feb 2, 1991–Nov 28, 1995	36	TN's focal and ad lib. observations of mature males. Gathering information from other researchers, research assistants, and TV crew during TN's fieldwork. Data processing from notes by research assistants	TN, MB, RK, HT, MiN, RN, KN, HH, RH, JM, MN, NI, LT
	SU's DB (1992)	Apr 19, 1992–Jul 17, 1992	4	SU's focal and ad lib. observations	SU
Huffman & Kalunde 1993	—	Dec 16, 1991	—	Ad lib. observations	MAH
Nakamura 1997	—	Jan 5, 1997	—	Ad lib. observations	MN
Zamma 2002	—	Jun 27, 2000	—	Ad lib. observations	KZ
Fujimoto & Shimada 2008	—	Oct 8, 2001–Nov 1, 2005	—	Ad lib. observations	MF, MaS
Nishie 2004	—	May 7, 2003–Sep 24, 2004	—	Ad lib. observations	HN
Hosaka 2015*	TN's DB (1994–2007)	Dec 24, 1994–Oct 24, 2007	154	TN's focal and ad lib. observations. Gathering information from other researchers, research assistants, and TV crew during TN's fieldwork. Data processing from notes by research assistants	RK, TN, MM, KA, ShK, RN, MB, RH, KZ, NC, MaS, EI, TS, SF, HN, MaM, MiN
	KH's DB (2000–2009)	Dec 2, 2000–Sep 10, 2009	5	KH's focal observations of mature males (342.9 h) and ad lib. observations (300.4 h)	KH
	MN's DB (1996–2010)	Aug 5, 1996–Jul 7, 2010		MN's focal and ad lib. observations	MN

* Duplicate data were retained only in the upper publication or DB for each publication.

** AK, Alimasi Kasulamemba; AM, Akiko Matsumoto; EI, Eiji Inoue; HH, Hitoshige Hayaki; HI, Hidemi Ishida; HN, Hitonaru Nishie; HT, Hiroyuki Takasaki; IK, Izack Kaseke; JM, John C. Mitani; KA, Kabumbe Athumani; KH, Kazuhiko Hosaka; KK, Kenji Kawanaka; KN, Kohshi Norikoshi; KZ, Koichiro Zamma; LT, Linda A. Turner; MAH, Michael A. Huffman; MaM, Matsuya Mitsue; MaS, Masaki Shimada; MB, Moshi Bunengwa; MF, Mariko Fujimoto; MH, Mariko Hiraiwa-Hasegawa; MiH, Miya Hamai; MiN, Miho Nakamura; MM, Moshi Matumula; MN, Michio Nakamura; MoS, Mohamedi Seifu; NC, Nadia Corp; NI, Noriko Itoh; RH, Rashidi Hawazi; RK, Rashidi Kitopeni; RN, Ramadhani Nyundo; SaK, Satoshi Kobayashi; SF, Shiho Fujita; ShK, Shabani Kabule; SM, Saidi Musa; SU, Shigeo Uehara; TH, Toshikazu Hasegawa; TN, Toshisada Nishida; TS, Tetsuya Sakamaki; TT, Takahiro Tsukahara; YT, Yukio Takahata.

colobus. The top four other prey species were blue duikers, bushbucks, red-tailed monkeys (*Cercopithecus ascanius*), and bushpigs (*Potamochoerus larvatus*), which together account for 18.8% of the prey (Hosaka et al. 2020).

II. Data collection

The dataset used in this study was compiled from data on chimpanzee predatory behavior collected at Mahale with respect to the predators' age–sex classes, prey's developmental stages, and their longitudinal changes. The cases were aggregated from published papers and supplemented with unpublished cases from original databases created from 1979 on (see Table 1 for the details of the dataset).

