DIET OF SAVANNA CHIMPANZEES IN THE UGALLA AREA, TANZANIA

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ABSTRACT We studied the diet of chimpanzees (*Pan troglodytes*) in the Ugalla savanna woodland area of western Tanzania. This area is the most eastern habitat and one of the driest and most open habitats of chimpanzees. Field surveys were conducted mainly at the Nguye and Bhukalai sites in Ugalla from 1995 to 2011, during which we collected 465 feces of chimpanzees. From the discernable components of the Ugalla chimpanzees' diet in the fecal samples we collected and recorded, we compared the diet of these chimpanzees with that of chimpanzees in wet habitats, especially Mahale and Gombe in Tanzania, in the literature. Chimpanzees in Ugalla had eaten 117 plant parts of 100 plant species, 1 bird species, at least 1 small mammal species, and at least 3 insect species, including termites and ants. These chimpanzees in Ugalla ate fewer plant species and plant parts, more underground storage organs of plants, and fewer vertebrates and invertebrates than did the chimpanzees in Mahale and Gombe.

Key Words: Chimpanzee; Diet; Savanna woodland; Dry habitat.

INTRODUCTION

Chimpanzees (*Pan troglodytes*) have varied diets that include many parts of plants and animals. The main component of their diet is fruits, particularly ripe ones (Goodall, 1968; Nishida, 1968; Nishida & Uehara, 1983; Tutin et al., 1997; Wrangham et al., 1998). They also feed on other parts of plants, such as flowers, seeds and pods, shoots and leaves, stems, bark and cambium, and underground storage organs (Goodall, 1968; Suzuki, 1969; Hladik, 1977; Nishida & Uehara, 1983; McGrew et al., 1988; Wrangham et al., 1998; Sugiyama & Koman, 1992; Tutin et al., 1997; Newton-Fisher, 1999; Basabose, 2002; Hunt & McGrew, 2002; Pruetz, 2006). Chimpanzees also prey on vertebrates and invertebrates (Goodall, 1968; Nishida & Uehara, 1983; Pruetz, 2006; Hernandez-Aguilar et al., 2007; Stewart & Piel, 2013). Moreover, chimpanzee diet is very varied depending on habitat, which ranges from the tropical rainforests to savanna woodlands (Goodall, 1968; Suzuki, 1969; Nishida & Uehara, 1983; Basabose, 2002; Hernandez-Aguilar, 2006; Pruetz, 2006).

In Tanzania, chimpanzee populations are found along the eastern shore of Lake Tanganyika, in the Ugalla area, the Masito area including the Kasakati site, Mahale Mountains National Park, Gombe Stream National Park, and other areas (Suzuki, 1969; Kano, 1972; Ogawa et al., 2007, 2014). Ugalla and Kasakati lie within the dry region, which annually receives <1,500 mm of rain (Suzuki, 1969; Hernandez-

Aguilar, 2006), whereas Mahale and Gombe belong to the wet region and annually receive >1,500 mm of rain (Clutton-Brock & Gillett, 1979; Goodall, 1986; Takasaki et al., 1990). Mahale is characterized by its extremely diverse vegetation, and the forest type which is most important for the survival of the chimpanzee is semi-deciduous and semi-evergreen gallery forest (Nishida, 1990). Also, chimpanzees at Mahale utilize both forest and woodland (Turner, 2000). Gombe is a mosaic of patches of evergreen forest, semi-deciduous forest, woodland, and grassland (Clutton-Brock, 1975). The dominant vegetation in Ugalla and Kasakati is woodland, with patchy forests and grasslands (Suzuki, 1969; Kano, 1972; Ogawa et al., 2007). Because of these differences in vegetation, we expected the diets of chimpanzees in Ugalla and Kasakati to be quite different from those in Mahale and Gombe.

Within the dry region, Ugalla has fewer forests than Kasakati (Suzuki, 1969) and is one of the driest and most open habitats of chimpanzees (Moore, 1992). It is considered similar to the environment of early hominids (Itani, 1979). Studying the feeding ecology of Ugalla chimpanzees is important not only for primate ecology but also for anthropology.

After studying the environment in Ugalla and the diet of chimpanzees reported in previous studies, we posed the following two hypotheses:

1. Chimpanzees in Ugalla eat fewer food items than those in the two wet habitats, Mahale and Gombe, as Pruetz (2006) reported that chimpanzees in the dry region ate fewer food items than chimpanzees in the wet region.
2. In Ugalla, woodland has more plant species eaten by chimpanzees than the forest, as Schoeninger et al. (1999) reported that carbon and nitrogen stable isotope ratios in Ugalla chimpanzee hair samples indicated that they primarily fed on plants in woodlands rather than those in forests or grasslands.

In order to test these hypotheses, we studied the diet of chimpanzees in the Ugalla area. We also investigated the diet of baboons (*Papio cynocephalus* and *P. anubis*) inhabiting the same study area to compare with that of chimpanzees.

METHODS

I. Study Area

Location. We conducted field surveys in the Ugalla area of western Tanzania, East Africa (05°09′–05°52′S, 30°23′–31°01′E; Fig. 1). Field surveys were conducted at the Nguye site, in the northwestern part of Ugalla (05°13.0′S, 30°27.5′E; Fig. 1) and the Bhukalai site, in central Ugalla (05°26.8′S, 30°44.1′E; Fig. 1). Ugalla, which covers 3,352 km^2 at elevations ranging from 980 to 1,712 m, is bounded by the Ugalla River to the east, the Malagarasi River to the north, Uvinza-Mpanda Road to the west, and the Niamansi Basin to the south (Fig. 1; Kano, 1972; Ogawa et al., 2007).

