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The Population and Habitat Preferences of Chimpanzees in Non-Protected Areas of Tanzania

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INTRODUCTION

Tanzania is the most eastern region of the distribution of eastern chimpanzees (*Pan troglodytes schweinfurthii*) (Kano 1972). According to Kano's survey in 1965–67 (Kano 1972), chimpanzees inhabited the eastern shore of Lake Tanganyika: a) Gombe (Gombe National Park), b) Lilanshimba, c) Ugalla, d) Masito, e) Mukuyu, f) Mahale (Mahale Mountains National Park), g) Karobwa, and h) Wansisi. In addition, Ogawa and others (1997) found the most southern chimpanzee population in i) Lwazi in 1996 (Figure 1). The geographical distribution of chimpanzee beds (Yoshikawa *et al.* 2008) and DNA variation (Inoue

et al. 2013) indicate that the chimpanzee population is continuous in c–h areas. This means that there are four local populations of chimpanzees in Tanzania: a) Gombe, b) Lilanshimba, so called “Greater Mahale” composed of c–h areas, and i) Lwazi, as well as an introduced population on Rubondo Island in Lake Victoria. Although chimpanzees still inhabit all areas in which they were found in 1960s (Kano 1972; Ogawa *et al.* 1997, 2004, 2006a, 2006b, 2007; Hernandez-Aguilar 2006; Moyer *et al.* 2006; Yoshikawa *et al.* 2008; Ndimuligo 2008; Plumptre *et al.* 2010), the population density of chimpanzees in non-protected areas has been significantly reduced from 1960s to 2000s (Yoshikawa *et al.* 2008). Proper conservational planning is essential to protect chimpanzees (Plumptre *et al.* 2010). However, chimpanzees in such areas have been much less studied than those in two national parks, a) Gombe and f) Mahale. Therefore, in addition to our extensive field surveys in 1994–2008 (Ogawa *et al.* 1997, 2004, 2006a, 2006b, 2007; Yoshikawa *et al.* 2008) and estimation of population densities of chimpanzees (Yoshikawa *et al.* 2008), we conducted further surveys in 2010–2011 and GIS analyses of chimpanzee habitats in non-protected areas of Tanzania.

METHODS

From 1994 to 2011, we conducted transect bed censuses in all chimpanzee habitats out of national parks: b, c, d, e, g, h, and i, (Ogawa *et al.* 1997, 2004, 2006a, 2006b, 2007; Yoshikawa *et al.* 2008) (Figure 1, Table 1). As a control, we conducted bed censuses at j) Mishamo, k) Sabaga, and l) Niamansi in non-habitats of chimpanzees (Figure 1, Table 1). We usually made a round trip from our base camp along the river to the top of a hill and walked on not only traditional paths, but also paths of wild animals and off-path. When we found a chimpanzee bed, we recorded location of the bed using GPS, vegetation of the bed site, and perpendicular distance between the bed and the census line. We chose the census lines whose tracks had been recorded by GPS and/or on 1/50,000 maps, and plotted the census lines on a vegetation map using ERDAS Imagine (Leica Geosystems GIS & Mapping) based on satellite images (ETM+). We then defined a census belt of 60 m width centered on the census line. This width was used, because the detection rate of a chimpanzee bed was constant within 30 m from the census lines. We further divided all of the census belts and defined 60 × 60-m quadrats along the census line. We then calculated (1) proportion of the area covered by evergreen forests, (2) average ground slope, and (3) average altitude in each quadrat using a 90 m SRTM digital elevation model. Using ArcGIS (ArcView 9.3.1) (ESRI), we calculated the distance between each bed cluster and the nearest evergreen forest with area ≥ 1 ha, and the distance between each study site and the nearest edge of the nearest human settlement with area approximately ≥ 10 ha.