This study covers the 46-year period from 1965 to 2010, and the period is divided into 10 subperiods [see Hosaka et al. (2020) for details on each study period]. The first 10 years were combined into Period 1 (1965–1974) due to the lack of sufficient data on hunting activities during this time. During this study period, the chimpanzees tended to be observed around the feeding sites using *ad libitum* sampling methods (Altmann 1974). The remaining years were divided into nine 4-year periods: Period 2 (1975–1978), Period 3 (1979–1982), Period 4 (1983–1986), Period 5 (1987–1990), Period 6 (1991–1994), Period 7 (1995–1998), Period 8 (1999–2002), Period 9 (2003–2006), and Period 10 (2007–2010). After Period 2, many researchers started taking the records by using the focal animal sampling method. The K group consisted of 21 individuals in 1966, but it declined in numbers through Periods 2–3, becoming extinct in 1983. The M group was estimated to consist of 60–80 individuals in 1968, and it was always larger than the K group. After Period 2, the population of the M group varied around 50–100.

In addition, we divided the study period into three periods (Period 3–5, Period 6–7, and Period 8–10), in order to exhibit temporal changes in the developmental stages of red colobus prey for each mature male chimpanzees, adolescent male chimpanzees, and mature/adolescent female and juvenile chimpanzees (see Figure 5).

III. Data analysis

This dataset was originally created to analyze more general patterns in the hunting behaviors, such as changes in the prey species, in a previous study (Hosaka et al. 2020). For this study, we extracted data on red colobus hunting from this dataset to analyze how such hunting has spread among M-group members. This dataset has several limitations. For example, the observation methods used were inconsistent, and the data produced often lacked the hunting-related information that would be necessary for detailed analyses (e.g., party size and composition in which hunting occurred and predator–prey interactions during encounters) because such data were recorded by only a few researchers.

In this study, a *hunting episode* is defined as an instance in which at least one chimpanzee engages in behavior that leads to prey capture, whether the result is success or failure. We use the term *killing episodes* to refer to successful hunting episodes. A *multiple-kill episode* is defined as the killing of two or more prey within an hour. Many hunting episodes were already in progress when the given observer arrived (responding to sounds of either predators or prey), making it difficult to identify the initiators of the hunt. Further, observations of the killing episodes often began after one or more prey had already been captured. A *captor* was only counted when the hunter that captured the prey could be identified. However, killing episodes in which the captor was unknown were also included in the analysis to determine whether the killing episodes were single or multiple, so long as

the number of prey killed was confirmed.

To compare changes in the diversity of age–sex classes of chimpanzee captors and developmental stages of red colobus prey, we used Shannon–Weaver's H' (= $-\Sigma P_i \mathrm{Log}_2 P_i$; $P_i = n_i/N$; where N is the total number of prey of the study period, and n_i is the number of the captors and prey in each age–sex class and developmental stage) as the diversity index. To identify any male chimpanzees that had been hunting frequently for red colobus over the long term, we used the following procedures. The average number of red colobus kills per mature/adolescent male in each observation year was calculated. Next, we extracted data representing the males that showed more killing activities than the upper limit of the 95% confidence limit of the average number of kills by mature/adolescent males in a year. Then, we checked to see if such males showed a high frequency of killings over several years.

Statistical analyses were conducted using Excel 2016 (Microsoft 2016) and Statistica (StatSoft Inc. 1999). All tests were two-tailed and a significance level of $p < 0.05$ was used.

IV. Background to this study

From 1965 to 2010, the hunting activities of Mahale chimpanzees shifted from sporadic hunting for small ungulates and primates to a specialized habit of hunting the red colobus (Figure 1). In total, red colobus hunts accounted for 586 hunting episodes (66.4% of all 882 hunting episodes) and 377 killing episodes (60.9% of all 619 killing episodes).

The most distinctive feature of red colobus hunting was that of multiple kills, an aspect that was not recorded in hunts for noncolobus primates, ungulates, or other mammals and was only seen in three cases among birds (Hosaka et al. 2020). The first multiple-kill episode observed for red colobus took place on November 1981 (Period 3), after which multiple-kill episodes increased, accounting for 20.0–40.0% of the killing episodes during Period 6 and thereafter (Table 2). Of the 528 red colobus prey, 284 (53.8%) were killed in single kills, and 244 (46.2%) were killed in multiple kills. In a multiple-kill episode, an average of 2.62 prey were killed.