Vegetation. The majority (86%) of the Ugalla area is covered by woodlands, locally called *miombo* woodland. The dominant plants in the woodlands are decid-

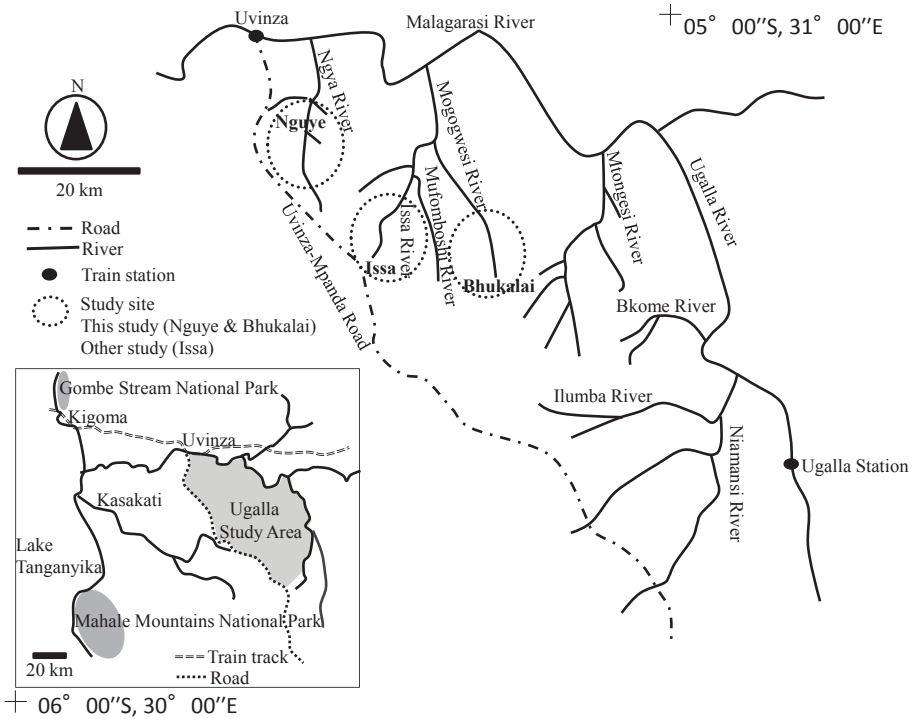

Fig. 1. Study area in Ugalla, Tanzania

uous trees of the genera *Brachystegia* and *Julbernardia*. Another 12% is grasslands and the remaining 2% is forests (Ogawa et al., 2007). The grassland habitat includes swamps with few trees, and wooded grasslands with scattered trees (canopy cover <20%; Pratt et al., 1966; Hernandez-Aguilar, 2006).

Climate. Annual rainfall in Ugalla measures 955 mm (Hernandez-Aguilar, 2006). The dry season (defined here as having monthly rainfall <100 mm) spans May to October, while the rainy season lasts from November to April (Hernandez-Aguilar, 2006). To observe the seasonality of chimpanzee diets, we divided the year into four equal periods: (1) the first half of the dry season (May–July), (2) the second half of the dry season (August–October), (3) the first half of the rainy season (November–January), and (4) the second half of the rainy season (February–April).

Average daily maximum temperature has been reported as highest in August (34°C) and lowest in November (28°C), and the average daily minimum temperature highest in January (17.2°C) and lowest in August (14.4°C; Hernandez-Aguilar, 2006).

II. Study Subjects

Chimpanzees (Fig. 2). Chimpanzees live in a fission–fusion society comprising multi-male and multi-female unit groups and form temporal sub-groups (Nishida,

Fig. 2. Chimpanzees (left side) and baboons (right side) in Ugalla recorded in camera traps

1968). Previous bed surveys estimated that eastern chimpanzees (*Pan troglodytes schweinfurthii*) inhabit the 3,352 km^2 Ugalla area (Ogawa et al., 2007) at a density of 0.10 individuals (>3- to 4-year-old individuals who make beds)/km^2 (Yoshikawa et al., 2008), which indicates that a total 335 individuals (>3 to 4 years old) inhabit this area (Ogawa et al., 2014). If the size of the unit group is considered to be 30–35 individuals >3- to 4-years-old (Ogawa et al., 2007), there should be approximately 10 unit groups, each with a home range of 335 km^2.

At Nguye, direct observations of feeding behavior in the literature found 14 individuals in the largest sub-groups, whereas bed counts identified 23 individuals in the largest sub-groups (Ogawa et al., 2007). Previous observations and bed counts found that chimpanzees at Nguye and Bhukalai temporally formed sub-groups with a mean of 3.3 individuals in the daytime and 5.2 individuals at night during the dry season (Ogawa et al., 2007), and 2.6 individuals in the daytime and 2.9 individuals at night during the rainy season (Ogawa, unpublished data).

Baboons (Fig. 2). To compare the diet selectivity between sympatric species in the study area, we also investigated the yellow baboon (*P. cynocephalus*) and the olive baboon (*P. anubis*) in Ugalla. The baboons in Ugalla formed multi-male and multi-female groups composed of 33.3 individuals. The home range of each group was about 5.0 km^2 and the density of groups was 0.17 groups/km^2 (Ogawa, 2000).

III. Data Collection

Fecal analyses. Ogawa and Yoshikawa conducted the Nguye site field surveys, and Ogawa the Bhukalai site field survey. Ogawa collected data during the dry season in 1995, 1996, 1999, and 2003. Yoshikawa collected data during the rainy season in 2007, all seasons from March 2008 to January 2009, and all seasons in 2010 and 2011.

We collected diet data on chimpanzees from fecal samples, feeding remains, and direct observations of feeding behavior. Although we directly observed chimpanzees as long as possible, most data in this study are based on fecal analyses. We recorded the species and plant parts consumed: fruits, flowers, seeds and pods, leaves, stems, and underground storage organs. Among the plants found in the chimpanzee feces, we listed only the ones that we were able to identify to the species level, although we found many unidentified seeds of fruits, leaves, and underground storage organs.

To record seasonal changes in chimpanzee diets, we used only fresh feces. We estimated the age of feces according to their moistness and the presence or absence of urine close to the feces. When we found feces under a chimpanzee bed, we estimated the age of the bed and used the feces only when the bed had green leaves.

We also studied food items eaten by baboons, using the same method as for chimpanzees, during the dry seasons in 1996 and 1999, and during all seasons from March 2008 to January 2009. We did not collect feces when we were not able to discriminate between feces of chimpanzees and baboons.

Review of the literature. Previous studies that reported the diet of chimpanzees in Ugalla were either short-term surveys at several sites in Ugalla (Nishida, 1989; Moore, 1994; Gen'ichi Idani, personal communication) or longer 1 year at the Issa site in the western part of Ugalla (Hernandez-Aguilar, 2006; Stewart & Piel, 2013; Fig. 1). We combined the results of our surveys with those from previous reports to compile a diet list for chimpanzees in the Ugalla area. We then compared the dietary components of chimpanzees in Ugalla with those in Mahale and Gombe.

RESULTS

I. Number of Fecal Samples

We collected a total of 465 chimpanzee feces in Ugalla. We determined the seasonal changes in chimpanzee diets on the basis of 399 fresh feces, including 114 in the first half of the dry season and 177 in the second half, and 42 in the first half of the rainy season and 66 in the second half. We also collected 196 fresh samples of baboon feces, including 104 and 60 in the first and second halves of the dry season, respectively, and 23 and 9 in the first and second halves of the rainy season, respectively.

