Int J Primatol (2007) 28:1397–1412
DOI 10.1007/s10764-007-9210-0

Sleeping Parties and Nest Distribution of Chimpanzees in the Savanna Woodland, Ugalla, Tanzania

Hideshi Ogawa · Gen'ich Idani · Jim Moore · Lilian Pintea · Adriana Hernandez-Aguilar

Received: 20 October 2005 / Revised: 11 July 2006 / Accepted: 11 August 2006 /
Published online: 20 November 2007

Abstract We conducted ecological studies of chimpanzees (*Pan troglodytes*) in the Ugalla area, western Tanzania. Ugalla is one of the driest habitats of chimpanzees and the Ugalla River is the eastern boundary of chimpanzee distribution. Most of Ugalla is occupied by savanna woodlands dominated by deciduous trees of *Brachystegia* and *Julbernardia*. Chimpanzees tended not to make nests in riverine forests in plains, but in small patchy forests dominated by *Monopetalanthus richardsiae* and valley forests dominated by *Julbernardia unijugata* on slopes in mountainous areas. We estimated population density of chimpanzees to be $7–9\times10^{-2}$ individuals/km^2 based on nest censuses, suggesting that $2–3\times10^2$ individuals inhabited the 3352 km^2 area of Ugalla. The size of the largest nest cluster (n=23) suggests that 1 unit group (community) comprised 30–35 individuals. In the daytime, chimpanzees formed small feeding parties (mean 2.0 individuals), but larger ones in the evening (mean 4.8 individuals and 5.2 individuals based on fresh nest clusters). The pattern might reduce the predation risk from large nocturnal carnivores such as lions and leopards. The sleeping sites may function as both a safe sleeping site and a meeting point for chimpanzees with a huge home range that may have difficulty in finding other members of their unit group.

H. Ogawa (✉)
School of International Liberal Studies, Chukyo University,
Tokodachi 101, Kaizu-cho, Toyota, Aichi 470-0393, Japan
e-mail: hogawa@lets.chukyo-u.ac.jp

G. Idani
Great Ape Research Institute (GARI), Hayashibara, 952-2 Numa, Tamano, Okayama 706-0316, Japan

J. Moore
Department of Anthropology, University of California, San Diego, La Jolla, CA 92093, USA

L. Pintea
Jane Goodall Institute, Arlington, VA 22203, USA

A. Hernandez-Aguilar
Department of Anthropology, University of Southern California, Los Angeles, CA 90089, USA

Keywords chimpanzee · nest distribution · party size · savanna woodland · Ugalla area

Introduction

Chimpanzees (*Pan troglodytes*) live in tropical rain forests and more open and dry areas in Africa (Kortlandt 1983; Teleki 1989), while other great apes are more restricted to tropical forests. In Tanzania, eastern chimpanzees (*Pan troglodytes schweinfurthii* or *P. marungensis* or both) live along the shore of Lake Tanganyika (Kano 1972; Massawe 1992; Nishida 1989; Ogawa *et al.* 1997). Although researchers have continuously studied and protected chimpanzees in Mahale and Gombe National Parks since the 1960s (Goodall 1986; Nishida 1990), comparatively little chimpanzee research has been done in Tanzania's savanna woodland environments (Itani 1979; Kano 1972; Moore 1994; Nishida 1989). Such research is important for understanding the variety and flexibility of chimpanzee adaptation and to illuminate models of early hominid behavioral ecology (Baldwin *et al.* 1981, 1982; Itani 1979; Kano 1972; McGrew *et al.* 1981; Moore 1992, 1996; Suzuki 1969).

Chimpanzees in savanna woodland areas have lower population density and larger home ranges (Baldwin *et al.* 1982; Kano 1972; Moore 1992) than those of chimpanzees in more forested areas (Boesch and Boesch 1989; Hashimoto 1995). Among savanna woodland environments, chimpanzees in Ugalla have very low population density (Itani 1979; Kano 1972). Kano (1972) estimated that the density of chimpanzees was 0.08 individuals/km^2 and the total number of chimpanzees >3–4 yr was *ca.* 200–240 individuals in the 2800-km^2 Ugalla area, yielding 5–6 unit groups in Ugalla if a unit group (community) comprised 40 individuals as in other areas (Kano 1972). If home ranges are nonoverlapping, the home range of each unit group is roughly 470–560 km^2 (Kano 1972). If 25–50% of the home range overlapped with the range of its neighboring unit group, the home range of chimpanzees in Ugalla might be as much as 700–750 km^2 (Itani 1979).

Sparse and patchily distributed food supplies in savanna woodlands may cause such low density and huge home range. If chimpanzees in savanna woodland environments form small parties, however, they may face high predation risk, because potential predators such as lions (*Panthera leo*), leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*), and spotted hyenas (*Crocuta crocuta*) inhabit the area, and because the distances between deciduous trees are long and the canopies are open. To understand chimpanzee adaptation to such open and dry circumstances, we conducted ecological surveys in the Ugalla area.

Methods

Study Area

Location and Geographical Features The Ugalla area (Fig. 1) is surrounded by the Ugalla River on the east, the Malagarasi River on the north, Uvinza-Mpanda Road on the west, and the Niamansi Basin on the south (Kano 1972). The Ugalla area covers 3352 km^2 with elevation of 980–1712 m. Compared to Kano's (1972) estimate, the

