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Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low male effective population size in bonobos (*Pan paniscus*)

JONAS ERIKSSON,*† HEIKE SIEDEL,* DIETER LUKAS,* MANFRED KAYSER,*‡ AXEL ERLER,*§ CHIE HASHIMOTO,¶ GOTTFRIED HOHMANN,* CHRISTOPHE BOESCH* and LINDA VIGILANT*

**Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany, †Department of Animal Ecology, Evolutionary Biology Centre (EBC), Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden, ‡Department of Forensic Molecular Biology, Erasmus University Medical Center Rotterdam, Dr Molewaterplein 50, 3015 GE Rotterdam, The Netherlands, §Department of Genomics, Technical University Dresden BIOTEC, Tatzberg 47-51, D-01307 Dresden, Germany, ¶Kyoto University Primate Research Institute, Kanrin, Inuyama, Aichi 484-8506, Japan*

Abstract

Dispersal is a rare event that is difficult to observe in slowly maturing, long-lived wild animal species such as the bonobo. In this study we used sex-linked (mitochondrial DNA sequence and Y-chromosome microsatellite) markers from the same set of individuals to estimate the magnitude of difference in effective dispersal between the sexes and to investigate the long-term demographic history of bonobos. We sampled 34 males from four distinct geographical areas across the bonobo distribution range. As predicted for a female-dispersing species, we found much higher levels of differentiation among local bonobo populations based upon Y-chromosomal than mtDNA genetic variation. Specifically, almost all of the Y-chromosomal variation distinguished populations, while nearly all of the mtDNA variation was shared between populations. Furthermore, genetic distance correlated with geographical distance for mtDNA but not for the Y chromosome. Female bonobos have a much higher migration rate and/or effective population size as compared to males, and the estimate for the mitochondrial TMRCA (time to most recent common ancestor) was approximately 10 times greater than the estimate for the Y chromosome (410 000 vs. 40 000–45 000). For humans the difference is merely a factor of two, suggesting a more stable demographic history in bonobos in comparison to humans.

Keywords: chimpanzee, Democratic Republic of Congo, genotyping, noninvasive samples, patrilocality

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Introduction

Because they are inherited without recombination, genetic markers transmitted by only one sex produce data that can be reconstructed as genealogies offering insights into population histories. The most widely used tool for such investigations is the maternally transmitted mitochondrial DNA (mtDNA) molecule. Since the 1980s, sequence variation of this rapidly evolving molecule has been examined in samples from numerous taxa and used to address topics such as the concordance between phylogenetic relationships and geographical origins (Avise 2000), the timing of population expansions (Harpending & Rogers 2000), and the effects of sex-specific dispersal on population relationships (Avise 1995). In contrast to work using mtDNA, research employing its male 'counterpart', the Y chromosome, has been minimal and primarily limited to studies in humans (Hammer 1995; Seielstad *et al*. 1998; Hammer *et al*. 2001, 2003; but see Burrows & Ryder 1997; Tosi *et al*. 2000; Stone *et al*. 2002).

The human Y chromosome is the best-characterized single chromosome among mammals, with a highly repetitive palindromic structure that is difficult to sequence and has hindered development of easily characterized markers (Skaletsky *et al*. 2003). Furthermore, in the segments of the Y chromosome that have been sequenced from humans and various other mammals, levels of nucleotide diversity

Correspondence: L. Vigilant, Fax: +49 341 3550299; E-mail: vigilant@eva.mpg.de.

Jonas Eriksson and Heike Siedel contributed equally to this work.

are much lower than would be expected from the reduced male effective population size and higher male mutation rate (lynx, wolf, reindeer, cattle, vole: Hellborg & Ellegren 2004; horse: Lindgren *et al*. 2004; sheep: Meadows *et al*. 2004). This means that while single nucleotide polymorphisms (SNPs) may be useful for inferring broad-scale population events such as the strong sex bias in the domestication of the horse (Lindgren *et al*. 2004), the African origin of modern humans (Hammer *et al*. 1998; Underhill *et al*. 2000; Ke *et al*. 2001), and the relatively higher nucleotide diversity of chimpanzees and bonobos as compared to humans (Stone *et al*. 2002) markers exhibiting higher levels of intraspecific variation are needed for studies examining more recent population histories.