Table 1. Diet of chimpanzees and baboons in the Ugalla area, Tanzania

Food species						Chimpanzee																Baboon		
Kingdom	Class	Order	Family	Species	Life form	Vegetation type	Part of plant	Season				Evidence	Source	Sampling site in Ugalla				Other study areas in Tanzania				Feeding record	Part of plant	Evidence
								Dry		Rainy				Nguye	Bhukalai	Issa	other	Mahale	Gombe	Kasakati				
								May - Jul.	Aug. - Oct.	Nov. - Jan.	Feb. - Apr.													
Plant																								
	DICOTYLEDONEAE																							
			ALOACEAE	*Aloe sp.*																		+	l	d
			ANACARDIACEAE	*Lannea schimperi*	t	w	f					f	H			+		+	-	-			
			ANACARDIACEAE	*Mangifera indica*	t	w	f					r	H			+		+	+	-			
			ANACARDIACEAE	*Pseudospondias microcarpa*	t	f	f		+	+		f	YO	+	+			+	+	+			
			ANACARDIACEAE	*Sclerocarya birrea*	t	w/f	f					f	H, YO	+		+		-	-	-			
			ANISOPHYLLEACEAE	*Anisophyllea pomifera* and/or *boehmii*	t	w	f	+	+	+		f	H, M, YO	+	+	+	+	-	+	-			
			ANNONACEAE	*Annona senegalensis*	t	w	f			+	+	f	H, N, YO	+		+	+	+	+	+	+	f	f
			ANNONACEAE	*Artabotrys collinus*	l	f	f	+		+	+	f	YO	+				-	-	-			
			ANNONACEAE	*Artabotrys monteiroae* or *stolzii*	l	f	f					f?	M				+	+	-	-			
			ANNONACEAE	*Hexalobus monopetalus*	t	w	f			+	+	f	H, YO	+		+		-	-	-			
			ANNONACEAE	*Monanthotaxis poggei*	s	f	f					f?	M				+	-	+	+			
			ANNONACEAE	*Monodora angolensis*	t	f	f	+	+			f	YO	+	+		+	-	-	-			
			ANNONACEAE	*Monodora* cf *junondii*	t/l	f	f					f	M				+	-	-	-			
			APOCYNACEAE	*Carissa spinarum*	t	f	f					f	H			+		-	-	-			
			APOCYNACEAE	*Diplorhynchus condylocarpon*	t	w/wg	f, s	+	+	+	+	f, r	H, YO	+		+		+	+	+	+	f, s	re
			APOCYNACEAE	*Landolphia owariensis*	l	f	f			+	+	f, r	H, YO	+		+		+	-	?			
			APOCYNACEAE	*Landolphia stolzii ?*	l	f	f					?	M				+	-	-	?			
			APOCYNACEAE	*Saba comorensis*	l	f	f	+	+		+	f	H, M, YO	+	+	+	+	+	-	+			
			ASCLEPIADACEAE	*Raphionacme welwitschii*	h	w	u					r	H			+		-	-	-			
			ASTERACEAE	*Aspilia pluriseta*	h	w	l					f	H			+		-	+	-			
			ASTERACEAE	*Guizotia scabra*	h	w	l					f	H			+		-	-	-			
			BORAGINACEAE	*Cordia africana*	t	f	f					f	N				+	+	+	+			
			BORAGINACEAE	*Trichodesma zeylanicum*	h	w	l					d, r	H			+		-	-	-			
			CAESALPINIACEAE	*Bauhinia thonningii*	t	w/wg	s					f, r	H			+		+	-	-			
			CAESALPINIACEAE	*Brachystegia bussei*	t	w	s, l, b, u,?	+		+	+	d, r	H, YO	+		+		+	+	+			
			CAESALPINIACEAE	*Brachystegia spiciformis*	t	w	s	+				d	YO		+			+	-	-			
			CAESALPINIACEAE	*Isoberlinia angolensis*	t	w	s	+				d	YO	+	+			-	-	+			
			CAESALPINIACEAE	*Julbernardia globiflora*	t	w	fl, l, s					d, f, r	H			+		-	-	+	+	s	f

