



Genetic Analyses Suggest Male Philopatry and Territoriality in Savanna-Woodland Chimpanzees (*Pan troglodytes schweinfurthii*) of Ugalla, Tanzania

Deborah L. Moore^{1,2} · Kevin E. Langergraber³ · Linda Vigilant²

Received: 27 June 2014 / Accepted: 16 January 2015 / Published online: 29 March 2015
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Abstract Socioecological models predict that as resources become more sparsely distributed, primate populations will occur at lower densities and this demographic shift may have some effect on social structure. In savanna-woodland habitats, chimpanzees live at lower densities and in larger home ranges compared to forested habitats, presumably because of more widely dispersed food availability. These factors may result in chimpanzee home ranges being economically undefendable, leading to a reduction in male philopatry and territoriality. To test this hypothesis, we genotyped 237 fecal samples collected from Ugalla at 12 autosomal and 13 Y-chromosome microsatellite loci. We considered individuals that were sampled together at the same place and time to have been associating in the same party; with repeated sampling of an individual in different places and with different associates, we established which individuals belonged to the same community and the community locations. We identified 44 females and 69 males, carrying four different Y-chromosome haplotypes. One Y-chromosome haplotype was prevalent and found throughout the study site. The three rarer haplotypes occurred in spatially discrete clusters, which corresponded with the locations of communities identified through analysis of autosomal genotypes. Together

Electronic supplementary material The online version of this article (doi:10.1007/s10764-015-9830-8) contains supplementary material, which is available to authorized users.

✉ Deborah L. Moore
deborah.moore97@gmail.com

¹ Department of Anthropology, University of Texas at San Antonio, San Antonio, Texas 78249, USA

² Department of Primatology, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

³ School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona 85287, USA

with an observation of an aggressive interaction, these results suggest that, like chimpanzees living in species-typical forest habitats, the chimpanzees of Ugalla are organized into male philopatric, territorial communities, and that this social structure is reliably expressed under a variety of ecological conditions. This study reminds us that primate social structures may be adaptive across a range of habitats, and/or subject to phylogenetic constraint.

Keywords Chimpanzees · Genetics · Philopatry · Savanna-woodland · Social structure · Socioecology

Introduction

Adaptation to current ecological conditions is a fundamental premise of evolutionary theory, and hypotheses and models are built around predictions generated by this assumption (Darwin 1859; Fuller *et al.* 2014; Pearce-Higgins *et al.* 2011; Scholander *et al.* 1950). Ecological determinism has been a particularly important school of thought in understanding the variation in social structure across our own order, Primates, and for understanding the evolution of our own species, *Homo sapiens* (Stanford 1999, 2003; Sterck *et al.* 1997; Wrangham 1979, 1996, 1999). The extensive variation present across primate social structures is seen as an array of adaptive responses to the diverse habitats and wide variety of foods exploited. Although many primate species exhibit social structures as predicted through socioecological modeling (Doran 1997; Koenig and Borries 2006; Mitani *et al.* 2002; Sugiura *et al.* 2000; Wrangham 1980), it is increasingly recognized that some primate species do not conform to these models (Harris 2007), and that either current socioecological models require refinement, or that the evolutionary history of a species, i.e., phylogeny, may be the fundamental determinant of social structure, regardless of current environmental conditions (Di Fiore and Rendall 1994; Thierry 2008, 2013). An important means toward understanding the relative importance of phylogeny and flexible adaptation in the formation of primate social structure is to investigate a population living in an understudied ecological niche for the particular species (Chapman and Rothman 2009).

Much of what we know of chimpanzees (*Pan troglodytes*) comes from the forested or forest-woodland long-term study sites of Gombe Stream Research Center (Goodall 1986), Mahale Mountains National Park (Nishida 1990), Tai National Park (Boesch and Boesch-Achermann 2000), and Kibale National Park (Watts and Mitani 2002). Chimpanzees occupying savanna-woodland habitats remain little studied because of the difficulty in habituating rarely encountered individuals that probably range more widely (Baldwin *et al.* 1982; Moore 1992). However, field sites of savanna-woodland chimpanzees have recently been established and early research is providing new insights into the behavioral variation present among chimpanzees (Pruetz 2007; Pruetz and Bertolani 2007).

At all sites where chimpanzees have been habituated and subject to long-term observations, they live in distinct communities, composed of individuals that are familiar with each other and occupy a spatially discrete home range, i.e., territory, that is defended against neighboring communities (Boesch and Boesch-Achermann 2000; Hiraiwa-Hasegawa *et al.* 1984). Within these communities, individuals forage in small,

fluid parties, and exhibit a high degree of fission–fusion dynamics (Aureli *et al.* 2008; Goodall 1986; Kummer 1971; Nishida 1968). The strong preference for ripe fruit among chimpanzees is thought to drive the fission–fusion system that enables flexible adjustment of foraging party size to fluctuations in fruit abundance and distribution (Wrangham 1980).

Chimpanzees are highly territorial, engaging in “boundary patrols” wherein they search for neighbors from other communities and sometimes attack and kill them (Amsler 2010; Watts and Mitani 2001; Wilson and Wrangham 2003). Boundary patrols and other forms of cooperative territorial behavior are primarily a male activity. Male chimpanzees that successfully cooperate to make incursions into neighboring communities and expand their territory can accrue several fitness benefits. In a study of the Kasakela community at Gombe National Park, Tanzania, researchers demonstrated that larger territories resulted in increased food availability and shorter interbirth intervals (Pusey *et al.* 2005; Williams *et al.* 2004). The reduction of community size due to lethal intercommunity aggression is responsible for (Gombe: Goodall 1986), and likely caused (Mahale: Nishida 1985), the transfers of parous females into the larger community, demonstrating that successful cooperation among males to expand their territory can also result in increased reproductive success through the addition of more adult females to their community. In addition, the most reproductively successful males at Ngogo are most often the males that participate in cooperative boundary patrols (Watts and Mitani 2001), and so will benefit most from the addition of well-fed and highly reproductive females. Moreover, these direct fitness benefits that males accrue from territoriality are supplemented by indirect fitness benefits resulting from male philopatry, as direct fitness benefits are shared among related community males, and represent a cost to less related males in other communities (Langergraber *et al.* 2011; Lukas *et al.* 2005; Vigilant *et al.* 2001).

