



## How old are chimpanzee communities? Time to the most recent common ancestor of the Y-chromosome in highly patrilineal societies



Kevin E. Langergraber<sup>a,b,\*</sup>, Carolyn Rowney<sup>b</sup>, Grit Schubert<sup>b,c</sup>, Cathy Crockford<sup>b</sup>, Catherine Hobaiter<sup>d</sup>, Roman Wittig<sup>b</sup>, Richard W. Wrangham<sup>e</sup>, Klaus Zuberbühler<sup>d,f</sup>, Linda Vigilant<sup>b</sup>

<sup>a</sup> Boston University, Department of Anthropology, 232 Bay State Road, Boston, MA 02215, USA

<sup>b</sup> Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, Leipzig 04103, Germany

<sup>c</sup> Robert Koch Institute, Epidemiology of Highly Pathogenic Organisms, Nordufer 20, Berlin 13353, Germany

<sup>d</sup> University of St. Andrews, School of Psychology and Neuroscience, Westburn Lane, St Andrews, Fife KY16 9JP, UK

<sup>e</sup> Harvard University, Department of Human Evolutionary Biology, 11 Divinity Avenue, Cambridge, MA 02138, USA

<sup>f</sup> University of Neuchâtel, Cognitive Science Center, Rue Emile-Argand 11, Neuchâtel 2000, Switzerland

### ARTICLE INFO

#### Article history:

Received 6 September 2013

Accepted 30 December 2013

Available online 25 February 2014

#### Keywords:

*Pan troglodytes*

Haplotype

Philopatry

Ancestry

Mutation rate

Paternity

Community formation

Dating

Culture

### ABSTRACT

Many human societies are patrilineal, with males passing on their name or descent group affiliation to their offspring. Y-chromosomes are also passed on from father to son, leading to the simple expectation that males sharing the same surname or descent group membership should have similar Y-chromosome haplotypes. Although several studies in patrilineal human societies have examined the correspondence between Y-chromosome variation and surname or descent group membership, similar studies in non-human animals are lacking. Chimpanzees represent an excellent species for examining the relationship between descent group membership and Y-chromosome variation because they live in strongly male philopatric communities that arise by a group-fissioning process. Here we take advantage of recent analytical advances in the calculation of the time to the most recent common male ancestor and a large sample size of 273 Y-chromosome short tandem repeat haplotypes to inform our understanding of the potential ages of eight communities of chimpanzees. We find that the times to the most recent common male ancestor of chimpanzee communities are several hundred to as much as over two thousand years. These genetic estimates of the great time depths of chimpanzee communities accord well with behavioral observations suggesting that community fissions are a very rare event and are similar to genetic estimates of the time depth of patrilineal human groups.

© 2014 Elsevier Ltd. All rights reserved.

### Introduction

Many human societies have cultural markers of shared ancestry. For example, in many modern societies individuals have surnames that they inherit from one of their parents, typically the father. Shared ancestry is an even more important organizing principle in many traditional societies, where the population is divided into tribes, tribes are divided into clans, and clans are divided into

lineages. At each level of the hierarchy, these descent groups claim to have a distinctive common ancestor. As with surnames in many modern societies, patrilineal societies in which a father transmits his descent group affiliation to his offspring are roughly twice as frequent as matrilineal societies (Burton et al., 1996).

Like surnames or descent group membership, Y-chromosomes are also passed on from father to son, leading to the simple expectation that males sharing the same surname or descent group membership should have similar Y-chromosome haplotypes, inherited from a shared paternal ancestor – perhaps the surname's or descent group's original founder (Jobling, 2001). The extent to which descent group membership is reflected in Y-chromosome identity or similarity depends on a number of factors (Jobling, 2001). Y-chromosomes are modified by mutation over time, and knowledge of the mutation rate is therefore important in assessing

\* Corresponding author.

E-mail addresses: [langergr@bu.edu](mailto:langergr@bu.edu), [klangerg@yahoo.com](mailto:klangerg@yahoo.com) (K.E. Langergraber), [rowney@eva.mpg.de](mailto:rowney@eva.mpg.de) (C. Rowney), [schubert@rki.de](mailto:schubert@rki.de) (G. Schubert), [crockford@eva.mpg.de](mailto:crockford@eva.mpg.de) (C. Crockford), [clh42@st-andrews.ac.uk](mailto:clh42@st-andrews.ac.uk) (C. Hobaiter), [wittig@eva.mpg.de](mailto:wittig@eva.mpg.de) (R. Wittig), [wrangham@fas.harvard.edu](mailto:wrangham@fas.harvard.edu) (R.W. Wrangham), [klaus.zuberbuehler@unine.ch](mailto:klaus.zuberbuehler@unine.ch) (K. Zuberbühler), [vigilant@eva.mpg.de](mailto:vigilant@eva.mpg.de) (L. Vigilant).

links between biological and cultural patrilineal descent and estimating the age of Y-chromosome lineages. Paternity by males from outside of the patrilineal descent group, or adoption of males from outside the descent group, will introduce exogenous Y-chromosome haplotypes into a descent group, which can create difficulties when relating the time to the most recent common ancestor (TMRCA) of a set of Y-chromosomes to the time when the descent group was founded.