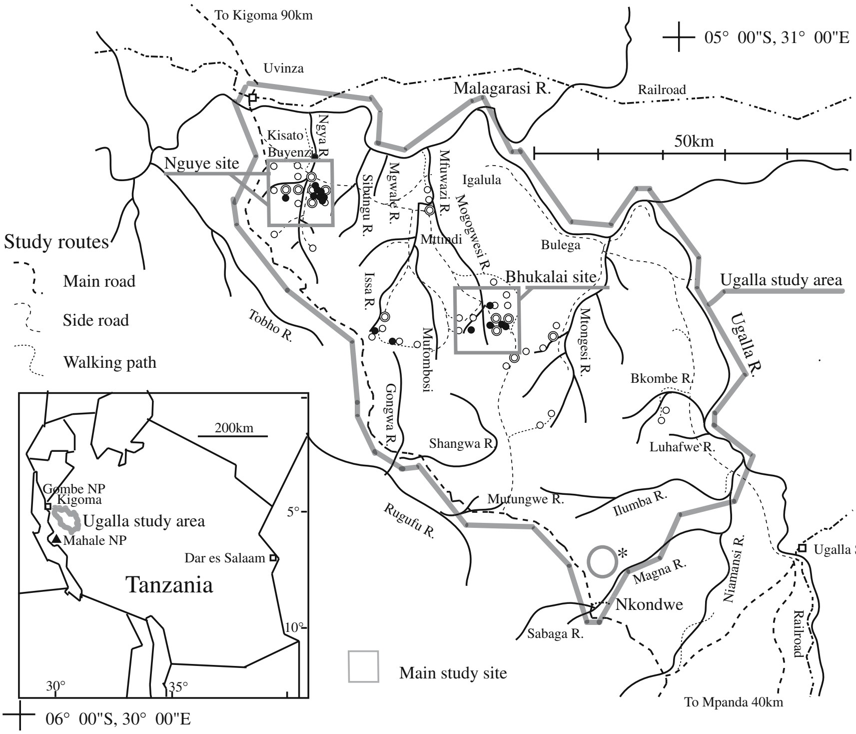

Fig. 1 Distribution of chimpanzee nests in the Ugalla area. ◎: the 2 km×2 km areas in which chimpanzee nest(s) were recorded in ≥2 different years. ○: the 2 km×2 km areas in which chimpanzee nest(s) were recorded in 1 yr. Some points were the area we visited only one time. ●: the place where we observed chimpanzees directly. Main study site: 2 main study sites, Bhukalai and Nguye, are shown by 10×10 km squares. Main road: unpaved road connecting Uvinza, Mpanda, and Ugalla Station. Roads are almost closed during the rainy season. Side road: roads for transportation of timbers. Walking route: traditional path, path of wild animals, and walking route for the nest census. Walking routes out of 2 main study sites, Bhukalai and Nguye, are shown, but walking routes in the Bhukalai and Nguye sites are not shown. All of the main roads, side roads, and walking routes were passed by Ogawa. The information above is based on Ogawa's record in 1994–2005. ○*: nests were found in 2005 (Piel and Stewart, *pers. comm.*).

3352 km^2 figure we adopted is derived from a regional GIS, and reflects slightly larger boundaries and accurate accounting for 3-dimensional relief. There is a plateau in west Ugalla and steep slopes or escarpments between that plateau and the plains along the Malagarasi and the Ugalla Rivers.

Climate The Tanzanian Directorate of Meteorology operates 2 rainfall stations near Uvinza (5°06′ S, 30°23′ E), at the northwest edge of the Ugalla area. Unfortunately, data obtained at different times show minor unreconciled differences, making it difficult to determine confidently precise averages for the site. However, the discrepancies do not affect the overall picture given significant orographic differences between the 2 Uvinza recording sites, the vast area under consideration, and the overall consistency of the data. For 1973–2005, mean annual rainfall is 980 mm (range: 750–1350 mm); for 16 of the years no rain fell during June-Aug. Defining a dry month as one with average rainfall ≤60 mm, average total rainfall during the May–Sept. dry season is 60±40 mm (*n*=26 complete years) and the average of *Q*, a seasonality index, is 108.3±35.9 (*n*=26; *Q* = [(no. of dry mo/no. of wet mo)×100]; Moore 1992). Because of this long dry season and geographical and geological features (Sutton and Roberts 1968), most streams in the Ugalla area dry up during the dry season. In this sense, Ugalla is one of the driest habitats in which chimpanzees live (Moore 1992).

Hernandez-Aguilar recorded daily temperature at Issa site in Ugalla. Daily maximum and minimum temperatures are available for Aug. 2002–June 2003. For 3 mo, data are partial (>15 d but less than the total days of the month). In June, we recorded data for 1 wk. Average daily maximum temperature was highest in Aug. (34°C) and lowest in Nov. (28°C). Average daily minimum temperature was highest in Jan. (17.2°C) and lowest in Aug. (14.4°C).

Vegetation The Ugalla area has 3 main vegetation types: 1) savanna woodland, 2) forest, and 3) grassland. Most of the Ugalla area is savanna (miomba) woodlands dominated by deciduous trees of *Brachystegia* and *Julbernardia*, and locally called miombo woodland (Itani 1979; Kano 1971, 1972; Nishida 1989; Moore 1994).

Study Periods and Study Sites

Ogawa conducted ecological surveys in Ugalla: 1) Aug. 15–Sept. 9 and Oct. 3–Nov. 13, 1995, (2) July 27–Aug. 31, 1996, (3) July 30–Aug. 21, 1997. Idani joined him during some parts of the periods. They also conducted a pilot study from Aug. 8 to 24 and from Oct. 12 to 14, 1994. Ogawa also studied from Aug. 5 to Sept. 4, 1999, and Feb. 21 to March 3, 2003, July 30 to Aug. 10, 2003, and Aug. 30 to Sept. 4, 2005. They established base camps at 1) the Bhukalai site (05°26.8′ S, 30°44.1′ E) close to the Mogogwesi (Bhukalai) River in central Ugalla and 2) the Nguye site (05°13.0′ S, 30°27.5′ E) close to the Ngya (Nguye) River in northwest Ugalla (Fig. 1). Ogawa stayed at Bhukalai site for 59 d and at Nguye for 89 d, and walked in the area of *ca.* 100 km^2 (10 km×10 km) around the base camps. Ogawa also drove a car, walked, and stayed at other sites in Ugalla for 61 d (Fig. 1).

Moore conducted surveys in 1988, 1992, and 1993, camping at Nguye, Mttindi, and Bulega (Fig. 1) as well as other sites. Henandez-Aguilar intensively studied nest distributions at Issa during 2002–2003.

Study Methods

We report on data collected independently by several groups. Methods differed between the teams; we described them separately. Combining data collected over >15 yr by independent teams using different methods is difficult (Plumptre and Cox 2006), and density estimation was not a primary goal for either Moore or Hernandez-Aguilar.

One of the main variables for using nest densities to estimate population density is the rate at which nests decay (Ihobe 2005), which has been difficult to establish with confidence at Ugalla, because nest decay in savanna woodland is typically slow. For example, A. Murorerowa, a local assistant working for Ogawa and Idani, marked 22 old nests in savanna woodland on Aug. 22, 2000 and 6 (27%) of them were recognizable on July 29, 2001. Thus, decay rates generally have exceeded study periods. In 1999–2000, he also located and monitored 5 fresh and 5 new nests in an evergreen valley forest at 3-mo intervals until they completely disintegrated. All nests lost all their leaves before 185 d but ≥9 were still identifiable nests. At 245 d, ≥4 were still present and by 276 d, 6 were completely disintegrated. We used the midpoint between the durations, 260 d, to estimate time to total disintegration of nests in an evergreen forest. Because 260 d exceeds the duration of wet/dry seasons, in the absence of data to the contrary, we assume that ignoring season of nest-building will not bias our data strongly in any direction. We do not have comparable data for nests in the savanna woodland, so we have applied this figure to all nests. We emphasize that more detailed study of nest decay rates in the Ugalla area is critical to refine the present population estimates. Kano (1972) used 180 d for his density estimates, and we also present Kano formula population estimates for comparison.