Conversely, studies of a variety of populations have shown that although territorial behavior is beneficial, it is not without its associated costs. For example, a study of the Ngogo community at Kibale demonstrated that male chimpanzees expend more energy, travel further distances, and spend more time traveling during boundary patrols than when not conducting patrols (Amsler 2010). Like the community at Kibale, patrolling at Taï occurs more frequently during periods of fruit abundance (Herbinger *et al.* 2001; Mitani and Watts 2005).

Thus, it is conceivable that the more widely distributed food resources in savanna-woodland environments may make it more difficult for male chimpanzees to accrue the direct and indirect fitness benefits of territoriality and philopatry. Socioecological models predict that as food availability decreases, individuals will have to travel over a larger area to meet their nutritional requirements, and thus home range sizes will increase and population densities decrease (Balcomb *et al.* 2000; Isbell 1991; Wrangham *et al.* 1993). Accordingly, chimpanzee population density should be much lower in savanna-woodland habitats than in forested environments, where published densities range from 2.5 to 9 individuals/km² (Boesch and Boesch-Achermann 2000; Chancellor *et al.* 2012; Chapman and Wrangham 1993; Nishida 1990; Pusey *et al.* 2008; Watts *et al.* 2006). In fact, the habituated savanna-woodland community of 28–36 individuals at Fongoli, Senegal occupies a range of ≥ 85 km² (Pruetz and Lindshield 2012), resulting in a maximum population density of only 0.42 individuals/km² (36/85). This suggests that the constraint of lower population density may be resolved by

both smaller community size *and* larger home ranges. Further, the boundaries of such a large home range would seem to be energetically indefensible, given that the daily path length of chimpanzees would make it difficult to frequently encounter and monitor such a large border, regardless of the number of foraging parties (Amsler 2010; Brown 1964; Lowen and Dunbar 1994; Mitani and Rodman 1979).

Some support for the indefensibility of large territories among savanna-woodland chimpanzees comes from Fongoli, where intercommunity interactions have not been reported; nor has any “border patrol” behavior been described, in contrast to findings from most long-term studies of chimpanzees living in forests (Boesch and Boesch-Achermann 2000; Goodall *et al.* 1979; Newton-Fisher 1999; Nishida 1990; Watts and Mitani 2001). However, the Fongoli chimpanzees have been habituated only since 2005 (Pruetz 2007), and Goodall (1986) did not report agonistic intercommunity encounters at Gombe until 14 yr after her research began.

The term savanna incorporates a range of ecological environments, but all are distinguished by a continuous C₄ grass understory (Ratnam *et al.* 2011). Savanna, rather than forest, is found in places with <1500 mm of rainfall and seasonal drought (Murphy and Bowman 2012). Much variation exists in the density and genera of tree cover (Ratnam *et al.* 2011). The savanna-woodland of the Ugalla region in western Tanzania is characterized by the tree genera *Julbernardia* and *Brachystegia*, known as “miombo woodland,” with small strips of forest that occur around rivers and comprise the *ca.* 2% of forest cover. The chimpanzee population density estimate for the Ugalla region, inferred using a spatially explicit genetic capture–recapture method (SECR), is 0.25 individuals/km² (CI 0.16–0.38) (Moore and Vigilant 2014a), which is 10 times lower than the lowest reported density for a forested site (Nishida 1990). Thus, to accommodate even a small community of 15 individuals, for example, a home range of *ca.* 60 km² is necessary (15/0.25 = 60), which is twice the size of the published community home range of Ngogo in Kibale National Park, an exceptionally large chimpanzee community (*ca.* 148 individuals) living in a forest environment (Amsler 2010). Recent evidence suggests that at least one community in Ugalla may contain a substantial number of individuals, with the genetic identification of 67 associating individuals (Rudicell *et al.* 2011). If this community occurs at a density of 0.25 individuals/km², they would occupy a home range of 268 km² (67/0.25 = 268), although it is not expected that chimpanzees are evenly distributed across the Ugalla landscape, and this community may inhabit an area at an unusually high density. Even twice the estimated Ugalla population density would be exceptionally low, and such conditions of low density and large range size characterizing the chimpanzee communities at Ugalla, therefore, may result in a shift in social structure. Specifically, there may be reduced selection pressure for male philopatric communities among the savanna chimpanzee population of Ugalla as a result of an increase in the cost of territorial defense.

Savanna-woodland habitats present logistical challenges for the study of chimpanzees. The low population densities limit opportunities for encounters by researchers, which exacerbates the difficulties of habituation of this species (Baldwin *et al.* 1982; Moore 1992). Remote techniques, such as the genetic survey applied in this study, provide information not otherwise attainable from unhabituated populations (Arandjelovic *et al.* 2010, 2011; Inoue *et al.* 2013; McGrew *et al.* 2004; Schubert *et al.* 2011). The characterization of DNA from noninvasively collected samples can

provide information such as group membership, sex-biased dispersal and dispersal events, paternity, and inter- and intracommunity relatedness (Arandjelovic *et al.* 2011; Langergraber *et al.* 2007; Schubert *et al.* 2011). Such surveys, conducted over large areas, also can provide population-level data such as estimates of genetic diversity (Moore and Vigilant 2014b) and evidence of population structure such as isolation by distance (IBD) (Wright 1943), adding a scale of analysis beyond that of the community.