Over the last two decades, several studies have compared Y-chromosomal variation and patrilineal descent group membership in a variety of human societies (Hammer et al., 1997; Thomas et al., 1998, 2003; Behar et al., 2003; Hammer et al., 2009; Strassmann et al., 2012; Raaum et al., 2013; Sanchez-Faddeev et al., 2013). For example, Chaix et al. (2004) examined Y-chromosome short tandem repeat (Y-STR) variation in several highly traditional Turkish groups that are hierarchically organized into patrilineal descent groups. They found that although members of the same lineage and (less often) members of the same clan generally shared a recent common male ancestor, members of the same tribe did not. These results suggest that tribes do not come about via a process of clans fissioning upon becoming too large, as is claimed by oral tradition, but rather by the fusion of clans that have different origins and the subsequent invention of a common ancestor, perhaps in an effort to enhance group unity (Chaix et al., 2004). However, Y-STR TMRCA calculations suggested that on average the last common male ancestor of the lineage existed  $\approx 15$  generations ( $\approx 450$  years) ago, a value that was in fairly good agreement with those from oral traditions. A study of Y-STR TMRCA of patrilineal descent groups also found a fairly close agreement with traditional knowledge of the timing of the settlements of six villages of Gujarati Patels in India, ranging from  $\approx 1000$  to 1700 years ago (Pemberton et al., 2012). Similarly, Y-STR TMRCA for men sharing the same surname in Britain and Ireland are broadly consistent with the timing of surname establishment in these countries ( $\approx 700$  years ago) (Sykes and Irven, 2000; Jobling, 2001; McEvoy and Bradley, 2006; King and Jobling, 2009a, b).

In contrast to humans, very little research has been done on the relationship between descent groups and Y-chromosome variation in non-human animals. Chimpanzees represent an excellent species for examining the relationship between social organization and Y-chromosome variation because they live in strongly male philopatric communities, with males spending their entire lives in their natal territory, and females typically dispersing to join another community at puberty, where they remain and reproduce for the rest of their lives (Mitani et al., 2002). Male chimpanzees are highly territorial, and along with humans are one of the few species in which members of one group engage in lethal levels of coalitional violence against members of other groups (Wilson and Wrangham, 2003). Chimpanzees are also well-known for their extensive between-community variability in tool usage, grooming and communicative behaviors, with each community showing a unique combination of these variations (Whiten et al., 1999, 2001; Langergraber et al., 2011). Given the social learning skills shown by chimpanzees in controlled experimental studies in captivity, as well as the distribution of these variants in relation to ecological and genetic differences between communities, at least some of the behavioral differences between chimpanzee communities are likely 'cultural' in nature (Whiten et al., 2005, 2007; Whiten and Mesoudi, 2008; Langergraber et al., 2011; Kamilar and Marshack, 2012). According to one author, the cultures of chimpanzee communities may even involve "a sense of identity, as our way of doing things differentiates us from the way others do things, i.e., 'us' and 'them'" (McGrew, 2004: 25). Thus, although they are probably not consciously aware of this fact themselves, the male chimpanzees living in a community share a common culture whose membership is determined by descent from a common male ancestor.

The process by which new chimpanzee communities are formed is poorly understood. Given the extremely high levels of aggression shown between members of different communities, it is highly unlikely that new chimpanzee communities form by the fusion of two previously existing chimpanzee communities, as apparently often occurs in patrilineal human societies when clans join to form tribes (Chaix et al., 2004). Rather, new chimpanzee communities probably come into existence when one community fissions into two communities. There has been only one apparent case of large-scale community fissioning in chimpanzees, when the single community of 15 males at Gombe purportedly fissioned into two communities of seven and eight males each (Goodall, 1986). However, other researchers argue that no community fission occurred, and that there always were two separate communities that were brought into unusually close contact by researchers who observed them at a banana provisioning station that happened to be located at the overlap zone between the two communities (Teleki et al., 1976). Community fissions may plausibly occur on a much smaller scale: there have been several reports of alpha males leaving their natal community after they are overturned (Nishida, 1983; Kawanaka, 1984; Goodall, 1986; Pruett, Personal communication), but so far none have been known to successfully attract females to start a viable reproductive community.

In both the multi-male and one-male fissioning scenarios, new chimpanzee communities are formed by a relatively small number of paternally related male founders. This has important implications for our understanding of the relationship between (1) the TMRCA of a set of extant chimpanzee Y-chromosome haplotypes in a community, and (2) the timing of when the community was originally founded. Although the former always occurs before (i.e., further back in time than) the latter, the distance between the timing of these two events decreases as the strength of the founder effect or bottleneck associated with the formation of the new community increases. Thus, the TMRCA of the Y-chromosome haplotypes of a chimpanzee community can give a reasonable estimate of the maximum possible ages of chimpanzee communities.

Here we calculate Y-STR TMRCA for eight communities of the East African subspecies of chimpanzees, *Pan troglodytes schweinfurthii*. We do not calculate Y-STR TMRCA for communities of the West African subspecies of chimpanzees, *Pan troglodytes verus*, as previous research suggests they do not practice strict male philopatry, and their Y-chromosome TMRCA would hence be potentially much older than the actual timing of community formation. Among West African chimpanzees in the Taï National Park, Ivory Coast, parentage analyses indicate a significant rate of extra-community paternities (Vigilant et al., 2001; Boesch et al., 2006), and there have been well-documented observations of dependent male offspring accompanying their mothers when they transferred between habituated study communities as adults (Boesch et al., 2008). In contrast, no extra-community paternities have ever been detected in chimpanzees from the East African subspecies (Constable et al., 2001; Inoue et al., 2008; Wroblewski et al., 2009; Newton-Fisher et al., 2010; Langergraber et al., 2013). Although as in the West African subspecies, East African females have been observed to transfer between communities with weaned male offspring, whether these males would have survived long enough to successfully reproduce is unclear (Williams et al., 2002, 2004). In the best documented case, two young males accompanied their mothers as they transferred from the K-group to the M-group following the death of most of the adult males in K-group and the dissolution of that community (Nishida et al., 1985). However, one of these juvenile males disappeared within a few years, while the other survived to adulthood but probably would have been killed by M-group males if not for protective interventions by human researchers (Nishida and Hiraiwa-Hasegawa, 1985; Nishida et al.,

