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Gene Flow Dynamics in Baboons

- The Influence of Social Systems -

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Für Tobi und Lina

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SUMMARY

The relationship between genes and behaviour has been of longstanding interest to evolutionary biologists. Certain behaviours can shape the genetic structure of natural populations, thereby altering their genetic diversity and influencing their evolutionary fate. Dispersal is the behaviour that mediates gene flow, the extent of which determines population genetic structure. Because both historic and contemporary gene flow are considered to have greatly impacted their evolutionary history, baboons (genus *Papio*) are especially intriguing to study the relationship between behaviour and population genetic structure. Both species-specific male- and female-biased dispersal can be observed in this genus, their current distribution was shaped by range expansion and contraction, and interspecific gene flow is prevalent.

In this thesis, I investigated how different dispersal patterns influence gene flow in baboons to contribute to a better understanding of the interrelation between behavioural ecology and genetic makeup of natural populations. I specifically addressed how differences in the social system of baboon species impact their genetic structure and also used the observed patterns to draw inferences about sex-biased dispersal in Guinea baboons, one of the least known members of the genus. I examined in detail how both historic and contemporary gene flow shape the genetic structure of Guinea baboons and whether we can draw inferences about human evolution from the analysis of range expansions in baboons. To answer these questions, I used a population genetic approach based on distribution-wide, geo-referenced faecal samples of baboons for which I analysed both autosomal microsatellites and part of the mitochondrial hypervariable region I.

I could show that the genetic structure of Guinea baboons is best explained by female-biased dispersal, both on a local and a distribution-wide scale. Female gene flow results in high intrapopulation diversity and a lack of genetic-geographic structuring in mitochondrial DNA. In contrast, there is significant structuring of nuclear markers on a global scale and males exhibit higher population structuring than females on a local scale, as expected if males are the more philopatric sex. Over the whole distribution, locally restricted dispersal appears to limit effective gene flow to a distance of below 200 km, resulting in a strong isolation-by-distance effect and genetically divergent populations. Signatures of population expansion, the clinal structure of genetic variation, and potential traces of allele surfing, point to an his-

toric west-ward expansion of Guinea baboons. Introgressive hybridization with olive baboons can be invoked to explain genetic patterns in the contact zone, but warrant further investigation. Additionally I could show the 'southern route' from Africa to Arabia could have been used by hamadryas baboons during the same time period in the Late Pleistocene as proposed for modern humans.

My study is the first comprehensive analysis of the genetic population structure in Guinea baboons and provides evidence for female-biased dispersal in this species. It corroborates the notion that the Guinea baboons' social system shares some important features with that of hamadryas baboons, suggesting similar evolutionary forces have acted to distinguish them from all other baboons. In conjunction with the importance of range expansions in shaping their distribution and genetic diversity, this strengthens baboons as an intriguing model to elucidate the processes that also influenced the evolution of our own species.

ZUSAMMENFASSUNG

Die Beziehung zwischen Genen und Verhalten ist in der Evolutionsbiologie von besonderem Interesse. Bestimmte Verhaltensweisen können die genetische Struktur natürlicher Populationen gestalten, dadurch deren genetische Diversität verändern und so ihr evolutives Schicksal beeinflussen. Abwanderung aus der Geburtsgruppe ist eine dieser Verhaltensweisen. Sie beeinflusst Genfluss, dessen Ausmaß die genetische Struktur von Populationen bestimmt. Paviane (Gattung *Papio*) sind ein besonders interessantes Forschungssystem um die Beziehung zwischen Verhalten und populationsgenetischer Struktur zu untersuchen. Die Evolution der Paviane wurde sowohl von historischem als auch gegenwärtigem Genfluss geprägt. Innerhalb dieser Gattung treten sowohl die überwiegende Abwanderung von Männchen als auch die überwiegende Abwanderung von Weibchen auf. Zudem wurde ihre gegenwärtige Verbreitung maßgeblich von Populationsausbreitung und –rückzug beeinflusst und es tritt häufig Genfluss zwischen verschiedenen Arten auf.

In meiner Doktorarbeit untersuchte ich, wie verschiedene Abwanderungsmuster den Genfluss bei Pavianen beeinflussen. Damit hoffe ich zu einem besseren Verständnis der Wechselbeziehung zwischen Verhaltensökologie und Genetik in natürlichen Populationen beizutragen.

Ich fokussierte mich darauf, wie Unterschiede in den Sozialsystemen unterschiedlicher Pavianarten deren genetische Struktur beeinflussen. Die beobachteten Muster nutzte ich, um auf das geschlechtsspezifische Abwanderungsmuster bei Guineapavianen zu schließen, eine der am wenigsten untersuchten Pavianarten. Zudem untersuchte ich, wie sowohl historischer als auch gegenwärtiger Genfluss die genetische Struktur der Guineapaviane formten und ob es möglich ist von der Populationsausbreitung der Paviane Rückschlüsse auf die menschliche Evolutionsgeschichte zu ziehen. Um diese Fragen zu beantworten nutzte ich einen populationsgenetischen Ansatz, basierend auf im gesamten Verbreitungsgebiet gesammelten Kotproben, deren exakter geographischer Ursprung bekannt war. Ich analysierte sowohl autosomale Mikrosatelliten als auch Sequenzen der mitochondrialen Hypervariablen Region I.

Meine Ergebnisse zeigen, dass die genetische Struktur der Guineapaviane am besten durch die überwiegende Abwanderung von Weibchen erklärt werden kann, sowohl in einem lokalen als auch im globalen Kontext. Weiblicher Genfluss führt zu einer hohen Diversität innerhalb von Populationen sowie einem Fehlen von genetisch-

geographischer Struktur in mitochondrialer DNA. Nukleäre DNA hingegen zeigt eine starke globale geographische Struktur und Männchen sind im Vergleich zu Weibchen durch eine stärkere lokale Struktur gekennzeichnet. Dies entspricht den Vorhersagen für ein System, in welchem hauptsächlich Weibchen abwandern und Männchen in ihrer Geburtsgruppe verbleiben.

Insgesamt scheint lokal begrenzte Abwanderung den wirksamen Genfluss auf eine Distanz unter 200 km zu beschränken, was zu einem starken Isolation-durch-Distanz Effekt und genetisch differenzierten Populationen führt. Anzeichen für Populationsausbreitung, die graduelle Struktur genetischer Variation, und mögliche Hinweise auf das "Allele-surfing" Phänomen, deuten auf eine historische westwärts gerichtete Ausbreitung von Guineapavianen hin. Introgressive Hybridisierung mit benachbarten Anubispavianen könnte genetische Muster im Bereich der Kontaktzone erklären, muss aber im Detail noch untersucht werden. Zusätzlich konnte ich zeigen, dass Mantelpaviane vermutlich im gleichen Zeitraum des Späten Pleistozäns von Afrika nach Arabien wanderten, wie Hypothesen für den modernen Menschen vorschlagen.

Meine Studie ist die erste umfassende Analyse der genetischen Populationsstruktur der Guineapaviane und liefert Belege für die überwiegende Abwanderung von Weibchen in dieser Art. Dies untersützt die Ansicht, dass das Sozialsystem der Guineapaviane einige vergleichbare Merkmale zum System der Mantelpaviane aufweist und deutet somit darauf hin, dass während der Evolution dieser beiden Arten besondere evolutionäre Drücke gewirkt haben, die sie von allen anderen Pavianarten abgrenzen.

In Kombination mit dem starken Einfluss von Populationsausbreitungen auf ihre Verbreitung und genetische Diversität, bekräftigt meine Arbeit Paviane als interssanten analogen Modellorganismus, der helfen kann, die Prozesse die während der Evolution des Menschen maßgeblich waren, aufzuklären.

CHAPTER 1: INTRODUCTION

The relationship between genes and behaviour has been of longstanding interest to evolutionary biologists. Clarifying the genetic basis of animal behaviours is essential to understand behavioural adaptations and the evolution of individual behavioural patterns (Rittschof & Robinson 2014). Tremendous advances in genomic techniques in recent years have enable scholars to pinpoint an increasing number of genetic variants underlying specific behavioural traits in animals (Flint 2003; Robinson 2004; Mackay *et al*. 2005; Robinson *et al*. 2008) and this progress will eventually help us to understand the mechanisms that form the basis of behavioural variation in natural populations. However, it is important to note that genes and behaviour are mutually influential. Firstly, sexual selection can drive changes in phenotypically preferred traits through mate choice, thereby promoting genetic changes underlying these traits (Kopp *et al*. 2000, 2003; Chenoweth & McGuigan 2010; Wilkinson *et al*. 2015). Secondly, individual behaviours may trigger or prevent gene expression through epigenetic modifications (Robinson *et al*. 2008; Tung *et al*. 2011). It has been shown, for instance, that in yellow baboons (*Papio cynocephalus*) the dominance rank of the mother impacts gene-expression of her offspring (Tung *et al*. 2011) and that maternal investment can alter the epigenomic state of offspring in laboratory rats (Weaver *et al*. 2004). Finally, behaviours that influence gene flow shape the genetic structure and diversity of natural populations, having a strong impact on the evolutionary trajectory of both populations and species. One of the main pathways through which behaviour directly influences gene flow is the movement of an organism (Slatkin 1985). Populations with high intra-population gene flow represent a panmictic and both genetically and phenotypically homogenous entity, while restricted intra-population gene flow may lead to several genetically differentiated populations with distinct gene pools that potentially react differently to selection pressures or might eventually diverge into separate species (Hutchison & Templeton 1999; Avise 2009). Hence, gene flow provides a powerful conceptual link between the behavioural ecology and the evolution of a population or species (Bohonak 1999).

In my thesis, I am investigating how different gene flow mechanisms shape the genetic structure of baboons. I especially focus on the influence of sex-biased dispersal on gene flow in one of the least investigated members of the genus, the Guinea baboon (*Papio papio*). In this introduction, I will first give an overview about some pathways of gene flow and molecular approaches to study it. Secondly, I will present

why baboons represent an intriguing study system to explore the interrelation of gene flow and behaviour, and finally, I will describe the major aims of this project.

1.1. Gene flow

Quantifying the spatial and temporal dynamics of natural populations' genetic structure can help us to elucidate their evolutionary trajectories. In concert with genetic drift, natural selection, and mutation, one of the main determinants of genetic structure is gene flow, the movement of alleles between and their integration in populations (Slatkin 1985). While it was previously assumed that gene flow maintains a species' homogeneity (Mayr 1942, 1963), its evolutionary importance was later questioned as being limited in nature and destructive by preventing local adaptation and speciation (Ehrlich & Raven 1969; Endler 1977). However, it is now widely acknowledged that gene flow is an essential microevolutionary force (Slatkin 1985; Bohonak 1999).

There is a suite of processes how gene flow, especially its direction and magnitude, affects the integrity of populations and even species, ranging from complete divergence (no gene flow) or amalgamation (strong gene flow) to introgression (unidirectional gene flow) and formation of new populations (Fig. 1.1) (Jacobsen & Omland 2011). In animals, the primary mechanism underlying gene flow is the movement of individuals (Slatkin 1985), the extent of which is shaped by individual behavioural patterns, ecological factors and landscape characteristics, demographic history, and interspecific relationships.

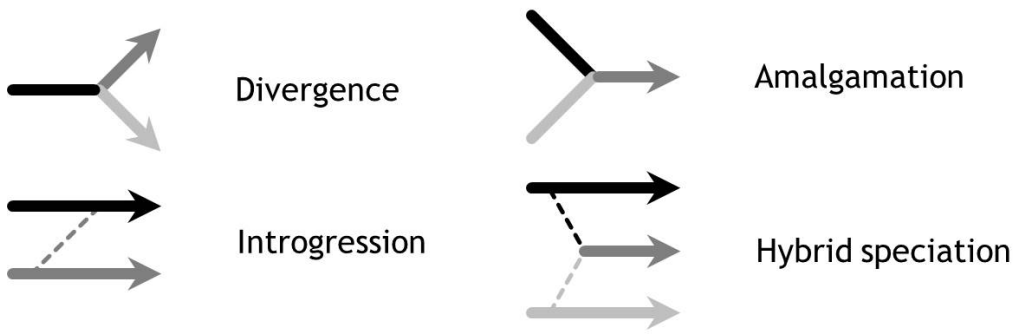

Fig. 1.1.: Evolutionary scenarios of the effects of gene flow (modified from Jacobsen & Omland 2011)

1.1.1. Dispersal

Dispersal, an animal's movement away from its natal area or group to reproduce (Pusey & Packer 1987; Clobert *et al*. 2001) is an important life history trait, which greatly affects the fitness of an individual. Beyond the individual level, dispersal has major implications for both the dynamics and the genetic makeup of populations (Bohonak 1999; Prugnolle & de Meeus 2002). Many taxa exhibit sex-biased dispersal, i.e. one sex shows a greater tendency to leave its natal area or to move further away than the other (Greenwood 1980; Pusey 1987). Male dispersal and female philopatry is predominant in mammals (Greenwood 1980), but exceptions can be found, e.g. in some non-human primates, equids, and some bats (Lukas & Clutton-Brock 2011), and presumably in the majority of human societies (Seielstad *et al*. 1998; Wilkins & Marlowe 2006; Lawson Handley & Perrin 2007; Marks *et al*. 2012).

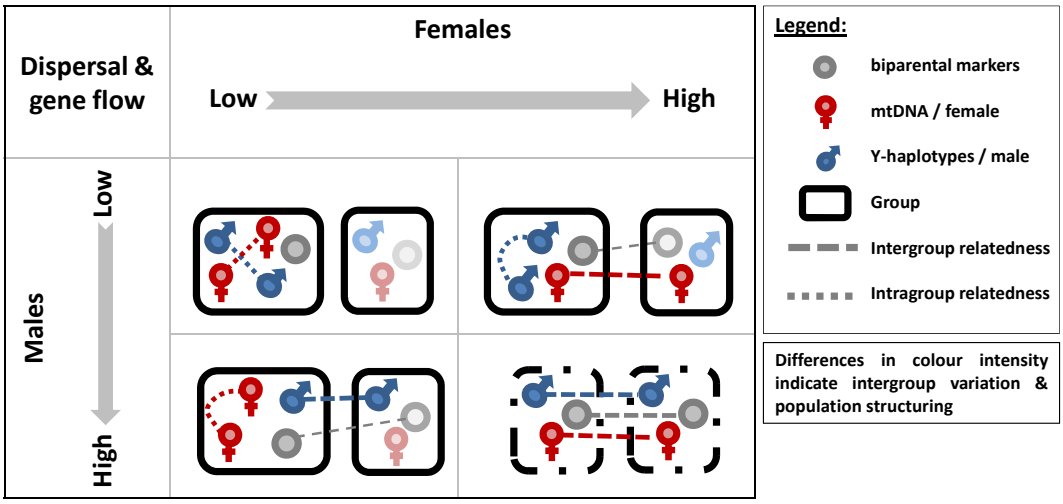

Fig. 1.2.: Impact of different patterns of dispersal and gene flow on genetic population structure and relatedness. Depending on the amount of gene flow among groups or populations and the genetic marker system under investigation, different patterns of population structure can be expected (modified from Avise 2004).

A sex-bias in dispersal translates into a specific genetic population structure. When dispersal is biased towards one sex, uniparentally inherited genetic markers show incongruent patterns in population structure (Avise 2004) (Fig. 1.2). In mammals, therefore, a stronger geographic structuring of the maternally inherited mitochondrial DNA (mtDNA), but not the paternally inherited Y-chromosomal haplotypes, is often observed (Avise 2004). Consequently, dispersal is a behaviour that connects

the social system of a species with its genetic diversity and represents a central factor in population genetics and population dynamics (Broquet & Petit 2009). In addition to its evolutionary force within species, it has been recently shown theoretically that differences in sex-biased dispersal have the power to significantly alter the spread rate of population expansions (Miller *et al*. 2011; Shaw & Kokko 2015).

1.1.2. Range Expansion

Dispersal strategies can strongly influence how populations shift their ranges (Ibrahim *et al*. 1996) and how they are capable of colonizing new regions. Range expansions may occur in response to geological events or climate fluctuations that produce environmental shifts thus creating new suitable habitats or dispersal corridors (Hewitt 2000; Parmesan & Yohe 2003). Moreover, populations may evolve novel adaptations that allow them to colonize previously inaccessible regions (Lee 2002; Gray *et al*. 2009; van Bocxlaer *et al*. 2010). The current distribution of populations is often a function of how they reacted to changing ecosystems. In particular, the isolation and reconnection of suitable areas have major impacts on dispersal and hence gene flow among populations. Accordingly, Plio-Pleistocene glacial climate oscillations and related range contractions and extensions account for a considerable amount of the present-day geographical distribution of populations and their genetic diversity in numerous climate zones and biomes (e.g. African savannah: deMenocal 1995, 2004; Arctander *et al*. 1999; Vrba 1999; Cerling *et al*. 2011; Lorenzen *et al*. 2012; Haus 2013). However, there is notable variation among taxa in how they respond to these extrinsic processes (Hewitt 1996, 2011; Bisconti *et al*. 2011; Haus 2013), and this is probably mainly attributable to differences in fundamental biological properties, such as dispersal capability and general adaptability.

Interestingly, range expansions also generate distinctive evolutionary forces at the expanding range margins, which influence and are also influenced by the dynamics of the expansion and resulting genetic patterns (Austerlitz *et al*. 1997; Klopfstein *et al*. 2006; Excoffier *et al*. 2009; Travis *et al*. 2010; White *et al*. 2013). These forces can be either of stochastic nature (Austerlitz *et al*. 1997; Hallatschek *et al*. 2007; Excoffier & Ray 2008; Slatkin & Excoffier 2012) or driven by altered selective pressures (Travis & Dytham 2002; Burton *et al*. 2010; Phillips *et al*. 2010; Datta *et al*. 2013). Especially increased dispersal and reproduction in expanding edge populations has been shown both theoretically (Travis & Dytham 2002; Burton *et al*. 2010; Shine *et al*. 2011) and empirically in several taxa throughout the animal kingdom (Simmons

& Thomas 2004; Phillips *et al*. 2006; Hughes *et al*. 2007; Moreau *et al*. 2011). However, to my knowledge, theoretical work is largely based on models of asexual organisms (but see Miller *et al*. 2011; Shaw & Kokko, 2015) and there is a lack of studies explicitly analysing the role of sex-bias in dispersal in the framework of range expansions.

1.1.3. Interspecific gene flow and introgression

By expanding their ranges, populations often come into contact with or invade the range of neighbouring populations. Both intra- and interspecific factors, such as mate recognition and reproductive isolation, determine the extent and magnitude of gene flow in this context. Natural hybridization may occur if individuals of distinct populations reproduce successfully (Arnold 1997). This phenomenon is now recognized to be widespread and considered a major evolutionary process (Barton & Hewitt 1985; Hewitt 1988; Arnold 1992, 1997, 2006; Mallet 2005; Schwenk *et al*. 2008; Abbott *et al*. 2013). The investigation of interspecific gene flow sheds light on the selective forces that separate species (Barton & Hewitt 1985), the mechanisms of reproductive isolation (Arnold 1992), the adaptive value of certain traits (McDonald *et al*. 2001), hybrid speciation (Mallet 2007; Nolte & Tautz 2010; Abbott *et al*. 2013) and the influence of introgression on species integrity (Payseur 2010).

Especially the role that interspecific gene flow has played throughout the evolution of our own lineage has attracted much attention (Jolly 2001; Holliday 2003; Stefansson *et al*. 2005; Trinkaus 2005; Arnold & Meyer 2006; Gibbons 2011); the most intensively investigated probably being the relationship between Neanderthals and modern humans (Duarte *et al*. 1999; Tattersall & Schwartz 1999; Plagnol & Wall 2006; Garrigan & Kingan 2007; Wolpoff 2009; Green *et al*. 2010; Sankararaman *et al*. 2012, 2014; Callaway 2014; Prüfer *et al*. 2014; Kelso & Prüfer 2014; Frantz *et al*. 2014) and lately Denisovans (Abi-Rached *et al*. 2011; Reich *et al*. 2011; Disotell 2012; Huerta-Sánchez *et al*. 2014).

Interspecific gene flow is most likely to occur between closely related species that diverged recently (Mallet 2005). It might either persist despite divergence or recur after isolation in cases of secondary contact. Depending on the strengths of selection and drift, certain genomic regions of one population can invade the genome of the other population, resulting in a mosaic genome (Arnold & Meyer 2006), a process called introgression (Mallet 2005). Depending on the sex-bias and symmetry in dispersal different introgression patterns will manifest. In mammals with male-biased dis-

persal, for instance, unidirectional gene flow can lead to nuclear swamping (Zinner *et al*. 2011a).

1.1.4. Approaches to study gene flow in natural populations

Molecular techniques are used to elucidate the amount of gene flow by investigating genetic patterns within and among natural populations. Hence, they constitute an indirect method to infer dispersal patterns and examine range expansions and interspecific relationships.

A first crucial factor in studies of gene flow is the choice of appropriate genetic markers. They need to be highly polymorphic and exhibit large variation over a rather small geographic scale to have enough resolution for intraspecific analyses and be informative on an appropriate time scale (Sunnucks 2000; Balkenhol *et al*. 2009; Garrick *et al*. 2010). In addition, their mode of inheritance is important. Due to their uniparental inheritance, in mammals, Y-chromosomal markers and mitochondrial DNA can provide insights into patrilines and matrilines of populations, respectively (Avise 2004; Eriksson *et al*. 2006; Hammond *et al*. 2006). Biparentally inherited, codominant markers (e.g. restriction fragment length polymorphism (RFLP), single nucleotide polymorphism (SNP), microsatellites) can be used to examine more general population genetic patterns. The recent revolution in DNA sequencing techniques has promised to enable the use of genomic scale data in population genetics and phylogenetics even for non-model organisms (Ekblom & Galindo 2011; McCormack *et al*. 2013; Perry 2014). However, newly developed techniques for genome-wide genotyping typically rely on high-quality samples (e.g. blood, tissue) (Bergey *et al*. 2013), which are often not available for natural populations of elusive or protected species, or request closely related model organisms for which genotyping arrays have been developed to allow cost-efficiency (VonHoldt *et al*. 2011). Methods for genome-wide sequencing of non-invasive samples are currently under development but still in the optimization phase (Tung et al. pers. comm). Consequently, studies based on non-invasive samples often rely on traditional markers, such as microsatellites (or short tandem repeats, STRs; simple sequence repeats, SSRs), which are highly polymorphic, relatively simple to amplify and type, and have been commonly applied in population-genetic studies of various species (Queller *et al*. 1993; Coote & Bruford 1996; Luikart & England 1999; Sunnucks 2000; Prugnolle & de Meeus 2002; Goudet *et al*. 2002; Lawson Handley & Perrin 2007; Mondol *et al*. 2009; Dickerson *et al*. 2010; Kanno *et al*. 2011; Gottelli *et al*. 2012; Roffler *et al*. 2014; Städele *et al*. 2015).

Their shortness (100 – 300 base pairs (bp)) makes them useful markers for degraded DNA samples extracted from faecal material (Bayes *et al*. 2000).

Several different statistical approaches have been developed to examine gene flow. Genetic distance between populations (e.g. Nei 1987) can be used to reconstruct dendrograms to reveal the relationship among populations. Genetic differentiation estimates, which measure the diversity among populations compared to the whole population (Wright 1949; Weir & Cockerham 1984; Excoffier *et al*. 1992), can be linked to migration rates (Slatkin & Voelm 1991; Cox & Durrett 2002). By correlating genetic and geographic distance inferences about dispersal distances can be drawn (Banks & Peakall 2012). Model-based Bayesian clustering algorithms assign individuals to differentiated groups (Pritchard *et al*. 2000; Corander & Marttinen 2006) and can incorporate spatial information (Guillot *et al*. 2005; Chen *et al*. 2007; François & Durand 2010). Ordination techniques, such as Principal Components Analysis (PCA) or multidimensional scaling, condense data to reveal the overall similarity of populations (Jombart *et al*. 2009). To specifically estimate migration rates, likelihood methods (Beerli & Palczewski 2010; Hey 2010) can be used. A new approach, Approximate Bayesian Computation (ABC) (Beaumont *et al*. 2002) allows to compare different hypothetical scenarios by model-based inferences in a Bayesian setting (Bertorelle *et al*. 2010; Csilléry *et al*. 2010). The strength of this last approach is that it accounts for the stochasticity of the involved demographic and genetic processes (Estoup & Guillemaud 2010) and can disentangle complex histories by accommodating several processes (e.g. divergence, migration, and population size change) in a statistically more solid framework (Knowles 2009). Sex differences in these processes can then be deduced from incongruence between results from differently inherited marker systems. For instance, a higher differentiation among populations in mitochondrial markers in comparison with nuclear and Y-chromosomal markers suggests stronger dispersal of males than of females.

1.2. Baboons as a study system

Like humans, non-human primates live in complex social systems and can therefore help to elucidate how behaviour and species-specific life-history attributes influences gene flow among highly social species. Baboons of the genus *Papio* (Erxleben 1777) belong to the family of Old World Monkeys (Cercopithecidae) and are among

the best studied primate taxa (Jolly 1993; Swedell & Leigh 2006; Swedell 2011). They have widely been used as a model to study the evolution of social systems using a comparative socio-ecological approach (Barton *et al*. 1996; Barrett 2009). This genus is especially intriguing to study the relationship between behaviour and gene flow as its evolutionary history was shaped by range expansion and contraction, both ancient and on-going hybridization have been described, and both species specific male- and female-biased dispersal can be observed (Swedell 2011; Anandam *et al*. 2013; Zinner, *et al*. 2013a).

1.2.1. Baboon phylogeography

Baboons are nearly continuously distributed throughout sub-Saharan Africa, only excluding the deep rainforests of Central and West Africa, and also occupy parts of the Arabian Peninsula (Fig. 1.3.). They range in a large variety of habitats, from semi-desert and savannah to rainforests and high-altitude mountains (Kingdon 1997), exhibiting high ecological flexibility (Whiten *et al*. 1987; Barton *et al*. 1996) with no apparent consistent ecological niche separation between species (Jolly 1993; Kamilar 2006).

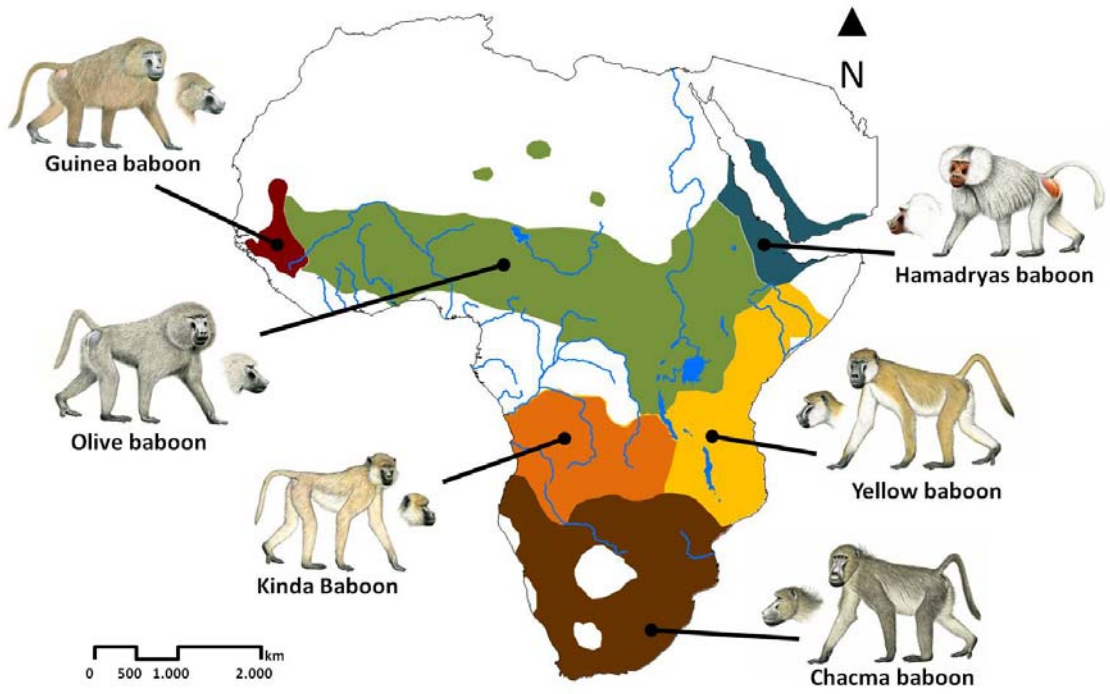

Fig.1.3.: Distribution of six commonly recognized baboon taxa (Zinner *et al*. 2011b). Drawings by Stephen Nash.

There are several phenotypically distinct, parapatric forms of baboons described that are either grouped as species or subspecies (Hill 1970; Jolly 1993; Groves 2001). According to the Biological Species Concept (BSC; Mayr 1942, 1963) they should be united into one single species *P. hamadryas* (Thorington & Groves 1970; Szalay & Delson 1979; Jolly 1993; Kamilar 2006), as both historic and current interbreeding between parapatric taxa has been observed and neighbouring populations usually differ in a stepped-cline fashion (Jolly 1993; Frost *et al*. 2003a; Kamilar 2006). However, acknowledging that there are six major diagnosable entities (Hill 1967; Hayes *et al*. 1990), and by adopting the Phylogenetic Species Concept (PSC; Cracraft 1983, 1989; Nixon & Wheeler 1990), most scholars currently distinguish six different baboon species: yellow baboon *Papio cyncocephalus* (including *P. c. cynocephalus* and *P. c. ibeanus*), chacma baboon *P. ursinus* (including *P. u. ursinus, P. u. griseipes,* and *P. u. ruacana*), Kinda baboon *P. kindae,* hamadryas baboon *P. hamadryas*, olive baboon *P. anubis*, and Guinea baboons *P. papio* (Groves 2001, 2005; Grubb *et al*. 2003; Swedell 2011; Zinner, Buba, *et al*. 2011; Anandam *et al*. 2013). I also adopt the six species concept here, on the one hand for consistency and convenience and on the other hand to accentuate the respective species-specific differences. However, I am aware that baboons are located in an ambiguous region of the speciation continuum (Nosil *et al*. 2009; Nosil & Feder 2012) and applying this taxonomic scheme is rather a philosophical decision rather than deeply rooted in an understanding of the pheno- and zygostructure of this genus and its intrarelationships (Jolly 1993), because "[B]aboon systematics is a tangle" (Groves 2001, p. 237).

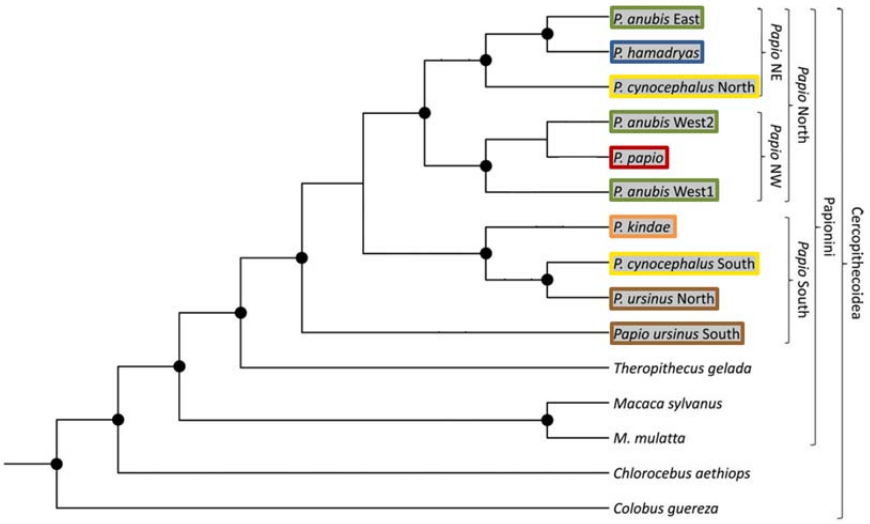

Fig.1.4.: Phylogeny of baboons (and outgroup taxa) based on whole mitochondrial genomes (modified from Zinner *et al*. 2013b).

Both fossil and molecular data point to an origin of the genus in southern Africa approximately 2.5 million years ago (mya), from where it dispersed to north and west (Benefit 1999; Newman *et al*. 2004; Zinner *et al*. 2009). The main radiation of baboons occurred during the Pleistocene and was probably shaped by climate oscillations that led to multiple phases of habitat isolation and reconnection. Reconstructions of the phylogeny and phylogeography of baboons have been mainly based on mitochondrial DNA (mtDNA) and revealed seven major haplogroups, which correspond to geographic distribution but show poly- and paraphylies in most species (Fig. 1.4.) (Zinner *et al*. 2009; Keller *et al*. 2010; Zinner *et al*. 2011b; Zinner *et al*. 2013b).

Introgressive hybridization has been invoked to explain the observed incongruence between the distribution of morphological traits compared to mtDNA haplotypes (Zinner *et al*. 2009; Keller *et al*. 2010). These discordances point to ancient hybridization in at least four different regions representing past taxon borders (Keller *et al*. 2010). However, our knowledge about active hybrid zones is incomplete (Jolly 1993; Groves 2001; Grubb *et al*. 2003; Tung *et al*. 2008; Burrell *et al*. 2010; Charpentier *et al*. 2012). Hybridization is assumed to occur wherever populations of the different taxa meet, because most species have been reported to interbreed successfully in captivity (Hill 1970) and no reproductive barriers have been observed. Although twelve boundary zones exist (Jolly 1993), only two present-day hybrid zones have been studied in more detail: the hybrid zone between olive and hamadryas baboons in the Awash National Park in Ethiopia (Nagel 1973; Shotake 1981; Phillips-Conroy *et al*. 1986; Bergman & Beehner 2004) and the hybrid zone between olive and yellow baboons in the Amboseli National Park in Kenya (Samuels & Altmann 1986; Alberts & Altmann 2001; Tung *et al*. 2008; Charpentier *et al*. 2012).

1.2.2. Baboon social systems and gene flow

The Awash hybrid zone is particularly interesting, since two baboon species with different social systems come into contact here (Woolley-Barker 1999). Hamadryas baboons live in a multi-level social organization with one-male-units as the smallest entities and exhibit a monandric-polygynous mating system (Kummer 1968; Abegglen 1984; Swedell & Plummer 2012). Female-biased dispersal (Sigg *et al*. 1982; Swedell 2011; Städele *et al*. 2015) is reflected in the absence of geographical mtDNA structuring (Hapke *et al*. 2001; Hammond *et al*. 2006). In contrast, olive baboons live in stable multi-male-multi-female groups, show promiscuous mating and male-biased dispersal (Packer 1975; Smuts 1985; Melnick & Pearl 1987; Swedell 2011). This pat-

tern usually leads to a strong geographical structuring of mtDNA haplotypes, but of neither Y-chromosomal nor autosomal markers (Burrell 2008; Burrell *et al*. 2011). Investigating hybridization between these taxa has the potential to elucidate the selective advantages of different mating systems (Bergman *et al*. 2008). Woolley-Barker (1999) described the hybrid zone as a "socially-constrained tension zone" (p.205), since selection was found to be both ecological and behavioural. Male hamadryas baboons in the contact zone tend to shift from philopatry to dispersal and it was suggested that they outplay olive baboon males in reproductive success (Woolley-Barker 1999; Phillips-Conroy & Jolly 2004).

In the second well-investigated hybrid zone in the Amboseli National Park, two species with similar social systems meet. In Amboseli, an increasing influx of olive baboon males has been observed over the last few decades (Alberts & Altmann 2001; Tung *et al*. 2008), leading to asymmetrical gene flow from olive to yellow baboon populations (Charpentier *et al*. 2012). It has been suggested that olive baboon males currently have fitness advantages over yellow baboon males in these habitats and therefore reproduce successfully within the yellow baboon population (Charpentier *et al*. 2008; Tung *et al*. 2008).

Apart from these two long-term studies focusing on specific populations in eastern Africa, data on active hybrid zones are scarce. Recent molecular genetic studies indicate gene transfer between Kinda baboons and their neighbouring taxa in Zambia (Burrell 2008; Jolly *et al*. 2011). In addition, hybridization is hypothesized in the overlapping regions of olive and Guinea baboons in West Africa (Tahiri-Zagret 1976; Jolly 1993), but has not yet been confirmed (Groves 2001).

1.2.3. Guinea baboons

Guinea baboons have a rather limited distribution on the north-western fringe of the baboon distribution in West Africa, where they occupy diverse habitats and climate zones, ranging from humid Guinean high forests in Guinea-Bissau to arid Saheli-an steppe in Mauretania (Galat-Luong *et al*. 2006; Oates *et al*. 2008). They have been proposed to share both morphological and behavioural features with the hamadryas baboon on the north-eastern fringe (Dunbar & Nathan 1972; Boese 1973, 1975; Anderson & McGrew 1984; Jolly 1993, 2009; Jolly & Phillips-Conroy 2006). Like the hamadryas baboon, the Guinea baboon has been suspected to live in a multi-level society with male philopatry and female dispersal (Jolly 2009). However, our knowledge about this species has been very limited until recently (Dunbar & Nathan

1972; Boese 1973; Fady 1973; Sharman 1981; Anderson & McGrew 1984; Barton 2000; Henzi & Barrett 2003; Galat-Luong *et al*. 2006; Maestripieri *et al*. 2007). Fortunately, data from a long-term study have been accumulating over the last years helping to clarify their social system: Guinea baboons form a multi-level society comparable to that of hamadryas baboons, but with some distinctive features such as high tolerance among males and greater freedom of females (Goffe & Fischer in prep.; Patzelt *et al*. 2011, 2014; Maciej *et al*. 2013a; Maciej *et al*. 2013b). The high tolerance among males could be a result of male philopatry and therefore high relatedness among males in the group, which could favour tolerance and cooperation through kin selection (Hamilton 1964a; b; Greenwood 1980).

1.2.4. Jolly's Frontier Hypothesis

The hypothesis that male Guinea baboons are philopatric is strengthened by a theoretical model established by Clifford Jolly (Jolly 2009), the so-called "Frontier Hypothesis". It stems from the failure to explain the differences in social systems among baboon species with differences in ecology (as would be expected by socio-ecological models (reviewed in Janson 2000; Ostner & Schülke 2012) and instead invokes demographic forces during the fast northward expansion of this genus to explain the increasing disposition for male philopatry and male-male cooperation from southern to northern populations (Jolly 2009). Jolly (2009) argues that a rapidly moving frontier of a dispersing population into an "empty" territory should act as a driving force favouring male philopatry because populations at the frontier of an expanding range have access to uncontested resources that are enhancing population growth and generating the expansion. Individuals in this population will vary in their propensity to disperse and this variation must have a genetic component to be acted on by natural selection (Roff & Fairbairn 2004). A male that moves backwards is removed from the frontier and does not contribute to the gene-pool of the frontier population's following generations. A male moving forward cannot find mates in the still uninhabited habitat and will not be able to reproduce. A male moving laterally might end up in a sink population in a less productive habitat, especially if the frontier is tapered. Males that do not disperse face the risk of inbreeding, but when frontier groups become large due to the uncontested resources, risk of inbreeding is reduced and there are enough unrelated females available for reproduction. Jolly (2009) concludes that "if this scenario is close to reality, one would expect genes predisposing to philopatry, whatever they might be, would accumulate at the frontier". He em-

phasizes the fact that this scenario is only possible if the potential for rapid expansion is extreme, i.e. if a founder population passes through a narrow gap in a barrier. Subsequently, however, the philopatric system would be self-sustainable.

1.2.5. Baboons as a model for human evolution

Baboons have been considered to represent a valuable analogous model for the study of human evolution (De Vore & Washburn 1963; Jolly 1970, 2001, 2009; Strum & Mitchell 1987; Barton *et al*. 1996; Holliday 2003; Elton 2006; Swedell & Plummer 2012; Strum 2012). They are the only extant primate taxon that evolved and radiated during the same time frame and habitat as hominins, in the Plio-Pleistocene savannahs and woodlands of Africa (Jolly 2001; Henzi & Barrett 2005). It is therefore assumed that baboons and early humans were exposed to similar selective pressures (Jolly 2001). For instance, climate fluctuations during this time triggered extensions and retractions of suitable habitat, probably leading to episodes of population isolation and reconnection (deMenocal 1995, 2004, 2011). These processes may have impacted both baboons and hominins in a similar way, leading to bouts of speciation and hybridization among closely related lineages (Zinner *et al*. 2009; Zinner *et al*. 2011b). Moreover, the plasticity in behaviour (Swedell 2011) and the formation of complex societies has been attributed to be an adaptation to the temporal and spatial variation of food resources, which resulted from these climate fluctuations, both in baboons and in humans (Whiten *et al*. 1987; Barton *et al*. 1996; Henzi & Barrett 2005; Grueter *et al*. 2012; Schreier & Swedell 2012). Multi-level societies have been suggested to form the basis of the evolution of the highly cooperative human societies (Rodseth *et al*. 1991; Chapais 2010; Silk & Boyd 2010; Grueter *et al*. 2012) and the multi-level societies of baboons provide a valuable comparative model to test this assumption and elucidate the underlying processes (Swedell & Plummer 2012; Grueter *et al*. 2012; Patzelt *et al*. 2014; Grueter 2014). In addition, sex-biased dispersal in humans exhibits plasticity and strikingly different patterns among populations, with the underlying causes of these differences are still being debated (Destro Bisol *et al*. 2012; Harcourt 2012). Baboons have the potential to also provide comparative data on this topic thus contributing to a better understanding of the evolution of human societies.

1.3. Aims and approaches

In my thesis, I aim to investigate how different dispersal patterns influence gene flow in baboons to contribute to a better understanding of the interrelation between behavioural ecology and genetic makeup of natural primate populations. I specifically want to address (i) if the genetic structure of Guinea baboons indicates male philopatry and female dispersal, both on a local (Chapter 2) and a distribution-wide scale (Chapter 3 and 4), (ii) how differences in the social system of baboons species impact their genetic structure (Chapter 3); (iii) how both historic and contemporary gene flow shape the genetic structure of Guinea baboons (Chapter 4); and (iv) whether we can draw inferences about human evolution from the analysis of range expansions in baboons (Chapter 5).

To answer these questions, I used a population genetic approach based on distribution-wide, geo-referenced faecal samples of baboons. These were obtained during field expeditions in West Africa, provided by several different collaborators or already available from previous projects directed by Dr. Dietmar Zinner at the German Primate Center. I analyzed both autosomal microsatellites and part of the mitochondrial hypervariable region I for these samples and also incorporated published records and pre-analyzed data provided by collaborators.

CHAPTER 2: POPULATION GENETIC INSIGHTS INTO THE SOCIAL ORGANIZATION OF GUINEA BABOONS (*PAPIO PAPIO*): EVIDENCE FOR FEMALE-BIASED DISPERSAL

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Author contributions: GHK, DZ and JF designed research, GHK collected data, GHK analyzed data, AP provided unpublished data, CR helped in genetic analyses and provided unpublished laboratory protocols. GHK wrote the manuscript. All authors discussed the results and contributed to the final manuscript.

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Abstract

Sex differences in philopatry and dispersal have important consequences on the genetic structure of populations, social groups, and social relationships within groups. Among mammals, male dispersal and female philopatry are most common and closely-related taxa typically exhibit similar dispersal patterns. However, among four well-studied species of baboons, only hamadryas baboons exhibit female dispersal, thus differing from their congenerics, which show female philopatry and close-knit female social relationships. Unitl recently knowledge of the Guinea baboon social system and dispersal pattern remained sparse. Previous observations suggested that the high degree of tolerance observed among male Guinea baboons could be due to kinship. This led us to hypothesize that this species exhibits male philopatry and female dispersal, conforming to the hamadryas pattern. We genotyped 165 individuals from five localities in the Niokolo-Koba National Park, Senegal, at 14 autosomal microsatellite loci and sequenced a fragment of the mitochondrial hypervariable region I (HVRI) of 55 individuals. We found evidence for higher population structuring in males than in females, as expected if males are the more philopatric sex. A comparison of relatedness between male-male and female-female dyads within and among communities, did not yield conclusive results. HVRI diversity within communities was high and did not differ between the sexes, also suggesting female gene flow. Our study is the first comprehensive analysis of the genetic population structure in Guinea baboons and provides evidence for female-biased dispersal in this species. In conjunction with their multilevel social organization, this finding parallels the observations for human hunter-gatherers and strengthens baboons as an intriguing model to elucidate the processes that shaped the highly cooperative societies of *Homo*.

Keywords

Social system, male philopatry, microsatellites, population structure, hypervariable region I

Introduction

Dispersal, an organism's movement away from its original site or group (Pusey & Packer 1987) has major implications for both the dynamics and the genetic makeup of populations (Bohonak 1999; Prugnolle & de Meeus 2002) and social groups (Hughes 1998; Hoelzer *et al*. 2004; Archie *et al*. 2008; Di Fiore 2012), and hence, on kinship related social relationships within groups (Lukas & Clutton-Brock 2011). Many taxa exhibit sex-biased dispersal, i.e. one sex shows a greater tendency to leave its natal area or to move further away than the other (Greenwood 1980; Pusey 1987). Male dispersal and female philopatry is predominant in mammals (Greenwood 1980), but exceptions can be found, e.g. in some non-human primates, equids, and some bats (Lukas & Clutton-Brock 2011), and presumably in the majority of human societies (Seielstad *et al*. 1998; Wilkins & Marlowe 2006; Lawson Handley & Perrin 2007; Marks *et al*. 2012).

In many social mammals, the aggregation of individuals and their social relationships are determined by kinship (Smith 2014) and, as a consequence of sex-biased dispersal, more social affiliation, tolerance, and cooperation is expected among the philopatric sex, due to kin selection (Hamilton 1964a; b; Greenwood 1980; Gouzoules 1984; Moore 1992; Clutton-Brock & Lukas 2012; Di Fiore 2012). Hence, in many mammalian species, philopatric and therefore related females form matrilines and gain fitness benefits from close social ties with their kin (Moses & Millar 1994; Gompper *et al*. 1997; Lambin & Yoccoz 1998; Chesser 1998; Silk *et al*. 2006a; Silk *et al*. 2006b; Broad *et al*. 2006; Silk 2007). This paradigm has been most thoroughly studied in primates (Sterck *et al*. 1997; Silk 2002, 2007; Langergraber 2012) with baboons, genus *Papio,* being one of the prime examples for female kin-based bonding in matrilocal multimale-multifemale groups (Sterck *et al*. 1997; Kapsalis 2004; Silk *et al*. 2006a; Silk *et al*. 2006b; Seyfarth *et al*. 2014) Baboons are distributed over most of sub-Saharan Africa, and comprise six commonly recognized species: chacma (*Papio ursinus*), Kinda (*P. kindae*), yellow (*P. cynocephalus*), olive (*P. anubis*), hamadryas (*P. hamadryas*), and Guinea baboons (*P. papio*) (Anandam *et al*. 2013). In contrast to the general female-bonded pattern, hamadryas baboons are prominent for exhibiting a multi-level society (Kummer 1968, 1995; Abegglen 1984; Zinner *et al*. 2001; Schreier & Swedell 2009; Grueter *et al*. 2012) with male philopatry and female-biased dispersal (Sigg *et al*. 1982; Hapke *et al*. 2001; Hammond *et al*. 2006; Kopp *et al*. 2014a; Städele *et al*. 2015). While female dispersal in hamadryas baboons is

behaviourally not analogous to female dispersal in other taxa (Swedell *et al*. 2011) the genetic effects are the same (Hammond *et al*. 2006; Kopp *et al*. 2014a; Städele *et al*. 2015). In spite of the fact that baboons are among the most intensively studied primates (Barrett & Henzi 2008), Guinea baboons are vastly understudied and our knowledge about their social system is still limited (Barton 2000; Henzi & Barrett 2003; Galat-Luong *et al*. 2006; Maestripieri *et al*. 2007; Patzelt *et al*. 2011, 2014; Maciej *et al*. 2013a). Compared to other baboon species they have a rather small distribution in West Africa, but occupy diverse habitats and climate zones, ranging from humid Guinean high forests in the South to arid Sahelian savannah in the North, occupying even isolated mountain ranges in the desert of Mauretania (Galat-Luong *et al*. 2006; Oates *et al*. 2008; Oates 2011; Anandam *et al*. 2013). They live in a multi-male-multi-female society, which is organized in a multi-layered way (Sharman 1981; Galat-Luong *et al*. 2006; Patzelt *et al*. 2011, 2014; Maciej *et al*. 2013a). Three to five adult males with several females and young form a party, which is assumed to be equivalent to the clan level in hamadryas baboons (Patzelt *et al*. 2014). Parties regularly associate in a gang of approximately 60 individuals (hamadryas band), and several gangs share a home range and aggregate in a community of more than 350 individuals (Maciej *et al*. 2013a; Patzelt *et al*. 2014). Subgrouping seems to be flexible both on a daily and a seasonal scale (Patzelt *et al*. 2011) and male Guinea baboons show a peculiar high degree of tolerance towards each other compared to other baboon taxa (Sharman 1981; Maciej *et al*. 2013b; Patzelt *et al*. 2014). This could be a consequence of male philopatry and therefore high relatedness among males within groups. A recent study on mitochondrial DNA (mtDNA) variation over the whole range of Guinea baboons found a high level of female-mediated gene flow, suggesting female-biased dispersal (Kopp *et al*. 2014a).

