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Out of Africa, but how and when? The case of hamadryas baboons (*Papio hamadryas*)



Gisela H. Kopp^{a,*}, Christian Roos^b, Thomas M. Butynski^{c,d,1}, Derek E. Wildman^e, Abdulaziz N. Alagaili^{f,g}, Linn F. Groeneveld^h, Dietmar Zinner^a

^a Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

^b Gene Bank of Primates and Primate Genetics Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

^c King Khalid Wildlife Research Centre, Saudi Wildlife Authority, P.O. Box 61681, Riyadh 11575, Saudi Arabia

^d Conservation Programs, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom

^e Center for Molecular Medicine and Genetics, Wayne State University School of Medicine, 540 E. Canfield Ave. 3240 Scott Hall, Detroit, MI 48220, USA

^f KSU Mammals Research Chair, Department of Zoology, College of Science, King Saud University, Riyadh, Saudi Arabia

^g Saudi Wildlife Authority, P.O. Box 61681, Riyadh 11575, Saudi Arabia

^h NordGen – Nordic Genetic Resource Center, Ås, Norway

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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.

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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

* Corresponding author.

E-mail addresses: gkopp@dpz.eu (G.H. Kopp), croos@dpz.eu (C. Roos), tbutynski@aol.com (T.M. Butynski), dwildman@med.wayne.edu (D.E. Wildman), aalagaili@ksu.edu.sa (A.N. Alagaili), linn.groeneveld@nordgen.org (L.F. Groeneveld), dzinner@gwdg.de (D. Zinner).

¹ Present affiliation: Lolldaiga Hills Research Programme, Sustainability Centre Eastern Africa, P.O. Box 149, Nanyuki 10400, Kenya.

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 and 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. 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 and 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; Drake et al., 2013; Larrasoña 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 palaeoceanographic and palaeoecological 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).

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 and 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 (*Papio kindae*), yellow (*Papio cynocephalus*), olive (*Papio anubis*), hamadryas (*Papio hamadryas*), and Guinea baboon (*Papio papio*) (Jolly, 1993, 2013; Kingdon, 1997; Szmulewicz et al., 1999; Groves, 2001; Frost et al., 2003; 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., 2011, 2013). 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., 2014). At present, this species inhabits Ethiopia, Eritrea, Somalia, Djibouti and possibly Sudan, and southwestern Arabia along the Red Sea from Yemen to south-western Saudi Arabia (Anandam et al., 2013; Swedell, 2013) (Fig. 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 and 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 *Papio arabicus* (Thomas, 1900) or *P. hamadryas arabicus* (Ellermann and Morrison-Scott, 1951; Harrison, 1964; Corbet, 1978; Harrison and 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. 1). To our knowledge, however, no *Papio* fossils or sub-fossils 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; Drake et al., 2013; Larrasoña et al., 2013).
- (ii) Hamadryas baboons immigrated to Arabia across the southern Red Sea (southern route; Fig. 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 and Fuller, 2009; Boivin et al., 2009) and the Bronze Age (c. 3500–1200 B.C.E.; Boivin and Fuller, 2009; Boivin et al., 2009), which had the potential for the translocation of baboons.

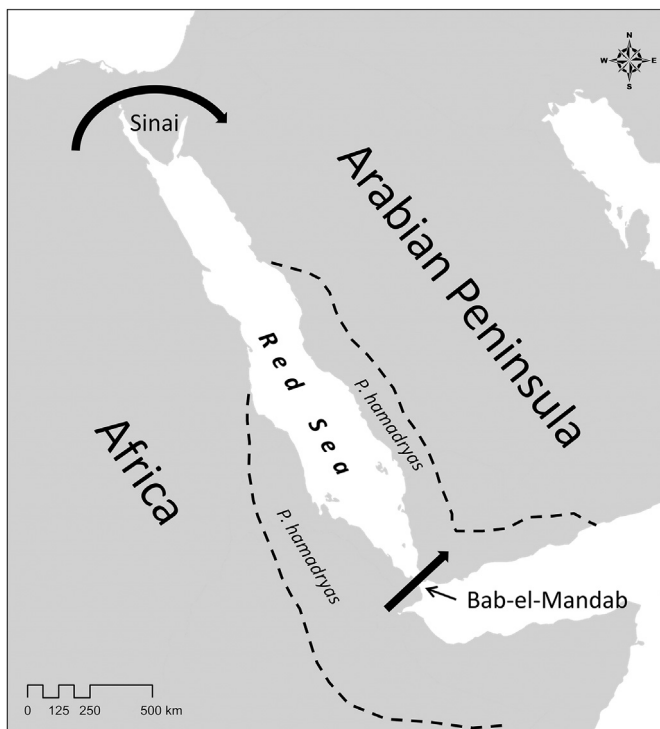


Figure 1. Geographic range and hypothetical immigration routes of hamadryas baboons from Africa into Arabia. Dashed lines indicate the approximate borders of the geographic range of hamadryas baboon in Africa and Arabia (after Yalden et al., 1977, 1996; Harrison and Bates, 1991). Thick arrows indicate the southern and northern dispersal routes.

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), analysed 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 palaeontologically documented 4 mya *Theropithecus-Papio* split (Delson, 1993; Goodman et al., 1998; Gundling and 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?