RESULTS

For GIS analyses, we used a total of 1,026 km census lines in chimpanzee habitats and 46 km in non-habitats, yielding 17,845 60 × 60-m quadrats along the census lines (Table 1). The area was occupied by savanna woodlands

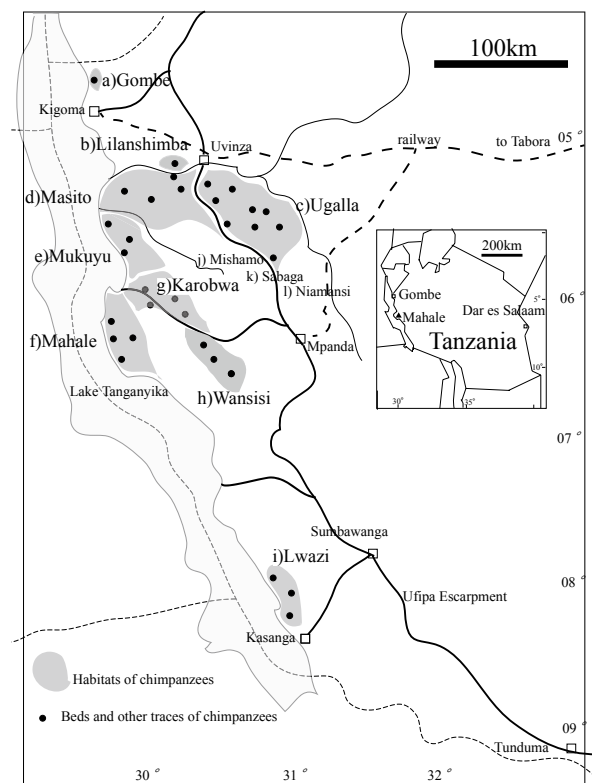


Figure 1. Distribution of chimpanzees in Tanzania.

(86.9%), evergreen forests (5.9%), and others such as grasslands, bamboo thickets, cultivated fields, and human settlements (7.2%).

In chimpanzee habitats, there were 665 beds in 186 quadrats, while there were no beds in 17,659 quadrats. Evergreen forests occupied more area, $25.0 \pm 35.5\%$ (mean \pm SD) (range: 0–100), in the quadrats with beds than in the quadrats without beds, $5.7 \pm 18.8\%$ (0–100) (Figure 2(1), Mann-Whitney U test, $n_1 = 186$, $n_2 = 17,659$, $z = 12.6$, $p < 0.05$). The slope of the ground was steeper, $10.1 \pm 7.1^\circ$ (0.6–30.8), in the quadrats with beds than the quadrats without beds, $6.5 \pm 22.8^\circ$ (0.1–37.7) (Figure 2(2), $z = 8.2$, $p < 0.05$). The difference was not significant between the altitude in the quadrats with beds, $1,217 \pm 154.8$ m (797–1,814), and those in the quadrats without beds, $1,216 \pm 182.0$ m (780–1,876) (Figure 2(3), $z = 1.5$, ns).

The ground slope and altitude of all quadrats with beds were between 0.6° and 30.8° , and between 797 m and 1,814 m. If we regard such quadrats as possible bed sites of chimpanzees, the possible bed sites were 97.4% in chimpanzee habitats and 100% in non-habitats (Table 1).

We recorded a total of 2,154 beds within and out of 30m from the census lines. Chimpanzees made 1,085 beds (50.4%) in forests, 1,020 beds (47.3%) in woodlands, and 49 beds (2.3%) in mixed vegetations (Table 1). Beds in woodlands were 0.15 km (0.01–0.64) from the nearest forest (Table 1).

The population density of chimpanzees was positively correlated with the proportion of forest in the area (Table 1, Kendall rank correlation test, $n = 10$: b–e, g–l areas, $\tau = 0.58$, $z = 2.3$, $p < 0.05$), and with the distance between the area and the nearest human settlement (Table 1, $\tau = 0.71$, $z = 2.9$, $p < 0.05$).

Table 1. Environments of chimpanzee habitats in Tanzania.