In our study we investigated the genetic structure of a Guinea baboon population in south-eastern Senegal to further elucidate their social system. We examined the genetic relatedness within one community and among several communities at different spatial scales using non-invasive genotyping of individuals. More specifically, we compared the relatedness between males and females, respectively, within and among communities as well as population structuring of autosomal markers over a broader spatial range. Differences could reveal sex-biased dispersal and philopatry, both important determinants of the social system of a species. Through the analysis of sequence information of the maternally transmitted mtDNA we aim to unveil matrilineal structures. Additionally we used a genetic capture-

recapture approach (Lukacs & Burnham 2005; Arandjelovic *et al*. 2011) to assess the stability of subgrouping on a short temporal scale, in order to evaluate if this methodolgy can be used to distinguish between structured multi-level societies and more flexible fission-fusion societies based on genetic samples only.

We hypothesized that Guinea baboons exhibit male philopatry and, as a consequence of inbreeding avoidance, female dispersal and therefore predicted to find (i) higher population structuring of males compared to females; (ii) higher relatedness among males within communities than among males of different communities and the reversed pattern for females; and (iii) a generally high diversity of mtDNA haplotypes within communities and no difference in mtDNA variation between males and females.

Methods

Field Work

The study was conducted at the Centre de Recherche de Primatologie (CRP) Simenti in the Niokolo Koba National Park (PNNK) in south-eastern Senegal (N13.03° W13.29°). Since 2007 a community of more than 350 Guinea baboons is under investigation.

We collected 452 fecal samples of the Simenti community between May and July 2009 during morning (0630-1130) and evening (1700-1900) follows. At that time, identification of individual baboons was not possible. Furthermore we collected additional samples at four localities inside the national park: potential neighboring communities are represented by Gue Damantan (n=62) and Camp du Lion (n=54) with a distance to Simenti of 3km and 6km, respectively. Lingue Kountou (n=53; 23km) and Niokolo (n=52; 62km) were chosen to enable comparisons over larger geographic scales (Fig. 2.1).

Fecal samples were collected and stored following the two-step protocol (Roeder *et al*. 2004; Nsubuga *et al*. 2004). For each sample consecutive number, date, time, and GPS coordinates were recorded. For the Simenti samples, we listed which samples were collected from the same gang. Due to large flight distance and poor visibility of the animals we were not able to assign sex and age classes to the samples, hence post- and pre-dispersal individuals cannot be distinguished in the

statistical analyses. All samples were stored in the field at ambient temperature for up to 3 months and at -20°C in the laboratory.

This project complied with the protocols approved by the German Primate Center, Göttingen, Germany, the animal care regulations and principles of the American Society of Primatologists for the ethical treatment of nonhuman primates, and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Permits for research and sample export were obtained from the Senegalese authorities and research adhered to the legal requirements of both Senegal and Germany.

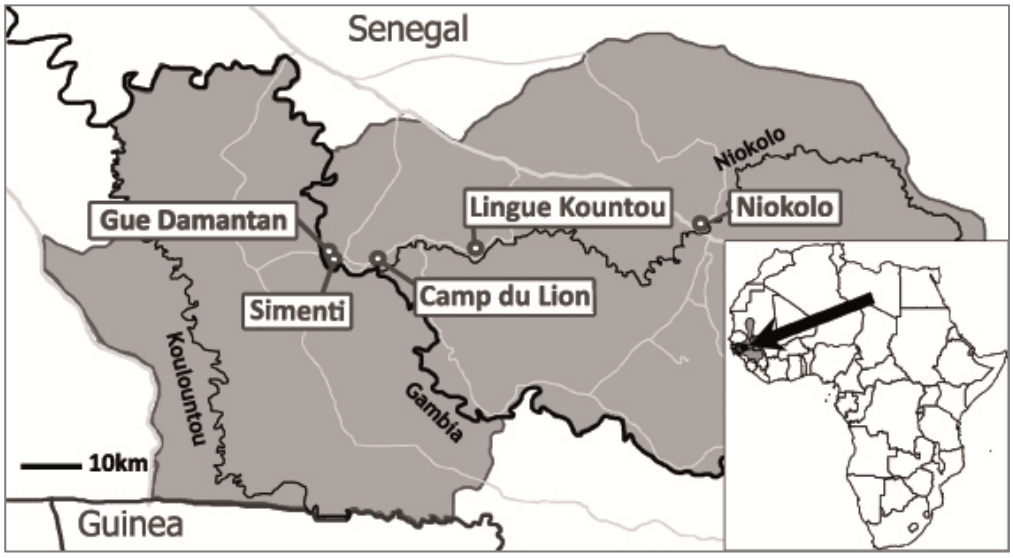

Figure 2.1: Sampling sites of Guinea baboon communities in the Niokolo Koba National Park, Senegal.

Genetic analysis

DNA was extracted using the QIAamp DNA Stool Mini Kit (Qiagen, Hilden, Germany) according to the protocol for isolation of DNA from stool for human DNA analysis with slight modifications (Haus *et al*. 2013). To determine the sex of individuals we used a PCR-based gonosomal sexing system (C. Roos unpubl.).

We genotyped all samples for which we reliably determined the sex at 15 autosomal microsatellite loci (Table 2.SI) developed in humans and reported to also amplify in baboons (Rogers *et al*. 2000; Roeder *et al*. 2009; Ferreira da Silva *et al*.

2014). Microsatellites were amplified in five multiplex reactions, containing two to four different primer pairs (Table 2.SII). Details on screening of microsatellites and laboratory procedures can be found in the supporting information. To assure accuracy, genotyping was repeated several times leading to a consensus genotype (multiple tubes approach (Navidi *et al*. 1992; Taberlet *et al*. 1996; Morin *et al*. 2001)).

For 55 samples we amplified and sequenced a fragment of the hypervariable region I (HVRI) of the mitochondrial genome comprising 339 base pairs (bp) following established protocols (Kopp *et al*. 2014a). MtDNA sequences were uploaded to GenBank and can be accessed through the following accession numbers: KF692784-788, 790-800, 811-814, 816, 818, 847-852, 856, 879-884, 886, 894, 895, 897-908, 910, 911, 913-915.

Statistical Analyses

Obtaining accurate microsatellite genotypes from fecal samples can be difficult due to low DNA quality and quantity or poor extract quality (PCR inhibitors) (Taberlet *et al*. 1999). We therefore rigorously evaluated genotyping errors and only included samples that passed our quality control (further details can be found in the supporting information). Genotype matching was performed using GIMLET 1.3.3 (Valière 2002) allowing one mismatch. Every duplicate genotype was excluded from the final dataset. The probability that a single genotype actually represents one single individual was calculated with the Probability of Identity $P_{(ID)}$ (Paetkau & Strobeck 1994) and the more conservative estimator Probability of Identity between sibs $P_{(ID)sib}$ (Evett & Weir 1998; Taberlet & Luikart 1999) as implemented in GIMLET. The final dataset was converted to the specific input file formats of each software program using CREATE 1.3 (Coombs *et al*. 2008).

Departures from Hardy-Weinberg Equilibrium (HWE) were tested with exact tests using the program GENEPOP 4.0.11 (default settings: dememorization number: 10,000; number of batches: 20; iterations per batch: 5000) (Raymond & Rousset 1995; Rousset 2008). Expected heterozygosity H_E and observed heterozygosity H_O were calculated in ARLEQUIN 3.5.1.2 (Excoffier & Lischer 2010). Allelic richness and F_{IS} were calculated in FSTAT 2.9.3.2 (Goudet 1995).

Population genetic parameters were calculated to investigate if there is any population structuring despite the fact that there are no obvious barriers for gene

flow between the sampling sites. First the program STRUCTURE 2.3.3 (Pritchard *et al*. 2000) was used, which is based on a Bayesian approach. It identifies the most likely number of populations (*K*) in a data set and the likelihood of an individual to belong to this population. Program settings were set to a total run length of 1,000,000 iterations, a burnin of 100,000, and values of *K* from 1 through 6. The analysis was repeated 10 times to assure the consistency of the results. We chose the admixture model as ancestry model and the correlated frequency model as allele frequency model (Falush *et al*. 2003). Furthermore we used the LOCPRIOR model that takes into account the sampling location of individuals as a prior information to assist the clustering if the signal is relatively weak (Hubisz *et al*. 2009). All other settings were left at their default value. To evaluate the most probable number of clusters, we employed the method suggested by Evanno et al. (2005) as implemented in STRUCTUREHARVESTER WEB v0.6.92 (Earl & VonHoldt 2011). To further investigate population structuring Weir & Cockerham's fixation index F_{ST} (Weir & Cockerham 1984) among the sampling sites was calculated in FSTAT and the relationship between geographic and genetic distances among sampling sites (isolation by distance; IBD) was tested with a Mantel test in GENEPOP using 1000 permutations.

We tested for sex-bias in dispersal by comparing several parameters between males and females. To begin with, population structure and IBD of females and males was examined with the same settings as in the analysis of the total population. To quantify the degree of population structuring, F_{ST} values were calculated for each sex separately and tested two-sided predicting males being philopatric with 1000 permutations using FSTAT. Sampling sites Gue Damantan, Simenti, Camp Du Lion and Lingue Kountou were grouped together as one cluster and Niokolo constituted a second cluster following the results from the population structure analysis. Allelic frequencies of the dispersing sex should be more homogeneous and therefore F_{ST} should be lower for the dispersing than for the philopatric sex. We refrained from testing other parameters available in the sex-biased dispersal test in FSTAT, on the one hand to avoid multiple testing and on the other hand because these parameters have been shown to perform poorly under certain conditions, whereas the F_{ST} statistic is the most powerful measure to detect sex-bias in dispersal, regardless of sampling scheme and magnitude (Goudet *et al*. 2002). Sex-biased dispersal should also influence the distribution of relatedness in a population. Pairwise relatedness coefficients *R* were calculated using the regression estimator derived by Queller & Goodnight (1989) as implemented in COANCESTRY 1.0 (Wang 2011). The average

relatedness of males and females within a gang, among gangs, and among communities, respectively, was compared (for within gang comparisons only dyads in the Simenti community were included). We tested for significance using a permutation test as implemented in the R package coin (Hothorn *et al*. 2008) in R 3.1.1 (R Development Core Team 2014) with 99999 Monte Carlo resamplings. A set of 14 microsatellites does not suffice to infer kinship reliably without any additional information and putative misclassification would lead to erroneous conclusions (Van Horn *et al*. 2008). With the absence of pedigree (e.g. known mother-offspring pairs) and demographic information (Harris *et al*. 2009; Arora *et al*. 2012), we therefore refrained from analyzing dyadic relatedness.

To visualize the genetic distances and frequencies of HVRI haplotypes, we generated a haplotype network in HAPSTAR 0.6 (Teacher & Griffiths 2011) based on pairwise distances output from ARLEQUIN 3.5.1.2. In order to assess the diversity of HVRI haplotypes we calculated levels of nucleotide and haplotype diversity for males and females, respectively, using DNASP version 5.10.1 (Librado & Rozas 2009), both for the whole study population and for every community separately, as well as for females and males, respectively. We tested for significance using the difference test in Statistica (StatSoft®).

To investigate the temporal stability of gangs we examined if individuals that were sampled multiple times on different days were repeatedly sampled with the same individuals in the same gang.

Results

From a total of 339 extracted and sexed samples 149 were determined as males and 113 as females, the rest was excluded because of no visible amplification product, ambiguous results or suspected contamination. The 211 successfully genotyped samples of the final data set yielded 165 different individuals (68 females and 97 males), that were typed at a minimum of 13 loci with a mean of 13.9 loci (Table 2.SIV). Loci had a good power to discriminate between individuals with a total $P_{(ID)sib}$ of 5.984×10^{-5} ($P_{(ID)}=2.080 \times 10^{-10}$). The quality of samples and estimated genotyping error rates (Table 2.SIII) fall in the normal range for non-invasive samples (Bayes *et al*. 2000; Smith *et al*. 2000; Lathuillière *et al*. 2001; Miquel *et al*. 2006; Arandjelovic *et al*. 2009) and allow population genetic analysis. While it cannot be

ruled out that some multilocus genotypes contain errors, they are sufficiently rare and should be distributed randomly throughout the dataset, thus not biasing the analysis of sex-biases.

All loci were polymorphic, with number of alleles ranging from three to seven (mean=5.36±SD 1.22) and a mean allelic richness of 3.76 (±SD 0.95). Loci showed no significant deviations from HWE. Expected and observed heterozygosity were similar (H_E=0.60±0.13; H_O=0.63±0.14), F_{IS} values ranged around zero with a mean of -0.068. Both nucleotide diversity and expected heterozygosity are lower in Guinea baboons than in their congenerics (Table 2.SV).

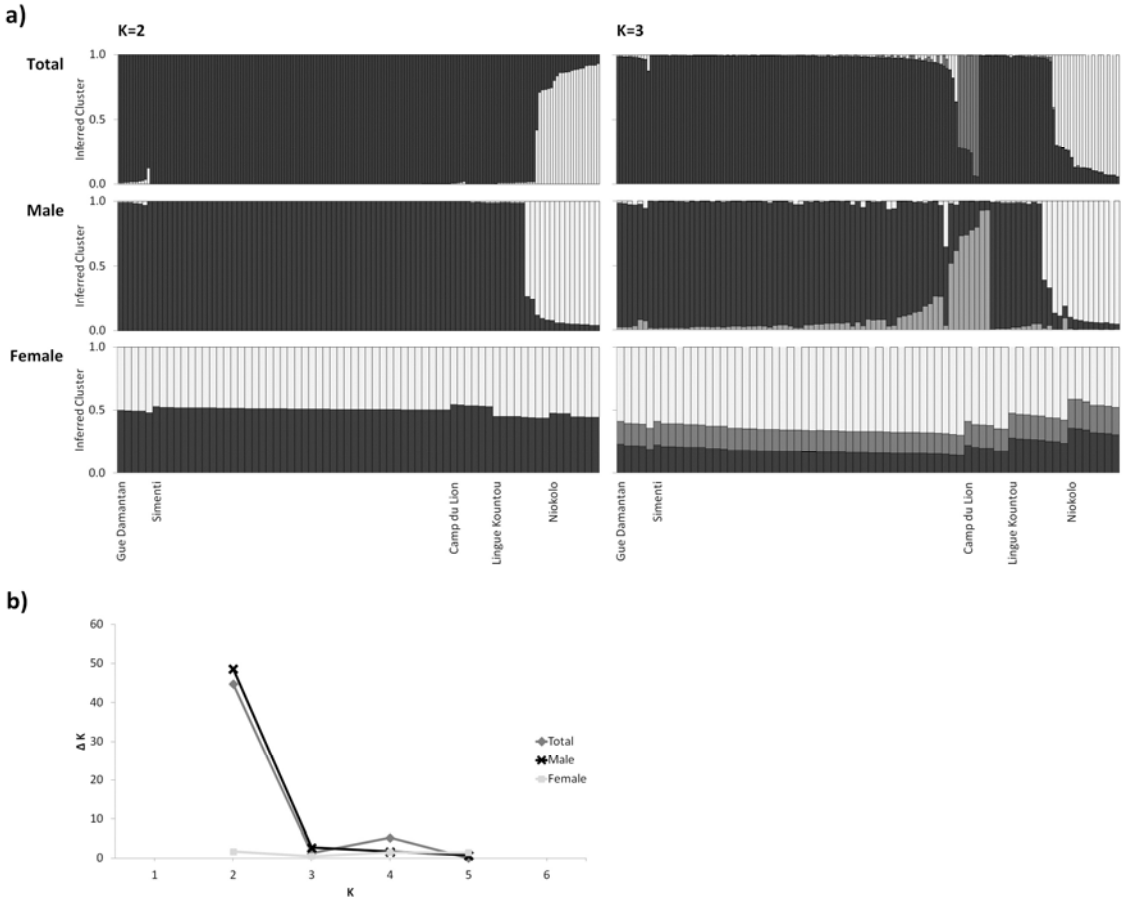

Figure 2.2: (a) Genetic population structure of male and female Guinea baboons as well as the total sample set using the software Structure and clustering of K=2 and K=3. (b) Inference of the most probable number of clusters (K) for the three data sets (male, female, total) using the ad hoc statistic ΔK [Evanno et al., 2005] returns K=2 as the most probable solution for both males and the total population but K=1 for females.

The STRUCTURE analysis revealed population structuring, with K=2 being the most probable (Fig. 2.2). Individuals from Niokolo were found to differ from all other

communities. There was a significant positive correlation between geographic and genetic distance, indicating IBD (r^2=0.600; p=0.039) (Fig. 2.3).

Sex-biased dispersal

The STRUCTURE analysis revealed differences in population structuring between males and females, respectively. For males K=2 was found to be the most probable, whereas females did not show any structuring (Fig. 2.2), indicating that male gene flow is more restricted, as expected for the philopatric sex. We also found a slight trend for IBD in males (r^2=0.559, p =0.127) but not in females (r^2=0.015, p=0.348) (Fig. 2.3). The comparison of F_{ST} values between the sexes also showed significantly higher values for males than for females, also suggesting a stronger population structure in males ($F_{ST♂}$=0.08, $F_{ST♀}$=0.02, p =0.018).

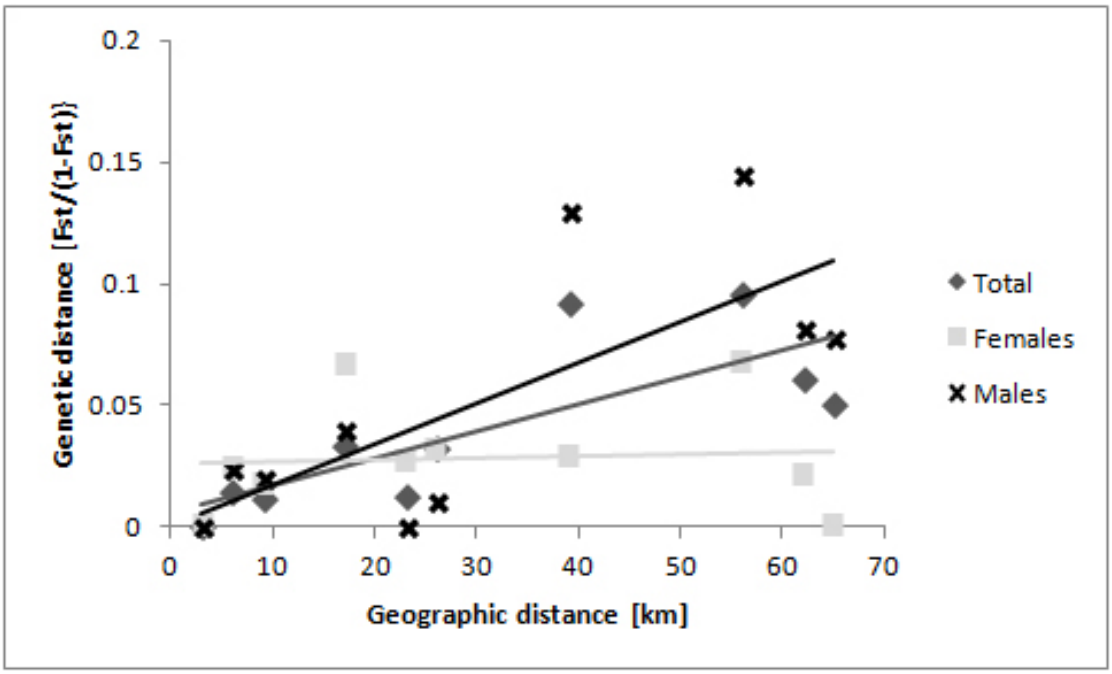

Figure 2.3: Correlations between genetic differentiation, as measured by F_{ST}, and geographic distance between sampling sites suggest that the total population shows evidence for Isolation-by-distance (r^2=0.600, p=0.039), there is a trend for IBD in males (r^2=0.559, p=0.127) but not in females (r^2=0.015, p=0.348).

The second approach to examine sex-biased dispersal was to analyse the effects of distance and sex on relatedness. Mean pairwise relatedness was significantly higher

among females than among males, both within and among communities. ($N_{♀}$=68, $N_{♂}$=97; $R_{♀within}$=0.0357 ± SD 0.2005, $R_{♂within}$=0.0092 ± SD 0.2143, Z=3.5618, p<0.001; $R_{♀among}$=-0.0203 ± SD 0.1891, $R_{♂among}$=-0.0446 ± SD 0.1982, Z=3.3397, p<0.001) and both males and females were less related among than within communities (females: Z=-6.7837, P<0.001; males: Z=-8.6657, P<0.001). For both male, female, and mixed-sex dyads mean pairwise relatedness decreased considerably from the gang to the community to the population level (Fig. 2.4a). Looking at the well-sampled Simenti community more closely, we found a small, but significant difference in the relatedness coefficients of male versus female dyads ($N_{♀Simenti}$ =42, $N_{♂Simenti}$ =66; $R_{♀Simenti}$=0.0344 ± SD 0.1952, $R_{♂Simenti}$=-0.0006 ± SD 0.2111; Z=4.1453, p<0.001; Fig. 2.4b).

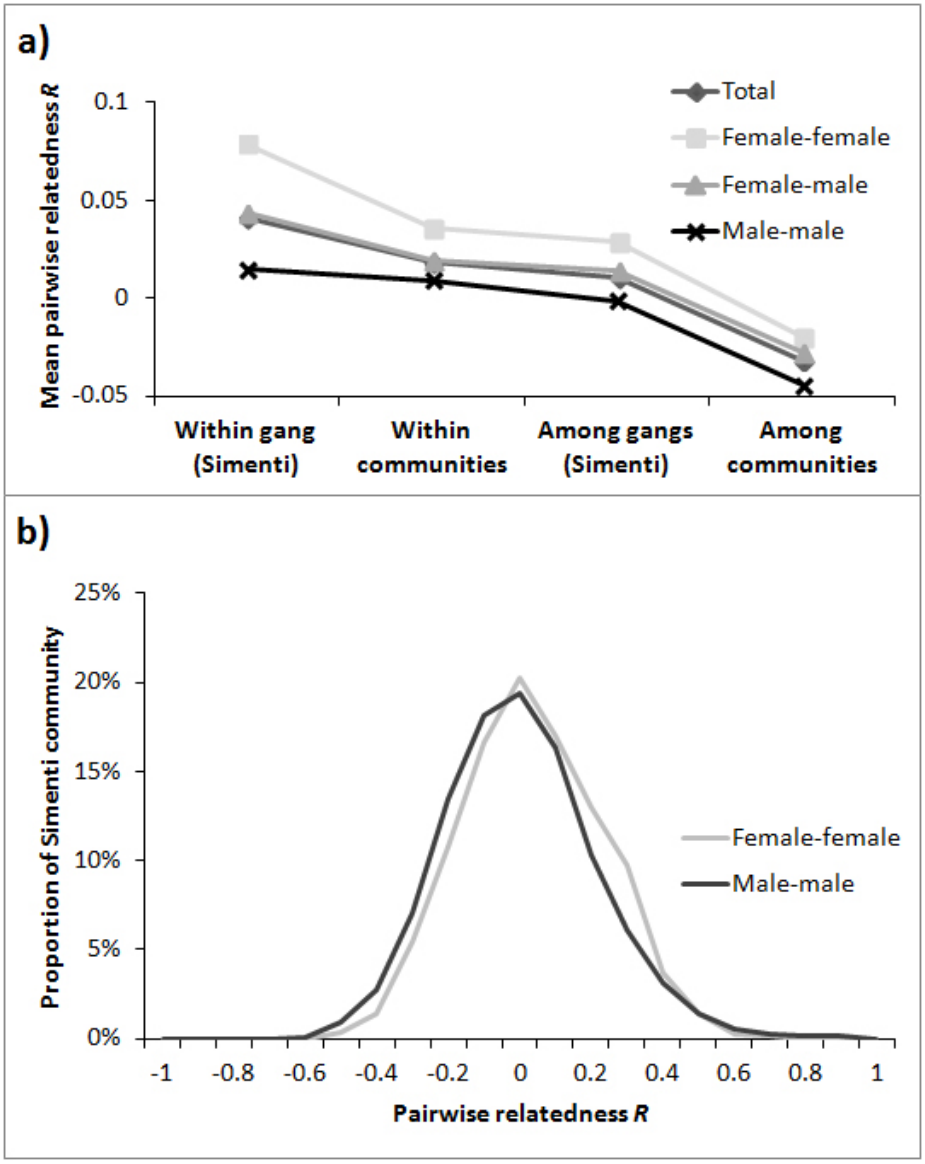

Figure 2.4: (a) Mean pairwise relatedness as inferred from autosomal microsatellites among male and female dyads within gangs of the Simenti community, within communities, among gangs of the Simenti community, and among communities. (Number of dyads: Female-female/within gangs=101; female-female/within community=1145; female-female/among gangs=760; female-female/among communities=1133; female-male/within gangs=236; female-male/within community=3559; female-male/among gangs=2536; female-male/among communities=3037; male-male/within gangs=170; male-male/within community=2681; male-male/among gangs=1975 ; male-male/among communities=1975; total/within gangs=507; total/within community=7385; total/among gangs=5271; total/among communities=6145; (b) Distribution of relatedness coefficients of male and female dyads in the Simenti community.

MtDNA diversity

The PNNK study population comprised 13 HVRI haplotypes with an overall haplotype diversity Hd of 0.798 (± SD 0.047) and nucleotide diversity π of 0.01030 (± SD 0.00134). The haplotype network revealed two coarse haplotype clusters divided by four mutational steps, albeit without any clear geographical signal (Fig. 2.5). One haplotype was very common (N=23) and was discovered in every community except Lingue Kountou, while several other haplotypes were only observed once. Within communities we found a median number of 3 haplotypes (range 2-6), mean Hd of 0.6334 (± 0.116), and mean π of 0.008032 (± 0.00473). On average, there was no considerable difference in within-community Hd between the sexes ($Hd_{♀}$=0.5788±0.3595, $N_{♀}$=25; $Hd_{♂}$=0.5974±0.1203, $N_{♂}$=30, p=0.7909), but π was nearly twice as high for females within communities than for males ($\pi_{♀}$=0.0101±0.0061, $N_{♀}$=25, $\pi_{♂}$=0.0055±0.0054, $N_{♂}$=30, p=0.0036).

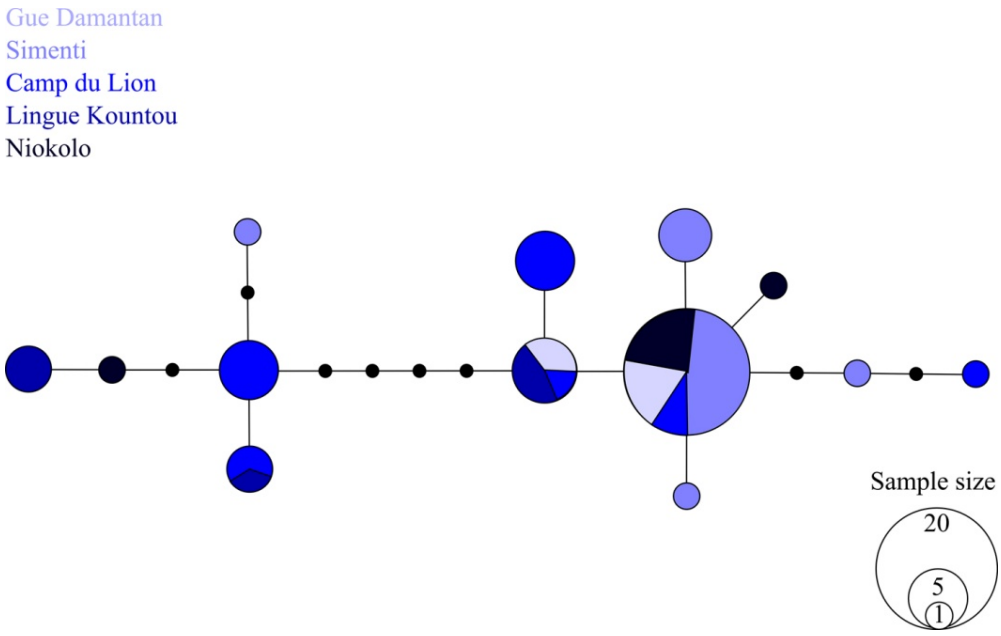

Figure 2.5: Network of HVRI haplotypes found in the Niokolo Koba National Park. Different haplotypes are colored according to the sampling sites where they were found.

Stability of gangs

19 individuals were sampled multiple times on two to three different days. Of these individuals 14 were sampled repeatedly together with the same other individual(s), resulting in six dyads and one triad (Fig. 2.6). These mostly consisted of individuals of the same sex, but one dyad and the triad also contained both a male and one or two females. Time span between repeated sampling varied between 1 and 48 days (mean: 11.6 days).

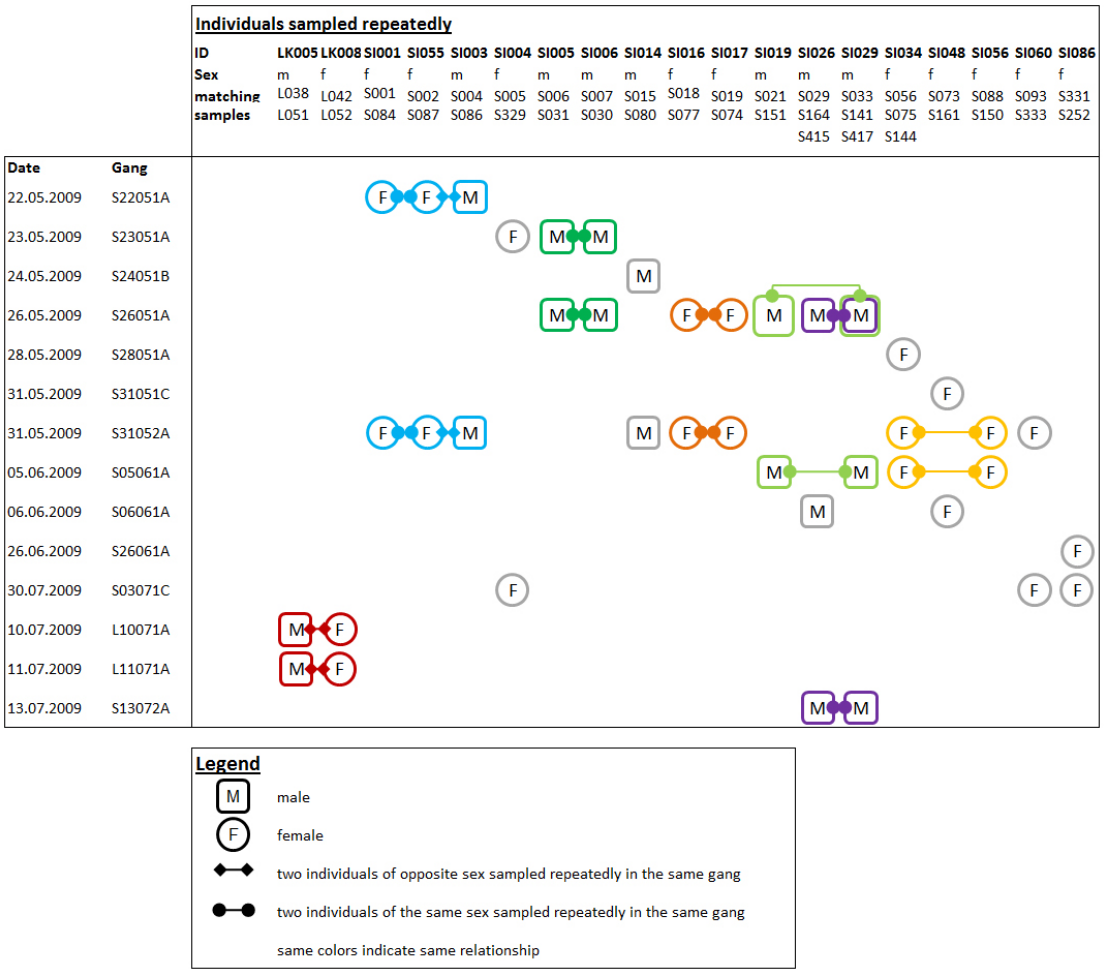

Figure 2.6: 14 individuals were repeatedly sampled with a least one other particular individual on different days.

Discussion

We investigated the genetic structure of a Guinea baboon population to gain a better understanding of their social system, specifically their dispersal pattern. We found differences in population structure between males and females, with significantly higher F_{ST} values for males. This structuring is probably attributable to a stronger IBD effect in males than in females, implying that male gene flow is more restricted than female gene flow, which is consistent with male philopatry and female-biased dispersal. The assessment of mean pairwise relatedness coefficients to infer sex-bias in dispersal, however, did not yield conclusive results: The finding that females are more closely related than males within communities is against our predictions for female dispersal, whereas the higher relatedness among females from different communities than among males from different communities is consistent with our predictions. It needs to be highlighted that the magnitude of differences in average relatedness is rather small and presumably arose out of the presence of a moderately larger number of related dyads among females. The PNNK population of Guinea baboons was characterized by a high mitochondrial haplotype diversity within communities, as expected for species with female dispersal (Städele *et al*. 2015), which leads to the accumulation of several haplotypes in single localities. Additionally, the fact that males and females show a similar haplotype diversity strongly supports the hypothesis of female dispersal.

One problem regarding the detection of sex-bias in dispersal and philopatry from genetic data was that we were not able to assign age-classes to the sampled individuals. Especially the sampling of mothers together with their dependent offspring is a potential source of error. Firstly, this inflates the relatedness within communities thus hampering the detection of differences in relatedness between males and females. This shortcoming of our study design might be a reason why our relatedness analyses failed to give conclusive results. Secondly, the sampling of mothers with their offspring complicates the examination of male dispersal via mtDNA variation, because pre-dispersal males, carrying the mtDNA variant of their resident mother, would weaken the predicted effect of higher male mtDNA variation. Hence, the inclusion of pre-dispersal individuals introduces a considerable amount of noise that may silence differences that are expected between males and females if sex-bias in dispersal exists (Prugnolle & de Meeus 2002). Accordingly, sex differences may actually be stronger than they are reported here. Furthermore, home range overlap

among the communities was unknown. Possibly, individuals that were treated as belonging to different communities actually belonged to the same. This applies specifically to animals of neighboring localities such as Simenti and Gue Damantan.

The fact that individuals were repeatedly sampled together indicates that the composition of gangs is stable over a substantial period of time, a finding that is now supported by behavioral observations (Patzelt *et al*. 2014). This fact and the finding that the average relatedness is higher in gangs as compared to the whole community corroborate the view that in Guinea baboons the gang constitutes an important social unit (Maciej *et al*. 2013b). A decrease in relatedness through the different levels of hierarchically structured societies has also been described in hamadryas baboons (Städele *et al*. 2015), female geladas (*Theropithecus gelada,* Snyder-Mackler *et al*. 2014) and elephants (*Loxondonta africana*, Wittemyer *et al*. 2009). In both geladas and elephants relatedness was found to be a predictor of group fission and fusion (Archie *et al*. 2006; Snyder-Mackler *et al*. 2014). Future studies will elucidate in detail the socio-genetic structure of the complex Guinea baboon society.

Overall, the relatedness of individuals within the Simenti community is extremely low, regardless of sex, and comparable to the values described for hamadryas baboons (Städele *et al*. 2015). This result is concordant with other studies, which showed that in large groups mean pairwise relatedness is not necessarily higher in the philopatric sex, because many unrelated dyads may dilute the effects of few highly related dyads (Lukas *et al*. 2005). Relatedness values are also affected by reproductive skew (Lukas *et al*. 2005). If one or a few males are able to monopolize reproduction over a long time period, the amount of paternal half-siblings in the group is high. In contrast, if reproductive skew is low because multiple males are able to reproduce, within group relatedness is expected to be relatively low. Long-term behavioral observations and paternity analyses will be needed to clarify the mating system of Guinea baboons.

The low relatedness among males within the community suggests that male tolerance is not conditional on kinship in this species, which is supported by Patzelt and colleagues (Patzelt *et al*. 2014), who found that relatedness did not predict the quality of male-male bonds in Guinea baboons. Similarly, in chimpanzees, cooperative behavior is not solely determined by kinship (Langergraber *et al*. 2007a). Still, male philopatry has the potential to facilitate the establishment of strong male bonds (Mitani *et al*. 2002; Langergraber *et al*. 2007a) through the early formation of peer groups that, in the absence of male dispersal, can persist from early childhood into

adulthood (Boese 1975). Moreover, this system obliges females to counterbalance the negative effects of dispersal, especially the unavailability of kin (Silk 2002). In some species unrelated females form strong bonds, which provide direct fitness benefits through social integration (Lehmann & Boesch 2009; Cameron *et al*. 2009), while in other species females regularly disperse together with or into groups with relatives to maintain kin associations (Starin 1994; Bradley *et al*. 2007).

Our finding of female-biased dispersal in this Guinea baboon population confirms and refines the results of a previous study, which, based on patterns of mtDNA variation, recovered female gene flow in both Guinea and hamadryas baboons species-wide (Kopp *et al*. 2014a). We cannot draw conclusion about the magnitude of the sex difference in dispersal and the social level at which this bias manifests , and are not rejecting that male philopatry might be weak. These questions, however, can only be ascertained by analyzing Y-chromosomal haplotypes in the future (Petit *et al*. 2002) and by incorporating detailed data on the multiple levels of the community (Städele *et al*. 2015). Unfortunately, we failed to find informative, polymorphic loci when screening several Y-chromosomal markers upon initiation of this study. An extremely low level of diversity on the Y-chromosome has also been described in hamadryas baboons (Lawson Handley *et al*. 2006; Städele *et al*. 2015) and is a common problem in mammalian non-model organisms (Greminger *et al*. 2010). Still, on average, females appear to migrate more often and/or further away than males in this population of Guinea baboons. Research on different populations throughout the range of Guinea baboons covering most of the habitats they occupy could help to evaluate how climatic and ecological variation as well as anthropogenic disturbances may alter dispersal behavior. Guinea baboons occupy a vast variety of habitats and climate zones (Galat-Luong *et al*. 2006; Oates *et al*. 2008; Oates 2011; Anandam *et al*. 2013) and poaching and habitat destruction is a major threat in certain regions of their range (Ferreira da Silva *et al*. 2014). A comparison of different populations would provide the data necessary to evaluate how flexibly this species can respond to ecological variables (Wikberg *et al*. 2012) and how strong it is influenced by evolutionary constraints.

Unfortunately, ecological and behavioral data on Guinea baboons that are required to investigate evolutionary causes of their dispersal pattern are still scarce. It remains unknown how costs and benefits of dispersal and philopatry are distributed among the sexes and how, for instance, the avoidance of local resource competition and inbreeding (Lukas & Clutton-Brock 2011; Clutton-Brock & Lukas 2012) shaped this

pattern. It is also premature to speculate on the analogy of female dispersal behavior in Guinea and hamadryas baboons. Still, given that female philopatry and male dispersal is most likely the ancestral state in the Papionini (Di Fiore & Rendall 1994; Lukas & Clutton-Brock 2011) it would be interesting to examine possible evolutionary causes for a sex reversal in dispersal in hamadryas and Guinea baboons. Jolly (2009) proposed that demographic factors in expanding frontier populations rather than ecological conditions led to male philopatry both in Guinea and hamadryas baboons, because neighboring olive baboons occupy the same habitats and this species usually exhibits male-biased dispersal (Packer 1975; Vinson *et al*. 2005). Other scholars have also questioned the direct effects of ecological factors on the evolution of female dispersal (Lukas & Clutton-Brock 2011). To test this hypothesis, a well-resolved phylogeny of baboons, especially of the northern clade including Guinea, hamadryas, and olive baboons (Boissinot *et al*. 2014) is needed (Pozzi *et al*. 2014). This will enable us to investigate whether Guinea and hamadryas baboons evolved female-biased dispersal independently or if it was inherited from their common ancestor, and if phylogeographic processes, such as range expansions (Jolly 2009), could have had an influence.

Conclusion

Our results corroborate that Guinea baboons are one of the few mammalian taxa characterized by female-biased dispersal. While the causes of this exceptional pattern remain unclear, it reinforces the view that the social system of this species should receive more attention in the future, in particular possible demographic and ecological factors influencing dispersal behavior. Their dispersal pattern in combination with their multilevel social organization and strong male-male bonds parallels the social system of humans and strengthens the case for the use of baboons as models to elucidate the processes that shaped the highly cooperative societies of *Homo*.

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CHAPTER 3: THE INFLUENCE OF SOCIAL SYSTEMS ON PATTERNS OF MITOCHONDRIAL DNA VARIATION IN BABOONS

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Abstract

Behavior is influenced by genes but can also shape the genetic structure of natural populations. Investigating this link is of great importance because behavioral processes can alter the genetic diversity on which selection acts. Gene flow is one of the main determinants of the genetic structure of a population and dispersal is the behavior that mediates gene flow. Baboons (genus *Papio*) are among the most intensely studied primate species and serve as a model system to investigate the evolution of social systems using a comparative approach. The general mammalian pattern of male dispersal and female philopatry has thus far been found in baboons, with the exception of hamadryas baboons (*P. hamadryas*). As yet, the lack of data on Guinea baboons (*P. papio*) creates a taxonomic gap in genus-wide comparative analyses. In our study we investigated the sex-biased dispersal pattern of Guinea baboons in comparison to hamadryas, olive, yellow and chacma baboons using sequences of the maternally transmitted mitochondrial hypervariable region I. Analyzing whole-range georeferenced samples (n=777), we found strong evidence for female-biased gene-flow in Guinea baboons and confirmed this pattern for hamadryas baboons, as shown by a lack of genetic-geographic structuring. Additionally, most genetic variation was found within and not among demes, in sharp contrast to the pattern observed in matrilocal primates including the other baboon taxa. Our results corroborate the notion that the Guinea baboons' social system shares some important features with that of hamadryas baboons, suggesting similar evolutionary forces have acted to distinguish them from all other baboons.

Keywords

Papio, social system, sex-biased dispersal, hypervariable region I, genetic population structure

Introduction

Clarifying the genetic basis of animal behavior is essential to understand its evolution. Advances in molecular techniques in recent years have enabled researchers to pinpoint an increasing number of genes underlying specific traits, which may eventually help to explain individual behavioral variation in natural populations (Tung *et al*. 2010). However, behavior and genes are mutually influential. For example, by triggering or preventing gene expression (Robinson *et al*. 2008; Tung *et al*. 2011) or by shaping the genetic structure of natural populations (Melnick & Pearl 1987; Altmann 1996; Bohonak 1999; Di Fiore 2003; Avise 2004). Investigating the influence of behavior on genetic structure is of great importance because behavioral processes can alter the genetic diversity upon which selection acts.

One of the main pathways through which behavior can directly influence genetic diversity and population genetic structure is dispersal. Dispersal, an animal's movement away from its natal area or group (Pusey & Packer 1987) is an important behavior underlying gene flow. Populations with high gene flow represent a panmictic and genetically more uniform entity, while restricted gene flow leads to several genetically differentiated demes (i.e. local interbreeding populations with distinct gene pools) that may react differently to selection pressures or may eventually diverge into separate species (Avise 2004).

Whereas birds tend to exhibit male philopatry and female-biased dispersal, in mammals male-biased dispersal and female philopatry are the norm, an observation that led Greenwood (Greenwood 1980) to hypothesize that the sex-bias in dispersal tightly correlates with the mating system. In group living species, the composition of the group (social organization, sensu (Kappeler & van Schaik 2002)) is immediately influenced by the immigration and emigration of individuals. Furthermore dispersal determines relatedness patterns within a group (Di Fiore 2003) and thus has profound impacts on the social relationships among individuals (social structure), as many social species preferably interact with close kin (Silk 2002; Seyfarth & Cheney 2012).

A sex-bias in dispersal translates into a specific pattern of genetic population structure. When dispersal is biased towards one sex, uniparentally inherited genetic markers show incongruent patterns in population structure (Avise 2004). In mammals, the general pattern of female philopatry and male dispersal is reflected in strong geographic structuring of the maternally inherited mitochondrial DNA (mtDNA), but not the paternally inherited Y-chromosomal haplotypes (Avise 2004). Consequently,

dispersal is a behavior that connects the social system of a species with its genetic diversity and represents a central factor in population genetics and population dynamics (Broquet & Petit 2009). Moreover, investigating the influence of dispersal patterns on the genetic variation of natural populations may help us to infer the social system of understudied taxa using genetic data (Di Fiore 2003).

The link between the social system and population genetic structure has been investigated in many species, including primates. *Papio* is among the best studied primate taxa and has widely been used as a model to study the evolution of social systems using a comparative socio-ecological approach (Barton *et al*. 1996; Barrett 2009). The wealth of data accumulated on their behavior and their wide distribution throughout Africa promotes them as a useful model to investigate the relationships between social systems and genetic structure.

In southern and eastern African baboons (yellow baboon *Papio cyncocephalus*, chacma baboon *P. ursinus*, Kinda baboon *P. kindae*), for example, in which the dispersing sex is male, a strong geographical structuring of mtDNA haplotypes, but of neither Y-chromosomal nor autosomal markers, reflects their matrilineal organization (Burrell 2008; Burrell *et al*. 2011). Interestingly, the phylogenetically closely related hamadryas baboon (*P. hamadryas*) exhibits a different social system in which male philopatry (Sigg *et al*. 1982; Swedell 2011) leads to a strikingly different genetic structure. For instance, there is no structuring of mitochondrial variation that corresponds to geography (Hapke *et al*. 2001; Hammond *et al*. 2006).

The Guinea baboon (*P. papio*), on the northwestern fringe of the baboon distribution, has been proposed to share some features with the hamadryas baboon on the northeastern fringe (Jolly 1993, 2009; Jolly & Phillips-Conroy 2006). Like the hamadryas baboon, the Guinea baboon is suspected to be characterized by male philopatry and female dispersal (Jolly 2009). A study using microsatellites indeed found evidence for female-mediated gene flow in a Guinea baboon population in Senegal (Fickenscher *et al*. 2011), whereas a similar study on a population in Guinea-Bissau did not find signatures of sex-biased dispersal, probably due to anthropogenic disturbance of the population and group compositions (Ferreira da Silva 2012). If the hypothesis that males are philopatric while females disperse in Guinea baboons is correct, we would expect to find little or no geographic structure in female specific genetic markers (mtDNA) in Guinea baboon. In contrast, if the geographic structure in mtDNA is strong, we would infer that gene flow in Guinea baboons is not female mediated, as in matrilocal primates.

In our study we investigate the taxon-wide pattern of female gene flow in Guinea, hamadryas, olive, yellow, and chacma baboons using sequences of the maternally transmitted mitochondrial hypervariable region I (HVRI). We infer common patterns by evaluating data over a wide range in order to overcome the noise induced by different local conditions in single populations. We reconstruct haplotype networks and test for isolation by distance to demonstrate the geographical distribution of genetic variation. We further estimate the hierarchical population structure. We expect to find a high diversity of mitochondrial haplotypes within demes and no significant variation among demes, with shared haplotypes existing between even distantly located demes.

Methods

Sample collection

Between 1995 and 2012 we collected fecal samples of free-ranging Guinea and hamadryas baboons covering the whole of their respective ranges. We also collected samples of olive, yellow, and chacma baboons for comparison. Fecal samples were stored either in ethanol or on silica, or according to the two-step method (Roeder *et al*. 2004; Nsubuga *et al*. 2004). Additionally, we analyzed available tissue samples of hamadryas baboons of known provenance provided by the King Khalid Wildlife Research Center (KKWRC), Saudi Arabia, and published sequences were downloaded from GenBank (Table 3.SI). In total, our dataset included 221 samples of hamadryas baboons (74 and 12 of these samples have previously been published by Hapke *et al*. (2001) and Winney *et al*. (2004), respectively) representing 27 different locations, 376 samples of Guinea baboons representing 62 different locations, 112 samples of olive baboons representing 25 different locations (18 of these samples have previously been published by Hapke *et al*. (2001), 44 samples of chacma baboons representing 17 different locations, and 24 samples of yellow baboons representing 11 different locations (Fig. 3.1; overview in Table 3.I; details in Table 3.SI). For each sampling site we recorded GPS coordinates (we only used general site-specific coordinates for our analysis because samples were usually found in a clumped fashion only separated by a few meters). We use sampling location as a proxy for social group, as most samples were collected from unhabituated animals that in some cases were not observed directly. However, to account for the uncertainty of whether samples actually represent the same social group we use the term “deme” to refer to samples

taken from the same location. Because the exact distribution of Guinea baboons in West Africa is unclear, we also collected samples outside of the range indicated in the literature and included them in the analysis if direct observation confirmed that the species was *P. papio*. For a subset of the hamadryas and Guinea baboon samples, we tested for repeated sampling of individuals using autosomal microsatellites (Hapke *et al*. 2001; Fickenscher *et al*. 2011; Ferreira da Silva 2012). For the remaining samples we did not explicitly test if samples originated from different individuals, as we followed some precautions in the sampling protocol (e.g. only one sampling session per site, a minimum distance between samples of two meters), that make double sampling negligible (Hapke *et al*. 2001; Fickenscher *et al*. 2011).