1985). Thompson et al. (2006) recently reported a purported case of large-scale transfer of adult females accompanied by dependent offspring into the Sonso community of chimpanzees in the Budongo Forest Reserve, Uganda. However, subsequent paternity and Y-chromosome analyses of the sons of these putative immigrant females showed that they were sired by Sonso males, and thus that these newly identified adult females were actually peripheral long-term residents of the Sonso community who had only just become sufficiently habituated for researchers to identify (Langergraber et al., in press). The absence of evidence for male gene flow between eastern chimpanzee communities, and hence the introduction of extraneous Y-chromosomes, is consistent with the much higher levels of lethal aggression towards members of other communities compared with the western subspecies (Wrangham and Glowacki, 2012). Finally, the absence or extreme rarity of between community male gene flow in eastern chimpanzees is supported by studies of Y-chromosome variation, which show that levels of between-community differentiation ( $F_{ST}$ ) for the Y-chromosome in East African chimpanzees (0.83) are 60% higher than West African (0.52) chimpanzees (Schubert et al., 2011), and 46% higher than the highest value reported for any patrilineal human society (0.57; Langergraber et al., 2007). Given the strong evidence for extra-patriline paternities, adoptions, and migrations in humans, researchers studying humans are forced to somewhat arbitrarily divide their sample of Y-chromosomes into ‘descent clusters’ of closely related haplotypes that share recent common ancestry and ‘exogenous’ haplotypes that are assumed to have been introduced from outside the community (Chaix et al., 2004; King and Jobling, 2009a; Raaum et al., 2013). However, given the lack of evidence for male between-community gene flow in eastern chimpanzees, we used all of the extant Y-chromosome haplotypes in a community to calculate TMRCA.

## Materials and methods

### Study communities and laboratory procedures

We genotyped 273 chimpanzees at 13 Y-STR loci, following procedures described in previous publications (Langergraber et al., 2007; Schubert et al., 2011). Briefly, we noninvasively collected chimpanzee fecal samples using the two-step ethanol-silica method, and extracted DNA using the QIAamp DNA stool kit with slight modifications of the manufacturer’s (QIAGEN) protocol (Nsubuga et al., 2004). We used a two-step amplification method, where we initially combined all primer pairs with template DNA in a multiplex PCR, then used dilutions of the resultant PCR products for amplification of each individual locus using fluorescently labeled forward primers and nested reverse primers in singleplex PCR reactions (Arandjelovic et al., 2009). We sampled chimpanzees from five different areas, four of which contained the East African subspecies (Budongo forest area, Uganda,  $N = 72$ ; Gishwati Forest Reserve, Uganda,  $N = 12$ ; Kibale National Park, Uganda,  $N = 92$ ; Semliki Wildlife Reserve, Uganda,  $N = 6$ ), and one of which contained the West African subspecies (Tai National Park, Ivory Coast,  $N = 91$ ). While we used the Y-STR haplotypes of all 273 individuals for our estimates of quality ( $q$ ) and the relationship between average squared distance (ASD) and mutation rate (see below), we only estimated Y-STR TMRCA for East African communities where we could unambiguously ascertain community membership from long-term observations of habituated or semi-habituated individually identified animals. This included four communities in the Budongo Forest Reserve (Busingiro,  $N = 16$ ; Kaniyo-Pabidi,  $N = 16$ ; Sonso,  $N = 18$ ; Waibira,  $N = 18$ ), one community in a remnant forest patch located about 5 km to the south of the Budongo Forest Reserve (Kasokwa,  $N = 4$ ), and three communities in Kibale



**Figure 1.** Map of locations of eight communities of East African chimpanzees.

National Park (Kanyantale,  $N = 25$ ; Kanyawara,  $N = 12$ ; Ngogo,  $N = 55$ ). The locations of these communities are shown in Fig. 1.

### Estimating Y-STR TMRCA

We calculated the TMRCA of community Y-STR haplotypes in generations ( $\bar{T}$ ) using the ASD method, which considers the ratio of the observed within-locus allele variance averaged across all sampled loci ( $\sigma_{ASD}$ ) divided by the mean of the locus-specific generational mutation rates ( $\bar{\mu}$ ), which represent the probability that a son has a different allele than his father:  $\bar{T} = \sigma_{ASD}/\bar{\mu}$  (Goldstein et al., 1995). The ancestral Y-STR haplotype of the MRCA was inferred separately for each community by calculating the median allele value for each locus (Sengupta et al., 2006; Bird, 2012). The central estimate for  $\bar{T}$  and its Monte Carlo simulation-derived confidence intervals were calculated in the Matlab program ‘YTime’ (Behar et al., 2003). Although the central estimate of  $\bar{T}$  is independent of the population’s genealogy, size or growth rate, the sizes of the confidence intervals of  $\bar{T}$  are influenced by these factors. As the growth history of the chimpanzee communities studied here was unknown, we assumed a no-growth, constant size scenario, which produces the most conservative (i.e., widest) confidence intervals. Because of the fact that Y-STR TMRCA always predates the timing of the founding of the community, Y-STR TMRCA are not informative as to the minimum age of a chimpanzee community, but rather only the maximum possible age of a community (Barbujani et al., 1998). Lower confidence limits are thus not informative in the context of the current study, and we therefore report only one-sided 95% upper confidence limits. The  $\bar{T}$  in generations was converted to  $\bar{T}$  in years by multiplying by 24, the average generation length in years for wild male chimpanzees (Langergraber et al., 2012).

As an exploratory analysis of the sources of variation among community Y-STR TMRCA, we compared the number of genotyped males per community with Y-STR TMRCA. Previous research on chimpanzees and other primates living in multi-male, multi-female groups has shown that the extent of male reproductive skew decreases as the number of males in the group increases (Alberts et al., 2003; Boesch et al., 2006; Kutsukake and Nunn, 2006;

Langergraber et al., 2013). Lower male reproductive skew means that the effective population size for the Y-chromosome is larger, with less chance of losing lineages due to drift.