To estimate population density of chimpanzees, Ogawa recorded information on chimpanzee nests along 4 4-km straight vegetation transects bellow per methods of Tutin and Fernandez (1984). In addition, on 97.6 km of walking routes in 1997, we recorded vegetation types while passing through 64% savanna woodlands, 32% along the edge of forests and savanna woodland, 3% in forests, and 1% in grassland. Because the proportions were broadly similar to those in the vegetation transects and Landsat satellite imagery, he treated the walking routes in 1995–1997 as nest transects (Fig. 1, Table 3). No one duplicated the route ≤12 mo. We measured distances on walking route via a pedometer. The mean distance of a 1-d walk is 9.4 km (Table 3). Because a pedometer has an accidental error, we calculated population density by summing ±10%. Before each daily walk, Ogawa planned the route. With 1:50,000 maps and a portable GPS, he usually made a round trip from the base camp to the tops of hills and walked not only on traditional paths but also paths of wild animals and off paths (see Plumptre and Reynolds 1997). He recorded the following information for each nest: age class of the nest [fresh (1 d), new (all leaves are green), recent (some leaves are green), old (all leaves are not green), and rotting (no leaves)]; perpendicular distance between the nest and the vegetation transect line or the walking route. He measured perpendicular distance via footsteps of local guides, or, when that was impossible, estimated by eye after he practiced estimating distance by eye.

Moore's 1988 nest density estimate is based exclusively on 7 formal vegetation transects of 2 km each, 1 at Nguye and 6 at Mttindi. He determined via a random number table to select UTM coordinates within a 5 km×5 km square centered on camp; he assigned transect directions to cardinal directions before this. He measured perpendicular distances to nests to the nearest meter with a 50-m surveyor's tape and recorded nest ages via the same categories Ogawa used.

To estimate the size of a sleeping party, Ogawa recorded the number of nests in each nest cluster, i.e., ≥1 nests that appeared to have been made on the same day, were located ≤ ca. 50 m diameter circle, and were < *ca.* 20 m apart from the closest nest.

Ogawa made 1 100 m×100 m vegetation quadrat in savanna woodland at Nguye, 1 50 m×50 m quadrat in a forest at Nguye, and 1 50 m×50 m quadrat in a forest at Bhukalai. He recorded the name, diameter at breast height (DBH), and height of all trees with ≥5 cm in DBH in the quadrats (Table 1). He also recorded the location of nests within and around the quadrats. He made 2 vegetation transects at

Table 1 Trees in the vegetation quadrats in woodland and two subtypes of forests

Vegetation subtype	*Brachystegia bussei* woodland		Kabamba-jike forest		Flat riverine forest[c]	
Location	Nguye site		Bhukalai site		Nguye site	
Range of survey	10,000 m^2 (100 m×100 m)		2500 m^2 (50 m×50 m)		2500 m^2 (50 m×50 m)	
Ratio of basal area[a]	0.14%		0.18%		0.54%	
Number of plants	234 (43, 61, 64, and 66 in each 50 m×50 m area)		140		303	
Number of species	36 (16, 19, 21, and 22 in each 50 m×50 m area)		10		30	
DBH of the largest tree	80.7 cm (51.9, 80.7, 50.9, and 46.4 in each 50 m× 50 m area)		94.7 cm		124.2 cm	
Dominant plants[b]	Name	%	Name	%	Name	%
	Brachystegia bussei	20.3	*Monopetalanthus richardsiae*	61.3	Unidentified	55.8
	Brachystegia boehmii	11.2	*Brachystegia microphylla*	13.4	*Pseudospondia microcarpa*	10.8
	Brachystegia spiciformis	10.6	*Strychnos spinosa*	11.8	Unidentified	8.2
	Pericopsis angolensis	9.4			*Pachystela brevipes*	6.7
	Pterocarpus tinctorius	9.3				
	Parinari curatellifolia	9.1				
	Diplorhynchus condylocarpon	9.1				

[a] $\{\Sigma\pi(\mathrm{DBH}/2)^2\}/\text{survey area}\}$.

[b] % of basal area of the species to the total basal area of all trees. The species with ≥5% are listed.

[c] This survey area is not necessarily representative of composition of plants in flat riverine forests because the quadrat was made in the place where 2 meandering streams join and the forest was wide, while most flat riverine forests are narrower.

Bhukalai, 1 at Shangwa, and 1 at Nkondwe, each of which was a 4-km straight line 4 m wide. He recorded the same data on plants in the area and data on nests along the lines.

Results

Habitat

Vegetation in Ugalla comprises 3 main types: 1) savanna woodland, 2) forest, and 3) grassland. Unlike other areas in western Tanzania, there were few bamboo thickets in Ugalla. Vegetation maps derived from 2001–2002 Landsat satellite imagery showed that 86% of the 3352-km^2 Ugalla area was occupied by savanna woodlands, 2% by forests, and 12% by grasslands. Four 4 km×4 m line transect vegetation surveys in Ugalla showed that 83% of 16 km occupied by savanna woodlands, 4% by forests, and 12% by grasslands, if grassland were defined as the place where a tree with ≥5 cm DBH was not present along >50 m transect line. Table 1 contains density of trees and dominant trees in 3 vegetation quadrats.

Savanna woodland is widely spread in western Tanzania. Deciduous 20-m trees are scattered over areas of grass (Graminae). The presence of groundcover dominated by C4 grasses defines a habitat as savanna (Moore 1992). The canopies of some woodland trees are not closed even during the rainy season. Savanna woodlands can be further divided into subtypes, e.g., *Brachystegia bussei* woodland or dry open forest (Combretum/Protea/Monotes savanna; Itani 1979; Kano 1971, 1972; Moore 1994; Suzuki 1969).