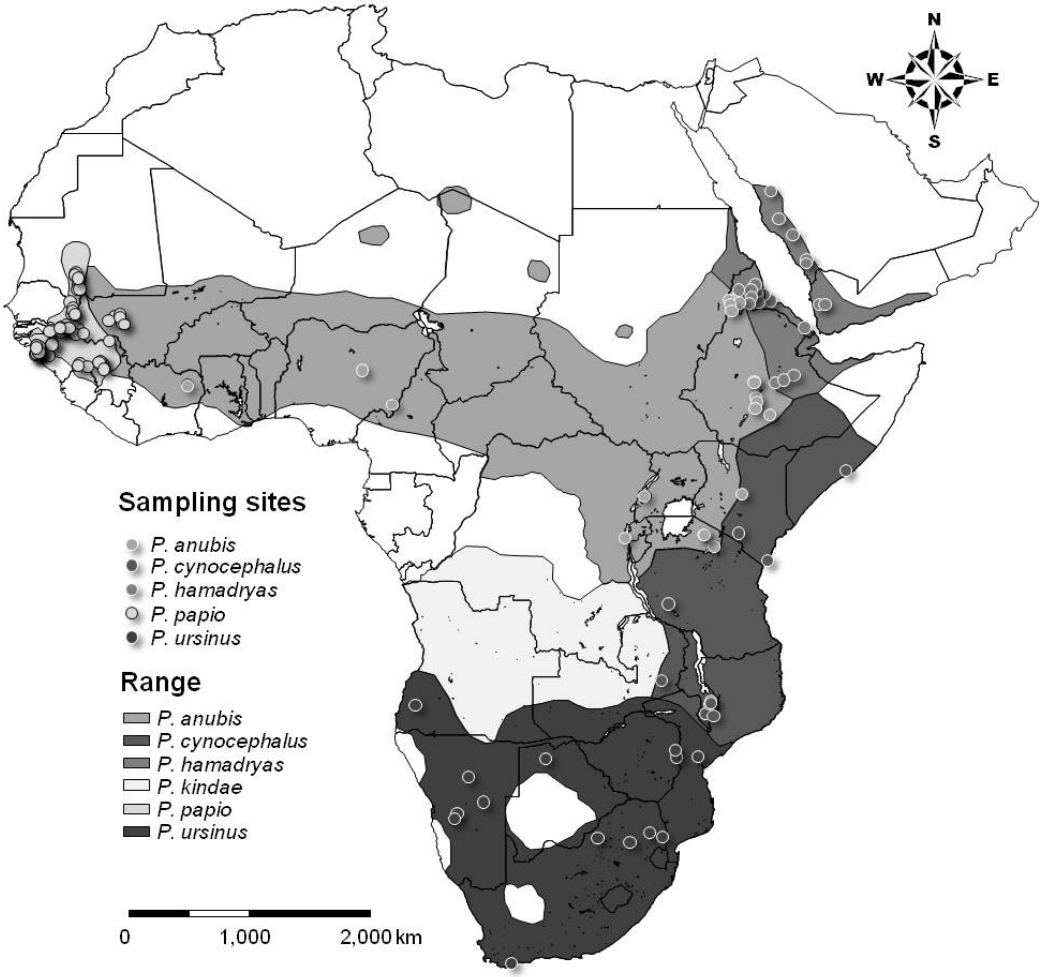

Figure 3.1: Distribution of baboons (Kingdon, 1997; Galat-Luong et al. 2006; Jolly 2007; Zinner et al. 2009) and sample locations used in this study.

This project complied with the protocols approved by the German Primate Center, Germany and the animal care regulations and principles of the International Primatological Society for the ethical treatment of non-human primates. Permits for research and sample export were obtained from the local authorities and research adhered to the legal requirements of the respective countries in which research was conducted.

Laboratory analyses

Total genomic DNA was extracted from fecal samples with the QIAamp DNA Stool Mini Kit (Qiagen, Hilden, Germany) and from tissue samples with the DNeasy Blood and Tissue Kit (Qiagen) according to the manufacturer's protocols with slight modifications (Haus *et al*. 2013). To avoid contamination we followed established protocols and performed extractions, PCR, and sequencing in separate laboratory rooms. All steps were monitored for contamination with negative (HPLC water) controls.

We amplified and sequenced a fragment of the HVRI of the mitochondrial genome (D-loop) comprising 341 base pairs (bp) using primers from previous studies (Hapke *et al*. 2001). PCR amplification was performed on a Sensoquest labcycler in a total volume of 30µl composed of 1.0µl DNA extract (20-40ng/µl), 19.6µl H_2O, 3.0µl 10x buffer (contains 15mM $MgCl_2$, Biotherm), 1.0µl forward primer (0.33µM; 5'-CTGGCGTTCTAACTTAAACT-3') and 1.0µl reverse primer (0.33µM; 5'-GTAGTATTACCCGAGCGG-3'), 0.2µl dNTPs (0.16mM), 4.0µl BT (0.6 mg/ml BSA + Triton) and 0.2µl BioTherm™ 5000 Taq Polymerase (1U; Genecraft, Germany). PCR conditions comprised a pre-denaturation step at 94°C for 2min, followed by 35-40 cycles at 94°C for 1min, 51°C for 1min, 72°C for 1min, and a single final extension step at 72°C for 5min. PCR products were checked on 1% agarose gels, excised and purified with the Qiagen Gel Extraction Kit (Qiagen). Both strands of each sample were sequenced on an ABI 3130*xL* sequencer using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Germany). We checked and aligned sequences manually in BIOEDIT 7.0.5.3 (Hall 1999).

To test for the accuracy of the sequences we amplified random samples and/or sequenced repeatedly. To avoid the amplification of nuclear mitochondrial insertions (numts), we selected primers highly specific to amplify only mitochondrial fragments of *Papio* (Hapke *et al*. 2001). We did not observe double peaks in chromatograms or sequence ambiguities when comparing both strands or repeatedly sequenced sam-

ples, which would indicate that numts could have flawed our analysis (Bensasson *et al*. 2001; Thalmann *et al*. 2004).

Statistical analyses

We estimated number of segregating sites *S*, nucleotide diversity π (Nei 1987), number of haplotypes and haplotype diversity hd (Nei 1987) for each species, both range-wide and separately for each deme, in DNASP 5.10.01 (Librado and Rozas 2009). Demes with only one sample were excluded from within-deme diversity calculations. To compare genetic variation within and among demes we performed a hierarchical analysis of molecular variance (AMOVA) (Excoffier *et al*. 1992) in ARLEQUIN 3.5.1.2 (Excoffier & Lischer 2010) using 10,000 permutations. For this analysis we grouped demes into distinct regions according to their geographic clustering, i.e. the distance to the next closest deme had to be smaller than 70km, as this is a distance that has been shown to affect population structure of nuclear markers in Guinea baboons for two different populations (Fickenscher *et al*. 2011; Ferreira da Silva 2012) (Fig. 3.4; overview in Table 3.I; details in Talbe 3.SI). Because the grouping may also affect the results of the AMOVA, we also ran the analysis with a weaker clustering, where the smallest distance had to be less than 150km. The fixation indices calculated in the AMOVAs, which are measures of genetic differentiation ranging from 0 (no differentiation, high gene flow) to 1 (complete differentiation, no gene flow), were used to evaluate the amount of gene flow within each species at the three respective spatial levels. Using 'ALLELES IN SPACE' (AIS) 1.0 (Miller 2005) we furthermore quantitatively analyzed the correlation between genetic and geographic distances with a Mantel test (Mantel 1967) for each species, testing for significance with 10,000 replicates. We split this analysis for hamadryas baboons for the Arabian and the African populations to account for the Red Sea acting as a major barrier to gene flow. To visualize the genetic distances and geographical distribution of haplotypes, we reconstructed a haplotype network using output data generated in ARLEQUIN and visualized using HAPSTAR 0.6 (Teacher & Griffiths 2011) for Guinea and hamadryas baboons, respectively (but not for the other species, where sampling was too sparse).

Results

The 221 hamadryas baboon samples yielded 93 different haplotypes with 84 segregating sites *S*, a haplotype diversity (hd) of 0.978 and nucleotide diversity (π) of

0.042. The 376 Guinea baboon samples yielded 104 different haplotypes with *S*=90, hd=0.947 and π=0.024. The remaining three species (chacma, yellow, and olive baboons) showed very similar hd values, but both π and *S* were considerably higher than in hamadryas and Guinea baboons (Table 3.I). When comparing the mean within-deme diversity indices hamadryas baboons showed slightly higher values than Guinea baboons (Table 3.I).

Separate hierarchical AMOVAs for each species revealed highly significant levels of structuring and comparable results for both Guinea and hamadryas baboons and a different pattern for chacma, yellow, and olive baboons (Table 3.II; Fig. 3.2). In Guinea and hamadryas baboons more than half of the species-wide genetic variation (Guinea baboons: 54%, hamadryas baboons: 54%) was a result of variation within demes (Table 3.II). Only a minor proportion of the genetic variation in these two species was explained by differences between demes (Guinea baboons: 7%, hamadryas baboons: 11%), whereas differentiation between regions contributed slightly more than a third of the genetic variation (Guinea baboons: 39%, hamadryas baboons: 34%) (Table 3.II). In contrast, within-deme diversity accounted for only 8%, 14%, and 14% of the variation in olive, yellow, and chacma baboons, respectively, while by far the highest percentage of genetic variation in these species was explained by variation among regions (olive baboons: 89%, yellow baboons: 75%, chacma baboons: 79%). Changing the clustering from 70 km to 150 km did not greatly affect the overall results and mainly reallocated some of the within-region variation to among-region variation (Table 3.II). The fixation indices are also considerably smaller in Guinea and hamadryas baboons than in the three matrilocal species indicating higher mitochondrial gene flow than in olive, yellow, and chacma baboons on all three spatial levels (among regions, among demes within regions, within demes; Table 3.II). We also compared our AMOVA results to published data on both matrilocal and patrilocal primate species. This comparison showed that the distribution of genetic variation in hamadryas and Guinea baboons is very similar to humans and chimpanzees (*Pan troglodytes*) (patrilocal), whereas the distribution of genetic variation in chacma, yellow, and olive baboons is more similar to macaques (*Macaca* spp.), orang-utans (*Pongo* spp.), and mouse lemurs (*Microcebus* spp.) (matrilocal) (Fig. 3.2).

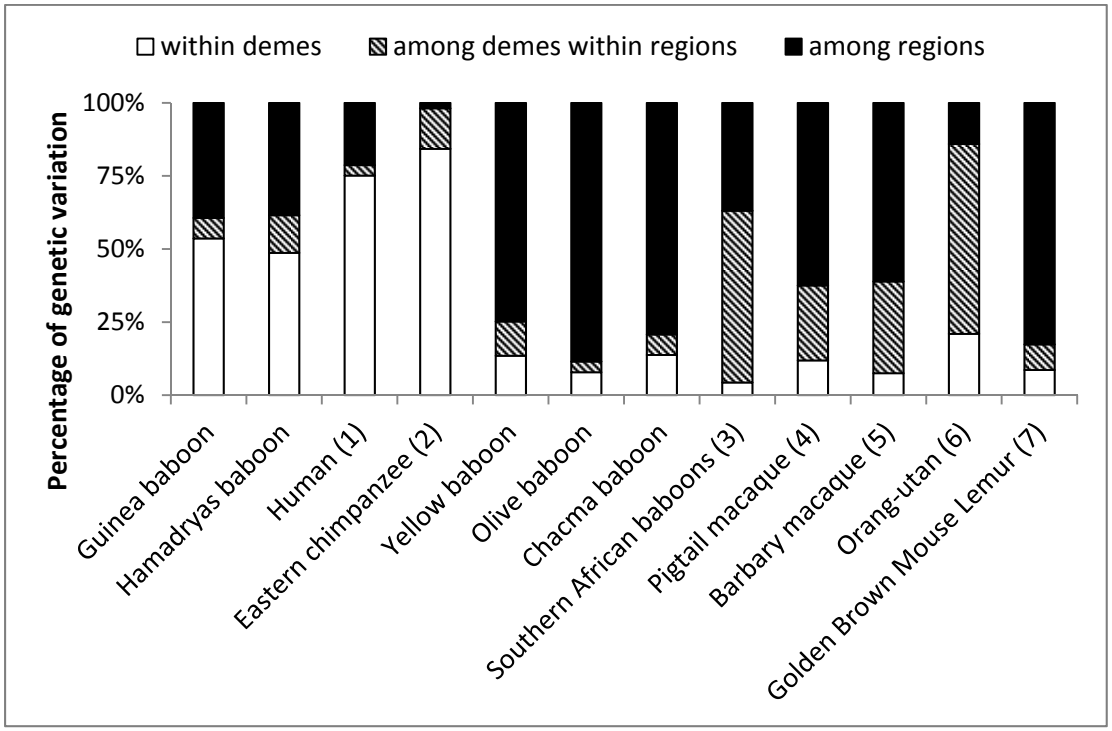

Figure 3.2: Analysis of Molecular Variance describing the hierarchical distribution of genetic variation for baboons in comparison to two patrilocal and four matrilocal primates [(1) Excoffier *et al*. 1992, (2) Goldberg & Ruvolo 1997, (3) Burrell 2008, (4) Rosenblum *et al*. 1997 (5) Modolo *et al*. 2005, (6) Nietlisbach *et al*. 2012, (7) Guschanski *et al*. 2006].

The Mantel test revealed significant correlations of genetic and geographic distance in all five species (Fig. 3.3). This isolation-by-distance effect was responsible for less than half of the variation in Guinea and hamadryas baboons with a lot of scatter around the regression line (Guinea baboons: $r=0.48$, $p<0.001$; hamadryas $baboons_{Africa}$: $r=0.34$, $p<0.001$; hamadryas $baboons_{Arabia}$: $r=0.25$, $p<0.001$). It was much stronger in the matrilocal baboons: IBD explained more than half of the variation in olive, chacma, and yellow baboons and reached a correlation coefficient as high as 0.90 in olive baboons (olive baboons: $r=0.90$, $p<0.001$; yellow baboons: $r=0.76$, $p<0.001$; chacma baboons: $r=0.54$, $p<0.001$).

Visualization of the haplotype networks (Fig. 3.4) showed that there were some haplotype clusters in both Guinea and hamadryas baboons, yet, these clusters were not very pronounced. In the Guinea baboons, network clusters only weakly corresponded to the geographic distribution of demes, with many haplotypes being found in several, and even very distant demes (Fig. 3.4a). Similarly, samples from geographically close demes frequently yielded haplotypes of very distant genetic relationships. The hamadryas baboon network showed a slightly more pronounced geo-

graphic clustering, separating most African from Arabian samples, with two distinct Arabian clades (Fig. 3.4b). Still, haplotypes within regions were very diverse and in some cases very distinct, for instance some Ethiopian samples clustered closer with Eritrean or Arabian samples than with other samples from Ethiopia. Moreover, several haplotypes in the Arabian clades were shared between demes over a distance of more than 1,000 km (Fig. 3.4b).

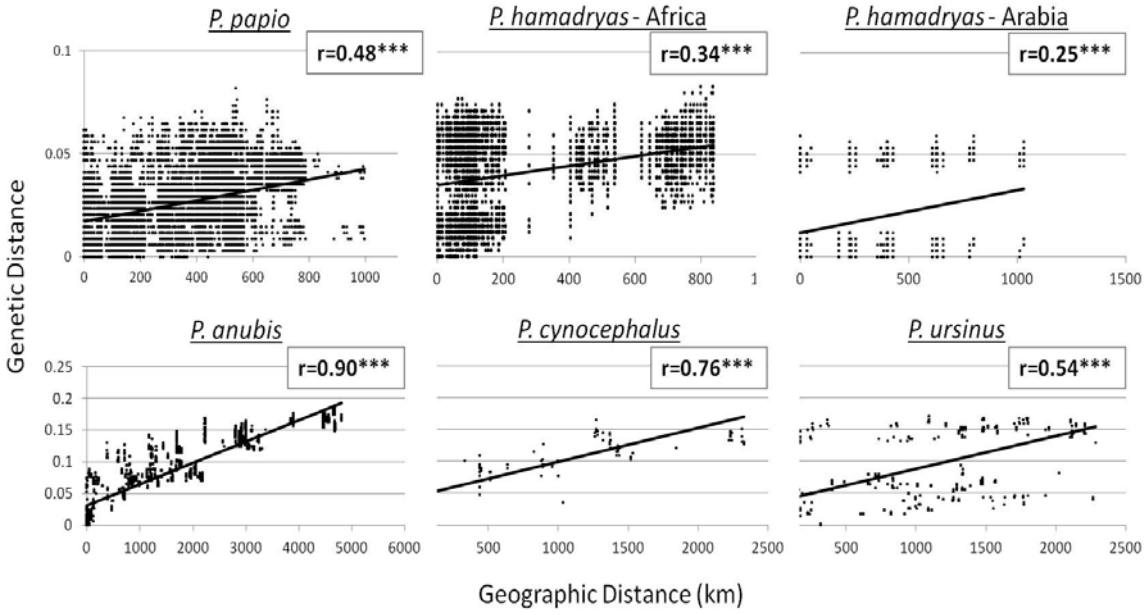

Figure 3.3: Plots of genetic distance vs. geographic distance for each baboon species with the results of Mantel tests. (r: Correlation of genetic and geographical distances; ***: p<0.001 (10,000 replicates)).

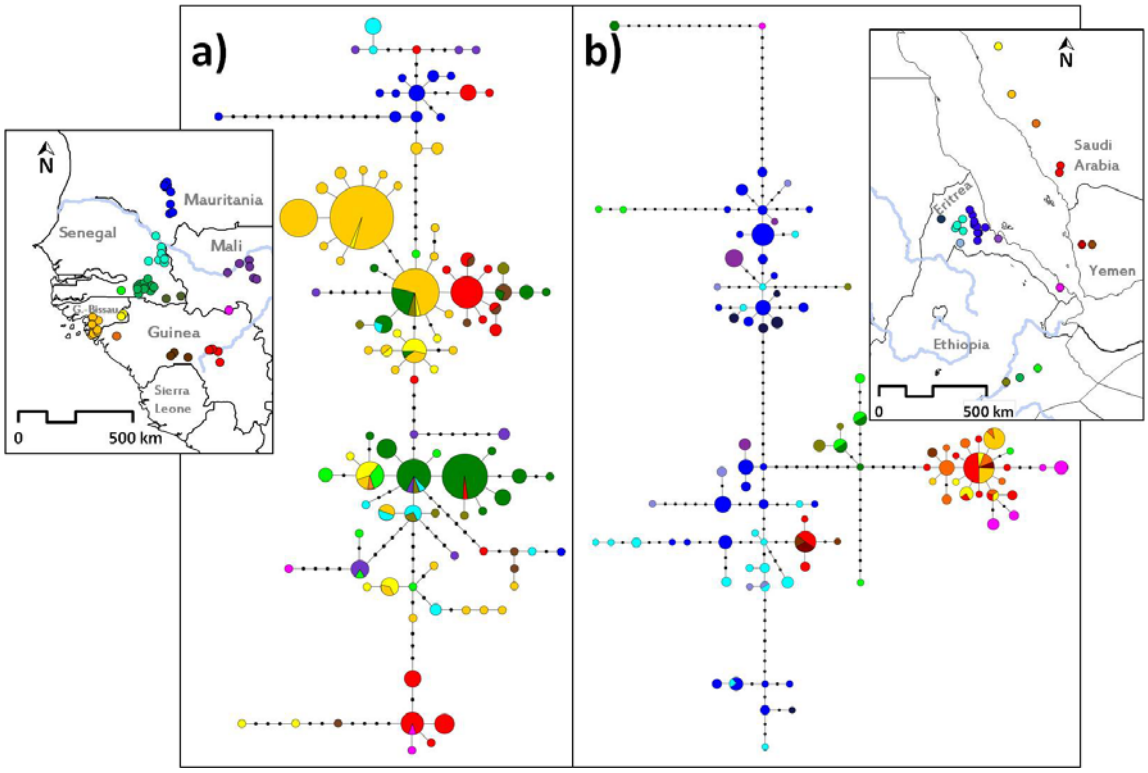

Figure 3.4: Haplotype network of mtDNA sequences and corresponding distribution of samples of (a) *Papio papio* and (b) *P. hamadryas*. One haplotype is represented by one circle and circle size corresponds to haplotype frequency. Branch length is proportional to mutational steps and each dot represents one mutated position. Haplotype color represents the different regions defined for the AMOVA (70km clustering) depicted on the map.

Table 3.1: Overview of collected samples and genetic diversity of baboons, species-wide and within demes*. The number of demes and regions corresponds to the 70km clustering of sampling locations used in the AMOVA. Genetic diversity within demes represents average values within one single deme, whereby demes with only one sample were excluded from the analysis.

Taxon	Species-wide						Within demes*			
	Number of demes (regions)	Number of samples	Number of haplotypes	Hd	π	*S*	median (min-max) number of samples	median (min-max) number of haplotypes	Mean Hd (±SD)	Mean π (±SD)
P. hamadryas	27 (15)	221	93	0.987	0.042	84	7 (2-25)	4 (1-11)	0.795 (±0.203)	0.025 (±0.012)
P. papio	62 (12)	376	104	0.947	0.024	90	4 (1-22)	3 (1-8)	0.703 (±0.318)	0.015 (±0.012)
P. ursinus	17 (14)	44	20	0.951	0.086	95	2 (1-5)	1 (1-3)	0.287 (±0.369)	0.013 (±0.020)
P. cynocephalus	11 (8)	24	17	0.949	0.076	94	1 (1-5)	1 (1-4)	0.76 (±0.258)	0.033 (±0.033)
P. anubis	25 (15)	112	42	0.949	0.092	129	4 (1-17)	2 (1-6)	0.518 (±0.307)	0.009 (±0.010)

Hd: haplotype diversity; π: nucleotide diversity, *S*: number of segregating sites; *: the term deme is used here to refer to sampling locations.

Table 3.2: Results of hierarchical AMOVA comparing the percentage of genetic variation explained by variation among regions, within regions, and within demes for each of the five baboon species for demes that are separated by a distance of at least 70km and 150km.

Taxon	Source of variation	df	Sum of squares	Variance component	Fixation index	*P*	Percent variation
P. papio 70km (150km)	Among regions	11 (3)	566.9 (97.0)	Va=1.77 (0.51)	ϕ_{CT}=0.39 (0.11)	<0.001	**39.36** (11.36)
	Among demes within regions	50 (58)	215.8 (685.6)	Vb=0.32 (1.56)	ϕ_{SC}=0.12 (0.39)	<0.001	**7.02** (34.9)
	Within demes	314 (314)	755.9 (755.9)	Vc=2.41 (2.41)	ϕ_{ST}=0.46 (0.46)	<0.001	**53.62** (53.73)
P. hamadryas 70km (150km)	Among regions	14 (7)	650.8 (529.5)	Va=2.53 (2.64)	ϕ_{CT}=0.34 (0.33)	<0.001	**34.19** (33.48)
	Among demes within regions	12 (19)	115.5 (236.8)	Vb=0.85 (1.22)	ϕ_{SC}=0.17 (0.23)	<0.01 (<0.001)	**11.48** (15.51)
	Within demes	194 (194)	780.9 (780.9)	Vc=4.03 (4.03)	ϕ_{ST}=0.46 (0.49)	<0.001	**54.32** (51.00)
P. cynocephalus 70km (150km)	Among regions	7 (5)	245.6 (190.1)	Va=12.28 (10.62)	ϕ_{CT}=0.75 (0.58)	<0.001	**74.82** (57.92)
	Among demes within regions	3 (5)	23.0 (78.5)	Vb=1.92 (5.50)	ϕ_{SC}=0.46 (0.71)	<0.001 (<0.01)	**11.69** (30.00)
	Within demes	13 (13)	28.8 (28.8)	Vc=2.22 (2.22)	ϕ_{ST}=0.87 (0.88)	<0.001 (<0.01)	**13.50** (12.08)
P. anubis 70km (150km)	Among regions	14 (11)	1573.9 (1478.3)	Va=15.80 (15.53)	ϕ_{CT}=0.88 (0.82)	<0.001	**88.50** (82.24)
	Among demes within regions	10 (13)	44.3 (139.9)	Vb=0.65 (1.95)	ϕ_{SC}=0.32 (0.58)	<0.001	**3.63** (10.32)
	Within demes	87 (87)	122.2 (122.2)	Vc=1.40 (1.40)	ϕ_{ST}=0.92 (0.92)	<0.001	**7.87** (7.44)
P. ursinus 70km (150km)	Among regions	13 (10)	565.5 (438.6)	Va=12.77 (4.73)	ϕ_{CT}=0.79 (0.29)	<0.001 (ns)	**79.25** (29.43)
	Among demes within regions	3 (6)	15.3 (142.2)	Vb=1.13 (9.12)	ϕ_{SC}=0.34 (0.80)	ns (<0.001)	**6.99** (56.78)
	Within demes	27 (27)	59.9 (59.9)	Vc=2.22 (2.22)	ϕ_{ST}=0.86 (0.86)	<0.001	**13.76** (13.80)

Discussion

Our results strongly support the hypothesis of female-biased gene flow in Guinea baboons: the female inherited mtDNA marker shows no clear genetic structure that would be consistent with the geographic distribution of our samples. Furthermore, it displays isolation-by-distance, which is consistent with neutral genetic drift driven by dispersal.

Genetic diversity, as inferred from number of haplotypes per species and hd, is comparable between Guinea and hamadryas baboons, both species-wide and at the level of single demes. Species-wide hd is furthermore very similar to all other baboon species. However, π is considerably higher in olive, yellow and chacma baboons compared to hamadryas and Guinea baboons. This probably reflects the more complex evolutionary history of the former three species which is characterized by multiple events of population isolation and reconnection, leading to deep divergences of haplogroups within these species (Zinner *et al*. 2009). The very low π in Guinea baboons compared to hamadryas baboons confirms results of a previous study based on a smaller sample size of Guinea baboons from Guinea-Bissau (Ferreira da Silva *et al*. 2013). The difference in π between Guinea and hamadryas baboons may either be due to a lower effective (female) population size N_e or a more recent origin of the species. However, the latter, is rather unlikely considering current divergence time estimations that do not suggest a more recent origin of Guinea baboons (Zinner *et al*. 2013b). A smaller effective population size in Guinea baboons could be the result of past demographic changes (e.g. bottlenecks, recent expansion), a smaller census size, less population substructuring or a different mating system. Nuclear microsatellite data also suggest that genetic diversity is lower in Guinea baboons than in other baboon species (Fickenscher *et al*. 2011; Ferreira da Silva 2012). A smaller census size and less substructuring are likely explanations, considering that Guinea baboons have the most restricted distribution of all baboon species (Anandam *et al*. 2013) and that hamadryas baboons comprise two subpopulations divided by the Red Sea. The similar haplotype diversity between all five species makes us confident that a comparative study of gene flow patterns is feasible and will not be affected by other factors that generally influence the genetic diversity of populations (e.g., differences in female reproductive skew, substructuring of species, differences in demographic history).

MtDNA variation was strikingly similar between Guinea and hamadryas baboons, with the highest proportion of genetic variation being explained by variation within demes. This indicates that female dispersal leads to the accumulation of several mitochondrial haplotypes within a group, a pattern also observed in other female-dispersing species, for example chimpanzees (Morin *et al*. 1994; Goldberg & Ruvolo 1997; Gagneux *et al*. 1999) and humans (Seielstad *et al*. 1998). In species with female philopatry, the restriction of female gene flow prohibits the exchange of mitochondrial haplotypes among demes, explaining our results of low genetic variation within demes, but high variation among demes and regions for olive, yellow and chacma baboons. A study of south African baboons observed similarly low within-deme variation (Burrell 2008). The higher among-deme and lower among-region variation observed by Burrell (Burrell 2008) relative to our results for chacma and yellow baboons might be explained by differences in sampling scheme. Our sampling in these species was sparser but included a broader range. Changing the clustering of the AMOVA to larger geographic regions largely eliminates the difference between these two studies.

Burrell (2008) furthermore reports that usually only one haplotype is observed in one specific deme, a pattern that we also observe in yellow and chacma baboons but treated with caution due to our low within-deme sampling. In olive baboons we find on average two haplotypes as compared to four and three in demes of hamadryas and Guinea baboons, respectively. While this difference in within-deme diversity seems to be rather minor, it is confirmed by the considerably lower within-deme π in olive relative to hamadryas and Guinea baboons. This suggests that even if several haplotypes are observed within a deme in olive baboons, these are much more closely related than in Guinea and hamadryas baboons.

A comparison of hierarchical distribution of mitogenetic variation between our results and different species with female dispersal and female philopatry, respectively, (Rosenblum *et al*. 1997; Modolo *et al*. 2005; Nietlisbach *et al*. 2012) supports our conclusion that Guinea baboons show the typical patterns of a species with female dispersal.

Additionally, the less pronounced effect of isolation-by-distance in Guinea and hamadryas baboons is evidence for higher rates of female gene flow in these two species. Although female transfer may be observed on rare occasions in female-philopatric species and has been reported for yellow (Rasmussen 1981) and olive baboons (Henzi & Barrett 2003), this apparently has no important impact on the genetic

make-up of populations. In hamadryas baboons, the Mantel test revealed the two distinct Arabian clusters that are visible in the haplotype network. These two distinct clusters have already been described in previous studies and are probably a result of the complex colonization history of the Arabian Peninsula by hamadryas baboons (Wildman *et al*. 2004; Winney *et al*. 2004).

There was a high degree of shared haplotypes between distant demes in Guinea baboons and, to a lesser extent, in hamadryas baboons. The fact that this pattern is less pronounced in hamadryas baboons could be due to the sampling scheme, which was much patchier in this species. Including more samples from the area between the Ethiopian and the Eritrean clusters may reveal a similar picture in hamadryas baboons to that in Guinea baboons. In both species we observe shared haplotypes over distances of more than 500km, a result comparable to, for instance, Eastern chimpanzees (*Pan troglodytes schweinfurthii,* Goldberg & Ruvolo 1997). These shared haplotypes could result from long-distance dispersal, but successive short dispersal events over several generations adding up to larger distances seem to be more likely considering the general biology of baboons. Alternatively the lack of strong geographic clustering may be explained by shared haplotypes representing ancient diversity and that these ancient lineages are incompletely sorted due to time constraints. Divergence time estimations and reconstructions of phylogeographic history suggest that Guinea baboons evolved during the same time period as all other baboon species (Zinner *et al*. 2011b; Zinner *et al*. 2013b). Consequently, Guinea baboons had as much time as the other species to develop genetic clusters and this strongly argues against the explanation of incomplete lineage sorting. Furthermore, in female philopatric species one haplotype reaches fixation extremely quickly within demes causing mitochondrial diversity to disappear rapidly (Hoelzer *et al*. 1998). This means that polymorphism caused by incomplete lineage sorting would be lost even over short evolutionary timescales, leading to a pattern of mitochondrial variation comparable to what we observed in chacma, yellow, and olive baboons.

Taken together, the results of our study constitute solid evidence for female-biased gene flow in both Guinea and hamadryas baboons, sharply contrasting with the pattern observed in all other baboon species and most mammals. Unfortunately we cannot distinguish between female dispersal in the narrow sense with our mtDNA data set (where single females or small groups of females migrate) and dispersal of social units, e.g., one-male, multi-female groups in hamadryas baboons (Swedell *et al*. 2011) or parties (Patzelt *et al*. 2011) in Guinea baboons. This question can only be

addressed by long-term observations of individually identified animals, and at the genetic level by including nuclear markers in future analysis. Whereas direct behavioral observations confirm female dispersal in hamadryas baboons (Swedell *et al*. 2011), our study is the first indication of a general species-wide pattern of female dispersal in Guinea baboons. These results corroborate the notion that the Guinea baboon's social system shares some important features with that of hamadryas baboons, suggesting that similar evolutionary forces have acted in their history to distinguish them from all other baboons. Although the details of female dispersal behavior in Guinea baboons remain to be clarified, our study adds to the knowledge of the biology of the genus *Papio* and improves our understanding of the link between behavior and genetics in primates.

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CHAPTER 4: GENETIC CLINES IN A SMALL WORLD – GENE FLOW DYNAMICS IN WEST AFRICAN BABOONS

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Abstract

The extent of gene flow within and among populations is one of the main determinants of genetic structure and thus directly influences the evolutionary fate of populations. Behavioural patterns, ecological factors and landscape characteristics, demographic history, and phylogenetic relationships are major contributors that shape gene flow within and among populations. In this study we investigate gene flow patterns over the whole distribution of West African Guinea baboons (*Papio papio*). We analysed sequence data of the mitochondrial hypervariable region I (D-loop) of 517 individuals and up to 23 nuclear microsatellite markers of 477 individuals. We specifically assessed the pattern and degree of gene flow in this species and how it is affected by features of social organization (i.e. sex-biased dispersal patterns), demographic history, and interaction with the neighbouring olive baboon (*P. anubis*). Our results reveal a lack of geographic structure in mitochondrial but significant global structuring of nuclear markers, which is probably attributable to female dependent gene flow. However, we could not detect consistent patterns among regions in sex-biased local structuring. Overall, locally restricted dispersal appears to limit effective gene flow to a distance of below 200 km, resulting in a strong isolation-by-distance effect and genetically divergent populations. Signatures of population expansion, the clinal structure of genetic variation, and potential traces of allele surfing point to an historic west-ward expansion of Guinea baboons. In contrast, landscape features appear to be a negligible factor. Introgressive hybridization with olive baboons can be invoked to explain genetic patterns in the contact zone, but warrant further investigation.

Keywords

Papio, sex-biased dispersal, genetic population structure, range expansion, allele surfing, microsatellites, hypervariable region I

Introduction

Quantifying the spatial and temporal dynamics of natural populations' genetic structure can help us to elucidate their evolutionary trajectories. In addition, information about the intraspecific distribution and magnitude of genetic diversity is essential as a baseline to evaluate interspecific relationships (Jolly 1993). The accuracy of phylogenetic reconstructions and species delimitation efforts, for instance, greatly rely on whether intraspecific diversity was assessed appropriately (Markolf *et al*. 2011). In concert with genetic drift, natural selection, and mutation, one of the main determinants of genetic structure is gene flow, i.e. the movement of alleles between populations (Slatkin 1985). In animals, the primary mechanism underlying gene flow is dispersal (Slatkin 1985), the extent of which is shaped by both intrinsic and extrinsic factors: individual behavioural patterns, ecological factors and landscape characteristics, demographic history, and phylogenetic relationships such as reproductive barriers.

Dispersal strategies can strongly influence how populations shift their ranges (Ibrahim *et al*. 1996) and how they are capable of colonizing new regions. Range expansions may occur in response to geological events or climate fluctuations that produce environmental shifts thus creating new suitable habitats and dispersal corridors (Hewitt 2000; Parmesan & Yohe 2003). The current distribution of populations is often a function of how they reacted to changing ecosystems. In particular, the isolation and reconnection of suitable habitats have major impacts on dispersal and hence gene flow among populations. However, there is notable variation among taxa in how they respond to these extrinsic processes (Hewitt 1996, 2011; Bisconti *et al*. 2011; Haus 2013), and this is probably mainly attributable to differences in fundamental biological properties, such as dispersal capability and general adaptability.

Interestingly, range expansions also generate distinctive evolutionary forces at the expanding range margins, which influence and are also influenced by the dynamics of the expansion and resulting genetic patterns (Austerlitz *et al*. 1997; Klopfstein *et al*. 2006; Excoffier *et al*. 2009; Travis *et al*. 2010; White *et al*. 2013). These forces can be either of stochastic nature (Austerlitz *et al*. 1997; Hallatschek *et al*. 2007; Excoffier & Ray 2008; Slatkin & Excoffier 2012) or driven by altered selective pressures (Travis & Dytham 2002; Burton *et al*. 2010; Phillips *et al*. 2010; Datta *et al*. 2013). Most importantly, allele frequency gradients might be created, and reduced genetic diversity but increased population structuring is expected in edge as com-

pared to core populations as a result of recurrent founder effects (Eckert *et al*. 2008; Excoffier *et al*. 2009). Furthermore, increased dispersal and reproduction in growing edge populations has been shown both theoretically (Travis & Dytham 2002; Burton *et al*. 2010; Shine *et al*. 2011) and empirically in several taxa throughout the animal kingdom (Simmons & Thomas 2004; Phillips *et al*. 2006; Hughes *et al*. 2007; Moreau *et al*. 2011). However, to our knowledge, theoretical work is largely based on models of asexual organisms (but see Miller et al., 2011; Shaw & Kokko, 2015) and there is a lack of studies explicitly analysing the role of sex-bias in dispersal in the framework of range expansions.

By expanding their ranges, populations often come into contact with or invade the range of neighbouring populations. Natural hybridization may occur if individuals of distinct populations reproduce successfully (Arnold 1997). This phenomenon is now recognized to be widespread and considered a major evolutionary process (Barton & Hewitt 1985; Hewitt 1988; Arnold 1992, 1997, 2006; Mallet 2005; Abbott *et al*. 2013). Interspecific gene flow is most likely to occur between closely related species that diverged recently (Mallet 2005). It might either persist despite divergence or recur after isolation in cases of secondary contact. Depending on the strengths of selection and drift, certain genomic regions of one population can invade the genome of the other population, resulting in a mosaic genome (Arnold & Meyer 2006), a process called introgression (Mallet 2005). Depending on the sex-bias and symmetry in dispersal different introgression patterns will manifest (Petit & Excoffier 2009). In mammals with male-biased dispersal, for instance, unidirectional gene flow can lead to nuclear swamping (Zinner *et al*. 2011a). To disentangle whether genetic signatures stem from historical or contemporary processes, a fine-scale assessment over the whole geographic range of a species is necessary (Zellmer & Knowles 2009; Guo 2012; Epps *et al*. 2013a).

In this study, we investigate the impact of contemporary and historical gene flow on the distribution of genetic diversity over the whole range of a generalist primate, the Guinea baboon (*Papio papio*). More specifically, we aim to draw inferences about the contribution of sex-biased dispersal, range expansion, and interspecific gene flow on the genetic structure of this species. Baboons represent an intriguing study taxon to investigate gene flow dynamics, as their evolutionary history was shaped by range expansion and contraction, both ancient and on-going hybridization have been described, and both species specific male- and female-biased dispersal can be observed (Swedell 2011; Anandam *et al*. 2013; Zinner *et al*. 2013a; Kopp *et al*. 2014a).

Guinea baboons have a rather limited distribution on the north-western fringe of the baboon distribution in West Africa (Kingdon 1997; Anandam *et al*. 2013), where they occupy diverse habitats and climate zones, ranging from humid Guinean high forests in Guinea-Bissau to arid Sahelian steppe in Mauretania (Galat-Luong *et al*. 2006; Oates *et al*. 2008). A genus-wide study on mitochondrial DNA (mtDNA) variation (Kopp *et al*. 2014a) as well as a small-scale population genetic study based on autosomal microsatellites and mtDNA found evidence for female-biased gene-flow in this species (Kopp *et al*. 2015). A study on a different population concluded that mtDNA variation is best explained by historic female gene flow (Ferreira da Silva *et al*. 2014). It has been suggested that Guinea baboons hybridize with the neighbouring olive baboons (*P. anubis*) in Mali (Grubb *et al*. 2003) but this species border has never been investigated. We compiled the first comprehensive, distribution-wide data set on Guinea baboon genetic variation including both uni- and bi-parentally inherited markers at a fine-scale spatial resolution in order to examine the pattern and degree of genetic structure of this species. This enabled us to investigate the impact of historical and contemporary range expansions, examine signatures of sex-biased dispersal, and explore interspecific gene flow. We hypothesized (i) that the historic range expansion of Guinea baboons left shallow genetic gradients as traces and that major rivers restrict gene flow; (ii) that female-biased dispersal leads to a stronger global structuring of nuclear compared to mitochondrial DNA and to a stronger regional structuring in males than in females; and (iii) that introgressive hybridization with the neighbouring olive baboon results in discordances between nuclear and mitochondrial data as well as the presence of foreign alleles on the eastern and southern edge of the Guinea baboon distribution.

Methods

Sample collection

We non-invasively collected faecal samples of wild Guinea baboons between 2009 and 2014 according to the two-step method (Roeder *et al*. 2004; Nsubuga *et al*. 2004). Some of these samples have already been analyzed for previous studies (Ferreira da Silva 2012; Patzelt *et al*. 2014; Kopp *et al*. 2014a; Kopp *et al*. 2015). In total, we included 104 sampling sites across the species' range (Fig. 4.1; Table 4.I). Because the exact distribution of Guinea baboons is insufficiently known (Oates *et al*. 2008; Oates 2011), we extended our sampling region east- and southwards, thereby potentially incorporating samples from the neighbouring olive baboon. For each sampling site we recorded GPS coordinates and used these general site-specific coordinates for our analysis because samples were usually found in a clumped fashion only separated by a few meters. One additional sample of unknown exact provenance in Côte d'Ivoire was included. It was obtained from Abidjan zoo and described as *P. anubis* morphologically but harboured the same mitochondrial haplotype as *P. papio* in a previous study (Zinner *et al*. 2011b). This led to the hypothesis that this sample represents a hybrid individual, making it a valuable data point for this study. For this sample we assigned coordinates within Côte d'Ivoire to enable us to use it in spatial analyses. We assigned sampling sites to 18 different "regions" based on their geographic location (Fig. 4.1, Table 4.I).

This project complied with the protocols approved by the German Primate Center, Germany and the animal care regulations and principles of the International Primatological Society for the ethical treatment of non-human primates. Permits for research and sample export were obtained from the local authorities and research adhered to the legal requirements of the respective countries in which research was conducted.

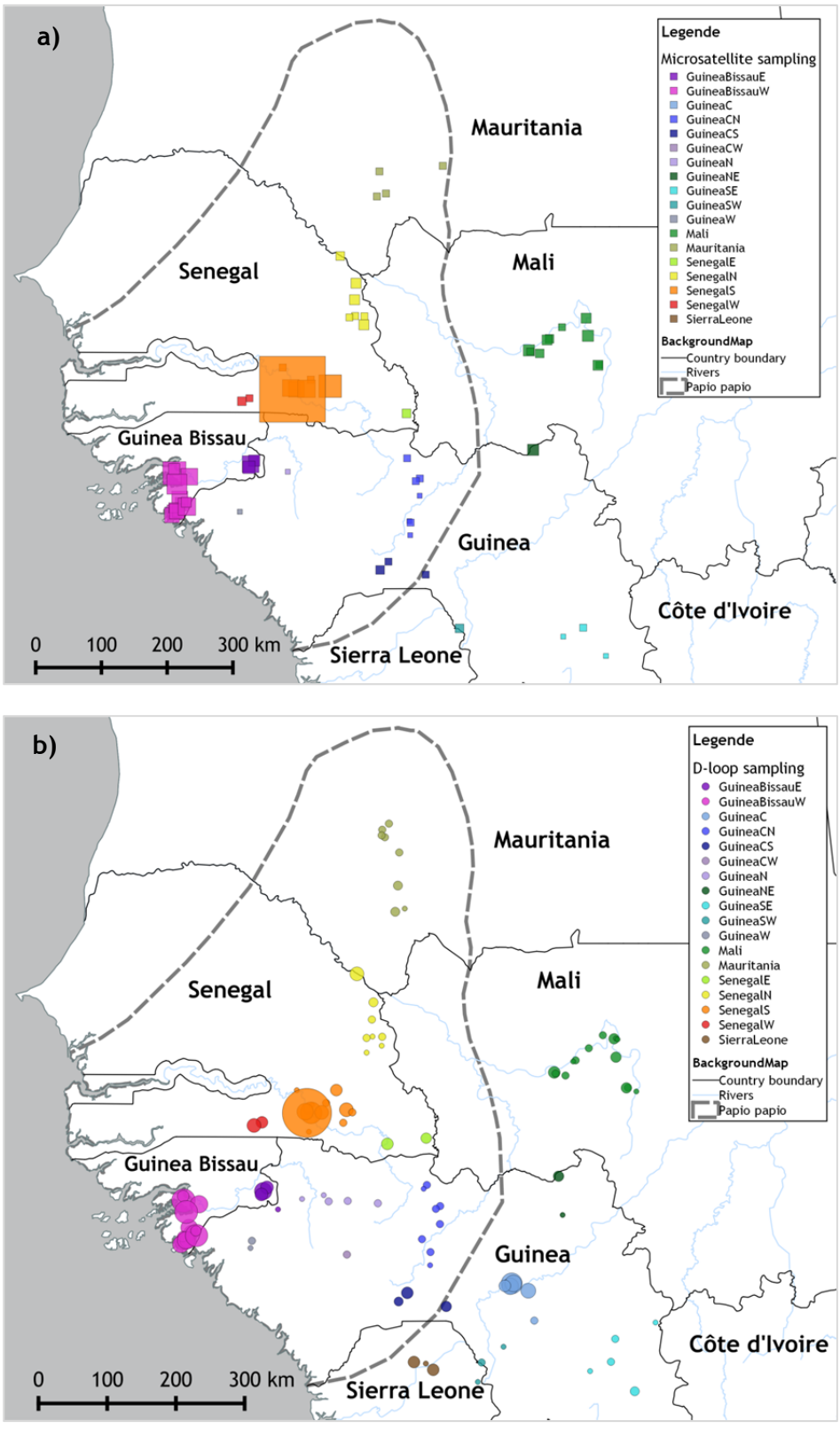


Fig. 4.1: Distribution of baboon samples analysed in this study using (a) microsatellites and (b) mitochondrial DNA sequences. Symbol colour reflects assignment to the respective region while symbol size corresponds to sample size (smalles circle/square: n=1, largest circle: n=87, largest square: n=171). IUCN distribution map of Guinea baboons (Oates *et al*. 2008) indicated by grey dashed line.

Table 4.I: Overview of samples analysed in this study (Dloop: number of D-loop sequences; Genotypes: number of individual genotypes).

