Direct Observations of Savanna Chimpanzees in the Ugalla Area, Tanzania: Characteristics of Their Party Size and Composition

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INTRODUCTION

Chimpanzees (Pan troglodytes) follow a fission–fusion grouping pattern, in which their unit-group (community) splits into parties (temporal sub-groups) (Nishida, 1968). The size and composition of the party is affected by food availability, predation pressure, and number of oestrous females (Doran, 1997). Chimpanzees vary widely in party size and composition as well as in their unit-group size, diet, and habitat use, because they inhabit both tropical rainforests and more open vegetation such as savanna woodland in eastern Africa (Kano, 1972; Hernandez-Aguilar, 2006; Ogawa et al., 2007, 2014) and forest-grassland mosaic in western Africa (Baldwin, 1979; Tutin et al., 1983; Pruett & Lindshield, 2012). However, few studies have directly observed chimpanzees in marginal habitats (e.g. Pruett et al., 2008) due to the difficulty in habituating wild chimpanzees in such areas.

The Ugalla area is the eastern-most chimpanzee habitat and one of the driest and most open (Kano, 1972), with many predators including lions (Panthera leo) and leopards (P. pardus) (Ogawa et al., 2007). Compared with chimpanzees in rainforests, chimpanzees in Ugalla might form larger parties to reduce predation risk, but may also form smaller parties due to small food patches and/or low fruit availability. If seasonal changes in food availability alter their party size, as with chimpanzees in other areas (Doran, 1997), chimpanzees in Ugalla might form smaller parties in the rainy season than in the dry season because less fruits are available in the rainy season (Yoshikawa et al., in preparation). Whereas chimpanzees form all-male parties in rainforests (Matsumoto-Oda et al., 1998), male chimpanzees in Ugalla are more likely to follow oestrus females to avoid losing them due to their huge home range (Ogawa et al., 2007). Less competition with other unit-groups for food resources and oestrus females may also reduce the necessity of forming all-male parties to defend territory. To investigate these predictions, we studied the party and habitat use characteristics of chimpanzees in the Ugalla savanna woodland area based on direct observations and data from camera traps.

MATERIALS AND METHODS

Study Area

We conducted field surveys in the Ugalla area of western Tanzania (Fig. 1, 05°09′–05°52′S, 30°23′–31°01′E). The majority (86.0%) of this area is covered by woodlands with scattered deciduous trees; 12.0% is grassland, and 2.0% is forest (Ogawa et al., 2014). The dry season (defined as monthly rainfall <100mm) spans from May to Oct., and the rainy season lasts from Nov. to Apr. We collected...
observational data on unhabituated chimpanzees at Nguye (Nguya) (05°13'S, 30°28'E; 90km²), Issa (05°23'S, 30°35'E; 85km²), and Bhukalai (05°27'S, 30°44'E; 120km²) (Fig. 1). These sites are >20km apart from one another, so they are likely to be in the home ranges of different unit-groups.

Study Subjects
A previous bed census found that the density of chimpanzees in Ugalla is 0.10 individuals/km² (≥4-yr-old individuals who make beds) (Yoshikawa et al., 2008), which implies that roughly 335 chimpanzees inhabit the 3,352km² area. Ogawa et al. (2007) estimated the unit-group size to be 30–35 individuals, based on the largest party composed of 23 chimpanzee beds, which indicates that there should be about 10 unit-groups, each with a home range of 335km².

We divided the chimpanzees into three age classes: adults (≥13-yr-old), adolescents and juveniles (5–12-yr-old), and infants (≤4-yr-old), based on age classes in an open habitat (Baldwin, 1979). We included adolescents and juveniles in a single class, because observational conditions sometimes made it difficult to distinguish them.

Study Periods and Sampling Methods
MY and/or HO stayed in Ugalla for 503 days from 1995 to 2012, and walked 2,053km and 1,152km in the dry and rainy seasons respectively, to find chimpanzees and conduct other research such as bed censuses and vegetation surveys.