CAESALPINIACEAE	*Julbernardia unijugata*	t	f	s	+	+			d, f, r	M, YO	+	+		+	-	-	-			
CAESALPINIACEAE	*Monopetalanthus richardsiae*	t	f	s	+	+			d	M, YO	+			+	-	-	-			
CAESALPINIACEAE	*Piliostigma thonningii*	t	w	s			+		f	YO	+				+	+	-			
CAESALPINIACEAE	*Tamarindus indica*	t	w	s					f	N				+	-	-	-			
CELASTRACEAE	*Maytenus senegalensis?*	t	?	f					f	H			+		-	-	-			
CELASTRACEAE	*Pleurostylia africana*	t	w	f					f	H			+		-	-	-			
																	-			
CHRYSOBALANACEAE	*Maranthes floribunda*	t	w	f		+			f	YO		+			-	-	-			
CHRYSOBALANACEAE	*Parinari curatellifolia*	t	w	f	+	+		+	d, f	H, M, YO	+	+	+	+	+	+	+	+	f	d, f
DIOSCOREACEAE	*Dioscorea odoratissima*	c	w	f	+			+	f	YO	+				+	+	-			
DICHAPETALACEAE	*Dichapetalum stuhlmannii*	l	f	f	+			+	f	YO	+				-	-	?	+	f	f
EUPHORBIACEAE	*Antidesma venosum*	t	w	f	+		+	+	f	H, YO	+		+		-	+	+	+	f	f
EUPHORBIACEAE	*Bridelia micrantha ?*	t	f	f					?	M				+	-	+	-			
EUPHORBIACEAE	*Pseudolachnostylis*	t	w	f					f	H			+		-	-	-			
EUPHORBIACEAE	*Uapaca kirkiana*	t	w	f		+	+	+	f, r	YO	+	+			+	+	+			
EUPHORBIACEAE	*Uapaca nitida*	t	w	f		+	+	+	f	YO	+	+			+	+	?			
FLACOURTIACEAE	*Flacourtia indica*	t	f	f					f	H			+		+	+	-			
GUTTIFERAE	*Garcinia huillensis*	t	w/f	f		+			f	H, YO	+	+	+		+	-	+			
GUTTIFERAE	*Garcinia volkensii*	s	f	f		+			f	YO		+			-	-	?			
LEGUMINOSAE	*Dalbergia fischeri*	l	f	s					f	H			+		-	-	-			
LEGUMINOSAE	*Dolichos kilimandscharicus*	h	w	u					f?, r	H			+		-	-	-			
LEGUMINOSAE	*Pterocarpus tinctorius*	t	w	fl, s	+	+	+		d, f, r	H, M, YO	+	+	+	+	+	+	-			
LOGANIACEAE	*Strychnos cocculoides*	t	w	f	(+)	(+)			f, r	M?, N, YO	(+)	(+)		+	-	+	?	(+)	f	f
LOGANIACEAE	*Strychnos innocua*	t	w	f	(+)	(+)			f, r	H, M?, YO	(+)	(+)	+	(+)	+	+	+	(+)	f	f
LOGANIACEAE	*Strychnos pungens*	t	w	f, l	(+)	(+)			d, f	H, M?, YO	(+)	(+)	+	(+)	-	-	?	(+)	f	f
LOGANIACEAE	*Strychnos spinosa*	t	w	f	(+)	(+)			f	M?, H?, YO	(+)	(+)		(+)	-	-	+	(+)	f	f
MALVACEAE	*Thespesia garckeana and/or Azanza garckeana*	t	w	f	+	+		+	d, f, r	H, M, YO	+	+	+	+	+	+	-	+	f	f
MENISPERMACEAE	*Tiliacora funifera*	l	f	f	+			+	d, f	YO	+				-	+	-	+	f	f
MORACEAE	*Ficus cyathistipula*	t	f	f	(+)	(+)	(+)	(+)	f	YO	(+)	(+)		(+)	+	-	?	(+)	f	f
MORACEAE	*Ficus dicranostyla*	t	w/f	f					r	H			+		?	-	?			
MORACEAE	*Ficus exasperata*	t	w/f	f, l					d, r	H			+		+	+	?			
MORACEAE	*Ficus lutea*	t	w/f	f	(+)	(+)	(+)	(+)	f	YO	(+)	(+)		(+)	?	-	?			
MORACEAE	*Ficus ottoniifolia*	t	w/f	f, l					d, r	H			+		?	-	?			
MORACEAE	*Ficus thonningii*	t	w/f	f	(+)	(+)	(+)	(+)	f	M, YO	(+)	(+)		(+)	+	-	?	(+)	f	f
MORACEAE	*Ficus vallis-choudae*	t	f	f	(+)	(+)	(+)	(+)	f	YO	(+)	(+)		(+)	+	+	?	(+)	f	f
MORACEAE	*Ficus variifolia*	t	w/f	f					d, r	H			+		?	-	?			
MORACEAE	*Ficus zanzibarica*	t	?	f	(+)	(+)	(+)	(+)	f	YO	(+)	(+)		(+)	?	-	?	(+)	f	f

MYRTACEAE	*Syzygium guineense*	t	f	f		+	+		d, f	H, YO	+	+	+	+	+	+	-			
OLACACEAE	*Ximenia caffra*	t	w	f					f	H			+		-	-	-			
OLEACEAE	*Chionanthus africana*	t	f	f					f	YO		+			-	-	-			
RHAMNACEAE	*Ziziphus abyssinica*	t	w/wg/g	f					f	H			+		-	-	-			
RUBIACEAE	*Canthium crassum ?*	t	w	f					?	M				+	+	+	+			
RUBIACEAE	*Canthium gueinzii*	s	w/f	f					f	H			+		?	-	?			
RUBIACEAE	*Fadogia quarrei*	h	w	u					r	H			+		-	-	-			
RUBIACEAE	*Keetia gueinzii/Canthium hispidum*	l	f	f	(+)	(+)	(+)	(+)	f	N, H, YO	(+)	(+)	+	+	-	+	+	(+)	f	f
RUBIACEAE	*Keetia venosa*	l	f	f	(+)	(+)	(+)	(+)	f	YO	(+)	(+)		(+)	+	-	-	(+)	f	f
RUBIACEAE	*Multidentia crassa*	t	w	f	+	+	+	+	f	YO	+	+			-	-	-	+	f	f
RUBIACEAE	*Psychotria peduncularis*	s	f	f	+	+		+	f	YO	+				+	-	-	+	f	f
RUBIACEAE	*Psychotria* sp.	h	w	f					f	H			+		-	-	-			
RUBIACEAE	*Psydrax livida*	t	w	f					r	H			+		-	-	-			
RUBIACEAE	*Psydrax parviflora*	t	f	f	+	+			f	YO		+			+	-	-			
RUBIACEAE	*Pyrostria lobulata*	t	f	f					f	H			+		-	-	-			
RUBIACEAE	*Vangueria volkensii*	t	f	f					f	H			+		-	-	-			
SAPINDACEAE	*Chrysophyllum* sp.	t	f	f	+	+			f, r	YO	+	+			-	-	-			
SAPINDACEAE	*Zanha africana*	t	w	f					f, r	H			+		-	-	-			
SAPINDACEAE	*Zanha golungensis*	t	w/f	f		+	+		f	YO	+				+	+	-			
SAPOTACEAE	*Afrosersalisia cerasifera*	t	f	f		+			d, f	YO	+	+			+	+	-			
SAPOTACEAE	*Manilkara mochisia*	t	w	f					f, r	H			+		-	-	-			
SMILACACEAE	*Smilax* sp.	h	w	u					r	H			+		?	-	-			
TILIACEAE	*Grewia mollis*	s	f	f	+	+			f	N, YO	+	+		+	+	+	-			
TILIACEAE	*Grewia platyclada*	s	f	f					f	N				+	+	+	-			
TILIACEAE	*Grewia rugosifolia*	s	w	f					f	H			+		-	-	-			
VERBENACEAE	*Clerodendrum formicarum*	s	f	f					f	YO	+				-	-	-			
VERBENACEAE	*Vitex doniana*	t	w	f	(+)	(+)	(+)	(+)	f	H?, M,YO	(+)	+	+	+	+	+	+	(+)	f	f
VERBENACEAE	*Vitex mombassae*	t	w	f	(+)	(+)	(+)	(+)	f	H?, YO	(+)	+	+		-	-	-	(+)	f	f
VITACEAE	*Ampelocissus obtusata*	h	w	f, st					f, r	H			+		-	-	-			
VITACEAE	*Cissus quarrei*	h	w	f					f	H			+		-	-	-			
VITACEAE	*Cissus rubiginosa*	c	w	f				+	f	H, YO	+		+		+	-	-			
MONOCOTYLEDONEAE																				
ARECACEAE	*Borassus aethiopum*	t	wg	f		+			f, r	H, N, YO			+	+	-	-	-			
ARECACEAE	*Elaeis guineense*	t	w	f		+			f	YO		+			-	+	-	+	f	f
TACCACEAE	*Tacca leontopetaloides*	h	w	f, l, st, u					f, r	H			+		+	-	-			