Fortunately, the sequencing of the human genome has facilitated the identification of a large number of highly variable microsatellite (also termed STRs for short tandem repeats) markers on the human Y chromosome (Kayser *et al*. 2004), many of which are useful in other primates (Erler *et al*. 2004). Humans and their closest living relatives, the chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*), appear to share the characteristic of male philopatry (in humans, usually termed 'patrilocality'), the tendency for males to remain in their natal group or place of origin while females typically disperse at onset of sexual maturity to reproduce in new social groups (Pusey 1979; Wrangham 1979; Greenwood 1980). Comparison of information from mtDNA sequence and Y-chromosome microsatellite analyses collected on a local or regional scale, such as of human communities known to practice predominantly patrilocality or matrilocality, have yielded relative levels of mtDNA and Y-chromosome diversity consistent with expectations. Specifically, lower Y-chromosome diversity is found in patrilocal as compared to matrilocal groups, and lower mtDNA diversity is found in matrilocal as compared to patrilocal groups (Salem *et al*. 1996; Oota *et al*. 2002). The distribution of genetic variation in humans on local and regional scales seems to support a history of patrilocality (Seielstad *et al*. 1998; Hammer *et al*. 2001; Kayser *et al*. 2003a), although the extent to which the two factors of patrilocality and polygyny have contributed to the pattern of global human genetic variation is currently under debate (Marlowe 2000; Dupanloup *et al*. 2003; Kayser *et al*. 2003b; Destro-Bisol *et al*. 2004b; Wilder *et al*. 2004a, b).

Sex-specific migration patterns and relative reproductive opportunities among males have likely varied throughout human history, with a particularly strong effect exerted by the transition from hunter-gatherer to settled societies (Marlowe 2000, 2004). In contrast, it seems reasonable to assume that the migration and reproductive skew patterns of contemporary chimpanzees or bonobos in the wild are representative of long-term species characteristics. As a consequence of male philopatry, it is expected that, in comparison to results from mtDNA analyses, the genetic variation evident from Y-chromosome microsatellite analysis would be more highly structured according to locality, as well as less variable within localities. However, it is not entirely clear how strictly individual chimpanzees or bonobos actually conform to expected dispersal patterns. Long-term behavioural studies of well-habituated individuals of both species have provided a large number of observations of young adolescent females disappearing from their native groups and, to a lesser extent, of new females joining a group of habituated individuals (Goodall 1983; Nishida 1990; Kano 1992; Pusey *et al*. 1997; Boesch & Boesch-Achermann 2000). But female migration is not ubiquitous in chimpanzees, as females also sometimes remain and reproduce in their natal group (Goodall 1986; Boesch & Boesch-Achermann 2000). In addition, some behavioural researchers have observed disappearances of male individuals from both bonobo and chimpanzee groups with a frequency and regularity difficult to attribute solely to natural mortality events, and have consequently suggested the possible existence of occasional male migration (Nishida & Hiraiwa-Hasegawa 1985; Sugiyama 1999). For bonobos in particular, the more egalitarian relations between the sexes and reduced levels of intergroup hostility as compared to chimpanzees (Wilson & Wrangham 2003) means that dispersal of males between groups is not entirely implausible. In fact, despite the relative paucity of observation hours of bonobos as compared to chimpanzees, one case of a bonobo male successfully joining a habituated group has been reported (Hohmann 2001). Here we address the topic of male- and female-mediated gene flow in bonobos by comparing the results of an examination of Y-chromosome microsatellite and mtDNA sequence variations in wild bonobos noninvasively sampled from multiple regions, and discuss the implications of our results for similar studies of human genetic variation.

Materials and methods

Sampling and individual identification

As was previously described in detail (Eriksson *et al*. 2004; Thalmann *et al*. 2005), noninvasive samples (faeces) were collected from multiple areas within the current range of bonobos (Fig. 1) and subjected to DNA extraction and quantification (Morin *et al*. 2001). Y-chromosome variation was examined in samples from four regions (NE, E, C, and S). Within each of the Eastern (E) and Central (C) regions, three distinct localities separated by a distance of at least 10 km and thereby approximating separate social communities (Eriksson *et al*. 2004) were sampled and are here termed 'populations'. The sex of each sampled individual was determined by use of a polymerase chain reaction (PCR) assay targeting the sex-chromosome-linked amelogenin gene (Bradley *et al*. 2001). Extracts producing

Fig. 1 The shaded area indicates the current estimated geographical distribution of bonobos within the Demographic Republic of Congo. Approximate geographical origins of samples used in this study are indicated by large circles and the black dots indicate separate populations collected within a region (NE, Northeast; C, Central; S, South; E, East).

two independent observations of the Y-chromosome fragment were attributed to males and four observations of only the X-chromosome product were required for extracts to be assigned to females. Sequences of the first hypervariable region (HV1) of the mtDNA were determined using primers L15996 and H16498 as described earlier (Eriksson *et al*. 2004). As previously detailed, comparisons of genotypes from three autosomal microsatellite markers (D11S2002, D5S1470, and D2s1326) were sufficient to determine whether samples from the same population of the same sex and mtDNA haplotype represented the same, or different individuals (Eriksson *et al*. 2004).

