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Contrasting demographic histories of the neighboring bonobo and chimpanzee

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Received: 5 March 2013 / Accepted: 10 July 2013
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Abstract The Pleistocene epoch was a period of dramatic climate change that had profound impacts on the population sizes of many animal species. How these species were shaped by past events is often unclear, hindering our understanding of the population dynamics resulting in present day populations. We analyzed complete mitochondrial genomes representing all four recognized chimpanzee subspecies and the bonobo to infer the recent demographic history and used simulations to exclude a confounding effect of population structure. Our genus-wide Bayesian coalescent-based analysis revealed surprisingly dissimilar demographic histories of the chimpanzee subspecies and the bonobo, despite their overlapping habitat requirements. Whereas the central and eastern chimpanzee subspecies were inferred to have expanded tenfold between around 50,000 and 80,000 years ago and today, the population size of the neighboring bonobo remained constant. The changes in population size are likely linked to changes

in habitat area due to climate oscillations during the late Pleistocene. Furthermore, the timing of population expansion for the rainforest-adapted chimpanzee is concurrent with the expansion of the savanna-adapted human, which could suggest a common response to changed climate conditions around 50,000–80,000 years ago.

Keywords *Pan* · Mitochondrial genome · Bayesian inference · Demography · MCMC

Introduction

The endangered chimpanzee and the bonobo are currently facing serious reductions in population size due to the expansion of human activity. However, in order to place this decline into context, it is important to know more about their historical population dynamics, including how they were influenced by environmental factors. In tropical Africa, the Pleistocene was characterized by humid interglacial periods alternating with arid glacial periods, leading to the expansion and contraction of forest habitats, respectively (de Menocal 2004; Cohen et al. 2007; Scholz et al. 2007; Cowling et al. 2008; Blome et al. 2012). Such changes likely affected the habitat conditions, distribution patterns, and population sizes of many large mammals in tropical Africa (Storz et al. 2002; Heller et al. 2008; Okello et al. 2008; Thalmann et al. 2011; Heller et al. 2012; Ting et al. 2012). The human population expansion and the subsequent exodus of humans from Africa within the last 70,000 years (for a review, see Endicott et al. 2009; Atkinson et al. 2009; Soares et al. 2009) mean that climate conditions during this period must have been favorable for at least some savanna-dwelling mammals. In contrast to humans, the African great apes—the chimpanzee (*Pan*

Sequence data from this article have been deposited in the DDBJ/EMBL/GenBank libraries under accession nos. JN191183–JN191235.

Electronic supplementary material The online version of this article (doi:10.1007/s10329-013-0373-3) contains supplementary material, which is available to authorized users.

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troglodytes), bonobo (*Pan paniscus*), and gorilla (*Gorilla*)—are primarily rainforest-dwelling species. For the Western gorilla (*Gorilla gorilla*) it has been found that, after the split into subspecies, the Western lowland gorilla (*Gorilla gorilla gorilla*) underwent continuous expansion and the Cross River gorilla (*Gorilla gorilla diehli*) underwent a contrasting recent reduction in population size (Anthony et al. 2007). However, the demographic histories of our closest relatives, the chimpanzee and bonobo, in the late Pleistocene are less well known.

Both the chimpanzee and bonobo likely arose as species in central equatorial Africa (Eriksson et al. 2004), but whereas the bonobo is presently confined to this region, the chimpanzee inhabits a wider region of equatorial Africa (Fig. 1). Today, these species' ranges are separated by the Congo River. Sub-structure has been identified in the bonobo, likely caused by Pleistocene paleoenvironmental changes and to a lesser degree by tributaries acting as barriers (Kawamoto et al. 2013). While the bonobo species is not taxonomically subdivided, four

subspecies of the chimpanzee are recognized: the West African chimpanzee (*Pan troglodytes verus*), the Nigeria–Cameroonian chimpanzee (*Pan troglodytes ellioti*), the Central African chimpanzee (*Pan troglodytes troglodytes*), and the East African chimpanzee (*Pan troglodytes schweinfurthii*) (Hill 1969; Grubb et al. 2003; Oates et al. 2009). Current knowledge of the demographic history of *Pan* is derived from demographic models assuming monotonous exponential growth from the time of subspecies divergence to the present (Won and Hey 2005; Becquet and Przeworski 2007; Becquet et al. 2007; Caswell et al. 2008; Hey 2010; Wegmann and Excoffier 2010; Fischer et al. 2011). These have shown that the bonobo and the chimpanzee subspecies were subject to past changes in population size, with equivocal evidence for both size decreases and expansions. Due to the miscellaneous approaches and the inclusion or exclusion of some of the recognised subspecies in/from previous studies, no complete and consistent genus-wide overview exists regarding the recent demographic histories of all members of the genus *Pan*.