The ASD method of estimating TMRCA assumes the Strict Stepwise Mutation Model (SSMM) of STR evolution, where alleles increase or decrease by one repeat size according to the locus-specific mutation rate (Kimura and Ohta, 1978). However, several factors, including microsatellite death (i.e., the loss of mutational activity at an STR) can result in departure from the SSSM model and a poor linear fit between ASD and time (Calabrese et al., 2001). Following Bird (2012), we performed two analyses to ensure that our TMRCA estimates were based on Y-STR loci that strictly conformed to the SSMM. We used all 273 chimpanzee Y-chromosome haplotypes for these two analyses.

First, we calculated Bird's (2012) measure of quality ( $q$ ) for each of our 13 microsatellite loci:

$$q = \frac{|K - S|}{r^2}$$

where  $K$  is kurtosis,  $S$  is skewness, and  $r$  is range of allele sizes (i.e., highest minus lowest allele value). This equation is based on previous research showing that for any particular locus, (1) its maximum range is the most important constraint on linearity in the SSMM, (2) that excess kurtosis is associated with microsatellite death, and that (3) excess skewness is associated with substantial departure from the allele distribution expected under the SSMM (Calabrese et al., 2001; Busby et al., 2012). Using this equation, a locus with a  $q$  value of 0 conforms perfectly to the SSMM, and  $q$  values of 0.07 or lower are considered as showing good to excellent conformity to the SSMM (Bird, 2012). Second, we calculated a linear regression to predict ASD from  $\bar{u}$  for the Y-STRs, with locus-specific mutation rates ( $\bar{u}$ ) as the values for the independent variable and locus-specific ASD as the values for the dependent variable (Bird, 2012).

As a sufficiently large number of father-son meiosis are not available to provide reliable estimates of locus-specific Y-STR mutation rates ( $\bar{u}$ ) for chimpanzees, we instead used rates from large-scale studies in humans (Ballantyne et al., 2010). For one of the 13 Y-STRs (DYS562), no human mutation rate was available, so we used the average mutation rate of the other loci in our TMRCA calculations, and excluded this locus from the linear regression between  $\bar{u}$  and ASD described in the previous paragraph. Previous research has shown no evidence of a length difference between chimpanzees and human Y-STRs, suggesting that the mutation rate of Y-STRs does not differ between the two species (Kayser et al., 2006). To test this more directly, we examined the locus-specific mutation rates ( $\bar{u}$ ) by counting the number of mutations between 104 father-son pairs (identified through parentage analyses of 19 autosomal microsatellite loci) of chimpanzees living in the Ngogo, Kanyawara, Sonso, Tai North, Tai Middle, and Tai South communities.

## Results

The allelic compositions of the Y-STR haplotypes, and their frequencies in the eight East African chimpanzee communities, are shown in the Supplementary Online Material (SOM Table 1). Median joining networks of the Y-STR haplotypes for each community are shown in SOM Figure 1 (Budongo) and 2 (Kibale).

We found that one locus (DYS392) had a  $q$  value of 92.0217; this locus was therefore not used in TMRCA calculations. The  $q$  value for the remaining 12 loci ranged from 0.00044 to 0.05847 (mean = 0.01503, s.d. = 0.01822), well below the suggested cut-off value of 0.07 (SOM Table 2). We also found a moderately strong and statistically significant relationship between ASD and  $\bar{u}$  ( $t = 3.818$ ,

$df = 10$ ,  $p = 0.004$ ,  $R^2 = 0.618$ ; SOM Figure 3). Despite the small sample size, both in terms of number of father-son pairs in chimpanzees and the number of Y-STR loci compared, we also found a moderately strong and statistically significant relationship between chimpanzee and human mutation rates ( $t = 3.198$ ,  $df = 10$ ,  $p = 0.011$ ,  $R^2 = 0.532$ ). Together, these results suggest that the Y-STR TMRCA estimates provided in this study should be reasonably accurate.

The central point estimates of the Y-STR TMRCA for the eight *Pt. schweinfurthii* chimpanzee communities ranged from 125 to 2625 years, with a median of 553 years (Table 1). These values were quite similar to those of eight patrilineal human descent groups, all of which represent the lowest levels in sets of hierarchically organized descent groups (median = 516 years, range = 397–930 years). Both the Budongo Forest area and Kibale National Park had a mixture of communities with both comparatively recent and older TMRCA. Contrary to what one might expect if genetic drift acts more strongly in communities with a smaller effective population size, there was no relationship between the number of genotyped Y-STR haplotypes per community and Y-STR TMRCA ( $r_s = -0.17$ ,  $N = 8$ ,  $p = 0.885$ ).

The two directly neighboring communities in Kibale National Park had very similar TMRCA estimates (Ngogo: 445, Kanyantale: 481). These communities also shared one haplotype, which was the most common haplotype in both chimpanzee communities (Ngogo: 33/55 = 60.0%; Kanyantale: 15/24 = 62.5%). Together, these results suggest that these two neighboring communities may have split from one another within the last 500 years.

As expected, the upper 95% one-sided confidence limits of the Y-STR TMRCA, which represent the maximum possible ages of community origin, are large relative to the central point estimates (median = 1513 years, range = 733–5188 years).

## Discussion

Genetic, archaeological, paleontological, and linguistic data are often used to investigate both the broad evolutionary history of humans as a species and the more recent history of specific cultural groups. Only in the past decade have researchers attempted similar small-scale studies of the history of specific groups of non-human primates. To date, these historical studies have been limited to archaeological data, with a recent high-profile paper introducing 'primate archaeology' as a new field, which has as a main goal the study of material accumulated at sites with high tool-use activity in order to understand the time depth of a particular cultural behavior

**Table 1**

Central point estimates and upper 95% one-sided confidence limits for Y-STR TMRCA in chimpanzee communities and patrilineal human groups.