Genetic surveys to deduce social structure have been used in studies of several chimpanzee populations, and such surveys can be used to determine the approximate composition and location of chimpanzees, and whether they conform to the species-typical pattern of male philopatry. Y chromosomes are passed from father to son, leading to the simple prediction that male chimpanzees from the same community should have the same or similar Y-chromosome haplotypes. The strength of the relationship between community membership and Y-chromosome similarity will depend on the frequency of paternity by males from outside of the community, either from extragroup copulations or when parous females transfer between communities accompanied by male offspring. Behavioral and genetic research suggests that both are exceedingly rare in chimpanzees, particularly in the East African subspecies (Langergraber *et al.* 2014a, b). Accordingly, there is a large degree of community structuring in Y-chromosome variation, with all communities showing multiple unique haplotypes and sharing only at most one, if any, haplotypes with other communities (Langergraber *et al.* 2007, 2014a, b; Schubert *et al.* 2011). The evolutionary relationships of Y-chromosome haplotypes can be further inferred through phylogenetic network analysis, and the movement of haplotypes across time and space may be traced.

The goal of this study is to elucidate the social structure of a population of unhabituated chimpanzees living in a savanna-woodland habitat at the edge of this species' geographic distribution, a habitat that may, therefore, represent their minimal ecological tolerance. To this end, we examine the distribution of individual genotypes and the Y-chromosome haplotypes of male chimpanzees across the Ugalla region of western Tanzania, a savanna-woodland habitat with a known low population density. Specifically, we address whether the distribution of Y-chromosome haplotypes, in combination with putative communities constructed through associating individuals identified through unique autosomal genotypes, provides evidence for the maintenance of male philopatric community structure. If this community structure is maintained, we expect to observe spatial clustering of Y-chromosome haplotypes, coincident with community ranges (inferred through associating individuals), as seen at long-term chimpanzee study sites (Arandjelovic *et al.* 2011; Langergraber *et al.* 2007). If spatial structure is not observed, we must consider that the Ugalla chimpanzees may be adopting an alternative social strategy to cope with this challenging savanna-woodland environment. Under male philopatry we also expect to see an absence of IBD at the Y chromosome. In contrast, if males are dispersing from their natal community, we expect that pairs of communities that are closer to one another will be more similar than one another at the Y chromosome than pairs of communities that are more distant from one another, i.e., positive IBD. Such a pattern is expected in the dispersing sex because dispersing individuals are more likely to travel shorter rather than longer distances (Wright 1943).

Methods

Study Site and Subjects

Eastern chimpanzees (*Pan troglodytes schweinfurthii*), one of four subspecies of chimpanzee (Oates *et al.* 2009; Schwarz 1934), are found from the western border of the Democratic Republic of Congo in central Africa to western Tanzania in East Africa. This study focuses on the population of chimpanzees in the Ugalla region of western Tanzania, located on the plateau stretching westward from the Eastern Arc Mountains. This region, covering *ca.* 3350 km², constitutes the easternmost range of chimpanzees, and is one of the most seasonal, dry, and open chimpanzee habitats (Hernandez-Aguilar *et al.* 2007; Kano 1971; Moore 1994; Ogawa *et al.* 2007). Although much of the region falls within the East Tongwe Forest Reserve, the area was specifically named by Kano (1971) and defined as the region bordered by the Mpanda–Uvinza road to the west, the Malagarasi River to the north, the Ugalla River to the east, and the Ilumba basin to the south (Moore 1994) (Fig. 1). The region is carved by deep valleys and the elevation of the area surveyed for this study ranges from 1095 m to 1919 m above sea level. Most precipitation occurs during the rainy season from November to April, with a marked dry season from May to October during which most rivers become dry (Hernandez-Aguilar *et al.* 2007; Moore 1994).

Collection Methods

Before the initiation of fieldwork, we established a survey grid within the Ugalla region over an area that was chosen based on previous chimpanzee nest surveys, existing remote sensing data, and accessibility by foot (Fig. 1) (Moyer *et al.* 2006; Ogawa *et al.* 2007). DLM conducted surveys from one permanent camp, and five temporary camps that were established across the survey area, and spent between 15 and 33 d at each camp. Accompanied by one field assistant, DLM searched the quadrats surrounding each camp based on a decision protocol wherein areas containing signs of chimpanzee presence, *i.e.*, feces, tracks, fresh nests, vocalizations, and/or observations, were searched again for 4 d, and areas with no evidence of chimpanzee presence were not searched again. We followed chimpanzees whenever they were heard, seen, or fresh tracks were detected, and any observed chimpanzee behavior was collected *ad libitum* in field notes. DLM uploaded daily track logs from a Garmin *etrex legend* GPS device to ArcGIS 9.3 each evening, and searched all quadrats within a minimum 4 km radius of camp prior to leaving the area.

We used the two-step ethanol–silica preservation method to collect all samples (Nsubuga *et al.* 2004). Samples were stored for ≤ 5 mo in the field and were shipped from Kigoma, Tanzania, to the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. Once in Leipzig, the samples were stored at 4°C for ≤ 18 mo before extraction of DNA.

Laboratory Methods

We used the QIAmp DNA stool kit (Qiagen) to extract DNA from all samples, according to manufacturer's instructions and amendments as per Nsubuga *et al.*

