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Differences in spatial genetic population structure between African and Asian elephant (*Loxodonta africana, Elephas maximus*) as revealed by sequence analysis of the mitochondrial Cyt *b* gene

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To assess spatial genetic population structure of both extant elephant species, we investigated sequence variation in 369bp of the mitochondrial Cyt *b* gene in 23 specimens of African elephant *Loxodonta africana* (Blumenbach, 1797) from three regions in the Southern part of Africa. In an integrated analysis, these results were compared to data of a previous study, where the same gene region had been analysed in 53 Asian elephants *Elephas maximus* (Linnaeus, 1758) from 5 different regions on Sri Lanka and Asian mainland. In *Loxodonta*, 14 polymorphic sites defined 6 different mitochondrial haplotypes with a mean sequence divergence of 2.085%. In *Elephas*, 6 polymorphic sites defined 8 different haplotypes with a mean sequence divergence of 0.942%. Compared to other mammals, genetic variation is high in *Loxodonta* and moderate in *Elephas*. The difference in genetic variation among the species could be explained either by a Pliocene bottleneck in *Elephas* or by different long term effective population sizes. In *Elephas*, a star like phylogeny of haplotypes was found, indicative of a population expansion after a bottleneck. In *Loxodonta*, very divergent mtDNA lineages coexisted, suggesting the absence of any bottleneck in population history. Within regional subpopulations, both species showed similar mean haplotype diversities, while mean nucleotide diversity within regions was higher in *Loxodonta* than in *Elephas*. This suggest larger long-term effective population sizes in *Loxodonta*, while short-term effective population sizes are presumably similar in both species. Spatial genetic population structure in *Loxodonta* is mainly determined by isolation-by--distance, while in *Elephas* it is impacted by human translocation. Human translocation might have prevented isolated small *Elephas* populations from severe genetic depletion.

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Introduction

At present, the order Proboscoidea is represented by only two extant species of the family Elephantidae, the African elephant *Loxodonta africana* (Blumenbach, 1797) and the Asian elephant *Elephas maximus* Linnaeus, 1758 (cf Yang *et al.*

1996, Shoshani *et al.* 1998, for details on elephantid phylogeny). Together with the extinct genus *Mammuthus* the two species share a common African ancestor living in the Pliocene (cf Haynes 1991, Yang *et al.* 1996, Shoshani *et al.* 1998). Within their distribution range, both species were formerly coherently distributed, the African elephant throughout entire Africa (cf Coppens *et al.* 1978), the Asian elephant from Persia through the Indian subcontinent into continental southern and southeastern Asia, into China up to the Yangtse Kiang, and on the islands Borneo, Sri Lanka, and Sumatra (cf Kurt 1992, Sukumar 1992). Both species experienced a decline in population sizes due to habitat fragmentation, hunting, poaching, and – especially in the case of Asian elephant – capturing, which has led to an incoherent distribution in subpopulations with presumably limited genetic exchange (cf Sukumar 1990, Kurt 1992, Georgiadis *et al.* 1994, Kurt *et al.* 1995, Barnes 1996). However, while this human threat might not have been significant before the 19th century for the African elephant, the Asian elephant has played an important role in the cultural, economic, and political life of Asia presumably for the last 4000 years, leading to severe impacts on population size more than 2000 years ago (cf Sukumar 1992, Sukumar *et al.* 1997). During this time, captive stocks of Asian elephants have been continuously replenished from the wild, and animals were frequently translocated (Kurt 1992, Sukumar *et al.* 1997). Today, about 1/4 of the world population of Asian elephant lives in captivity (Santiapillai and Jackson 1990, Sukumar 1992).

In this framework, the present study aims at a comparison of levels of genetic variation within subpopulations as well as genetic differentiation among subpopulations for the two extant elephant species, both providing an insight into their phylogeography and assessing the genetic effects of the different schemes of human impact on the species. We made use of the superior suitability of mitochondrial DNA for phylogeographic studies (cf Avise 1994) and choose a part of the mitochondrial cytochrome *b* (Cyt *b*)-gene as a marker system, which had already been demonstrated to be sufficiently polymorphic in elephants (Hartl *et al.* 1996).