	Central point estimate	Upper 95% C.I.
Budongo Forest area		
Kasokwa	125	733
Waibira	462	1372
Busingiro	625	1626
Kanyiyjo-Pabidi	2059	4226
Sonso	2625	5188
Kibale National Park		
Ngogo	445	1345
Kanyantale	481	1399
Kanyawara	1740	3731
Turkish pastoralists (Chaix et al., 2004)		
OTU parilineage	397	1389
KZ parilineage	415	1451
TK parilineage	516	1806
Yeman tribal village (Raaum et al., 2013)		
Patrilineage P1	555	1080
Patrilineage P2	930	1870

(Haslam et al., 2009). For example, excavations of behaviorally modified stones with food residue at chimpanzee nut cracking sites were dated to 4300 years ago, before the appearance of human agriculture in the area, and therefore suggesting that chimpanzee nut-cracking culture was independently invented by the chimpanzees themselves rather than learned from humans (Mercader et al., 2002, 2007). In the current manuscript, we have shown that genetic studies also have the potential to shed light on the time depth of non-human primate groups and their cultures.

We found that Y-STR TMRCA of chimpanzee communities were several hundred to as much as over two thousand years old. As we noted in the Introduction, if exogenous Y-chromosomes of males born outside the community are introduced through emigration, this would lead to Y-chromosome TMRCA that overestimate the actual time of community formation. Although the available observational and genetic data indicate that male gene flow among East African chimpanzee communities is extremely rare, it is of course impossible to prove the complete absence of a phenomenon, especially one that is expected to be infrequent. Interestingly, the community in our study that had the oldest Y-chromosome TMRCA (2625 years), the Sonso community in Budongo Forest Reserve, Uganda, was conjectured in previous research to have experienced a large scale immigration event of several adult females and their offspring, some of whom were male (Emery Thompson et al., 2006). This inference of the transfer of adult females with offspring was largely based on new identifications of several individuals during a relatively narrow period of time, several years after the onset of long-term study and well after the last adult female had previously been identified. However, subsequent genetic research found Sonso fathers for most of the putative immigrant offspring, while those male offspring for whom not all Sonso candidate fathers could be genotyped nevertheless had Y-chromosome haplotypes that were common in Sonso males but absent in four other communities in the Budongo area (Langergraber et al., in press). These results suggest that the newly identified adult females were actually peripheral long-term residents of the Sonso community who had only just become sufficiently habituated for researchers to identify. Thus, the very old Y-chromosome TMRCA of the Sonso community cannot be explained by the recent introduction of exogenous Y-chromosomes, and instead may indicate an older male immigration event or perhaps even a very ancient date of community formation.

Our genetic estimates of the great time depths of chimpanzee communities accord well with behavioral observations suggesting that community fissions are a very rare event. Considering only the 13 chimpanzee communities that have been the subject of continuous scientific study of habituated and identified individuals, as of 2013 chimpanzees have been observed for a total of approximately 313 years where they were sufficiently well known to detect the presence or absence of a fission event. Only one community fission event has been observed during this time, and even this case is controversial (Table 2).

Communities of chimpanzees appear to exist as stable entities for much longer than do groups of female-philopatric primate species, where many permanent group fissions have been observed (e.g., Van Horn et al., 2007 and references therein). Empirical and theoretical work suggests that primate groups fission when group size increases to the point where the costs of group-living exceed its benefits (van Schaik, 1983). However, the factors that limit reproductive success differ between females (i.e., access to food) and males (i.e., access to mates), and may show different relationships with group size (Trivers, 1972). While it is clear that in many primate species females decrease their access to food as within-group feeding competition increases with group size (Majolo et al., 2008), male chimpanzees may actually increase their access to mates as community size increases (Boesch et al., 2006;

**Table 2**

Number of years of continuous scientific study of individually identified and habituated chimpanzees.

Community	Beginning	End (2013 is ongoing)	Duration
Tai National Park, East group	2009	2013	4
Gombe Stream National Park, Kahama community	1972	1977	5
Fongoli community, Senegal	2005	2013	8
Tai National Park, Middle group	2000	2013	13
Tai National Park, South group	1997	2013	16
Ngogo community, Kibale National Park	1995	2013	18
Sonso community, Budongo Forest Reserve	1990	2013	23
Kanyawara community, Kibale National Park	1987	2013	26
Tai National Park, North group	1982	2013	31
Mahale Mountains National Park, K group	1977	2013	36
Bossou community, Guinea	1976	2013	37
Mahale Mountains National Park, M group	1967	2013	46
Gombe Stream National Park, Kasekela community	1963	2013	50
Total			313

Langergraber et al., 2013). The positive relationship between paternity success and community size in male chimpanzees presumably occurs because communities with more males can acquire and defend larger territories, which in turn attract more females and allow them to reproduce more often (Nishida et al., 1985; Williams et al., 2004; Mitani et al., 2010). Even if male chimpanzees were to have higher access to mates in a smaller community, this benefit can be outweighed by the costs of high levels of between-group competition: after the main community at Gombe fissioned into two communities, the males of the larger community systematically killed all of the males of the smaller community (Goodall, 1986).

Whatever the reason for the great time depths of chimpanzee communities, their existence raises interesting questions about the mechanisms promoting stability in group differences in behavior. Among primates, there is more evidence of immigrants adopting the behavior of their new group than there is of long-term group members adopting the behaviors of immigrants (van de Waal et al., 2010; van de Waal et al., 2013). There is also some evidence to suggest that primate social learning may involve conformity: the tendency of individuals to adopt the behavioral variant that is performed by the majority of individuals (Dindo et al., 2009; Claidière and Whiten, 2012; van de Waal et al., 2013). If the cultures of chimpanzee communities are very resistant to the introduction of variants introduced by immigrants, this would suggest a great time depth to the cultures themselves, perhaps on the order of the timing of the founding of the community itself. Assuming that new cultural variants arise over time through innovation, we might expect a positive relationship between Y-STR TMRCA and the number of cultural behavioral variants that a chimpanzee community possesses. However, the three communities for which both types of data were available (Kanyawara, Ngogo and Sonso) showed a very similar number of cultural behaviors (range: 9–11) despite a wide range of Y-STR TMRCA estimates (445–2625 years) (Langergraber et al., 2011).