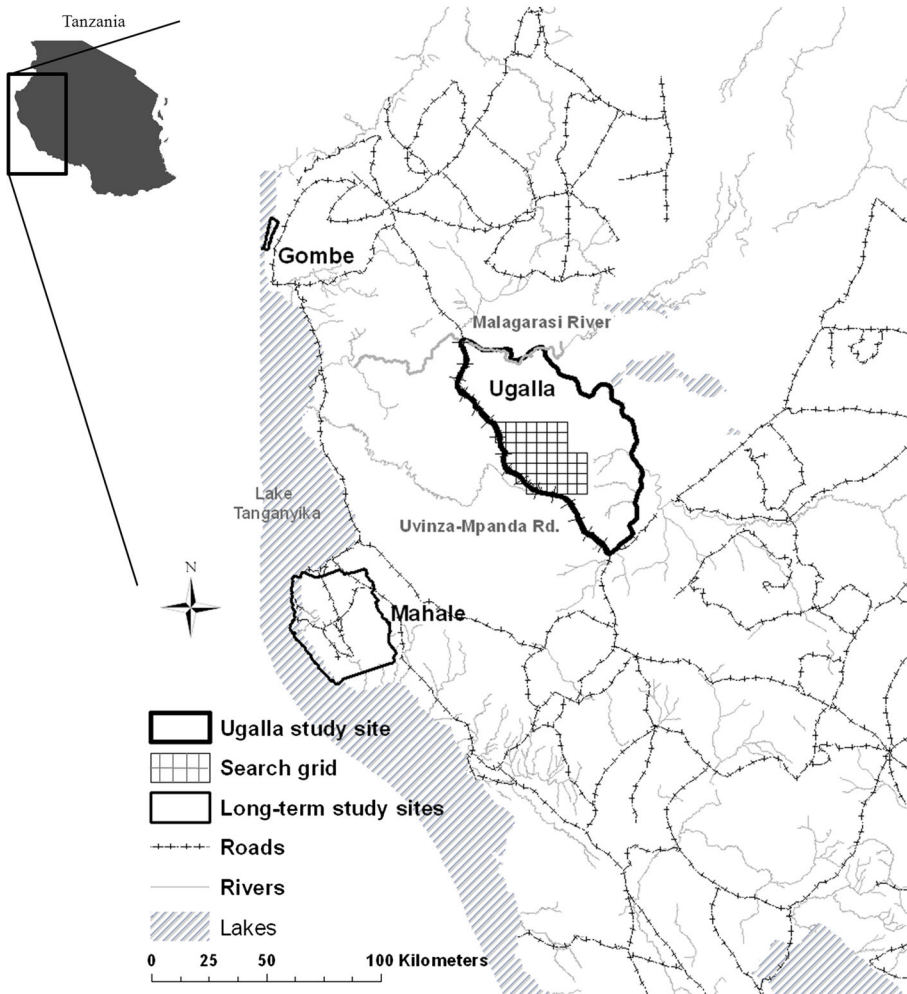


Fig. 1 Location of the Ugalla region in Tanzania, demonstrating boundaries and surveyed area, and relative to well-known long-term chimpanzee study sites Mahale Mountains National Park and Gombe Stream National Park. (Modified from Moore and Vigilant 2014a).

(2004). All extracts were amplified at the X–Y homologous amelogenin locus and electrophoresed on a 2.5 % agarose gel for 30 min at 80 V to assess the presence or absence of DNA and later to determine sex (Bradley *et al.* 2001). Following a multiplex procedure (Arandjelovic *et al.* 2009), we then amplified all extracts at 19 autosomal microsatellite loci using unlabeled forward and reverse primers in a single polymerase chain reaction (PCR) cycle, and at 12 of these 19 loci in a second single-locus PCR cycle, using fluorescently labeled forward primers and nested reverse primers (Table I). [We performed the second step only for 12 of the 19 loci because previous research showed that 8–12 loci are sufficient to identify unique individuals (Arandjelovic *et al.* 2011; Inoue *et al.* 2008), but we wanted to have the option to go back easily and genotype the other seven loci had this turned out not to be the case for our study

TABLE I Microsatellite loci used in genotyping Ugalla chimpanzees

Locus	No. of alleles	No. of typed individuals	Allele size ranges (bp)	Heterozygosity	
				Observed	Expected
Autosomal ^a					
D3s2459	11	107	168–222	0.542	0.542
D2s1326	10	111	179–219	0.838	0.828
D14s306	9	110	185–225	0.727	0.789
D7s2204	8	109	156–184	0.771	0.792
D7s817	7	113	106–148	0.796	0.821
D1s1622	7	99	237–265	0.505	0.508
D5s1470	6	111	166–186	0.676	0.591
D6s1056	6	110	230–250	0.727	0.706
D5s1457	6	112	102–126	0.643	0.651
D2s1329	6	110	173–201	0.782	0.786
D16s2624	6	102	106–130	0.49	0.509
D11s2002	5	110	133–149	0.736	0.704

^a Seven additional loci (D1s1656, D3s3038, D4s1627, D9s910, D10s676, D12s666, D18s536) were amplified in the first single PCR reaction, but not amplified in the second single locus PCR reactions.

population.] We performed from 3 to 12 independent amplifications for each sample at these 12 loci, based on the requirement that heterozygote alleles must be seen in two independent reactions and homozygote alleles must be seen in between three and five independent reactions, depending on the amount of template DNA in the extract (Arandjelovic *et al.* 2009). We used only samples that yielded confirmed alleles based on this protocol at eight or more loci in further analyses.

Once the sex of each extract was determined, we amplified those identified as male in the same two-step multiplex procedure, at 13 microsatellite loci on the Y chromosome (DYS510, DYS520, DYS612, DYS632, DYS517, DYS502, DYS439, DYS392, DYS562, DYS588, DYS533, DYS630, DYS469) in both steps. We examined the 13 loci for polymorphisms, and identified Y-chromosome haplotypes for the Ugalla samples. We conducted phylogenetic analysis of the haplotypes using the software NETWORK 4.6.1.0 (Bandelt *et al.* 1999) to investigate the evolutionary relationships of the Ugalla Y-chromosome haplotypes.

We electrophoresed PCR products from the autosomal and Y-chromosome amplifications on an ABI PRISM 3100 Genetic Analyser. We assigned genotypes and haplotypes based on allele sizes, which were determined using an internal size standard (ROX labeled HD400) and Genemapper version 3.7 (Applied Biosystems).