Location code	Location name	Region	Country	Longitude	Latitude	Dloop	Genotypes
AB	Abreirîz	Mauritania	Mauritania	-11.007265	16.422665	0	2
AC	Amindara Catobo	GuineaBissauW	Guinea Bissau	-14.97698	11.28059	8	7
AF	Ain Farfara	Mauritania	Mauritania	-12.16086	17.04272	2	0
AI	Boé Aicum	GuineaBissauE	Guinea Bissau	-13.93178	11.88762	11	11
AM	Boé Aicum Montanha	GuineaBissauE	Guinea Bissau	-13.87702	11.94172	6	5
AN	Aouînet Nanâga	Mauritania	Mauritania	-12.19912	17.15248	2	0
Ass	Mont Assirik	SenegalS	Senegal	-12.76667	12.88333	2	0
BA	Bandiagara	GuineaN	Guinea	-13.3663	11.773	1	1
Bak	Bakaria	GuineaC	Guinea	-10.31542	10.54267	16	0
BB	Belly Baobabwald	SenegalN	Senegal	-12.34072	14.13944	1	2
BBL	Boé Béli	GuineaBissauE	Guinea Bissau	-13.95713	11.83922	6	6
BC	Botchê Cule	GuineaBissauW	Guinea Bissau	-15.00971	11.35542	10	10
BD	Badi	SenegalS	Senegal	-13.22282	13.14267	1	0
BE	Berdo	Mali	Mali	-9.19301	13.96921	2	2
BI	Bira	SenegalS	Senegal	-13.44228	13.35725	1	2
BN	Bani	GuineaCN	Guinea	-11.62073	11.18792	2	0
BR	Berber	Mali	Mali	-8.82611	14.10676	4	4
BS	Bensely	GuineaCN	Guinea	-11.35616	11.6696	2	2
BU	Bubatchingue	GuineaBissauW	Guinea Bissau	-15.09168	11.7501	20	21
BY	Beli	GuineaCN	Guinea	-11.51498	11.02083	0	1
BZ	Bangko	GuineaSE	Guinea	-8.80754	9.73482	2	0
CA	Canamina	GuineaBissauW	Guinea Bissau	-15.08817	11.15442	11	9
CB	Cabedu	GuineaBissauW	Guinea Bissau	-15.12815	11.11149	10	9
CDI	Abidjan Zoo	CDI	Cote d'Ivoire	-9.50000*	7.5000*	1	1
CK	Bakar Conte	GuineaBissauW	Guinea Bissau	-14.86451	11.69654	11	11
CL	Camp du Lion	SenegalS	Senegal	-13.23463	13.0282	17	10
CM	Cambeque	GuineaBissauW	Guinea Bissau	-15.02566	11.17161	10	6
CQ	Caiquene	GuineaBissauW	Guinea Bissau	-15.10157	11.22527	4	4
CT	Catomboi	GuineaBissauW	Guinea Bissau	-15.05494	11.17154	11	9
DB	Diara Baka	GuineaW	Guinea	-14.11705	11.05829	1	0
DD	Dorodounga	Mali	Mali	-9.69587	13.61725	5	5
DI	Didikourou	GuineaNE	Guinea	-9.57419	11.54022	1	0
DK	Dokoro	GuineaCN	Guinea	-11.35935	11.40775	2	1
DL	Dalaba	SenegalS	Senegal	-13.26691	12.75181	1	0
DN	Dienoundiala	SenegalS	Senegal	-13.0162	13.17205	2	2
DO	Dondonya	SierraLeone	Sierra Leone	-11.45714	9.285	5	0
DS	Donguel Sigon	GuineaN	Guinea	-12.26307	11.7107	2	0
DU	Dumakuni	GuineaSE	Guinea	-8.87047	9.4007	2	2
FD	Fassori Dounga	Mali	Mali	-9.53247	13.57138	2	3
FK	Farakorodou	Mali	Mali	-9.67698	13.60088	2	2
GA	Guelta Galoûal	Mauritania	Mauritania	-11.97107	16.3388	3	2
GB	Guebombol	GuineaBissauW	Guinea Bissau	-15.0951	11.81303	5	5
GD	Gue Damantan	SenegalS	Senegal	-13.31968	13.04499	10	11
GK	Gabanikoro	Mali	Mali	-8.98882	14.15853	2	0
GL	Guelenwil	GuineaCW	Guinea	-12.71322	10.96385	2	0
GM	Gamon	SenegalS	Senegal	-12.86736	13.35923	5	0
GU	Guelta Goumbel	Mauritania	Mauritania	-12.00986	15.95708	3	2
HN	Hore Nioma	GuineaCN	Guinea	-11.54979	11.97686	2	2
KA	Kababongtini	GuineaSE	Guinea	-8.52417	8.97195	3	1
KB	Koussan Barrage	SenegalN	Senegal	-12.42742	14.11863	2	2
KD	Kendo	Mali	Mali	-8.62625	13.39549	2	2
Ked	Kedougou	SenegalE	Senegal	-12.12472	12.57556	5	0
KF	Kayanga Forêt classee	SenegalW	Senegal	-13.94963	12.8899	5	2
KG	Kamagboboi	SierraLeone	Sierra Leone	-11.73762	9.39756	5	0
KI	Kalan I	Mali	Mali	-9.38394	13.79255	2	3
KK	Kouroukoumba	Mali	Mali	-9.42076	13.77619	1	4
KL	Koullore	GuineaW	Guinea	-14.09571	11.16404	2	1
KM	Kamaro	GuineaSW	Guinea	-10.43402	9.62044	1	0
KN	nördlich von Kidira	SenegalN	Senegal	-12.32751	14.63811	3	4

Kou	Kouroukorodgi	GuineaC	Guinea	-10.07305	10.43605	8	0
KR	Kourounkanke	GuineaSE	Guinea	-9.17404	9.26567	1	1
KS	Kasenga	GuineaN	Guinea	-13.0506	11.82842	1	0
KT	Kotifara	Mali	Mali	-8.64568	13.39143	4	4
KW	Kewedji	GuineaCN	Guinea	-11.50284	10.80774	1	1
KX	Kondaybaya	SierraLeone	Sierra Leone	-11.56429	9.37605	1	0
KY	Kayanga	SenegalW	Senegal	-14.06561	12.84416	7	3
LA	Laout	Mauritania	Mauritania	-12.10167	17.24083	2	0
LG	Lorge	GuineaCN	Guinea	-11.41861	11.62917	2	2
LK	Lingue Kountou	SenegalS	Senegal	-13.08025	13.03378	7	12
LM	Loma	GuineaSW	Sierra Leone	-10.80765	9.10805	1	0
LN	Lenjele	GuineaCS	Guinea	-11.83477	10.40548	5	2
LY	Leysere	GuineaCS	Guinea	-11.26792	10.20729	4	2
Mar	Mare	GuineaC	Guinea	-10.33702	10.50143	10	0
MB	Mare Bendougou	Mali	Mali	-8.79814	13.83853	4	5
MD	Madina	GuineaCN	Guinea	-11.59589	11.92189	1	0
ML	Marela	GuineaCN	Guinea	-11.49739	10.99949	2	2
MT	Marteneblendou	Mali	Mali	-8.79971	14.11138	1	0
MU	Moudéri	SenegalN	Mauritania	-12.56762	15.05263	7	3
MY	Guelta Meyla	Mauritania	Mauritania	-11.87175	16.00255	1	2
NJ	Nafadji	SenegalE	Senegal	-11.55947	12.65923	4	3
NK	Niokolo	SenegalS	Senegal	-12.72078	13.07348	7	20
NS	südlich von Niokolo	SenegalS	Senegal	-12.63451	13.03531	2	0
NT	Nienta	GuineaNE	Guinea	-9.63293	12.10501	4	5
NY	Nyalama	GuineaN	Guinea	-12.70155	11.74452	2	0
OI	Oumm Icheglâne	Mauritania	Mauritania	-12.20785	17.0703	2	0
PG	Porto Gandamael	GuineaBissauW	Guinea Bissau	-14.9013	11.24092	18	12
QS	Quebo Sutuba	GuineaBissauW	Guinea Bissau	-14.91079	11.30911	4	4
SF	Sinthiou Fissa	SenegalN	Senegal	-12.34977	14.38698	2	4
SI	Simenti	SenegalS	Senegal	-13.29485	13.02626	87	171
SO	Fôret classée de Soyah	GuineaCS	Guinea	-11.96087	10.27998	3	3
SP	Senta Pont	GuineaBissauE	Guinea	-13.71624	11.62104	1	0
SS	Sr Soares	GuineaBissauW	Guinea Bissau	-15.05308	11.58412	19	16
SY	Samba Yaye	SenegalN	Senegal	-12.20762	14.00541	1	4
Tam	Tambo	GuineaC	Guinea	-10.29207	10.54283	10	0
TB	Touba	GuineaN	Guinea	-12.97937	11.73811	2	0
TF	Tacoutala Falemeufer	SenegalN	Senegal	-12.19996	14.13581	2	2
TJ	Taja	Mali	Mali	-8.77454	14.0976	1	0
TS	Trig Seiouaddé	Mauritania	Mauritania	-11.95168	16.82082	2	0
TT	Traverse de Tiko	Mali	Mali	-8.50145	13.33944	1	0
WF	Wendow Fode	SenegalN	Senegal	-12.42664	13.90499	1	0
WK	Wulonkoro	GuineaSW	Guinea	-10.75277	9.39091	2	3
Woy	Woyumba	GuineaC	Guinea	-10.41442	10.50847	5	0
WS	Wasaba	GuineaC	Guinea	-9.98602	10.00156	2	0
WT	Worontomonkoni	GuineaSE	Guinea	-8.22175	9.97359	1	0
total						517	477

***** For the sample from CDI, for which exact provenance was not known, we assigned coordinates within Côte d'Ivoire to enable us to use this sample in spatial analyses.

Genetic analyses

Total genomic DNA was extracted from faecal samples with the QIAamp DNA Stool Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's protocols with slight modifications (Haus *et al.* 2013). To avoid contamination we followed established protocols and performed extractions, PCR, and sequencing in separate labora-

tory rooms. All steps were monitored for contamination with negative (HPLC water) controls.

We amplified and sequenced a fragment of the hypervariable region I (HVRI) of the mitochondrial genome (D-loop) comprising 341 base pairs for 517 individuals. Laboratory procedures and post-sequencing processing followed established protocols (Kopp *et al*. 2014a).

We used a PCR-based gonosomal sexing system (C. Roos unpubl.) to determine the sex of sampled individuals. We genotyped 477 samples (229 females, 240 males, 8 undetermined sex) at 9 to 23 (mean 16.2) autosomal microsatellite loci using published protocols (Ferreira da Silva *et al*. 2014; Patzelt *et al*. 2014; Kopp *et al*. 2015). To assure accuracy, genotyping was repeated at least four times leading to a consensus genotype (multiple tubes approach (Navidi *et al*. 1992; Taberlet *et al*. 1996; Morin *et al*. 2001)). Obtaining accurate microsatellite genotypes from faecal samples can be difficult due to low DNA quality and quantity or poor extract quality (Taberlet *et al*. 1999). We therefore evaluated genotyping errors following standard procedures (Kopp *et al*. 2015) and only included samples that passed our quality control (i.e. having a quality index QI_{sample} (Miquel *et al*. 2006) over 0.5). Because genotyping was performed in different laboratories, we standardized allele scoring to avoid errors due to dye shifts (Sutton *et al*. 2011).

Statistical analyses

Summary statistics

To assess the diversity of D-loop sequences we calculated number of segregating sites *S*, nucleotide diversity π (Nei 1987), and haplotype diversity *Hd* using DNASP version 5.10.1 (Librado & Rozas 2009).

For microsatellites we tested for departures from Hardy-Weinberg equilibrium (HWE) with an exact test in GENEPOP 4.0.11 (default settings: dememorization number: 10,000; number of batches: 20; iterations per batch: 5,000) (Raymond & Rousset 1995; Rousset 2008), both for the whole dataset and in every region. We calculated mean number of different alleles per locus *Na*, expected heterozygosity H_E and observed heterozygosity H_O in ARLEQUIN 3.5.1.2 (Excoffier & Lischer 2010). The same program was used to assess average gene diversity H_S, and the Garza-Williamson index, which can be used to detect reductions in population size (Garza & Williamson 2001). Inbreeding coefficients F_{IS} were calculated in FSTAT 2.9.3.2

(Goudet 1995). Number of private alleles *Np,* and pairwise F_{ST} values among regions were estimated in GenAlEx.

Spatial structure of genetic diversity and differentiation

We visualized the relationships among D-loop haplotypes by generating a network in HAPSTAR 0.6 (Teacher & Griffiths 2011) based on pairwise distances calculated in ARLEQUIN. Using 'ALLELES IN SPACE' (AIS) 1.0 (Miller 2005) we quantitatively analysed the correlation between genetic and geographic distances with a Mantel test (Mantel 1967) testing for significance with 10,000 replicates.

Using the multilocus genotype dataset, we reconstructed a neighbour-joining (NJ) tree to evaluate the relationship between regions in POPTREE2 (Takezaki *et al*. 2010) based on Nei's genetic distance (D_A, Nei *et al*. 1983) and 1,000 bootstraps.

We investigated the nuclear genetic population structure with a suite of approaches to reach a reliable interpretation, including a Bayesian clustering algorithm, a spatially explicit Bayesian clustering method, a multivariate cluster analysis, and a multivariate spatial method. For a first assessment of the large-scale genetic structure of the species, we analysed our multilocus genotypes with STRUCTURE 2.3.4. (Pritchard *et al*. 2000) which employs a Bayesian clustering algorithm to identify the most likely number of populations and each individual's assignment probablity. A total of 1,000,000 Markov Chain Monte Carlo steps were run including a burn-in of 100,000. We evaluated a number of populations K from 1 to 10, with 10 replicates to assure convergence of results between runs. We used the admixture as ancestry and the correlated frequency as allele frequency model (Falush *et al*. 2003). To narrow down the most probable number of clusters, we evaluated the mean likelihood L(K) and variance per K and employed the ΔK method (Evanno *et al*. 2005) as implemented in STRUCTUREHARVESTER WEB v0.6.92 (Earl & VonHoldt 2011). Structure outputs were post-processed with CLUMPP 1.1.2 (Jakobsson & Rosenberg 2007) to average results over runs, using the Greedy option with random input orders, 1,000 repeats and G' similarity statistic. Averaged cluster membership probabilities of individuals across runs were interpolated on a geographic map with QGIS 2.8.1-Wien (QGIS Development Team 2015) using inverse distance weighting (IDW) and a distance coefficient P=3. Secondly, in order to incorporate prior spatial information in the Bayesian analysis, we ran the georeferenced multi-locus dataset in TESS 2.3.1 (Chen *et al*. 2007; Durand *et al*. 2009), which implements a Bayesian clustering algorithm with inference being based on a spatial individual network. We

ran 100,000 iterations with a burnin of 20,000 and evaluated 2-10 clusters K with 10 replicates. Coordinate uncertainty was set to 1 and we used the admixture model (BMY, Durand *et al*. 2009), correlated frequencies and spatial model, with null allele model set to false. The most probable number of clusters was selected by identifying K at which Deviance Information Criterion (DIC) values plateaued. Results were post-processed as above.

In addition, we analysed the same dataset with two multivariate methods. These "ordination in reduced space" techniques summarize a complex multivariate dataset into a small set of uncorrelated synthetic variables. The main advantage of these methods is that specific population genetic models (e.g. HWE) are not assumed and they are thus capable of revealing more complex structures, such as clinal variation (Jombart *et al*. 2009). Discriminant Analysis of Prinicpal Components (DAPC, Jombart *et al*. 2010) was used to identify and describe genetic clusters and run with the package ADEGENET 1.4-2 (Jombart 2008; Jombart & Ahmed 2011) in R 3.1.1. (R Development Core Team 2014). This technique aims to maximize variation among while minimizing variation within clusters by first transforming data in a Principal Component Analysis (PCA) and subsequently submitting the retrieved PCA factors to a Discriminant Analysis (DA). We identified the optimal number of clusters based on the Bayesian Information Criterion (BIC) (Jombart *et al*. 2010) using the *find.clusters* function. Sixty principal components (PCs), which cumulatively explained more than 90% of the observed variation in the data, were retained to be analysed in the DA, where we retained all eigenvalues. Using the *loading.plot* function, we assessed which alleles contributed most to the observed pattern.

To explicitely incorporate spatial information, a spatial principal component analysis (sPCA, Jombart *et al*. 2008), as implemented in ADEGENET, was used to investigate genetic variance and spatial patterns. sPCA assesses spatial autocorrelation through Moran's *I* to disentangle global structures (i.e. spatially close individuals are also genetically similar) from local structures (i.e. genetic dissimilarty among closely located individuals). We used individual multilocus genotypes and a connection network which defined neighbouring entities based on their pairwise geographic distance of 0 – 200 km (Fig. 4.7a). Missing data were replaced by mean allele frequencies. A screeplot of the eigenvalues was used to assess the interpretability of the principal components and we retained the first two positive and one negative axes. To support the interpretation of global and local patterns, we ran the global and local Monte Carlo tests in ADEGENET (Jombart *et al*. 2008) against

the null hypothesis of absence of spatial patterns with 9999 permutations. Again, we checked the contributions of alleles to rule out that observed patterns were solely driven by extreme outliers.

To assess whether genetic diversity can be explained by an isolation-by-distance effect (IBD) the correlation between genetic and geographic distances was analyzed with a Mantel test in AIS. In order to examine the spatial scale of gene flow in more detail, we performed a spatial autocorrelation analysis for the whole dataset, for males and females separately, and within inferred clusters. We specified distance classes of 30 km and calculated the autocorrelation coefficient *r* as a measure of genetic similarity between all individual dyads within the respective distance classes in GENALEX 6.501 (Peakall & Smouse 2012). Missing locus data was interpolated for the respective individuals from average genetic distance. 95% confidence intervals around *r* were estimated with 999 bootstraps and significance assessed with 999 permutations.

Regional and distribution-wide demographic history

Using the D-loop data, we computed Tajima's *D* statistic (Tajima 1989) and Fu's F_S (Fu 1997) in ARLEQUIN. A negative value of these estimates indicates that the population has undergone a demographic expansion in selectively neutral genes. To more precisely investigate the demographic history we calculated a mismatch distribution (Rogers & Harpending 1992) in ARLEQUIN 3.5.1.3 (Excoffier & Lischer 2010) with 1,000 bootstraps. We tested both the model for demographic expansion and the model for spatial expansion. We then calculated the time since expansion with $\tau = 2\mu t$ (μ: mutation rate. t: number of generations since expansion) applying a generation time of 12 years (Rogers & Kidd 1996) and the specific mutation rate of primate HVRI of 20% per million years (Jensen-Seaman & Kidd 2001).

The influence of bottlenecks on nuclear genetic diversity was evaluated using BOTTLENECK 1.2.02 (Cornuet & Luikart 1997) with the two-phase mutation model (TPM, 30% variance, 70% stepwise mutations) and 1,000 iterations for the whole distribution and four inferred clusters.

Results

Descriptive summary statistics

The 517 analysed D-loop sequences yielded 131 haplotypes, with 98 segregating sites *S*, haplotype diversity *Hd*=0.9486 and nucleotide diversity π=0.02396. In the microsatellite dataset, we found no departures from HWE in most regions and over the whole distribution (Table 4.II). F_{IS} ranged around zero (mean -0.002). Expected and observed heterozygosity were similar among regions, ranging from 0.57 to 0.68 and 0.54 to 0.67, respectively. Mean number of alleles *Na* ranged from 2.8 to 5.0 within regions, with 7.1 for the whole data set. About half of the regions, mainly those in the east, harboured private alleles (Table 4.II).

Spatial structure

The D-loop haplotype network did not reveal any obvious clusters corresponding to geographic locations and did not distinguish between samples from inside and outside the range of Guinea baboons (Fig. 4.2). Most regions harboured haplotypes distributed over the whole network. The CDI sample, putatively stemming from an olive baboon individual, clusters with samples from south-eastern Guinea and is identical to the main haplotype of that region. Moreover, the network showed several star-shaped patterns indicating population expansions. The Mantel test revealed a significant correlation between genetic and geographic distance (R^2=0.47, p<0.001; Fig. 4.3a), although there was vast variation around the regression line and genetic distance was in general very low.

The topology of the microsatellite NJ tree roughly corresponded to geography and revealed the deepest splits distinguishing the most southern regions from the rest (Fig. 4.4). However, bootstrap support of most nodes was rather low. Genetic differentiation among regions as measured by F_{ST} varied between 0 (no differentiation) and 0.6 (strong differentiation), with the most eastern populations being most distinct (Table 4.III).

Table 4.II: Microsatellite summary statistics for each region

Region	n	H_o	H_e	HWE	Hs	F_{IS}	Na	Np	GW
CDI	1	/	/	/	0.68	/	/	0.17	0.27
Guinea Bissau E	22	0.55	0.62	*	0.64	0.11	4.3	0	0.31
GuineaBissau W	123	0.57	0.57	ns	0.57	0.00	4.6	0	0.29
Guinea CN	11	0.53	0.59	ns	0.58	0.11	3.9	0	0.35
Guinea CS	7	0.57	0.60	ns	0.53	0.06	3.4	0	0.38
Guinea N	1	/	/	/	0.52	/	/	0	0.41
Guinea NE	5	0.64	0.65	ns	0.65	0.01	3.6	0	0.35
Guinea SE	4	0.61	0.63	ns	0.62	0.06	3.2	0.26	0.31
Guinea SW	3	0.61	0.68	ns	0.57	0.13	2.8	0.17	0.30
Guinea W	1	/	/	/	0.57	/	/	0	0.34
Mali	34	0.58	0.62	ns	0.61	0.05	5.0	0.22	0.34
Mauritania	8	0.57	0.64	ns	0.57	0.07	3.7	0.04	0.30
Senegal E	3	0.67	0.66	ns	0.52	-0.01	2.9	0.04	0.36
Senegal N	21	0.54	0.58	ns	0.57	0.06	4.4	0.17	0.33
Senegal S	228	0.60	0.57	***	0.58	-0.05	4.8	0.22	0.36
Senegal W	5	0.55	0.58	ns	0.59	0.06	3.0	0	0.37

n: sample size; HWE: departures from HWE, *p<0.05, **p<0.01, ***p<0.001, ns: not significant, / not estimated due to small sample size; Hs: average gene diversity over loci; F_{IS}: inbreeding coefficient; Na: mean number of alleles; Np: mean number of private alleles; GW: Garza-Williamson index

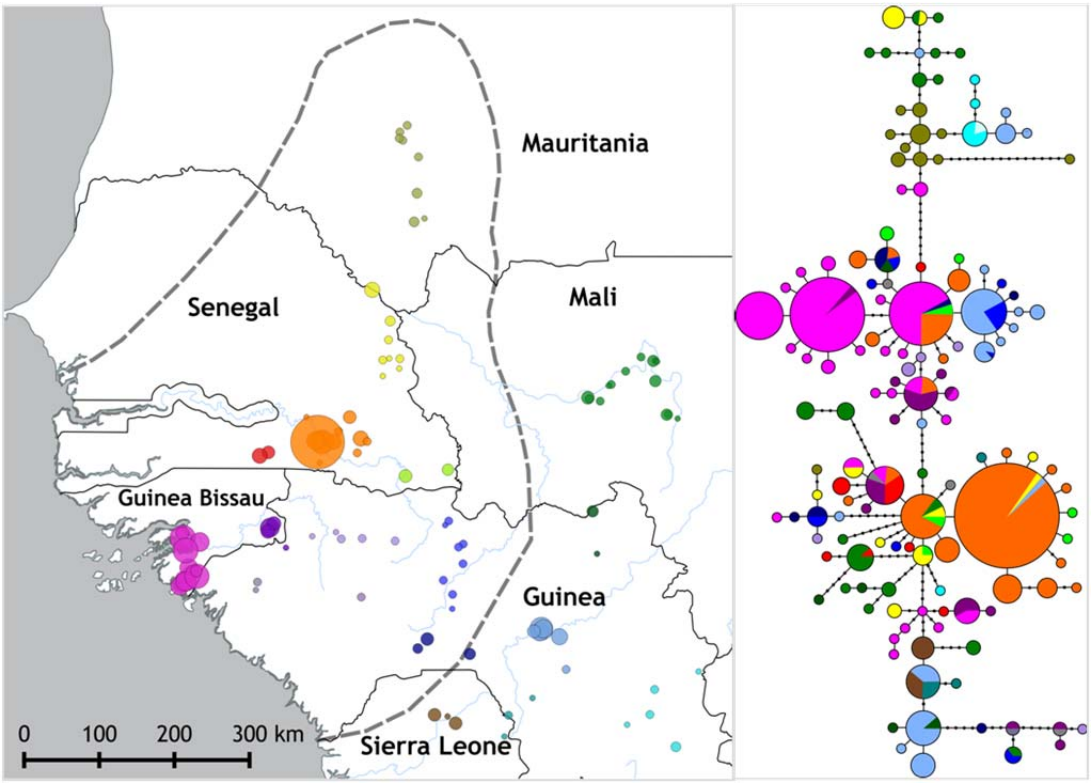


Fig. 4.2: Haplotype network of D-loop sequences. Circle size indicates sample size and colours correspond to sampling regions. The CDI sample (white) clusters with samples from south-eastern Guinea (turquoise) and is identical to the main haplotype of that region. IUCN distribution map of Guinea baboons (Oates *et al*. 2008) indicated by grey dashed line.

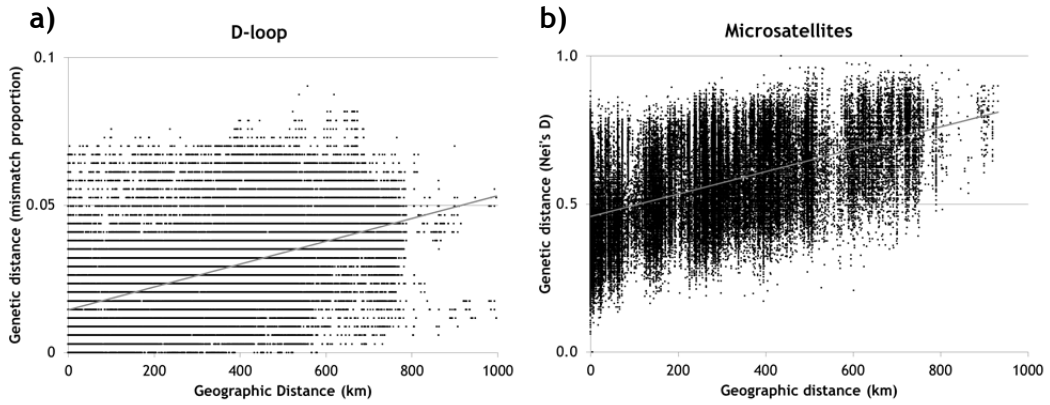


Fig. 4.3: Mantel test showing the correlation between genetic and geographic distance for (a) D-loop dataset (R^2=0.47, p<0.001) and (b) multilocus genotype dataset (R^2=0.51, p<0.001).

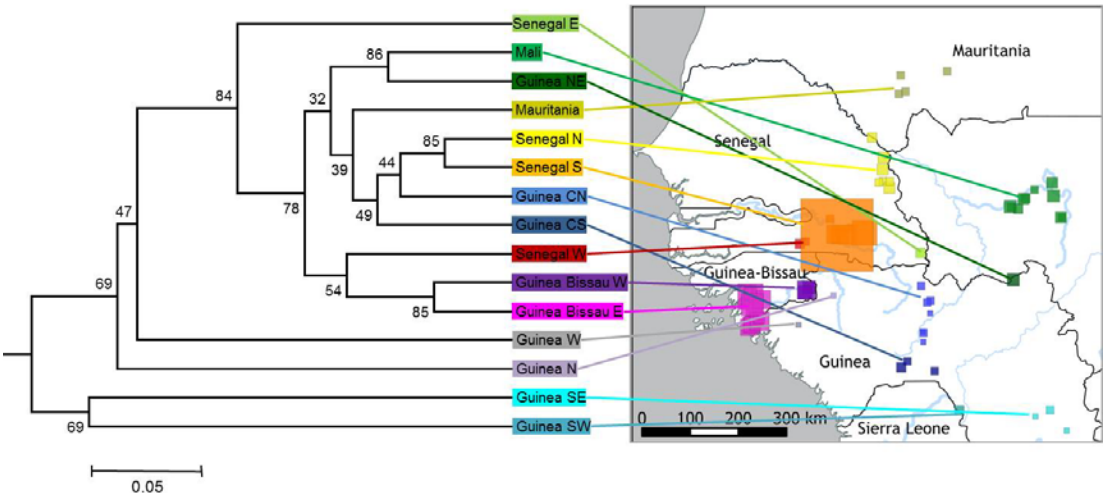


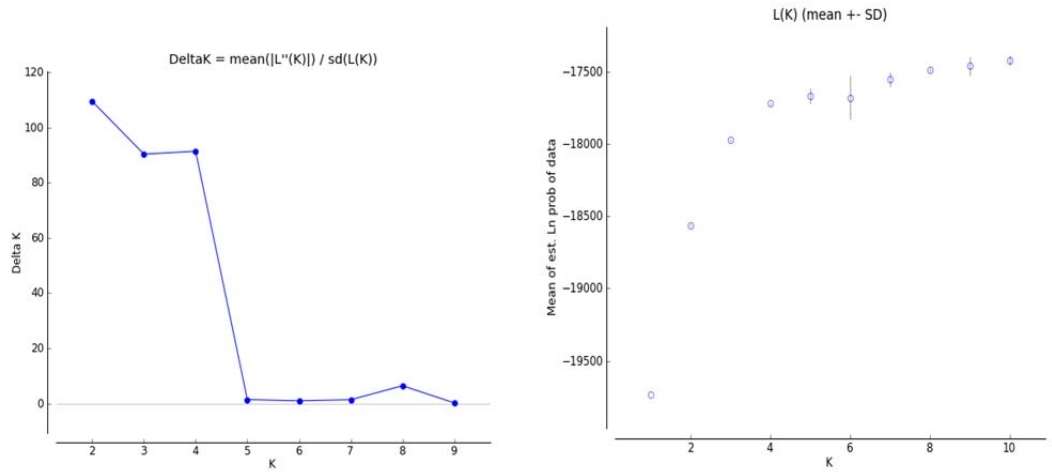
Fig. 4.4: Neighbour-joining tree of regions with more than one sample based on Nei's genetic distance among multilocus genotypes. Numbers indicate bootstrap support of respective nodes.

Table 4.III: Pairwise F_{ST} values among regions, darker shading indicates stronger differentiation

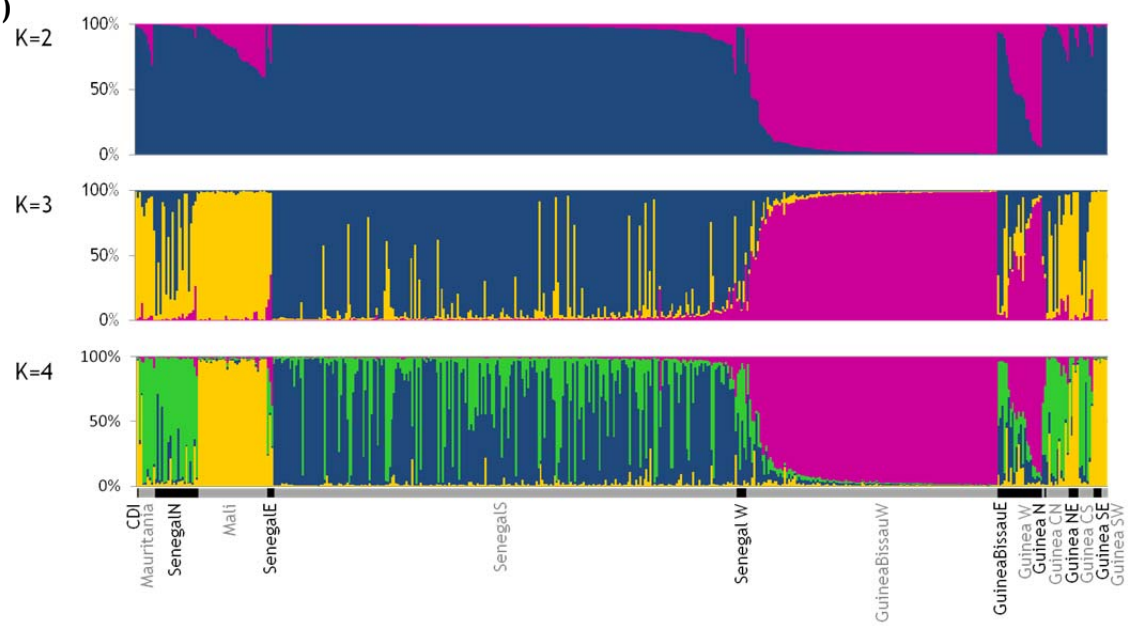
	CDI	Maur	SenN	Mali	SenE	SenS	SenW	GBiW	GBiE	GuiW	GuiN	GuiCN	GuiNE	GuiCS	GuiSE	GuiSW
CDI	0.0															
Maur	0.4	0.0														
SenN	0.3	0.1	0.0													
Mali	0.3	0.1	0.0	0.0												
SenE	0.4	0.1	0.1	0.1	0.0											
SenS	0.3	0.1	0.0	0.1	0.1	0.0										
SenW	0.3	0.1	0.1	0.1	0.1	0.1	0.0									
GBiW	0.6	0.4	0.4	0.4	0.4	0.3	0.4	0.0								
GBiE	0.5	0.4	0.3	0.3	0.4	0.3	0.3	0.5	0.0							
GuiW	0.5	0.3	0.2	0.2	0.3	0.2	0.2	0.5	0.5	0.0						
GuiN	0.5	0.2	0.2	0.2	0.3	0.2	0.2	0.5	0.5	0.4	0.0					
GuiCN	0.3	0.1	0.0	0.1	0.1	0.0	0.1	0.4	0.3	0.2	0.2	0.0				
GuiNE	0.3	0.1	0.0	0.1	0.1	0.1	0.1	0.4	0.3	0.2	0.2	0.1	0.0			
GuiCS	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.4	0.4	0.2	0.3	0.0	0.1	0.0		
GuiSE	0.3	0.2	0.1	0.1	0.2	0.1	0.2	0.4	0.4	0.3	0.2	0.1	0.1	0.2	0.0	
GuiSW	0.4	0.2	0.2	0.2	0.3	0.2	0.2	0.5	0.4	0.4	0.3	0.2	0.2	0.2	0.2	0.0

Bayesian cluster analysis of the individual multilocus genotypes in STRUCTURE revealed several genetic clusters. Two to four clusters appeared to suit the data best (Fig. 4.5a) and there was considerable admixture among clusters (Fig. 4.5b). Interpolation of inferred cluster membership probabilities indicated a strong geographical component in the data, with an eastern, one to two central, and a western cluster as well as admixture zones between these clusters (Fig. 4.5c, d). In the K=4 solution, the most eastern cluster fell outside of the assumed distribution range of Guinea baboons (Fig. 4.5d).

a)



b)



c)

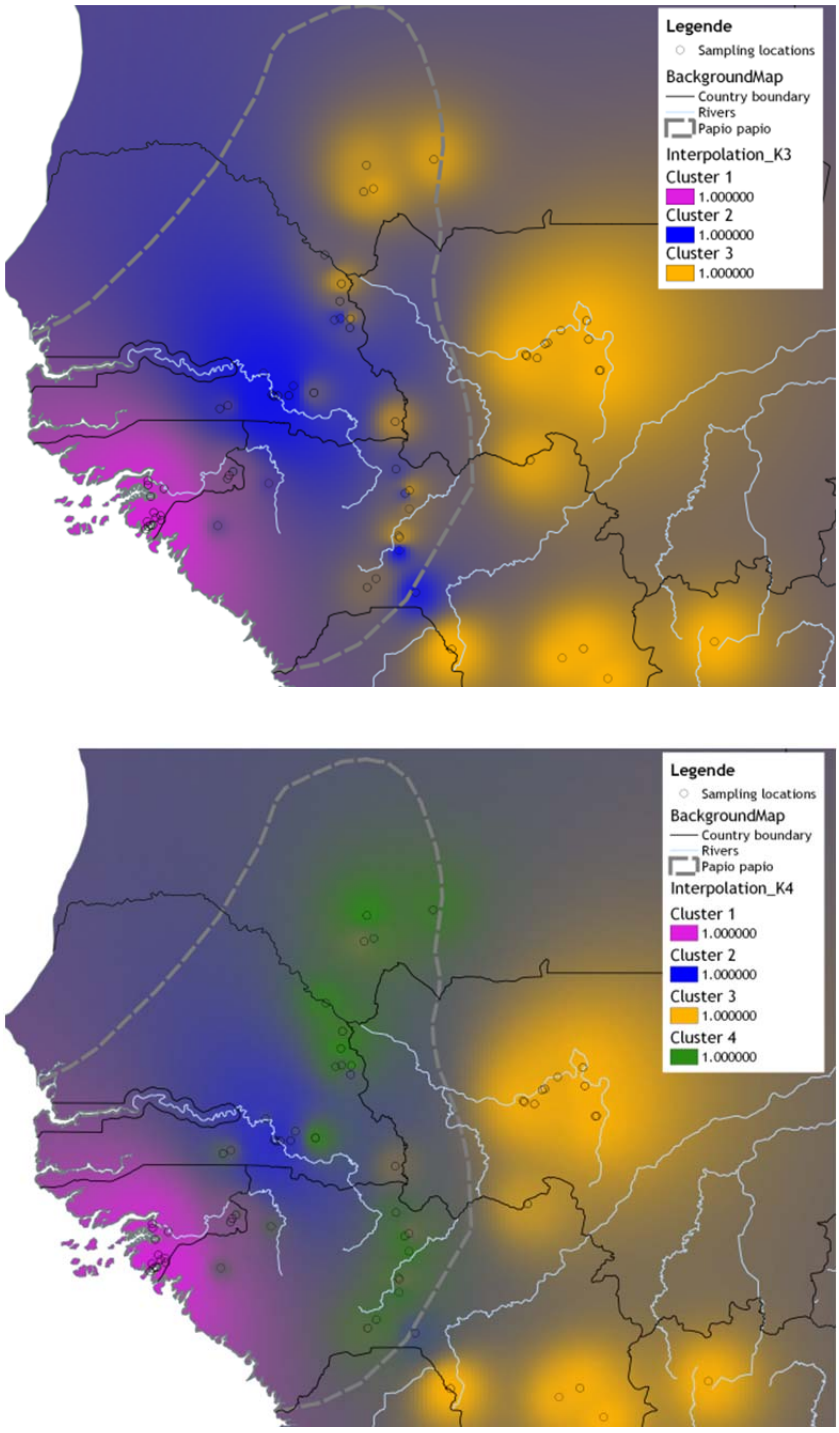
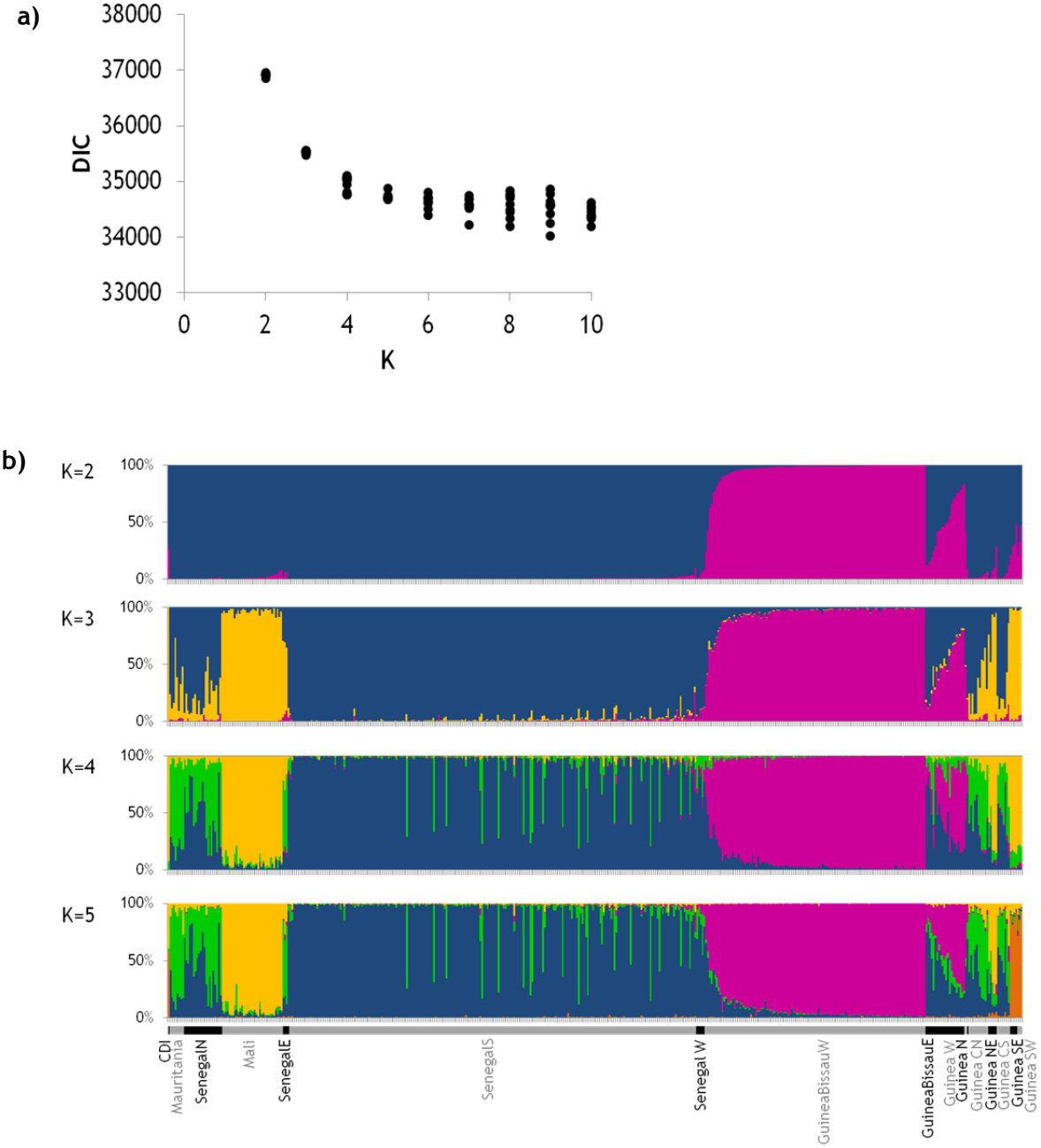


Fig. 4.4: Bayesian cluster analysis (a) Inference of the most likely number of clusters with ΔK (Evanno *et al.* 2005) and mean likelihood L(K) suggests two to four genetic clusters. (b) Barplot of individual cluster membership probabilities inferred by STRUCTURE for K=2, K=3, and K=4 populations (x-axis: individuals sorted by region, y-axis: cluster membership probabilities, colours: cluster 1-4); (c) Cluster membership probabilities (different clusters indicated by different colors) for K=3 and K=4 interpolated on map of sampling locations (black circles). IUCN distribution map of Guinea baboons (Oates *et al.* 2008) indicated by grey dashed line.

Results from the spatially explicit Bayesian cluster analysis in TESS matched the results obtained by the analysis without spatial priors (Fig.4.5). The general picture with distinct eastern and western clusters was replicated, but spatial clustering was overall stronger with more distinct well-defined clusters. There were small differences in individual assignment probabilities and the most probable number of inferred clusters was slightly higher with three to five clusters (Fig.4.5a). The fifth cluster, which was not detected by STRUCTURE, separated the southern from the eastern regions (Fig.4.5b, c).



c)

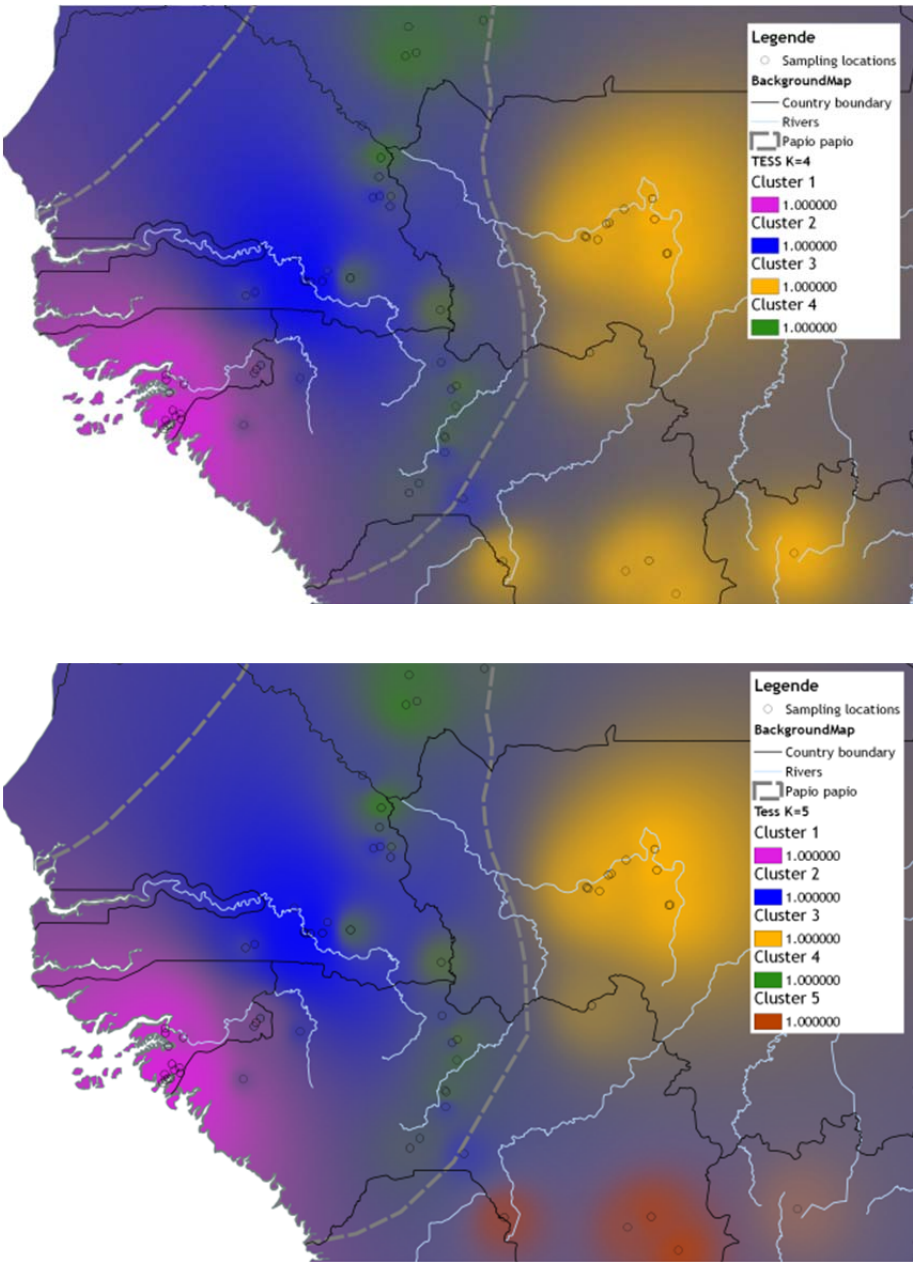


Fig. 4.5: Spatial Bayesian cluster analysis (a) Inference of the most likely number of clusters using the DIC suggests five to six genetic clusters; (b) Barplot of individual cluster membership probabilities inferred by TESS for K=2, K=3, K=4, and K=5 populations (x-axis: individuals sorted by region, y-axis: cluster membership probabilities, colours: cluster 1-5); (c) Cluster membership probabilities (different clusters indicated by different colors) for K=4 and K=5 interpolated on map of sampling locations (black circles). IUCN distribution map of Guinea baboons (Oates *et al*. 2008) indicated by grey dashed line.

The DAPC largely supported the Bayesian results and indicated four to ten clusters to best describe the data (Fig. 4.6a). The first axis separated individuals along an east-west direction and the second axis distinguished the central, eastern, and southern regions (Fig. 4.6b). When four clusters were considered, the posterior probabilities of individual cluster membership generally followed the patterns of the Bayesian analyses with distinct eastern and western clusters, but with slight differences in assignment probabilities (Fig. 4.6c). Furthermore, DAPC revealed that the genetic structure followed a clinal pattern of differentiation with clusters merging into each other (Fig. 4.6.b). When more clusters were considered, the southern cluster identified by TESS was eventually detected. The contribution of different alleles to the axes was relatively well distributed, with three and five alleles of different loci falling above the threshold of 0.05 for axis one and two, respectively.

The sPCA indicated that there was both a significant global (p<0.001) and local spatial structure (p<0.01). We identified two interpretable eigenvalues for global structure (Fig. 4.7b), with axis 1 having an eigenvalue of 0.402, composed of variance 0.595 and spatial autocorrelation *I* of 0.675, and axis 2 with an eigenvalue of 0.170 (variance: 0.272, I=0.624). Interpolation of individual lagged scores on a geographical map revealed that the first axis mainly distinguished the most western locations from the rest (Fig. 4.7c). The second axis showed a smoother genetic cline from west to east, with highest values outside of the range of Guinea baboons (Fig. 4.7.d). Five different alleles were the main contributors to axis one and there was again no suspicious pattern. Two of these alleles (D7s503-162 and D12s375-161) had already been identified with high loadings in the DAPC. Both occur at varying frequencies in multiple regions, but reach considerable higher frequencies in the western cluster (Fig. 4.8).