Material and methods

A total of 23 specimens of African elephant were collected in three regions of the southern part of Africa in Northwest Namibia (Ovambo, Etoscha, $n = 18$), in Northeast Namibia (Caprivi, Bushmanland, $n = 4$), and at Kruger National Park/South Africa ($n = 1$). Samples consisted either of dry skin tissue from the ears of dead animals or of ethanol preserved skin tissue collected with a biopsy gun from live animals. From all samples, total DNA was extracted using the Super Quik Gene Kit (Analytical Genetic Testing Center, Denver) according to manufacturer's instructions.

Using the primers L14724 and H15149 developed by Irwin *et al.* (1991), a part of the mitochondrial cytochrome *b* gene was amplified by PCR (cf Hartl *et al.* 1996 for experimental details). Sequencing was performed either with the Sequitherm Cycle Sequencing Kit (Epicentre, Madison) and a direct blot sequencing device (Hoefer, San Francisco) or with the Amersham Thermosequenase Dye Terminator Kit (Amersham, Buckinghamshire) and an ABI 373 automatic sequencer (PE Applied Biosystems, Foster City), using both PCR primers for sequencing of the respective strand.

Mitochondrial haplotypes were defined based on 369bp scored sequence. In the subsequent data analysis, the corresponding cytochrome *b* sequences of 53 specimens of Asian elephant from 5 geographic regions (Hartl *et al.* 1996) were included for comparison of the two elephant species. For this purpose, sequences were truncated to the overlapping region of 307bp (position 34 to 340 in Hartl *et al.* 1996). Note that sequence truncation did not alter the number of distinct haplotypes. Based on pairwise nucleotide divergence among haplotypes, nucleotide diversities (π) were calculated within and among regions for the two elephant species (cf Quinn and White 1987). Within regions, haplotype diversities (δ) were estimated (cf Nei and Tajima 1981). Standard errors were estimated by bootstrap resampling (1000 replicates) over nucleotides for π and by jackknife resampling over specimens for δ (cf Efron 1982). Multiple pairwise comparison of δ and π were performed as sequential Bonferroni test (cf Sokal and Rohlf 1995). In an analysis of molecular variance (AMOVA, Excoffier *et al.* 1992), the total genetic variation detected was proportionally assigned to the three levels (1) among species, (2) among regions, and (3) within regions. Haplotypic correlation at the respective levels was described by the ϕ-statistic (Excoffier *et al.* 1992). Correlation (Pearson's product-moment-correlation coefficient; cf Sokal and Rohlf 1995) between geographic and genetic distance was calculated. On the Asian mainland, geographic distances were measured as terrestrial distances. Net nucleotide diversity among sampling locales was used as genetic distance measure. Relationships among the mitochondrial haplotypes were investigated in a Maximum-Parsimony (MP)-analysis and presented as median graphs (Bandelt 1992).

Results

The analysed 23 specimens of African elephant comprised 6 different haplotypes defined by 1–12 nucleotide polymorphisms at a total of 14 polymorphic sites (Table 1). One substitution (306) was a transversion and two substitutions (85, 145) occured at the first codon position, while 11 were third codon position transitions. The 53 Asian elephants analysed by Hartl *et al.* (1996) comprised 8 different haplotypes, differing from one another by 1–6 polymorphisms at 6 polymorphic sites, all third codon position transitions (Table 1). All these specimens (*Loxodonta* and *Elephas*) showed two fixed transversions (81, 129), when compared to the sequence of a *Loxodonta* specimen of unknown African origin published by Irwin *et al.* (1991). Haplotype LOX I was by far the most abundant type found in the analysed specimens (Table 2). Three other haplotypes (LOX II, IV, VI) were quite closely related to the abundant LOX I, while LOX III and LOX V presumably represented distant mtDNA lineages (Fig. 1a). In Asian elephant, two mtDNA lineages were found, both represented by one abundant (ELE V, ELE VI) and several closely related less abundant haplotypes (Fig. 1b). Mean sequence divergence among *Loxodonta* haplotypes was about twice as high as among *Elephas* haplotypes, a difference statistically highly significant (Table 7).