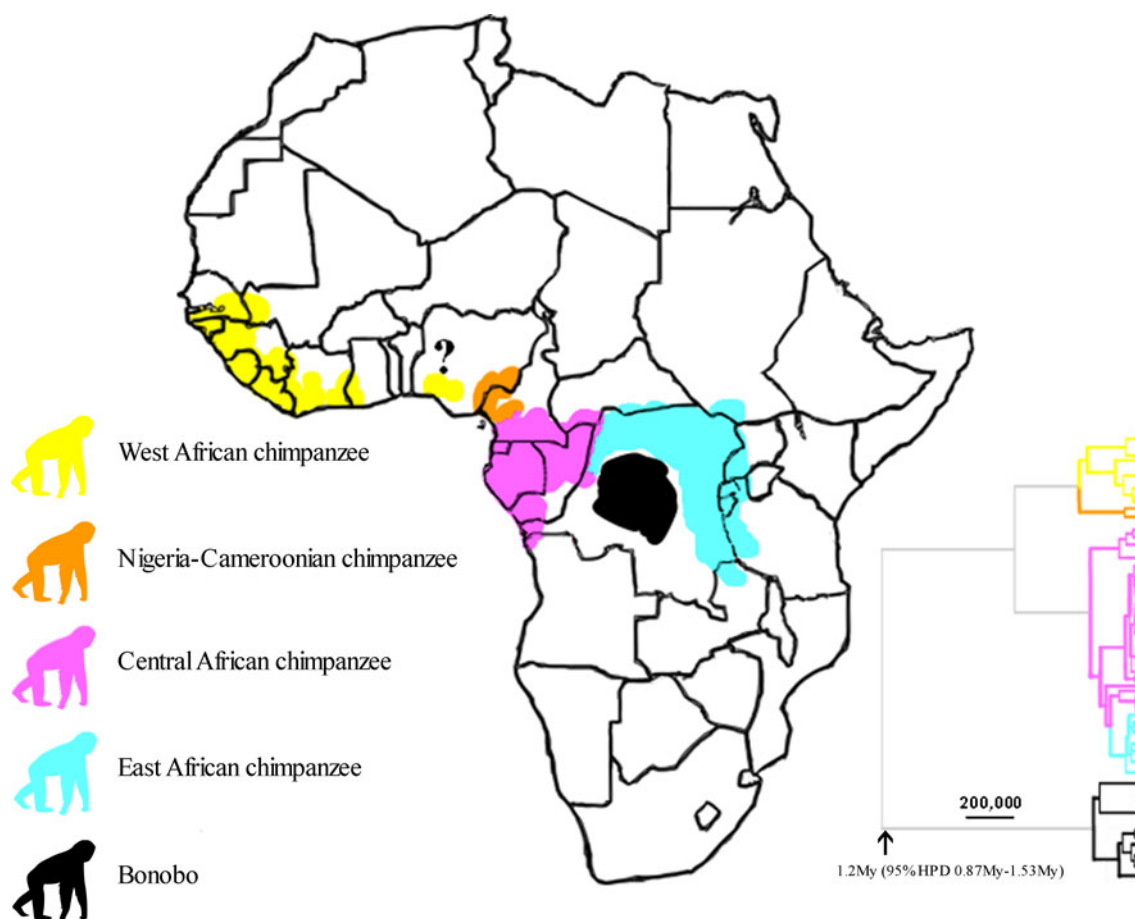


Fig. 1 Geographical distribution ranges throughout Africa and mitogenome phylogenetic relationship for the chimpanzee subspecies and the bonobo. The ranges of the subspecies and their phylogenetic positions are colour coded: *yellow* for the West African chimpanzee, *orange* for the Nigeria–Cameroonian chimpanzee, *pink* for the Central

African chimpanzee, *turquoise* for the East African chimpanzee, and *black* for the bonobo. On the map, the *question mark* indicates a dispute about whether the chimpanzees inhabiting the area west of the Niger River in Nigeria should be phylogenetically grouped with the West African chimpanzee or the Nigeria–Cameroonian chimpanzee

Mitochondrial DNA has been widely applied to infer demographic population history. Despite some limitations (notably the fact that mitochondrial DNA is maternally inherited and thus only captures the history of the maternal lineage, and the lack of recombination), mitochondrial genomes (mitogenomes) have played a vital role in understanding the recent demographic history of humans (Ingman et al. 2000; Atkinson et al. 2008, 2009; Endicott and Ho 2008; Endicott et al. 2009), including the genus *Pan* (Gagneux et al. 1999; Stone et al. 2010; Bjork et al. 2011; Zsurka et al. 2010). However, most demographic history inference methods make simplifying biological assumptions; in particular, they do not take population structure and migration into account. Recent studies have highlighted the potentially confounding effects of population structure and migration when inferring population size dynamics (Stadler et al. 2009; Chikhi et al. 2010; Peter et al. 2010). This can contribute to false signals of population size changes.

In contrast to previous studies, we present a demographic analysis of the recent demographic histories of all four chimpanzee subspecies and the bonobo, providing insight into what forces shaped present-day populations. Bayesian skyline plots (BSPs) allow inference of demographic history by exploring rather than conditioning on a specific parametric demographic model. We performed BSP analyses of 88 complete mitogenomes to understand the demographic history for each taxon, enabling us to infer more complex demographic dynamics in the recent past than achieved by previous studies (Won and Hey 2005; Becquet and Przeworski 2007; Becquet et al. 2007; Caswell et al. 2008; Hey 2010; Peter et al. 2010; Wegmann and Excoffier 2010; Fischer et al. 2011). Specifically, we wanted to assess whether the reported population size expansions (Wegmann and Excoffier 2010) were contemporary with those inferred by similar analyses of the gorilla and humans, and hence occurred more recently than previously assumed. This would allow us to evaluate which factors are likely to have influenced recent *Pan* dynamics, and whether such factors had a similar influence on all five species of African hominids. To test the robustness of our inferred population size dynamics, we included simulations of competing demographic structure scenarios to contrast the potential effects of structure and migration.