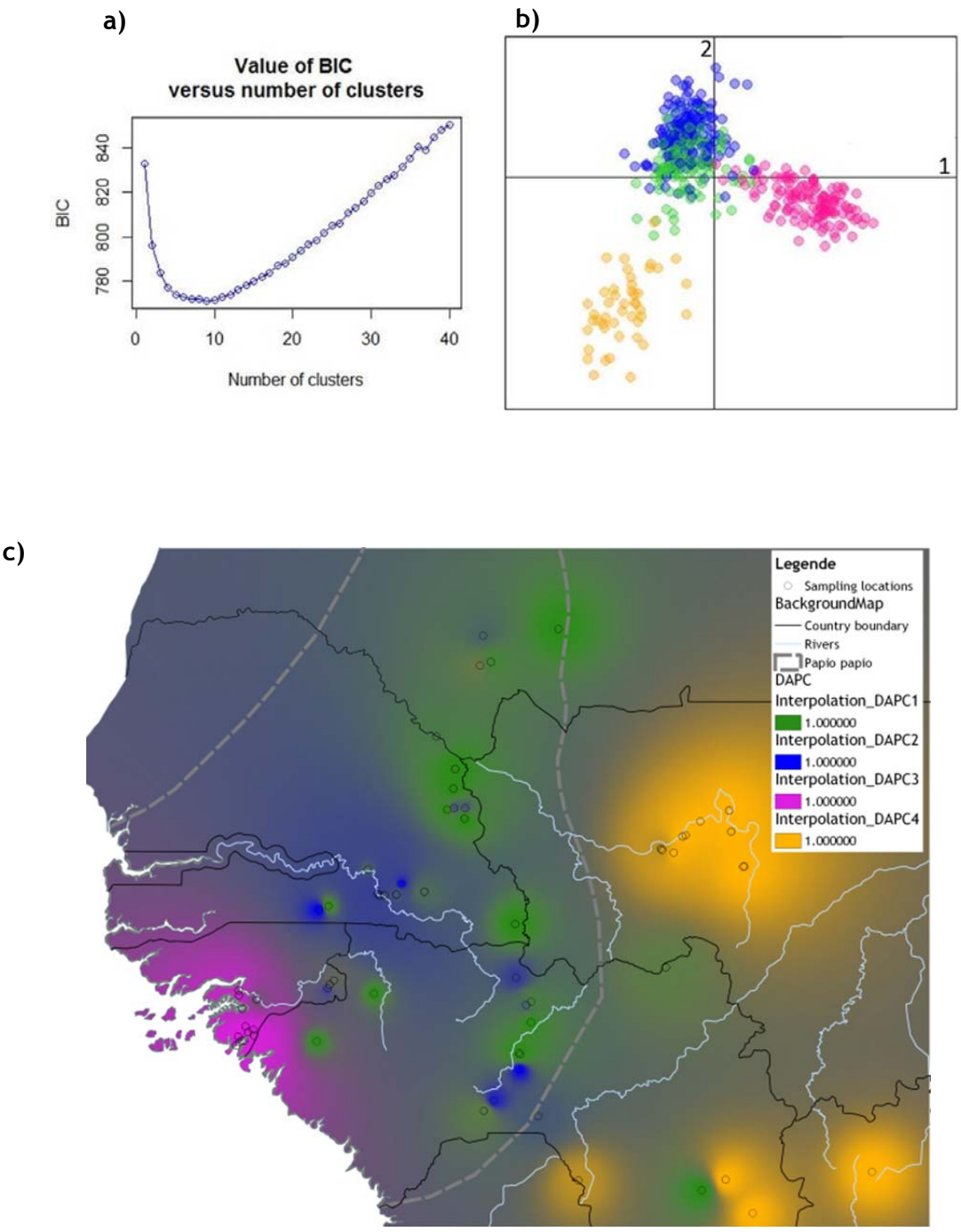


Fig 4.6: DAPC (a) Decrease of BIC as a function of the number of clusters for DAPC; (b) scatterplot of the first two principal components of the DAPC. Dots represent individuals and four clusters are shown by different colours (matching colour code of Structure analysis); (c) interpolation of posterior probabilities of K=4 cluster membership (different clusters indicated by different colors) on map of sampling locations (black circles). IUCN distribution map of Guinea baboons (Oates *et al*. 2008) indicated by grey dashed line.

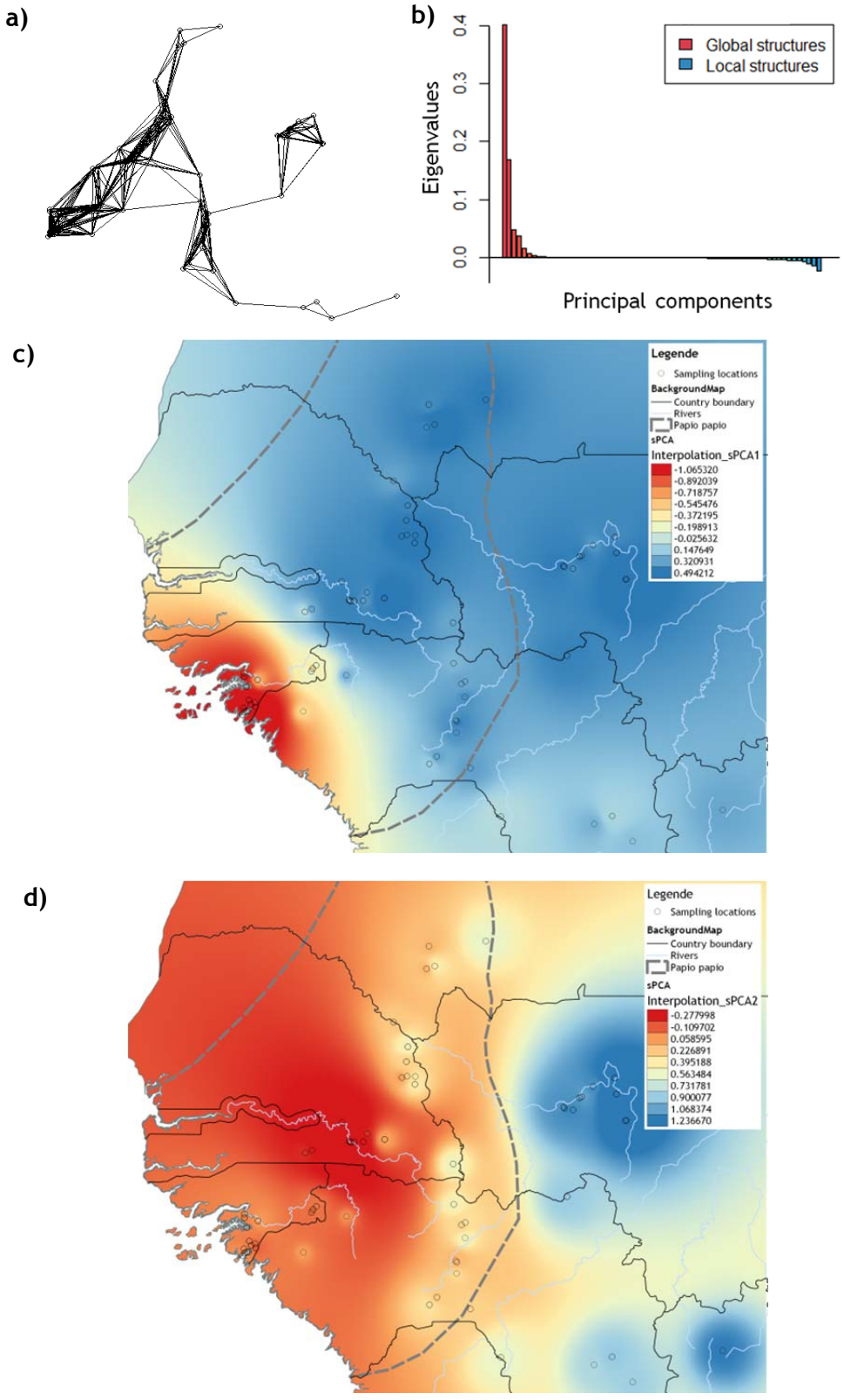


Fig 4.7: sPCA (a) Connection network defining neighbouring entities based on pairwise distance of 0-200km used to define spatial weightings in sPCA. (b) Screeplot of sPCA, positive values (red) indicate global structures while local patterns are indicated by negative values (blue). Individual lagged scores of (c) PC 1 (I=0.675) and (d) PC 2 (I=0.624) interpolated on map of sampling locations.

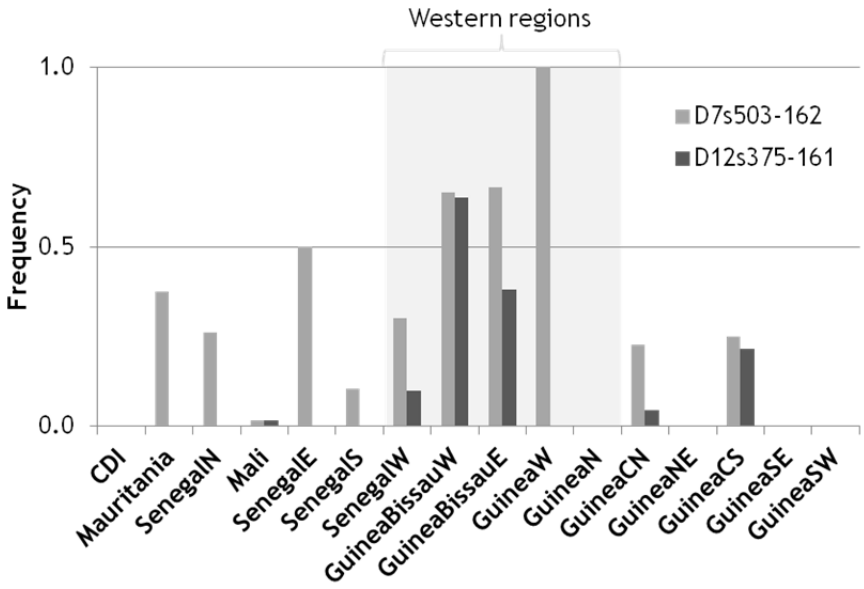


Fig 4.8: Allele frequencies per region for two alleles that were identified as strong contributors to genetic structuring in DAPC and sPCA. Both occur in considerably high frequencies in the western regions of the Guinea baboon distribution.

The Mantel test revealed a strong correlation of genetic and geographic distance (R^2=0.51, p<0.001; Fig. 4.3b). The spatial autocorrelation analyses indicated that the strongest effect of distance on genetic similarity is observable up to about 100-180km (Fig. 4.8). On a global scale, this effect seemed to be slightly more pronounced in females than in males, but within clusters this was not supported as a common pattern. A sharper decrease in *r* for males appeared in clusters West, East, and K=3Central, while it was stronger for females in cluster K=4Central.

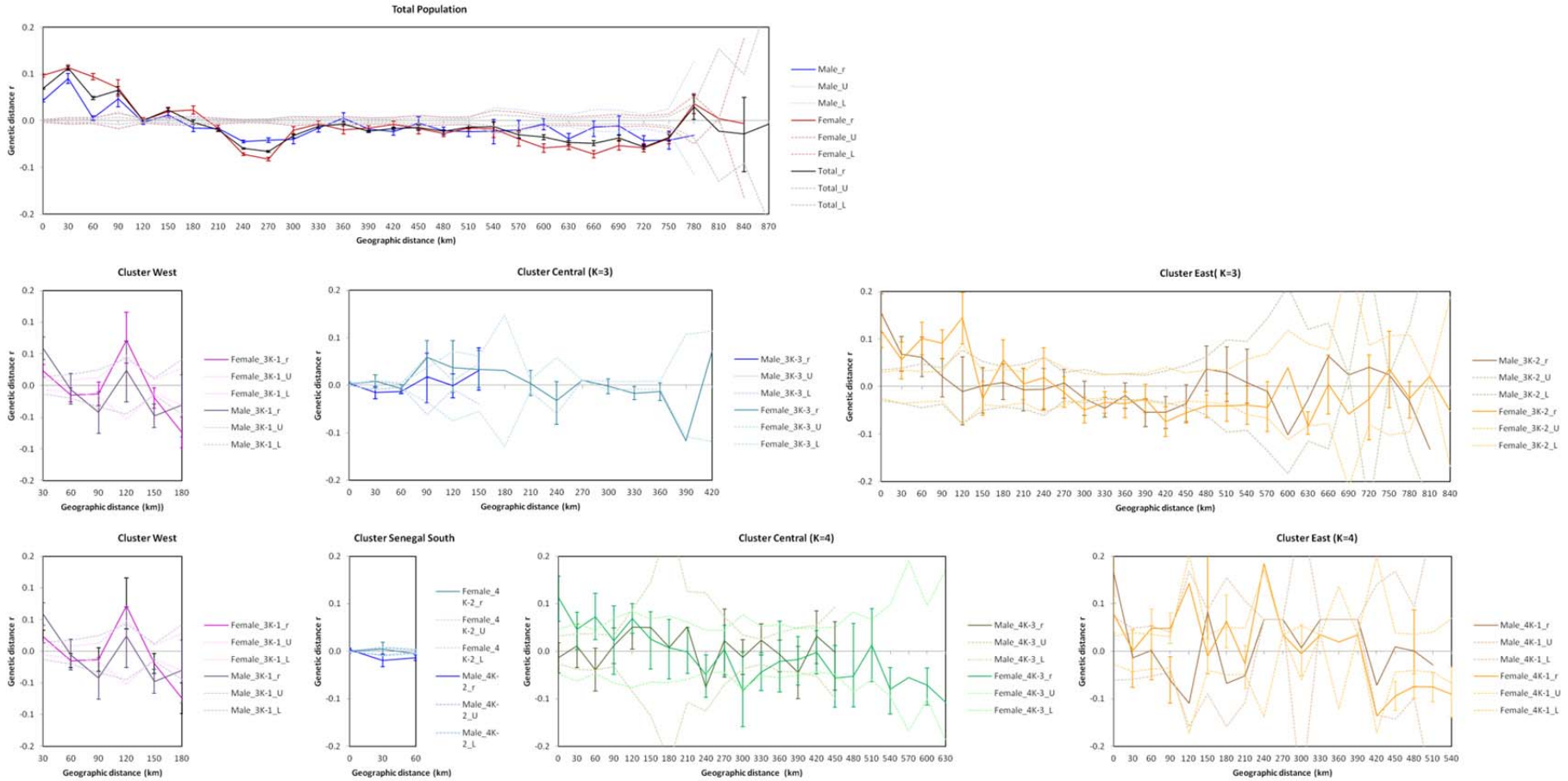


Fig. 4.8: Spatial autocorrelation based on 30km distance classes for the whole distribution and for inferred clusters (STRUCTURE K=3, K=4). Genetic distance r is represented by the solid line with upper and lower 95% confidence intervals by dotted lines. Different colours within graphs indicate females and males, respectively.

Demographic history

The unimodal shape of the D-loop mismatch distribution indicated a population expansion in Guinea baboons and did not significantly differ from the expansion model (sudden expansion model, p=0.69; spatial expansion model, p=0.80; Fig. 4.9). An estimated τ of 9.33 specified a time since expansion of approximately 828,000 years. Both neutrality tests also pointed towards a demographic expansion (Tajima's D=-1.3, p=0.06; Fu's F_S=-23.94, p=0.002).

Neither regional nor global bottlenecks were detected in the microsatellite data (whole dataset: p=0.515, Cluster East: p=0.444, Cluster Senegal: p=0.525, Cluster Central: p=0.44, Cluster West: p=0.14).

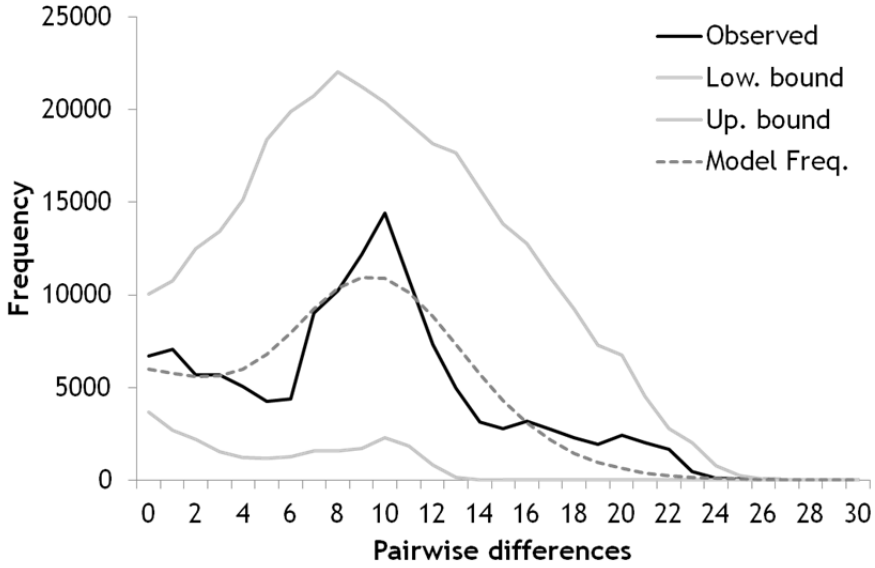


Fig. 4.9: Mismatch distribution showing the frequency of pairwise differences in the D-loop sequences compared to assumptions under a model of population expansion (sudden expansion model, p=0.69).

Discussion

Our analyses of genetic variation in Guinea baboons revealed patterns that are best explained by the interplay of historic and contemporary gene flow. In concordance with a previous study based on a smaller sample set (Kopp *et al*. 2014a), no clear geographic pattern could be revealed in the mitochondrial data. Although a significant IBD effect was found, the low genetic distance among haplotypes indicates that gene flow is more influential than genetic drift, suggesting a global panmictic population (Hutchison & Templeton 1999; Phillipsen *et al*. 2015a). In contrast, at least three genetically differentiated populations could be identified in the microsatellite data, irrespective of the algorithm employed: a western, a central, and an eastern population. These populations were not limited by sharp boundaries but rather merged into each other in gradual transition zones. The central population and its admixture zone to the eastern population are probably sub-structured further and an additional south-eastern population might exist, but the exact nature of these patterns could not be reliably resolved due to disagreement among the different methods. Most likely, the global structure that we were able to identify does not depict genetically distinct clusters in the strict sense, but reflects strong clinal patterns maintained by spatially restricted gene flow. This interpretation is corroborated by the Mantel test, which indicates a strong IBD effect resembling regional equilibrium states of gene flow and genetic drift characteristic for species with moderate dispersal (Hutchison & Templeton 1999; Phillipsen *et al*. 2015b). Similarly, the spatial autocorrelation analysis supports that effective gene flow is restricted to below 200 km. In addition, both the distribution of BIC values over the number of clusters and the clinal arrangement of clusters in the DAPC scatterplot exhibit a pattern that closely resembles data simulated under a one-dimensional stepping stone model of migration (Jombart *et al*. 2010). The stepping stone model denotes a short distance migration pattern, with gene flow only occurring between adjacent populations (Kimura & Weiss 1964). Dispersal in baboons normally occurs over short distances mainly to neighbouring groups (Packer 1975, 1979; Samuels & Altmann 1986; Alberts & Altmann 1995; Rogers & Kidd 1996; Tung *et al*. 2008). Our results demonstrate that this behavioural pattern is apparently also well reflected in the nuclear genetic structure of Guinea baboons, with gene flow being effectively restricted to a distance of less than 200 km leading to genetic clines. An alternative explanation to individual short-distance dispersal could be the fission of groups and movement of whole groups, a scenario quite plausible for expanding populations.

Interestingly, we could not detect a general sex-specific influence on nuclear gene flow. Male and female gene flow occur at the same scale if the whole distribution is considered. We have demonstrated previously that in a Senegalese population of Guinea baboons male gene flow is more restricted than female gene flow on a local scale (Kopp *et al*. 2015). However, this pattern apparently only impacts the local genetic structure of populations but is concealed in distribution wide analyses by more global and historic effects. The duality of both global and local genetic structures is supported by our sPCA and a detailed fine-scale sampling, optimally covering a distance of around 200km, of several populations is needed for reliable inferences of regional variation. This could help to assess the impact of sex-biased dispersal and reveal more subtle differences among regions. Our mtDNA results support that female gene flow is generally more pronounced in Guinea baboons than in most of its congenerics (Kopp *et al*. 2014a). The global discordance between the structuring of mitochondrial and nuclear variation is in steep contrast for the patterns observed in female philopatric species (Chakraborty *et al*. 2015). Y-chromosomal data needs to be incorporated to unequivocally ascertain sex-specific differences in dispersal magnitude and distance.

Present day landscape features that would have the potential to act as barriers to gene flow, such as rivers, do not fully explain the distribution of genetic populations in Guinea baboons. Rivers are generally considered to pose only incomplete barriers to the movement of baboons (Zinner *et al*. 2011a). In West Africa, strong seasonality in water level and land bridges during the dry season enable individuals to cross even major rivers like the Gambia or the Niger (Kopp, pers. obs.), thereby maintaining gene flow. Similarly, current climatic or ecological gradients do not seem to influence genetic structuring strongly, as we would expect clusters to be arranged according to latitude in this case. However, we did not explicitly test for correlations between genetic and landscape variables and do not rule out that more complex ecological features or historic climatic or geographic conditions played a role. Historic climate conditions are assumed to have triggered the phylogeography of baboons in general (Zinner *et al*. 2011b) and most likely also left traces in the genetic structure of Guinea baboons. The D-loop sequences exhibit a clear pattern of population expansion which could have occurred in concert with a range expansion. The considerably higher frequency of particular alleles on the western edge of the distribution, the putative expansion front, in comparison to core regions, might be explained by the surfing phenomenon. This process, during which otherwise rare alleles increase

to high frequencies at the wave front due to stochastic effects (Edmonds *et al*. 2004; Hallatschek & Nelson 2008), is theoretically very well supported and is increasingly being documented in empirical studies in natural populations (Melo-Ferreira *et al*. 2011, 2014; Graciá *et al*. 2013; Tollis & Boissinot 2013; Pierce *et al*. 2014). A westward range expansion of Guinea baboons could also have generated the observed cline in nuclear genetic variation. A pattern of clinal variation along the axis of expansion can be commonly detected (Excoffier *et al*. 2009) and is, for example, also characteristic for humans (Cavalli-Sforza *et al*. 1993; Ramachandran *et al*. 2005; Lawson Handley *et al*. 2007). Interpretation of clinal variation, though, can be problematic, as clinal patterns can also arise due to mathematical artefacts and are extremely likely to occur when gene flow is triggered by short-range dispersal (Novembre & Stephens 2008). This is mainly attributable to the covariance between spatial and genetic data, if this is not controlled for (Novembre & Stephens 2008; Frichot *et al*. 2012). Moreover, allele surfing phenomena during range expansions as well as admixture with local populations and traces of ancient introgression can lead to genetic structuring perpendicular to the direction of expansion (Francois *et al*. 2010). We therefore refrain from drawing definite conclusions about the settlement of Guinea baboons in West Africa without integration of other approaches. Still, we suggest that their current genetic pattern reflects both their historic range expansion and contemporary short-range dispersal and can develop hypotheses for further explicit testing.

The eastern population, falling outside of the known range of Guinea baboons (Oates *et al*. 2008), could potentially represent the neighbouring olive baboon population harbouring Guinea baboon mtDNA due to introgressive hybridization and forming a narrow zone of admixture with the central population. Two processes are conceivable to explain this pattern: Guinea baboon females moving eastwards into the olive baboon range (mitochondrial capture) or male olive baboons moving westwards into the Guinea baboon range (nuclear swamping). Both scenarios are equally plausible (and also not mutually exclusive) given the respective sex-bias in dispersal of the two species. Considering the similarity between hamadryas and Guinea baboon social organization (Patzelt *et al*. 2014), however, it is possible that Guinea baboon female dispersal occurs over shorter distances (to neighbouring gangs within the same community) than dispersal of olive baboon males, which can disperse over 20km or further, especially if secondary and tertiary dispersal events are included. Noticeably, the occurrence of private alleles is skewed to the eastern part of the Guinea baboon

distribution. These alleles could be either interpreted as stemming from admixture with olive baboons or representing ancient Guinea baboon alleles that were lost during a west-ward expansion. Our field observations identified sampled individuals in Mali as phenotypic Guinea baboons and this data was recently used to update the Guinea baboon distribution map (Anandam *et al*. 2013), but we cannot discard that they exhibit a certain degree of admixture. The samples from Côte d'Ivoire and Sierra Leone are considered to stem from phenotypic olive baboons leading us to speculate that introgressive hybridization might occur. It has been reported that eastern Guinea baboon individuals have darker and less red pelage than individuals from the west, suggesting admixture between olive and Guinea baboons in the eastern part of the Guinea baboon distribution (Jolly 1993). Unfortunately, morphological species identification of sampled individuals was not possible during this project in other regions outside the known range of Guinea baboons and we still lack distribution wide quantitative morphological data to investigate gradients in phenotype. Museum collections could potentially provide accessible resources to test the concordance between nuclear genetic and phenotypic variation.

Surprisingly, the most consistently identified population is located in the extreme West of the Guinea baboon distribution. Strongly differentiated clusters at habitat edges have been observed in simulations of range expansions and been attributed to the joint effects of IBD and geographic bottlenecks (Burton & Travis 2008; Francois *et al*. 2010; Nullmeier & Hallatschek 2013). Although we did not detect traces of genetic bottlenecks in this cluster, the NJ tree suggests that it is nested within the central population. Together with the above described allele surfing this supports the western population to result from a westward range expansion.

Overall, two different phylogeographic scenarios seem to be most plausible for explaining the observed patterns of genetic variation: (i) a simple westward expansion leading to a genetic cline and differentiation of populations due to IBD effects, (ii) an initial westward expansion, followed by a period of isolation (establishment of Cluster West) and subsequent secondary contact with Cluster East leading to the formation of Cluster Central. Pinpointing the exact taxon border between Guinea and olive baboons with an extended eastward sampling, both genetically and phenotypically, will help to distinguish between these scenarios.

In conclusion, our results indicate an interplay of intrinsic and extrinsic factors in shaping the genetic structure of Guinea baboons. Short-distance dispersal, historic range expansion, and introgression lead to pronounced spatial genetic patterns even

over a rather restricted distribution range. This emphasizes the importance to consider intraspecific genetic variation in broader analyses of interspecific relationships (Markolf *et al*. 2011). The restriction of dispersal to short distances has the potential to create strong genetic clines, which could be misinterpreted as distinct clusters if sampling is too heterogeneous (Schwartz & McKelvey 2009). We assume that in many cases, in which species delimitation is based solely on genetic clustering approaches and samples are not obtained from the whole distribution, the underestimation of intraspecific variation leads to an overestimation of interspecific differentiation. Indeed, studies employing a fine scale sampling have proven to reveal more nuanced pictures than work based on fewer samples, which often provide clear but oversimplistic conclusions (Markolf *et al*. 2011; VonHoldt *et al*. 2011; Kutschera *et al*. 2014; Wood *et al*. 2014; Fünfstück *et al*. 2015; Botero *et al*. 2015). Many species borders, which seem to be well-defined sharp boundaries given restricted data sets, might in fact be better represented by more or less steep clines of genetic variation if genetic samples were taken at an appropriate fine scale (Merker *et al*. 2009; Fünfstück *et al*. 2015). This is of particular relevance for phylogenetic projects, which are regularly based on only a few individuals per species and often lack precise information about provenance because high-quality samples were taken from captive individuals (Chan *et al*. 2013). Especially genomic projects often neglect whole-taxon sampling in favour of increasing statistical power through number of basepairs (Soltis *et al*. 2004). In light of our results we suppose that this will lead to exciting intra- and interspecific patterns being overlooked and urge to fully appreciate a population-genomic approach.

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CHAPTER 5: OUT OF AFRICA BUT HOW AND WHEN? THE CASE OF HAMADRYAS BABOONS (*PAPIO HAMADRYAS*)

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Author contributions: DZ conceived project, GHK and DZ designed research, DZ and GHK collected data, GHK, DZ, CR and LFG analyzed data, TMB, DEW, and ANA provided samples.GHK and DZ wrote the manuscript. All authors discussed the results and contributed to the final manuscript.

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Abstract

Many species of Arabian mammals are considered to be of Afrotropical origin and for most of them the Red Sea has constituted an obstacle for dispersal since the Miocene-Pliocene transition. There are two possible routes, the 'northern' and the 'southern', for terrestrial mammals (including humans) to move between Africa and Arabia. The 'northern route', crossing the Sinai Peninsula, is confirmed for several taxa by an extensive fossil record, especially from northern Egypt and the Levant, whereas the 'southern route', across the Bab-el-Mandab Strait, which links the Red Sea with the Gulf of Aden, is more controversial, although post-Pliocene terrestrial crossings of the Red Sea might have been possible during glacial maxima when sea levels were low.

Hamadryas baboons (*Papio hamadryas*) are the only baboon taxon to disperse out of Africa and still inhabit Arabia. In this study, we investigate the origin of Arabian hamadryas baboons using mitochondrial sequence data from 294 samples collected in Arabia and Northeast Africa. Through the analysis of the geographic distribution of genetic diversity, the timing of population expansions, and divergence time estimates combined with palaeoecological data, we test: (i) if Arabian and African hamadryas baboons are genetically distinct; (ii) if Arabian baboons exhibit population substructure; and (iii) when, and via which route, baboons colonized Arabia.

Our results suggest that hamadryas baboons colonized Arabia during the Late Pleistocene (130–12 kya [thousands of years ago]) and also moved back to Africa. We reject the hypothesis that hamadryas baboons were introduced to Arabia by humans, because the initial colonization considerably predates the earliest records of human seafaring in this region. Our results strongly suggest that the 'southern route' from Africa to Arabia could have been used by hamadryas baboons during the same time period as proposed for modern humans.

Keywords

HVRI; Arabia; Pleistocene; Divergence time estimates; Population structure; primate

Introduction

When modern humans (*Homo sapiens*) dispersed out of Africa is a central question in the study of human evolution. Recently discovered archaeological evidence in Jebel Faya, United Arab Emirates, points to the presence of modern humans in Arabia by ca. 125 thousand years ago (kya) (Armitage *et al*. 2011). That study stresses the Bab-el-Mandab Strait in the southern Red Sea as a possible immigration route during glacial maxima, when sea levels were low, as an alternative to a northern route via the Sinai Peninsula (Beyin 2006, 2011). Humans are not the only mammal that evolved in Africa and colonized Arabia. Many species of Arabian mammals are considered to be of Afrotropical origin (Delany 1989), with 62 species in nine orders known to occur on both sides of the Red Sea (Harrison & Bates 1991; Yalden *et al*. 1996). These taxa colonized Arabia at different times. For most of them the Red Sea has constituted an obstacle for dispersal since the Miocene-Pliocene transition 5.3 million years ago (mya) (Fernandes *et al*. 2006; Bailey *et al*. 2007; Bailey 2009). There are two routes, the 'northern' and the 'southern', that would have enabled terrestrial mammals to move between Africa and Arabia (Beyin 2006, 2011; Bailey 2009) (Fig. 5.1). The 'northern route', crossing the Sinai Peninsula, is confirmed for several taxa by an extensive fossil record, especially from northern Egypt and the Levant (Tchernov 1992; Cavalli-Sforza *et al*. 1993; Lahr & Foley 1994). Immigrations via this route presumably occurred during several 'Green Sahara Periods' when humid conditions opened dispersal corridors across the eastern Sahara for savannah species (Blome *et al*. 2012; Larrasoaña *et al*. 2013; Drake *et al*. 2013). The 'southern route', across the Bab-el-Mandab Strait, which links the Red Sea with the Gulf of Aden, is more controversial, although post-Pliocene (2.5 mya) terrestrial crossings of the Red Sea might have been possible during glacial maxima when sea levels were low (Bailey *et al*. 2007). There is, however, disagreement as to whether the paleoceanographic and paleoecological data are compatible with the scenario of land bridges (Rohling 1994; deMenocal 1995; Rohling *et al*. 1998, 2009; Siddall *et al*. 2003; Fernandes *et al*. 2006).

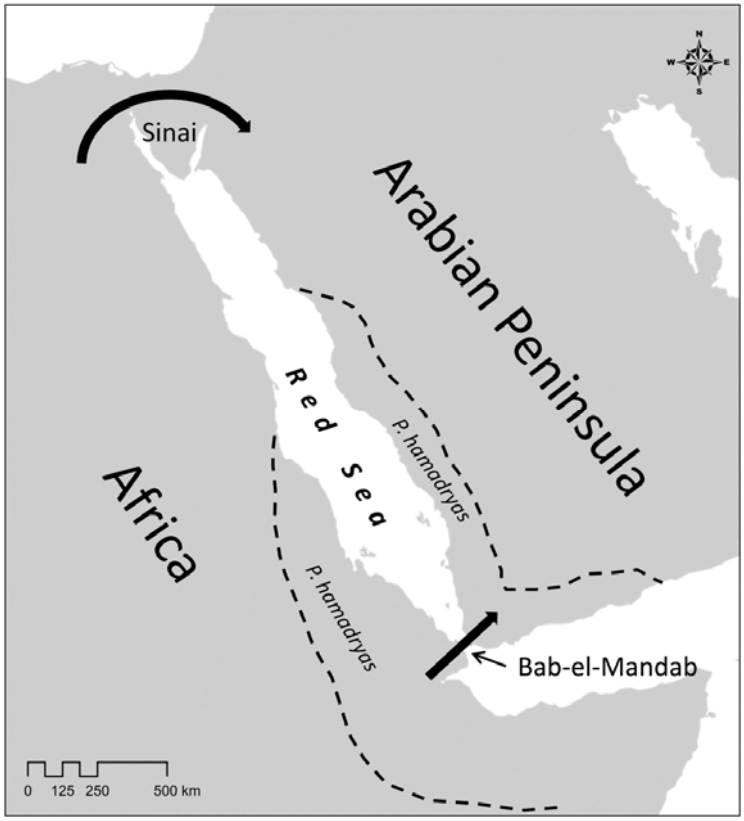

Figure 5.1: Geographic range and hypothetical immigration routes of hamadryas baboons from Africa into Arabia. Dashed lines indicate the approximate borders of the geographic range of hamadryas baboon in Africa and Arabia (after Yalden et al., 1977, 1996; Harrison and Bates, 1991). Thick arrows indicate the southern and northern dispersal routes.

Baboons (*Papio* spp.) have been proposed as an analogous model for human evolution as they evolved during the same period and in the same habitats (Jolly 1970, 2001; Strum & Mitchell 1987; Rodseth *et al*. 1991; Elton 2006). At present, five or six species of baboons are usually recognized, although their taxonomic status is still debated: chacma (*Papio ursinus*), Kinda (*P. kindae*), yellow (*P. cynocephalus*), olive (*P. anubis*), hamadryas (*P. hamadryas*), and Guinea baboon (*P. papio*) (Jolly 1993, 2013; Kingdon 1997; Szmulewicz *et al*. 1999; Groves 2001; Frost *et al*. 2003b; Grubb *et al*. 2003; Zinner *et al*. 2009; Anandam *et al*. 2013; Butynski *et al*. 2013). The fossil record and mitochondrial sequence data both suggest that modern *Papio* originated in southern Africa ca. 2.5 mya, from where they dispersed to the north and west (Benefit 1999; Newman *et al*. 2004; Zinner *et al*. 2011b; Zinner *et al*. 2013b). The current distribution of *Papio* includes much of sub-Saharan Africa, excluding most of the central and West African rain forests. The hamadryas baboon is the only baboon

found outside of Africa and one of the few primate species exhibiting female-biased dispersal (Hapke *et al*. 2001; Hammond *et al*. 2006; Kopp *et al*. 2014a). At present, this species inhabits Ethiopia, Eritrea, Somalia, Djibouti and possibly Sudan, and south-western Arabia along the Red Sea from Yemen to south-western Saudi Arabia (Anandam *et al*. 2013; Swedell 2013) (Fig. 5.1). Cranial and dental remains of *Papio* sp. from the Middle Pleistocene (800 – 200 kya) recovered at Asbole, Ethiopia, show strong affinities to extant *P. hamadryas* (Alemseged & Geraads 2000), indicating a long presence of hamadryas baboons on the African side of the Red Sea.

The hamadryas baboons of Arabia were thought to be smaller than those in Africa and, as such, referred to as *P. arabicus* (Thomas 1900) or *P. hamadryas arabicus* (Ellermann & Morrison-Scott 1951; Harrison 1964; Corbet 1978; Harrison & Bates 1991). Kummer *et al*. (1981) found, however, that hamadryas baboons on both sides of the Red Sea are morphologically and behaviourally similar. Groves (2001, 2005) also found no significant differences between African and Arabian representatives of this species and, as such, considers hamadryas baboons as monotypic.

Three hypotheses have been put forth to explain the presence of hamadryas baboons in Arabia (Kummer 1995):

(i) Hamadryas baboons in Arabia are remnants of a past continuous distribution around the Red Sea (northern route; Fig. 5.1). To our knowledge, however, no *Papio* fossils or subfossils have been discovered in the Levant, in northern Egypt, or in northwestern Arabia. Dispersal events could have been favoured during Green Sahara Periods, e.g., in Marine Isotopic Stage (MIS) 5 (130–71 kya; Blome *et al*. 2012; Larrasoaña *et al*. 2013; Drake *et al*. 2013).

(ii) Hamadryas baboons immigrated to Arabia across the southern Red Sea (southern route; Fig. 5.1), e.g., via a temporary land bridge, during periods of sea level lowstand of the Red Sea (MIS 12: ca. 440 kya; MIS 10: ca. 340 kya; MIS 6: ca. 130 kya; MIS 4: ca. 65 kya; MIS 2: ca. 20 kya; Rohling 1994; Rohling *et al*. 1998, 2009).

(iii) Hamadryas baboons were introduced into Arabia by humans (Thomas 1900; Kummer *et al*. 1981). Ancient Egyptians are known to have translocated baboons. For example, there are drawings from the Eighteenth Dynasty (1540–1304 Before the Common Era [B.C.E.]) in which boats from Punt (which is probably Eritrea) brought hamadryas baboons to Egypt (Kummer 1995; Moritz *et al*. 2010). It is conceivable that these ships reached Arabia (Phillips 1997). Moreover, there is evidence for trade between Northeast Africa and Arabia during earlier times, e.g., in the Predynastic

Period (5000–3100 B.C.E.; Ward 2006; Boivin *et al*. 2009; Boivin & Fuller 2009) and the Bronze Age (c. 3500–1200 B.C.E.; Boivin *et al*. 2009; Boivin & Fuller 2009), which had the potential for the translocation of baboons.

To date, there are three population genetic studies that focus on the origin of Arabian hamadryas baboons. The first study investigated the phylogeography of Arabian hamadryas baboons (Winney *et al*. 2004) using 168 base pair (bp) sequences of the mitochondrial hypervariable region I (HVRI) of 107 baboon samples from four sites in Saudi Arabia plus sequences published by Hapke *et al*. (2001) from 10 sites in Eritrea. Of the three clades recovered, Clade 1 is found only in Arabia, Clade 2 is mainly African but also present in the southernmost sampling location in Arabia, and Clade 3 is found only in Africa. Divergence dates were calculated based on the human/chimpanzee split and on the transition/transversion ratio, leading to estimates of the most recent common ancestor of all clades at 443–316 kya. Divergence dates within Clades 1 and 2 were estimated at 119–85 kya and 219–156 kya, respectively. Winney *et al*. (2004) concluded that, assuming an African origin of hamadryas baboons and a later colonization of Arabia, the divergence time estimates point to immigration events before humans could have played a role. The Winney *et al*. (2004) study has some limitations, namely (i) a sampling regime that does not include Yemen, Ethiopia or any region close to Bab-el-Mandab, (ii) rough divergence estimates without confidence intervals, and (iii) analysis based on only a very short, highly variable, fragment of one mitochondrial DNA (mtDNA) locus.

A second study, by Wildman (2000) and Wildman *et al*. (2004), analyzed 47 baboon samples, including hamadryas baboons from five sites in Yemen, three sites in Saudi Arabia, and one site in Ethiopia. Based on a different and less variable mitochondrial marker (Brown Region, 896 bp; Brown *et al*. 1982) than the Winney *et al*. (2004) study, they found three clades: the exclusively Arabian Clade IIA (part of Winney's Clade 2), Clade IIB, which includes hamadryas baboons of Arabia and Ethiopia with a purely Arabian subclade (Winney's Clade 1), and Clade IIC, which includes African hamadryas and olive baboons (Winney's Clade 3). Due to the trichotomy of Clade II, this study did not draw a conclusion on where hamadryas baboons evolved, but argued that an African origin is most parsimonious. Calibrated with a paleontologically documented 4 mya *Theropithecus-Papio* split (Delson 1993; Goodman *et al*. 1998; Gundling & Hill 2000), they dated the colonization of Arabia close to the origin of hamadryas baboons (ca. 400 kya) and excluded gene flow between Africa and Arabia after ca. 35 kya. They thereby also rejected the hypothesis of human introduction.

Wildman (2000) and Wildman *et al*. (2004) suggested that hamadryas baboons colonized Arabia multiple times via the southern route with a first dispersal event in the Middle Pleistocene (after 400 kya).

A third study, by Fernandes (2009), reviewed the data on the origin of Arabian baboons (Wildman *et al*. 2004; Winney *et al*. 2004) and applied two Bayesian coalescent approaches to resolve the discordance between the estimated colonization times of the two earlier studies. He concluded that hamadryas baboons colonized Arabia twice, and suggested two northern expansions into Arabia during interglacial periods [MIS 9e (ca. 330 kya) or MIS 7c (ca. 220 kya), and the second half of MIS 5e (120–110 kya) or the end of MIS 5a (ca. 80 kya)]. However, the estimates provided by the two approaches differed considerably and, in our opinion, the very large confidence intervals make it impossible to draw conclusions about the most probable immigration route.

In our study, we investigate the origin of Arabian hamadryas baboons. We use mitochondrial sequence data from 294 baboon samples collected in Arabia and in Northeast Africa. These enable us to more accurately determine the distribution of the clades and to assess whether the pure Arabian clade found in the earlier studies is, in fact, only present in Arabia. We sequenced three mtDNA markers, summing up to a total length of 2373 bp, to obtain a better resolution of divergence time estimates. Furthermore, we conducted more sophisticated Bayesian time divergence estimates including confidence intervals and calibrated with a *Theropithecus-Papio* split of 5 mya based on new fossil evidence (Jablonski *et al*. 2008; Frost *et al*. 2014). The main research questions are: (i) Are Arabian hamadryas baboons genetically distinct from African hamadryas baboons? (ii) Do Arabian baboons exhibit population substructure? (iii) When, and via which route, did baboons colonize Arabia?

Methods

Sample collection

We non-invasively obtained baboon faecal samples at 37 sites in Eritrea, Ethiopia, and Yemen, identified species based on phenotypic characters, and recorded the GPS coordinates of each sampling site (Fig. 5.2, Table 5.I). Fresh samples were preserved in 90% ethanol. Dry samples were preserved in plastic tubes without an additive. Samples were stored at ambient temperature for up to six months in the field and at -20°C upon arrival in the laboratory. Additionally, tissue samples of Arabian hamadryas baboons were provided by the King Khalid Wildlife Research Centre (KKWRC), Saudi Arabia. Ear tissue was taken from anaesthetized animals, which were live-trapped and released during a population genetic survey (Winney *et al*. 2004; Hammond *et al*. 2006). We also included mtDNA sequence information from one yellow baboon museum specimen from Somalia (Zinner *et al*. 2008). Sample collection, as well as capturing and handling procedures of baboons, complied with the laws of the respective countries of origin and Germany and the guidelines from the International Primatological Society.

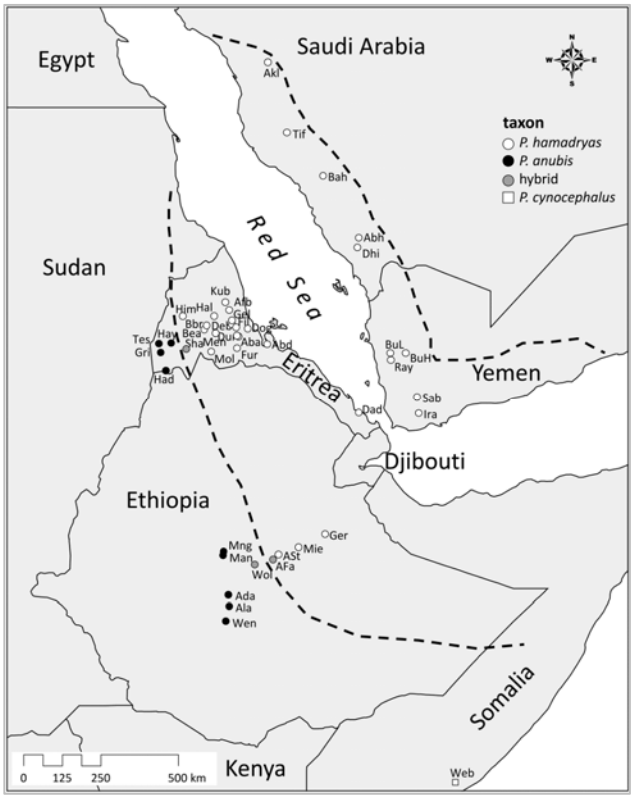

Figure 5.2: Baboon sampling sites (see also Table 5.I) in Africa and Arabia. Dashed lines indicate approximate geographic range of hamadryas baboons in Africa and Arabia.

Table 5.I: Geographic coordinates (decimal degrees) of *Papio* sampling sites and sample sizes.

No.	Taxon	Country	Site	Code	Sample size	Longitude	Latitude
1	Ph	Saudi Arabia	Abha	Abh	25	42.505228	18.216389
2	Ph	Saudi Arabia	Al Akhal	Akl	6	39.859444	23.315556
3	Ph	Saudi Arabia	Baha	Bah	15	41.466667	20.016667
4	Ph	Saudi Arabia	Dhilafa Escp.	Dhi	4	42.466667	17.933333
5	Ph	Saudi Arabia	Taif	Tif	15	40.415833	21.270278
6	Ph	Yemen	Bura'a Forest A	BuH	4	43.416667	14.866667
7	Ph	Yemen	Bura'a Forest B	BuL	5	43.866944	14.867222
8	Ph	Yemen	Jebel Iraf	Ira	1	44.250000	13.116667
9	Ph	Yemen	Jebel Raymah	Ray	1	43.433333	14.666667
10	Ph	Yemen	Jebel Sabir	Sab	1	44.200000	13.583333
11	Ph	Eritrea	Mt. Abagamsei	Aba	14	39.018620	15.349100
12	Ph	Eritrea	Abdur	Abd	11	39.845850	15.128570
13	Ph	Eritrea	Afabet	Afb	3	38.749583	16.120166
14	Ph	Eritrea	Barka Bridge	Bbr	7	38.020380	15.555120
15	Ph	Eritrea	R. Baeat	Bea	2	38.094270	15.671570
16	Ph	Eritrea	Dada (Bolo)	Dad	13	42.508889	13.129630
17	Ph	Eritrea	Debresina	Deb	3	38.825930	15.705350
18	Ph	Eritrea	Dogali	Dog	6	39.284730	15.579080
19	Ph	Eritrea	Durfo	Dur	7	38.964580	15.373700
20	Ph	Eritrea	Filfil Bridge	Fil	6	38.944450	15.614420
21	Ph	Eritrea	Furrus	Fur	9	38.971150	15.011480
22	Ph	Eritrea	Geleb	Gel	7	38.824070	15.821430
23	Ph	Eritrea	Halhal	Hal	7	38.314330	15.941370
24	Ph	Eritrea	Af Himbol	Him	9	37.397100	15.945050
25	Ph	Eritrea	Kubkub	Kub	11	38.632170	16.344820
26	Ph	Eritrea	Mensura	Men	5	38.351230	15.445980
27	Ph	Eritrea	Molki	Mol	7	38.221700	14.909080
28	PX	Eritrea	R. Shackat	Sha	4	37.499350	14.983100
29	Pa	Eritrea	R. Griset	Gri	8	36.760180	14.883220
30	Pa	Eritrea	R. Hadejemi	Had	6	36.907100	14.358270
31	Pa	Eritrea	Haykota	Hay	17	37.066000	15.156950
32	Pa	Eritrea	Tesseney	Tes	9	36.701420	15.145100
33	Ph	Ethiopia	Awash Station	ASt	5	40.177750	8.992683
34	Ph	Ethiopia	Gerba Luku	Ger	10	41.534000	9.587400
35	Ph	Ethiopia	Mieso	Mie	7	40.764083	9.203533
36	PX	Ethiopia	Awash Falls	AFa	5	40.019167	8.842683
37	PX	Ethiopia	Wolenkiti	Wol	5	39.487883	8.694583
38	Pa	Ethiopia	Adami Tulu	Ada	4	38.714933	7.825583
39	Pa	Ethiopia	Alambada	Ala	3	38.747683	7.504633
40	Pa	Ethiopia	Managasha 1	Mng	1	38.583333	9.083333
41	Pa	Ethiopia	Managasha 2	Man	6	38.571250	8.968383
42	Pa	Ethiopia	Wendo Genet	Wen	1	38.649650	7.071267
43	Pc	Somalia	Webi Shebelli	Web	1	45.433333	2.420833

Ph = *Papio hamadryas*; Pa = *P. anubis*; PX = phenotypic hybrids between *P. hamadryas* and *P. anubis*; Pc = *P. cynocephalus*. Longitude and latitude in decimal degrees.

DNA extraction, PCR amplification, and sequencing

DNA from tissue and faeces was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) and QiAamp DNA Stool Mini Kit (Qiagen), respectively. Extraction was according to the manufacturer's protocols with slight modifications (Haus *et al*. 2013). To prevent contamination, laboratory procedures followed standard protocols (Goossens *et al*. 2000; Karanth *et al*. 2005; Osterholz *et al*. 2008; Roos *et al*. 2008). DNA extraction, PCR, gel extraction, and sequencing were performed in separate laboratories. All PCR reactions were performed with negative (HPLC-purified water) controls.

We analysed three mitochondrial markers, as these allowed us to include published data sets in the statistical analyses and they could reliably be amplified from low quality samples. Furthermore, since mtDNA is transmitted via the maternal lineage, and because in hamadryas baboons females are the predominant dispersing sex, these markers are expected to give a good indication of the population history of this species. We amplified and sequenced a 338 bp fragment of the mitochondrial HVRI (Hapke *et al*. 2001) of all samples. For a subset, representing all major mitochondrial clades discovered in the HVRI analysis, we also sequenced 896bp of the Brown Region and 1140bp of the cytochrome *b* gene (cyt *b*) using established protocols (Zinner *et al*. 2009). Brown Region and cyt *b* were both amplified via two overlapping fragments to ensure that sequences were obtained even if the DNA was degraded (as can be expected in faecal samples). To prevent amplification of nuclear pseudogenes, we used primers known to solely amplify the mitochondrial fragment (Zinner *et al*. 2009). The PCR conditions for amplifications comprised a pre-denaturation step at 94°C for 2 min, followed by 40 cycles at 94°C for 1 min, 51°C (HVRI)/56°C (Brown Region)/60°C (cyt *b*) for 1 min and 72°C for 1 min, and a final extension step at 72°C for 5 min. The results of the PCR amplifications were checked on 1% agarose gels. The PCR products were cleaned with the Qiagen PCR Purification Kit and subsequently sequenced on an ABI 3130*xL* sequencer using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems).