Of the total variation found in the mitochondrial Cyt *b* gene, 81.3% could be attributed to divergence among the two elephant species, while the remaining variation was mainly due to within region variation (17%), as revealed by the analysis of molecular variance (AMOVA; Table 3). Only 1.7% of the variation was due to divergence among geographical regions (Table 3). Excluding among species divergence from the AMOVA, the percentage of variation due to geographic

Table 1. Mitochondrial haplotypes found in the analysed African elephants (LOX I – VI) compared to a published African elephant sequence (LOX; Irwin *et al.* 1991), Asian elephant (ELE I – VIII confer to MAX I – VIII in Hartl *et al.* 1996) and Siberian woolly mammoth (MAM I – II, Hagelberg *et al.* 1994). Only polymorphic positions are given. Positions are numbered by vertical digits according to Hartl *et al.* 1996. ! – indicates transversions, * – substitutions at 1. or 2. position of the amino acid code of the Cyt *b* gene.

Haplotypes	0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 3 3 3 3 3 3 4 6 7 8 8 0 1 2 3 4 4 5 5 6 6 7 9 0 1 1 2 4 6 6 7 7 0 0 1 2 3 3 5 6 5 1 5 2 7 9 2 4 5 0 6 2 5 1 5 7 6 9 8 6 4 7 0 3 0 6 5 1 0 6 ! * ! * ! !
LOX	T T C A A C A A A A T C C T T C T T T A C A C T C C A C G C G T
LOX I	. . . C . . . C G . . . . . T . . . G . . . . . T . . . . .
LOX II	. . . C . . . C G . . . . . T . . . G . . . . . T G G . . . .
LOX III	. . . C G . . C G . C . . C . . . C . . . . T C . . G . A . . C
LOX IV	. . . C . . . C G . . . . . T . . . G . . . . . T G . . . . .
LOX V	. . . C G . . C G . . . . . T . . . G . . T C . . . . A . . C
LOX VI	. . . C . . C . . . . . G . . . . .
ELE I	C C T C . T G C . . . . . C T . C C C . G T C T . . . A T A C
ELE II	C C T C . . G C . . . . . C T C C C C . G T C T . . . A . A C
ELE III	C C T C . . G C . . . . . C T . C C C . G T C . . . . A T A C
ELE IV	C C T C . . . C . . . . . C T . C C C . . T C T . . . A . A C
ELE V	C C T C . . G C . . . . . C T . C C C . G T C T . . . A T A C
ELE VI	C C T C . . . C . . . . . C T . C C C . . T . . . . . A . A C
ELE VII	C C T C . . . C . . . . . C T . C C C . . T C . . . . A . A C
ELE VIII	C C T C . . G C . . . . . C T . C C C . G T C T . . . A . A C
MAM I	. . C G . . T . . . T . . . C . . T C
MAM II	. . C . G . T T . . T . C . C T . T C

Table 2. Frequencies of African elephant haplotypes found in this study at different regions (NWN – North West Namibia, NEN – North East Namibia, KNP – Kruger National Park).

Haplotypes	NWN	NEN	KNP
LOX I	14	2	–
LOX II	1	–	–
LOX III	2	1	–
LOX IV	1	–	–
LOX V	–	1	–
LOX VI	–	–	1

divergence was twice as high in *Loxodonta* (15.1%) as compared to *Elephas* (7.5%; Table 3). This was corroborated by another measure of genetic divergence, the mean net nucleotide diversity among regions, in *Loxodonta* being more than 5 times the value of *Elephas*, a difference statistically highly significant (Table 7).