Identification of Individuals

Using CERVUS 3.0 (Kalinowski *et al.* 2007), we determined how many autosomal loci were necessary to confidently assign individual identifications to matching genotypes, given the allele frequencies of our samples. We found the probability that two

samples with the same genotype were not from two different individuals (including two full siblings), i.e., $P_{ID_{sibs}}$ was <0.001 . We first ran all of the extracts amplified at eight or more loci through the “identity analysis” function of CERVUS allowing for mismatches at two loci, and then examined these genotypes at the mismatched loci for errors or to re-genotype for cases of ambiguity. We then re-ran the identity analysis with no mismatches allowed, and matching genotypes were assigned an individual identification number.

Community Assignment

We assigned individuals to communities as per methods in Arandjelovic *et al.* (2011), wherein researchers collected feces of unhabituated chimpanzees over 132 km² of Loango National Park. Individuals whose feces were collected at the same time and location were assumed to be “associating” in the same “party,” and thus represent members of the same community. Associates of associates were also assumed to belong to the same community; for example, if individual A was found associating with individual B, and at a later time and place was found associating with individual C, then all three individuals were assumed to be members of the same community, even though individuals B and C were never found in direct association. This method provides the maximum number of communities, owing to the inability to sample all associations and because entire chimpanzee communities are rarely found together.

We then used ArcGIS version 10.1 (ESRI) to map all occurrences of individuals and minimum convex polygons (MCPs) were drawn around individuals linked by association to determine the locations of the minimum home ranges/territories of the communities. Individuals that were unlinked to any of the individuals identified as belonging to the same community, but nevertheless were sampled within the MCP, were also assumed to be members of the same community (Arandjelovic *et al.* 2011). Males were also mapped according to their Y-chromosome haplotype to investigate the distribution of Y-chromosome haplotypes and determine whether they were geographically clustered.

Population Structure

Using the communities established by the methods above, we conducted an IBD analysis to determine whether the genetic differentiation of Y-chromosome haplotypes between putative communities could be described as a function of geographic distance. We estimated genetic differentiation of the Y chromosomes, i.e., fixation index (F_{st}), between 12 communities containing 1–13 males (average 4.5) using Arlequin v.3.5.1.2 (Excoffier and Lischer 2010). Three males were excluded from this analysis because of the lack of association of their sample with any other individuals, and thus an inability to assign them to a community. From the MCPs drawn around each putative community, we obtained the centroid coordinates and measured the distance between each community using these points. We then conducted a matrix correlation between the geographic and genetic distances, i.e., F_{st} values, using the IBDWS vers. 3.23 Web Service (Jensen *et al.* 2005) to determine whether a pattern of IBD was present among the Ugalla males.

Ethical Note

This study complied with protocols approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Texas at San Antonio (#PA001-05/14A0), and was approved by Tanzanian government authorities (COSTECH Permit No. 2009-143-ER-2009-05).

Results

Samples and Individuals

We collected 237 samples from a surveyed area of 624 km² comprising 39 4 × 4 km² quadrats. Of the 237 extracts analyzed, a total of 197 extracts provided usable genotypes, which represents an 83% success rate. The 197 genotypes were on average 95% complete, with 137 (70%) of the samples successfully amplified at all 12 autosomal microsatellite loci.

Based on the heterozygosity values of the 12 microsatellite loci analyzed, a minimum of 8 loci were required to confidently ($P_{ID_{sibs}} = 0.00058$) determine that matching genotypes were from the same individual and not from full siblings (Table I). We identified 113 individuals from the 197 extracts analyzed, comprising 44 females and 69 males.

Associations

The 113 individuals were sampled from one to five times (Table II). Using these association linkages, we determined 13 potential communities comprising 2–22 individuals, but 11 individuals were not initially linked to any community because of their lack of association with any other individual [Table III and Electronic Supplementary Material (ESM) Appendix S1 for full list of Ugalla communities]. We mapped all occurrences of individuals and minimum MCPs were drawn around associating individuals to approximate spatial occurrence of the 13 inferred communities (Fig. 2). Of the 11 unlinked individuals, two were located within an MCP and were assigned to that community.

Y Chromosome

Of the 13 Y-chromosome microsatellite loci genotyped, 10 loci were monomorphic while 3 loci had 2 alleles each. Haplotypes were based on combinations of Y-

TABLE II Sampling and resampling of individual chimpanzees in Ugalla region, collected between July 2009 and April 2010

No. of times sampled	No. of individuals	Males/females (N)
1	85	48/37
2	21	14/7
3	5	5/0
4	1	1/0
5	1	1/0

TABLE III A portion of the spreadsheet linking chimpanzee individuals by association to two (UG1 and UG2) of the possible 13 communities at Ugalla (see ESM Appendix S1 for the full table). For example, the parties linked from July 27, August 1, and August 6 (outlined) were linked by the presence of individual U006 (in bold) in all three parties. Individual U006 was sampled once on July 27, three times on August 1, and twice on August 8. Similarly, individuals that were sampled on more than one occasion were used to link other individuals, creating putative communities across the Ugalla region

	Group assignment	UG1													UG2														
	Ind. ID	U001	U002	U012	U013	U014	U015	U016	U003	U004	U006	U007	U008	U009	U010	U011	U017	U018	U019	U020	U022	U023	U024	U025	U026	U027	U028	U029	U030
	Sex	M	M	M	F	F	F	M	F	F	M	F	M	M	M	M	F	M	F	M	M	F	F	M	F	F	F	M	F
Date Sampled	22/7/09	1	1																										
	23/7/09							1																					
	27/7/09									1	1	1	1	1	1	1	1												
	30/7/09		1	1	1	1	1	1																					
	1/8/09										3							1											
	2/8/09							1					1		1		1	1	1										
	4/8/09											1	1	1	1		1		1	1	1	1	1	1	1	1	1	1	1
	6/8/09									1	2	1							1		1		1		1	1	1	1	1

chromosome loci, and each of the four haplotypes found was assigned a label (Table IV and ESM Appendix S2 for full list of Ugalla males and their haplotypes). Eight males were not completely genotyped and could not be assigned to a haplotype.