Analyses

Sequences were checked, edited and aligned manually using BIOEDIT 7.5.0.2 (Hall 1999). The data set was complemented with published orthologous sequences from Eritrea and Saudi Arabia available in GenBank (AF275384-475 (Hapke *et al*. 2001); AY247444-447, 453, 459, 460, 530, 533, 534, 547, 548 (Winney *et al*. 2004)). The re-

sulting final data set comprised 294 HVRI sequences from 43 localities (10 Arabia and 33 Africa, including eight *P. anubis* sites and three *P. anubis* x *P. hamadryas* hybrid sites in Eritrea and Ethiopia). For divergence time estimates we used 73 concatenated Brown Region + cyt *b* + HVRI sequences from 28 sites (nine Arabia and 19 Africa, including seven *P. anubis* sites in Eritrea and Ethiopia, and one *P. anubis* x *P. hamadryas* hybrid site in Ethiopia) comprising 52 haplotypes. As outgroups, we used orthologous sequences from *Theropithecus gelada* and 17 *Papio* spp. samples from other regions in Africa, including 15 *P. anubis* samples from southern Ethiopia and one *P. cynocephalus* sample from south-eastern Somalia. The final alignment comprised 70 sequences (52 + 18). All sequences were deposited in GenBank (details of samples, amplified loci per sample, and accession numbers are given in Table 5.SI).

We used the HVRI data set to investigate the genetic population structure of hamadryas baboons in detail. To visualize the relationship between haplotypes, we reconstructed a median-joining haplotype network (Bandelt *et al*. 1999) using NETWORK version 4.6.1.1 (2012 Fluxus Technology Ltd.). Here we left out the 15 Ethiopian olive baboons, as they are too distantly related. Hence, only 280 samples were included in the network analysis.

To compare genetic diversity for hamadryas baboons in Africa and Arabia, we calculated haplotype diversity (*Hd*) and nucleotide diversity (π) using DNASP 5.10.1 (Librado & Rozas 2009), and tested the differences for significance using Statistica 10 (StatSoft®). Additionally, we investigated the distribution of genetic diversity in the Arabian population by calculating Hd and π for each sampling locality (excluding localities with only one sample).

To investigate whether the Arabian baboon population expanded after the colonization event, we calculated mismatch distributions for both Arabian clades in ARLEQUIN 3.5.1.3 (Excoffier & Lischer 2010) with 1000 bootstraps. We tested both the model for demographic expansion and the model for spatial expansion. We then calculated the time since expansion with $\tau = 2\mu t$ (μ: mutation rate, t: number of generations since expansion). Here we applied a generation time of 12 years (Rogers & Kidd 1996) and the specific mutation rate of primate HVRI of 15–20% per million years (Jensen-Seaman & Kidd 2001).

To estimate divergence times between clades, we concatenated the Brown Region, cyt *b,* and HVRI sequences (n = 70), and applied a Bayesian Markov Chain Monte Carlo method, which employs a relaxed molecular clock approach (Drummond *et al*.

2006) as implemented in BEAST 1.6.1 (Drummond & Rambaut 2007). The three loci were partitioned, each with its optimal nucleotide substitution model (Brown Region: TrN + G; cyt *b*: HKY + G; HVRI: HKY + I+ G) as chosen with the Bayesian information criterion (BIC) in JMODELTEST 0.1.1 (Posada 2008). We assumed a relaxed uncorrelated lognormal model of lineage variation and a Birth-Death Process prior for branching rates. As calibration point, we applied the fossil-based split of *Theropithecus* and *Papio* 5.0 ± 1.0 mya (Jablonski *et al*. 2008; Frost *et al*. 2014). Four replicates were run for 25 million generations with tree and parameter sampling occurring every 100 generations. The adequacy of a 10% burn-in and convergence of all parameters was assessed by visual inspection of the trace of the parameters across generations using TRACER 1.5 (Rambaut *et al*. 2003). The sampling distributions were combined (25% burn-in) using LOGCOMBINER 1.6.1 (Rambaut & Drummond 2002a). A consensus chronogram with node height distribution was generated and visualized with TREEANNOTATOR 1.6.1 (Rambaut & Drummond 2002b) and FIGTREE 1.3.1 (Rambaut 2006).

Results

The 294 baboon samples comprised 109 HVRI haplotypes. The subset of 73 samples for which we analysed the Brown Region, cyt *b*, and HVRI, comprised 52 haplotypes.

Haplotype network

The HVRI haplotype network reveals three major clades (Fig. 5.3). Clade X is strictly African and consists of Eritrean and a few Ethiopian hamadryas baboons, and phenotypical *P. hamadryas* x *P. anubis* hybrids from Ethiopia. Clade Y is more complex, encompassing Eritrean hamadryas and olive baboons, Eritrean hybrids, and Arabian hamadryas baboons. Clade Z is comprised of Ethiopian, Eritrean, and Arabian hamadryas baboons. Two Arabian clades are identifiable. Clade Arab_Y comprises four haplotypes and clusters closely with Eritrean baboons. Clade Arab_Z consists mainly of haplotypes found in Arabia but also some haplotypes found in Eritrea from sampling locations closest to the Bab-el-Mandab Strait (Dad) and one haplotype from Gerba Luku, Ethiopia (0317PHGer). Clade Arab_Z clusters more closely with Ethiopian baboons.

Population genetics of Arabian baboons

Whereas the three northern Arabia sampling locations (Akla, Taif, and Baha) harbour only haplotypes of Clade Arab_Z, both Clades Arab_Z and Arab_Y are represented in all other locations in Arabia (Fig. 5.4). One haplotype (H1) of Clade Arab_Z is found in every sampling location in Arabia.

Haplotype diversity and nucleotide diversity are both significantly higher in the African than in the Arabian hamadryas baboon populations (n_{Africa} =149, n_{Arabia} =77, Hd_{Africa} ±SD=0.983±0.003, Hd_{Arabia} ±SD=0.871±0.026, p<0.001; π_{Africa} ±SD=0.04251±0.00088, π_{Arabia} ±SD=0.01920±0.00243, p<0.001). Haplotype diversity and nucleotide diversity are both significantly higher (p<0.001) in Clade Arab_Z (n=61) than in Clade Arab_Y (n=16): Hd_Z ±S =0.825±0.040), Hd_Y ±SD=0.533±0.142) and π_Z ±SD=0.00431±S0.00046, π_Y ±SD=0.00218±0.00076.

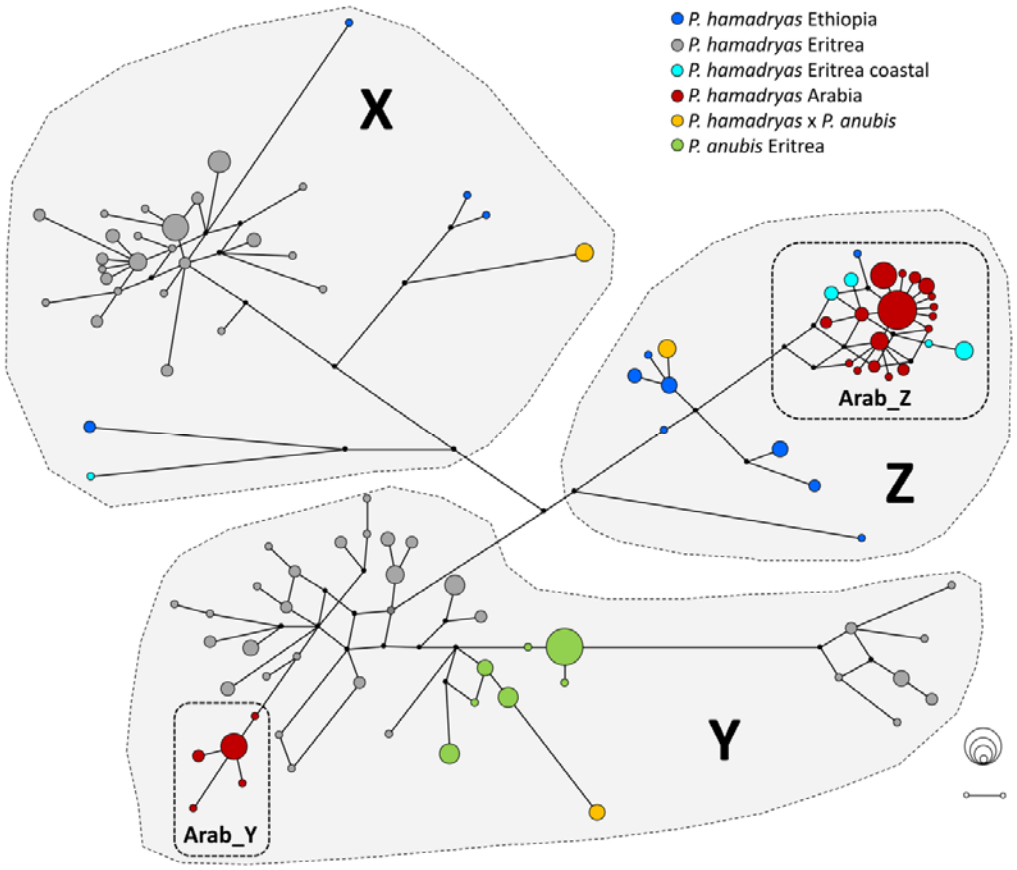

Figure 5.3: Median-joining HVRI haplotype network of hamadryas baboons with the three major clades X, Y, and Z indicated by grey shading and the two Arabian clades Arab_Y and Arab_Z indicated by dashed boxes (n = 280, 338 bp). Scale bar = 1 pairwise difference; node sizes are proportional to haplotype frequencies (scale indicates 1, 5, 10 and 20).

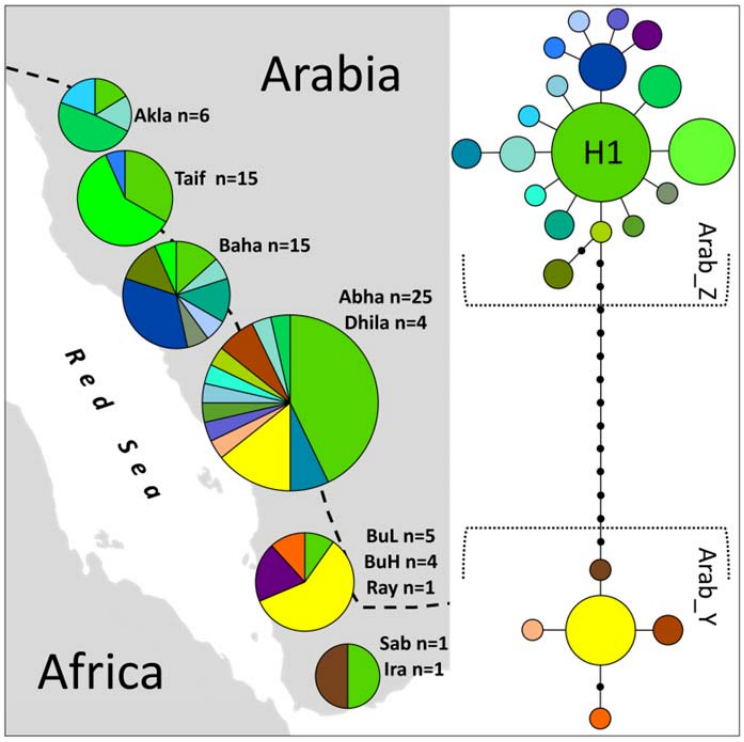

Figure 5.4: HVRI haplotypes network of Arabian hamadryas baboons showing the spatial distribution and frequency of haplotypes.

When genetic diversity for Arabian hamadryas baboons is depicted from south to north, a decrease is observed in nucleotide diversity but not in haplotype diversity (Fig. 5.5). Both Arabian clades probably underwent a population expansion, as neither the demographic nor the spatial expansion model is rejected at $\alpha = 5\%$ (Table 5.II). The expansion of Clade Arab_Z occurred twice as early as the expansion of Clade Arab_Y, as indicated by a τ value, which is twice as high (Table 5.II).

Phylogenetic tree and divergence time estimates

Similar to the network, the phylogenetic tree reconstruction, based on concatenated Brown + cyt *b* + HVRI sequences, reveals the three distinct Clades X, Y, and Z, all of which include African hamadryas baboons (Fig. 5.6). Clade X is purely African and includes both hamadryas and olive baboons. Clade Y is more complex, encompassing Eritrean hamadryas and olive baboons, as well as Arabian hamadryas baboons. Clade Z comprises Ethiopian, coastal Eritrean, and Arabian hamadryas baboons. African hamadryas baboons in Clades Y and Z are basal to Arabian hamadryas baboons, pointing to an African origin for this species.

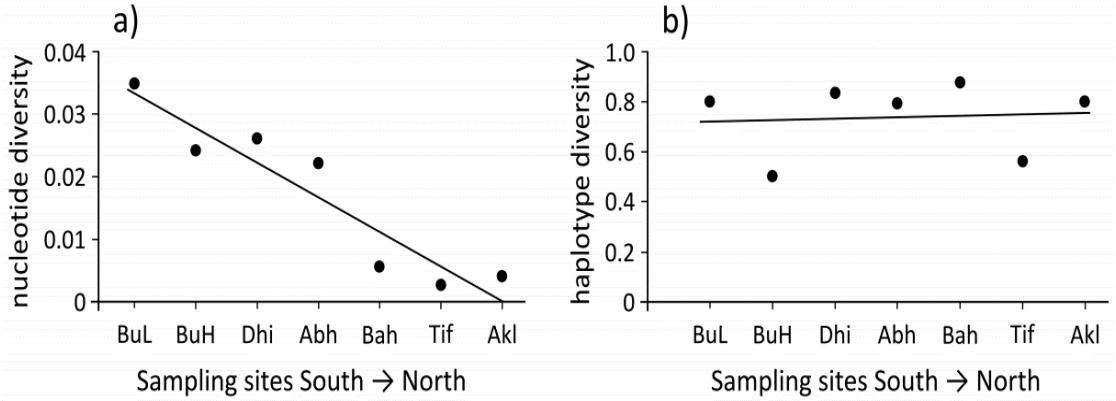

Figure 5.5: South-north gradients in Arabian hamadryas baboons in (a) nucleotide diversity and (b) haplotype diversity.

Table 5.II: Analysis of mismatch distribution to test for population expansion for both Arabian hamadryas baboon lineages Arab_Z and Arab_Y. Calculations are based on a 338 bp fragment of the mitochondrial HVRI and tested for significance with 1000 bootstraps. Time since expansion is calculated with $\tau = 2\mu t$ (μ: mutation rate, t: number of generations since expansion; ka = thousand years) applying a generation time of 12 years and the specific mutation rate of primate HVRI of 15–20% per million years.

HVRI clade	Demographic expansion		Spatial expansion		Time since expansion (ka)	
	τ (confid. interval)	*P*	τ (confid. interval)	*P*	15% [μ=5.07*10^{-5}]	20% [μ=6.76*10^{-5}]
Arab_Z	1.566 (1.062-2.271)	0.14	1.565 (0.692-2.058)	0.085	185 (82-269)	139 (61-202)
Arab_Y	0.824 (0.000-1.803)	0.999	0.804 (0.227-1.958)	0.85	98 (0-232)	73 (0-174)

In Clade Z, Arabian and coastal Eritrean baboons are estimated to have diverged from the Ethiopian population 150.4 kya (95% confidence interval: 221.8–87.5). Arabian lineages diverged from coastal Eritrean baboons 77.2 (119.1–41.4) kya. The first split within Clade Arab_Z is estimated at 54.7 (84.7–28.2) kya and the lineage of the Ethiopian sample (0317PHGer) within this clade split off ca. 28.0 (47.4–12.4) kya. In Clade Y, Arabian baboons diverged from Eritrean baboons 61.6 (96.4–28.1) kya. The first split within Clade Arab_Y is estimated at 30.6 (55.2–10.5) kya (Fig. 5.6). It can be assumed that baboons immigrated to Arabia between the divergence of the African and Arabian lineages and the first splits within the Arabian lineages (i.e., be-

tween 150 and 31 kya). This time period includes sea level lowstands around 130 kya and 65 kya (Fig. 5.7). The confidence intervals are, however, large and all divergence time estimates span periods of sea level lowstands as well as Green Sahara Periods (Fig. 5.7).

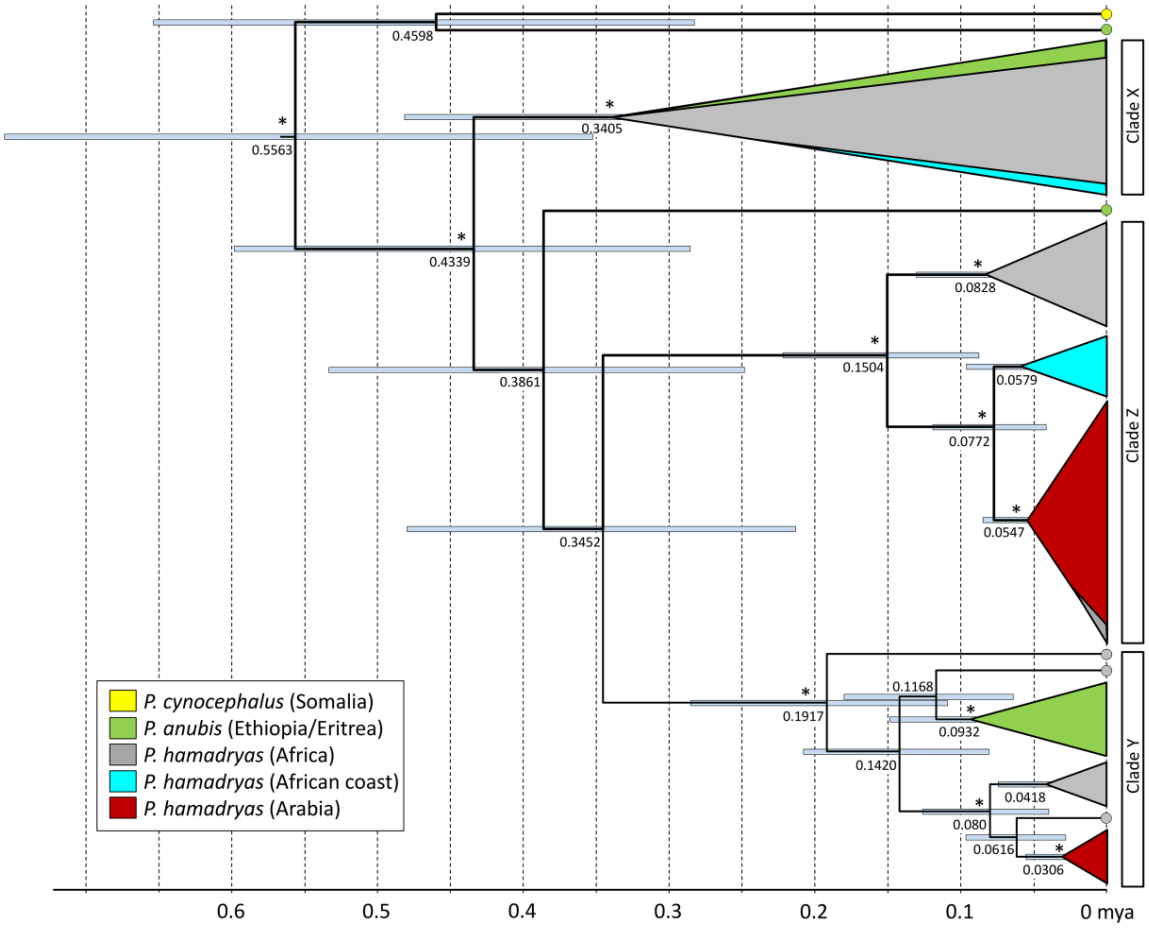

Figure 5.6: Bayesian divergence time estimations of Northeast African and Arabian baboon mtDNA lineages (concatenated Brown region + cyt *b* + HVRI, 2373 bp) based on 52 unique Northeast African and Arabian hamadryas baboon haplotypes, 17 other *Papio,* and one *Theropithecus* haplotype. In order to conserve space, only the Northeast African and Arabian parts of the tree are depicted. Clades are collapsed and represented as solid triangles. Node values are divergence time estimates in mya, with blue bars across nodes representing their 95% highest posterior density intervals. Stars demark nodes with high posterior probabilities (>0.95).

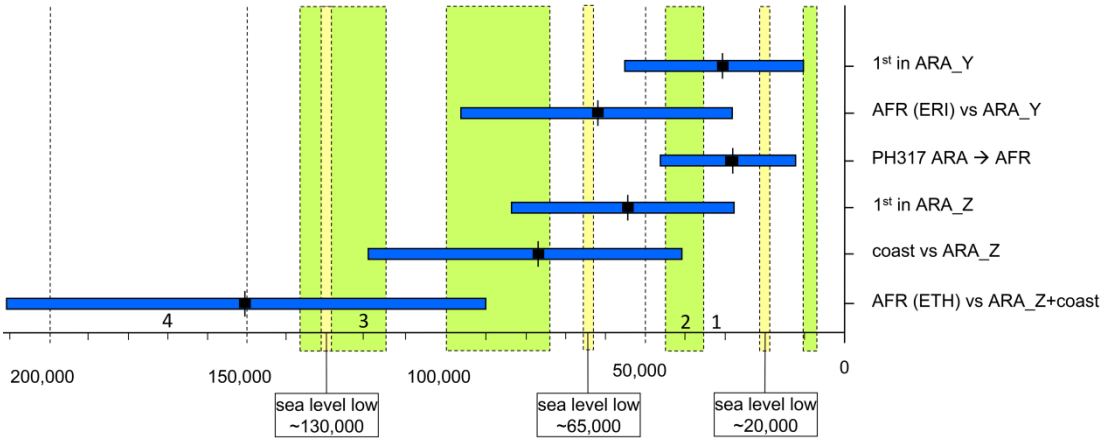

Figure 5.7: Divergence ages between African and Arabian hamadryas baboon mtDNA clades in relation to Red Sea sea level lowstands (yellow; (Rohling 1994; Rohling *et al*. 1998, 2009)) and Green Sahara Periods (green; (Blome *et al*. 2012; Drake *et al*. 2013)). Numbers 1 to 4 refer to estimated colonization times of other African mammals into Arabia: (1) white-tailed mongoose *Ichneumia albicauda* (Fernandes 2011); (2) cheetah *Acinonyx jubatus* (Charruau *et al*. 2011); (3) striped hyena *Hyaena hyaena* (Rohland *et al*. 2005); (4) leopard *Panthera pardus* (Uphyrkina *et al*. 2001).

Discussion

Our large data set allows us to reconcile and refine previous population genetic studies on hamadryas baboons and thereby elucidate the phylogeographic history of this species. Our results indicate that Arabian hamadryas baboons are genetically distinct from African hamadryas baboons; they form two mitochondrial clades and share no haplotypes.

African hamadryas baboon populations do not form clear monophyletic geographic clusters. This is likely attributable to the female-biased dispersal pattern in this species, which reduces the correlation between geography and mitochondrial genetic structuring. This is in support of a recent study that discusses this topic in detail (Kopp *et al*. 2014a). The inclusion of Ethiopian and Eritrean olive baboons in the network is probably due to introgression of hamadryas populations by male olive baboons. This has likely resulted in nuclear swamping and a phenotypical olive baboon population carrying hamadryas baboon mitochondria (Wildman *et al*. 2004; Zinner *et al*. 2009).

The phylogenetic tree reconstruction and the comparison of genetic diversity both support an African origin for hamadryas baboons. Firstly, the African population is basal in the phylogenetic tree, whereas the Arabian clades are derived and nested

within the African population. This is in congruence with previous molecular studies on the origin of hamadryas baboons (Wildman *et al*. 2004; Winney *et al*. 2004) and also fits with the fossil record (Alemseged & Geraads 2000). Secondly, one expects the highest genetic diversity in the region of origin (Austerlitz *et al*. 1997; Ramachandran *et al*. 2005; Excoffier *et al*. 2009), and the African population harbours a higher mitochondrial genetic diversity than the Arabian population. It cannot be concluded, however, that the immigration to Arabia imposed a bottleneck effect, as Lawson Handley et al. (Lawson Handley *et al*. 2006) found that allelic richness, averaged over seven autosomal loci, is not significantly different between African and Arabian hamadryas baboon populations.

The Arabian baboon population is mitochondrially structured and composed of two discrete mitochondrial clades. This can be explained by either two independent colonization events of Arabia or by a founding population that was already mitrochondrially structured. Two factors support the first alternative. Firstly, the dissimilar geographic distributions of the two clades in Arabia are better explained by two colonization events (Wildman 2000; Wildman *et al*. 2004; Winney *et al*. 2004; Fernandes 2009). Clade Arab_Y, which diverged from the Eritrean hamadryas population, is restricted to the southern part of the Arabian distribution, while Clade Arab_Z, which diverged from the Ethiopian population, is found in every Arabian sampling location. Secondly, genetic diversity is higher in Clade Arab_Z and population expansion and radiation of this clade seem to be slightly less recent than of Clade Arab_Y. This makes it more likely that Clade Arab_Z colonized Arabia before Clade Arab_Y, despite the fact that the confidence intervals of divergence time estimates overlap to a great extent.

The Clade Arab_Z includes some African samples: one from a very distant location in Ethiopia (Gerba Luku, Ger) and several from the sampling site closest to the Bab-el-Mandab Strait on the coast of Eritrea (Dada, Dad). The close relationship between Arabian and coastal Eritrean baboons indicates natural colonization via the Bab-el-Mandab Strait. Our results cannot resolve whether the coastal Eritrean clade is originally African or represents a back-migration from Arabia to Africa. The most likely explanation for the sample from Gerba Luku (located on an ancient trade route in the Rift Valley) is that humans translocated baboons inland from the coast. Even today, infant and juvenile baboons are kept as pets by nomads and carried over long distances in Eritrea and Ethiopia (DZ, personal observation).

We aimed to infer the colonization route of hamadryas baboons to Arabia through the geographic distribution of genetic diversity, the timing of population expansions, and divergence time estimates, but the results are ambiguous. There are several alternative scenarios that could explain the decline in genetic diversity in Arabia from south to north. First, this gradient could indicate that hamadryas baboons colonized Arabia in the south and then expanded northwards, gradually losing genetic diversity by serial founder effects (Ramachandran *et al*. 2005; Henn *et al*. 2012). Second, the observed pattern could be the result of an initial colonization via the northern route by Clade Arab_Z during Green Sahara Periods followed by a more recent colonization, via the southern route, by individuals belonging to Clade Arab_Y. Third, this pattern is in concordance with immigration to Arabia via the northern route followed by a retraction of the Arabian population to a southern refugium during dry periods and subsequent northward expansion during humid periods. The two latter scenarios would, however, still involve back-immigrations of Clade Arab_Z individuals to Africa via a southern route in order to explain the occurrence of closely related haplotype(s) in Africa near the Bab-el-Mandab Strait.

The star-like structure of the Arabian clades and mismatch distributions suggest that, after the colonization of Arabia, both clades expanded. The estimated expansion times are both less recent than the estimated divergence times and fit with colonization events during MIS 6 (ca. 130 kya). These estimates are directly derived from the assumed mutation rate. If we assumed a higher mutation rate, because substitution rates are elevated close to the tips (Ho *et al*. 2011), the time estimates of population expansions in Arabia would correspond better with the divergence times estimates.

Combining divergence time estimates with climatic data could help to identify the most probable of the above-mentioned scenarios. One has to bear in mind, however, that proposed periods of sea level lowstands and the existence of a land bridge across the southern Red Sea are still highly debated (Fernandes *et al*. 2006; Bailey 2009), that climatic reconstructions are far from precise (Drake *et al*. 2013), and that the confidence intervals of our divergence time estimates span large intervals. Therefore, it is vital to stress the limitations of the data. In concordance with previous studies (Wildman 2000; Wildman *et al*. 2004; Winney *et al*. 2004), our divergence times are not recent enough to support an original introduction of hamadryas baboons to Arabia by humans (which would have occurred within the last 10 kya). Our estimates, however, locate the divergence between African and Arabian baboons as

222–28 kya. This is more recent than previously thought and within the same time frame proposed for the out-of-Africa migration of modern humans, the Late Pleistocene.

The entire time span from the divergence of the Arabian population from the African population to the onset of diversification within the Arabian clades needs to be considered as the critical period for the colonization. Our divergence time estimates do not have the power to resolve whether the two Arabian clades diverged from the African source population at different times. This is because of the inclusion of African samples in Clade Arab_Z, low support values within Clade Y, and a great overlap of confidence intervals. If coastal Eritrean baboons in Clade Z represent a back-immigration to Africa, the colonization of Arabia in this clade broadly coincides with the proposed period of the sea level lowstand in MIS 6 (ca. 130 kya). The alternative scenario for Clade Z and the divergence time estimates for Clade Y are both in concordance with colonization events during MIS 4 (ca. 65 kya; Rohling 1994; Rohling *et al*. 1998, 2009) (Fig. 5.7). Colonizing events during MIS 2 (ca. 20 kya) cannot be rejected as the first splits within the Arabian Clade Arab_Y (i.e., the onset of diversification within this clade) occurred during this period.

Studies of other terrestrial Afro-Arabian mammals, such as white-tailed mongoose *Ichneumia albicauda* (Fernandes 2011), cheetah *Acinonyx jubatus* (Charruau *et al*. 2011), striped hyena *Hyaena hyaena* (Rohland *et al*. 2005), and leopard *Panthera pardus* (Uphyrkina *et al*. 2001) do not reveal any congruent pattern (Fig. 5.7). For humans, MIS 5 (ca. 130–71 kya) is identified as the climatic period most probable for dispersal for both immigration routes (Drake *et al*. 2013). Immigrations by hamadryas baboons through the northern route were probably feasible during major Green Sahara Periods (Blome *et al*. 2012; Larrasoaña *et al*. 2013; Drake *et al*. 2013), which fall well within the divergence confidence intervals of both Arabian clades. Hamadryas baboons historically (3000–2000 B.C.E.) occurred farther north to Upper Egypt and olive baboons penetrated the Sahara (Smith, 1969 and Arnold, 1995 cited in Masseti & Bruner 2009). There is, however, to our knowledge, no archaeological evidence for baboons on the Sinai Peninsula, the Levant or northern Arabia to support a historic occurrence along the northern route.

It is important to note that dispersal via the southern route might have occurred by means other than land bridges (Bailey *et al*. 2007), e.g., over-water dispersal, as has been proposed in a variety of contexts for other mammals, including primates (Yoder *et al*. 2003; de Queiroz 2005; Fernandes *et al*. 2006; Fernandes 2011).

Independent of the route the baboons took, an interesting question remains, 'Why did hamadryas baboons not emigrate farther east into Oman?', especially because humans are proposed to have emigrated eastward through southern Arabia between 70 kya and 50 kya (Kivisild *et al*. 1999; Oppenheimer 2012a; b). Favourable humid conditions in southern Arabia likely occurred around 125.0 kya, 100.0 kya and 80.0 kya, whereas from 75.0 kya to 10.5 kya arid conditions prevailed and turned southern Arabia into a natural barrier for baboon dispersal (Yan & Petit-Maire 1994; Rosenberg *et al*. 2012; Groucutt & Petraglia 2012).

Our results favour the southern route hypothesis over the northern route hypothesis, and also indicate a more recent and complex colonization of Arabia than previously thought (Wildman *et al*. 2004; Winney *et al*. 2004; Fernandes 2009). The close relationship between the Arabian population and the African population nearest to the Bab-el-Mandab Strait supports the hypothesis that this region served as an important dispersal corridor between Africa and Arabia (Wildman 2000; Kivisild *et al*. 2004). We conclude that (i) the present distribution and diversity of hamadryas baboons is shaped by a colonization of Arabia from Africa via a southern route in the Late Pleistocene and by back-immigrations to Africa, and (ii) that humans did not play a role in the original colonization of Arabia by hamadryas baboons.

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CHAPTER 6: GENERAL DISCUSSION

In the previous chapters I presented that (i) the genetic structure of Guinea baboons indicates female-biased dispersal, both on a local and a distribution-wide scale; (ii) differences in the social systems of baboon species leave characteristic footprints in their genetic structure; (iii) both historic and contemporary gene flow, namely a westward range-expansion, short-distance dispersal, and possibly introgressive hybridization, have shaped the genetic structure of Guinea baboons; and (iv) the 'southern route' from Africa to Arabia could have been used by hamadryas baboons during the same time period as proposed for modern humans. In the following general discussion I am revisiting these main findings to unify them into a comprehensive picture about the interrelation between the behavioural ecology and distribution of genetic variation in natural populations. In the first part I will outline how the obtained insights contribute to a better understanding of the Guinea baboon social system and the evolution of social systems in baboons in general. In the second part I will put my findings into a broader context about the importance of species-specific life-history attributes in shaping the genetic structure of natural populations. Finally, I will describe remaining challenges and provide an outlook on exciting future research avenues.

6.1. Female-biased dispersal in Guinea baboons: Implications for the evolution of baboon social systems

While Guinea baboons were until recently commonly neglected in discussions about the evolution of baboon social systems due to data deficiency, the accumulation of studies on their social system over the last years have led to an increased appreciation of this species to elucidate the evolution of complex societies (Grueter 2014). Based on observations of high male-male tolerance in this species (Patzelt *et al*. 2014) and the recognition of shared features between Guinea and hamadryas baboons (Jolly 2009) we hypothesized that Guinea baboons are characterized by male philopatry and female-biased dispersal. In the previous chapters I compiled several lines of evidence that support these hypotheses while also identifying aspects that warrant further investigation.

6.1.1. Evidence for female-biased dispersal in Guinea baboons

On a local scale, Guinea baboon males exhibit a stronger population structure of autosomal genetic variation than females (Chapter 2 (Kopp *et al*. 2015)). This can be attributed to more restricted gene flow in males as compared to females, resulting in an increased Isolation-by-Distance (IBD) effect, which is consistent with male philopatry and female-biased dispersal. A high level of female gene flow is also supported by a high local mitochondrial diversity, which is most likely caused by the accumulation of multiple haplotypes in single localities due to immigrating females (Chapter 2/Kopp *et al*. 2015, Chapter 3/Kopp *et al*. 2014a). On a global scale, female gene flow prevents the emergence of strong geographical clusters of mitochondrial variation (Chapter 3/Kopp *et al*. 2014a, Chapter 4) while restricted dispersal still leads to genetically differentiated populations if nuclear variation is considered (Chapter 4). With the lack of informative Y-chromosomal markers I could not confront the question of male gene flow directly, but had to rely on indirect evidence from the discordance of mitochondrial and autosomal data. This discordance is considered to arise from sex-differences in gene flow (Di Fiore 2012) and a comparative approach including species with confirmed sex-bias in dispersal helps to verify my conclusions. A similar pattern to the one I describe in Guinea baboons characterizes other male-philopatric species (e.g. hamadryas baboon Chapter 3/Kopp *et al*. 2014a, Hapke *et al*. 2001; Hammond *et al*. 2006, human *Homo sapiens* and chimpanzee *Pan troglodytes* Langergraber *et al*. 2007b) but stands in sharp contrast to the genetic structure of species with female philopatry, both within the baboon genus (Chapter 3 /Kopp *et al*. 2014a, Burrell 2008) and in other taxa (e.g. Arunachal macaque *Macaca munzala* Chakraborty *et al*. 2015; rhesus macaque *Macaca mulatta* Melnick & Hoelzer 1992; Orang-utan *Pongo pygmaeus* Nater *et al*. 2011; Nietlisbach *et al*. 2012; sperm whales *Physeter macrocephalus* Lyrholm *et al*. 1999; big brown bat *Eptesicus fuscus* Turmelle *et al*. 2011; Mexican black iguana *Ctenosaura pectinata* Zarza *et al*. 2011).

Interestingly, the strong local and global signatures of sex-biased gene flow are not readily detectable on the regional scale (Chapter 4). This could on the one hand be either the result of an inadequate sampling scheme or exemplify how strong signatures of historic gene flow can overshadow the traces of contemporary processes. On the other hand it is conceivable that the sex-bias in dispersal is not consistent over different spatial scales (Fontanillas *et al*. 2004; Gauffre *et al*. 2009) or that there are intraspecific regional differences in dispersal behaviour and hence gene flow. These differences could stem from climatic and ecological variation changing

the cost-benefit balance of individual dispersal decisions. Plasticity in dispersal has indeed been described in several species (Seychelle warblers *Acrocephalus sechellensis* Eikenaar *et al*. 2010; red deer *Cervus elaphus* Pérez-González & Carranza 2009; spider monkeys *Ateles belzebuth* Di Fiore *et al*. 2009; sand dune tuco-tuco *Ctenomys australis* Mora *et al*. 2010; Eurasian badger *Meles meles* Frantz *et al*. 2010; Central American squirrel monkey *Saimiri oerstedii* Blair & Melnick 2012; black-and-white colobous *Colobus vellerosus* Wikberg *et al*. 2012; red colobus *Procolobus rufomitratus* Miyamoto *et al*. 2013). Additionally, anthropogenic disturbance could force individuals to alter their dispersal behaviour (Ferreira da Silva 2012). Because Guinea baboons occupy a variety of habitats and climate zones (Galat-Luong *et al*. 2006; Oates *et al*. 2008; Oates 2011; Anandam *et al*. 2013) and inhabit both undisturbed and severely human-mediated landscapes (Ferreira da Silva *et al*. 2014) they constitute an intriguing study species to evaluate intraspecific variation in dispersal behaviour and its underlying causes. Besides the need of more and detailed ecological and behavioural data from individual populations for elucidating the ultimate causes and proximate mechanisms of female-biased dispersal in Guinea baboons, the comparison of different populations could shed light on how flexible this species can respond to ecological changes and how strong it is influence by phylogenetic inertia.

It is important to acknowledge that, although the presented evidence for female-biased dispersal in Guinea baboons is strong, my results do not permit conclusions about the extent of this bias and solely support that females apparently disperse further and/or more often than males. The multilevel structure of the Guinea baboon society renders it even more complicated to deduce precise behavioural patterns from the genetic data at hand (Fontanillas *et al*. 2004; Gauffre *et al*. 2009). Behavioural observations in Guinea baboons suggest that transfer of females among parties and gangs is common (Goffe & Fischer in prep.) leading to the question at which social level the sex-bias in dispersal manifests. For hamadryas baboons, living in a superficially similar society as Guinea baboons, dispersal behaviour was argued to not be a mere inversion in sex-bias of the dispersal behaviour in other taxa but to be based on completely different mechanisms (Swedell *et al*. 2011). Genetic data suggest that in this species males are philopatric at the clan level and females disperse more than males among bands (Städele *et al*. 2015). For Guinea baboons, differences in genetic relatedness across the different layers of their social organization together with behavioural observations indicate that the gang

constitutes an important social entity (Chapter 2/Kopp *et al*. 2015, Maciej *et al*. 2013b; Patzelt *et al*. 2014). Conclusively, if dispersal behaviour in Guinea baboons is analogous to hamadryas baboons, we would expect that the gang is the level at which males are philopatric and females disperse. However, the analogy of the Guinea and the hamadryas system is far from clear and a comprehensive genetical and behavioural data set will be needed to elucidate this question.

Strikingly, the deduced male philopatry does not translate into above average relatedness among males within the Guinea baboon community (Chapter 2/Kopp *et al*. 2015). Similarly, relatedness was found to not predict the quality of social bonds among males (Patzelt *et al*. 2014). At first, these finding seems to challenge the kinship-based link between philopatry and tolerance. Indeed, it has been questioned if tolerance and cooperative behavior are solely conditional on kinship (Langergraber *et al*. 2007a). Still, male philopatry has the potential to facilitate the establishment of strong male bonds (Mitani *et al*. 2002; Langergraber *et al*. 2007a) through the early formation of peer groups that, in the absence of male dispersal, can persist from early childhood into adulthood (Boese 1975).

6.1.2. Scenarios for the evolution of female-biased dispersal in Guinea and hamadryas baboons

In addition to similarities in their morphology (Jolly 1993, 2003; Kingdon 1997; Groves 2001; Frost *et al*. 2003b), the superficial resemblance of their multilevel societies (Patzelt *et al*. 2014) and presumably their mating system (Goffe & Fischer in prep.; Jolly & Phillips-Conroy 2006), my results confirm female-biased dispersal as a shared characteristic of Guinea and hamadryas baboons. The lack of long-term behavioural and ecological data on Guinea baboons restricts the identification of the ultimate causes for this pattern. While differences in ecology are commonly invoked to explain the evolution of different social systems in primates (reviewed in Janson 2000; Ostner & Schülke 2012), they appear to be of little explanatory power in the baboon genus (Henzi & Barrett 2003, 2005; Barrett 2009; Jolly 2012). Female philopatry and male dispersal are most likely the ancestral state in the Papionini (Di Fiore & Rendall 1994; Lukas & Clutton-Brock 2011) and the question arises which forces triggered the switch to an opposite pattern in both Guinea and hamadryas baboons. A first crucial step to answer this question is to investigate whether this shared pattern represents autapomorphic traits resulting from convergent evolution or if it is a homologous, synapomorphic trait derived from a common ancestor. A well-resolved

phylogeny is indispensable to discriminate between these two alternatives (Pozzi *et al*. 2014). Both species are placed within the northern clade of the baboon phylogeny, which excludes chacma, southern yellow, and Kinda baboons but also includes olive and northern yellow baboons (Zinner *et al*. 2013b; Boissinot *et al*. 2014). Olive baboons currently separating the distribution of Guinea and hamadryas baboons, occupy comparable habitats and live in multi-male-multi-female groups with male-biased dispersal (Packer 1975; Vinson *et al*. 2005). The relationships within the northern clade are not well understood as are the phylogeographic processes that formed it (Zinner *et al*. 2011b; Zinner *et al*. 2013b). If the olive baboon is basal to Guinea and hamadryas baboons, the most parsimonious explanation for female-biased dispersal would be that it represents a synapormphy that evolved in the common ancestor of Guinea and hamadryas baboons. However, if olive baboons are phylogenetically nested between the other two species or diverged last, female-biased dispersal could either be a synapomorphic trait (that was subsequently lost in olive baboons) or represent autapomorphies in the other two species as a result of convergent evolution. I speculate that female-biased dispersal in Guinea and hamadryas baboons represents a synapomorphy based on two arguments. Firstly, homology appears to be the most parsimonious explanation for the suite of characters shared between these two species that comprise both morphological and behavioural traits. The nuanced differences in these traits could have arisen through independent evolution since the two taxa diverged. Secondly, a more recent common ancestor of Guinea and hamadryas baboons appears likely in the hypothetical reconstruction of the phylogeographic history of baboons (Zinner *et al*. 2011b). This reconstruction suggests a colonization of the northern savannah belt by baboons with subsequent isolation of this northern population from the southern population(s) (Kingdon 1997; Zinner *et al*. 2011b). Whether this northern population was panmictic, exhibited clinal variation or already diverged into separate, for instance western and eastern populations, is unclear. When dispersal corridors opened again, olive baboons invaded from the south and split the distribution of contemporary Guinea and hamadryas baboons, either by completely replacing or hybridizing with the local populations (Kingdon 1997; Jolly 2003; Zinner, Buba, *et al*. 2011). Under this scenario, the inclusion of olive baboons in the northern clade and their split into a northeastern and –western haplogroup can be explained by introgressive hybridization (Zinner *et al*. 2011b). Additionally, this scenario also includes the possibility that contemporary Guinea baboons actually represent a hybrid species, formed by the interbreeding of

ancient olive and a hamadryas-related proto-Guinea baboon. Although this is highly speculative, it could explain the similarities in behaviour of Guinea baboons and baboons of P. *hamadryas x P. anubis* hybrid groups (Beehner 2003; Bergman & Beehner 2004). Under this scenario, the distinct Western cluster in Guinea baboons (Chapter 4) could represent the original Guinea baboon population while the other clusters exhibit different levels of introgression. However, than we would expect female-biased dispersal to be more pronounced in this western populations, and there is currently no evidence supporting that.

Even if we were able to decide on the evolutionary history of female-biased dispersal in Guinea baboons, the ultimate adaptive value of this behaviour would remain to be determined. Meta-analyses suggest that in mammals, habitual female dispersal mainly arises as a consequence of inbreeding avoidance in reaction to increased male tenure length (Lukas & Clutton-Brock 2011; Clutton-Brock & Lukas 2012). While this conclusion provides a testable hypothesis for baboons, the "Why?" question is merely transferred from the evolution of dispersal to the evolution of male tenure length. Jolly's "Frontier Hypothesis" (Jolly 2009) is shifting the attention from ecological explanations to the importance of demographic factors. Its advantage is that it can be embedded into phylogeographic scenarios and profits from the growing evidence about the peculiar evolutionary forces during range expansions (Excoffier *et al*. 2009). Furthermore, it can not only be invoked to explain the evolution of sex-biased dispersal and male social relationships in baboons, but also the evolution of multi-level systems (Grueter *et al*. 2012). To me it is conspicuous that several primate species with female-biased dispersal also live in multi-level or fission-fusion societies (e.g. chimpanzee, hamadryas baboon, proboscis monkey *Nasalis larvatus*, spider monkey *Ateles* spp., Muriqui *Brachyteles* spp.; Lukas & Clutton-Brock 2011; Grueter *et al*. 2012). While these multi-level and fission-fusion societies, respectively, should not be equated and represent different phenomena (Grueter *et al*. 2012) they both comprise sublevels imbedded in a stable higher grouping level. The joint occurrence of female-biased dispersal and multi-level or fission-fusion societies could indicate that either these two patterns emerge due to similar evolutionary forces or that one feature is an important catalyst for the other. One hypothesis, if the latter is the case, could be that in nested societies the dispersal costs for females are reduced, because they are able to disperse to familiar groups within the higher level grouping. Whether there is indeed a correlation between these two patterns, both within the primate order and maybe among mammals in general, has, to

my knowledge, not been systematically examined but could help to identify their evolutionary origins.

6.1.3. Strengthening baboons as a model for human evolution

The multi-level social organization and strong male-male bonds of Guinea baboons (Patzelt *et al*. 2014) have been recognized to elucidate the processes that shaped the highly cooperative societies of humans (Grueter 2014). The female-biased dispersal pattern described here (Chapter2/Kopp *et al*. 2015; Chapter 3/Kopp *et al*. 2014a) adds another facette to the Guinea baboon social system which parallels the social system of humans. Until now the hamadryas baboon was considered to be the only nonhuman primate taxon sharing these characteristic features with humans (Swedell & Plummer 2012). By identifying these features also in the Guinea baboon we ascertain that the hamadryas baboon system is not a extreme peculiarity but that important insights might be gained from pinpointing the adaptive value of these traits in both species. For instance, the hypothesis that the hamadryas baboon system is an adaptation to arid habitats (Jolly 1993; Schreier & Swedell 2012) appears to not be directly transferable to the Guinea baboon thus also questioning its generalization to humans. A crucial next step will be to evaluate the nuanced interspecific differences as well as intraspecific plasticity in these behavioural traits in baboons to provide comparative data for understanding their variability across human societies.

In addition to these analogous behavioural traits, baboons parallel humans in their rapid expansion during the Plio-Pleistocene (Jolly 2009; Zinner *et al*. 2011b). In his "Frontier Hypothesis", Jolly (2009) develops a scenario in which this rapid range expansion could have provided the arena for male philopatry to evolve. Although highly speculative and awaiting both empirical and theoretical corroboration, this hypothesis fits into the growing body of literature demonstrating the distinctive evolutionary forces acting in the edge populations of range expansions (Excoffier *et al*. 2009). In Guinea baboons, an historic range expansion and contemporary, spatially restricted dispersal appear to be the most plausible explanation for the current distribution of genetic diversity (Chapter 4). Although the sampling of my project turned out to be spatially too limited to unambiguously characterize the taxon boundary of West African baboons, taken together with previous studies (Zinner *et al*. 2009; Keller *et al*. 2010) it hints to genetic clines being a better representation of baboon genetic diversity than sharply defined clusters (Chapter 4). Human genetic diversity also appears

to be mainly clinal with a strong positive correlation between genetic and geographic distance (Serre & Pääbo 2004; Manica *et al*. 2005; Ramachandran *et al*. 2005; Lawson Handley *et al*. 2007). The decreasing genetic diversity in human populations from East Africa along likely colonization routes into Eurasia and the Americas confirms the African origin of modern humans (Prugnolle *et al*. 2005). We identify a similar pattern in the out-of-Africa dispersal of hamadryas baboons (Chapter 5/Kopp *et al*. 2014b). The "southern route" from Africa to Arabia could have been used by both hamadryas baboons and modern humans during the same time period during the Late Pleistocene (Chapter 5/Kopp *et al*. 2014b). The observation that geographic distance explains most of the observed variance in both humans (Manica *et al*. 2005; Prugnolle *et al*. 2005) and some baboon species (Chapter 3/Kopp *et al*. 2014a, Chapter 4) does not rule out that slight discontinuities in dispersal exist (Rosenberg *et al*. 2005) and genetic diversity in both taxa can probably be best explained by a synthetic model in which distance explains most of the variance but discontinuities due to restricted dispersal can generate cluster-like patterns (Lawson Handley *et al*. 2007).