Of the 377 red colobus killing episodes, 375 were observed in the M group, but only two

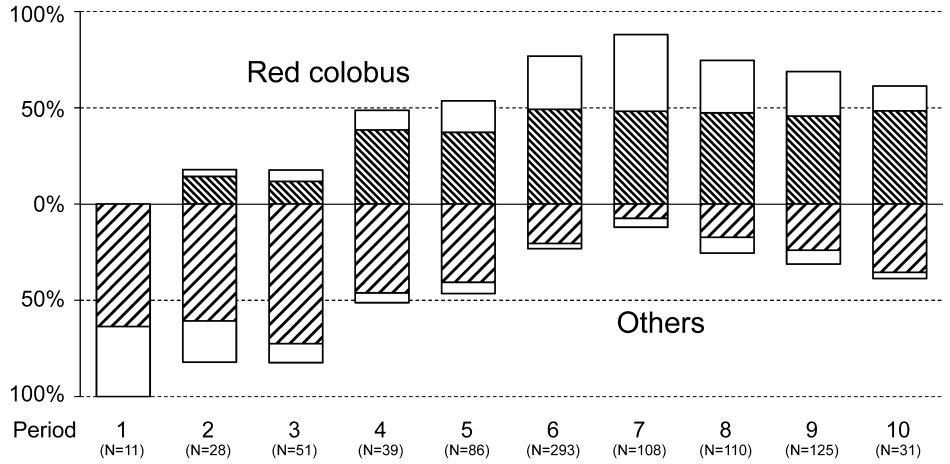

Figure 1 Long-term changes in the red colobus hunting and killing episodes (above the horizontal solid line) and those for other prey (below the horizontal solid line) at Mahale. Shaded areas show killing episodes.

Table 2 Number of the red colobus prey per killing episode

	No. of prey	Study period										Total
		1	2	3	4	5	6	7	8	9	10	
Single kills	1	0	4	5	9	29	107	41	34	43	12	284
Multiple kills	2	0	0	1	1	3	24	8	14*	8	3	62
	3	0	0	0	5	0	7	2	4*	3	0	21
	4	0	0	0	0	0	2	0	0	2	0	4
	5	0	0	0	0	0	2	0	0	0	0	2
	7	0	0	0	0	0	0	1	0	0	0	1
	8	0	0	0	0	0	0	0	0	1	0	1
	9	0	0	0	0	0	2	0	0	0	0	2
	Total number of prey in multiple kills	0	0	2	17	6	105	29	38*	41	6	244
% of multiple-kill episodes to all kill episodes		—	0.0	16.7	40.0	9.4	25.7	21.2	34.6	24.6	20.0	24.7
% of prey in the multiple kills to all prey		—	0.0	28.6	65.4	17.1	49.5	41.4	52.8	48.8	33.3	46.2
Mean number of prey per multiple-kill episode		—	—	2.00	2.83	2.00	2.84	2.64	2.22	2.93	2.00	2.62

* In each of two multiple-kill episodes recorded in Period 8, a prey of unidentified species was included. Thus, the number of the red colobus prey was 38 instead of 40.

were observed in the K group. Both of the cases recorded for the K group were single-kill episodes, and the age–sex classes were unknown for both captors and prey. Therefore, all of the following analyses concern red colobus hunting in the M group.

Results

I. Long-term changes in the contribution to prey captures by age–sex classes of the chimpanzees

Of the 235 red colobus killing episodes for which the captor was observed, mature male chimpanzees were 58.5% of the total (Figure 2). Their proportion decreased over the study period from 100.0% in Period 3 and 81.8% in Period 4 to 50–60% in the later periods (except for Period 10).