We defined a forest by the near-total dominance of evergreen trees. Trees in forests grew more densely than trees in savanna woodlands (Table 1). Forests in Ugalla were of 3 subtypes: 1) *Kabamba-jike forest*: *Monopetalanthus richardsiae*, locally called kabamba-jike, formed small patchy forests beside cliffs, escarpments, and springs. Some of the forests were ≤3000 m^2. Dry riverine forest (Itani 1979) and upper scarp edge (Moore 1994) refer to the same vegetation. Conversely, moist riverine forest (Itani 1979) are close to flowing water (Kano 1972; Moore 1994). 2) *Valley forest*: This is a kind of riverine forest located mainly in valleys. Evergreen trees of 20–30 m formed a deep forest, and some valley forests were ≤200 m wide. Most valley forests were dominated by *Julbernardia unijugata*, locally called kabamba-dume. Researchers identified *Monopetalanthus richardsiae* and *Julbernardia unijugata* as *Cynometra* spp. in some earlier reports (Kabamba: Moore 1994; Kamama: Nishida and Uehara 1981). Gallery forest (Nishida 1989) might be the same vegetation. 3) *Flat riverine forest*: Narrow riverine forests are along streams and rivers in plains. The width was <50 m and the forests were not necessarily continuous along streams. Unlike in kabamba-jike forests and valley forests, dominant trees varied in flat riverine forests.

There are 2 subtypes of grasslands. Riverine grassland: Along rivers, there were grasslands dominated by Gramineae or Cyperaceae such as *Cyperus papyrus*. During the rainy season, they resembled a swamp called Mbuga (Itani 1979), swamp (Kano 1972), and lower valley bottom grassland (Nishida 1989). Plateau grassland: On the plateau, there were dry grasslands that included areas with exposed rocks and few plants except for *Xerophyta spekei*.

Table 2 shows large mammals living in Ugalla (Itani 1979; Kano 1972; Nishida 1989). We very rarely saw giraffe (*Graffa camelopardalis*), zebra (*Equus burchellii*), and wild dog (*Lycaon pictus*), and giraffe and zebra may have become locally extinct during our study period. Impala (*Acepyceros melampus*) was also very rare.

Table 2 also shows primate species in Ugalla. The same primate species as reported in the 1960s (Kano 1971) continue to inhabit Ugalla. Red-tailed monkeys (*Cercopithecus ascanius*), known to inhabit western and southern Ugalla based on information from local people (Kano 1971) and vocalization (Nishida 1989) and in northwestern and central Ugalla. Blue monkeys (*Cercopithecus mitis*), which we did not confirm in western Ugalla (Kano 1971), live in both of western and eastern Ugalla. The 2 *Cercopithecus* spp. live only in forests. Many yellow baboons (*Papio cynocephalus*) inhabit Ugalla. In addition, we observed olive baboons (*Papio anubis*), which before lived only to the north of the Malagarasi River, in northwestern Ugalla. Green monkeys (*Cercopithecus aethiops*) live at Nkobdwe, Bulega, and upper Nguye, but at very low densities on other sites. We saw no red colobus (*Colobus badius*). At least 2 species of *Galago* are present.

Human Activity

Wa-Tongwe people originally lived in Ugalla but were resettled to nearby villages under the government's emigration policy in the late 1960s, and only some people temporally

Table 2 Primates and large mammals in Ugalla

English name	Scientific name	Evidence
Proboscidea		
Elephant	*Loxodonta africana*	Direct observation
Tubulidentata		
Ant bear	*Orycteropus afer*	Nest
Artiodactylas		
Hippopatamus	*Hippopotamus amphibius*	Direct observation
Warthog	*Potamochoerus aethiopicus*	Direct observation
Bushpig	*Potamochoerus porcus*	Direct observation
Black buffalo	*Syncerus caffer*	Direct observation
Eland	*Taurotragus oryx*	Direct observation by local guides and horns of a carcass
Waterbuck	*Kobus defassa*	Direct observation
Roan antelope	*Hippotragus equinus*	Direct observation
Sable antelope	*Hippotragus nige*	Direct observation[a]
Lichtenstein hartbeest	*Alcelaphus lichtensteini*	Direct observation
Bushbuck	*Tragelaphus scriptus*	Direct observation
Sitatunga	*Tragelaphus spekei*	Direct observation by local guides[b]
Greater kudu	*Tragelaphus strepsiceros*	Direct observation by local guides[b]
Lesser kudu	*Tragelaphus imberbis*	Direct observation by local guides[b]
Klipspringer	*Oreotragus oreotragus*	Direct observation
Common duiker	*Sylvicapra grimmia*	Direct observation
Impala	*Acepyceros melampus*	Direct observation by local guides[b]
Giraffe	*Graffa camelopardalis*	Direct observation
Plains zebra	*Equus burchellii*	Direct observation
Carnivora		
Lion	*Panthera leo*	Direct observation
Leopard	*Panthera pardus*	Direct observation
Spotted hyena	*Crocuta crocuta*	Footprints, feces, and vocalization
Wild dog	*Licaob pictus*	Direct observation
Side-striped jackal	*Canis adustus*	Direct observation
Black-backed jakal	*Canis mesomelas*	Direct observation
Primates		
Chimpanzee	*Pan troglodytes*	Direct observation
Yellow baboon	*Papio cynocephalus*	Direct observation
Olive baboon	*Papio anubis*	Direct observation
Green monkey	*Cercopithecus aethiops*	Direct observation
Redtail monkey	*Cercopithecus ascanius*	Direct observation
Blue monkey	*Cercopithecus mitis*	Direct observation
Red colobus	*Procolobus pennantii*	Direct observation
Great galago	*Galago crassicaudatus*	Direct observation by local guides[c]
Lesser galago	*Galago senegalensis*	Direct observation by local guides[c]

All primates and large-sized mammals inhabiting the Ugalla area are listed.
Direct observation: No number on "direct observation" = directly observed Ogawa and/or Idani.
[a] Directly observed by Moore, Herandez-Aguilar, and other researchers (Piel, *pers. comm.*; Nishida 1989).
[b] Directly observed by the local guides of Ogawa's and Idani's.
[c] At least 1 species of galago was observed and 2 different species were heard by Ogawa. His local guides say 2 galago species inhabit Ugalla, probably great galago and lesser galago.

used the Ugalla area for honey gathering, fishing, and hunting from then until the 1990s. Limited commercial harvest of specific trees, *Pterocarpus angolensis* and *Pterocarpus tinctorius*, has been conducted in the Tongwe East Forest Reserve in Ugalla (5°25–5° 50′ S, 30°40–31°05′ E), via hand pit-sawing techniques. People burn grasses during the dry season. Although the brush fires had direct and indirect influences on vegetation and wild animals, trees did not die from brush fires; lightning-strike fires also occur and miombo woodland is considered fire-adapted (Kikula 1986). In the late 1990s, small farms (shambaa) began to expand southward from Uvinza along Mpanda-Uvinza Road. Since 1997, several people have immigrated into Nguye and Kisato, northwestern Ugalla, and made *ca.* 5 farmer's huts and cultivated fields. A professional hunter's camp was built on the east bank of the Ugalla River in 1993 and the Ugalla area is a Niensi game control area now.