ZINGIBERACEAE	*Aframomum angustifolium*	h	f	f, st	(+)	(+)	(+)	(+)	f, r	YO	(+)	(+)		(+)	?	?	-	(+)	f	f
ZINGIBERACEAE	*Aframomum mala*	h	w/f	f, st	(+)	(+)	(+)	(+)	f, r	H, YO	(+)	(+)	+	(+)	+	?	-	(+)	f	f
ZINGIBERACEAE	*Costus macranthus*	h	w/wg	u					r	H			+		-	-	-			
Animal																				
MAMMALIA																				
RODENTIA																				
SCIURIDAE? or MUROIDEA?	Unidentified								d, f	H,N, I	+		+	+	+	-	-	+		f
AVES																				
PLOCEIDEA?																				
	Steganura paradisaea?					+			f	YO		+			?	?	-			
INSECTA																				
COLEOPTERA																				
	Unidentified					+			f	H, YO	+	+	+		+	+	-			
HYMENOPTERA																				
FORMICIDAE	Unidentified					+	+	+	d, f	H, YO	+	+	+		+	+	+	+		f
ISOPTERA																				
TERMITIDAE	*Macrotermes* sp.				+	+	+	+	d, f, r	H, SP, YO	+	+	+		+	+	+	+		f

Data and Notes.

In the dietary components of chimpanzees and baboons in Ugalla, Tanzania, only the plants identifed the species level and data from previous studies by other researchers were used.

Type of plant: t = tree, l = liana, h = herb, s = shrub, g = grass, c = climber.

Type of habitat: w = woodland, f = forest, g = grassland, wg = wooded grassland. ? = unknown.

Part of plant eaten: f = fruit, fl = flower, s = seed or pod, l = leaf or shoot, st = stem, b = bark or cambium, u = underground storage organ. ? = unknown. Seasons when chimpanzees ate the species are shown, using data from the current study. + = Ate during that period. Blank = Unknown whether eaten in that season. (+) = Chimpanzees probably ate the species during that period, but there was no proof because seeds of that species in chimpanzee feces looked similar to those of another species in the same genus. Dry = During the dry season. Rainy = During the rainy season.

Evidence: Evidence from this study is shown. d = Direct observation. f = Feces. r = Remnants including wadges. ? = Unknown.

Source: H = Hernandez-Aguilar, 2006; I = Idani, personal communication; M = Moore, 1994; N = Nishida, 1989; SP = Stewart & Piel, 2013; YO = Yoshikawa & Ogawa, the present study.

Sampling sites in Ugalla: Data for Nguye and Bhukalai came from this study. Data for Issa came from Hernandez-Aguilar (2006). Data for other sites came from this study, Moore (1994), and Nishida (1989). + = Ate. Blank = Unknown. Other study areas: Mahale is from Nishida & Uehara (1983) and Itoh (2004). Kasakati, from Suzuki (1969). Gombe, Wrangham (1975). + = Ate. - = Unknown. ? = Not identified in the cited reference, but they may be identical.

Feeding: + = Baboons ate the species. Blank: Unknown.

Note 1: *Saba comorensis* was probably identified as *Saba* sp. in Moore, 1994.

Note 2: *Monopetalanthus richardsiae* and *Julbernardia unijugata* were identified as *Cynometra* sp. 1 and *Cynometra* sp. 2, before identification by botanists changed (Moore, 1994).

Note 3: Chimpanzees probably ate these 4 species in the genus *Strychnos*, but we are uncertain because seeds of those species in chimpanzee feces look similar to one another. Moore (1994) recorded *Strychnos* sp. 4 as chimpanzee food, and it is probably 1 of the 4 species. Hernandez-Aguilar (2006) recorded *Strychnos* sp. as chimpanzee food, and it is probably 1 of the 4 species.

Note 4: Chimpanzees probably ate these 5 species in the genus *Ficus*, but we are uncertain because seeds of those species in chimpanzee feces look similar to one another.

Note 5: Chimpanzees probably ate these 2 species in the genus *Keetia*, but we are uncertain because seeds in chimpanzee feces look similar.

Note 6: *Psydrax parviflora* was probably identified as *Psydrax* sp. 1 in Hernandez-Aguilar, 2006.

Note 7: *Grewia mollis* was probably identified as *Grewia* sp. in Nishida, 1989.

Note 8: Chimpanzees probably ate these 2 species in the genus *Vitex*, but we are uncertain because seeds in feces look similar. Hernandez-Aguilar (2006) recorded *Vitex* sp. 1 and sp. 2 as chimpanzee food, and these are probably the 2 species.

Note 9: Chimpanzees probably ate these 2 species in the genus *Aframomum*, but we are uncertain because seeds in feces look similar. Moore (1994) recorded *Aframomum* sp. 4, which is probably *Aframomum mala*.

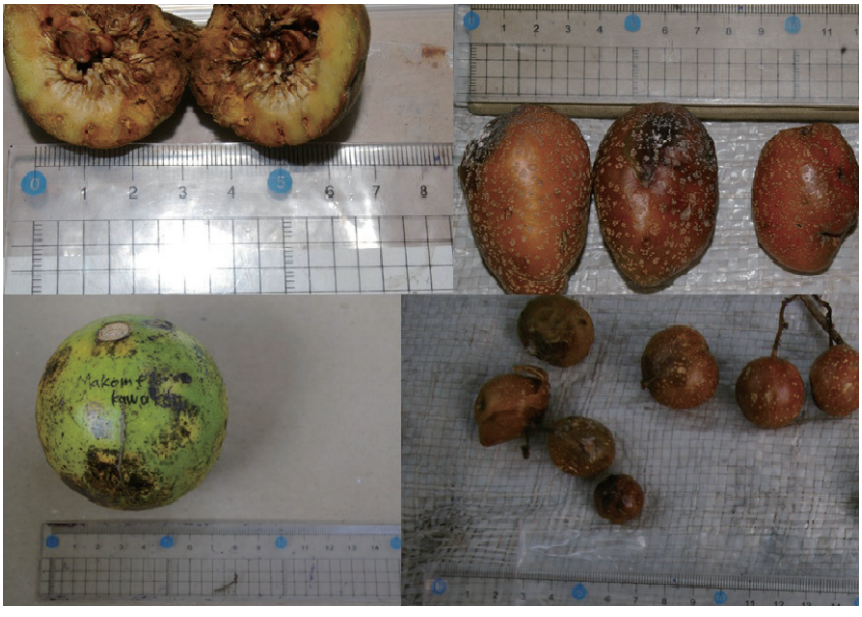

Fig. 3. Foods eaten by chimpanzees during the second half of the dry season in Ugalla