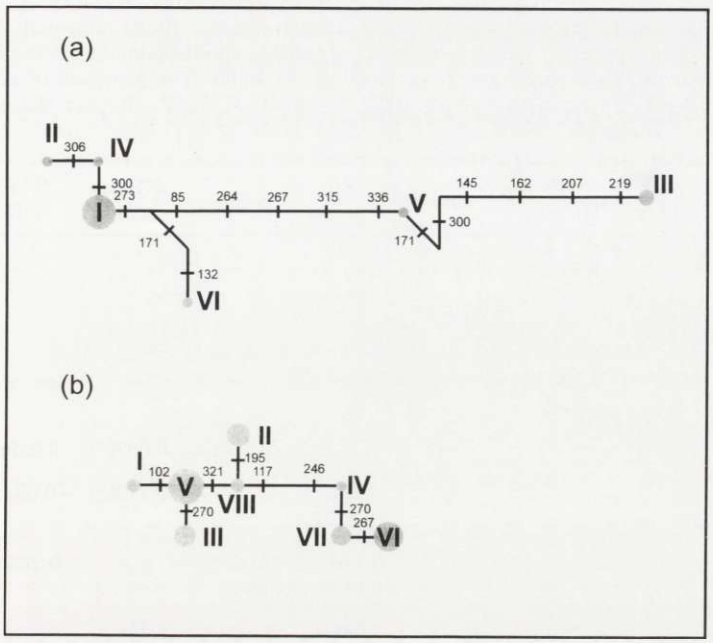

Fig. 1. Parsimonious networks (arranged as median graphs) of the relationships among haplotypes of African (a) and Asian (b) elephant (data for the Asian elephant from Hartl *et al.* 1996). Haplotypes are given as grey circles with size of circle area proportional to absolute haplotype frequency. Roman numbers refer to haplotypes (LOX in a, ELE in b). Arabic numbers indicate nucleotide position of polymorphism. Three homoplasious mutations were found, two in *Loxodonta* (position 171 and 300) and one in *Elephas* (position 270).

Table 3. Hierarchical analysis of molecular variance (AMOVA; cf Excoffier *et al.* 1992) of Cyt *b* sequence variation in elephants within and among regions and among the two elephant species (data for the Asian elephant calculated from Hartl *et al.* 1996). 1–3: analysis for both species; 2a–3a and 2b–3b: separate analysis for *Loxodonta* and *Elephas*, respectively (ns – $p > 0.1$, (*) – $p < 0.1$, *** – $p < 0.001$).

Level	Source of variation	Variance	% total	ϕ statistic	p
1	Among species	6.486	81.3	$\phi_{CT} = 0.813$	0.000***
2	Among regions within species	0.137	1.7	$\phi_{SC} = 0.092$	0.088(*)
3	Within regions	1.357	17.0	$\phi_{ST} = 0.830$	0.000***
2a	Among *Loxodonta* regions	0.303	15.1	–	–
3a	Within *Loxodonta* regions	1.706	84.9	$\phi_{ST} = 0.151$	0.173ns
2b	Among *Elephas* regions	0.101	7.5	–	–
3b	Within *Elephas* regions	1.243	92.5	$\phi_{ST} = 0.075$	0.063(*)

Net nucleotide diversity among regions was significant for all pairwise comparisons within species, while pairwise ϕ_{ST} values were only significant at $p < 0.1$ among several regions of *Elephas* (Table 4).

Table 4. Above diagonal: Pairwise ϕ_{ST} distances among regions. Below diagonal: Net nucleotide diversities among regions (in %). Values are given only within species (standard error in parenthesis; data for the Asian elephant calculated from Hartl *et al.* 1996). The significance of divergence is indicated (ns – $p > 0.1$, (*) – $p < 0.1$, * – $p < 0.05$; ** – $p < 0.01$, KNP – Kruger National Park, Mya – Myanmar, Thai – Thailand).

Location	NW Namibia	NE Namibia	KNP	Sri Lanka	S India	NE Ind N Mya	S Mya N Thai	E Thai Vietnam
NW Namibia	–	0.125ns	0.315ns	–	–	–	–	–
NE Namibia	0.328** (0.119)	–	−0.167ns	–	–	–	–	–
KNP	0.892* (0.478)	1.118* (0.432)	–	–	–	–	–	–
Sri Lanka	–	–	–	–	−0.065ns	0.097(*)	0.029ns	0.130(*)
S India	–	–	–	0.024(*) (0.017)	–	0.119(*)	−0.034ns	0.110ns
NE India N Mya	–	–	–	0.119* (0.057)	0.140* (0.069)	–	0.163(*)	−0.007ns
S Mya N Thai	–	–	–	0.095(*) (0.060)	0.080(*) (0.057)	0.198(*) (0.122)	–	0.124(*)
E Thai Vietnam	–	–	–	0.236* (0.109)	0.186* (0.099)	0.142* (0.070)	0.187* (0.107)	–

Table 5. Haplotype diversity (δ) and nucleotide diversity (π; in %) in analysed regions of African and Asian elephant (Kruger National Park data excluded because of small sample size; data for the Asian elephant calculated from Hartl *et al.* 1996; Mya – Myanmar, Thai – Thailand).