Y-chromosome microsatellite genotyping

Individuals were characterized using 12 microsatellite loci developed in humans and reported to also amplify in chimpanzees (DYS502, DYS520, DYS533, DYS562, DYS510, DYS517, DYS612, DYS630, DYS469 and DYS632 — Erler *et al*. 2004; DYS439 — Gusmao *et al*. 2002a; and DYS392 — Gusmao *et al*. 2002b) (Table 1). These loci are a subset of an initial group of 31 loci selected for testing in three males and one female each of bonobos, western chimpanzees (*Pan troglodytes verus*) and eastern chimpanzees (*Pan troglodytes troglodytes*). The 19 loci that appeared less variable and so were not used further included DYS501, DYS565, DYS588, DYS508, DYS587, DYS634, DYS638, DYS504, DYS536, DYS472, DYS483, DYS473, DYS546, DYS541, DYS571, DYS577, DYS485, DYS538, and DYS575 (Erler *et al*. 2004). PCR amplifications were performed under the following conditions modified from Erler *et al*. (2004): Super*Taq*® (HT Biotechnology) was premixed at a 2:1 ratio with *Taq*Start® monoclonal antibody (BD Biosciences Clontech) to enable a hot start protocol. PCR amplifications were performed in a total volume of 20 μL composed of 1.25X PCR Super*Taq*® buffer, an additional 0.8 mM $MgCl_2$ for a final concentration of 2.3 mM $MgCl_2$, 250 nM each primer, 250 μM each dNTP, 16 μg BSA, 0.33 U Super*Taq*®, and 2 μL of DNA extract. Annealing temperatures (T_a) and primer sequences are listed in Table 1. Touchdown amplifications were performed in an MJ Research thermal cycler (DNA Engine® PTC-200) with a 3-min activation step at 94 °C; followed by eight cycles at 94 °C for 60 s (T_a +4 °C) minus 0.5 °C per subsequent

Table 1 Names, sequences of repeat motifs, annealing temperatures (T_a) and primer sequences for Y-chromosome microsatellite loci analyzed in bonobos

Locus ID	Repeat	T_a (°C)	Primer F (5′–3′)	Primer R (5′–3′)
DYS630	GAAA	65	GCCTTTGGACAGAGCAAGAC	AGCCATGGAAAGCTGTGAGT
DYS562	CTAT	60	GGGTGTATAAAGAGGGGCATA	GGTAAAGGTTATCACGCCATC
DYS520	GATA	58	AACAGCCTGCCCAACATAGT	ACCATCATGCCCTGCAATA
DYS517	GAAA	60	TAATCGTCCCATTTTGAGCA	TGCAATCCCAAACTCAGAAA
DYS612	CTT	58	CCCCCATGCCAGTAAGAATA	TGAGGGAAGGCAAAAGAAAA
DYS439	GATA	58	TCCTGAATGGTACTTCCTAGGTTT	GCCTGGCTTGGAATTCTTTT
DYS510	GATA	60	TTTTTCCTCCCTTACCACAGA	TCTGGAGAAGACAGAACTTGTCA
DYS469	CTT	58	TTTGGGGACTGAATTCAAAA	CCCCAGCTGGTAAAATGAGT
DYS533	CTAT	58	CATCTAACATCTTTGTCATCTACC	TGATCAGTTCTTAACTCAACCA
DYS392	TAT	58	TCATTAATCTAGCTTTTAAAAACAA	AGACCCAGTTGATGCAATGT
DYS502	ATA	58	CAGCAAGCCACCATACCATA	TGTGCTTTTGGAGTTTGGAG
DYS632	*	60	GGCCGTTGCAAAATAAACTG	TCTGGGCAACAGAAGGCGAC

Locus ID refers to the names of the human homologues listed in the Genome Database (GDB).
*Monomorphic in our sample and thus not sequenced.

cycle for 60 s, 60 °C for 60 s (except for DYS630, which was 65 °C for 60 s); followed by 32 cycles at 94 °C for 60 s, T_a for 60 s, 60 °C for 60 s (except for DYS630 at 65 °C for 120 s as annealing and extension steps) and 72 °C for 30 min as final extension. All sets of amplifications contained male human and chimpanzee positive controls to confirm success of the PCRs and multiple negative controls to monitor contamination. Initial PCRs from each locus also included as one control a DNA from a female bonobo to serve as a check that amplification did not occur from additional loci not on the Y chromosome. Success of the PCRs was confirmed by visualization of 5 μL of product under UV light after electrophoresis on 2.8% agarose gels containing ethidium bromide. The forward primers were fluorescently labelled (HEX, 6-FAM or NED), and all successful reactions were further analysed through determination of PCR fragment length by capillary electrophoresis (ABI310, Applied Biosystems) relative to an internal size standard (HD400) using GENE SCAN (Applied Biosystems) software.

Data analysis

In order to confirm the identity of the sequence motif of the microsatellite repeat unit, and to determine the relationship between amplified fragment length and the actual length of just the segment consisting of tandem repeats of the microsatellite repeat unit, at least two alleles of different lengths were sequenced for each locus. PCR products were cloned using the TOPO® TA Cloning Kit (Invitrogen). A minimum of three clones per allele were analysed.