Nest Distributions and Party Sizes

Distribution and Population Density of Chimpanzees Chimpanzee nests were distributed widely in the Ugalla area, though with possible lacunae on plains and plateaus, e.g., Bulega and Mfuwazi Basin (05°11′ S, 31°38′ E, downstream of the Issa River), and showed clear concentrations at others, e.g., Issa area (Fig. 1). Local people at Nkondwe reported hearing chimpanzees 1 or 2 times/yr, and nests occurred north of Nkondwe (Piel, A. and Stewart, F., *pers. comm.*; Fig. 1). However, at the Niamansi River and the road from Ugalla Station to Mpanda-Uvinza Road, no nest occurred, and local people said that they have never heard chimpanzees in the area. The northern portion of the Niamansi Basin (north of the Magna River) appeared to be the southern limit of the chimpanzee habitat.

Ogawa observed 455 nests along 298.2 km of vegetation transect lines and walking routes. Maximum perpendicular distance was *ca.* 70 m, but >90% (413) fell ≤35 m of the routes. Assuming that a nest remains for 260 d and all nests ≤35 m on each side are located, the population density of chimpanzees >3–4 yr was $7–9\times10^{-2}$ individuals/km^2, based on 413 nests ≤35 m each side of the 298.2-km vegetation transect lines and walking routes: $\text{density} = \{(413 \times (1/260)\}/\{298.2 \times (70/1000)\} = 0.076\ \text{individuals}/\text{km}^2$ (Table 3). The same assumption shows that the density was $8–10\times10^{-2}$ individuals/km^2 at Bhukalai based on 143 nests along the 87.8 km, and $5–7\times10^{-2}$ individuals/km^2 at Nguye based on 111 nests along the 98.7-km (Table 3).

While Kano (1972) recorded 350 nests along his 250-km walking route, Ogawa recorded 455 nests along his 298.2-km vegetation transect lines and walking routes. The difference in number of nests relative to the walking distance is not significant ($\chi^2=1.5$, df=1, n.s.), though there was slight difference between 0.079 and 0.086 individuals/km^2, if Kano's (1972) assumptions are used for both studies: a nest disappears in 180 days and 70% of nests ≤70 m of each side of the walking route were located.

Moore recorded 8 nests visible from the transect line along the 14 km of transects and the density estimate derived is for comparative purposes only. The greatest perpendicular distance was 73 m, and 2/8 were ≥50 m from the transect line. Using Kano's (1972) model yields an estimate of 0.032 individuals/km^2. At least 3 potentially overlapping explanations for this lower density estimate are possible: 1) Moore's estimate, coming from only 14 km of transect, is unrepresentative, 2) estimates based on walking routes instead of true transects were biased toward

Table 3 Number of nests and density of chimpanzees

Site	Census line	Month and year	Number of days for census	Distance of census (km)	Number of nests	Population density (individuals/km^2)
Bhukalai	Walking route	Aug., 1996	6	66.5	63	0.05
Bhukalai	Walking route	Aug., 1997	2	13.3	44	0.18
Bhukalai	Straight transect	Aug., 1995	1	4.0	22	0.30
Bhukalai	Straight transect	Aug., 1996	1	4.0	14	0.19
Subtotal			10	87.8	143	0.09
Nguye	Walking route	July and Aug., 1996	6	80.2	98	0.07
Nguye	Walking route	July and Aug., 1997	6	18.5	13	0.04
Subtotal			12	98.7	111	0.06
Others	Walking route	Sept., 1995	1	5.5	0	0.00
Others	Walking route	Aug., 1996	6	32.3	72	0.12
Others	Walking route	Aug., 1997	3	65.8	87	0.07
Others	Straight transect	Aug., 1996	2	8.0	0	0.00
Total			34	298.2	413	0.08

Number of nests: number of nests recorded ≤35 m from the census line. Walking route: census lines were walking routes. Straight transect: census lines were straight for a vegetation line transect survey. Population density of chimpanzees >3–4 yr was calculated, assuming that a nest remains for 260 d and all nests ≤35 m each side were found.

habitats or topographies more likely to contain nests, and 3) the Mttindi area tends to be little used by chimpanzees, for either ecological or social reasons, e.g., near the boundary between two communities.

Choice of Nest Trees and Sleeping Sites Chimpanzees mainly inhabited mountainous areas between northwest Ugalla and southeast Ugalla (Fig. 1). We found no evidence in the plains at Igalula, Bulega, Mfuwazi Basin, and Niamansi Basin.

In 1995–1997, Ogawa and Idani recorded a total of 982 chimpanzee nests in 237 nest clusters in Ugalla. Chimpanzees made 70 (29.5%) nest clusters in savanna woodlands, 92 (38.8%) in kabamba-jike forests, 47(19.8%) in valley forests, 22 (9.3%) in flat riverine forests, and 6 (2.5%) over 2 vegetation types. In July and Aug., when most deciduous trees are leafless, only 1 (1.0%) fresh, we recorded new and recent nest clusters in savanna woodlands and 31 (56.4%) in kabamba-jike forests, 18 (32.7%) in valley forests, 4 (7.3%) in flat riverine forests, and 1(1.8%) over 2 vegetation types. Chimpanzees made 388 (39.5%) nests in *Monopetalanthus richardsiae*, 245 (24.9%) nests in *Julbernardia unijugata*, 72 (7.3%) nests in *Brachystegia bussei*, 23 (2.3%) nests in *Pterocarpus tinctorius*, and 20 (2.0%) nests in *Brachystegia microphylla* (Table 4). Comparison between 404 nest trees in kabamba-jike forests and 140 trees with ≥5 cm DBH in the vegetation quadrat in a kabamba-jike forest shows that chimpanzees selected nesting trees nonrandomly (χ^2 test, $df=4$, $\chi^2=499.2$, $p<0.05$) and slept in *Monopetalanthus richardsiae* more frequently than expected (χ^2 test, $df=1$, $\chi^2=290.8$, $p<0.05$). Comparison between 288 nest trees in woodland and 234 trees with ≥5 cm DBH in the vegetation quadrat in a woodland shows that chimpanzees also selected trees nonrandomly in this habitat (χ^2 test, $df=9$, $\chi^2=260.7$, $p<0.05$), preferring *Brachystegia bussei* (χ^2 test, $df=1$, $\chi^2=15.4$, $p<0.05$) and *Pterocarpus tinctorius* (χ^2 test, $df=1$, $\chi^2=4.58$, $p<0.05$).