Methods

Samples

A total of 39 Central African, 17 West African, 13 East African, and 4 Nigeria–Cameroonian chimpanzees as well as 15 bonobo samples were included in this study (see

Online Resource 1 in the Electronic supplementary material, ESM). Of these, 53 were newly generated complete mitogenome sequences from wild-caught individuals, or first-generation individuals of wild-born parents with known geographical origins. If unknown, subspecies status was determined based on microsatellite (Hvilsom et al. 2013) and mitochondrial DNA D-loop data before inclusion in the present study. The additional 35 sequences were obtained from GenBank (see Online Resource 1 in the ESM) (Stone et al. 2010; Zsurka et al. 2010; Bjork et al. 2011). The origin of the bonobo samples from the study by Zsurka et al. (2010) was only known for a subset (eight) of the samples. The remaining samples were collected from various biobanks where no information on origin or relatedness was available. Hence, we proceeded with the eight samples, which—after excluding related samples based on studbook information—were reduced to a subset of four sequences from Zsurka et al. (2010); see Online Resource 1 in the ESM.

Laboratory methods

Genomic DNA was extracted directly from EDTA whole-blood samples using a DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA), following the manufacturer's instructions. All blood samples were taken during routine health checks, and Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) permits were obtained.

The mitogenome (≈ 16 kb) was amplified in two fragments, each ≈ 9 kb, by complementary PCRs, creating overlapping fragments. The 25- μ l PCR reactions were optimized to contain 50 ng DNA, a 0.4 μ M concentration of each primer; forward 5' CCCTATTAACCACTCACGG GAGC and reverse 5' CCAATTAGGTGCATGAGTAGG TGG (fragment 1) as well as forward 5' AT CTATTCGCTTCATTCGCTGCC and reverse 5' AC GCCGGTTTCTATTGACTTGGG (fragment 2); 200 μ M each of dATP, dCTP, dGTP and dTTP; 2.5 μ l 10 \times PCR buffer; 2.0 mM MgCl₂; and 1 U Platinum Taq High Fidelity Polymerase (Invitrogen, Carlsbad, CA, USA). Negative controls were included in each amplification set to check for contamination. Amplification included 94 °C for 2 min followed by 30 cycles of 94 °C for 30 s, 59 °C for 30 s, 68 °C for 10 min, respectively; these were followed by 72 °C for 7 min and a hold at 4 °C. The PCR products were purified with the QIAquick Purification Kit (Qiagen). Sequences were generated on the Solexa sequencing platform using the Illumina genome analyzer at Beijing Genomics Institute (Shenzen, China), to an average of 2,000 \times coverage. Paired end reads (100 bp long) were assembled into genomic sequences using Geneious 5.0.4 (Biomatters Ltd., Auckland, New Zealand) by mapping to either the chimpanzee or bonobo reference mitochondrial

sequences (NC_001643 and NC_001644 obtained from Genbank) using “high sensitivity” settings. As an additional test of these assemblies, we also mapped the paired end reads to subspecies-specific reference mitogenomes obtained from Genbank to evaluate the effect of mapping to subspecies instead of species-specific sequences. No discrepancies were found when comparing the sequences generated by these two assembly methods. The consensus sequences were finally inspected for obvious alignment errors, misreads, single-base indels, and chimera sequence artefacts. Sequence data from this article have been deposited in the DDBJ/EMBL/GenBank libraries under accession nos. JN191183–JN191235.

Data set

The chimpanzee and bonobo sequences were aligned with reference sequences (NC001643) and (NC001644), respectively. Multiple sequence alignments were performed using ClustalW2 (Larkin et al. 2007) in Geneious using the default settings. One full mitogenome alignment was created containing the four chimpanzee subspecies and bonobo sequences. As in previous studies, a subset containing a concatenated partitioned alignment (14,501 bp) of loop regions of the two ribosomal RNA (rRNA) genes (12S and 16S), 12 protein coding genes (CDS), and the D-loop was used for analysis, as this was found to be most suitable for mitogenome analyses, allowing for different evolutionary models for different functional regions (Endicott and Ho 2008). The remaining sections of the mitogenomes were discarded from the analyses, including the ND6 gene due to its atypical substitution pattern and nucleotide composition (Saccone et al. 1999).

Selection can affect demographic analyses. Hence we scanned for signs of selection along the mitogenome. After applying Bonferroni correction, no evidence of either positive or negative selection was found (see Online Resource 2 in the ESM), and we thus disregarded an impact of selection on the interpretation of the demographic results.

Genetic diversity

Measures of diversity and tests of neutrality were performed with the program DnaSP 5.0 (Librado and Rozas 2009). The genetic diversities of the chimpanzee subspecies and the bonobo, and that overall were estimated as the nucleotide diversity (π) (equation 10.5 in Nei 1987). Tajima’s D statistic was calculated to test for deviations from the neutral frequency distribution (Tajima 1989). We also applied Fu’s F , as this statistic has been shown to be more powerful in the detection of deviations from neutrality and thereby when testing for population expansions (Fu 1997).