A party was defined as a group of chimpanzees that were seen together during a continuous observation. We started data recording when we found a chimpanzee, and stopped it when the chimpanzee(s) disappeared from view. Though we could not always observe all chimpanzees during the continuous observation, we regarded all of them as party members. Party sizes are shown as the mean±SD individuals, excluding infants that slept with their mothers and did not forage independently. Referring to Tutin et al., (1983) and Suzuki (1969), we classified party types as: 1) lone male; 2) lone female; 3) mother–infant; 4) consort; 5) all-male; 6) all-female; and 7) mixed (Table 1).

We also recorded the number of oestrous females with swollen sexual skin in the party, activities (feeding, resting, moving, or engaging in social behaviour) of the majority (≥50%) of individuals in the party, and locations (in trees or on the ground; in forests, woodlands, or grasslands) of each individual, when they were first seen. For parties of ≥2 chimpanzees, 89.6%±20.4% (range 20.0–100.0%) of all party members were visible at the start of each observation.

We set nine camera traps (Trophy Cam, Bushnell) 1m above the ground on a tree trunk from 31 Jul. to 14 Aug. 2012 at Nguye in Ugalla. We set five camera traps at paths in valley forests dominated by Monopetalanthus richardsiae and Julbernardia unijugata, which chimpanzees frequently used as sleeping sites; two camera traps that recorded the bottom of and around fruiting Parinari curatellifolia in woodlands; and two camera traps in riverine forests. They recorded a 60-s movie clip when activated. A party was defined as a group of chimpanzees that were photographed by the same camera trap within 10min.

RESULTS
We found 52 parties of chimpanzees at the Nguye, Issa, and Bhukalai sites. These data were pooled and analysed together, because all three sites are savanna woodland areas. The total observation time was 24.7h, and mean observation time of a party was 29.0min (range 10s to 3h 22.0min). When chimpanzees noticed the observer(s), they never threatened them, but ran away immediately. We did not encounter multiple groups on the same day.

The party size was 3.1±2.2 (range 1–10) individuals. If infants were included, the party size was 3.7±2.8 (range 1–14). We recorded 14 (26.9%) parties composed of 1 individual, 32 (61.5%) parties with 2–5 individuals, 4 (7.7%) parties with 6–9 individuals, and 2 (3.8%) parties with 10 individuals. Both of the largest parties were found in the dry season. Chimpanzees formed smaller parties in the rainy season (2.0±1.1 individuals) than in the dry season (3.6±2.4 individuals) (Fig. 2, Mann-Whitney U-test, n1=17, n2=34, z=−2.6, p<0.05). On 2 Aug. 2011 in the dry season, we observed that chimpanzees divided a party into two.

Though the party size may have been underestimated when the observation time was too short, we found no significant differences in party size between observations of <1h and ≥1h (Mann-Whitney U-test, n1=43, n2=9, z=−1.8, ns). Mean observation time did not differ significantly between the dry and rainy seasons (Mann-Whitney U-test, n1=17, n2=33, z=−1.0, ns).

Table 1 lists the number of observations of each party type. We found a lone male eight times, whereas we found a lone female only once and three mother–infant parties. We did not find any all-male or all-female parties, but found four consort parties. Mixed parties comprised 28 (53.8%) of the 52 observations, and they contained more adult females (1.9 individuals) than adult males (1.4 individuals) (Wilcoxon signed-rank test, n=28, z=−2.0, p<0.05). Parties with infants included 17 (85.0%) mixed parties and 3 (15.0%) mother–infant parties. Mixed parties with oestrous female(s) had a size of 5.7±3.8 individuals, whereas parties with no oestrous
Chimpanzees formed larger parties in woodlands (4.1 individuals) than in forests (3.1 individuals) (Mann-Whitney U-test, n1=31, n2=25, z=–2.1, p<0.05). Party size was 3.2±2.5 in trees and 2.9±1.4 on the ground (Mann-Whitney U-test, n1=31, n2=17, z=–0.4, ns). We found 31 (59.6%) parties in forests, 20 (38.5%) in woodlands, and no party in grasslands (Table 2). Only 2.0% of the area was covered by forests, and chimpanzees were more likely to stay in forests than in woodlands (chi-square test, df=1, χ²=24.7, p<0.05). Chimpanzees rested more frequently in forests than they did in woodlands, whereas they fed and moved more frequently in woodlands than in forests, though the difference was not significant (Table 2, chi-square test, df=2, χ²=0.75, ns). Chimpanzees formed larger parties in woodlands (4.1±2.5 individuals) than in forests (3.1±2.7 individuals) (Mann-Whitney U-test, n1=31, n2=20, z=–2.1, p<0.05).