Ultimately, testing such hypotheses about the links between genetic and cultural co-evolution will require more accurate and precise TMRCA estimates. Here we have attempted to account for the inherent uncertainty involved in the estimation process by evaluating the conformity of our Y-STR loci to the SSSM process. Further improvements in reducing the amount of uncertainty surrounding TMRCA estimates could be made by genotyping a larger number of well-behaved Y-STR loci (Bird, 2012) and perhaps eventually through large-scale sequencing when this becomes a routine possibility on non-invasively collected samples (Perry et al., 2010).

## Acknowledgments

Thanks to C. Tennie and especially S. C. Bird for useful discussions and advice; the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and Makerere University Biological Field Station for permission and logistical support of research in Uganda; J. Lloyd for providing Kanyantale samples; E. Otali and M. Muller for Kanyawara samples; J.C. Mitani, D. Watts, J. Lwanga, J. Fenton, A. Magoba, G. Mbabazi, L. Ndagizi, and A. Tumusiime for Ngogo samples and other research assistance; V. Reynolds for Sonso samples; and Z. Zommers for Busingiro, Kaniyo-Pabidi, Kasokwa and Sonso samples. This study was funded by Boston University, the Max Planck Society, the Alexander von Humboldt Foundation, the US National Science Foundation (BCS-0215622 and IOB-0516644), the Leakey Foundation, and the Detroit Zoological Institute.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2013.12.005>