Bayesian analyses of the demographic history

The timing and magnitude of past demographic events were inferred through Bayesian Markov chain Monte Carlo (MCMC) coalescent-based analysis of the mitogenomes using the program BEAST v.1.6.1 (Drummond and Rambaut 2007). As dates are completely dependent on the substitution rates used, we inferred the rates (see Online Resources 3 and 6 in the ESM), using a root time calibration with a normally distributed prior mean of 1.2 million years (My), and with 95 % of the density between 0.87 and 1.53 My ago, on the basis of the earliest well-supported date for *Pan* divergence (Won and Hey 2005; Becquet and Przeworski 2007; Becquet et al. 2007; Caswell et al. 2008; Hey 2010; Wegmann and Excoffier 2010; Stone et al. 2010). Subsequently, the substitution rates were used to estimate changes in population size over time for the four chimpanzee subspecies and the bonobo using a separate concatenated partition, comprising rRNA, CDS, and D-loop to permit a separate evolutionary model for each partition and allow for different patterns of rate heterogeneity. Based on results from the exploratory runs (see Online Resource 5 in the ESM), we applied the extended Bayesian skyline plot (EBSP) model to the datasets using the HKY nucleotide substitution model with gamma-distributed rates among sites for all partitions (see Online Resource 5 in the ESM). Preliminary analyses of the rate coefficient of variation indicating how much the rate of evolution varies from lineage to lineage showed little evidence of rate heterogeneity of branch rates, except for the West African chimpanzee and in the CDS for the Central African chimpanzee (results not shown). Hence, for all other chimpanzee subspecies and the bonobo, we applied a strict molecular clock. The remaining parameters were given uninformative wide prior distributions. We followed the same approach as Endicott and Ho (2008) but used a piecewise linear model as a prior for the demographic history and ran three independent chains as above.

Lastly, we compared three different tree priors in order to test alternative demographic models and how well these fitted our data. The objective was to test whether the EBSP model was a better fit to our data than the simpler exponential growth and constant demographic models. We applied the same evolutionary model as described for the EBSP, and the subsequent Bayes factor test was performed in Tracer by importance sampling the marginal likelihoods of each of the three models (Suchard et al. 2001).

Effects of population structure, migration, and sampling scheme

The skyline plot method assumes that the populations are panmictic and receive no gene flow from other populations.

Population structure and migration between subspecies can give rise to false signals of population size changes (Stadler et al. 2009; Peter et al. 2010), and can for example lead to false signals of population decline or the mitigation of actual population expansions. Consequently, it can be difficult to distinguish between populations that are structured and a panmictic population that has changed in size. As population structure may well exist in chimpanzee subspecies (Becquet and Przeworski 2007; Becquet et al. 2007; Wegmann and Excoffier 2010), we wanted to assess whether population structure and migration were likely to bias the signal detected in the skyline plots for the Central African and East African chimpanzee subspecies (see “Results”) (Heller et al. 2013). We thus performed simulations to test four biologically plausible alternative demographic scenarios for the two subspecies (see Online Resource 7 in the ESM) as well as to assess the impact of gene flow. As a final test, we simulated what we assumed to be the biologically most realistic scenario: internal subspecies structure with high migration between demes combined with low immigration (constituting limited gene flow from other subspecies, see Online Resource 7 in the ESM). For the intrasubspecies island model (see Online Resource 7 in the ESM) only, we assessed the impact of sampling scheme when low values of M (number of migrants) were explored, since the effect of sampling scheme becomes negligible at high numbers of migrants, i.e., $M > 10$ (Peter et al. 2010). Using Bayesian Serial SimCoal (BayeSSC) (Chan et al. 2006), we simulated 100,000 data sets for each scenario using settings imitating the actual data in terms of number of samples and population size. The sequence length was the same as the actual data, 14,501 bp, evolving according to the HKY substitution model with parameter values inferred in BEAST. Simulations were carried out under the assumption that the chimpanzee generation time is 25 years (Langergraber et al. 2012).

We assessed the reliability of the inferred population size dynamics by performing approximate Bayesian computation (ABC) analyses of the simulated scenarios. The 1,000 simulations with the lowest Euclidean distances were retained, and the selected uncorrelated summary statistics were extracted and compared to the values calculated from the actual data. The selected informative summary statistics included number of haplotypes, nucleotide diversity, Tajima’s D , and the most recent common ancestor (MRCA), the latter estimated from BEAST. The scenario that produced summary statistics closest to the values from the actual data was considered most suitable. The ABC-toolbox package (Wegmann et al. 2010) was applied to assess the different simulated scenarios and perform model selection by comparing the marginal density of each scenario using Bayes factors. We validated the ABC results by

using pseudo-observed data sets (PODs) to evaluate bias in parameter posterior estimates (Wegmann et al. 2009) (see Online Resource 8 in the ESM). Finally, we estimated the coefficient of variation from multiple regression of the summary statistics against each of the model parameters (Neuenschwander et al. 2008). This provided an estimate of the information content of the summary statistics with regards to the model parameters.