Species	*Loxodonta africana*		*Elephas maximus*				
Location	NW Namibia	NE Namibia	Sri Lanka	S India	NE India N Mya	S Mya N Thai	E Thai Vietnam
n	18	4	14	9	11	8	11
δ	0.399	0.833	0.835	0.667	0.800	0.750	0.655
(SE)	(0.039)	(0.192)	(0.020)	(0.056)	(0.020)	(0.022)	(0.040)
π	0.791	1.697	0.759	0.616	0.823	0.525	0.773
(SE)	(0.226)	(0.487)	(0.286)	(0.275)	(0.340)	(0.255)	(0.338)

Levels of genetic variation within two regions of African and five regions of Asian elephant are given in Table 5. Haplotype diversity (δ) was significantly lower in the NW Namibia population of *Loxodonta* than in all other analysed regions of both *Loxodonta* and *Elephas* (Table 5, 6). Among regions in *Elephas*, was significantly lower in south India (compared to Sri Lanka) and east Thailand/

Table 6. Pairwise comparisons of within region haplotype diversity (δ, upper triangular) and nucleotide diversity (π, lower triangular) in regions for African and Asian elephant. Given are rounded *p* values (*t*-test) and significance in sequential Bonferroni tests (ns – not significant, (*) – significant at experimentwise error rate (α) = 0.1, * – significant at α = 0.05, ** – significant at α = 0.01, *** – significant at α = 0.001) (Kruger National Park data excluded because of small sample size; data for the Asian elephant calculated from Hartl *et al.* 1996; Mya – Myanmar, Thai – Thailand).

Species	*Loxodonta africana*		*Elephas maximus*				
Location	NW Namibia	NE Namibia	Sri Lanka	S India	NE India N Mya	S Mya N Thai	E Thai Vietnam
NW Namibia	–	0.001 *	0.000 ***	0.001 **	0.000 ***	0.000 ***	0.000 **
NE Namibia	0.103 ns	–	0.985 ns	0.286 ns	0.775 ns	0.545 ns	0.186 ns
Sri Lanka	0.930 ns	0.136 ns	–	0.003 *	0.235 ns	0.013 ns	0.000 **
S India	0.645 ns	0.063 ns	0.737 ns	–	0.026 ns	0.208 ns	0.860 ns
NE India N Mya	0.936 ns	0.194 ns	0.886 ns	0.652 ns	–	0.114 ns	0.004 (*)
S Mya N Thai	0.492 ns	0.039 ns	0.589 ns	0.813 ns	0.522 ns	–	0.626 ns
E Thai Vietnam	0.964 ns	0.170 ns	0.975 ns	0.731 ns	0.918 ns	0.620 ns	–

Table 7. Comparison of population genetic measures between African and Asian elephant (standard errors in parentheses; statistical methods: [a]*t*-test for hederoscedastic data; [b]*t*-test for homoscedastic data, data log-transformed to reach homoscedasticity).

Measure	*Loxodonta*	*Elephas*	*p*
n	23	53	–
No of haplotypes	6	8	–
No of polymorphic sites	14	6	–
Mean sequence divergence among haplotypes (%)	2.085 (0.322)	0.942 (0.089)	0.003[a]
Mean haplotype diversity within regions	0.616 (0.217)	0.741 (0.036)	0.666[a]
Mean nucleotide diversity within regions (%)	1.244 (0.453)	0.699 (0.056)	0.089[b]
Mean net nucleotide diversity among regions (%)	0.779 (0.235)	0.141 (0.020)	0.002[b]

/Vietnam (compared to Sri Lanka and NE India/North Myanmar; Tables 5, 6). Among the two elephant species, no significant difference in mean values of δ were obtained (Table 7). Within species, no significant differences in within region nucleotide diversity (π) were detected (Tables 5, 6). However, comparing mean values among the two species, genetic variation was significantly higher in