Fig. 4. Foods eaten by chimpanzees during the second half of the rainy season in Ugalla

II. Plants Eaten by Chimpanzees

1. Plant species

Chimpanzees in Ugalla consumed a total of 100 plant species belonging to 72 genera and 34 families (Table 1, Figs. 3 & 4). Chimpanzees consumed 12 species of the family Rubiaceae, 9 species of Moraceae, 9 species of Caesalpiniaceae, and 7 species of Annonaceae. The genus *Strychnos* included 4 food species, and the genus *Ficus* had 9 species. As some seeds of certain species found in chimpanzee feces closely resembled congeners, we were unable to distinguish them (Table 1). We found that 39 plant species were eaten by both Ugalla and Mahale chimpanzees. Mahale chimpanzees ate 39.0% of the 100 plant species eaten by Ugalla chimpanzees, and Ugalla chimpanzees ate 19.7% of the 198 plant species eaten by Mahale chimpanzees.

We found that 33 plant species were eaten by both Ugalla and Gombe chimpanzees. Gombe chimpanzees ate 33.0% of the 100 plant species eaten by Ugalla chimpanzees, and Ugalla chimpanzees ate 22.4% of the 147 plant species (calculated from Wrangham, 1975) that were eaten by Gombe chimpanzees. Ugalla and Kasakati chimpanzees had 18 plant species in common in their diets; Kasakati chimpanzees ate 18.0% of the 100 plant species eaten by Ugalla chimpanzees, and Ugalla chimpanzees ate 23.1% of the 78 plant species eaten by Kasakati chimpanzees.

Baboons ate 27 plant parts from 26 plant species, 1 species of rodent, and at least 2 insect species. Baboons ate 25 of the 100 plant species (25.0%) eaten by chimpanzees, while chimpanzees ate all except for 1 of the 26 plant species (96.2%) eaten by baboons (Table 1).

2. Plant parts

Ugalla chimpanzees ate a total of 117 plant parts of a variety of species: 81 (69.2%) fruits, 2 (1.7%) flowers, 12 (10.3%) seeds and pods, 9 (7.7%) leaves and shoots, 4 (3.4%) stems, 7 (6.0%) underground storage organs, 1 (0.9%) bark and cambium, and 1 (0.9%) unknown item (Tables 1 & 2).

Table 2. Number of plant parts eaten by chimpanzees of Ugalla, Kasakati, Mahale, and Gombe, Tanzania

Study area		Fruit	Flower	Seed & pod	Leaf & shoot	Stem	USO	Bark & cambium	Unknown	Total	Source
Ugalla	Number	81	2	12	9	4	7	1	1	117	Table 1 of this study
	%	69.2	1.7	10.3	7.7	3.4	6.0	0.9	0.9	100	
Kasakati	Number	61	4	16	5	2	Present			88	Suzuki, 1969
	%	69.3	4.5	18.2	5.7	2.3				100	
Mahale	Number	100	29	15	117	36	0	31		328	Nishida & Uehara, 1983
	%	30.5	8.8	4.6	35.7	11.0	0.0	9.5		100	
Gombe	Number	86	19	14	54	15	0	13		201	Wrangam, 1977
	%	42.8	9.5	7.0	26.9	7.5	0.0	6.5		100	

Note: USO = underground storage organ

Table 3. Life forms of plants eaten by chimpanzees of Ugalla and Mahale in Tanzania

Study area		Tree	Herb	Shrub	Liana	Climber	Tree/ Liana	Parasite	Herb/ Shrub	Shrub/ Liana	Shrub/ Tree	Shrub/ Liana/ Tree	Total	Source
Ugalla	Number	65	14	8	10	2	1						100	Table 1 of this study
	%	65.0	14.0	8.0	10.0	2.0	1.0						100	
Mahale	Number	83	29	18	52			1	1	3	4	1	192	Nishida & Uehara, 1983
	%	43.2	15.1	9.4	27.1			0.5	0.5	1.6	2.1	0.5	100	

Table 4. Vegetation types of plants eaten by chimpanzees of Ugalla, Kasakati, and Mahale, Tanzania

Study area		Woodland	Forest	Woodland/ Forest	Woodland / Wooded grassland	Woodland/ Wooded grassland/ Grassland	Wooded grassland	Lakeshore	Woodland/ Lakeshore	Lakeshore/ Woodland	Unknown	Total	Source
Ugalla	Number	47	35	11	3	1	1				2	100	Table 1 of this study
	%	47.0	35.0	11.0	3.0	1.0	1.0				2.0	100	
Kasakati	Number	20	54				4					78	Suzuki, 1969
	%	25.6	69.2				5.1					100	
Mahale	Number	73	80	21				10	4	3	1	192	Nishida & Uehara, 1983
	%	38.0	41.7	10.9				5.2	2.1	1.6	0.5	100	

Baboons ate a total of 27 plant parts of a variety of species: 24 (88.9%) fruits, 2 (7.4%) seeds, and 1 (3.7%) leaf (Table 1).

3. Life forms of plants

The life forms of the food plant species included 65 (65.0%) trees, 14 (14.0%) herbs, 8 (8.0%) shrubs, 10 (10.0%) lianas, 2 (2.0%) climbers, and 1 (1.0%) tree/liana (Tables 1 & 3).

III. Diet in Each Vegetation Type

The plant species identified in the Ugalla chimpanzee diets inhabit various vegetation types: 47 (47.0%) grow in woodlands, 35 (35.0%) in forests, 11 (11.0%) in woodlands and/or forests, 3 (3.0%) in woodlands and/or wooded grasslands, 1 (1.0%) in woodlands/wooded grasslands/grasslands, 1 (1.0%) in wooded grasslands, and 2 (2.0%) in unknown vegetation (Tables 1 & 4). Mahale chimpanzees ate 73 plant species in woodlands and 80 plant species in forests (Nishida & Uehara, 1983), and Kasakati chimpanzees ate 20 plant species in woodlands and 54 plant species in forests (Suzuki, 1969) (Table 4).

Ugalla and Mahale chimpanzees had more food species in common from woodlands (17 species; Table 1) than from forests (15 species; Table 1). Ugalla and Gombe chimpanzees had more food species in common from woodlands (18 species; Table 1) than from forests (12 species; Table 1).