Because of complete linkage of all loci on the nonrecombining portion of the Y chromosome, composite Y-chromosome genotypes represent haplotypes. We used ARLEQUIN 2.0 (Schneider *et al*. 2000) to estimate haplotype (gene) diversity (*h*) and its standard deviation (SD) (Nei 1987) from both mtDNA and Y-chromosome data as well as mean pairwise sequence differences (MPD) for mtDNA and mean pairwise step differences (MPSD, assuming a stepwise-mutation model for microsatellites) for Y-chromosome microsatellite haplotypes (Nei & Li 1979). In order to avoid biases that might arise from the use of unmatched data sets, the mtDNA data were limited to sequences from the same males analysed for Y-chromosome variation.

Reconstruction of Y and mtDNA phylogenies were performed by means of the median-joining (MJ) method (Bandelt *et al*. 1995) and the Y-haplotype relationships were in addition analysed using the reduced median-joining (RM) network method (Bandelt *et al*. 1999), both as implemented in NETWORK 4.0.0.0 (Fluxus TechnologyLtd, 2003). For network calculations, each Y microsatellite locus was weighted equally due to inadequate knowledge of the mutation rates of individual loci in humans (Kayser *et al*. 2000). In all RM analyses, the RM reduction threshold was set to the default value of 2; that is, character conflicts are resolved into subtrees only if the weight of at least two characters opposes one conflicting character weight.

In order to investigate the apportionment of genetic variation as a reflection of sex differences in dispersal rate, a decomposition of the total variance of both systems (mtDNA and Y) was done using an analysis of molecular variance (AMOVA, Excoffier *et al*. 1992) as implemented in ARLEQUIN 2.0 (Schneider *et al*. 2000). This approach is analogous to an analysis of variance in which the correlation among haplotype distances (F_{ST}, R_{ST}) at various hierarchical levels are used as *F*-statistic analogues (Excoffier *et al*. 1992; Slatkin 1995). The parameter $N\nu$ was estimated using the formula $N\nu = (1/F_{ST}) - 1$ assuming an island model of migration for a haploid system (Cavalli-Sforza & Bodmer 1971). *N* represents the effective population size and ν incorporates migration (*m*) and mutation (μ) as $\nu = m + \mu - m\mu$. Because the mutation rates for Y-chromosome microsatellites and the rapidly evolving sites of the mtDNA HV1 are similar, and both are substantially lower than the effective number of migrants per generation, we follow other workers in assuming that ν approximates *m* (Seielstad *et al*. 1998; Destro-Bisol *et al*. 2004b).

A matrix correlation test (Mantel 1967) using 5000 permutations was used to assess the statistical significances of the correlations between genetic distances inferred from either Y-STR or mtDNA haplotypes and geographical distances between regions (computer program MATMAN version 1.0, Noldus Information Technology). Due to the limited number of groups sampled within each geographically separated region, the genetic and geographical distance between each individual was used. Both the shortest possible geographical distance (without regard for geographical barriers) and distance as measured around the large rivers were tested.

Finally, we used the program BATWING (Wilson *et al*. 2003) to draw inferences regarding male bonobo population history from the Y-chromosome haplotypes. The program uses a Markov chain Monte Carlo simulation algorithm, based on the coalescent model and using a stepwise-mutation model for microsatellite evolution, to provide estimates of the mutation rate, male effective population size (N_e) and the time back to the most recent common ancestor (TMRCA) of all haplotypes. This program was preferred over an approach using a rejection algorithm (Tavare *et al*. 1997) because the modest size of our data set allows convergence within BATWING in a reasonable time while making full use of the data instead of relying on summary statistics. Previous analysis of human Y-microsatellite data found a strong signal of exponential population growth (Tavare *et al*. 1997), so initial runs allowed for simultaneous estimation of changes in population size and growth rate. However, for bonobos this procedure did not indicate a clear signal of population growth (data not shown), in line with previous mtDNA analysis that also showed no signal of growth in bonobos (Eriksson *et al*. 2004). In addition,

values obtained under a model of constant population size were nearly identical with a model allowing growth, but had reduced uncertainty in their estimations, and so all final analyses were performed under the assumption of no population growth.

As input factors, we used the same four sets of priors described in a previous analysis (Macpherson *et al*. 2004) of a human data set (Cann *et al*. 2002). The sets were coded as P, K, W and Z by the authors following their original descriptions in (Pritchard *et al*. 1999; Kayser *et al*. 2000; Wilson *et al*. 2003; Zhivotovsky *et al*. 2004), and cover a range of assumptions concerning effective population size and mutation rate. Given our comparatively small number of haplotypes, the limited number of possible arrangements allowed the program to exploit extremes within single runs, given the allowed number of changes per run (40 changes to the tree, 100 changes of the parameters). This was confirmed by the autocorrelation function, which had values below 0.01 already after a lag of three for nearly all estimates. In addition, we choose a 'badness' value of 0.1, which forced the initial tree to one, based on the maximum-parsimony method. These factors allowed the program to immediately converge towards the final parameter space and the distribution of the first 2000 samples, which were initially allowed as burn-in, was identical to the total distribution.