Adolescent male chimpanzees accounted for 45.5 cases (19.4%), nearly the same level as the 41 cases (17.4%) observed among mature female chimpanzees. Adolescent female and juvenile chimpanzees also killed a small number of red colobus (3.0% and 1.7%). Thus, at Mahale, chimpanzees other than mature males participated in red colobus killing, although some variation by age–sex classes was seen. This tendency was slightly higher for cases of multiple kills than cases of single kills (Fig. 4 of Hosaka et al. 2020), but there was no statistical difference (chi-squared test: $\chi^2 = 15.748$, $df = 12$, $p > 0.30$).

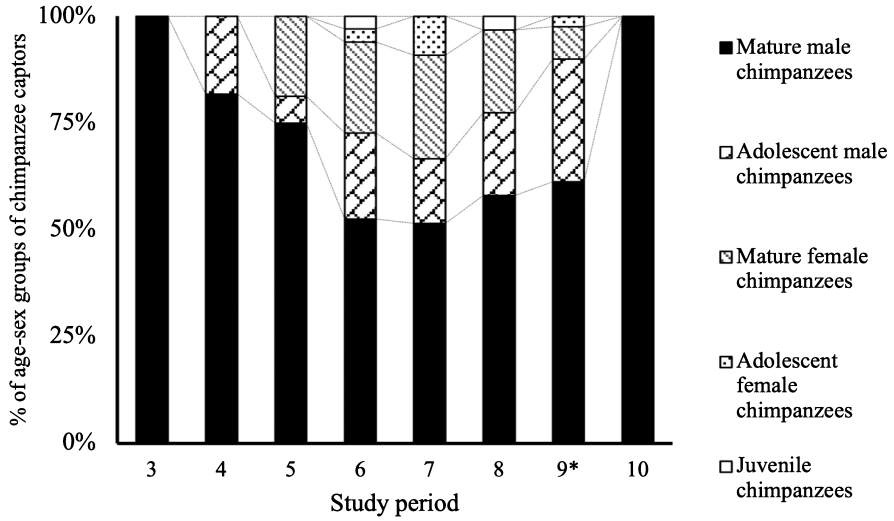

Figure 2 Long-term changes of the M-group chimpanzee captors in the kills of red colobus. The dataset is the same as that used to make Figures 3–5 in Hosaka et al. (2020). *At a hunting episode recorded in Period 9, a mature male and an adolescent male chimpanzees were observed to seize the prey at the same time, giving 0.5 points to each.

II. Long-term changes in the developmental stages of red colobus captured by chimpanzees

Developmental stages were recorded for 339 killed red colobus prey: 80 adults (23.6%), 79 adolescents (23.3%), 95 juveniles (28.0%), and 85 infants (25.1%). This composition was not significantly different from that of a red colobus group reported by Ihobe (2002) at Mahale: 11 adults (40.7%), 7 adolescents (25.9%), 6 juveniles (22.2%), and 3 infants (11.1%) ($\chi^2 = 5.362$, $df = 3$, $p = 0.147$). Note that adult male colobus was unlikely to be captured. Of the 27 adult prey animals for which the sex was known, only one was a male red colobus, and the remaining 26 were females.

A significant difference was seen between the study periods in terms of the proportion of developmental stages of red colobus prey ($\chi^2 = 36.333$, $df = 21$, $p = 0.020$). With the exception of Period 10, the proportion of infant prey increased as time passed (Figure 3). The proportion of juvenile prey was high in Period 3, but it declined during the study period. The proportion of adolescent prey increased from Periods 3 through 7 before decreasing in Period 8 and later. The proportion of adult prey was comparatively high in Periods 3 and 4, it decreased through Periods 5–7, and then it increased during Periods 9 and 10. The diversity index values for the developmental stages of prey surged from Period 3 to Period 4, remaining stable at high values after Period 5.