Results

Mitogenome diversity

The 14,501-bp concatenated alignment of the chimpanzee subspecies and bonobo contained 3,133 segregating sites. The rRNA region was found to harbor approximately twice as many segregating sites as the D-loop, and six times as many as the protein-coding genes (CDS) per 1,000 bp (Table 1). Nucleotide diversity (π) for the concatenated alignment spanned within subspecies from 0.00271 to 0.00725 (Table 1). The West African chimpanzee, Central African chimpanzee, and the bonobo were found to harbor roughly the same amount of nucleotide diversity, but only the Central African chimpanzee had an excess of low-frequency polymorphisms relative to neutral expectations (Table 1). We found the Nigeria–Cameroonian and East African chimpanzee to harbor the lowest nucleotide diversity. However, it should be noted that the sample size of the Nigeria–Cameroonian subspecies was low ($n = 4$), and perhaps not large enough to capture the majority of the diversity. To address this, we randomly drew a subset of four individuals from each of the other populations. Results showed that four samples captured the nucleotide diversity well compared to estimates produced by five- to tenfold more samples.

Recent demographic histories of the chimpanzee subspecies and the bonobo

We estimated the time of the most recent common ancestor (tMRCA) for the species overall and for the individual subspecies using concatenated alignment (Table 2). The different mitochondrial partitions yielded varied estimates for substitution rates (see Online Resource 6 in the ESM) and were lower than for the closest genetic relative—humans (Endicott and Ho 2008). In addition, we found rate heterogeneity among lineages for all partitions of the West African chimpanzee and for protein-coding genes (CDS) only of the Central African chimpanzee, indicating a departure from the assumption of a molecular clock, in contrast to previous findings (Bjork et al. 2011).

Table 1 General statistics of mtDNA diversity

	Partition	Length	Segregating sites	π	Tajima's D	Fu's F
West African chimpanzee		14,501	307	0.00725	0.6469	-0.891
Nigeria-Cameroonian chimpanzee		14,501	82	0.00287	-0.7540	1.890
Central African chimpanzee		14,501	588	0.00619	-1.4182	-7.309*
East African chimpanzee		14,501	175	0.00271	-1.4081	-1.633
Bonobo		14,501	339	0.00676	0.2131	-2.041
Overall		14,501	3,133	0.02254	0.8626	-
	rRNA	2,521	1,657	-	-1.6164	-
	CDS	10,824	1,182	-	0.0575	-
	D-loop	1,156	294	-	-0.1681	-

Tajima's test of the entire concatenated alignments for the chimpanzee subspecies and the bonobo did not produce significant P values ($P > 0.10$). When looking at Tajima's D values for synonymous and nonsynonymous sites, only the Central African chimpanzee produced a significant P value ($P < 0.01$) for the latter (nonsynonymous Tajima's $D = -2.1915$)

A negative Tajima's D signifies an excess of low-frequency polymorphisms (rare alleles), indicating population size expansion and/or purifying selection. A positive Tajima's D signifies low levels of low- and high-frequency polymorphisms, indicating a decrease in population size and/or balancing selection. To further test for population expansion, we applied Fu's F . The test only produced a significant negative value for the Central African chimpanzee, supporting a population expansion

* Significance $P < 0.001$

Table 2 Demographic parameter estimates for the chimpanzee and bonobo

ID	Current N_e^a		Ancestral N_e^b		Age of mtDNA ancestor (in thousands of years)	
	Mean	95 % HPD	Mean	95 % HPD	Mean	95 % HPD
West African chimpanzee	36,000	197-104,712	16,000	5,273-29,896	289	179-413
Nigeria-Cameroonian chimpanzee	8,000	5-21,527	6,000	815-14,588	101	61-149
Central African chimpanzee	183,000	45,857-385,005	18,000	6,321-32,214	254	167-355
East African chimpanzee	53,000	1,665-108,162	4,000	0-15,629	80	51-113
Central African chimpanzee and East African chimpanzee	-	-	-	-	295	295-396
West African chimpanzee and Nigeria-Cameroonian chimpanzee	-	-	-	-	376	239-511
Bonobo	56,000	1,550-115,000	20,000	0-37,200	286	190-406
Chimpanzee	-	-	-	-	712	458-994

We also report the age of the mtDNA ancestor for the two major chimpanzee clusters (the Central African chimpanzee and the East African chimpanzee as well as the West African chimpanzee and the Nigeria-Cameroonian chimpanzee), according to the mtDNA genome phylogeny (see Online Resource 5 in the ESM). The estimates were inferred under the EBSP model

^a Population size estimates in BEAST are provided as $N \times g$, so the inferred values were divided by the generation time $g = 25$ years to produce estimates of N_e

^b Ancestral N_e estimates at the age of the mtDNA ancestor

The Bayes factor test comparing the three alternative demographic models revealed that the EBSP model fitted the Central African chimpanzee data significantly better than the constant model and exponential growth model (Table 3). For the Nigeria-Cameroonian chimpanzee and the bonobo, the EBSP and constant size models were an equally good fit, and both models fit the data significantly better than the exponential growth model. For the East African chimpanzee, the EBSP was only weakly favored over the second best model, the constant model. Contrasting the EBSP, exponential, and constant models of the

West African chimpanzee pointed to low and inconclusive Bayes factors (Kass and Raftery 1995).