6.2. The interplay of historic and contemporary gene flow

While the overall genetic diversity in Guinea baboons is best described as a cline, cluster-like patterns are identifiable (Chapter 4). In my opinion, the most plausible explanation for this pattern is that historic gene flow during a westward range expansion led to a gradient in allele frequencies while contemporary dispersal is restricted to short distances shaping structures that are perceived as clusters in the nuclear data (Chapter 4). More complex scenarios such as allele surfing in edge populations as well as historic and ongoing hybridization with olive baboons could be incorporated in this hypothesis and be invoked to explain the spatial arrangement of the clusters (Chapter 4). My findings highlight the importance of jointly evaluating the influence of both historical and contemporary gene flow when investigating the spatial pattern of genetic variation (Zellmer & Knowles 2009; Guo 2012; Epps *et al*. 2013b). The restriction of dispersal and hence gene flow to short distances appears to be imposed by the social system of the species emphasizing the need to consider species-specific life-history attributes as important factors in shaping the genetic structure of natural populations (Bolliger *et al*. 2014). The restriction in gene flow could furthermore enable populations to evolve local adaptations in response to lo-

cally specific selection regimes (Bamshad & Wooding 2003; Serre & Pääbo 2004; Peng *et al*. 2011). Taken together, this underlines the importance of considering intraspecific genetic variation in broader analyses of interspecific relationships (Markolf *et al*. 2011). If samples are not obtained homogeneously from the whole distribution of a species (Schwartz & McKelvey 2009) erroneous conclusions might be drawn form an underestimation of intraspecific diversity and a resulting overestimation of interspecific differentiation. Studies employing a fine-scale sampling have proven to reveal more nuanced results than work based on fewer samples, which often provide seemingly clear but over simplistic conclusions (Markolf *et al*. 2011; VonHoldt *et al*. 2011; Kutschera *et al*. 2014; Wood *et al*. 2014; Fünfstück *et al*. 2015; Botero *et al*. 2015). This is of particular relevance for phylogenetic projects, which are regularly based on only a few individuals per species and often lack precise information about provenance because high-quality samples were taken from captive individuals (Chan *et al*. 2013). Hence, in cases where the investigated taxa are permeable to gene flow and not panmictic, it is crucial to examine their internal structure and variation (Jolly 1993). Especially genomic projects often neglect whole-taxon sampling in favour of increasing statistical power through number of basepairs (Soltis *et al*. 2004). In light of our results we suppose that this will lead to exciting intra- and interspecific patterns being overlooked and urge to fully appreciate a population-genomic approach.

6.3. Conclusions: Future challenges and research avenues

My project provides the first solid evidence for female-biased dispersal in Guinea baboons and strengthens baboons as an intriguing model to elucidate processes and selective pressures that impacted the evolution of humans. It suggests that the current genetic make-up of this species is shaped by a historic range expansion and contemporary locally-restricted dispersal and emphasizes the importance of considering intraspecific genetic variation. To close this thesis, I am summarizing the questions that remained unsolved or emerged from this project.

Firstly, the details of female dispersal behaviour in Guinea baboons need to be clarified in order to understand the ultimate causes of this unusual pattern. This includes the magnitude of sex-bias as well as the dispersal distance, in particular at which level of the society a sex-bias manifests. Long-term behavioural, genetic, and ecological data is needed to solve this question. Additionally, the development and

investigation of informative Y-chromosomal markers is critical to examine the extent of male philopatry. Comparative data from other populations could help to evaluate the plasticity of dispersal behaviour and how both ecological and demographic factors could have influenced its evolution.

Secondly, without confidence in the phylogenetic relationship of Guinea and hamadryas baboons we can only speculate whether their shared features represent synapomorphic or autapomorphic traits. Distinguishing between these possibilities, however, is crucial to understand the processes that led to the evolution of multi-level societies with female-biased dispersal. Analysis of several baboon genomes, representing all six species, is currently under way and will hopefully help to solve this question.

Thirdly, sampling needs to be extended east- and southwards and incorporate both genetic and phenotypic data to locate the taxon border of West African baboons. This will help to characterize the extent of interspecific gene flow and to distinguish between the different phylogeographic scenarios outlined above. It could also verify whether the clinal pattern of genetic variation indeed extends beyond the taxon border. Unfortunately, habitat alteration and degradation led to the extinction of baboon populations in some of the regions of interest and the current political situation in the respective countries hampers sampling efforts. Museum collections could provide an alternative sample source to circumvent these problems.

Fourthly, a quantitative analysis of genetic variation in relation to landscape variables could uncover correlations that were overlooked in this project. Such an analysis should include both past and present features to accommodate potential time lags between changes in the environment and in genetic variation. Moreover, including adaptive genetic variation in the analysis could uncover different selective regimes in populations occupying different habitats.

Fifthly, extending the analyses provided here to the genome-scale could give a more detailed picture of both neutral and adaptive intraspecific variation, for example on difference in gene flow among genomic regions. With genome-scale sequencing becoming increasingly cost-effective and a reference genome available this theoretically appears to be feasible. However, current protocols struggle with factoring in the low quality of DNA obtained from faecal samples, especially the low quantity of endogenous target DNA, or are not economical when hundreds of samples should be analyzed. The development of a methodology specifically tailored to non-invasively

collected samples is currently in the optimization phase at Duke University. A pilot study on samples from my project gave promising preliminary results making me confident that this research avenue can be pursued in the near future.

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APPENDIX

Supplementary material, Chapter II

Genetic analyses

We used 15 autosomal microsatellite loci. In a first step one Y-chromosomal and 13 autosomal microsatellites were amplified for every sample in singleplex reactions to examine their allele-size and polymorphism. The Y-chromosomal marker did not amplify and was excluded, as was one autosomal microsatellite that turned out to be monomorphic. In a second step a multiplex strategy (Ferreira da Silva 2012) was adopted and optimized that contained three additional microsatellites. This resulted in five multiplex reactions, containing two to four different primer pairs (Table 2.SII). Singleplex PCR amplifications were performed in a total volume of 30µl, composed of 1.0µl fecal DNA extract (20-40ng/µl), 19.6µl H_2O, 3.0µl 10x buffer, 1.0µl of each primer (10pmol/µl; forward primer end-labelled with fluorescent-dye; Table 2.SI), 0.2µl dNTPs, 4.0µl BT (0.6 mg/ml of bovine serum albumin [BSA] + Triton) and 0.2µl BioTherm™ Taq DNA polymerase. PCR conditions comprised a pre-denaturation step at 94°C for 2min, followed by 35 cycles at 94°C for 20s, optimal annealing temperature T_a for 30s, 72°C for 30s, and a single final extension step at 72°C for 5min. Multiplex PCR amplifications were performed in a total volume of 10µl, composed of 1.2µl DNA extract, 2.65µl H_2O, 5.0µl Qiagen Multiplex PCR Kit Mastermix (contains HotStartTaq® DNA Polymerase, Multiplex PCR Buffer (contains 6mM $MgCl_2$), dNTP Mix; Qiagen, Valencia, California, U.S.A), 1.0µl Primermix (containing 0.1-0.6µM of 2-4 primer pairs; Table 2.SII) and 0.15µl BT. PCR conditions comprised a pre-denaturation and polymerase activation step at 95°C for 15min, followed by 40 cycles at 94°C for 30s, optimal annealing temperature T_a for 40s, 72°C for 40s, and a single final extension step at 72°C for 30min. All sets of amplifications contained negative controls with HPLC water to monitor contamination. PCR amplification success was confirmed by visualization of 2µl of product under UV light after electrophoresis on 1% (singleplex) or 2% (multiplex) agarose gels containing ethidium bromide. Concentration of DNA was estimated by comparison with 2µl pUC19 DNA (Fermentas, Burlington, Ontario, Canada) with known concentration of 5ng/µl and 10ng/µl, respectively. 0.5 µl appropriately diluted PCR product was mixed with 9.9µl Hi-Di™ Formamide (Applied Biosystems, Foster City, CA, U.S.A.) and 0.1µl

GeneScan™-400HD ROX® Size Standard (Applied Biosystems) and further analyzed through determination of PCR fragment length by capillary electrophoresis on an ABI 3130xL Genetic Analyser (16 capillary sequencer, Applied Biosystems). Fragment length was rated relative to the size standard using PEAK SCANNER™ v1.0 (Applied Biosystems). For markers that were used with different fluorescent tags in singleplex and multiplex PCR, respectively (D10S611, D14S306), differences in allele size due to these tags (Sutton *et al*. 2011) were evaluated by comparing singleplex and multiplex results.

Genotyping errors

In a study on yellow baboons that tested the reliability of microsatellite genotyping from fecal DNA compared to blood derived DNA, two and three repetitions for heterozygotes and homozygotes, respectively, proved to suffice, but the fact that only fresh faecal samples were used was highlighted (Bayes *et al*. 2000). Samples used in our study were generally fresh (normally collected within an hour after defecation) and DNA concentration was high. Furthermore samples with very low concentrations were already excluded after sex determination. We accepted heterozygosity if repeated at least two times and homozygosity if repeated at least four times. In addition we used Quality indices (*QI*) that indicate the reliability of the data by evaluating the percentage of PCR reactions that yield the "true" result (i.e. the consensus genotype; (Miquel *et al*. 2006)). We calculated the *global QI* as well as *QI per locus* and *QI per sample*. To improve the quality of the data set, loci were only included in further analysis if their *QI* was above 0.5 and subsequently all samples with a *QI* below 0.6 were excluded. Three types of error were estimated from all amplifications for each locus, whereby multiplex PCRs were not counted as one amplification but as the number of markers they combined to account for the fact that they sometimes only partially amplified: allelic dropout (ADO; replicates missing one allele of the consensus genotype as a proportion of all positive amplifications of individuals determined as heterozygous), occurrence of false alleles (FA; replicates showing a false allele as a proportion of all positive amplifications) (Broquet & Petit 2004) and amplification failure (proportion of failed amplification attempts for all amplification attempts). Null alleles, long allele dropout and erroneous scoring due to stuttering were estimated using the Monte Carlo simulation (bootstrap) method implemented in MICRO-CHECKER 2.2.3 (Van Oosterhout *et al*. 2004), with a Bonferroni adjusted 95% confidence interval and 1000 repetitions.

2,134 out of 20,467 microsatellite amplifications performed in total failed, leading to an overall amplification success of 89.6% in the raw data set. We found substantial differences in *QI* and error rates of both samples and loci, with a global *QI* of 0.72. After excluding locus D1S533 (QI_{Locus}=0.40) and 52 samples (QI_{Sample}<0.60) amplification success increased to 97.2% and global *QI* to 0.84, ADO dropped to 16.3% and FA to 4.7% (Table 2.SIII). No locus showed evidence for null alleles and stuttering apparently did not result in scoring errors.

Table 2.SI: List of microsatellite loci used in this study (dyes in brackets were used in multiplex PCR; grey loci were tried but later excluded; T_a=optimal annealing temperature).

Locus ID	Repeat	Genbank	Primer F 5'-3' Primer R 5'-3'	Dye	T_a(°C)
D1S533	GATA	G07788	CAT CCC CCC CAA AAA ATA TA TTG CTA ATC AAA TAA CAA TGG G	Fam	55
D2S1326	CTAT	G08136	AGA CAG TCA AGA ATA ACT GCC C CTG TGG CTC AAA AGC TGA AT	Tet	56
D3S1766	ATCT	NT_022517.18	ACC ACA TGA GCC AAT TCT GT ACC CAA TTA TGG TGT TGT TAC C	Cys	58
D3S1768	GATA	G08287	GGT TGC TGC CAA AGA TTA GA CAC TGT GAT TTG CTG TTG GA	Tet	56
D4S243	GATA	M87736	TCA GTC TCT CTT TCT CCT TGC A TAG GAG CCT GTG GTC CTG TT	Fam	60
D5S1457	GATA	G08431	TAG GTT CTG GGC ATG TCT GT TGC TTG GCA CAC TTC AGG	Fam	58
D6S501	CTAT	G08551	GCT GGA AAC TGA TAA GGG CT GCC ACC CTG GCT AAG TTA CT	Tet	58
D7S503	CA	Z16870	ATG ACT TGG AGT AAT GGG AAC CTT TAA TCA GGA TAC AGAC	Cys	54
D7S2204	AGAT	G08635	TCA TGA CAA AAC AGA AAT TAA GTG AGT AAA TGG AAT TGC TTG TTA CC	Fam	57
D8S1106	GATA	G09378	TTG TTT ACC CCT GCA TCA CT TTC TCA GAA TTG CTC ATA GTG C	Tet	58
D10S611	GATA	G08794	CAT ACA GGA AAC TGT GTA GTG C CTG TAT TTA TGT GTG TGG ATG G	Tet (Cys)	60
D12S375	GATA	G08936	TTG TTG AGG GTC TTT CTC CA TCT TCT TAT TTG GAA AAG TAA CCC	Fam	57
D13S159	CA	Z16691	GCT GTG ACT TTT AGG CCA AA TGT GAT GTC TAC AAC TCC AGG	Hex	58
D13S765	GATA	G09003	TGT AAC TTA CTT CAA ATG GCT CA TTG AAA CTT ACA GAC AGC TTG	Tet	58
D14S306	GATA	G09055	AAA GCT ACA TCC AAA TTA GGT AGG TGA CAA AGA AAC TAA AAT GTC CC	Fam (Cys)	62
D21S1442	GATA	G08071	CTC CTC CCC ACT GCA GAC TCT CCA GAA TCA CAT GAG CC	Fam	58
DYS391	GATA	G09613	CTA TTC ATT CAA TCA TAC ACC CA GAT TCT TTG TGG TGG GTC TG	Tet	58

Table 2.SII: Details of Multiplex PCRs.

Multiplex Mix	Marker	Ta (°C)	Primer Concentration (uM)	Allele Range (bp)
M1 57°C	D3S1766	58	0.1	194-202
	D12S375	57	0.1	165-181
	D7S503	54	0.6	140-158
	S13S765	58	0.15	197-213
M2 55°C	D1S533	55	0.4	187-203
	D14S306	62	0.2	163-279
	D2S1326	56	0.3	251-263
M3 59°C	D10S611	60	0.1	133-141
	D6S501	58	0.5	176-188
	D8S1106	58	0.1	144-160
M4 57°C	D3S1768	56	0.1	193-209
	D5S1457	58	0.1	121-129
	D7S2204	57	0.4	232-248
M5 58°C	D21S1442	58	0.4	226-246
	D4S243	60	0.1	147-171

Table 2.SIII: Genotyping errors

Locus	D2S1326	D3S1768	D4S243	D5S1457	D6S501	D7S2204	D8S1106	D10S611	D12S375	D13S765	D14S306	D21S1442	D3S1766	D7S503	mean
Amplifications	1048	1030	890	1022	968	900	962	981	1061	1089	1005	890	886	897	
positive	716	896	772	772	817	738	829	773	940	976	869	573	800	810	
negative	108	7	1	18	6	57	9	23	19	18	43	55	13	9	
Ampl. Success	0.89695	0.9932	0.99888	0.98239	0.9938	0.93667	0.99064	0.97655	0.98209	0.98347	0.95721	0.9382	0.98533	0.98997	
heterozygotes	121	127	171	102	155	154	115	138	165	107	114	156	76	162	
Amplifications	574	590	703	472	688	628	503	624	822	546	508	627	302	674	
homozygotes	88	84	39	107	56	55	95	71	45	104	97	45	135	45	
Amplifications	467	440	181	533	280	263	455	346	232	543	497	211	584	206	
no consensus	2	0	1	2	0	2	1	2	1	0	0	10	0	4	
allelic dropout	169	72	72	151	107	61	76	111	42	72	65	140	58	30	
ADO	0.325	0.12308	0.10256	0.32543	0.1562	0.10499	0.15323	0.18257	0.05198	0.13508	0.13458	0.23973	0.19595	0.04505	**0.163**
false alleles	48	55	39	64	38	36	45	63	53	23	28	78	15	31	
FA	0.05145	0.05376	0.04417	0.06484	0.0395	0.04311	0.04737	0.06653	0.05121	0.02148	0.02911	0.09861	0.01718	0.03559	**0.047**
QI/locus	0.71976	0.88288	0.8841	0.78051	0.85624	0.83188	0.87075	0.80411	0.8922	0.89875	0.87433	0.68276	0.90979	0.9109	

Amplifications	total	negative	success
	13629	386	**0.97168**

QI global
0.84278492

Table 2.SIV: Genotypes. Individual Genotypes of 165 Guinea baboons.

Ego	Sex	Pop	D2S1326		D3S1768		D4S243		D5S1457		D6S501		D7S2204		D8S1106		D10s611		D12S375		D13S765		D14S306		D21S1442		D3S1766		D7S503	
CL001	m	C	243	255	205	205	159	159	125	125	180	184	240	244	152	152	137	137	169	177	201	201	171	175	230	238	194	194	156	158
CL002	f	C	255	259	197	197	159	159	125	129	184	188	236	240	152	152	141	141	169	181	205	209	167	171	234	242	194	202	144	158
CL003	m	C	251	255	205	205	155	159	125	125	180	184	236	244	148	152	137	141	169	177	201	205	171	171	0	0	194	202	144	144
CL004	f	C	255	255	205	205	159	159	125	129	176	180	240	244	152	156	137	137	177	177	201	201	167	171	234	234	194	202	144	144
CL005	f	C	255	255	197	205	155	159	125	129	176	180	240	240	152	156	0	0	169	177	197	201	167	171	230	234	194	194	156	158
CL006	f	C	251	255	197	205	155	159	125	125	176	184	232	240	152	152	137	141	173	173	201	205	167	171	230	234	194	194	0	0
CL007	m	C	251	255	205	205	159	171	121	125	180	180	240	240	148	152	137	137	173	177	201	205	167	167	238	242	194	194	144	156
CL008	m	C	251	255	205	205	159	171	121	125	172	180	240	240	148	152	129	137	173	177	201	205	167	167	238	242	194	194	144	156
CL009	m	C	251	255	205	205	159	163	121	125	180	184	244	248	152	152	137	141	169	173	201	205	167	171	230	238	194	194	150	156
CL010	f	C	255	255	205	209	159	159	125	125	184	184	240	240	152	156	137	141	169	173	201	201	167	171	230	230	194	202	156	158
CL011	f	C	255	255	205	205	159	171	129	129	180	180	240	240	152	152	137	141	169	181	205	205	167	171	230	242	194	194	156	158
GD001	f	G	251	255	205	209	159	163	125	125	180	184	236	244	144	152	137	141	169	177	201	201	167	167	238	242	194	194	144	156
GD002	f	G	255	255	197	197	159	163	125	129	180	184	232	236	148	152	141	141	165	173	201	205	167	167	238	238	194	194	144	158
GD003	m	G	251	255	205	209	159	163	125	129	180	184	244	248	152	152	0	0	165	169	201	205	167	167	226	230	194	198	156	158
GD004	m	G	251	255	205	205	163	163	125	129	188	188	232	240	152	152	137	141	169	173	201	205	167	171	230	242	194	194	158	158
GD005	f	G	251	255	201	205	155	159	129	129	180	180	240	248	152	156	137	137	173	177	201	205	167	167	230	238	194	194	156	158
GD006	m	G	251	255	205	205	159	159	129	129	180	184	232	240	152	156	137	141	177	177	201	201	167	171	234	238	194	202	144	156
GD007	f	G	251	255	205	205	155	163	125	125	176	184	240	240	152	152	137	141	0	0	201	201	167	175	230	242	194	202	156	158
GD008	m	G	251	255	205	205	155	163	125	129	184	188	236	240	152	156	133	137	169	169	201	201	171	171	238	238	194	194	156	156
GD009	m	G	239	255	205	205	155	159	125	125	184	184	236	236	152	156	137	137	173	173	201	201	159	167	234	242	194	194	158	158
GD010	m	G	255	255	205	209	159	163	125	129	180	184	240	248	152	152	137	141	173	181	205	205	167	167	242	246	194	194	156	156
GD011	f	G	255	255	205	205	155	159	125	125	184	188	232	236	152	156	137	137	165	169	201	201	163	167	230	242	194	202	144	156
LK001	m	L	251	255	197	205	159	163	125	125	176	180	232	244	152	156	137	137	177	177	201	205	167	175	230	230	194	194	144	156
LK002	f	L	255	255	205	205	155	159	125	129	180	184	232	232	144	156	137	137	169	177	197	205	167	171	230	238	194	194	156	158
LK003	f	L	255	255	205	209	155	159	125	129	180	184	232	240	148	148	137	141	169	169	201	205	167	171	234	238	194	202	150	156
LK004	f	L	251	251	205	205	163	167	125	125	176	184	240	244	156	156	137	137	177	177	201	205	167	171	230	238	194	202	154	158
LK005	m	L	251	259	205	205	155	167	125	125	180	184	232	240	152	152	137	141	177	181	205	209	167	171	230	238	194	202	156	158
LK006	f	L	251	259	205	205	155	159	125	125	176	184	232	232	152	152	137	137	169	177	197	201	167	167	230	234	194	202	150	154
LK007	f	L	251	259	197	205	155	163	125	125	176	184	232	232	152	152	137	137	169	177	197	201	167	167	230	234	194	202	150	154
LK008	f	L	251	255	197	205	159	163	125	125	180	184	240	244	156	156	137	137	173	173	201	201	171	171	230	238	194	202	154	156
LK009	m	L	255	255	205	205	155	159	125	129	180	184	232	240	152	152	137	141	173	181	205	205	167	171	230	238	194	202	156	158
LK010	f	L	251	255	205	205	159	163	125	129	180	184	232	244	152	152	137	141	169	173	201	205	171	171	238	246	194	202	156	156
LK011	m	L	251	255	197	205	159	163	125	129	176	184	232	240	152	152	137	141	169	173	201	205	167	171	234	238	194	194	0	0
LK012	m	L	255	255	205	205	155	159	125	125	176	176	232	240	156	156	137	141	169	177	197	205	167	167	230	238	194	194	154	156
LK013	f	L	251	255	197	205	155	159	125	129	180	184	240	244	156	156	133	137	173	173	201	201	171	171	230	238	194	202	154	156
NK001	m	N	255	259	197	205	147	163	125	129	180	180	236	236	156	156	137	141	169	173	201	205	167	171	230	246	194	194	144	158
NK002	m	N	259	259	197	209	163	163	125	129	180	180	236	236	152	156	133	141	165	173	201	201	171	171	230	246	194	194	144	154
NK003	m	N	259	259	197	205	147	163	125	129	180	184	236	244	152	156	137	141	173	173	201	201	171	171	0	0	194	194	144	154
NK004	m	N	255	259	197	205	147	163	125	125	180	180	236	236	152	156	133	137	173	173	201	201	167	171	230	238	194	194	144	144
NK005	m	N	259	259	197	205	147	163	125	129	176	180	0	0	152	156	137	141	169	173	201	201	167	167	226	230	194	194	144	158
NK006	m	N	0	0	197	205	147	163	125	129	180	180	236	236	152	156	137	141	169	173	201	201	167	171	230	238	194	194	144	158
NK007	f	N	255	259	197	205	159	163	125	125	180	184	236	244	152	156	133	137	169	173	201	205	167	171	234	242	194	194	144	158
NK008	m	N	255	255	201	201	147	155	121	125	184	184	240	240	156	156	137	141	165	165	201	201	167	167	234	238	194	194	156	156
NK009	m	N	255	259	201	205	147	151	125	129	176	184	236	236	148	152	133	137	165	173	201	201	167	167	238	238	194	202	144	156
NK010	f	N	255	255	193	205	151	159	125	125	180	184	236	236	152	156	137	141	165	169	201	209	167	167	238	238	194	202	148	156

Ego	Sex	Pop	D2S1326		D3S1768		D4S243		D5S1457		D6S501		D7S2204		D8S1106		D10s611		D12S375		D13S765		D14S306		D21S1442		D3S1766		D7S503	
NK011	f	N	243	255	201	205	147	151	125	125	176	184	232	240	156	156	137	137	165	169	201	205	167	171	238	238	194	194	144	156
NK012	m	N	255	263	201	201	147	159	125	129	176	184	232	236	152	156	137	141	173	177	205	213	167	167	238	242	194	194	144	156
NK013	m	N	255	259	201	205	147	151	125	129	176	184	236	236	152	156	133	141	165	173	201	201	167	167	238	238	194	202	144	156
NK014	f	N	251	255	205	205	151	155	125	129	180	184	232	236	152	152	137	141	169	177	201	201	167	171	230	238	202	202	148	148
NK015	m	N	255	259	197	205	151	163	125	129	180	180	236	240	152	152	137	137	169	173	201	205	167	179	230	238	194	202	144	158
NK016	f	N	0	0	201	205	163	163	125	129	180	180	236	244	156	156	137	141	169	173	205	205	171	175	230	238	194	194	156	158
NK017	m	N	259	259	197	205	147	163	121	125	184	184	240	240	156	156	137	141	165	169	201	201	167	167	238	246	194	194	144	156
NK018	m	N	255	259	201	205	159	163	125	125	180	184	236	236	152	156	137	141	173	173	201	205	167	171	0	0	194	194	156	156
NK019	f	N	255	259	201	205	147	151	125	125	184	184	232	240	0	0	137	141	165	169	201	205	171	179	238	238	194	194	144	156
NK020	f	N	255	259	197	205	147	159	121	129	180	184	0	0	148	152	137	141	177	177	201	201	167	171	238	242	194	194	144	156
NK021	m	N	255	255	197	205	159	163	125	129	180	184	236	240	156	156	137	141	165	169	201	201	167	179	0	0	194	194	144	156
NK022	m	N	251	255	201	205	151	159	125	129	176	184	228	236	148	156	137	141	169	177	201	205	171	179	234	238	194	202	156	158
SI001	f	S	255	255	197	201	159	163	125	129	180	184	232	236	152	156	137	141	169	173	201	201	167	167	230	238	194	202	144	156
SI003	m	S	255	255	197	209	159	163	125	129	180	184	232	240	148	152	137	141	169	169	201	201	167	167	238	242	194	194	154	156
SI004	f	S	255	255	205	205	155	159	125	125	180	188	232	236	148	156	141	141	165	169	201	201	167	175	230	242	194	194	154	154
SI005	m	S	251	255	205	205	155	163	125	129	176	180	236	240	152	156	137	141	165	169	201	201	167	171	238	242	194	202	144	158
SI006	m	S	255	255	205	205	159	159	125	129	184	188	232	232	148	152	137	137	173	173	201	209	167	171	238	242	194	202	156	158
SI007	m	S	251	255	197	209	159	163	125	125	180	184	232	240	148	152	137	141	169	177	201	205	171	171	230	238	194	202	156	156
SI008	f	S	255	255	197	205	155	159	121	121	180	184	232	240	144	152	137	137	169	173	201	201	171	175	238	238	194	202	144	144
SI009	m	S	255	263	201	209	155	159	125	125	180	180	240	244	152	152	133	137	173	181	205	205	167	171	230	230	194	202	150	156
SI010	m	S	243	251	197	205	155	159	125	125	180	184	232	232	144	152	137	137	165	173	201	209	167	171	0	0	194	194	144	158
SI011	m	S	255	255	197	205	155	159	125	125	176	180	236	236	152	152	133	141	177	177	201	205	167	167	242	242	194	194	0	0
SI012	f	S	255	255	205	209	155	159	121	125	180	184	232	236	144	152	133	137	165	169	201	201	171	171	234	238	194	194	144	148
SI013	f	S	251	255	201	205	159	159	125	125	180	180	232	244	156	156	137	137	165	177	201	205	167	167	234	246	194	202	156	156
SI014	m	S	251	251	197	205	159	159	125	125	184	184	232	240	152	156	137	141	177	181	201	201	171	171	238	242	194	194	144	154
SI015	m	S	251	251	197	205	159	163	125	125	184	184	232	240	152	156	137	141	177	181	201	201	167	167	238	242	194	194	152	158
SI016	f	S	255	255	197	205	155	159	125	125	188	188	232	236	152	152	137	137	173	177	201	201	167	167	238	242	194	194	152	156
SI017	f	S	251	255	205	205	159	163	125	125	180	184	232	236	152	156	137	137	173	177	201	201	167	171	230	238	194	194	154	158
SI018	m	S	255	255	197	205	159	163	125	125	184	184	240	244	152	152	133	137	169	169	201	201	171	175	238	242	194	198	144	156
SI019	m	S	251	255	205	205	163	163	125	125	180	184	236	240	148	152	137	137	173	177	201	201	167	167	226	230	194	194	148	158
SI020	m	S	251	255	205	205	159	163	125	125	180	184	232	236	152	156	137	137	177	177	201	201	167	167	226	238	194	194	148	158
SI021	m	S	251	255	197	205	155	159	125	129	184	188	236	236	152	152	133	137	169	177	201	201	167	171	226	238	194	194	156	156
SI022	m	S	251	255	193	205	159	163	125	125	184	184	232	236	152	156	137	141	173	177	201	201	167	171	226	242	194	194	154	158
SI023	m	S	251	255	201	205	155	159	125	129	184	184	232	240	156	156	137	137	169	173	201	205	171	171	230	238	194	202	0	0
SI024	f	S	251	255	197	205	159	159	125	129	180	188	232	240	148	152	141	141	177	181	201	205	167	171	230	242	194	194	144	156
SI025	m	S	255	255	197	205	159	163	129	129	180	180	232	244	152	156	137	141	169	177	201	205	175	175	230	230	194	202	156	156
SI026	m	S	255	255	205	205	155	159	125	125	184	184	232	232	156	156	137	141	169	173	205	209	167	171	230	230	194	202	156	156
SI028	f	S	251	255	197	205	155	159	125	129	180	184	232	232	152	160	137	141	165	181	201	201	167	171	234	238	194	202	152	154
SI029	m	S	251	255	197	205	155	155	125	125	180	184	232	240	156	160	137	141	165	181	201	201	171	171	234	242	202	202	152	156
SI030	f	S	251	255	205	205	155	163	125	125	176	180	240	244	152	152	137	141	169	169	201	205	171	175	238	238	194	202	144	158
SI031	m	S	251	255	197	205	155	155	125	125	180	184	232	240	156	160	137	141	165	181	201	205	171	171	230	238	194	202	152	156
SI032	m	S	251	251	201	205	155	155	125	129	180	184	236	240	152	160	137	141	165	181	201	201	167	175	230	234	202	202	156	158
SI033	f	S	255	255	197	205	155	163	125	125	184	184	232	236	152	152	137	141	165	173	201	201	171	171	230	242	194	202	154	154
SI034	f	S	251	255	197	205	159	163	125	125	180	184	232	236	152	156	137	137	173	177	201	205	167	167	226	238	194	194	148	152
SI035	f	S	251	255	197	205	147	163	125	129	180	184	236	240	152	152	137	141	173	177	201	201	167	171	230	230	194	194	156	158

Ego	Sex	Pop	D2S1326		D3S1768		D4S243		D5S1457		D6S501		D7S2204		D8S1106		D10s611		D12S375		D13S765		D14S306		D21S1442		D3S1766		D7S503	
SI036	m	S	251	251	197	205	151	159	121	125	184	184	236	244	156	156	133	137	173	177	201	201	171	171	230	230	194	198	148	156
SI037	m	S	255	255	205	205	147	159	125	129	180	184	232	232	152	156	137	137	169	177	201	205	167	167	230	238	194	202	156	158
SI038	m	S	255	255	197	205	147	159	125	125	180	184	236	240	152	156	137	141	169	177	201	205	167	175	230	238	194	202	156	156
SI039	m	S	251	251	205	205	155	159	125	125	180	180	232	240	152	152	133	137	169	181	205	209	167	167	230	234	194	202	156	158
SI040	m	S	255	255	205	205	159	163	121	125	180	184	236	240	152	156	137	141	173	173	201	205	167	171	230	234	194	202	144	156
SI041	m	S	251	251	205	205	155	159	125	125	180	184	232	240	152	156	133	141	169	177	201	205	167	167	230	234	194	202	144	156
SI042	m	S	255	259	197	205	159	163	125	129	180	184	236	240	152	156	137	137	173	173	201	205	167	171	234	238	194	202	144	156
SI043	f	S	255	255	205	205	159	163	121	125	176	180	240	244	152	156	137	137	173	173	201	201	171	171	230	242	194	194	144	156
SI044	m	S	251	255	205	205	159	167	125	129	180	184	232	240	152	156	133	137	173	177	205	205	171	171	230	230	194	194	158	158
SI045	f	S	251	251	197	205	159	159	125	125	180	184	232	232	152	156	133	137	169	173	201	201	167	175	230	238	198	202	144	148
SI046	m	S	255	255	197	197	159	163	125	129	180	184	232	240	152	152	137	137	173	173	201	201	167	167	230	230	194	194	156	158
SI047	m	S	255	255	197	205	155	159	125	125	176	176	244	244	152	152	137	141	169	169	201	209	167	175	230	242	194	202	144	158
SI048	f	S	255	255	197	205	159	159	125	125	180	184	232	236	152	156	141	141	173	177	201	201	167	171	226	242	194	194	148	148
SI049	f	S	251	255	197	205	159	163	125	125	184	184	236	240	152	152	137	141	177	177	201	201	171	171	230	242	194	194	148	158
SI050	m	S	251	255	205	205	159	163	125	129	180	184	236	240	152	152	141	141	169	177	201	205	167	171	226	226	194	202	148	156
SI051	f	S	255	255	197	209	155	159	125	129	184	188	232	240	152	152	137	141	169	177	201	201	167	175	238	238	194	202	154	156
SI052	f	S	251	255	205	205	155	159	0	0	176	184	232	236	152	152	141	141	177	181	201	201	167	171	230	242	194	194	154	156
SI053	m	S	251	255	205	209	155	159	125	129	176	188	232	240	152	152	137	141	177	181	201	205	167	171	238	238	194	194	154	154
SI054	f	S	251	255	205	205	155	163	125	129	180	184	232	240	148	152	137	141	177	177	201	205	167	171	230	238	194	202	154	158
SI055	f	S	255	255	197	205	155	163	125	125	180	188	232	240	152	152	141	141	169	177	201	205	167	175	238	242	194	194	156	156
SI056	f	S	251	255	205	205	155	163	125	129	180	184	240	240	148	152	137	141	169	177	201	205	167	167	230	242	194	194	154	156
SI057	f	S	251	255	205	205	159	159	125	125	184	188	232	240	152	152	137	141	173	181	201	201	167	171	242	242	194	194	154	156
SI058	m	S	251	255	201	205	155	159	125	125	176	184	232	240	156	156	129	137	169	173	201	205	171	171	230	230	202	202	156	156
SI059	m	S	251	255	197	205	155	155	125	129	180	184	232	240	156	160	133	141	165	181	201	201	171	171	234	242	202	202	152	156
SI060	f	S	255	255	197	205	155	155	125	129	176	184	232	240	152	156	137	137	173	177	201	201	171	175	230	242	202	202	156	156
SI061	m	S	251	255	205	205	163	163	125	129	180	180	232	244	152	152	137	137	169	177	201	205	175	175	230	238	194	202	156	158
SI062	f	S	251	255	197	205	155	159	125	125	180	188	232	240	148	152	137	141	177	181	201	205	167	171	230	242	194	194	144	156
SI063	f	S	251	255	205	209	159	163	125	129	176	176	240	240	152	152	137	137	169	177	201	205	171	171	0	0	194	202	144	156
SI064	f	S	251	255	205	205	159	159	125	129	180	184	232	240	156	156	137	141	169	181	201	205	171	171	230	242	194	194	156	158
SI065	m	S	255	255	197	205	159	163	125	125	180	184	232	240	152	156	137	141	169	173	201	201	167	171	238	242	194	194	154	158
SI066	m	S	251	255	205	209	159	163	125	125	176	180	236	244	152	156	137	137	169	173	201	205	167	171	238	242	194	194	144	156
SI067	m	S	251	255	205	205	155	155	125	125	180	180	236	236	152	152	137	141	177	177	201	205	167	167	230	242	194	194	154	156
SI068	f	S	239	251	205	205	159	163	125	125	184	184	240	240	152	152	137	141	169	173	205	205	167	171	230	230	194	194	144	156
SI069	m	S	255	255	201	201	155	159	125	129	180	184	232	236	152	156	137	141	177	181	201	209	167	171	234	238	194	194	156	156
SI070	f	S	251	255	205	205	159	163	125	129	180	184	236	240	152	152	137	137	169	177	201	201	167	171	230	242	194	202	144	154
SI071	m	S	255	255	205	205	155	163	125	129	180	184	240	240	152	152	137	141	165	181	205	205	167	167	230	238	194	194	156	158
SI072	f	S	255	255	205	209	155	159	125	125	176	180	236	244	152	156	137	141	165	169	201	201	167	167	230	238	194	194	144	154
SI073	f	S	251	255	197	205	159	163	125	129	180	180	232	244	152	152	137	141	173	173	201	201	167	167	230	234	194	194	148	158
SI074	f	S	247	251	205	209	159	163	125	125	180	184	244	244	148	156	137	141	165	181	201	201	167	175	230	242	194	194	144	158
SI076	f	S	255	255	197	205	155	159	125	129	180	184	232	232	152	156	137	141	173	177	205	205	167	171	230	246	194	194	144	156
SI077	m	S	251	255	197	209	155	163	125	129	176	184	236	240	152	156	137	137	169	169	201	201	167	167	230	234	194	194	148	156
SI078	m	S	255	255	205	205	155	159	125	125	180	180	240	248	152	156	137	137	169	177	201	201	167	167	230	238	194	194	156	156
SI079	m	S	255	255	205	205	159	163	0	0	176	188	232	232	152	152	133	137	173	173	201	209	167	171	238	246	194	194	156	158
SI080	m	S	251	255	197	205	155	159	125	125	184	188	236	236	152	152	137	137	169	177	201	201	167	167	226	238	194	194	156	156
SI081	m	S	251	259	205	205	159	163	125	125	180	184	232	236	152	156	137	141	177	177	201	201	167	167	226	238	194	194	148	158

Ego	Sex	Pop	D2S1326		D3S1768		D4S243		D5S1457		D6S501		D7S2204		D8S1106		D10s611		D12S375		D13S765		D14S306		D21S1442		D3S1766		D7S503	
SI082	m	S	251	255	205	205	155	159	125	129	180	180	232	240	152	160	133	137	177	181	201	201	171	175	234	242	194	202	154	158
SI083	m	S	251	255	205	205	155	159	129	129	180	180	232	240	152	160	137	137	177	181	201	201	171	175	234	242	194	202	154	158
SI084	f	S	251	255	205	205	155	163	125	125	180	180	236	244	152	156	137	137	169	181	201	205	171	171	238	242	202	202	156	158
SI085	m	S	251	255	205	205	159	163	129	133	184	188	236	240	152	152	137	141	169	177	201	205	167	167	238	242	194	202	154	156
SI086	f	S	255	259	205	205	155	159	125	129	176	184	232	236	152	156	137	137	169	177	201	205	167	171	230	230	194	194	144	148
SI087	f	S	251	255	205	209	159	167	125	129	180	184	236	240	152	152	141	141	177	181	201	201	167	167	230	230	194	194	144	148
SI088	m	S	255	255	201	205	159	163	125	125	180	184	232	236	152	152	137	137	177	181	197	201	167	167	238	238	194	194	156	158
SI089	m	S	255	255	197	205	155	155	125	129	176	184	236	240	152	156	137	141	165	165	201	201	163	167	234	242	194	194	144	158
SI090	f	S	251	255	205	205	159	159	125	125	176	184	236	248	152	156	137	141	169	169	201	205	163	175	230	230	194	194	154	158
SI091	m	S	251	255	201	205	155	159	125	129	180	184	236	240	152	152	137	141	177	181	201	205	167	171	230	238	194	194	144	158
SI092	f	S	255	255	201	205	159	163	125	125	180	184	232	236	152	156	137	137	177	181	197	201	167	171	238	238	194	194	156	158
SI093	m	S	255	255	197	205	155	155	125	125	176	184	236	248	152	156	137	141	165	165	201	201	163	167	242	242	194	194	144	158
SI094	m	S	251	255	197	205	159	167	125	129	188	188	232	240	152	152	137	141	169	169	201	205	167	167	230	230	194	194	156	156
SI095	f	S	251	255	205	209	167	167	125	125	184	188	232	244	156	156	137	141	169	181	201	205	167	167	230	238	194	194	144	156
SI096	m	S	251	255	197	205	155	159	125	129	188	188	240	240	152	152	133	137	169	173	205	205	167	167	238	242	194	202	156	156
SI097	m	S	251	251	197	209	159	167	125	125	184	188	232	240	152	156	137	137	169	181	201	205	167	167	238	242	194	194	144	156
SI099	m	S	255	255	205	205	159	159	125	125	176	180	232	236	152	156	137	141	169	181	201	209	167	167	230	238	194	202	156	158
SI100	f	S	255	255	197	205	155	159	125	125	184	188	240	240	152	156	137	141	165	173	201	205	167	167	230	242	194	194	144	148
SI101	m	S	251	255	205	209	155	163	125	125	180	188	236	244	152	156	137	141	169	177	201	201	167	167	230	238	194	194	144	156
SI102	m	S	255	255	197	205	159	163	125	125	184	184	236	240	152	156	137	141	169	173	201	201	167	171	230	242	194	194	144	144
SI103	m	S	255	255	197	209	155	163	125	125	180	184	232	240	152	152	137	137	177	177	205	209	167	175	238	238	194	202	144	150
SI104	m	S	251	263	197	209	159	163	129	129	184	184	232	240	152	152	137	137	165	181	205	209	167	171	238	238	194	202	144	144
SI105	f	S	255	255	197	205	155	159	125	129	180	184	240	240	152	152	137	141	169	173	205	205	167	171	234	238	194	194	144	150
SI106	m	S	251	255	205	205	155	159	121	125	184	184	236	240	152	152	133	137	173	177	201	205	163	171	230	238	194	194	144	158
SI107	m	S	251	255	205	205	159	167	125	129	180	188	232	232	144	152	133	137	173	177	201	205	167	171	234	238	202	202	154	156
SI108	m	S	255	263	205	209	159	159	125	125	180	180	244	244	144	152	137	137	165	173	205	213	171	171	230	238	194	194	150	150
SI109	m	S	255	255	205	205	155	163	125	125	176	180	236	244	152	156	137	137	173	173	201	205	167	167	230	238	194	194	144	156
SI110	m	S	251	255	205	205	159	163	125	125	184	184	236	240	152	152	137	137	169	177	201	205	167	171	226	226	194	202	148	156
SI111	m	S	251	255	197	205	159	163	125	125	180	184	236	240	152	152	137	137	173	177	201	201	167	171	230	238	194	194	148	158
SI112	f	S	255	255	197	205	159	163	125	125	184	188	232	240	152	152	137	141	173	181	201	205	167	171	238	242	194	194	152	156

Table 2.SV: Population genetic parameters of different baboon taxa

Taxon	Location	H_E	F_{ST}	F_{IS}	Relatedness	Reference
P. papio	Niokolo-Koba,Senegal	0.60	0.025-0.085	-0.068	♀ =♂=0	this study
	Guinea-Bissau	0.43	/	/	/	(Ferreira da Silva 2012)
P. cynocephalus	Tana River,Kenya; Mikumi, Tanzania	0.73-0.79	0.069	/	/	(St George *et al*. 1998)
	Mikumi, Tanzania	/	0.022	-0.030	♀ >0 w/in ♀ <0 among ♂>0 w/in	(Vinson 2005)
	Amboseli, Kenya	/	/	/	♀ >♂	(Altmann 1996)]
	Zambia	0.65-0.70	0.020	0.086	/	(Burrell 2008)
P. ursinus	Tsaobis, Namibia	0.50-0.80	0.044	-0.065	/	(Huchard *et al*. 2010)
P. u. griseipes	Zambia	0.56-0.72	0.022	0.053	/	(Burrell 2008)
P. kindae	Zambia	0.75	0.033	0.027	/	(Burrell 2008)
P. hamadryas	Arabia	/	0.148	0.037	/	(Hammond *et al*. 2006)
	Awash, Ethopia	0.68	0.016	0.163	high	(Woolley-Barker 1999)
P. hamadryas x anubis	Awash, Ethopia	0.63-0.72	0.026-0.029	-0.022-0.162	low	(Woolley-Barker 1999)
P. anubis	Awash, Ethopia	0.68	0.035	0.071	♀ >♂	(Woolley-Barker 1999)
	Gombe	/	/	-0.040	♀ =0 ♂<0	(Vinson 2005)

Supplementary material, Chapter III

Table 3.SI: Sampling sites and number of samples collected.