Area	Location	Bed census		Census distance (km)	Number of beds ¹	Proportion of evergreen forest (%) ²	Ground slope (°) ²	Altitude (m) ²	Proportion of possible bed site (%) ³	Bed site		Distance to human settlement (km)	Density of chimpanzees ⁵ (individuals/km ²)	Habitat range (km ²)	Number of chimpanzees (individuals)	Reference
		Study periods	Location							Number of beds in evergreen forest ⁴	Distance from woodland beds to evergreen forest (km)					
Habitat																
Non-protected area																
b) Lilanshimba	05°07'-05°14'S 30°07'-30°14'E	Jul '01, Aug '06		119	35 (187)	7.6	5.6 (0.5-29.1)	1,115 (911-1,302)	99.7	31 (16.6%)	0.13 (0.01-0.64)	14.4	0.02 (0.01-0.05)	140	3 (1-7)	Ogawa <i>et al.</i> 2006b; Yoshikawa <i>et al.</i> 2008
c) Ugalla	05°09'-05°52'S 30°23'-31°01'E	Sep '95, Aug '96, Aug '97, Jul '01, Feb '03, Jul '03, Aug '07, Aug '08, Dec '10-Mar '11		488	379 (1,512)	4.1	5.7 (0.1-33.5)	1,210 (1,041-1,621)	97.7	938 (62.0%)	0.15 (0.01-0.62)	32.5	0.10 (0.07-0.18)	3,350	335 (235-603)	Hernandez-Aguilar 2006; Ogawa <i>et al.</i> 2007; Yoshikawa <i>et al.</i> 2008; this study
d) Masito	05°10'-05°35'S 29°50'-30°35'E	Aug '03, Aug '05		78	71 (102)	8.7	5.4 (0.2-31.5)	1,072 (795-1,315)	99.1	39 (38.2%)	0.19 (0.04-0.51)	16.5	0.12 (0.04-0.49)	2,200	264 (88-1,078)	Yoshikawa <i>et al.</i> 2008
e) Mukuyu	05°22'-05°51'S 29°44'-30°07'E	Aug '05		31	26 (52)	7.9	7.8 (0.1-25.9)	890 (780-1,027)	89.3	3 (5.8%)	0.08 (0.01-0.24)	8.3	0.05 (0.02-0.08)	1,100	55 (22-198)	Yoshikawa <i>et al.</i> 2008
g) Karobwa	05°51'-06°10'S 29°55'-30°31'E	Aug '03		125	95 (154)	16.9	8.1 (0.2-37.7)	1,241 (967-1,876)	97.5	47 (30.5%)	0.10 (0.01-0.36)	15.5	0.03 (0.02-0.08)	900	29 (18-72)	Ogawa <i>et al.</i> 2006a; Yoshikawa <i>et al.</i> 2008
h) Wansisi	06°19'-06°38'S 30°27'-30°43'E	Aug '01		47	17 (78)	0.3	7.2 (0.5-22.1)	1,422 (1,178-1,823)	99.2	0 (0.0%)	0.16 (0.08-0.36)	13.6	0.02 (0.02-0.08)	500	10 (5-40)	Ogawa <i>et al.</i> 2004; Yoshikawa <i>et al.</i> 2008
i) Lwazi	07°48'-08°28'S 30°55'-31°10'E	Aug '01, Jul '03, Aug '05		138	42 (69)	2.9	6.8 (0.2-29.1)	1,349 (780-1,889)	94.5	27 (39.1%)	0.14 (0.01-0.43)	11.7	0.01 (0.00-0.03)	1,250	18 (0-38)	Ogawa <i>et al.</i> 1997; Yoshikawa <i>et al.</i> 2008
<i>Subtotal</i>	05°07'-08°28'S 29°44'-31°01'E			1,026 (2,154)	665 (2,154)	6.2 (0.1-37.7)	6.2 (0.1-37.7)	1,211 (780-1,889)	97.4	1,085 (50.4%)	0.15 (0.01-0.64)	20.3	0.05	9,440	714	
Protected area (national park)																
a) Gombe	04°37'-04°45'S 29°36'-29°40'E	Sep '03, Aug '08 ⁶		0	-	-	-	-	-	-	-	-	-	52	approx 100	Moyer <i>et al.</i> 2006; Ndumiligo 2008; Plumptre <i>et al.</i> 2010
f) Mahale	05°43'-06°30'S 29°45'-30°13'E	Sep '94 ⁶		0	-	-	-	-	-	-	-	-	-	1,600	approx 500	Kano 1972; Moyer <i>et al.</i> 2006; Ndumiligo 2008
<i>Total</i>														11,092	approx 1,300	
Non-habitat																
j) Mishamo, k) Sabaga, l) Niamansi		Aug '03, Sep '05, Aug '06		46	0	0.5	3.4 (0.2-19.1)	1,357 (1,105-1,602)	100.0	-	-	6.8	0.00	-	0	this study

1. Numbers of beds within 30 m from the census line are shown. Total numbers of beds found in the areas are shown in parentheses.