In agreement with the Bayes factor tests, the inferred skyline plots of the chimpanzee subspecies differed among subspecies (Fig. 2). The subspecies inhabiting the western part of equatorial Africa (the West African and the Nigeria-Cameroonian chimpanzee) had more stable demographic trajectories (Fig. 2, Online Resource 9a,b in the ESM) than the subspecies inhabiting the central/eastern part of equatorial Africa (the Central African and East African chimpanzees) (Fig. 2, Online Resource 9c,d in the

ESM). This pattern was confirmed by examining the EBSP parameter demographic.popsizchanges (DPSC), which estimates the minimum number of population size changes required to yield the observed genealogies. For the two latter subspecies, the 95 % highest posterior density (HPD) of DPSC excluded 0, strongly supporting a population size change, whereas the 95 % HPD interval for this parameter in the remaining chimpanzee subspecies and the bonobo included 0. The East African chimpanzee experienced a

more than tenfold expansion from 80,000 years before the present (YBP) to the present (Fig. 2 and Online Resource 9d in the ESM). The EBSP showed a constant population size of the Central African chimpanzee, on the order of 18,000 until 50,000 years ago, followed by a tenfold expansion to a current effective population size (N_e) of 183,000 (Fig. 2 and Online Resource 9c in the ESM), which was also supported by significant negative Tajima’s D and Fu’s F estimates (Table 1). A difference was found

Table 3 Bayes factor (BF) tests comparing demographic models for the chimpanzee subspecies and the bonobo

Population	Model	ln P (model) ($\times 10^4$)	sd ($\times 10^4$)	BF compared with		
				EBSP	Exponential	Constant size
West African chimpanzee	EBSP	-2.18	0.12	-	0.83	0.97
	Exponential	-2.18	0.13	1.20	-	1.17
	Constant size	-2.18	0.10	1.03	0.86	-
Nigeria-Cameroonian chimpanzee	EBSP	-1.99	0.08	-	35.7***	1.38
	Exponential	-1.99	0.10	0.03	-	0.04
	Constant size	-1.99	0.08	0.73	25.8***	-
Central African chimpanzee	EBSP	-2.52	0.19	-	6.2×10^7 ****	6×10^8 ****
	Exponential	-2.52	0.19	0	-	9.62**
	Constant size	-2.52	0.19	0	0.10	-
East African chimpanzee	EBSP	-2.09	0.09	-	8.19**	1.44
	Exponential	-2.09	0.10	0.12	-	0.18
	Constant size	-2.09	0.10	0.70	5.69**	-
Bonobo	EBSP	-2.18	0.12	-	917****	0.97
	Exponential	-2.18	0.14	0.001	-	0.001
	Constant size	-2.18	0.11	1.03	945****	-

The BF comparisons were done row by column. The marginal tree likelihood of the model [ln P (model)] and standard deviation (sd) of this estimate are shown

For the Bayes factor interpretation, the following symbols denote * weak, ** positive, *** strong, **** very strong evidence in favor of the row model compared to the column model (Kass and Raftery 1995)

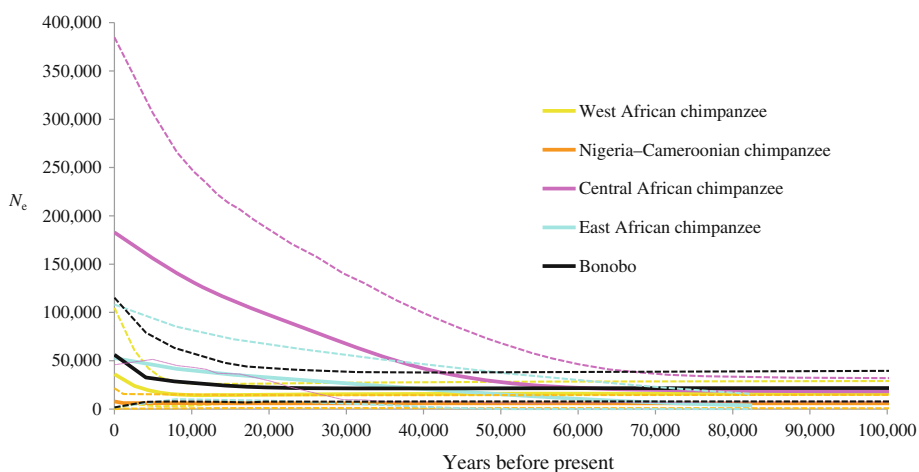


Fig. 2 Inferred historical effective population size plots for the chimpanzee subspecies and the bonobo. The inference is based on the extended Bayesian skyline plot (EBSP) demographic model, which was shown to have either most or equally good support based on a

Bayes factor model comparison. *Solid lines* represent the mean inferred effective population size (N_e), *dashed lines* indicate the 95 % highest posterior density (HPD) intervals, representing the combined phylogenetic and coalescent uncertainty

between the neighboring populations of the bonobo and the Central African/East African chimpanzee subspecies, with the bonobo having a constant population size back through time (N_e remaining roughly constant at 20,000; Fig. 2 and Online Resource 9e in the ESM), and the Central African and East African chimpanzees, which exhibited a tenfold expansion in population size. The effective sample sizes (ESSs) were generally high for all parameters, indicating good MCMC mixing in the combined chains.

In order to test the effect of the demographic prior on the posterior estimates, the EBSP model was run without data. The resulting EBSPs were flat with inferred population sizes of between 10^{-20} and 500, very different from the EBSPs including the data. We can therefore conclude that the priors alone were not responsible for producing the variable EBSP signal observed for the chimpanzee subspecies and bonobo.