Adult and infant red colobus prey were more likely to be killed by mature male chimpanzees (Figure 4). By contrast, adolescent and juvenile red colobus prey were often killed by adolescent male and mature female chimpanzees. These differences were statistically significant (ANOVA, $df = 3$, $F = 4.107$, $p = 0.008$).

III. Long-term changes in the relationship between the age–sex classes of the captors and developmental stages of the prey

In the M group, the proportion of developmental stages of the red colobus that were

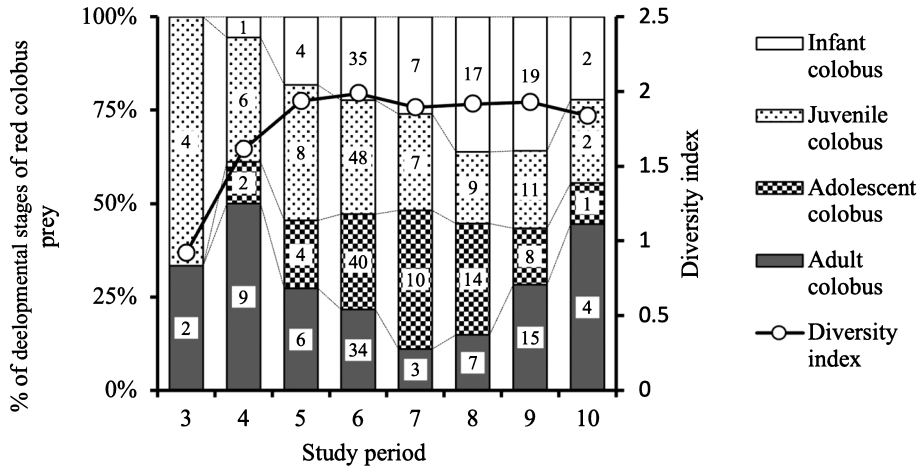

Figure 3 Long-term changes in the developmental stages of prey in the red colobus kills by the M-group chimpanzees. The diversity index was calculated using Shannon–Weaver's H'.

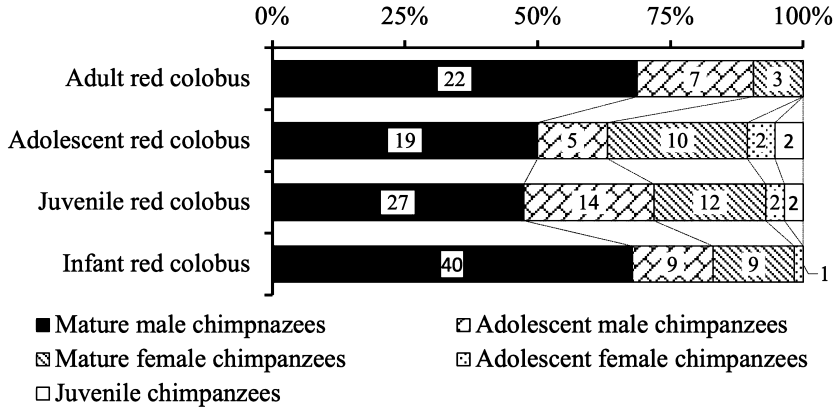

Figure 4 Relationship between the age–sex compositions of the chimpanzee captors in the M group and the compositions of the developmental stages of red colobus prey.

preyed on by mature male chimpanzees showed several significant long-term changes (χ^2 = 18.366, *df* = 6, *p* = 0.005; Figure 5a). As time went on, the proportion of adult prey decreased, while the proportion of younger prey increased. The values of the diversity index for the developmental stages of prey increased over Periods 3–5 to the Periods 6–7, and then they decreased slightly in Periods 8–10.

The proportion of developmental stages of red colobus preyed on by adolescent male chimpanzees exhibited long-term changes in a similar direction, but these changes were not significant (χ^2 = 8.689, *df* = 6, *p* = 0.192; Figure 5b). The values of the diversity indices showed a consistent upward trend.