## References

- Alberts, S.C., Watts, H.E., Altmann, J., 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim. Behav.* 65, 821–840.
- Arandjelovic, M., Guschanski, K., Schubert, G., Harris, T.R., Thalman, O., Siedel, H., Vigilant, L., 2009. Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. *Mol. Ecol. Resources* 9, 28–36.
- Ballantyne, K.N., Goedbloed, M., Fang, R., Schaap, O., Lao, O., Wollstein, A., Choi, Y., van Duijn, K., Vermeulen, M., Brauer, S., 2010. Mutability of Y-chromosomal microsatellites: rates, characteristics, molecular bases, and forensic implications. *Am. J. Hum. Genet.* 87, 341–353.
- Barbujani, G., Bertorelle, G., Chikhi, L., 1998. Evidence for Paleolithic and Neolithic gene flow in Europe. *Am. J. Hum. Genet.* 62, 488.
- Behar, D.M., Thomas, M.G., Skorecki, K., Hammer, M.F., Bulygina, E., Rosengarten, D., Jones, A.L., Held, K., Moses, V., Goldstein, D., 2003. Multiple origins of Ashkenazi Levites: Y chromosome evidence for both Near Eastern and European ancestries. *Am. J. Hum. Genet.* 73, 768–779.
- Bird, S.C., 2012. Towards improvements in the estimation of the coalescent: implications for the most effective use of Y chromosome short tandem repeat mutation rates. *PLoS One* 7, e48638.
- Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., Normand, E., 2008. Intergroup conflicts among chimpanzees in Tai National Park: lethal violence and the female perspective. *Am. J. Primatol.* 70, 519–532.
- Boesch, C., Kohou, G., Nene, H., Vigilant, L., 2006. Male competition and paternity in wild chimpanzees of the Tai forest. *Am. J. Phys. Anthropol.* 130, 103–115.
- Burton, M.L., Moore, C.C., Whiting, J.W.M., Kimball Romney, A., 1996. Regions based on social structure. *Curr. Anthropol.* 37, 87–123.
- Busby, G.B., Brisighelli, F., Sánchez-Diz, P., Ramos-Luis, E., Martínez-Cadenas, C., Thomas, M.G., Bradley, D.G., Gusmão, L., Winney, B., Bodmer, W., 2012. The peopling of Europe and the cautionary tale of Y chromosome lineage R-M269. *P. Roy. Soc. Lond. B. Bio.* 279, 884–892.
- Calabrese, P.P., Durrett, R.T., Aquadro, C.F., 2001. Dynamics of microsatellite divergence under stepwise mutation and proportional slippage/point mutation models. *Genetics* 159, 839–852.
- Chaix, R., Austerlitz, F., Khegay, T., Jacquesson, S., Hammer, M.F., Heyer, E., Quintana-Murci, L., 2004. The genetic or mythical ancestry of descent groups: lessons from the Y chromosome. *Am. J. Hum. Genet.* 75, 1113–1116.
- Claidière, N., Whiten, A., 2012. Integrating the study of conformity and culture in humans and nonhuman animals. *Psychol. Bull.* 138, 126.
- Constable, J.L., Ashley, M.V., Goodall, J., Pusey, A.E., 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Mol. Ecol.* 10, 1279–1300.
- Dindo, M., Whiten, A., de Waal, F.B., 2009. In-group conformity sustains different foraging traditions in capuchin monkeys (*Cebus apella*). *PLoS One* 4, e7858.
- Goldstein, D.B., Ruiz Linares, A., Cavalli-Sforza, L.L., Feldman, M.W., 1995. Genetic absolute dating based on microsatellites and the origin of modern humans. *Proc. Natl. Acad. Sci.* 92, 6723–6727.
- Goodall, J., 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Harvard University Press, Cambridge.
- Hammer, M.F., Behar, D.M., Karafet, T.M., Mendez, F.L., Hallmark, B., Erez, T., Zhivotovskiy, L.A., Rosset, S., Skorecki, K., 2009. Extended Y chromosome haplotypes resolve multiple and unique lineages of the Jewish priesthood. *Hum. Genet.* 126, 707–717.
- Hammer, M.F., Skorecki, K., Selig, S., Blazer, S., Rappaport, B., Bradman, R., Bradman, N., Waburton, P.J., Ismajlowicz, M., 1997. Y chromosomes of Jewish priests. *Nature* 385, 32–35.
- Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de La Torre, I., DeStefano, A., Du, A., Hardy, B., Harris, J., Marchant, L., 2009. Primate archaeology. *Nature* 460, 339–344.
- Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O., Nishida, T., 2008. Relatedness in wild chimpanzees: influence of paternity, male philopatry, and demographic factors. *Am. J. Phys. Anthropol.* 137, 256–262.
- Jobling, M.A., 2001. In the name of the father: surnames and genetics. *Trends Genet.* 17, 353–357.
- Kamilar, J.M., Marshack, J.L., 2012. Does geography or ecology best explain 'cultural' variation among chimpanzee communities? *J. Hum. Evol.* 62, 256–260.
- Kawanaka, K., 1984. Association, ranging, and the social unit in chimpanzees of the Mahale Mountains, Tanzania. *Int. J. Primatol.* 5, 411–434.
- Kayser, M., Vowles, E.J., Kappe, D., Amos, W., 2006. Microsatellite length differences between humans and chimpanzees at autosomal loci are not found at equivalent haploid Y chromosomal loci. *Genetics* 173, 2179–2186.
- Kimura, M., Ohta, T., 1978. Stepwise mutation model and distribution of allelic frequencies in a finite population. *Proc. Natl. Acad. Sci.* 75, 2868–2872.
- King, T.E., Jobling, M.A., 2009a. Founders, drift, and infidelity: the relationship between Y chromosome diversity and patrilineal surnames. *Mol. Biol. Evol.* 26, 1093–1102.
- King, T.E., Jobling, M.A., 2009b. What's in a name? Y chromosomes, surnames and the genetic genealogy revolution. *Trends Genet.* 25, 351–360.
- Kutsukake, N., Nunn, C.L., 2006. Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. *Behav. Ecol. Sociobiol.* 60, 695–706.
- Langergraber, K.E., Siedel, H., Mitani, J.C., Wrangham, R.W., Reynolds, V., Hunt, K.D., Vigilant, L., 2007. The genetic signature of sex-biased migration in patrilineal chimpanzees and humans. *PLoS One* 10, e973.
- Langergraber, K.E., Boesch, C., Inoue, E., Inoue-Murayama, M., Mitani, J.C., Nishida, T., Pusey, A., Reynolds, V., Schubert, G., Wrangham, R.W., Wroblewski, E., Vigilant, L., 2011. Genetic and 'cultural' similarity in wild chimpanzees. *P. Roy. Soc. Lond. B. Bio.* 278, 408–416.
- Langergraber, K.E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., Inoue-Murayama, M., Mitani, J.C., Muller, M.N., Robbins, M.M., Schubert, G., Stoinski, T.S., Viola, B., Watts, D., Wittig, R.M., Wrangham, R.W., Zuberbühler, K., Pääbo, S., Vigilant, L., 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proc. Natl. Acad. Sci.* 109, 15716–15721.
- Langergraber, K.E., Mitani, J.C., Watts, D.P., Vigilant, L., 2013. Male–female socio-spatial relationships and reproduction in wild chimpanzees. *Behav. Ecol. Sociobiol.* 67, 861–873.
- Langergraber, K.E., Rowney, C., Crockford, C., Wittig, R., Zuberbühler, K., Vigilant, L., 2014. Genetic analyses suggest no immigration of adult females and their offspring into the Sonso community of chimpanzees in the Budongo Forest Reserve, Uganda. *Am. J. Primatol.* (In press).
- Majolo, B., de Bortoli Vizioli, A., Schino, G., 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. *Anim. Behav.* 76, 1235–1247.
- McEvoy, B., Bradley, D.G., 2006. Y-chromosomes and the extent of patrilineal ancestry in Irish surnames. *Hum. Genet.* 119, 212–219.
- McGrew, W.C., 2004. *The Cultured Chimpanzee: Reflections on Cultural Primatology*. Cambridge University Press, Cambridge.
- Mercader, J., Panger, M., Boesch, C., 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296, 1452–1455.
- Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. *Proc. Natl. Acad. Sci.* 104, 3043–3048.
- Mitani, J.C., Watts, D.P., Muller, M.N., 2002. Recent developments in the study of wild chimpanzee behavior. *Evol. Anthropol.* 11, 9–25.
- Mitani, J.C., Watts, D.P., Amsler, S.J., 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Curr. Biol.* 20, R507–R508.
- Newton-Fisher, N.E., Thompson, M.E., Reynolds, V., Boesch, C., Vigilant, L., 2010. Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *Am. J. Phys. Anthropol.* 142, 417–428.
- Nishida, T., 1983. Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates* 24, 318–336.
- Nishida, T., Hiraiwa-Hasegawa, M., 1985. Responses to a stranger mother-son pair in the wild chimpanzee: a case report. *Primates* 26, 1–13.
- Nishida, T., Hiraiwa-Hasegawa, M., Hasegawa, K., Y., T., 1985. Group extinction and female transfer in wild chimpanzees in the Mahale Mountains National Park, Tanzania. *Z. Tierpsychol.* 67, 281–301.
- Nsubuga, A.M., Robbins, M.M., Roeder, A.D., Morin, P.A., Boesch, C., Vigilant, L., 2004. Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. *Mol. Ecol.* 13, 2089–2094.
- Pemberton, T.J., Li, F.Y., Hanson, E.K., Mehta, N.U., Choi, S., Ballantyne, J., Belmont, J.W., Rosenberg, N.A., Tyler-Smith, C., Patel, P.I., 2012. Impact of restricted marital practices on genetic variation in an endogamous Gujarati group. *Am. J. Phys. Anthropol.* 149, 92–103.
- Perry, G.H., Marioni, J.C., Melsted, P., Gilad, Y., 2010. Genomic-scale capture and sequencing of endogenous DNA from feces. *Mol. Ecol.* 19, 5332–5344.
- Raaum, R.L., Al-Meerri, A., Mulligan, C.J., 2013. Culture modifies expectations of kinship and sex-biased dispersal patterns: A case study of patrilineality and patrilocal inheritance in tribal Yemen. *Am. J. Phys. Anthropol.*