Based on 549 nests of which we recorded all of the following data, mean nest height is 13.4 m (range: 3–30, SD: 5.1), mean DBH of a nest tree is 36.9 cm (range: 4.3–121.3, SD: 19.3), and mean height of a nest tree is 19.8 m (range: 5–35, SD: 5.5). The minimum DBH of a nest tree was 4.3 cm and its height was 5 m. However, the remaining 548 (99.8%) nest trees were ≥5.0 cm in DBH, and 528 (96.2%) were ≥10.0 cm in DBH. Nest height correlates with the height of a nest tree (Kendall rank correlation, $\tau=0.50$, $p<0.05$).

In 3 nest clusters comprising 10 new nests, 4 new nests, and 6 recent nests in vegetation quadrats, mean and SD of the distance between nests is 28.6±16.4, 18.2±6.3, 9.2±6.2 m, the mean and SD of the distance to a closest nest is 7.8±8.1, 12.0±6.9, and 5.5±3.8 m, respectively. Subjects made multiple nests in some trees.

Party Size We recorded a total of 563 fresh, new, and recent nests in 104 nest clusters. The mean size of a nest cluster is 5.4 nests (range: 1–23). The size is 5.2 in

Table 4 Number of nest trees of chimpanzees

Name of tree	Savanna woodland	Vegetation	Valley forest	Flat riverine forest	Total	%
		Kabamba-jike forest				
Monopetalanthus richardsiae		388			388	39.5
Julbernardia unijugata			225	20	245	24.9
Brachystegia bussei	72				72	7.3
Pterocarpus tinctorius	23				23	2.3
Brachystegia microphylla	19	1			20	2.0
Julbernardia paniculata	12				12	1.2
Brachystegia microcarpa	9				9	0.9
Syzygium guineense				7	7	0.7
Brachystegia spiciformis	5				5	0.5
Others[a]	148	15	2	36	201	20.5
Total	288	404	227	63	982	100.0

Trees in which chimpanzees made ≥5 nests are listed.

[a] Total number of nests in unidentified trees and trees of which the name was not recorded.

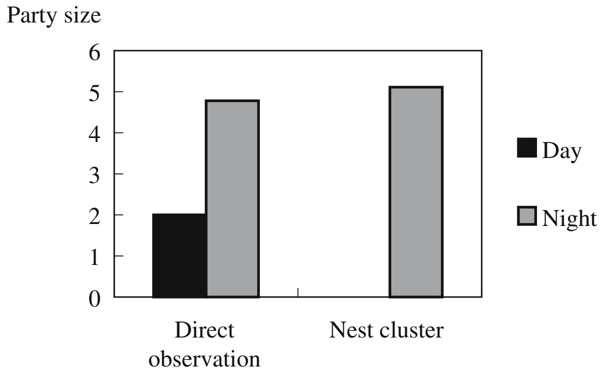

Fig. 2 Change of party size between day and night. Party size: the average number of chimpanzees >3–4 yr or average number of nests in a nest cluster. Direct observation: chimpanzee(s) were directly observed. Day: 10 parties were found between 9:30 A.M. and 5:00 P.M. Night: 9 parties were found before 9:30 A.M. or after 5:30 P.M.. Nest cluster: 17 fresh nest clusters were found on the same day in one place. All nests were regarded as night nests.

fresh nests (range: 1–19), 5.3 in new nests (range: 1–19), and 5.5 in recent nests (range: 1–23) (Kruskal-Wallis, n_1=17, n_2=35, n_3=55, H=0.11, n.s.). Mean cluster size is 5.0 at Bhukalai and 5.9 at Nguye (Mann-Whitney *U*-test, n_1=68, n_2=25, $z=-0.23$, n.s.).

Since 1995, Ogawa and Idani have directly observed a total of 74 chimpanzees including 11 infants in 19 parties. The average party size is 3.3 individuals >3–4 yr (n=19, range=1–12). If parties are divided to halves based on time of observations, daytime parties between 9:30 A.M. and 5:00 P.M. average 2.0 individuals (n=10, range=1–4), while morning parties before 9:30 A.M. or evening parties after 5:30 P.M. average 4.8 individuals (n=9, range=1–12) (Mann-Whitney *U*-test, n_1=10, n_2=9, $z=-2.25$, $p<0.05$) (Fig. 2). Daytime party size is smaller than the size of fresh nest clusters (Mann-Whitney *U*-test, n_1=10, n_2=17, $Z=-1.97$, $p<0.05$; Fig. 2).

Discussion

Number, Population Density, and the Size of a Unit Group of Chimpanzees

Ugalla is the most eastern and marginal known habitat of chimpanzees (Kano 1972; Kortlandt 1983). Our observation of nest distribution showed that chimpanzees still inhabit the same area as in the 1960s. In addition, direct comparison with Kano's data (1972) shows that the population of chimpanzees in the Ugalla area has been stable since the 1960s.

However, the population density of chimpanzees in the Ugalla area, $7–9\times10^{-2}$ individuals/km^2, is very low, while densities in more forested areas at the coast of the Lake Tanganyika are 1.29–1.93 (Goodall 1968) and 1.0 individual/km^2 (Nishida 1968), and densities in tropical rain forests in other countries are >0.2 individuals/km^2: 2.92 (Boesch and Boesch 1989), 2.5 (Hashimoto 1995), 1.45–2.38 (Ghiglieri

1984), 0.20 (Hoppe-Dominik 1991), 0.31–1.53 (Jones and Sabater 1971), 0.3 (Kano and Asato 1994), 1.30 (Mitani 1992), 2.90–3.90 (Reynolds and Reynolds 1965), and 0.32 (Tutin and Fernandez 1984). Only in disturbed areas have researchers reported comparably low densities: 0.035 (Hoppe-Dominik 1991) and 0.01–0.03 (Carrol 1986). In addition, even among savanna woodland areas, chimpanzee density in the Ugalla area is lower than in other savanna woodland areas of Tanzania (Suzuki 1969; Kano 1972; Moore, unpublished data) and as low as 0.09 individuals/km^2 in the western marginal habitat at Mt. Assirik, Senegal (Baldwin *et al.* 1982).

Conversely, the largest nest cluster had 23 nests in Ugalla. The size of nest clusters might be overestimated, if chimpanzees slept at the same place in a series of days and nests were located at a later time. However, that there is no significant difference between the size of fresh nest clusters and that of new and recent nest clusters suggests that nest age did not bias the estimated size of a sleeping party. The size of the unit group is considered to be 30–35 individuals >3–4 yr because the largest party was 64% of the unit group in Gombe (Teleki 1977) and 73% in Kasakati, Tanzania (Izawa 1970). The size is within the range of number of chimpanzees >3–4 yr in a unit group in other areas in Tanzania (Goodall 1986; Itani and Suzuki 1967; Izawa 1970; Nishida 1968; Nishida *et al.* 1990), but <40 in Z group in Kasakati (Izawa 1970) and 80 in M group in Mahale (Nishida *et al*. 1990).