One haplotype (A) occurred at a high frequency among the Ugalla males, while the remaining three (B–D) were less prevalent (Fig. 2a). The most frequent haplotype (A) was found throughout the study site and in each of the putative communities, but each of the rare haplotypes (B–D) occurred in spatial clusters, with each cluster separated by distances ranging from *ca.* 6–20 km. The only exception to the geographic clustering of rare haplotypes was the occurrence of a male carrying haplotype B, which was found in proximity of males carrying haplotype C (Fig. 2b). This exception may be explained, however, by a behavioral observation of a putative intercommunity encounter. DLM observed an encounter between two parties of chimpanzees; one party came over a ridge and comprising *ca.* 14 individuals, and the other party was at the bottom of the valley and out of view. At least 4 males from the party of 14 were observed to display, and continuous pant-hoots were heard from both parties. Both parties retreated

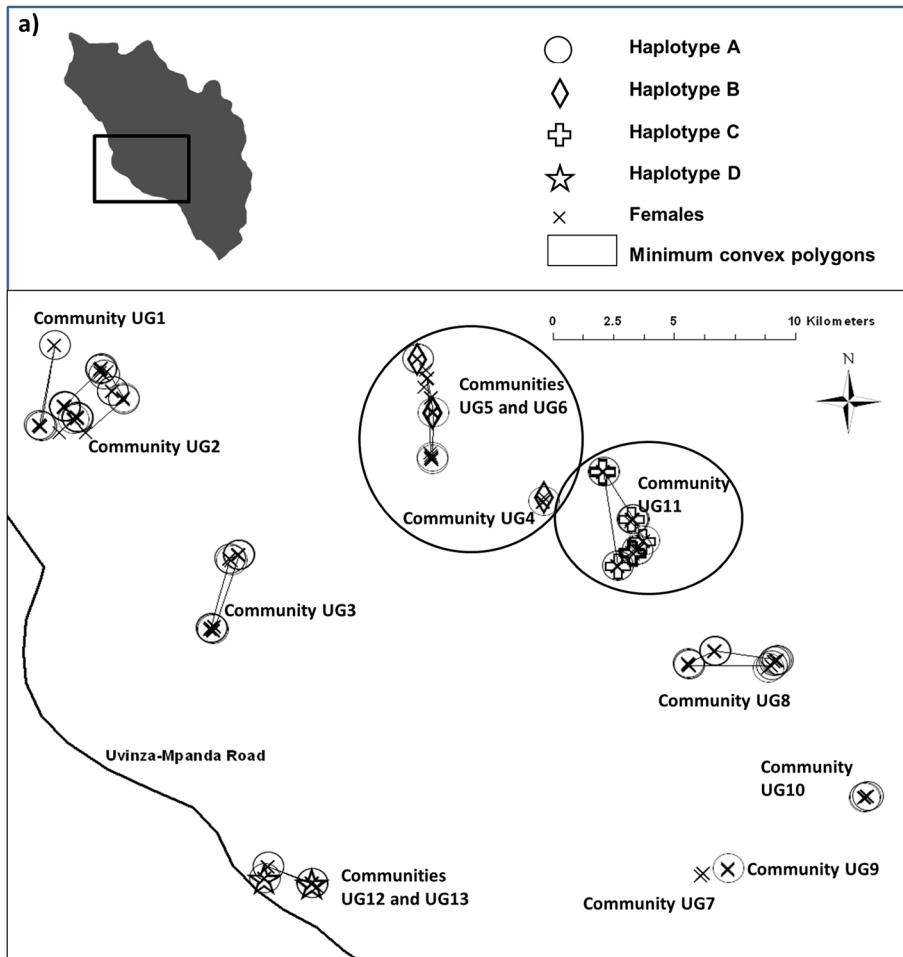


Fig. 2 Map of surveyed area of Ugalla region: **(a)** All sampled locations of chimpanzee individuals with male Y-chromosome haplotypes. Minimum convex polygons (MCPs) based on associating individuals and indicating putative communities are labeled. Geographic clustering of rarer haplotypes B–D are indicated by circles. (Note: individuals collected together are not discernible at this scale.) **(b)** Putative communities UG4, UG5, UG6, and UG11 based on associating individuals, and containing rarer Y-chromosome haplotypes B and C, and indicating the site of the possible intercommunity encounter that was witnessed.

in opposite directions. The encounter lasted *ca.* 5 min, during which time the human observers were undetected by the chimpanzees. These observations were consistent with accounts of hostile intercommunity encounters among habituated populations, most of which involve auditory/vocal rather than physical contact (Boesch *et al.* 2008; Watts *et al.* 2006). We were able to collect four fecal samples, one from the party on the ridge and three from the valley below. The male from the top of the ridge is of the rare haplotype B, while the male from the valley carries the haplotype A. Unfortunately, these four individuals were never resampled, preventing linking them to any other communities based on associations. If we link the male from the ridge to his conspecifics bearing the rare haplotype B, however, a picture emerges of two neighboring communities defined by Y-chromosome haplotypes. Further, the clusters of rare