2. Mean numbers in each 60 × 60-m quadrat are shown. Ranges are shown in parentheses.

3. Percentages of the quadrats whose ground slope was between 0.6° and 30.8°, and whose altitude was between 797 m and 1,814 m are shown.

4. % = (Number of beds in forests) / (Number of all beds) × 100.

5. Densities of individuals excluding immature sleeping with their mother are shown with 95% confidence intervals in parentheses (Yoshikawa *et al.* 2008).

6. We did not conduct a bed census, but stayed during the periods in the areas: a and f.

7. The location was 05°38'S, 30°28'E at j, 05°58'S, 30°45'E at k, and 05°56'S, 30°57'E at l.

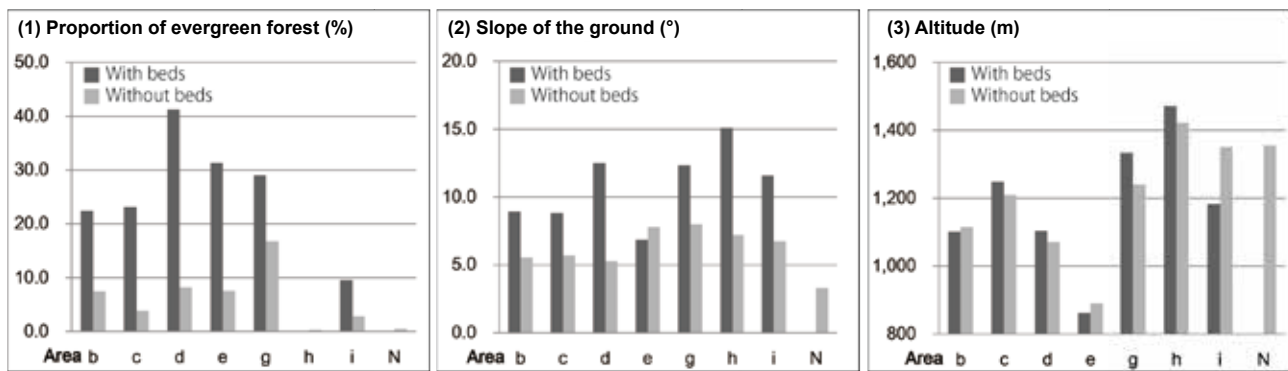


Figure 2. Conditions in quadrats containing chimpanzee beds in Tanzania.

(1) Percentage of evergreen forest area, (2) slope of the ground, and (3) altitude are compared between 60×60-m quadrats containing chimpanzee beds and quadrats without beds. With beds: quadrats containing beds. Without beds: quadrats without beds. Area: b=Lilanshimba, c=Ugalla, d=Masito, e=Mukuyu, g=Karobwa, h=Wansisi, i=Lwazi, N=non-habitat: j) Mishamo, k) Sabaga, and l) Niamansi.

DISCUSSION

Most of chimpanzee habitats in Tanzania are savanna woodlands (locally called “miombo” woodlands) dominated by deciduous trees of *Brachystegia* and *Julbernardia* with small proportion of evergreen riverine forests (Kano 1972). However, 47.3% of beds were in forests and all beds were within 0.64 km from a forest. In addition, the quadrats with chimpanzee beds had a greater proportion of forest than the quadrats without beds. Evergreen forests are indispensable for chimpanzees to make beds especially during the dry season, when most woodland trees lose their leaves (Hernandez-Aguilar 2006; Ogawa *et al.* 2007). In addition, forests provide chimpanzees with safe sleeping sites. Because forests have fewer grasses and more trees than woodlands, carnivores such as lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) are not able to hide themselves for hunting, and chimpanzees can more easily escape into trees (Hernandez-Aguilar 2006). In addition to forests, hilly areas are also critical for chimpanzees in Tanzania, as they prefer making beds in steep slopes (Kano 1972; Hernandez-Aguilar 2006; Ogawa *et al.* 2007). As a result, chimpanzee habitats in Tanzania had many evergreen forests and hilly areas.