For mature/adolescent female and juvenile chimpanzees, there was no significant difference in the proportion of developmental stages of prey (χ^2 = 11.480, *df* = 6, *p* = 0.075; Figure 5c). The values for the diversity indices showed a curve similar to that of the mature male chimpanzees.

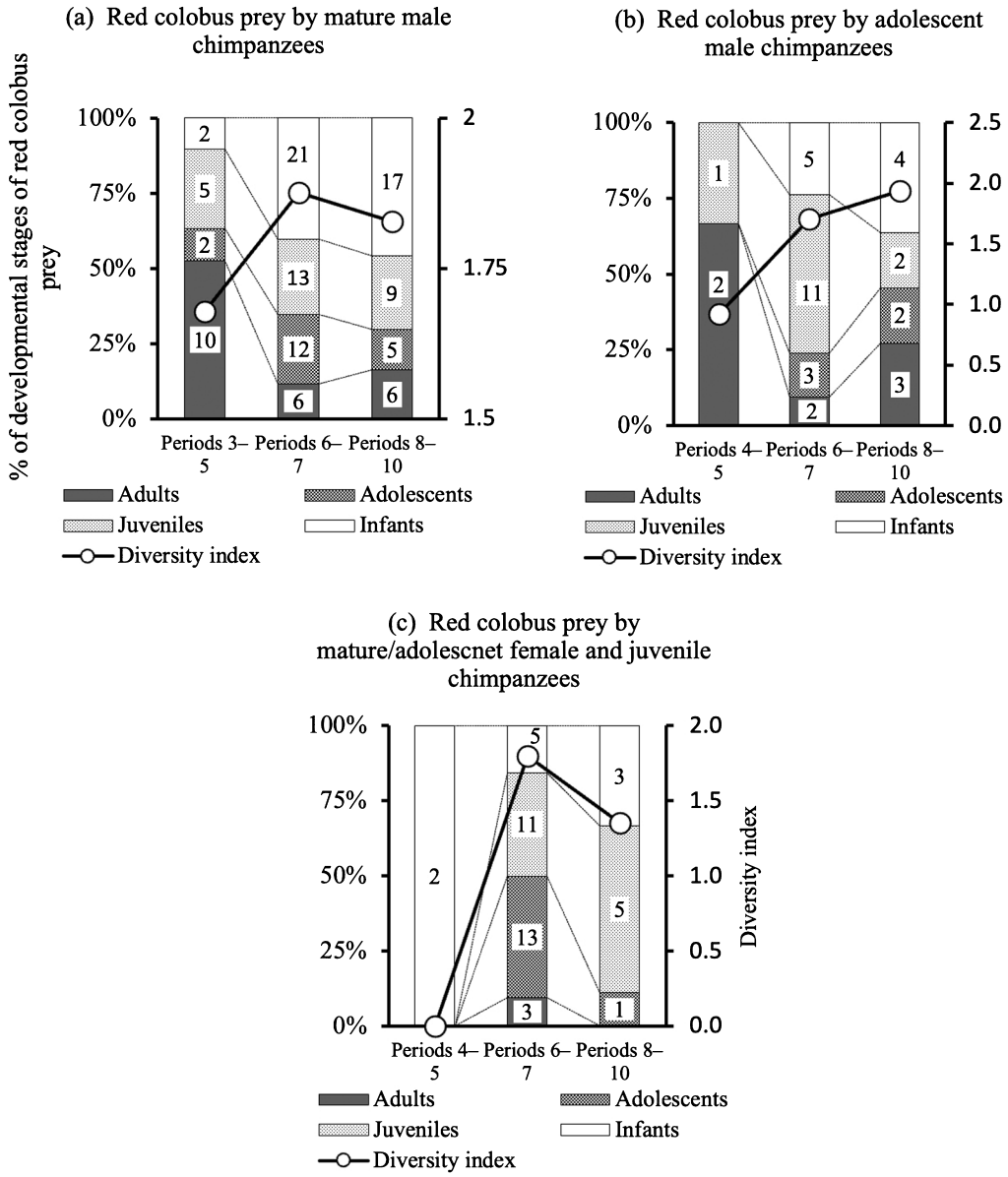

Figure 5 Long-term changes in the relationship between the chimpanzee captors in the M group and the red colobus prey: (a) mature male chimpanzees, (b) adolescent male chimpanzees, and (c) mature female and other chimpanzees. The diversity index was calculated using Shannon–Weaver's H'.