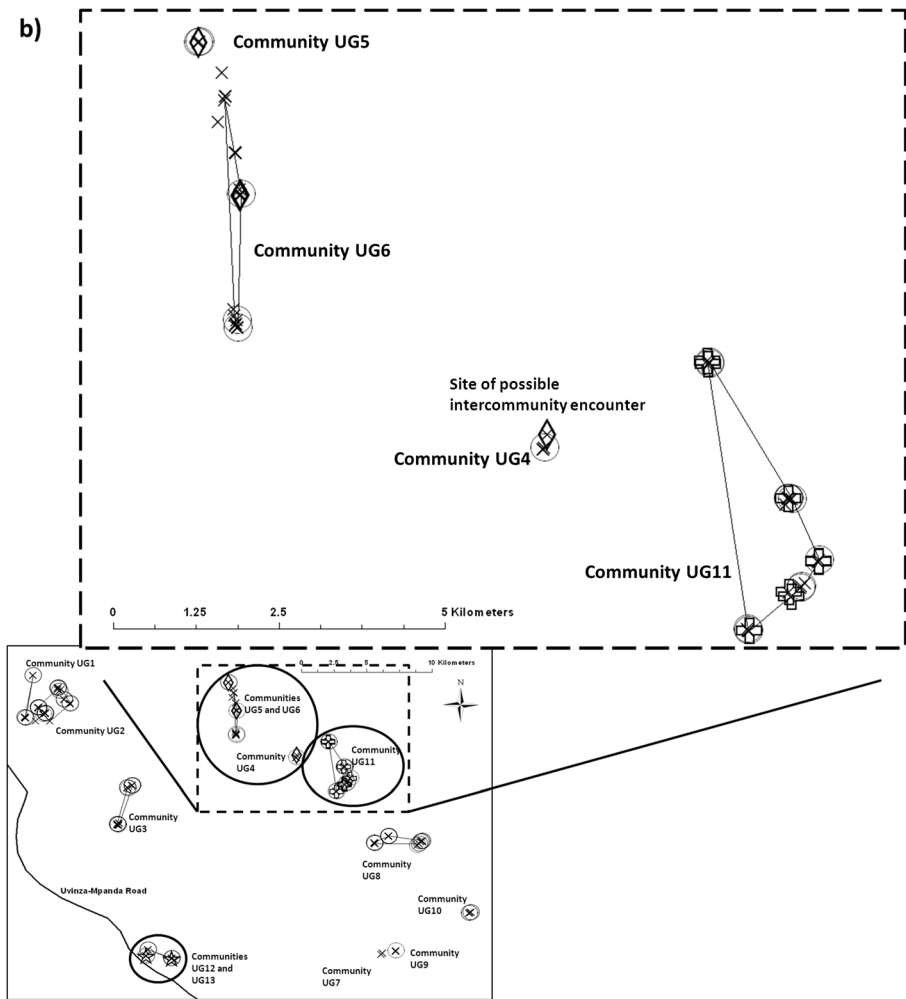


Fig. 2 (continued).

haplotypes were spatially coincident with the MCPs drawn around the putative communities that were identified through analysis of autosomal genotypes.

The phylogenetic network diagram generated in NETWORK 4.6.1.0 (Bandelt *et al.* 1999) suggests that each of the rarer Ugalla haplotypes emerged independently from the putative ancestral haplotype A. We found no evidence for positive IBD in intercommunity Y-chromosome variation ($r = 0.1837$, $P = 0.0767$).

Discussion

We found evidence of chimpanzee presence throughout the surveyed region of Ugalla, and we identified 113 individuals from the 237 samples collected. Of these individuals, the 69 males detected carried 4 Y-chromosome haplotypes, 1 that was prevalent across the entire study site and 3 more rare haplotypes, each of which were found in close

TABLE IV Y-Chromosome haplotypes of male chimpanzees from the Ugalla sample, collected between July 2009 and April 2010, with unique alleles in bold (see ESM Appendix S2 for full list of Ugalla males and their Y-chromosome haplotypes)

Haplotype	No. of individuals	DyS510	DyS520	DyS612	DyS632	Dys517	DyS502	DyS439	DyS392	DyS562	DyS588	DyS533	DyS630	DyS469
A	52	183	152	192	132	179	187	234	171	173	169	202	181	213
B	4	183	152	192	192	179	187	238	171	173	169	202	181	213
C	2	179	152	192	192	179	187	234	171	173	169	202	181	213
D	3	183	152	192	192	179	187	234	171	173	169	202	177	213

proximity to one another and at a considerable distance from other such geographic clusters of Y-chromosome haplotypes. The spatial clustering of the rare Y-chromosome haplotypes in the Ugalla population meets our prediction for male philopatric community structure and is consistent with the community structure present at all previously studied chimpanzee study sites. Further, these clusters are coincident with putative communities constructed through associating individuals and may indicate the approximate locations of male philopatric communities in the Ugalla region.

Community designation according to the clustered distribution of rare haplotypes is further supported by the branching pattern of the phylogenetic network of the four Ugalla Y-chromosome haplotypes. Each of the rarer Ugalla haplotypes is one mutation away from the putative ancestral haplotype and more than one mutation away from another rare haplotype. The most parsimonious explanation for this network is that each of the rare haplotypes, B–D, emerged in isolation from each other, and is descended from haplotype A. Any alternative explanations would involve back mutations to a specific allele, which is extremely unlikely. The emergence of novel haplotypes in isolation from others is consistent with territorial, male philopatric communities with restricted male-mediated gene flow, and thus the location of these haplotypes could signify the general locations of different chimpanzee communities.

We also found no pattern of IBD at the Y chromosome, as would be expected if males were dispersing from their natal communities and following the typical pattern of dispersers in more often joining closer rather than more distant communities (Wright 1943). It should be noted, however, that the number of communities used to test for IBD is likely inflated because of the methods used, and members of neighboring “communities” may be part of the same community. In addition, some of the communities were represented by few males, which might increase the variance in F_{st} (fixation index) estimations. Even if we found IBD, however, this would not necessarily indicate that males are dispersing rather than philopatric; one would also expect to find that geographically proximal communities were more similar at the Y than geographically distant communities even if males were strictly philopatric but new communities were formed via fissioning as their size increased, as has been observed to occur at Gombe (Goodall 1986). Furthermore, the pattern of unique haplotype clusters observed at Ugalla is consistent with studies of habituated western chimpanzees (Schubert *et al.* 2011) and eastern chimpanzees (Langergraber *et al.* 2007), with known systems of female dispersal and male philopatry.