However, the quality of chimpanzee habitats has become worse over time, caused by habitat destruction for cultivation, firewood, charcoal, and commercial use of timbers (Ogawa *et al.* 1997, 2004, 2006a, 2006b, 2007). The population density of chimpanzees shows that the number of chimpanzees outside national parks in Tanzania has been reduced from approximately 1,300 (Kano 1972) to 700 (Yoshikawa *et al.* 2008) during the last 40 years. Even including 100 chimpanzees in a) Gombe and its surrounding area (Moyer *et al.* 2006; Ndimuligo 2008; Plumptre *et al.* 2010) and 500 chimpanzees in f) Mahale (Kano 1972; Moyer *et al.* 2006; Plumptre *et al.* 2010), the total number of chimpanzees in Tanzania may be no more than 1,300 individuals. Although another survey estimated that 2,800 chimpanzees inhabited Tanzania (Moyer *et al.* 2006; Plumptre *et al.* 2010), both surveys showed that more than half of all Tanzanian chimpanzees inhabited non-protected areas. The estimated population of chimpanzees in Tanzania ranges from 1,300 to 2,800. However, similar methods of bed censuses in 1960s (Kano

1972) and 2000s (Yoshikawa *et al.* 2008) indicate that the population of chimpanzees in non-protected areas of Tanzania has been remarkably reduced.

A huge continuous habitat, Greater Mahale, is precious property of Tanzania. In e) Mukuyu and g) Karobwa, however, people originally from Burundi set many snares around the Mishamo settlement. Such poachers actually killed chimpanzees in these areas (Ogawa *et al.* 2006a). In b) Lilanshimba, the Lugufu settlement for Congolese refugees was established within chimpanzee habitat in 1997, and cultivation and poaching by these refugees have reduced chimpanzees (Ogawa *et al.* 2006b). Small isolated populations in b) Lilanshimba and i) Lwazi may be faced with extinction. It is urgently necessary to protect chimpanzees in these two areas, as well as chimpanzees in Greater Mahale.

We found that the population density of chimpanzees is lower in areas close to human settlements. To make matters worse, more and more immigrant farmers cultivated fields except for steep hills in e) Mukuyu and g) Karobwa, and h) Wansisi (Ogawa *et al.* 2004, 2006a). Such haphazard deforestation reduces chimpanzee habitats and does not necessarily benefit future generations of Tanzanian people. It is necessary to adopt sustainable management of trees and other natural resources. Effective conservation plans are possible, because chimpanzees prefer hilly areas which are not suitable for cultivation. Especially, c) Ugalla and d) Masito still have habitats where only a few local people temporally visit. In collaboration with researchers, the Tanzanian government has to make and conduct proper conservation planning to protect chimpanzees and their habitats in Tanzania.