- Sanchez-Faddeev, H., Pijpe, J., van Bodegom, D., van der Hulle, T., van der Gaag, K.J., Eriksson, U.K., Spear, T., Westendorp, R.G.J., de Knijff, P., 2013. Ancestral stories of Ghanaian Bimoba reflect millennia-old genetic lineages. *PLoS One* 8, e65690.
- Schubert, G., Stoneking, C.J., Arandjelovic, M., Boesch, C., Eckhardt, N., Hohmann, G., Langergraber, K., Lukas, D., Vigilant, L., 2011. Male-mediated gene flow in patrilocal primates. *PLoS One* 6, e21514.
- Sengupta, S., Zhitovskiy, L.A., King, R., Mehdi, S., Edmonds, C.A., Chow, C.-E.T., Lin, A.A., Mitra, M., Sil, S.K., Ramesh, A., 2006. Polarity and temporality of high-resolution Y-chromosome distributions in India identify both indigenous and exogenous expansions and reveal minor genetic influence of Central Asian pastoralists. *Am. J. Hum. Genet.* 78, 202–221.
- Strassmann, B.I., Kurapati, N.T., Hug, B.F., Burke, E.E., Gillespie, B.W., Karafet, T.M., Hammer, M.F., 2012. Religion as a means to assure paternity. *Proc. Natl. Acad. Sci.* 109, 9781–9785.
- Sykes, B., Irven, C., 2000. Surnames and the Y chromosome. *Am. J. Hum. Genet.* 66, 1417–1419.
- Teleki, G., Hunt, E., Pflifferling, J., 1976. Demographic observations (1963–1973) on the chimpanzees of Gombe National Park, Tanzania. *J. Hum. Evol.* 5, 559–598.
- Thomas, M.G., Parfitt, T., Weiss, D.A., Skorecki, K., Wilson, J.F., le Roux, M., Bradman, N., Goldstein, D.B., 2003. Y chromosomes traveling south: the Cohen modal haplotype and the origins of the Lemba—the “Black Jews of Southern Africa”. *Am. J. Hum. Genet.* 66, 674–686.
- Thomas, M.G., Skorecki, K., Ben-Amid, H., Parfitt, T., Bradman, N., Goldstein, D.B., 1998. Origins of old testament priests. *Nature* 394, 138–140.
- Thompson, M.E., Newton-Fisher, N., Reynolds, V., 2006. Probable community transfer of parous adult female chimpanzees in the Budongo Forest, Uganda. *Int. J. Primatol* 27, 1601–1617.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), *Sexual Selection and the Descent of Man*. Aldine Publishing Company, Chicago, pp. 136–207.
- van de Waal, E., Renevey, N., Favre, C.M., Bshary, R., 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *P. Roy. Soc. Lond. B. Bio* 277, 2105–2111.
- van de Waal, E., Borgeaud, C., Whiten, A., 2013. Potent social learning and conformity shape a wild primate's foraging decisions. *Science* 340, 483–485.
- Van Horn, R.C., Buchan, J.C., Altmann, J., Alberts, S.C., 2007. Divided destinies: group choice by female savannah baboons during social group fission. *Behav. Ecol. Sociobiol.* 61, 1823–1837.
- van Schaik, C.P., 1983. Why are diurnal primates living in groups? *Behav.* 87, 120–144.
- Vigilant, L., Hofreiter, M., Siedel, H., Boesch, C., 2001. Paternity and relatedness in wild chimpanzee communities. *Proc. Natl. Acad. Sci.* 98, 12890–12895.
- Whiten, A., Mesoudi, A., 2008. Establishing an experimental science of culture: animal social diffusion experiments. *Philos. Trans. R. Soc. B. Biol. Sci.* 363, 3477–3488.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. *Nature* 399, 682–685.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wrangham, R.W., Boesch, C., 2001. Charting cultural variation in chimpanzees. *Behaviour* 138, 1481–1516.
- Whiten, A., Horner, V., de Waal, F.B.M., 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature* 437, 737–740.
- Whiten, A., Spiteri, A., Horner, V., Bonnie, K.E., Lambeth, S.P., Schapiro, S.J., de Waal, F.B.M., 2007. Transmission of multiple traditions within and between chimpanzee groups. *Curr. Biol.* 17, 1038–1043.
- Williams, J.M., Pusey, A.E., Carlis, J.V., Farm, B.P., Goodall, J., 2002. Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. *Anim. Behav.* 63, 347–360.
- Williams, J.M., Oehlert, G., Pusey, A.E., 2004. Why do male chimpanzees defend a group range? *Anim. Behav.* 68, 523–532.
- Wilson, M., Wrangham, R.W., 2003. Intergroup relationships in chimpanzees. *Annual Review of Anthropology* 32, 363–392.
- Wrangham, R.W., Glowacki, L., 2012. Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. *Hum. Nat.* 23, 5–29.
- Wroblewski, E.E., Murray, C.M., Keele, B.F., Schumacher-Stankey, J.C., Hahn, B.H., Pusey, A.E., 2009. Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Anim. Behav.* 77, 873–885.