Comparing simulations with actual data

In order to evaluate the robustness of our inferred population size changes for the Central African and East African chimpanzees, we simulated different types of demographic scenarios to explore the types of genetic signals produced by different demographic processes. We assessed both the impact of internal subspecies structure and external gene flow among subspecies, as well as combined internal and external migration. Evaluation of the alternative demographic scenarios was based on ABC. Bayes factors were used to perform model selection of the different scenarios (see Online Resources 10 and 11 in the ESM). Our ABC analyses showed that an actual population expansion was required for both subspecies to adequately explain the observed summary statistics. For both subspecies, the Bayes factor test strongly favored the population expansion model mimicking the skyline plot from the actual data (Popexp) and an island model with population expansion, high migration between and sampling from all demes (Incomplete_M15_expo) over the pure structured or sampling scheme models (see also Online Resource 7 in the ESM for a description of the models). We can thus conclude that inter-subspecies gene flow as well as intra-subspecies structure is unlikely to be responsible for the EBSP population expansion signal for the Central African and East African chimpanzees. When assessing the impact of internal structure for the Central African chimpanzee, both models showed a good fit to the observed data (P values of 0.70 and 0.79, respectively). With a Bayes factor of 1.62 in support of the island model with population expansion, high migration between and sampling from all demes, this model was only weakly favored over the population expansion model (see Online Resource 10 in the ESM). For the East African chimpanzee models, we observed P values

of 0.87 and 0.80 and a Bayes factor of 1.0 for both models (see Online Resource 11 in the ESM). As these models were equally supported (and are substantially similar because the high migration rate approaches panmixia; see “Discussion”), we only report parameter estimates and validation statistics for the single-deme population expansion (Popexp) model for both subspecies (see below).

To corroborate the EBSP signal of population size changes for the Central African and East African chimpanzees, we obtained posterior estimates of the expansion time and growth rate using ABC on the simulations from Popexp. For the Central African/East African chimpanzee subspecies, the simulated estimates produced unimodal posterior densities with mode values for the expansion factors of 10.02/9.54 and 51,200/58,100 YBP for the onset of expansion time, respectively. This agrees with the signal observed in the skyline plots and shows that the full-likelihood methods and ABC converged on the same result. Parameter estimation bias was not found, as was evident from the test of parameter quantile coverage in the PODs (see Online Resource 8 in the ESM). Reasonably high coefficients of variation confirmed that the summary statistics contained adequate information about most model parameters (see Online Resource 8 in the ESM).

Discussion

Despite a considerable focus on the demographic history of *Pan*, relatively little is known about the most recent past, for which comparable information is available for the other hominids. We used BSPs to look at the recent history of the entire *Pan* genus based on complete mitogenomes. Although mitochondrial DNA analyses reflect the genetic history of a single linkage group, our parameter estimates are in overall agreement (but see below) with previous findings based on a wide range of genetic loci (Won and Hey 2005; Anthony et al. 2007; Becquet et al. 2007; Caswell et al. 2008; Stone et al. 2010; Wegmann and Excoffier 2010; Zsurka et al. 2010), leading us to conclude that the parameter estimates reported here realistically reflect the demographic history of the genus *Pan*.

Demographic comparison

We found evidence of significant recent population expansions in the Central African and East African chimpanzee subspecies only, which together with our finding of constant population sizes for the West African, the Nigeria–Cameroonian chimpanzee, and the bonobo complements earlier studies by focusing on continuous population changes in the recent past (Fischer et al. 2006; Anthony et al. 2007; Wegmann and Excoffier 2010). The EBSPs for

the latter two did show a small tendency towards a recent expansion, but this was not supported by Bayes factor tests and therefore disregarded.

Contrasting actual data with simulated competing scenarios yielded evidence that population structure alone was unlikely to produce the expansion signal observed in the Central African and East African chimpanzee subspecies. For both subspecies, the Bayes factor test of population expansion (Popexp) versus the island model with population expansion, high migration between and sampling from all demes (Icomplete_M15_expo) yielded indecisive Bayes factors. This is reassuring, since the latter model mimics an almost unstructured population due to the high level of gene flow. The island model with population expansion, low migration between and sampling from all demes (Icomplete_M0.5_expo) mimics a heavy population structure, but this model was clearly not supported in the ABC model selection.

We do not regard the dissimilar chimpanzee subspecies and the bonobo histories to be due to missing signals of expansion caused by substructure (see Stadler et al. 2009). Firstly, we find it unlikely that population structure should have a substantially different effect on our analyses of the chimpanzee subspecies and the bonobo. Furthermore, although the timing of population expansion has been identified as a factor affecting the strength of an expansion signal (Stadler et al. 2009), the inferred expansions in the Central African and East African chimpanzee subspecies make it unlikely that we have missed a signal in the West African, the Nigeria–Cameroonian chimpanzee, and the bonobo that occurred in a similar time frame.