The posterior probabilities were, therefore, based on the total of 12 000 samples and the presented values are the modes of the resulting unimodal distributions. To transform the estimated length of the tree measured in generations into an estimate of time to the most recent common ancestor, a generation time of 25 years was assumed for bonobos as was done for humans (Macpherson *et al*. 2004).

Results

Comparison of molecular sexing results, HV1 sequences, and autosomal microsatellite genotypes as detailed in Eriksson *et al*. (2004) revealed that DNAs from a total of 34 different males were successfully sampled from the following regions: Central = 18, South = 10, East = 4 and Northeast = 2 (Fig. 1). Within the Central and Eastern regions, the following numbers of unique males were sampled from each of three localities, here termed populations: C1 = 7, C2 = 5, C3 = 6, E1 = 1, E2 = 1, E3 = 2.

Y-chromosome microsatellites

Of the 31 loci initially tested in three males and one female each of bonobos, western chimpanzees, and eastern chimpanzees, 19 (listed in the methods section) either amplified poorly or produced only single alleles for all male representatives of each of the three taxa. A total of 12 loci were found to reproducibly yield single products from males only, with at least two different alleles seen in bonobos or one of the chimp subspecies, and these loci were then genotyped in all individuals. Of these loci, one (DYS632) was monomorphic in our sample and two (DYS469 and DYS392) provided completely nonindependent information in our sample, resulting in a total of 10 informative loci. The sequences of the variable repeat units are shown in Table 1. The 34 individuals analysed revealed a total of 13 different Y-chromosome microsatellite haplotypes as shown in Table 2. No haplotypes were shared among the regions, and there was only one case of haplotype sharing across populations within a region (Table 2, haplotype F found in C2 and C3).

Table 2 Y-chromosome microsatellite haplotypes in bonobos

Locality	*N*	Hp ID	DYS439	DYS502	DYS520	DYS533	DYS562	DYS510	DYS517	DYS612	DYS630	DYS469	DYS392
C1	6	A	12	9	14	7	10	11	16	7	15	18	16
	1	B	13	9	14	7	10	11	16	7	15	18	16
C2	5	F	12	13	14	9	9	11	14	12	14	14	11
C3	1	F	12	13	14	9	9	11	14	12	14	14	11
	1	E	11	12	14	10	10	12	16	12	14	14	11
	3	C	11	12	16	10	10	12	16	12	14	14	11
	1	D	11	12	16	10	10	11	16	12	14	14	11
E1	1	G	14	12	13	11	11	11	16	12	17	14	11
E2	1	H	13	12	13	11	11	11	16	12	16	14	11
E3	2	I	13	12	13	10	11	11	15	12	16	14	11
S	3	J	12	11	14	9	9	11	14	15	15	14	11
	6	K	12	11	14	9	9	11	14	15	14	14	11
	1	L	12	11	14	9	9	?	15	15	?	14	11
NE	2	M	12	12	13	10	10	12	14	11	12	14	11

Locality indicates sample collection location as indicated on Fig. 1, *N* is the number of individuals sharing the haplotype, Hp ID indicates the name of the haplotype. Individual genotypes at a locus are given as number of repeat units. The question marks indicate missing data.

Table 3 Comparison of Y-chromosome and mtDNA haplotype variability in samples of bonobo males from different regions and in total

		Y chromosome			mtDNA		
Region	*N*	#Hp	$h \pm SD$	MPSD ± SD	#Hp	$h \pm SD$	MPD ± SD
Central	18	6	0.784 ± 0.061	5.08 ± 2.59	10	0.942 ± 0.036	16.16 ± 7.61
East	4	3	0.833 ± 0.222	2.33 ± 1.59	4	1.000 ± 0.178	12.34 ± 7.09
South	10	3	0.600 ± 0.130	0.67 ± 0.56	4	0.750 ± 0.112	14.52 ± 7.19
Northeast	2	1	—	—	2	—	—
Total	34	13	0.906 ± 0.025	5.48 ± 2.71	20	0.966 ± 0.016	17.59 ± 8.02

Sample size (*N*), number of haplotypes (#Hp), haplotype (gene) diversity (*h*), mean pairwise stepwise difference (MPSD), mean pairwise sequence difference (MPD).

Comparison of Y-chromosome and mtDNA haplotype variation

In a previous study using a larger data set consisting of both males and females, the distribution of mtDNA variation (F_{ST} values) of the three populations sampled within each of the Central and East regions indicated no significant within-region differentiation. Because of this fact, and the small sample sizes of males available for this study, we compared the Y-chromosome and mtDNA diversity in these 34 males at the regional level and were compelled to eliminate the Northeast region (two individuals) from some of the calculations presented in Table 3.