IV. Did specific male chimpanzees consistently show frequent red colobus killing activities over a long period?

The average number of kills by mature/adolescent males was calculated for each year from 1983 to 2010. In 34 male-years (defined as total number of observation years counted for each male), 18 males were observed in more killing episodes than the upper limit of the 95% confidence limit of the average number of kills (Table 3a). However, this high

Table 3 Number of years in which 18 mature/adolescent males in the M group exhibited frequent killing and the number of cases in which such highly frequent killing continuously lasted for 1–3 years

Males	(a) No. of years in which each male exhibited frequent killings*			(b) No. of cases in which the frequent killings lasted continuously for 1–3 years		
	Alpha status	Non alpha status	Total	1 year	2 years	3 years
DE	1 (3)	2 (23)	3 (26)	3		
NT	4 (13)	—	4 (13)	2	1	
AL	1 (4)	1 (15)	2 (19)	2		
BB	—	2 (20)	2 (20)	2		
DW	—	2 (13)	2 (13)	2		
NS	1 (2)	1 (12)	2 (14)	2		
PM	1 (2)	1 (11)	2 (13)	2		
SU	—	2 (10)	2 (10)	2		
BA	—	1 (11)	1 (11)	1		
CD	—	1 (10)	1 (10)	1		
FN	4 (7)	0 (16)	4 (23)	1		1
KI	—	1 (5)	1 (5)	1		
MA	—	1 (22)	1 (22)	1		
MU	—	1 (11)	1 (11)	1		
OR	—	1 (10)	1 (10)	1		
PR	—	1 (10)	1 (10)	1		
LJ	—	2 (9)	2 (9)		1	
TB	—	2 (12)	2 (12)		1	
Total	12 (31)	22 (220)	34 (251)	25	3	1

* "Frequent killing" was defined as instances when a single male showed more killing activities than the upper limit of the 95% confidence limit of the average number of kills by mature/adolescent males in a year. Numbers in parentheses are the total observation years.

frequency of hunting lasted only 1.17 years (SD = 0.46, n = 29) for each male. The longest case went on for 3 years (Table 3b).

The data indicated that male chimpanzees tended to perform more frequent red colobus killing in years when they had alpha status. Indeed, alpha males were frequently observed participating in killing activities in 12 of 31 male-years, whereas other males were frequently observed in killing in 22 of 220 male-years (Table 3a); this difference was significant ($\chi^2 = 19.124$, $df = 1$, $p < 0.0001$).

Discussion

This study extends previous results (Hosaka et al. 2020), which indicated that the hunting habits of the M-group chimpanzees altered from sporadic hunting to habitual hunting for red colobus, presenting the pattern of the spread of such new hunting habits within the age–sex interaction between chimpanzee predators and red colobus prey. Our data indicate that not only had the various age–sex classes of chimpanzees, including mature/adolescent female chimpanzees, become to participate in red colobus hunting and had multiple-kills increased over time as Hosaka et al. (2020) showed, but also the developmental stages of

the red colobus prey diversified over time. In particular, infant red colobus became to be frequently caught by mature male chimpanzees. Although no specific male chimpanzees contributed in red colobus hunting more than others continuously over the years, but alpha male chimpanzees tended to kill the red colobus more frequently.