The population density, $7–9 \times 10^{-2}$ individuals/km^2, means that the total number of chimpanzees in the Ugalla area is $2–3 \times 10^2$ individuals. If the unit groups are all about the same size, then 7–9 unit groups live in Ugalla. If 7–9 unit groups divide the 3352-km^2 Ugalla area, each unit group should have a $4–5 \times 10^2$ km^2 home range. This home range size is larger than the 120 km^2 (Izawa 1970) or 200 km^2 (Suzuki 1969) estimated for Kasakati, another savanna woodland area in Tanzania, and the 275–338 km^2 estimated for Mt. Assirik, Senegal (Baldwin *et al.* 1982; Tutin *et al.* 1983). However, chimpanzees did not uniformly use the areas in their home range. The overall Ugalla area includes plains where there was no nest, e.g., Bulega and Mfuwazi Basin. We located few nests in flat riverine forests, and many in kabamba-jike forests, valley forests, and savanna woodlands in mountainous areas (Itani 1979; Kano 1972; Nishida 1989). Suzuki (1969) estimated that the density within actual habitat of chimpanzees is higher than the average density in the whole Kasakati area. Chimpanzees in Ugalla might be ranging in smaller parts of their annual home range for a certain period of time.

Choice of Sleeping Site and Sleeping Party

Chimpanzees in Ugalla did not often sleep in flat riverine forests, but frequently slept in kabamba-jike forests and valley forests. They made many nests in the dominant trees of kabamba-jike forests, valley forests, and *Brachystegia bussei* woodlands. During the dry season when deciduous trees are leafless, they have to make a nest in evergreen forests. However, compared to the proportion of vegetation types, chimpanzees prefer a kabamba-jike forest and a valley forest as their sleeping site during both the dry season and the rainy season. Kano (1972) believed that the distribution of chimpanzees in Tanzania was consistent with the distribution of *Brachystegia bussei*. In Ugalla, *Brachystegia bussei* occurred in mountainous areas (Kano 1972), which also had many kabamba-jike forests and valley forests. In addition to food distribution, the location of kabamba-jike forests and valley forests as sleeping sites may affect the ranging of Ugalla chimpanzees.

Chimpanzees formed larger parties in the morning and evening than during the daytime. In addition, nest clusters showed that they formed larger sleeping parties at night than in the daytime.

In the daytime, chimpanzees might form small feeding parties to exploit food resources in small food patches. Chimpanzees in Ugalla feed on fruits and other parts of plants not only in forests but also in savanna woodlands (Kano 1972; Moore 1994; Nishida 1989; Schoeninger *et al.* 1999). The DBH of most fruiting trees in the area is <100 cm. The food patches are too small to supply feeding sites for a large party, though there were the exceptions of fruits of big trees of *Ficus* and legumes of *Brachystegia* and *Julbernardia* spp. in the first half of the dry season (Kano 1972; Suzuki 1969).

In contrast, chimpanzees formed larger parties for sleeping. Because the grouping patterns of chimpanzees are affected by predation risk (Boesch 1991), the larger sleeping parties in Ugalla might be caused by predation pressure from large carnivores such as lions and leopards. The density of trees in savanna woodland is so low that chimpanzees cannot move arboreally between neighboring trees in some areas. Originally, chimpanzees might have evolved a fission-fusion society to change the size and composition of parties, depending on food resources, because their body size is larger than that of other primates and their main foods are not distributed uniformly (Wrangham 1979). For example, Ogawa (1995) observed that chimpanzees in Nouabale-Ndoki National Park, Republic of Congo, that fed on fruits in a big *Ficus*, divided into smaller parties, and most of them left the tree in several directions in the evening. In contrast, chimpanzees in Ugalla used their fission-fusion society so that they form a small feeding party and a large sleeping party.

Further, the sleeping sites might provide chimpanzees with a meeting point as well as a safe sleeping site. Because Ugalla chimpanzees have a huge home range, they might have difficulty finding other members of their unit group. Indeed sleeping sites are limited to evergreen forests in the dry season, but they frequently reuse the same sleeping site (Hernandez-Aguilar, *unpub. data*). Chimpanzees might gather at the sleeping site not only for safety, but also to meet other chimpanzees that had been in another party (cf. Moore 1996).

Acknowledgments We thank Takayoshi Kano, Masaomi Kanaomi, Hosea Y. Kayumbo, Edeus T. Massawe, Junichiro Itani, Toshisada Nishida, Are Thune Paulsen, Toshimichi Nemoto, Alexander Piel, Fiona Stewart, and Kirit Vaitha for their suggestions and cooperation of the survey; Emanweli K. Sehele, Batromeo Kadyugenze, Arfani Murorerowa, Moshi Rajabu, Ramadhani Bilali, Busoti Juma, Abdall Saidi, and other local assistants for their help; Frank Mbago, Yahya Abeid, and other members of Herbarium, Dar es Salaam University, and Kaji Vollesen for plant identification; Daiji Kimura and offices of Meteorology for the data on vegetation and weather. The data and primary responsibility for this article are those of H. Ogawa and G. Idani, with J. Moore, A. Hernandez-Aguilar, and L. Pintea contributing unpublished data, discussion, and assistance with writing during H. Ogawa's sabbatical at University of California, San Diego. The Tanzanian authorities (Costech and Tawiri) granted permission for the study. A Grand-in-Aid for Scientific Research of MEXT, Japan (06061064; 09041160; 1257597; 17255005) and Global Environment Research Fund F061 provided funding for H. Ogawa and G. Idani. The Leakey Foundation and UCSD Committer on Research provided funding for J. Moore, and the NSF and Leakey Foundation provided funding for A. Hernandez-Aguilar.

References

Baldwin, P. J., McGrew, W. C., & Tutin, C. E. G. (1982). Wild-ranging chimpanzees at Mt. Assirik, Senegal. *International Journal of Primatology, 3*, 367–385.

Baldwin, P. J., Sabaster, P. J., McGrew, W. C., & Tutin, C. E. G. (1981). Comparison of nests made by different populations of chimpanzees. *Primates*, *22*, 474–486.

Boesch, C. (1991). The effects of leopard predation pattern in grouping patterns in forest chimpanzees. *Behaviour, 117*, 220–241.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Primatology, 78*, 547–573.

Carrol, R. W. (1986). Status of the lowland gorilla and other wildlife in the Dzanga-Sangha region of southweatern Central African Republic. *Primate Conservation, 7*, 38–41.