A greater number of mtDNA than Y-chromosome haplotypes were found in our sample (mtDNA: 20 vs. Y: 13) and accordingly the estimated total average haplotype diversity was significantly greater for mtDNA than for the Y chromosome (mtDNA: 0.966, Y: 0.906, $t = 11.8$, d.f. = 66 $P < 0.001$) (Table 3). As was found for the Y chromosome, the only occurrences of mtDNA haplotype sharing were observed among populations within the Central region. Among regions, the Y-chromosome and mtDNA haplotype diversity was significantly lower in South than in Central and East (Y: one-way ANOVA $F_{2,31} = 10.52$, $P < 0.01$, $r^2 = 0.42$; Tukey's post hoc test, $P < 0.01$ and mtDNA: one-way ANOVA $F_{2,31} = 17.82$, $P < 0.01$, $r^2 = 0.58$; Tukey's post hoc test, $P < 0.01$). There were significant differences among regions in the extent to which their Y chromosomes differed from one another, with the Central region having the highest mean pairwise stepwise difference (MPSD) and South the lowest (one-way ANOVA $F_{2,31} = 15.13$, $P < 0.01$, $r^2 = 0.51$; Tukey's post hoc test, $P < 0.01$). This is consistent with a higher mean pairwise sequence difference (MPD) of mtDNA sequences from the Central region, although this was only significantly greater when using the larger data set of both males and females (Eriksson *et al*. 2004) and not significant in the reduced data set of only males.

Regional differentiation according to mtDNA and Y-chromosome data

We obtained the same results when reconstructing the relationships among the Y-chromosome haplotypes using either median-joining (MJ) or reduced median-joining (RM) networks. For the mtDNA haplotypes only the MJ network was used as the RM network method is not able to handle multistate data. It is apparent (Fig. 2) that Y-chromosome microsatellite haplotypes from the same population within a region tend to be closely associated, and haplotypes within the East and within the South regions are each very similar, as was also evident from the low number of pairwise differences among haplotypes within each of these two regions. In contrast, little geographical structure at the regional or population level is evident in the mtDNA network. Haplotypes from the Central region are the most dispersed on each of the two networks.

In order to quantify the effect of geographical origin upon the distribution of genetic variation, a decomposition of the total variance of both systems (mtDNA and Y chromosome) was done using AMOVA (Table 4). The results show a strongly contrasting pattern between the two genetic systems. Nearly all (97.5%) of the variation on the Y chromosome is found between populations, while most (88.0%) mtDNA variation is found within single populations. We calculated *Nv*, the product of effective population size and migration rate, from both the mtDNA and Y-chromosome data and obtained 7.333 and 0.026, respectively. This yields an mtDNA/Y-chromosome ratio of *Nv* of 282.04,

Table 4 AMOVA assessment of population structure in bonobos for Y-chromosome and mtDNA haplotypic variation

	Variation within populations (%)	Variation between populations (%)	F_{ST}
Y chromosome	2.6	97.4	0.975
mtDNA	88.0	12.0	0.120

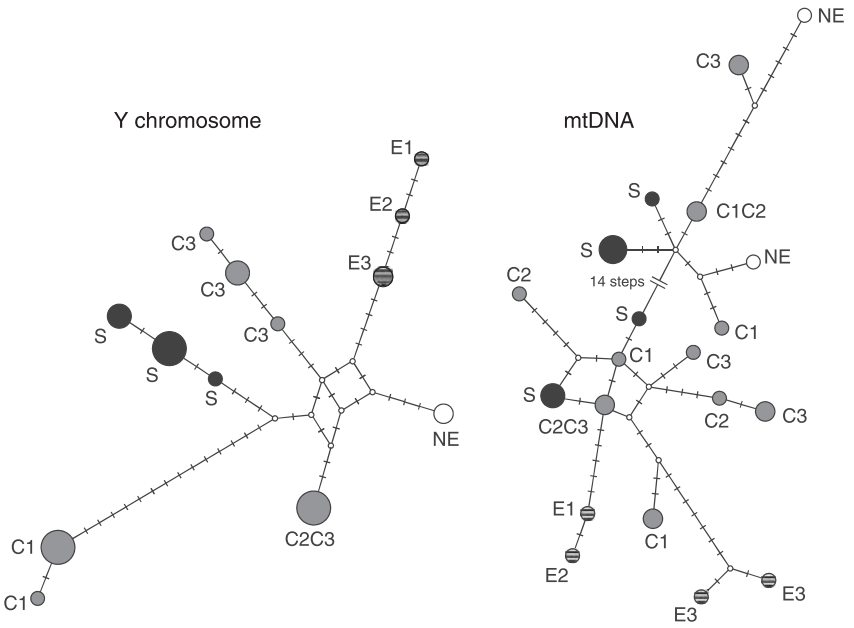

Fig. 2 Networks of bonobo Y-chromosome and mtDNA haplotypes composed from analysis of the same individuals. The size of the circles are proportional to the number of individuals sharing each haplotype. Letters indicate geographical origins of haplotypes as listed in Table 2 (C, Central; S, South; E, East; and NE, Northeastern regions).

indicating a tremendously greater female than male effective population size and/or migration rate in bonobos.