How the age–sex composition of both chimpanzee as hunters and red colobus as prey became more diverse over time? A systematic study of the predator–prey relationships between the M-group chimpanzees and sympatric primates started during the latter half of the 1990s by Ihobe (2002). He found that red-tailed monkeys avoided hunting by immediately moving in the opposite direction when they heard chimpanzee calls. In contrast, red colobus frequently adopted a *stand-and-defend strategy*, in which females and offspring moved lower in the trees to hide silently within leafy vegetation, and males moved further down to defend the females and offspring. However, this anti-predator strategy may not be effective against the hunting by chimpanzees (Hosaka & Ihobe 2015). While red colobus monkeys remained in the trees without fleeing, chimpanzees scattered around and climbed the tree and find hidden colobus (particularly female colobus). In addition, some chimpanzees remained below the trees with red colobus staying as "bystander," and they occasionally caught the escaping red colobus who typically jumped to the neighboring trees or the ground to avoid attacks by the other chimpanzees. Hosaka (2015) called this low-cost hunting habit *wait-for-monkey-to-fall strategy*.

Comparing with the results of the present study, in the early stages of red colobus hunting by the Mahale chimpanzees (i.e., Periods 2 and 3), most of the hunts ended in single kills, in which adult or juvenile prey were sporadically hunted by mature/adolescent male chimpanzees. In contrast, after Period 4, the rate of multiple kills and the cases of captures by female chimpanzees began to increase. These changes may be due to chimpanzees developing the *wait-for-monkey-to-fall strategy* against red colobus's a *stand-and-defend strategy*. In such hunting scenes, some bystander chimpanzees may have monitored both hunters and prey and swiftly exploited opportunities once the prey had moved closer to them while fleeing (Hosaka et al. 2001). Such changes in hunting habits could give chimpanzees other than mature males the opportunity to kill the red colobus. In addition, mature male chimpanzees may have gradually developed hunting tactics to snatch infant colobus from their mothers as shown in Figure 5a. Although no observational data were provided in this study, a mature or adolescent male chimpanzee caught infant red colobus more often. They may have developed a hunting technique to find a female red colobus with dependent offspring hidden in a thicket of vines near the canopy, and to snatch infant colobus from their mothers. Consequently, the diversities of both age–sex classes of the captor and developmental stages of the prey might have increased over time. Thus, female participation in red colobus hunting became non-negligible (Hosaka et al. 2020).

We found that few males maintained high hunting contributions over a long period at Mahale. On the other hand, we found that male chimpanzees tended to kill red colobus more frequently during the period that they occupied the alpha position. This tendency suggests that some social factors may affect hunting motivation in male chimpanzees. Hosaka (2015) argued for the existence of some periods of exceptionally high hunting frequency when social relations among high-ranking males were intense over alpha status. Among Mahale chimpanzees, Nishida et al. (1992) reported that an alpha male of the M group (NT in Table 3) showed a consistent tendency to share meat with particular members of the group in line with frequent grooming and proximity relations; the authors proposed the hypothesis that meat sharing may be a coalition strategy practiced by alpha males. This strategy could be associated with the high killing frequency of alpha males observed in the present study. The relationship between this high frequency of killing among alpha males

and the hunting techniques noted in this study is unknown. However, it is possible that alpha males actively employ a specific tactic (e.g., the *rush-to-hunt*) to improve hunting success, considering that the proportion of infants in red colobus kills by mature males increased over time.

Future studies should compare the hunting behavior across multiple chimpanzee field sites using focal sampling data that includes females and immatures to address the following questions: first, it is necessary to examine which chimpanzees initiate group hunting of the red colobus. Previous studies at other field sites have only analyzed the focal sampling data of the mature males, based on the assumption that hunters are predominantly males (e.g., Gilby et al. 2015). However, as suggested by Hosaka et al. (2020) and our own investigations, the contribution of females to prey captures at Mahale cannot be ignored. These analyses also allow for an assessment of the impact hunters, which remains unresolved in this study. In addition, the hunting tactics employed by chimpanzees of each age–sex class and their success should be explored in each field. We hope that such studies will advance our understanding of chimpanzee hunting behavior.

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