Generally, the inferred current population sizes are somewhat higher than those inferred using nuclear markers, but of the same order of magnitude (Becquet and Przeworski 2007; Hey 2010; Wegmann and Excoffier 2010; Fischer et al. 2011). It should be noted that the differences in demographic models among previous studies and the present study could account for some of the discrepancies in population size estimates. We report a current effective population size for the Central African chimpanzee of ~183,000 diploid individuals, which is in agreement with previous findings. However, our estimate of the current East African chimpanzee population size was 1.5–5.5 times higher than previously reported (Caswell et al. 2008; Hey 2010; Wegmann and Excoffier 2010, Fischer et al. 2011). The inferred ancestral N_e values of the Nigeria–Cameroonian and East African chimpanzees were lower (6,000 and 4,000, respectively) than those inferred for the West African and Central African chimpanzees and the bonobo (16,000, 18,000, and 10,000, respectively) (Table 2), and could be indicative of an ancestral population bottleneck somewhere in the period from subspecies divergence to mitochondrial tMRCA, as reported by Wegmann and Excoffier (2010) for

the East African chimpanzee. We find convincing evidence for a tenfold population expansion in both the Central African and the East African chimpanzee. This is greater than the twofold expansion in the Central African, but comparable to the eightfold expansion in the East African chimpanzee previously reported (Wegmann and Excoffier 2010). However, our study differs from previous studies in suggesting that these expansions occurred only within the last ~80,000 years, whereas previous models suggest that the expansions happened monotonously since the divergence of the subspecies, i.e., within the last ~100,000–550,000 years.

Pan history in context

The most notable feature of the *Pan* distribution is the separation into roughly two African ecoregions, Central and Western Africa (Fig. 1). Evidence suggests that the forest range of equatorial Africa was most stable throughout the late Pleistocene in Central Africa and more fragmented and fluctuating in the western part (Cowling et al. 2008). Surprisingly, we found a striking difference between the neighboring populations of the bonobo and the Central African/East African chimpanzee subspecies. One plausible explanation is that although the same climatic fluctuations were affecting the bonobo and the Central African/East African chimpanzee subspecies, the bonobo population was restricted by geographical barriers, preventing an expansion. The two *Pan* species have overlapping habitat requirements, but the Congo basin forest inhabited by the bonobo is crossed by several large rivers which bound the current geographical range of the species (Eriksson et al. 2004). Under this interpretation, although environmental and habitat conditions appear to have been improving for many other Central African large mammals in the late Pleistocene (see above), the population size of the bonobo remained constant because the main rivers were acting as barriers to migration, as has been observed in other Central African primates (Colyn et al. 1991; Anthony et al. 2007).

In general terms, the African equatorial region has been subject to successive cycles of pluvials, leading to expansion of forest cover, and interpluvials, leading to contraction of forest cover (de Menocal 2004; Cohen et al. 2007; Scholz et al. 2007; Cowling et al. 2008; Blome et al. 2012). The timescale of the demographic inference presented here covers the Last Glacial Maximum (LGM; roughly 26,200–19,000 YBP Clark et al. 2009), which was associated with substantial aridification and receding forests in equatorial Africa. Interestingly—and in agreement with evidence from other African mammals (Storz et al. 2002; Heller et al. 2008; Okello et al. 2008; Thalmann et al. 2011; Heller et al. 2012)—this did not lead to significant

population declines in the *Pan* genus. In addition, we did not find evidence of a population decline in the mid-Holocene, which has been identified for other African species and ascribed to either climate change or a cultural transition in humans (Heller et al. 2008; Heller et al. 2012).

The late Pleistocene expansions inferred in the Central African and East African chimpanzee subspecies agree with and are roughly contemporaneous with expansions inferred for savannah-adapted humans, which could suggest a common response to changed conditions around 50,000–80,000 YBP, as supported by paleorecords (Cohen et al. 2007; Scholz et al. 2007). The possibility of a concurrent continent-wide expansion of humans and other large mammals at 50,000–80,000 YBP (Atkinson et al. 2008; Heller et al. 2012; this study)—despite very variable habitat requirements—is tantalizing and warrants further study. The tenfold expansions for the Central African and East African chimpanzee subspecies also resemble the magnitude of expansion found for Western lowland gorillas—although from \approx 18,000 years ago (Thalmann et al. 2011). The two taxa share the same geographical range in Africa, but whereas the chimpanzee is a generalist, the gorilla is a closed-canopy specialist. Whether the climatic fluctuation that took place from 50,000 to 20,000 YBP, causing repeated contraction and expansion of forest belts, would favor a generalist more than the specialist is yet to be answered.

In this study, we have been able to infer the dates of recent past demographic events and trace the underlying dynamics on a finer scale than achieved by previous studies. We found that, despite sharing the same general habitat type and having proximate distribution ranges, the East African and Central African chimpanzee subspecies and the bonobo have dissimilar demographic histories. These differences in demographic history possibly arose due to geographical factors such as the presence of geographical barriers or lack of suitable habitat. Regardless of the contrasting ecological preferences of the savanna-adapted human and primarily rainforest-adapted chimpanzee, both species experienced similar population expansions in regard to both timing and magnitude.

We have shown that BSP coupled with simulations and ABC provides a powerful and robust framework for inferring detailed aspects of recent demographic history. Our findings add to the knowledge about the history of *Pan* and have allowed us to put it into the context of other co-distributed mammals.

Acknowledgments For generously providing samples, we thank Professor Dr. Werner Schempp (University of Freiburg), Ronald Bontrop (Biomedical Primate Research Centre), and Furuviiksparken, Sweden. Thanks to Sandra Abel Nielsen for sharing her research protocol and to Amal Al Chaer and Tanja Normann Gade for their invaluable assistance. For financial support we thank 15. Juni Fund,

Torben & Alice Frimodts Fund, H.R. & Grete S. Frederiksen Fund, the Danish Council for Independent Research | Natural Sciences, as well as the Industrial PhD program, Danish Agency for Science, Technology and Innovation.

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