In a previous analysis using a larger data set, we showed that the genetic distances between regions inferred from mtDNA data were significantly correlated with geographical distances between regions when geographical distances were calculated including detours around major rivers, but not when straight-line distances were used (Eriksson *et al*. 2004). Using this smaller, male-only data set, we also found a significant, although weak, correlation with geographical distances bypassing rivers for the mtDNA genetic distances (Mantel test: $r^2 = 0.2$, $P = 0.03$) but not for the Y-chromosome genetic distances (Mantel test: $r^2 = -0.08$, $P = 0.51$).

Bonobo male population history

Using the coalescence model of genealogy and the stepwise microsatellite mutation model for microsatellite evolution (Wilson *et al*. 2003), we made inferences about the population history of bonobo males. As expected, the use of the different sets of priors for the Bayesian analysis produced somewhat divergent results with broad confidence intervals (Table 5). This was most obvious with prior set P, in which an unrealistically high male effective population size of 36 000 was initially assumed, and the resulting modal estimate of male N_e was the highest at 1700 and the TMRCA was greatest at 95 000 years. When we compared the final trees obtained using BATWING for each prior set with the network shown in Fig. 2, we found that both the K and the W sets had converged on a topology similar to that shown, while for the Z set one sequence fell at a divergent place (data not shown). This discrepancy using the Z set was not due to nonconvergence, as repeated analyses gave identical results, and it resulted in a longer tree and consequently in a greater TMRCA as compared to that which would be obtained using the network in Fig. 2. These considerations

Table 5 Priors and results from Bayesian calculation of male effective population size and the time to the most recent common ancestor of bonobo males

	Priors			Parameter estimates		
Prior set	N_e	N_e (range)	μ	N_e (95% CI)	TMRCA (95% CI)	μ (95% CI)
P	36 000	large	0.0008	1700 (1000–8000)	95 000 (55 000–265 000)	0.0008 (0.0004–0.0014)
W	3 000	large	0.0022	900 (500–2100)	45 000 (30 000–110 000)	0.0019 (0.0012–0.0031)
K	1 000	narrow	0.0024	700 (300–2200)	40 000 (15 000–135 000)	0.0012 (0.0007–0.0039)
Z	1 000	narrow	0.00069	1100 (600–2600)	65 000 (30 000–220 000)	0.0010 (0.0004–0.0024)

Priors are described in Macpherson *et al*. (2004) and the following publications: Pritchard *et al*. (1999); Kayser *et al*. (2000); Wilson *et al*. (2003); Zhivotovsky *et al*. (2004). Prior values are means, and the posterior parameter estimates are the most frequent values (modes). N_e is the effective male population size and μ is the mutation rate per locus per generation.

regarding sets P and Z led us to focus upon the results from sets W and K, which were largely consistent with one another and also overlapped the confidence intervals from the other sets.

The effective male population size of 700–900 estimated for bonobos was slightly lower than the mean of 1000–1500 estimated using various priors for humans (Macpherson *et al*. 2004), and the intervals containing 95% of values were 300–2200 and 150–4500, respectively, and similarly large in humans. The modal value of the TMRCA, or coalescent of the bonobo Y-microsatellite sample, was estimated at about 40 000–45 000 years ago in contrast to the 60 000–90 000 estimated for humans. However, both of these estimates are associated with large, flat probability distributions, so that 95% of the values for bonobos fall within the range of 15 000–135 000 years ago and for humans the comparable interval is 20 000–180 000 years ago. It is important to note that the bonobo TMRCA estimate could be influenced by the relatively small sample size and additional samples would theoretically be expected to increase this estimate.

For both bonobos and humans, the maternally inherited mitochondrial HV1 sequences have deeper TMRCAs as compared to those estimated from the Y-microsatellite data. Specifically, the TMRCA of the HV1 of these bonobo males was estimated (by using the maximum divergence between two sequences in the data set and a mutation rate of 7.5×10^{-8} per site per year) at about 410 000 years ago (SD = 47 000), while the comparable estimate for humans is 160 000 years (Tamura & Nei 1993). Addition of sequences from females (Eriksson *et al*. 2004) increases the bonobo HV1 TMRCA somewhat to 460 000 years ago (SD = 21 000).

Discussion

One of the goals of this study was to compare levels of diversity among samples of bonobos collected from different regions. This examination of Y-chromosome microsatellite variation is in accordance with our previous results from mtDNA sequence analysis (Eriksson *et al*. 2004) in showing the highest level of diversity (as measured by mean pairwise differences) within the Central region. The limited sample size means that this result must be interpreted with caution, but would be consistent with a scenario in which bonobo populations in this region have experienced a stable population history and retained comparatively high levels of variation. This region corresponds to the Salonga National Park, an area which affords partially effective protection of bonobos (Inogwabini *et al*. 2005).