Goodall, J. (1968). The behavior of free-living chimpanzees in the Gombe stream area. *Animal Behaviour Monographs, 1*, 16–311.

Goodall, J. (1986). *The chimpanzees in Gombe: Patterns of behavior*. Cambridge: Harvard University Press.

Ghiglieri, M. P. (1984). *The chimpanzees of Kibale forest: A field study of ecology and social structure*. New York: Columbia University Press.

Hashimoto, C. (1995). Population census of the chimpanzees in the Kalinzu forest,Uganda: Comparison between methods with nest census. *Primates, 36*, 477–488.

Hoppe-Dominik, B. (1991). Distribution and status of chimpanzees (*Pan troglodytes*) on the Ivory Coast. *Primate Report, 31*, 45–47.

Ihobe, H. (2005). Life span of chimpanzee beds at the Mahale Mountains National Park, Tanzania. *Pan Africa News, 12*, 10–12.

Itani, J. (1979). Distribution and adaptation of chimpanzees in an arid area. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes* (pp. 55–71). Menlo Park, CA: Benjamin/Cummings.

Itani, J., & Suzuki, A. (1967). The social unit of chimpanzees. *Primates, 8*, 355–381.

Izawa, K. (1970). Unit groups of chimpanzees and their nomadism in the savanna woodland. *Primates, 2*, 1–46.

Jones, C., & Sabater, P. J. (1971). Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, Weat Africa. *Bibliotheca Primatologica, 13*, 1–96.

Kano, T. (1971). Distribution of primates on the eastern shore of Lake Tanganyika. *Primates, 12*, 281–304.

Kano, T. (1972). Distribution and adaptation of the chimpanzee on the eastern shore of Lake Tanganyika. *Kyoto University African Studies, 7*, 37–129.

Kano, T., & Asato, R. (1994). Hunting pressure on chimpanzees and gorillas in the Motaba river are, northeastern Congo. *African Study Monographs, 15*, 143–162.

Kikula, I. S. (1986). Environmental effects of Tanzania's villagisation program. Ph.D. thesis, Griffith University, Brisbane.

Kortlandt, A. (1983). Marginal habitats of chimpanzees. *Journal of Human Evolution, 12*, 231–278.

Massawe, E. T. (1992). Assessment of the status of chimpanzee populations in western Tanzania. *African Study Monographs, 13*, 35–55.

McGrew, W. C., Baldwin, P. J., & Tutin, C. E. G. (1981). Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, west Africa. *Journal of Human Evolution, 10*, 227–244.

Mitani, M. (1992). Preliminary results of the studies on wild western lowland gorillas and other sympatric diurnal primates in the Ndoki Forest, northern Congo. In N. Itoigawa, Y. Sugiyama, C. P. Sackett, R. K. R. Thompson (Eds.), *Topics in primatology, vol. 2: Behavior, ecology, and conservation* (pp. 99–118). Tokyo: University of Tohyo Press.

Moore, J. (1992). "Savanna" chimpanzees. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. B. M. de Waal (Eds.), *Topics in primatology, vol. 1: Human origins* (pp. 99–118). Tokyo: University of Tokyo Press.

Moore, J. (1994). Plants of the Tongwe east reserve (Ugalla), Tanzania. *Tropics, 3*, 333–340.

Moore, J. (1996). Savanna chimpanzees, referential models and the last common ancestor. In W. C. McGrew, L. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 275–292). Cambridge: Cambridge University Press.

Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates, 9*, 167–224.

Nishida, T. (1989). A note on chimpanzee ecology of the Ugalla area, Tanzania. *Primates, 30*, 129–138.

Nishida, T. (1990). A quarter century of research in the Mahale Mountains. In T. Nishida (Ed.), *The chimpanzees of the Mahale mountains: Sexual and life history strategies* (pp. 3–35). Tokyo: University of Tokyo Press.

Nishida, T., Takasaki, H., & Takahata, Y. (1990). Demography and reproductive profiles. In T. Nishida (Ed.), *The chimpanzees of the Mahale mountains: Sexual and life history strategies* (pp. 63–97). Tokyo: University of Tokyo Press.

Nishida, T., & Uehara, S. (1981). Kitongwe name of plants: A preliminary listing. *African Study Monographs, 1*, 109–131.

Ogawa, H. (1995). Feeding and sleeping parties of Tschego Chimpanzees (Pan troglodytes troglodytes) in the Nouabale-Ndoki national park. Rapport Annuel 1994–1995 pour Recherches Scientifiques Cooperatives par Equipes Japonaises et Congolaises, pp. 54–58.

Ogawa, H., Kanamori, M., & Mukeni, S. H. (1997). The Discovery of chimpanzees in the Loasi River area, Tanzania: A new southern distribution Limit. *Pan Africa News, 4*, 1–3.

Plumptre, A. J., & Cox, D. (2006). Counting primates for conservation: Primate surveys in Uganda. *Primates, 47*, 65–73.

Plumptre, A. J., & Reynolds, V. (1997). Nesting behavior of chimpanzees: Implications for censuses. *International Journal of Primatology, 18*, 475–485.

Reynolds, V., & Reynolds, F. (1965). Chimpanzees in the Budongo Forest. In I. deVore (Ed.), *Primate behavior: Field studies of monkeys and apes* (pp. 468–524). San Francisco: Holt, Rinehart and Winston.

Schoeninger, M., Moore, J., & Sept, J. (1999). Subsistence strategies of two "savanna" chimpanzee populations: The stable isotope evidence. *American Journal of Primatology, 49*, 297–314.

Sutton, J. E. G., & Roberts, A. D. (1968). Uvinza and its salt industry. *Azania, 3*, 45–869.

Suzuki, A. (1969). An ecological study of chimpanzees in a savanna woodland. *Primates, 10*, 103–148.

Teleki, G. (1977). *The predatory behavior of wild chimpanzees*. Lewisburg, PA: Bucknell University Press.

Teleki, G. (1989). Population status of wild chimpanzees (*Pan troglodytes*) and threats to survival. In G. H. Paul & A. M. Linda (Eds.), *Understanding chimpanzees* (pp. 312–353). Cambridge, MA: Harvard University Press.

Tutin, C., & Fernandez, M. (1984). Nationwide census of gorilla (*Gorilla g. Gorilla*) and chimpanzee (*Pan t. troglodytes*) population in Gabon. *American Journal of Primatology, 6*, 313–336.

Tutin, C. E. G., McGrew, W. C., & Baldwin, P. J. (1983). Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. *Primates, 24*, 154–173.

Wrangham, R. W. (1979). On the evolution of ape social systems. *Social Science Information, 18*, 335–368.