Another possibility is that geographic clusters of Y-chromosome haplotypes do not represent different communities, but instead represent male neighborhoods within a single community. This possibility is suggested by previous research in several East African chimpanzee communities showing that like females, male chimpanzees also show long-term tendencies to range preferentially in certain areas of the territory, i.e., spatial “neighborhoods,” over others (Emery Thompson *et al.* 2007; Gilby and Wrangham 2008; Langergraber *et al.* 2009, 2013; Machanda 2009; Murray *et al.* 2008; Newton-Fisher 2002). At Ngogo, males and females that preferentially range in the same neighborhood also are particularly likely to reproduce, producing sons with both similar ranging patterns (inherited from the son’s mother: Murray *et al.* 2008) and similar Y chromosomes (Langergraber *et al.* 2013). However, this “reproductive neighborhood” explanation is unlikely to explain the geographic pattern of Y-chromosome variation we observed at Ugalla, where haplotype clusters were much

too geographically distant from one another, e.g., 20 km between haplotypes C and D, to represent male neighborhoods within the same community, unless community home range size was exceptionally large. For example, if we draw a minimum convex polygon around just the three rare haplotypes, we obtain a polygon with an area of 261 km². This would be the *minimum* area of their home range, and is therefore unlikely to represent one community. The probable intercommunity encounter that was witnessed in the area between the occurrence of haplotypes B and C provides further evidence to support this conclusion. The more likely explanation, therefore, is that the haplotype clusters represent different chimpanzee communities.

This examination of social structure in the unhabituated Ugalla chimpanzee population provides evidence that these savanna-woodland chimpanzees are living in male philopatric, territorial communities, despite the social constraint of an extremely low population density and the energetic constraint of putatively large home ranges. Although determining whether male philopatry and territoriality are functionally adaptive under these constraints was of course beyond the scope of this study, their existence among chimpanzees living in the Ugalla region shows that these behavioral patterns are nevertheless expressed under a wide variety of ecological conditions. The apparent persistence of male philopatry and territoriality at Ugalla also provides support for the premise that this social structure is a shared trait among chimpanzees, bonobos, and our earliest ancestors, as they occupied a similar habitat (Cerling *et al.* 2010, 2011; Domínguez-Rodrigo 2014; Langergraber *et al.* 2007; White *et al.* 2009; Wilson and Wrangham 2003; WoldeGabriel *et al.* 2009). Of course, male philopatry and territoriality may be a derived trait among the genus *Pan*, and recent critiques of the chimpanzee model for human origins suggested the use of a “comparative convergence approach” (Vaesen 2014, p. 12) that includes, among other things, a more inclusive phylogenetic comparison (Duda and Zrzavý 2013; Vaesen 2014). In a study that adhered to this mandate, Duda and Zrzavý (2013) conducted a phylogenetic analysis of 65 characters, which included morphological, behavioral, and socioecological traits, among 6 species of great apes, humans, and 12 “outgroup” primate species, in an effort to reconstruct the last common ancestor (LCA) of chimpanzees and humans. Using maximum-parsimony and maximum-likelihood character optimization analyses of these 65 traits, their findings indicated that the LCA may have had a more “fluid” bisexual dispersal pattern, although it was likely female biased. This finding converges with those of Hill *et al.* (2011), who found that although many hunter–gatherer societies—thought to represent the social structure characterizing humans for most of their evolutionary history—are multilocal, living with either the husband or wife’s kin groups, males actually live with their male kin more frequently than females live with their female kin. This tendency toward patrilocality, therefore, may be an ancestral trait present in the LCA, and strongly selected for in the lineage leading to extant chimpanzees, resulting in the strict male philopatry we see today across a variety of habitats. More broadly, this study reminds us that social structures may be adaptive across a wide range of ecological conditions.

From a methodological perspective, this study is one of the first to systematically survey and describe a population of savanna-woodland chimpanzees through the noninvasive collection of genetic material (*cf.* McGrew *et al.* 2004). Although the geographic clustering of rare Y-chromosome haplotypes certainly is suggestive of community locations and male-philopatric community structure in this region, a more

widely surveyed area and a higher rate of individual recaptures would strengthen the initial portrayal of the Ugalla population presented here. It also may be argued that concentration of effort in a smaller area over a longer time scale would provide enhanced information on range use of the Ugalla chimpanzees. In this study, the furthest distance between recaptures for an individual was *ca.* 3.7 km, and the longest time between recaptures was 29 d. A higher sampling effort would produce more recaptures of individuals, and also may provide more informative individual ranging information.

If we are to expand our knowledge of this Endangered species (IUCN 2014) across its full geographic and ecological range, thereby documenting the full socioecological flexibility and repertoire of our closest relative, novel approaches such as the one used in this study must be employed. Given the enormous difficulties of habituating savanna chimpanzees and the further hardship of monitoring them across massive home ranges, this study demonstrates an innovative approach that provides first indications of community structure. What remains is the application of these and other methods to describe how this structure functions in a context of highly seasonal, widely distributed resources.

Acknowledgments We thank the Tanzania Wildlife Research Institute (TAWIRI) and the Tanzania Commission for Science and Technology (COSTECH) for permission to conduct the fieldwork for this study. We are very grateful to Mimi Arandjelovic for her extensive support and assistance throughout these analyses and the writing of this manuscript. D. L. Moore thanks James Moore, Fiona Stewart, and Alex Piel for introducing her to the Ugalla site, and is especially grateful to Carolyn Ehardt for introducing her to Tanzania, and for her support and advice throughout the conception and execution of this project. We also thank the editor and anonymous reviewers for valuable suggestions, which improved the manuscript. This research was supported through funding by The Margot Marsh Biodiversity Foundation, The Leakey Foundation, the Wenner-Gren Foundation, the Lambda Alpha Anthropology Honor Society, the Max Planck Institute for Evolutionary Anthropology, and the Department of Anthropology at the University of Texas at San Antonio.

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