As we predicted based upon the expectation of predominantly or exclusively male philopatry in bonobos, we found much higher levels of differentiation among local populations based upon Y-chromosomal than mtDNA genetic variation. While the vast majority (88%) of the total mtDNA variation was found within local populations, nearly all (97.4%) of the Y-chromosomal variation distinguished local populations, suggesting negligible levels of male-mediated gene flow between populations. The parameter $N\nu$ represents the product of effective population size and migration plus mutation rate, and the ratio of mtDNA to Y-chromosome $N\nu$ in bonobos was estimated at 282, indicating much higher female effective population size and/or rate of gene flow. In comparison, $N\nu$ for humans has been estimated from comparable data on sub-Saharan populations as 1.76 for food-producer and 0.11 for hunter-gatherer populations (Destro-Bisol *et al*. 2004a). The difference between the two ratios in humans has been interpreted as reflecting greater roles of patrilocality (male philopatry) and polygyny (increased male reproductive skew) in food-producing populations (Destro-Bisol *et al*. 2004a). This strongly suggests that contradictions among other studies (Seielstad *et al*. 1998; Hammer *et al*. 2001; Wilder *et al*. 2004b) concerning relative levels of male and female gene flow in humans have likely arisen out of a failure to systematically distinguish between samples from hunter-gatherers and food-producers. Although a female-to-male $N\nu$ ratio greater than one is supported by the vast majority of human populations, changing mobility and cultural practices in recent human history make it difficult to ascertain the relative importance of the two factors of patrilocality (i.e. higher female migration rate) and polygyny in producing this result (Dupanloup *et al*. 2003; Wilder *et al*. 2004a).

In contrast, in bonobos, as well as in other close relatives of humans such as chimpanzees, the distribution of genetic variation observed is expected to reflect consistent, long-term demographic patterns. There are several reasons to suggest that the remarkably high female-to-male $N\nu$ ratio in bonobos more strongly reflects higher female gene flow, rather than vastly different female and male effective population sizes. The first is the consideration that chimpanzees and bonobos have been described as one of the rare mammalian species to exhibit female dispersal as a result of the routine observation of females joining and reproducing in new groups. However, in some studies a small percentage (~10%) of paternities within chimpanzee groups cannot be attributed to males from within the group, suggesting that a modest amount of male-mediated gene flow among groups may also occur (Vigilant *et al*. 2001; Boesch *et al*. in press). Genetic analyses have in addition provided information relevant to the question of male effective population size by examining the extent to which reproduction is unevenly distributed among the males. In particular, studies of wild bonobos and chimpanzees have revealed that while reproductive success among group males is indeed biased towards males with high social rank, multiple adult males concurrently sire offspring belonging to their social group (Gerloff *et al*. 1999; Constable *et al*. 2001; Vigilant *et al*. 2001; Lukas *et al*. 2005). Furthermore,

males typically enjoy a high social rank status and its associated reproductive benefits for only a portion of their reproductive careers (Constable *et al*. 2001; Boesch *et al*. in press), further increasing the sharing of reproduction among the males. While these are qualitative rather than quantitative arguments, long-term data should soon allow for the estimation of skew indices (Nonacs *et al*. 2004; Widdig *et al*. 2004; Bradley *et al*. 2005) and so provide quantitative insights into the relationship between male reproductive skew and effective population size in bonobos and chimpanzees. When estimated from the data presented here, the male effective population size in bonobos is small and similar to that suggested from comparable data in humans, but these estimates are associated with large confidence intervals.

The estimates of the TMRCAs derived from the bonobo mtDNA HV1 and Y-chromosome microsatellite data are substantially different. At about 410 000 years ago, the estimate for the mitochondrial TMRCA is approximately 10 times greater than the estimate for the Y-chromosome TMRCA. In contrast, in humans the mitochondrial TMRCA at about 160 000 years ago is only about twice the depth of the Y-chromosome TMRCA of 60 000–90 000 years ago. Therefore, while the Y-chromosome TMRCAs are similar between humans and bonobos, the HV1 TMRCAs are quite different. A likely reason for this difference is the contrasting demographic histories of the two species. Patterns of genetic variation in humans suggest that humans underwent a population bottleneck and subsequent expansion (Sherry *et al*. 1994; Reich & Goldstein 1998; Ke *et al*. 2001), leading to a more recent mtDNA coalescent, in contrast to the stable demographic history suggested by the mtDNA and Y-chromosome data from bonobos.

In slowly maturing, long-lived wild animal species, dispersal is a rare event that is difficult to observe. This study demonstrates the potential of genetic analyses focusing on sex-linked markers for estimating the magnitude of difference in effective dispersal between the sexes, as well as investigating the long-term demographic history of species.

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This research comprises part of J. Eriksson's dissertation research on genetic variation in bonobos. H. Siedel is interested in adapting methods to meet the challenges of using noninvasive samples for genetic research on wild primates. D. Lukas explores analytical and modelling approaches for understanding the effects of social structure upon population genetic variation. M. Kayser and A. Erler focus mainly upon understanding human genetic variation and are also interested in the applicability of human markers in other species. C. Hashimoto, G. Hohmann and C. Boesch are field researchers with a strong appreciation of inter-disciplinary approaches. L. Vigilant is interested in using patterns of genetic variation to understand the social evolution of the great apes.