IV. Animals Preyed on by Chimpanzees

1. Vertebrates

Chimpanzees preyed on 1 bird and at least 1 mammal species (Table 1). Among the 465 fecal samples that we collected, only 1 (0.2%) contained bird feathers. Although precise identification was unavailable, the species appeared to be paradise whydah (*Steganura paradisea*), a bird with a body mass of approximately 20 g. None (0.0%) of the fecal samples contained mammal remains, although Gen'ichi Idani (personal communication) found at least 3 fecal samples that contained rodent hairs at Nguye and also observed a chimpanzee attempting to catch a small mammal, possibly a squirrel, in a tree. Hernandez-Aguilar (2006) recorded 1 fecal sample that contained the bones of a small mammal, again possibly a squirrel, at Issa.

2. Invertebrates

Chimpanzees ate at least 3 insect species (belonging to the orders Coleoptera, Hymenoptera, and Isoptera; Table 1). Of the 465 feces, 11 (2.4%) contained invertebrates, most of which were ants (Formicidae). Because we were not able to identify them to the species level, the exact number of insect species consumed remains unknown.

DISCUSSION

I. Plants Eaten by Chimpanzees

1. Plant species

Ugalla chimpanzees ate fewer plant species and fewer plant parts than did those in Mahale and Gombe (Table 5). Our data seemed to support the first hypothesis, but there remain some issues. First, an explanation for the finding that chimpanzees in Ugalla ate fewer plant species and fewer plant parts than did chimpanzees in Mahale and Gombe is that different sampling methods were used in the different study sites. In Ugalla, our information came from the fecal samples we collected and analyzed, whereas in Mahale and Gombe, much of the data were collected by direct observations. The fecal analysis revealed information about undigested fecal material only, and the digested portion of the diet remained unknown. Second, the study periods in Ugalla were shorter than those in Mahale and Gombe. The shorter study period may have caused the lower number of food species observed in the period. Third, the number of plant species and parts consumed might also have been affected by the availability of food resources in each habitat. Fewer species might be present in Ugalla than in Mahale and Gombe, because most of the Ugalla area is composed of woodlands, which generally con-

Table 5. Number of plant species and plant parts eaten by chimpanzees in the dry and wet regions

Study area			Number of Plant species	Number of Plant parts	Source	Main sampling methods
Dry region						
Ugalla	,	Tanzania	100	117	This study	Fecal analysis/Direct observation/ Food remains
Kasakati	,	Tanzania	78	88	Suzuki, 1969	Fecal analysis/Direct observation/ Food remains
Fongoli	,	Senegal	47	60	Pruetz, 2006	Fecal analysis/Direct observation
Assirik	,	Senegal	43	60	McGrew et al.,1988	Fecal analysis/Direct observation/ Food remains
Semliki	,	Uganda	-	36	Hunt & McGrew, 2002	Fecal analysis/Direct observation/ Food remains
Wet region						
Mahale	,	Tanzania	198	328	Nishida & Uehara, 1983	Direct observation
Gombe	,	Tanzania	-	201	Wrangham, 1977	Direct observation
Budongo	,	Uganda	56	87	Newton-Fisher, 1999	Direct observation
Kanyawara	,	Uganda	112	-	Wrangham et al., 1991	Fecal analysis/Direct observation/ Food remains
Ipassa	,	Gabon	-	141	Hladik, 1977	Direct observation
Lope	,	Gabon	-	182	Tutin et al., 1997	Fecal analysis/Direct observation
Kahuzi-Biega	,	DRC	114	171	Basabose, 2002	Direct observation/Food remains
Bossou	,	Guinea	200	246	Sugiyama & Koman, 1992	Direct observation

Note: We incorporated data on Ugalla from Table 6.2 in Pruetz (2006).

Fig. 5. Fruits of *Parinari curatellifolia*

Fig. 6. Fruits of *Aframomum mala*

tain fewer species than do forests (Yoshikawa et al., in preparation).

The 8 study areas in Table 5 in the wet region are Kanyawara in Uganda (Wrangham et al., 1991), Ipassa in Gabon (Hladik, 1977), Lope in Gabon (Tutin et al., 1997), Kahuzi-Biega in the Democratic Republic of the Congo (Basabose, 2002), Bossou in Guinea (Sugiyama & Koman, 1992), Budongo in Uganda (Newton-Fisher, 1999), Mahale (Nishida & Uehara, 1983), and Gombe (Wrangham, 1977). As shown in Table 5, the number of plant species eaten by chimpanzees was 136.0 ± 62.0 SD (range: 56–200), and the number of plant parts eaten by chimpanzees was 193.7 ± 77.1 SD (range: 87–328). The 5 study areas in Table 5 in the dry region are Ugalla in Tanzania (this study), Kasakati in Tanzania (Suzuki, 1969), Fongoli in Senegal (Pruetz, 2006), Assirik in Senegal (McGrew et al., 1988), and Semliki in Uganda (Hunt & McGrew, 2002). As shown in Table 5 and in contrast to the results from the wet region, the number of plant species eaten by chimpanzees in the dry region was only 67.0 ± 27.0 SD (range: 43–100), and the number of plant parts eaten by chimpanzees was only 72.2 ± 31.1 SD (range: 36–117). Ugalla chimpanzees ate fewer plant species and fewer plant parts than did chimpanzees in all of the habitats in the wet region, with the exception of Budongo.

Among Ugalla, Kasakati and Assirik where data were collected by the same sampling method, chimpanzees at Ugalla ate more species (100 species; this study) than did those at Kasakati (78 species; Suzuki, 1969) and Assirik (41 species; McGrew et al.,1988) (Table 5). Also, Ugalla chimpanzees ate more plant species than did chimpanzees in other dry habitats, including Fongoli in Senegal (Pruetz, 2006) and Semliki in Uganda (Hunt & McGrew, 2002) (Table 5). The reason that chimpanzees appeared to eat fewer plant species and parts in Kasakati than in Ugalla may have been related to the duration of the study periods. Suzuki (1969) spent 376 days in Kasakati, whereas we spent 654 days, over the course of 7 years from 1995 to 2011, in Ugalla (including 143 days spent by Ogawa, 289 days spent by Yoshikawa, and 222 days spent by local research assistants), although we spent more time there during the dry season in several years. Due to the shorter study periods in Kasakati, those data may underestimate the number of plant species and parts. Even at Assirik and Fongoli in Senegal, chimpanzees ate only 43–47 plant species and 60 plant parts (McGrew et al., 1988; Pruetz, 2006). In Fongoli, chimpanzees depended heavily on a few fruits each month (Pruetz, 2006). In contrast, chimpanzees in Ugalla frequently ate fruits of *Parinari curatellifolia* (Fig. 5), *Aframomum* spp. (Fig. 6), *Keetia* spp., and *Thespesia garckeana* (or *Azanza garckeana*) simultaneously during many months of the year (Yoshikawa et al., in preparation). These favorite fruits of Ugalla chimpanzees were scattered within their huge home range, with the exception of *Aframomum* spp., and therefore chimpanzees foraged widely to find them. When they were foraging, they might tend to eat various other plants as well. This foraging pattern of Ugalla chimpanzees may result in the larger variation in their diet than was present in the diet of Fongoli chimpanzees.