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REFERENCES

- Hernandez-Aguilar A 2006. *Ecological and Nesting Patterns of Chimpanzees (Pan troglodytes) in Issa, Ugalla, Western Tanzania*. Ph.D. thesis, University of Southern California.
- Inoue E, Tashiro Y, Ogawa H, Inoue-Murayama M, Nishida T, Takenaka O 2013. Gene flow and genetic diversity of chimpanzee populations in East Africa. *Primate Conserv* 26:67–74.
- Kano T 1972. Distribution and adaptation of the chimpanzee on the eastern shore of Lake Tanganyika. *Kyoto Univ Afr Stud* 7:37–129.
- Moyer D, Plumptre AJ, Pintea L, Hernandez-Aguilar A, Moore J, Stewart F, Davenport TRB, Piel A, Kamenya S, Mugabe H, Mpunga N, Mwangoka M 2006. *Surveys of Chimpanzees and Other Biodiversity in Western Tanzania*. Unpublished report. Arlington, VA: United States Fish and Wildlife Service (USFWS).
- Ndimuligo SA 2008. *Assessment of Chimpanzee (Pan troglodytes) Population and Habitat in Kwitanga Forest, Western Tanzania*. Master's dissertation, University of Witwatersrand, Johannesburg.
- Ogawa H, Kanamori M, Mukeni SH 1997. The discovery of chimpanzees in the Loasi River area, Tanzania: A new southern distribution limit. *Pan Afr News* 4:1–3.
- Ogawa H, Moore J, Kanamori M, Kamenya S 2004. Report on the chimpanzees of the Wansisi and Makomayo areas, Tanzania. *Pan Afr News* 11:3–5.
- Ogawa H, Moore J, Kamenya S 2006a. Chimpanzees in the Ntakata and Kakungu areas, Tanzania. *Primate Conserv* 21:97–101.
- Ogawa H, Sakamaki T, Idani G 2006b. The influence of Congolese refugees on chimpanzees in the Lilanshimba area, Tanzania. *Pan Afr News* 13:21–22.
- Ogawa H, Idani G, Moore J, Pintea L, Hernandez-Aguilar A 2007. Sleeping parties and nest distribution of chimpanzees in the savanna woodland area, Ugalla, Tanzania. *Int J Primatol* 28:1397–1412.
- Plumptre AJ, Rose R, Nangendo G, Williamson EA, Didier K, Hart J, Mulindahabi F, Hicks C, Griffin B, Ogawa H, Nixon S, Pintea L, Vosper A, McLennan M, Amsini F, McNeillage A, Makana JR, Kanamori M, Hernandez-Aguilar A, Piel A, Stewart F, Moore J, Zamma K, Nakamura M, Kamenya S, Idani G, Sakamaki T, Yoshikawa M, Greer D, Tranquilli S, Beyers R, Hashimoto C, Furuichi T, Bennett E 2010. *Eastern Chimpanzee (Pan troglodytes schweinfurthii): Status Survey and Conservation Action Plan 2010–2020*. ISBN978-2-8317-1246-8. IUCN, Gland, Switzerland.
- Yoshikawa M, Ogawa H, Sakamaki T, Idani G 2008. Population density of chimpanzees in Tanzania. *Pan Afr News* 15:17–20.

<NOTE>

Well Digging by Semliki Chimpanzees: New Data on Laterality and Possible Significance of Hydrology

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INTRODUCTION

The wild chimpanzees (*Pan troglodytes schweinfurthii*) of Toro-Semliki Wildlife Reserve, Uganda, are the only population of wild apes yet reported to dig wells for drinking water¹. They dig holes by hand in sandy riverbeds, then drink the water collected there by mouth or with 'sponges' made of leaves. We previously reported that the excavated tailings of this digging were often 'bilobed' in distribution on the substrate, that is, clearly divided into separate piles of sand to the left and right sides of the hole (McGrew *et al.* 2007). Because these piles were symmetrical in volume, we inferred that the chimpanzees were manually ambilateral, that is, that they did not favour one hand or the other in digging. That is, we inferred that had their digging been right-biased, then the rightside pile of sand would have been bigger.

However, our first report was no more than a pilot study, as it was done with only 2 days (July) of intensive etho-archaeological data collection over less than 1 km of riverbed, only in the dry season. Furthermore, it was done with only a single measure, 'volume'. Here we report a longer study done over 6 months (May–Nov.) over more than 5 km of riverbed, done in both wet and dry seasons. The aim of the follow-up study was to replicate and extend the pilot study's findings, but in the process several unexpected factors were revealed, chiefly hydrological ones.

In the first study in 2006, flow of surface water in the bed of the Mugiri River had ceased, leaving only scattered, stagnant pools. In some places, the sandy substrate was still moist, but in others it was dry. In the second study in 2008, surface water flow never ceased, though it varied in depth and volume, and the sand in the riverbed was always moist. Thus, environmental affordance of drinking water for the chimpanzees showed marked inter-annual variation.

With regard to laterality, we expected (as in the pilot study) that if the chimpanzees were manually biased at population-level to one side or another, then overall either left or right piles of tailings (lobes) would be larger. If there was no bias in the pooled data, then we expected no difference in any left- versus right-side measurements.