Sitecode	Sampling site	Country	Region (AMOVA)	Longitude	Latitude	Number of samples	Taxon	Collector	GenBank Accession Nr.
Aba	Arborobo	Eritrea	Ph1	39.01862	15.34910	14	*P.h.*	D.Zinner	AF275397-410
Abd	Abdur	Eritrea	Ph2	39.84585	15.12857	11	*P.h.*	D.Zinner	AF275411-21
Afb	Afabet	Eritrea	Ph1	38.74958	16.12012	3	*P.h.*	D.Zinner	KF693023-5
Bbr	Barka Bridge	Eritrea	Ph3	38.02038	15.55512	7	*P.h.*	D.Zinner	AF275445-51
Bea	Baeat	Eritrea	Ph3	38.09427	15.67157	2	*P.h.*	D.Zinner	KF692967-8
Dad	Dada	Eritrea	Ph6	42.35120	13.11402	11	*P.h.*	D.Berhane	KF693088-98
Deb	Debresina	Eritrea	Ph1	38.82593	15.70535	3	*P.h.*	D.Zinner	AF275428-30
Dog	Dogali	Eritrea	Ph1	39.28473	15.57908	6	*P.h.*	D.Zinner	AF275422-7
Dur	Durfo	Eritrea	Ph1	38.96458	15.37370	7	*P.h.*	D.Zinner	AF275393-6
Fil	Filfil	Eritrea	Ph1	38.94445	15.61442	6	*P.h.*	D.Zinner	KF692995-3000
Fur	Furrus	Eritrea	Ph1	38.97115	15.01148	9	*P.h.*	D.Zinner	AF275384-92
Gel	Geleb	Eritrea	Ph1	38.82407	15.82143	7	*P.h.*	D.Zinner	AF275431-7
Hal	Halhal	Eritrea	Ph3	38.31433	15.94137	7	*P.h.*	D.Zinner	KF692988-94
Him	Af Himbol	Eritrea	Ph4	37.39710	15.94505	9	*P.h.*	D.Zinner	KF692975-83
Kub	Kubkub	Eritrea	Ph1	38.63217	16.34482	11	*P.h.*	D.Zinner	AF275452-7; KF692969-73
Men	Mensura	Eritrea	Ph3	38.35123	15.44598	5	*P.h.*	D.Zinner	KF692974; KF692984-7
Mol	Molki	Eritrea	Ph5	38.22170	14.90908	7	*P.h.*	D.Zinner	AF275438-AF275444
ASt	Awash Station	Ethiopia	Ph7	40.17775	8.99269	5	*P.h.*	D.Zinner	KF693001-5
Ger	Gerba Luku/Erer Gota	Ethiopia	Ph9	41.53400	9.58740	10	*P.h.*	D.Zinner	KF693006-15
Mie	Mieso	Ethiopia	Ph8	40.76408	9.20353	7	*P.h.*	D.Zinner	KF693016-22
Abh	Abha	Saudi Arabia	Ph10	42.50523	18.21639	25	*P.h.*	KKWRC	AY247444-7; AY247453; AY247459-60; KF693026-43
Akl	Al Akhal	Saudi Arabia	Ph11	39.85944	23.31556	6	*P.h.*	KKWRC	AY247547-8; KF693044-7

Sitecode	Sampling site	Country	Region (AMOVA)	Longitude	Latitude	Number of samples	Taxon	Collector	GenBank Accession Nr.
Bah	Baha	Saudi Arabia	Ph12	41.46667	20.01667	15	*P.h.*	KKWRC	AY247530; KF693048-61
Dhi	Dhilafa Escp.	Saudi Arabia	Ph10	42.46667	17.93333	4	*P.h.*	K.Nasher	KF693075-8
Tif	Taif	Saudi Arabia	Ph13	40.41583	21.27028	15	*P.h.*	KKWRC	AY247533-4; KF693062-74
BuH	Bura'a Forest, Hodaidah A	Yemen	Ph14	43.41667	14.86667	4	*P.h.*	K.Nasher	KF693079-82
BuL	Bura'a Forest, Hodaidah B	Yemen	Ph15	43.86694	14.86722	5	*P.h.*	K.Nasher	KF693083-7
Bak	Bakaria	Guinea	Pp11	-10.31542	10.54267	16	*P. p.*	M.C.Huynen	KF692711-26
DB	Diara Baka	Guinea	Pp14	-14.11705	11.05829	1	*P. p.*	G.H.Kopp	KF692801
Kou	Kouroukorodgi	Guinea	Pp11	-10.07305	10.43605	8	*P. p.*	M.C.Huynen	KF692753-60
LN	Lenjele	Guinea	Pp10	-11.83477	10.40548	3	*P. p.*	G.H.Kopp	KF692857-9
LY	Leysere	Guinea	Pp10	-11.26792	10.20729	4	*P. p.*	G.H.Kopp	KF692860-3
Mar	Mare	Guinea	Pp11	-10.33702	10.50143	10	*P. p.*	M.C.Huynen	KF692727-36
NT	Nienta	Guinea	Pp9	-9.63293	12.10501	3	*P. p.*	G.H.Kopp	KF692890-2
SO	Soyah	Guinea	Pp10	-11.96087	10.27998	2	*P. p.*	G.H.Kopp	KF692916-7
Tam	Tambo	Guinea	Pp11	-10.29207	10.54283	10	*P. p.*	M.C.Huynen	KF692737-46
Woy	Woyumba	Guinea	Pp11	-10.41442	10.50847	6	*P. p.*	M.C.Huynen	KF692747-52
WS	Wasaba	Guinea	Pp11	-9.98602	10.00156	1	*P. p.*	G.H.Kopp	KF692922
AC	Amindara Catobo	Guinea-Bissau	Pp7	-14.97698	11.28059	8	*P. p.*	M.J.Ferreira Silva	KC312729-36
AI	Boé Aicum	Guinea-Bissau	Pp6	-13.93178	11.88762	11	*P. p.*	M.J.Ferreira Silva	KC312859-69
AM	Boé Aicum Montanha	Guinea-Bissau	Pp6	-13.87702	11.94172	6	*P. p.*	M.J.Ferreira Silva	KC312870-5
BBL	Boé Béli	Guinea-Bissau	Pp6	-13.95713	11.83922	6	*P. p.*	M.J.Ferreira Silva	KC312853-8
BC	Botchê Cule	Guinea-Bissau	Pp7	-15.00971	11.35542	10	*P. p.*	M.J.Ferreira Silva	KC312765-74
BU	Bubatchingue	Guinea-Bissau	Pp7	-15.09168	11.75010	20	*P. p.*	M.J.Ferreira Silva	KC312797-816
CA	Canamina	Guinea-Bissau	Pp7	-15.08817	11.15442	11	*P. p.*	M.J.Ferreira Silva	KC312786-96
CB	Cabedu	Guinea-Bissau	Pp7	-15.12815	11.11149	10	*P. p.*	M.J.Ferreira Silva	KC312737-46
CK	Bakar Conte	Guinea-Bissau	Pp7	-14.86451	11.69654	11	*P. p.*	M.J.Ferreira Silva	KC312817-28

Sitecode	Sampling site	Country	Region (AMOVA)	Longitude	Latitude	Number of samples	Taxon	Collector	GenBank Accession Nr.
CM	Cambeque	Guinea-Bissau	Pp7	-15.02566	11.17161	10	*P. p.*	M.J.Ferreira Silva	KC312751-60
CQ	Caiquene	Guinea-Bissau	Pp7	-15.10157	11.22527	4	*P. p.*	M.J.Ferreira Silva	KC312747-50
CT	Catomboi	Guinea-Bissau	Pp7	-15.05494	11.17154	11	*P. p.*	M.J.Ferreira Silva	KC312776-85
GB	Guembombol	Guinea-Bissau	Pp7	-15.09510	11.81303	5	*P. p.*	M.J.Ferreira Silva	KC312848-52
PG	Port Gandamael	Guinea-Bissau	Pp7	-14.90130	11.24092	18	*P. p.*	M.J.Ferreira Silva	KC312711-28
QS	Quebo Sutuba	Guinea-Bissau	Pp7	-14.91079	11.30911	4	*P. p.*	M.J.Ferreira Silva	KC312761-4
SS	Sr Soares	Guinea-Bissau	Pp7	-15.05308	11.58412	19	*P. p.*	M.J.Ferreira Silva	KC312829-47
BE	Berdo	Mali	Pp8	-9.19301	13.96921	1	*P. p.*	G.H.Kopp	KF692779
BR	Berber	Mali	Pp8	-8.82611	14.10676	4	*P. p.*	G.H.Kopp	KF692780-3
DD	Dorodounga	Mali	Pp8	-9.69587	13.61725	3	*P. p.*	G.H.Kopp	KF692802-4
KT	Kotifara	Mali	Pp8	-8.64568	13.39143	1	*P. p.*	G.H.Kopp	KF692839
MB	Mare Bendougou	Mali	Pp8	-8.79814	13.83853	3	*P. p.*	G.H.Kopp	KF692864-6
TT	Traverse de Tiko	Mali	Pp8	-8.50145	13.33944	1	*P. p.*	G.H.Kopp	KF692921
AF	Ain Farfara	Mauretania	Pp1	-12.16086	17.04272	2	*P. p.*	J.C.Brito	KF692761-2
AN	Aouînet Nanâga	Mauretania	Pp1	-12.19912	17.15248	2	*P. p.*	J.C.Brito	KF692774-5
GA	Guelta Galoûal	Mauretania	Pp1	-11.97107	16.33880	3	*P. p.*	J.C.Brito	KF692808-10
GU	Guelta Goumbel	Mauretania	Pp1	-12.00986	15.95708	3	*P. p.*	J.C.Brito	KF692826-8
LA	Laout	Mauretania	Pp1	-12.10167	17.24083	2	*P. p.*	J.C.Brito	KF692776-7
MU	Moudéri	Mauretania	Pp2	-12.56762	15.05263	7	*P. p.*	J.C.Brito	KF692867-73
MY	Guelta Meyla	Mauretania	Pp1	-11.87175	16.00255	1	*P. p.*	J.C.Brito	KF692874
OI	Oumm Icheglâne	Mauretania	Pp1	-12.20785	17.07030	2	*P. p.*	J.C.Brito	KF692763-4
TS	Trig Seiouaddé	Mauretania	Pp1	-11.95168	16.82082	2	*P. p.*	J.C.Brito	F692772-3
Ass	Mont Assirik	Senegal	Pp3	-12.76667	12.88333	2	*P. p.*	K.Hammerschmidt	KF692770-1
BD	Badi	Senegal	Pp3	-13.22282	13.14267	1	*P. p.*	G.H.Kopp	KF692778
CL	Camp du Lion	Senegal	Pp3	-13.23463	13.02820	17	*P. p.*	G.H.Kopp	KF692784-800
DL	Dalaba	Senegal	Pp3	-13.26691	12.75181	1	*P. p.*	G.H.Kopp	KF692805

Sitecode	Sampling site	Country	Region (AMOVA)	Longitude	Latitude	Number of samples	Taxon	Collector	GenBank Accession Nr.
DN	Dienoundiala	Senegal	Pp3	-13.01620	13.17205	2	*P. p.*	G.H.Kopp	KF692806-7
GD/GGD	Gue Damantan	Senegal	Pp3	-13.31968	13.04499	10	*P. p.*	G.H.Kopp	KF692811-20
GM	Gamon	Senegal	Pp3	-12.86736	13.35923	5	*P. p.*	G.H.Kopp	KF692821-5
KB	Koussan Barrage	Senegal	Pp2	-12.42742	14.11863	2	*P. p.*	G.H.Kopp	KF692829-30
Ked	Kedougou	Senegal	Pp4	-12.12472	12.57556	5	*P. p.*	K.Hammerschmidt	KF692765-9
KF	Kayanga Forêt classée	Senegal	Pp5	-13.94963	12.88990	5	*P. p.*	G.H.Kopp	KF692831-5
KN	Kidira Nord	Senegal	Pp2	-12.32751	14.63811	3	*P. p.*	G.H.Kopp	KF692836-8
KY	Kayanga	Senegal	Pp5	-14.06561	12.84416	7	*P. p.*	G.H.Kopp	KF692840-6
LK	Lingue Kountou	Senegal	Pp3	-13.08025	13.03378	10	*P. p.*	G.H.Kopp	KF692847-56
NJ	Nafadji	Senegal	Pp4	-11.55947	12.65923	4	*P. p.*	G.H.Kopp	KF692875-8
NK	Niokolo	Senegal	Pp3	-12.72078	13.07348	9	*P. p.*	G.H.Kopp	KF692879-87
NS	Niokolo Sud	Senegal	Pp3	-12.63451	13.03531	2	*P. p.*	G.H.Kopp	KF692888-9
SF	Sinthiou Fissa	Senegal	Pp2	-12.34977	14.38698	1	*P. p.*	G.H.Kopp	KF692893
SI	Simenti	Senegal	Pp3	-13.29485	13.02626	22	*P. p.*	G.H.Kopp	KF692894-915
SY	Samba Yaye	Senegal	Pp2	-12.20762	14.00541	1	*P. p.*	G.H.Kopp	KF692918
TF	Tacoutala Faleme	Senegal	Pp2	-12.19996	14.13581	2	*P. p.*	G.H.Kopp	KF692919-20
Pil	Pilanesberg Game Reserve	South Africa	Pu1	26.87805	-25.11111	4	*P. u.*	K.Slater	KF692923-6
Bly	Blyde River, Blyde-poort	South Africa	Pu3	30.78049	-24.66667	5	*P. u.*	K.Slater	KF692927-31
Swa	Blyde River, Swadini	South Africa	Pu3	30.79000	-24.68000	4	*P. u.*	K.Slater	KF692932-5
Hop	DeHoop Nature Reserve	South Africa	Pu12	20.40658	-34.45621	5	*P. u.*	D.Zinner	KF692936-40
Los	Loskop Nature Reserve	South Africa	Pu2	29.28162	-25.42147	4	*P. u.*	D.Zinner	KF692941-4
Hak	Hakos Gästefarm	Namibia	Pu9	16.36463	-23.23708	2	*P. u.*	Y.Warren	KF692945-6
Wat	Waterburg Plateau	Namibia	Pu10	17.24221	-20.50450	4	*P. u.*	Y.Warren	KF692947-50

Sitecode	Sampling site	Country	Region (AMOVA)	Longitude	Latitude	Number of samples	Taxon	Collector	GenBank Accession Nr.
Sp1	Namib Spreetshoogte 1	Namibia	Pu9	16.20160	-23.73322	1	*P. u.*	Y.Warren	KF692951
Sp2	Namib Spreetshoogte 1	Namibia	Pu9	16.20555	-23.64758	2	*P. u.*	Y.Warren	KF692952-3
Mor	Moremi Wildlife Reserve	Botswana	Pu5	23.00000	-19.18349	5	*P. u.*	J.Fischer	KF692954-8
Kru	Krüger National Park	South Africa	Pu4	31.70000	-25.00000	2	*P. u.*	C.Scheid	KF692959-60
Bin	Bindura	Zimbabwe	Pu13	31.63793	-13.26840	1	*P. u.*	C.Katsvanga	KF692961
Nya	Nyanga	Zimbabwe	Pu7	32.81283	-19.05781	1	*P. u.*	C.Katsvanga	KF692962
Vum	Vumba	Zimbabwe	Pu8	32.66133	-18.52769	1	*P. u.*	C.Katsvanga	KF692963
Gor	Gorongosa National Park	Mozambique	Pu11	34.36111	-18.97833	1	*P. u.*	M.Metz	KF692964
Oka	Okasewa Ranch	Namibia	Pu6	18.34910	-22.41203	1	*P. u.*	C.Keller	KF692965
Lub	Sera Leba, Luban-go	Angola	Pu14	13.24167	-15.14167	1	*P. u.*	C.Smida	KF692966
Hay	Haykota, Ruba Gash	Eritrea	Pa1	37.06600	15.15695	17	*P. a.*	H.Shoshani, D.Berhane, D.Zinner	AF275458-69; KF693146-50
Tes	Tesseney, Ruba Gash	Eritrea	Pa1	36.70142	15.14510	9	*P. a.*	D.Berhane, D.Zinner	AF275470-5; KF693129-31
KoN	Komoe North	Ivory Coast	Pa15	-3.79000	8.80000	6	*P. a.*	B.Kunz	KF693099-104
KoS	Komoe south	Ivory Coast	Pa15	-3.82000	8.74750	4	*P. a.*	B.Kunz	KF693105-8
Kwa	Kwano	Nigeria	Pa13	11.58333	7.31667	5	*P. a.*	J.Bovensiepen	KF693109-13
Gas	Gashaka Crop Raiding Gr.	Nigeria	Pa13	11.50000	7.35000	10	*P. a.*	J.Bovensiepen, Y.Warren	KF693114; KF693116-24
Mng	Managascha	Ethiopia	Pa4	38.58333	9.08333	1	*P. a.*	Museum König, Bonn/D.Zinner	KF693115
Sha	Shakata, Ruba	Eritrea	Pa2	37.49935	14.98310	4	*P. a.*	D.Zinner	KF693125-8
Gri	Griset, Ruba	Eritrea	Pa1	36.76018	14.88322	8	*P. a.*	D.Zinner	KF693132-9
Had	Hadejemi, Ruba Setit	Eritrea	Pa3	36.90710	14.35827	6	*P. a.*	D.Zinner	KF693140-5

Sitecode	Sampling site	Country	Region (AMOVA)	Longitude	Latitude	Number of samples	Taxon	Collector	GenBank Accession Nr.
Ngo	Ngorongoro	Tanzania	Pa11	35.59039	-3.28206	5	*P. a.*	H.Hofer	KF693151-5
Ada	Adami Tulu	Ethiopia	Pa5	38.71493	7.82558	5	*P. a.*	D.Zinner	KF693156-60
Ala	Alambada	Ethiopia	Pa5	38.74768	7.50463	3	*P. a.*	D.Zinner	KF693161-3
Wen	Wendo Genet	Ethiopia	Pa6	38.64965	7.07127	4	*P. a.*	D.Zinner	KF693164-7
Man	Managasha National Park	Ethiopia	Pa4	38.57125	8.96838	6	*P. a.*	D.Zinner	KF693168-73
Sr1	Serengeti 1	Tanzania	Pa10	34.85236	-2.43100	3	*P. a.*	M.East	KF693174; KF693177-8
Nr1	Serengeti Nir	Tanzania	Pa10	34.79355	-2.42233	1	*P. a.*	M.East	KF693175
Nr2	Seronera River	Tanzania	Pa10	34.80128	-2.42647	1	*P. a.*	M.East	KF693176
Sr2	Serengeti 2	Tanzania	Pa10	34.85567	-2.42614	3	*P. a.*	M.East	KF693179-81
Kb1	Kibale Forest 1	Uganda	Pa9	30.43333	0.51667	3	*P. a.*	S.Telen	KF693182-4
Kb2	Kibale Forest 2	Uganda	Pa9	30.40000	0.48333	3	*P. a.*	S.Telen	KF693185-7
sBu	South Bukavu	DRC	Pa12	28.91092	-2.68258	2	*P. a.*	A.Basabose	KF693188-9
Kur	Kura (Plateau State) NB	Nigeria	Pa14	9.26667	9.91667	1	*P. a.*	U.Buba	KF693190
Har	Harenna 2	Ethiopia	Pa7	39.73718	6.61577	1	*P. a.*	S.Doeschner	KF693191
ArP	Archers Post	Kenya	Pa8	37.67356	0.62466	1	*P. a.*	D.Oettinghaus	KF693192
Mic	Michiru MountainsCons. A1	Malawi	Pc1	34.91667	-15.75000	2	*P. c.*	K.Lorenz	KF693193-4
LCr	JB, Liwonde National Park	Malawi	Pc3	35.33333	-14.86667	2	*P. c.*	K.Lorenz	KF693195-6
LNb	Liwonde National Park	Malawi	Pc3	35.30000	-14.96667	5	*P. c.*	K.Lorenz	KF693197-201
Mu1	Mulanje Mt. 1	Malawi	Pc2	35.50000	-15.96667	1	*P. c.*	K.Lorenz	KF693202
Mu2	Mulanje Mt. 2	Malawi	Pc2	35.51667	-15.95000	1	*P. c.*	K.Lorenz	KF693203
LCh	Liwonde National Park	Malawi	Pc3	35.25000	-15.03333	5	*P. c.*	K.Lorenz	KF693204-8
Ruk	Lake Rukwa	Tanzania	Pc5	32.15517	-7.582967	1	*P. c.*	Humboldt Museum Berlin/D.Zinner	KF693209
LuS	South Luangwa NP	Zambia	Pc4	31.637933	-13.26840	4	*P. c.*	O.Behlert	KF693210-3

Sitecode	Sampling site	Country	Region (AMOVA)	Longitude	Latitude	Number of samples	Taxon	Collector	GenBank Accession Nr.
Web	Webi Shebelli	Somalia	Pc8	45.43333	2.42083	1	*P. c.*	Zool. Sammlung München/D.Zinner	KF693214
Dia	Diani Beach	Kenya	Pc6	39.55000	-4.32000	1	*P. c.*	A.Bauer	KF693215
Amb	Amboseli	Kenya	Pc7	37.39000	-2.29000	1	*P. c.*	K.Hammerschmidt	KF693216

P.h.=Papio hamadryas, *P.p.=Papio papio*, *P.u.=Papio ursinus*, *P.a.=Papio anubis*, *P.c.=Papio cynocephalus;* KKWRC=King Khalid Wildlife Research Center, Saudi Arabia.

Supplementary material, Chapter V

Table 5.SI: Origin, haplotype and NCBI GenBank accession numbers of baboon samples included in genetic analyses.

No.	ID	Site	Code	Country	Taxon	Source	Haplotype	GenBank dloop	GenBank Cyt b	GenBank Brown
1	Abh024**	Abha	Abh	ARA	Ph	KKWRC	59	AY247447	KM267380	KM267452
2	Abh030**	Abha	Abh	ARA	Ph	KKWRC	67	KF693027	KM267381	KM267453
3	Abh070**	Abha	Abh	ARA	Ph	KKWRC	36	KF693037	KM267386	KM267458
4	Abh088**	Abha	Abh	ARA	Ph	KKWRC	38	KF693041	KM267388	KM267460
5	Abh021	Abha	Abh	ARA	Ph	KKWRC	67	AY247444		
6	Abh022	Abha	Abh	ARA	Ph	KKWRC	67	AY247445		
7	Abh023	Abha	Abh	ARA	Ph	KKWRC	35	AY247446		
8	Abh027	Abha	Abh	ARA	Ph	KKWRC	67	KF693026		
9	Abh031	Abha	Abh	ARA	Ph	KKWRC	64	AY247453		
10	Abh041	Abha	Abh	ARA	Ph	KKWRC	36	KF693028		
11	Abh046**	Abha	Abh	ARA	Ph	KKWRC	70	KF693029	KM267382	KM267454
12	Abh049	Abha	Abh	ARA	Ph	KKWRC	67	KF693030		
13	Abh050	Abha	Abh	ARA	Ph	KKWRC	36	AY247459		
14	Abh051	Abha	Abh	ARA	Ph	KKWRC	67	AY247460		
15	Abh055*	Abha	Abh	ARA	Ph	KKWRC	67	KF693031	KM267383	KM267455
16	Abh056	Abha	Abh	ARA	Ph	KKWRC	73	KF693032		
17	Abh060	Abha	Abh	ARA	Ph	KKWRC	67	KF693033		
18	Abh063	Abha	Abh	ARA	Ph	KKWRC	61	KF693034		
19	Abh065*	Abha	Abh	ARA	Ph	KKWRC	38	KF693035	KM267384	KM267456
20	Abh068**	Abha	Abh	ARA	Ph	KKWRC	58	KF693036	KM267385	KM267457
21	Abh078	Abha	Abh	ARA	Ph	KKWRC	67	KF693038		
22	Abh085	Abha	Abh	ARA	Ph	KKWRC	67	KF693039		
23	Abh086*	Abha	Abh	ARA	Ph	KKWRC	67	KF693040	KM267387	KM267459
24	Abh094	Abha	Abh	ARA	Ph	KKWRC	36	KF693042		
25	Abh095	Abha	Abh	ARA	Ph	KKWRC	71	KF693043		
26	Akl001**	Al Akhal	Akl	ARA	Ph	KKWRC	67	KF693044	KM267389	KM267461
27	Akl002**	Al Akhal	Akl	ARA	Ph	KKWRC	71	AY247547	KM267390	KM267462
28	Akl003	Al Akhal	Akl	ARA	Ph	KKWRC	71	AY247548		
29	Akl004**	Al Akhal	Akl	ARA	Ph	KKWRC	68	KF693045	KM267391	KM267463
30	Akl005*	Al Akhal	Akl	ARA	Ph	KKWRC	71	KF693046	KM267392	KM267464
31	Akl006	Al Akhal	Akl	ARA	Ph	KKWRC	58	KF693047		
32	Bah005**	Baha	Bah	ARA	Ph	KKWRC	72	KF693051	KM267395	KM267467
33	Bah014**	Baha	Bah	ARA	Ph	KKWRC	53	KF693056	KM267398	KM267470
34	Bah002	Baha	Bah	ARA	Ph	KKWRC	58	KF693048		
35	Bah003*	Baha	Bah	ARA	Ph	KKWRC	72	KF693049	KM267393	KM267465
36	Bah004**	Baha	Bah	ARA	Ph	KKWRC	66	KF693050	KM267394	KM267466
37	Bah006	Baha	Bah	ARA	Ph	KKWRC	69	KF693052		
38	Bah009*	Baha	Bah	ARA	Ph	KKWRC	67	KF693053	KM267396	KM267468
39	Bah010	Baha	Bah	ARA	Ph	KKWRC	67	KF693054		
40	Bah012**	Baha	Bah	ARA	Ph	KKWRC	65	KF693055	KM267397	KM267469
41	Bah015	Baha	Bah	ARA	Ph	KKWRC	53	KF693057		
42	Bah016	Baha	Bah	ARA	Ph	KKWRC	74	KF693058		
43	Bah019	Baha	Bah	ARA	Ph	KKWRC	65	KF693059		
44	Bah021	Baha	Bah	ARA	Ph	KKWRC	65	KF693060		
45	Bah022	Baha	Bah	ARA	Ph	KKWRC	65	KF693061		
46	Bah023	Baha	Bah	ARA	Ph	KKWRC	65	AY247530		
47	0117PHDhi	Dhilafa Escp.	Dhi	ARA	Ph	K.Nasher	67	KF693075		
48	0118PHDhi	Dhilafa Escp.	Dhi	ARA	Ph	K.Nasher	59	KF693076		
49	0119PHDhi	Dhilafa Escp.	Dhi	ARA	Ph	K.Nasher	67	KF693077		
50	0120PHDhi	Dhilafa Escp.	Dhi	ARA	Ph	K.Nasher	36	KF693078		
51	Tif005**	Taif	Tif	ARA	Ph	KKWRC	74	KF693064	KM267402	KM267474
52	Tif010**	Taif	Tif	ARA	Ph	KKWRC	63	KF693068	KM267403	KM267475
53	Tif001	Taif	Tif	ARA	Ph	KKWRC	67	KF693062		
54	Tif002	Taif	Tif	ARA	Ph	KKWRC	74	KF693063		
55	Tif003	Taif	Tif	ARA	Ph	KKWRC	67	AY247533		
56	Tif004	Taif	Tif	ARA	Ph	KKWRC	74	AY247534		
57	Tif006	Taif	Tif	ARA	Ph	KKWRC	67	KF693065		
58	Tif007	Taif	Tif	ARA	Ph	KKWRC	74	KF693066		

59	Tif008	Taif	Tif	ARA	Ph	KKWRC	67	KF693067		
60	Tif013	Taif	Tif	ARA	Ph	KKWRC	74	KF693069		
61	Tif014	Taif	Tif	ARA	Ph	KKWRC	74	KF693070		
62	Tif015	Taif	Tif	ARA	Ph	KKWRC	74	KF693071		
63	Tif017	Taif	Tif	ARA	Ph	KKWRC	67	KF693072		
64	Tif019*	Taif	Tif	ARA	Ph	KKWRC	74	KF693073	KM267404	KM267476
65	Tif022	Taif	Tif	ARA	Ph	KKWRC	74	KF693074		
66	0413PHBuH*	Bura'a ForestA	BuH	YEM	Ph	KN	36	KM267327	KM267364	KM267436
67	0414PHBuH	Bura'a ForestA	BuH	YEM	Ph	KN	36	KF693079	EU885446	EU885805
68	0415PHBuH*	Bura'a ForestA	BuH	YEM	Ph	KN	67	KF693080	KM267365	KM267437
69	0416PHBuH	Bura'a ForestA	BuH	YEM	Ph	KN	36	KF693081		
70	0417PHBuL**	Bura'a ForestB	BuL	YEM	Ph	KN	62	KF693082	KM267366	KM267438
71	0418PHBuL	Bura'a ForestB	BuL	YEM	Ph	KN	62	KF693083		
72	0419PHBuL	Bura'a ForestB	BuL	YEM	Ph	KN	37	KF693084		
73	0420PHBuL	Bura'a ForestB	BuL	YEM	Ph	KN	36	KF693085		
74	0421PHBuL	Bura'a ForestB	BuL	YEM	Ph	KN	36	KF693086		
75	DW104PHIra**	Jebel Iraf	Ira	YEM	Ph	DW	34	KM267331	KM267400	KM267472
76	DW037PHRay**	Jebel Raymah	Ray	YEM	Ph	DW	36	KM267330	KM267399	KM267471
77	DW167PHSab*	Jebel Sabir	Sab	YEM	Ph	DW	67	KM267332	KM267401	KM267473
78	0014PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	81	AF275397		
79	0015PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	102	AF275398		
80	0016PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	41	AF275399		
81	0017PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	81	AF275400		
82	0018PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	100	AF275401		
83	0019PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	102	AF275402		
84	0020PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	43	AF275403		
85	0021PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	100	AF275404		
86	0022PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	41	AF275405		
87	0023PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	81	AF275406		
88	0024PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	102	AF275407		
89	0025PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	102	AF275408		
90	0026PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	18	AF275409		
91	0027PHAba	Mt.Abagamsei	Aba	ERI	Ph	DZ	40	AF275410		
92	0037PHAbd**	Abdur	Abd	ERI	Ph	DZ	93	AF275420	EU885441	EU885800
93	0028PHAbd	Abdur	Abd	ERI	Ph	DZ	93	AF275411		
94	0029PHAbd	Abdur	Abd	ERI	Ph	DZ	93	AF275412		
95	0030PHAbd	Abdur	Abd	ERI	Ph	DZ	42	AF275413		
96	0031PHAbd	Abdur	Abd	ERI	Ph	DZ	99	AF275414		
97	0032PHAbd	Abdur	Abd	ERI	Ph	DZ	42	AF275415		
98	0033PHAbd	Abdur	Abd	ERI	Ph	DZ	93	AF275416		
99	0034PHAbd	Abdur	Abd	ERI	Ph	DZ	93	AF275417		
100	0035PHAbd	Abdur	Abd	ERI	Ph	DZ	93	AF275418		
101	0036PHAbd	Abdur	Abd	ERI	Ph	DZ	93	AF275419		
102	0038PHAbd	Abdur	Abd	ERI	Ph	DZ	42	AF275421		
103	0391PHAfb**	Afabet	Afb	ERI	Ph	DZ	81	KF693023	EU885443	EU885802
104	0395PHAfb	Afabet	Afb	ERI	Ph	DZ	7	KF693024		
105	0396PHAfb	Afabet	Afb	ERI	Ph	DZ	94	KF693025		
106	0064PHBbr	Barka Bridge	Bbr	ERI	Ph	DZ	32	AF275445		
107	0065PHBbr	Barka Bridge	Bbr	ERI	Ph	DZ	82	AF275446		
108	0066PHBbr	Barka Bridge	Bbr	ERI	Ph	DZ	27	AF275447		
109	0067PHBbr	Barka Bridge	Bbr	ERI	Ph	DZ	24	AF275448		
110	0068PHBbr	Barka Bridge	Bbr	ERI	Ph	DZ	25	AF275449		
111	0069PHBbr	Barka Bridge	Bbr	ERI	Ph	DZ	24	AF275450		
112	0070PHBbr	Barka Bridge	Bbr	ERI	Ph	DZ	33	AF275451		
113	0062PHBea	R. Baeat	Bea	ERI	Ph	DZ	27	KF692967		
114	0063PHBea	R. Baeat	Bea	ERI	Ph	DZ	27	KF692968		
115	1594PHDad**	Dada (Bolo)	Dad	ERI	Ph	DZ	54	KF693089	KM267368	KM267440
116	1595PHDad**	Dada (Bolo)	Dad	ERI	Ph	DZ	103	KF693088	KM267369	KM267441
117	1597PHDad**	Dada (Bolo)	Dad	ERI	Ph	DZ	57	KF693096	KM267371	KM267443
118	1598PHDad**	Dada (Bolo)	Dad	ERI	Ph	DZ	56	KF693095	KM267372	KM267444
119	1604PHDad**	Dada (Bolo)	Dad	ERI	Ph	DZ	55	KF693093	KM267378	KM267450
120	1593PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	57	KF693098	KM267367	KM267439
121	1596PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	54	KF693090	KM267370	KM267442
122	1599PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	57	KF693097	KM267373	KM267445
123	1600PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	54	KF693091	KM267374	KM267446
124	1601PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	54	KM267328	KM267375	KM267447
125	1602PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	54	KF693092	KM267376	KM267448
126	1603PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	56	KF693094	KM267377	KM267449

127	1605PHDad*	Dada (Bolo)	Dad	ERI	Ph	DZ	56	KM267329	KM267379	KM267451
128	0045PHDeb	Debresina	Deb	ERI	Ph	DZ	88	AF275428		
129	0046PHDeb	Debresina	Deb	ERI	Ph	DZ	81	AF275429		
130	0047PHDeb	Debresina	Deb	ERI	Ph	DZ	85	AF275430		
131	0039PHDog	Dogali	Dog	ERI	Ph	DZ	40	AF275422		
132	0040PHDog	Dogali	Dog	ERI	Ph	DZ	102	AF275423		
133	0041PHDog	Dogali	Dog	ERI	Ph	DZ	40	AF275424		
134	0042PHDog	Dogali	Dog	ERI	Ph	DZ	23	AF275425		
135	0043PHDog	Dogali	Dog	ERI	Ph	DZ	23	AF275426		
136	0044PHDog	Dogali	Dog	ERI	Ph	DZ	40	AF275427		
137	0240PHDur**	Durfo	Dur	ERI	Ph	DZ	44	KM267314	KM267348	KM267420
138	0010PHDur	Durfo	Dur	ERI	Ph	DZ	95	AF275393		
139	0011PHDur	Durfo	Dur	ERI	Ph	DZ	102	AF275394		
140	0012PHDur	Durfo	Dur	ERI	Ph	DZ	102	AF275395		
141	0013PHDur	Durfo	Dur	ERI	Ph	DZ	102	AF275396		
142	0241PHDur	Durfo	Dur	ERI	Ph	DZ	97	KM267315		
143	0243PhDur	Durfo	Dur	ERI	Ph	DZ	95	KM267316		
144	0232PHFil**	Filfil Bridge	Fil	ERI	Ph	DZ	23	KF692995	KM267344	KM267416
145	0235PHFil**	Filfil Bridge	Fil	ERI	Ph	DZ	83	KF692996	KM267345	KM267417
146	0238PHFil**	Filfil Bridge	Fil	ERI	Ph	DZ	39	KF692999	KM267347	KM267419
147	0236PHFil**	Filfil Bridge	Fil	ERI	Ph	DZ	23	KF692997	KM267346	KM267418
148	0237PHFil	Filfil Bridge	Fil	ERI	Ph	DZ	8	KF692998		
149	0239PHFil	Filfil Bridge	Fil	ERI	Ph	DZ	40	KF693000		
150	0001PHFur	Furrus	Fur	ERI	Ph	DZ	18	AF275384		
151	0002PHFur	Furrus	Fur	ERI	Ph	DZ	18	AF275385		
152	0003PHFur	Furrus	Fur	ERI	Ph	DZ	89	AF275386		
153	0004PHFur	Furrus	Fur	ERI	Ph	DZ	101	AF275387		
154	0005PHFur	Furrus	Fur	ERI	Ph	DZ	18	AF275388		
155	0006PHFur	Furrus	Fur	ERI	Ph	DZ	98	AF275389		
156	0007PHFur	Furrus	Fur	ERI	Ph	DZ	18	AF275390		
157	0008PHFur	Furrus	Fur	ERI	Ph	DZ	18	AF275391		
158	0009PHFur	Furrus	Fur	ERI	Ph	DZ	98	AF275392		
159	0048PHGel	Geleb	Gel	ERI	Ph	DZ	102	AF275431		
160	0049PHGel	Geleb	Gel	ERI	Ph	DZ	9	AF275432		
161	0050PHGel	Geleb	Gel	ERI	Ph	DZ	102	AF275433		
162	0051PHGel	Geleb	Gel	ERI	Ph	DZ	88	AF275434		
163	0052PHGel	Geleb	Gel	ERI	Ph	DZ	9	AF275435		
164	0053PHGel	Geleb	Gel	ERI	Ph	DZ	9	AF275436		
165	0054PHGel	Geleb	Gel	ERI	Ph	DZ	95	AF275437		
166	0223PHHal	Halhal	Hal	ERI	Ph	DZ	20	KF692988		
167	0225PHHal	Halhal	Hal	ERI	Ph	DZ	21	KF692989		
168	0226PHHal	Halhal	Hal	ERI	Ph	DZ	90	KF692990		
169	0227PHHal	Halhal	Hal	ERI	Ph	DZ	20	KF692991		
170	0229PHHal	Halhal	Hal	ERI	Ph	DZ	22	KF692992		
171	0230PHHal	Halhal	Hal	ERI	Ph	DZ	4	KF692993		
172	0231PHHal	Halhal	Hal	ERI	Ph	DZ	9	KF692994		
173	0209PHHim**	Af Himbol	Him	ERI	Ph	DZ	5	KF692978	KM267342	KM267414
174	0206PHHim	Af Himbol	Him	ERI	Ph	DZ	80	KF692975		
175	0207PHHim	Af Himbol	Him	ERI	Ph	DZ	84	KF692976		
176	0208PHHim	Af Himbol	Him	ERI	Ph	DZ	86	KF692977		
177	0210PHHim	Af Himbol	Him	ERI	Ph	DZ	84	KF692979		
178	0211PHHim	Af Himbol	Him	ERI	Ph	DZ	80	KF692980		
179	0212PHHim	Af Himbol	Him	ERI	Ph	DZ	84	KF692981		
180	0213PHHim	Af Himbol	Him	ERI	Ph	DZ	87	KF692982		
181	0214PHHim	Af Himbol	Him	ERI	Ph	DZ	87	KF692983		
182	0074PHKub**	Kubkub	Kub	ERI	Ph	DZ	94	AF275455	EU885442	EU885801
183	0071PHKub	Kubkub	Kub	ERI	Ph	DZ	8	AF275452		
184	0072PHKub	Kubkub	Kub	ERI	Ph	DZ	10	AF275453		
185	0073PHKub	Kubkub	Kub	ERI	Ph	DZ	6	AF275454		
186	0075PHKub	Kubkub	Kub	ERI	Ph	DZ	17	AF275456		
187	0076PHKub	Kubkub	Kub	ERI	Ph	DZ	17	AF275457		
188	0110PHKub	Kubkub	Kub	ERI	Ph	DZ	85	KF692969		
189	0111PHKub	Kubkub	Kub	ERI	Ph	DZ	10	KF692970		
190	0112PHKub	Kubkub	Kub	ERI	Ph	DZ	102	KF692971		
191	0113PHKub	Kubkub	Kub	ERI	Ph	DZ	26	KF692972		
192	0114PHKub	Kubkub	Kub	ERI	Ph	DZ	78	KF692973		
193	0215PHMen**	Mensura	Men	ERI	Ph	DZ	30	KF692984	KM267343	KM267415
194	0115PHMen	Mensura	Men	ERI	Ph	DZ	79	KF692974		

195	0217PHMen	Mensura	Men	ERI	Ph	DZ	30	KF692985		
196	0218PHMen	Mensura	Men	ERI	Ph	DZ	31	KF692986		
197	0220PHMen	Mensura	Men	ERI	Ph	DZ	29	KF692987		
198	0055PHMol	Molki	Mol	ERI	Ph	DZ	19	AF275438		
199	0056PHMol	Molki	Mol	ERI	Ph	DZ	92	AF275439		
200	0057PHMol	Molki	Mol	ERI	Ph	DZ	28	AF275440		
201	0058PHMol	Molki	Mol	ERI	Ph	DZ	29	AF275441		
202	0059PHMol	Molki	Mol	ERI	Ph	DZ	19	AF275442		
203	0060PHMol	Molki	Mol	ERI	Ph	DZ	96	AF275443		
204	0061PHMol	Molki	Mol	ERI	Ph	DZ	11	AF275444		
205	0175PASha	R. Shackat	Sha	ERI	Px	DZ	15	KF693125		
206	0176PASha	R. Shackat	Sha	ERI	Px	DZ	15	KF693126		
207	0177PASha	R. Shackat	Sha	ERI	Px	DZ	15	KF693127		
208	0178PASha	R. Shackat	Sha	ERI	Px	DZ	15	KF693128		
209	0184PAGri**	R. Griset	Gri	ERI	Pa	DZ	14	KF693132	EU885422	EU885781
210	0185PAGri	R. Griset	Gri	ERI	Pa	DZ	14	KF693133		
211	0186PAGri	R. Griset	Gri	ERI	Pa	DZ	14	KF693134		
212	0187PAGri	R. Griset	Gri	ERI	Pa	DZ	14	KF693135		
213	0188PAGri	R. Griset	Gri	ERI	Pa	DZ	14	KF693136		
214	0189PAGri	R. Griset	Gri	ERI	Pa	DZ	14	KF693137		
215	0190PAGri	R. Griset	Gri	ERI	Pa	DZ	13	KF693138		
216	0191PAGri	R. Griset	Gri	ERI	Pa	DZ	12	KF693139		
217	0194PAHad**	R. Hadejemi	Had	ERI	Pa	DZ	16	KF693142	KM267340	KM267412
218	0192PAHad	R. Hadejemi	Had	ERI	Pa	DZ	16	KF693140		
219	0193PAHad	R. Hadejemi	Had	ERI	Pa	DZ	16	KF693141		
220	0195PAHad	R. Hadejemi	Had	ERI	Pa	DZ	16	KF693143		
221	0196PAHad	R. Hadejemi	Had	ERI	Pa	DZ	16	KF693144		
222	0197PAHad	R. Hadejemi	Had	ERI	Pa	DZ	16	KF693145		
223	0077PAHay**	Haykota	Hay	ERI	Pa	DZ	2	AF275458	KM267338	KM267409
224	0078PAHay	Haykota	Hay	ERI	Pa	DZ	3	AF275459		
225	0079PAHay	Haykota	Hay	ERI	Pa	DZ	2	AF275460		
226	0080PAHay	Haykota	Hay	ERI	Pa	DZ	2	AF275461		
227	0081PAHay	Haykota	Hay	ERI	Pa	DZ	2	AF275462		
228	0082PAHay	Haykota	Hay	ERI	Pa	DZ	2	AF275463		
229	0083PAHay	Haykota	Hay	ERI	Pa	DZ	2	AF275464		
230	0084PAHay	Haykota	Hay	ERI	Pa	DZ	12	AF275465		
231	0085PAHay	Haykota	Hay	ERI	Pa	DZ	12	AF275466		
232	0086PAHay	Haykota	Hay	ERI	Pa	DZ	2	AF275467		
233	0087PAHay	Haykota	Hay	ERI	Pa	DZ	12	AF275468		
234	0088PAHay	Haykota	Hay	ERI	Pa	DZ	2	AF275469		
235	0200PAHay**	Haykota	Hay	ERI	Pa	DZ	2	KF693146	KM267341	KM267413
236	0201PAHay	Haykota	Hay	ERI	Pa	DZ	2	KF693147		
237	0202PAHay	Haykota	Hay	ERI	Pa	DZ	2	KF693148		
238	0203PAHay	Haykota	Hay	ERI	Pa	DZ	2	KF693149		
239	0204PAHay	Haykota	Hay	ERI	Pa	DZ	2	KF693150		
240	0181PATes**	Tesseney	Tes	ERI	Pa	DZ	1	KF693129	KM267339	KM267410
241	0089PATes	Tesseney	Tes	ERI	Pa	DZ	2	AF275470		
242	0090PATes	Tesseney	Tes	ERI	Pa	DZ	2	AF275471		
243	0091PATes	Tesseney	Tes	ERI	Pa	DZ	2	AF275472		
244	0092PATes	Tesseney	Tes	ERI	Pa	DZ	2	AF275473		
245	0093PATes	Tesseney	Tes	ERI	Pa	DZ	2	AF275474		
246	0094PATes	Tesseney	Tes	ERI	Pa	DZ	2	AF275475		
247	0182PATes	Tesseney	Tes	ERI	Pa	DZ	2	KF693130		
248	0183PATes	Tesseney	Tes	ERI	Pa	DZ	2	KF693131		
249	0301PHASt**	Awash Station	ASt	ETH	Ph	DZ	91	KF693002	EU885444	EU885803
250	0300PHASt**	Awash Station	ASt	ETH	Ph	DZ	48	KF693001	KM267349	KM267421
251	0302PHASt**	Awash Station	ASt	ETH	Ph	DZ	47	KF693003	KM267350	KM267422
252	0303PHASt	Awash Station	ASt	ETH	Ph	DZ	48	KF693004		
253	0304PHASt	Awash Station	ASt	ETH	Ph	DZ	48	KF693005		
254	0316PHGer**	Gerba Luku	Ger	ETH	Ph	DZ	77	KF693012	KM267353	KM267425
255	0319PHGer**	Gerba Luku	Ger	ETH	Ph	DZ	49	KF693015	EU885445	EU885804
256	0310PHGer	Gerba Luku	Ger	ETH	Ph	DZ	76	KF693006		
257	0311PHGer	Gerba Luku	Ger	ETH	Ph	DZ	49	KF693007		
258	0312PHGer**	Gerba Luku	Ger	ETH	Ph	DZ	51	KF693008	KM267351	KM267423
259	0313PHGer**	Gerba Luku	Ger	ETH	Ph	DZ	52	KF693009	KM267352	KM267424
260	0314PHGer	Gerba Luku	Ger	ETH	Ph	DZ	45	KF693010		
261	0315PHGer	Gerba Luku	Ger	ETH	Ph	DZ	51	KF693011		
262	0317PHGer**	Gerba Luku	Ger	ETH	Ph	DZ	60	KF693013	KM267354	KM267426

263	0318PHGer	Gerba Luku	Ger	ETH	Ph	DZ	52	KF693014		
264	0320PHMie**	Mieso	Mie	ETH	Ph	DZ	104	KF693016	KM267355	KM267427
265	0321PHMie	Mieso	Mie	ETH	Ph	DZ	51	KF693017		
266	0322PHMie**	Mieso	Mie	ETH	Ph	DZ	50	KF693018	KM267356	KM267428
267	0323PHMie	Mieso	Mie	ETH	Ph	DZ	104	KF693019		
268	0324PHMie	Mieso	Mie	ETH	Ph	DZ	49	KF693020		
269	0325PHMie	Mieso	Mie	ETH	Ph	DZ	49	KF693021		
270	0326PHMie	Mieso	Mie	ETH	Ph	DZ	51	KF693022		
271	0305PXAFa	Awash Falls	AFa	ETH	Px	DZ	75	KM267317		
272	0306PXAFa	Awash Falls	AFa	ETH	Px	DZ	75	KM267318		
273	0307PXAFa	Awash Falls	AFa	ETH	Px	DZ	75	KM267319		
274	0308PXAFa	Awash Falls	AFa	ETH	Px	DZ	75	KM267320		
275	0309PXAFa	Awash Falls	AFa	ETH	Px	DZ	75	KM267321		
276	0327PXWol**	Wolenkiti	Wol	ETH	Px	DZ	46	KM267322	KM267357	KM267429
277	0328PXWol	Wolenkiti	Wol	ETH	Px	DZ	46	KM267323		
278	0329PXWol	Wolenkiti	Wol	ETH	Px	DZ	46	KM267324		
279	0330PXWol	Wolenkiti	Wol	ETH	Px	DZ	46	KM267325		
280	0331PXWol	Wolenkiti	Wol	ETH	Px	DZ	46	KM267326		
281	0332PAAda**	Adami Tulu	Ada	ETH	Pa	DZ	107	KF693156	KM267358	KM267430
282	0334PAAda*	Adami Tulu	Ada	ETH	Pa	DZ	107	KF693158	KM267359	KM267431
283	0335PAAda*	Adami Tulu	Ada	ETH	Pa	DZ	107	KF693157	KM267360	KM267432
284	0336PAAda*	Adami Tulu	Ada	ETH	Pa	DZ	107	KF693159	KM267361	KM267433
285	0338PAAla**	Alambada	Ala	ETH	Pa	DZ	105	KF693160	KM267362	KM267434
286	0337PAAla	Alambada	Ala	ETH	Pa	DZ	106	KF693162		
287	0339PAAla	Alambada	Ala	ETH	Pa	DZ	105	KF693161		
288	0159PAMan	Managasha 1	Mng	ETH	Pa	ZFMK	109	KF693163		
289	0349PAMan**	Managasha 2	Man	ETH	Pa	DZ	108	KF693115	EU885424	EU885783
290	0344PAMan	Managasha 2	Man	ETH	Pa	DZ	109	KF693173		
291	0345PAMan	Managasha 2	Man	ETH	Pa	DZ	109	KF693168		
292	0346PAMan	Managasha 2	Man	ETH	Pa	DZ	109	KF693169		
293	0347PAMan	Managasha 2	Man	ETH	Pa	DZ	109	KF693170		
294	0348PAMan	Managasha 2	Man	ETH	Pa	DZ	108	KF693171		
o01	0340PAWen**	Wendo Genet	Wen	ETH	Pa	DZ		KF693164	KM267363	KM267435
o02	0507PCWeb**	Webi Shebelli	Web	SOM	Pc	ZSM		KF693214	KM267337	KM267408
o03	0529PCDia**			KEN	Pc	DZ		KF693215	EU885429	EU885788
o04	0448PAKib**			UGA	Pa	DZ		KF693187	EU885420	EU885779
o05	0549PAChi**			NIG	Pa	DZ		KM267336	EU885458	EU885775
o06	0547PAKem**			NIG	Pa	DZ		KM267335	EU885454	EU885771
o07	0552PAKur**			NIG	Pa	DZ		KF693190	EU885460	EU885777
o08	0523PPKed**			SEN	Pp	DZ		KF692769	EU885462	EU885809
o09	0252PPBak**			GUI	Pp	DZ		KF692711	EU885463	EU885810
o10	0101PAKoS**			CDI	Pa	DZ		KF693105	KM267407	KM267479
o11	0096PAKoN**			CDI	Pa	DZ		KF693100	EU885450	EU885767
o12	0288PCMu2**			MLW	Pc	DZ		KF693203	EU885434	EU885793
o13	0151PCMic**			MLW	Pc	DZ		KF693194	EU885433	EU885792
o14	0422PUPil**			RSA	Pu	DZ		KF692923	EU885470	EU885817
o15	0492PUMor**			BOT	Pu	DZ		KM267334	EU885469	EU885816
o16	0484PUSpr**			NAM	Pu	DZ		KF692952	KM267406	KM267478
o17	0463PUHop**			RSA	Pu	DZ		KF692938	EU885486	EU885833
o18	0459Tg1**			zoo	Tgl	DZ		KM267333	KM267405	KM267477

Countries: ARA = Saudi Arabia; YEM = Yemen; ERI = Eritrea; ETH = Ethiopia; SOM = Somalia

Taxa: Pa = *Papio anubis*; Pc = *P. cynocephalus*; Ph = *P. hamadryas*; Px = phenotypic hybrid Pa x Ph

Source: KKWRC = King Khalid Wildlife Research Centre, Thumamah, Saudi Arabia; KN = Karim Nasher; DW = Derek Wildman; DZ = Dietmar Zinner; ZSM = Zoologische Staatssammlung München, Germany; ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

* We sequenced the 'Brown Region' (896 bp) and the complete cytochrome *b* gene (1140 bp) of these samples (n = 73).

** We used these 52 unique haplotypes of the concatenated Brown Region + cyt *b* + HVRI sequences to estimate divergence ages.

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