In addition to other animals including a leopard, camera traps recorded chimpanzees in 15 movie clips on 1 to 5 Aug. 2012 in valley forests dominated by Monopetalanthus richardiae along the Lutanda (05°13.8’S, 30°26.5’E) and Kalalikele (05°13.9’S, 30°28.3’E) Rivers. The camera traps recorded 12 parties with 1.4±0.7 individuals, which was smaller than the party size based on direct observations, though direct comparison is difficult because the definition of party was not the same (Mann-Whitney U-test, n1=12, n2=52, z=–3.1, p<0.05).

Information on identified chimpanzees showed where, how long, and with whom they stayed. Using camera traps, we identified 14 chimpanzees: 3 adult males, 2 adult females, and 2 infants in a valley forest from 1 to 5 Aug. 2012; 1 adult male, 3 adult females, and 3 infants in another valley forest located 3.4km away from 2 to 4 Aug. 2012. An adult female and an infant were observed for 3 consecutive days in the same valley forest. There was no overlap of individuals between the two valley forests.

**DISCUSSION**

Chimpanzees in Ugalla formed parties averaging 3.1 individuals. The observed party separation strongly suggests that they have a fission–fusion society similar to those in other areas (Tutin et al., 1983; Newton-Fisher et al., 2000). If they have a unit-group, the largest party size, 10 individuals, indicates that their unit-group was composed of 14–16

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**Table 1. Chimpanzee party type in the Ugalla savanna woodland area.**

| Party type       | Rainy season Number (%) | Dry season Number (%) | Total Number (%) |
|------------------|-------------------------|-----------------------|------------------|
| 1) Lone male     | 3 (16.7)                | 5 (14.7)              | 8 (15.4)         |
| 2) Lone female   | 0 (0.0)                 | 1 (2.9)               | 1 (1.9)          |
| 3) Mother–infant | 2 (11.1)                | 1 (2.9)               | 3 (5.8)          |
| 4) Consort       | 3 (16.7)                | 1 (2.9)               | 4 (7.7)          |
| 5) All-male      | 0 (0.0)                 | 0 (0.0)               | 0 (0.0)          |
| 6) All-female    | 0 (0.0)                 | 0 (0.0)               | 0 (0.0)          |
| 7) Mixed         | 8 (44.4)                | 20 (58.8)             | 28 (53.8)        |
| Unknown          | 2 (11.1)                | 6 (17.6)              | 8 (15.4)         |
| **Total**        | 18 (100.0)              | 34 (100.0)            | 52 (100.0)       |

1) lone male, a group composed of a single male; 2) lone female, a group composed of a single female with no infant(s); 3) mother–infant, a group composed of one adult female and her infant(s); 4) consort, a group composed of one adult male and one adult female; 5) all-male, a group composed of ≥2 adult males with no females; 6) all-female, a group composed of ≥2 adult females with no males; and 7) mixed, a group composed of both ≥1 adult male(s) and ≥1 adult female(s).

