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

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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.

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

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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 ≈15 generations (≈450 years) ago, a value that was in fairly good agreement with those from oral traditions. A study of Y-STR TMRCAs of patrilines 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 ≈1000 to 1700 years ago (Pemberton et al., 2012). Similarly, Y-STR TMRCAs for men sharing the same surname in Britain and Ireland are broadly consistent with the timing of surname establishment in these countries (≈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 coalitionary 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 chimpanzees 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; Pruetz, 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 TMRCAS 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 TMRCAs 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.,