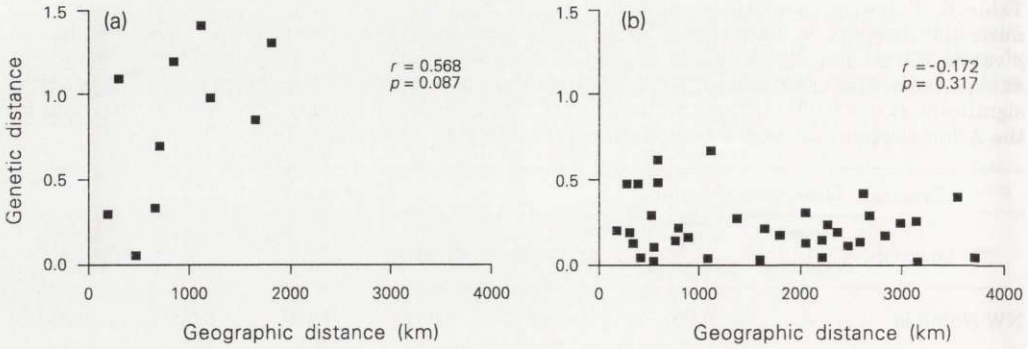

Fig. 2. Correlation between approximate geographic and genetic distance (net nucleotide diversity in % among sampling locales) for African (a) and Asian (b) elephant (data for the Asian elephant from Hartl *et al.* 1996).

Loxodonta than in *Elephas* (Table 7). In *Loxodonta*, geographic and genetic distance were significantly positively correlated (Fig. 2a), while such a correlation was absent in *Elephas* (Fig. 2b).

Discussion

Levels of genetic variation in elephants

Allozyme studies (*Elephas, Loxodonta*: Drysdale and Florkiewicz 1989, *Loxodonta*: Coetzee *et al.* 1993, *Elephas*: Nozawa and Shotake 1990, Hartl *et al.* 1995, Tiedemann *et al.* 1996), DNA fingerprinting (*Elephas*: Bischof and Duffield 1994), mitochondrial DNA RFLP analysis (*Loxodonta*: Georgiadis *et al.* 1994), and previous DNA sequencing of the mitochondrial cyt *b* gene (*Elephas*: Hartl *et al.* 1996) have demonstrated a considerable amount of genetic variation to be present in elephants, apparently indicative of the absence of a recent population bottleneck.

The present study confirms high levels of genetic variation to be present at least in *Loxodonta*: The mean divergence among haplotypes of *Loxodonta* (2.09%) almost reached the level found in the highly polymorphic fur seal species *Arctocephalus forsteri* (3.40 %; Lento *et al.* 1997). The maximum divergence among haplotypes in *Loxodonta* (3.91%) exceeded values for many canids (eg coyote *Canis latrans* – 2.5%, Lehman and Wayne 1991; red fox *Vulpes vulpes* – 1.2%, Geffen *et al.* 1992; gray wolf *Canis lupus* – 0.8%, Wayne *et al.* 1992). The mean divergence among *Elephas* haplotypes (0.94%) was moderate and exceeded eg variation levels in some less variable fur seal species (*A. pusillus* – 0.47%, *A. tropicalis* – 0.55%, *A. gazella* – 0.37%, Lento *et al.* 1997). The maximum divergence among haplotypes in *Elephas* (1.95%) exceeded values for red fox and wolf (see above). Hence, we conclude that none of the two extant elephant species has undergone a recent dramatic population bottleneck.

However, much more sequence variation was found in the cytochrome *b* gene of *Loxodonta* than in *Elephas* (cf Table 7, Fig. 1). Two possible explanations may account for this result: First, *Elephas* may have gone through an ancient population bottleneck, possibly as far back as when the species invaded Asia out of Africa during the Pliocene (Haynes 1991). Divergence rates in the cytochrome *b* gene have been estimated to be about 0.15 to 0.2% per million years (Ozawa *et al.* 1997) and are probably as high as 0.3% per million years within the Elephantidae (Irwin *et al.* 1991). Thus, if the invasion of Asia by *Elephas* might have caused a population bottleneck and genetic depletion, it might take some million years to regain a mean divergence of about 1%, as found in extant Asian elephant. Second, the different levels of genetic variation in the two elephant species might by indicative of different long term effective population sizes (N_e). For the African elephant, long term effective female population size ($N_{e(f)}$) has been estimated to be at least 50 000 (Georgiadis *et al.* 1994). For the Asian elephant, guesses on former population sizes give about 375 000 individuals at 330 BC (cf Hartl *et al.* 1996), before severe human impact started. If we assume half of this number to be females and adopt the relationship described by Avise *et al.* (1988) that effective population sizes are two to three orders of magnitudes smaller than census population sizes, $N_{e(f)}$ could be less than 2 000 in *Elephas*, hence significantly smaller than in *Loxodonta*.