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**Table 2. Activity of chimpanzees at each location and vegetation type in the Ugalla savanna woodland area.**

| Activity       | Location (in trees or on the ground) | Vegetation | All |
|----------------|--------------------------------------|------------|-----|
|                | Tree & Ground | Forest | Woodland | Forest & Woodland | Grassland | Number (%) |
| Feeding        | 16 (51.6) | 1 (25.0) | 11 (35.5) | 8 (40.0) | 0 (0.0) | 0 (0.0) | 19 (36.5) |
| Resting        | 13 (41.9) | 0 (0.0) | 11 (35.5) | 5 (25.0) | 0 (0.0) | 0 (0.0) | 16 (30.8) |
| Moving         | 1 (3.2) | 0 (0.0) | 6 (20.0) | 0 (0.0) | 0 (0.0) | 0 (0.0) | 1 (1.92) |
| Social behaviour | 1 (3.2) | 1 (3.2) | 1 (5.0) | 1 (100.0) | 0 (0.0) | 3 (5.8) |
| Unknown        | 0 (0.0) | 3 (75.0) | 1 (25.0) | 1 (100.0) | 0 (0.0) | 52 (100.0) |
| **Total**      | 31 (100.0) | 4 (100.0) | 31 (100.0) | 20 (100.0) | 1 (100.0) | 0 (0.0) | 52 (100.0) |
individuals because the largest party was 64% and 73% of the unit groups in Gombe and Kasakati, Tanzania, respectively (Izawa, 1970; Teleki, 1977). This unit-group size is smaller than in other open habitats: 35 in Fongoli (Pruetz & Paco, 2009) and 28 in Assirik (Tutin et al., 1983). Assuming that 14–16 individuals formed a unit-group in Ugalla, 19.4–22.1% of the chimpanzees in the same unit-group foraged together, similar to chimpanzees in other areas (Nishida, 1968; Tutin et al., 1983). However, Itani and Suzuki (1967) observed a group of 34 individuals (43 including infants) at Filabanga, 50 km west of Ugalla. Bed counts revealed that chimpanzees formed a sleeping party of 23 individuals at Nguye in Ugalla (Ogawa et al., 2007). Chimpanzees may sometime form a large party composed of almost all unit-group members in a savanna woodland area.

Chimpanzees in Ugalla formed smaller parties than chimpanzees in other open areas (Tutin et al., 1983; Pruetz & Paco, 2009) and in tropical rainforests (Boesch, 1996; Matsumoto-Oda et al., 1998; Newton-Fisher et al., 2000). This may be because less food was available in smaller food patches in Ugalla than in other areas (Yoshikawa & Ogawa, 2015; Piel et al., 2017). Chimpanzees in other habitats gather around *Ficus* spp., *Saba* spp., and *Landolphia* sp. fruits (Nishida, 1991; Kuroda et al., 1996; Wrangham et al., 1996), but these plants are not abundant in Ugalla (Yoshikawa et al., in preparation). Chimpanzees in Ugalla may be able to form a large party only when they can access large food patches, such as *Parinari curatellifolia* fruit in the dry season (Yoshikawa et al., in preparation). Conversely, chimpanzees formed smaller parties in the rainy season than in the dry season. Ripe fruit is less abundant in the rainy season than in the dry season in Ugalla (Yoshikawa et al., in preparation). As with chimpanzees in other habitats (Goodall, 1986), chimpanzees in Ugalla might reduce feeding competition by forming smaller parties.

In contrast, chimpanzees might reduce predation risk by forming larger parties in the dry season, similar to chimpanzees in other areas (Itani and Suzuki, 1967). Unlike in Fongoli, another open habitat, the predation risk in Ugalla is likely to be high (Stewart et al., 2013). Predation pressure may be even higher in the dry season, because most streams dry up in Ugalla and lions can wait for a prey at the limited water sites (Andrew et al., 2016). Kano (1972) reported an encounter between a lion and chimpanzees in the dry season at Issa in Ugalla. Additionally, the canopy in woodlands is open in the dry season, as most woodland trees lose their leaves, and the distance between trees is much longer than in forests. Therefore, woodlands are likely to be more dangerous, as chimpanzees must travel on the ground. Actually, we did not record any parties in grasslands, and we found only one lone female party. Though we found three mother–infant parties, as lactating females with infants tend to spend more time alone with their infants (Wrangham et al., 1992), there were more mixed parties with infants than there were mother–infant parties, and mixed parties contained more females than males. In order to reduce predation risk, females might gather more frequently than males. Nevertheless, chimpanzees in Ugalla spent 32.7% of the time on the ground. This may be why the chimpanzees formed larger parties in woodlands than in forests, though this difference might be related to the fact that more individuals were visible in woodlands. Together, these results indicate that predation pressure affected party size and composition.