Baboons in Ugalla had a simpler diet, and the food species of chimpanzees and baboons mostly did not overlap. Baboons ate only 25 of the 100 plant species eaten by chimpanzees, while chimpanzees ate almost all the plant species that

were eaten by baboons. Although we collected 196 baboon feces, the samples apparently did not cover all the food types eaten by baboons in Ugalla. We might have collected some feces from the same group of baboons who foraged together.

2. Plant parts

As with chimpanzees in other study areas (McGrew et al., 1988; Sugiyama & Koman, 1992; Tutin & Fernandez, 1993; Wrangham, 1977), our results show that chimpanzees in Ugalla ate fruits much more often than any other plant parts. However, Ugalla chimpanzees may eat more shoots and leaves than are shown in our results, because fecal analyses underestimate the amount of digested materials. Shoots and young leaves are readily available, particularly during the first half of the rainy season, while herbs wither and deciduous trees lose their leaves during the dry season. Like chimpanzees in other *miombo* woodlands (Suzuki, 1969), Ugalla chimpanzees may eat the legumes of many species, including those of *Brachystegia bussei* and *Monopetalanthus richardsiae*, especially during the first half of the dry season.

Whereas chimpanzees in rainforests infrequently ate the underground storage organs of plants (Hunt & McGrew, 2002), our study found that chimpanzees readily ate them at Nguye and at Issa in Ugalla (Hernandez-Aguilar et al., 2007). As did chimpanzees in other habitats, Ugalla chimpanzees ate fruits of *Ficus* spp. throughout the year. Underground storage organs may be another important food for Ugalla chimpanzees that help to compensate for the smaller number of edible plants available in this region, relative to the wet region. Digging sites made by chimpanzees were observed only during the rainy season (Hernandez-Aguilar et al., 2007). We also found evidence of underground storage organs in chimpanzee feces, mainly in January and February during the rainy season. Chimpanzees mainly prefer fruits and particularly ripe fruits, but fruit availability change over the seasons in Mahale (Itoh, 2004). As in Mahale, the availability changed with the seasons in Ugalla, and our phenology data indicated that there were few ripe fruits during the first half of rainy season (Yoshikawa, unpublished data). Therefore, Ugalla chimpanzees may eat the underground storage organs of plants as a seasonal fallback food.

3. Life forms of plants

Of the plant species eaten by chimpanzees in Mahale, 43.2% were trees and 27.1% were lianas, indicating that lianas are an important plant to produce food for Mahale chimpanzees (Nishida & Uehara, 1983; Turner, 2000; Itoh, 2004). Compared with Mahale, 65.0% of the plants eaten by chimpanzees in Ugalla were trees, and only 10.0% were lianas (Table 3). Liana were rare in the woodland habitat that dominates the Ugalla area (Hernandez-Aguilar, 2006), and chimpanzees there did not depend on them as did the Mahale chimpanzees.

II. Diet in Each Vegetation Type

The diet of Ugalla chimpanzees included 47 (47.0%) plant species in woodlands and 35 (35.0%) plant species in forests (Table 4). Woodlands in Ugalla contained

many plant species eaten by chimpanzees, compared with other types of vegetation. The results support the second hypothesis. As at Ugalla, woodlands at Assirik and Fongoli in Senegal contain more plant species consumed by chimpanzees than do other vegetation types at these sites, where only 2–3% of the area is forested (McGrew et al., 1988; Pruetz, 2006). At Kasakati, 58.9% of the area is woodland, 9.9% is forested, and 31.2% is grassland and savanna (Suzuki, 1969). The woodlands are an indispensable habitat for chimpanzees in the dry region.

The Ugalla area consists primarily of woodlands (86%) with some grasslands (12%) and a small forested area (2%) (Ogawa et al., 2007), but 35% of plant species eaten by chimpanzees in this area were from forests. The forest vegetation may have many plant species eaten by the chimpanzees, despite the small area.

III. Animals Eaten by Chimpanzees

There are at least 50 mammalian species in Ugalla (Iida et al., 2012), and 82 mammalian species in Mahale (Moyer, 2006).

Chimpanzees in Ugalla ate only 5 animal species, including 3 insect species (Table 1), although the number might be underestimated, because we did not identify the animal species. We recorded insects in 2.4% of feces in Ugalla, compared with 7.5% of feces in Kasakati (calculated from Suzuki, 1966). Chimpanzees ate at least 25 insect species in Mahale (Uehara & Nishida, 1983) and 13 insect species in Gombe (Wrangham, 1977). Assuming that our numbers are underestimated, it is still clear that chimpanzees in Ugalla ate fewer invertebrate animal species than did chimpanzees in Mahale (Nishida & Uehara, 1983) and Gombe (Wrangham, 1977).

Further, we found no evidence of chimpanzees having eaten primates and large mammals. It has been reported that chimpanzees hunted monkeys exclusively in groups, and large subgroup size increased the frequency and the success rate of such a hunt (Boesch & Boesch, 1989; Mitani & Watts, 1999). Chimpanzees in Mahale were reported to have formed a sub-group of 15.5 individuals (Itoh & Nishida, 2007). In contrast, the average sub-group of chimpanzees in Ugalla was observed to be only 3.3 individuals (Ogawa et al., 2007). Thus, the reason that Ugalla chimpanzees did not eat many vertebrates may be that their population has a small sub-group size, which may make it difficult for them to hunt large mammals and monkeys.

SUMMARY

1. Ugalla chimpanzees in the dry region in Tanzania ate fewer plant species and a smaller number of plant parts than did Mahale and Gombe chimpanzees in the wet region in Tanzania.

2. Ugalla chimpanzees ate a larger number of plant species and more types of plant parts than did chimpanzees in other dry habitats, including Kasakati in Tanzania, Assirik in Senegal, and Fongoli in Senegal.

3. Ugalla chimpanzees ate underground storage organs from more plant species than did Mahale and Gombe chimpanzees.

4. Ugalla chimpanzees ate fewer and smaller amounts of vertebrates and invertebrates than did Mahale and Gombe chimpanzees.

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