Relationship among mitochondrial haplotypes

In Asian elephant, a so-called star like phylogeny among mitochondrial haplotypes was found for each of the two observed lineages, consisting of an abundant haplotype (ELE V and ELE VI, respectively; cf Fig 1b), from which several closely related less abundant haplotypes can be derived. Such a phylogeny is typical for species having experienced population expansion after a bottleneck (Avise *et al.* 1984). While such star like phylogeny in the rapidly evolving mitochondrial control region has been considered indicative of a Pleistocene bottleneck in several mammalian species (eg harbour seal *Phoca vitulina*, Stanley *et al.* 1996; roe deer *Capreolus capreolus*, Wiehler and Tiedemann 1998; harbour porpoise *Phocoena phocoena*, Rosel *et al.* 1998), in the slowly evolving cytochrome *b* gene it is considered indicative of a more ancient bottleneck and might hence provide further evidence for an ancient bottleneck having occurred in the course of the invasion of *Elephas* into Asia.

In African elephant, the relationship among mitochondrial haplotypes seems to be strikingly different (Fig. 1a): Though haplotypes closely related to the most abundant type LOX I occured (LOX II, LOX IV), also single very divergent haplotypes were found (LOX III, LOX V), occuring in the same regions as LOX I (cf Table 2). Though our limited and geographically biased sampling does not allow reliable relative frequency estimations of the divergent lineages in *Loxodonta*, the coexistence of these lineages again suggests a large long term effective population size, where different divergent lineages could be maintained. The coexistence of divergent mitochondrial lineages in African elephant has also been revealed in an RFLP study on populations of Zimbabwe, Tanzania, and Botswana, while in Kenya

and South Africa only one major lineage was found (Georgiadis *et al.* 1994). These authors also concluded that $N_{e(f)}$ must be large in *Loxodonta*.

Genetic differentiation among geographic regions

Within geographic regions, both extant elephant species exhibited similar mean levels of haplotypic diversity (δ), while mean within region nucleotide diversity (π) was significantly higher in *Loxodonta* (Table 7). Contrasting these two values can provide insight into long term vs short term effective population size (cf Wiehler and Tiedemann 1998). While the higher values of π in *Loxodonta* are again indicative of a larger long-term effective population size, δ values much more reflect short term effective population size, since it is a measure affected by the number and frequency of haplotypes, but not by haplotype divergence (Nei and Tajima 1981). This could indicate that short term effective population sizes for regional subpopulations are similar in both elephant species. Given the fragmentation and decline of regional subpopulations of Asian elephant due to human impact (Kurt *et al.* 1995), it is unlikely that regional elephant subpopulation sizes are equal in both elephant species. However, an effective population size in *Elephas* which is comparable to that in *Loxodonta* may also result from more pronounced gene flow among subpopulations in the former species. This is corroborated by the much less obvious divergence among regions in *Elephas* compared to that in *Loxodonta*, as indicated by the AMOVA (Table 3) and the differences in mean net nucleotide diversity among regions (Table 7). However, due to habitat fragmentation in Asia, pronounced gene flow among adjacent regions is unlikely to occur. Hence, the most likely cause for gene flow among regions in Asian elephant is translocation by humans (Kurt 1992, Sukumar *et al.* 1997). This hypothesis is corroborated by the lack of correlation between geographic and genetic distance in *Elephas* (Fig. 2b), and by the very low genetic divergence among elephants from South Myanmar/North Thailand vs. South India/Sri Lanka (Table 4), since between these areas intensive translocation in historical times is documented.

On the contrary, translocation has not occured in African elephant. A pronounced genetic divergence among regional subpopulations could be found (Tables 3, 4, 7). Geographic and genetic divergence of regional subpopulations are significantly correlated (Fig. 2a), indicating isolation-by-distance to be the paramount factor affecting subpopulation segregation, in congruence with the results of previous studies (Georgiadis *et al.* 1994, Siegismund and Arctander 1995). Among the analysed regional subpopulations of *Loxodonta*, the NW Namibia region is peculiar for its decreased haplotype diversity (δ), which could be indicative of a small short-term effective population size, having caused genetic depletion by random genetic drift.

In conclusion, geographic patterns of genetic population structure are strikingly different among the two extant elephant species: In *Loxodonta*, isolation-by--distance is of paramount importance in determining gene flow among regions, while gene flow among *Elephas* regional subpopulations is to a considerable extent

due to human translocation. In this framework, translocation among *Elephas* subpopulations might even have prevented genetic depletion which otherwise should be expected in relatively small, isolated local subpopulations.

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