Mixed parties with oestrous female(s) averaged 5.7 individuals, whereas parties with no oestrous females averaged 4.0 individuals. We also found four consort parties. Male chimpanzees might try to forage with oestrous females because the population density is very low and males have difficulty finding oestrous females.

We did not find any all-male parties, similar to in other open habitats (Suzuki, 1969; Tutin et al., 1983). Their huge home range and low population density may reduce the necessity to patrol the border of their territory and defend females in their unit-group.

Camera traps identified 14 chimpanzees at Nguye in Ugalla. However, they did not record all members in the parties or the grouping pattern of chimpanzees. Further use of camera traps, as well as drones and GPS telemeters, may clarify the composition of parties and unit-groups, home ranges, and habitat use of unhabituated chimpanzees.

Though the limited number of observations on unhabituated chimpanzees restricts some conclusions, the findings indicate that chimpanzees in Ugalla changed their party size and composition depending on fruit abundance, predation pressure, and number of oestrous females, as with chimpanzees in other areas. However, chimpanzees in Ugalla did not form all-male parties but rather consort, and formed large parties in woodlands, suggesting anti-predation and reproductive strategies for adapting to a savanna woodland area.

**ACKNOWLEDGMENTS**

We are grateful to G Idani, T Kano, T Nishida, J Moore, ET Massawe, HY Kayumbo, A Hernandez-Aguilar, T Sakamaki, K Zamma, M Nakamura, M Koganewa, and T Nemoto. This study was permitted by the Tanzanian authorities (COSTECH and TAWIRI) and financially supported by a
Grants-in-Aid for Scientific Research of MEXT, Japan (C06061064; B1257597; A17255005; C22570223; 11J07921), Global Environment Research Fund F061, the Environment Research and Technology Development Fund (D-1007) of the Ministry of the Environment, Japan, the Advanced Studies on Primate Origins of Human Evolution (AS-HOPE), and International Training Program (ITP-HOPE), Japan Society for the Promotion of Science.

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Direct Observations of Savanna Chimpanzees in the Ugalla Area, Tanzania: Characteristics of Their Party Size and Composition

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We studied wild chimpanzees (\textit{Pan troglodytes}) in the Ugalla savanna woodland area of Tanzania from 1995 to 2012. Ugalla is the eastern-most chimpanzee habitat and is one of the driest and most open areas. From 52 direct observations of unhabituated chimpanzees, we found 59.6\% of parties (temporal sub-groups in a unit-group) in trees and 32.7\% on the ground; 59.6\% of parties were observed in forests, 38.5\% in woodlands, and none in grasslands. The mean±SD party size (excluding infants) was 3.1±2.2 (range 1–10) individuals. Party sizes were smaller in the rainy season (2.0 individuals) than in the dry season (3.6 individuals). This suggests that chimpanzees reduce feeding competition by forming smaller parties, especially in the rainy season when fruit availability is low and/or food patches are small. We found a lone male eight times, whereas we found a lone female only once. Mixed parties contained more females (1.9 individuals) than males (1.4 individuals). Mothers with infants might join a mixed party to reduce predation risk. The size of mixed parties with oestrous female(s) averaged 5.7 individuals, whereas that with no oestrous female averaged 4.0 individuals. We found four consort parties but no all-male party. This suggests that male chimpanzees in Ugalla frequently foraged with oestrous females but did not patrol their territory because their home range is huge and their population density is very low. Chimpanzees in Ugalla changed their party size and composition according to their feeding, anti-predation, and reproductive strategies to adapt to a savanna woodland area.

Key words: chimpanzee, party, savanna woodland, direct observation, food availability, predation pressure