Materials and 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. 2, Table 1). 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.

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 896 bp of the Brown Region and 1140 bp 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

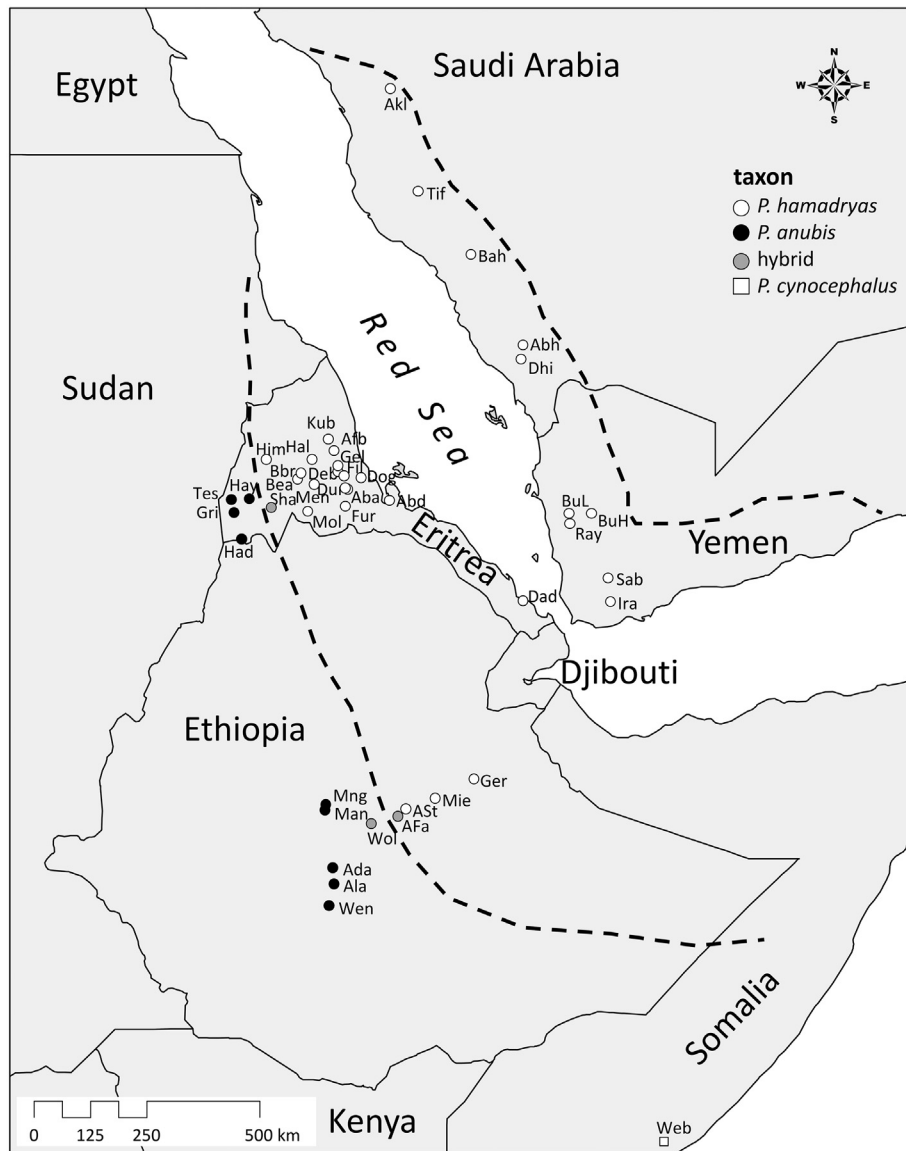


Figure 2. Baboon sampling sites (see also Table 1) in Africa and Arabia. Dashed lines indicate approximate geographic range of hamadryas baboons in Africa and Arabia.

subsequently sequenced on an ABI 3130xL 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-AF275475 (Hapke et al., 2001); AY247444-AY247447, AY247453, AY247459, AY247460, AY247530, AY247533, AY247534, AY247547, AY247548 (Winney et al., 2004)]. The resulting final data set comprised 294 HVRI sequences from 43 localities (10 Arabia and 33 Africa, including eight *P. anubis* sites and three *P. anubis* × *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* × *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 Appendix A, Supplementary Online Material [SOM] Table S1).

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 (H_d) and nucleotide diversity (π) using DnaSP 5.10.1 (Librado and 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 H_d and π for each sampling locality (excluding localities with only one sample).

Table 1
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. Grisat	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.

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 and 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 and Kidd, 1996) and the specific mutation rate of primate HVRI of 15–20% per million years (Jensen-Seaman and 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 and 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 a 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 and Drummond, 2002a). A consensus chronogram with node height distribution was generated and visualized with TreeAnnotator 1.6.1 (Rambaut and 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. 3). Clade X is strictly African and consists of Eritrean and a few Ethiopian hamadryas baboons, and phenotypic *P. hamadryas* × *P. anubis* hybrids from Ethiopia. Clade Y is more complex, encompassing Eritrean hamadryas and olive baboons, Eritrean hybrids, and Arabian hamadryas baboons. Clade Z comprises 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. 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 ($n_{Africa} = 149$, $n_{Arabia} = 77$, $Hd_{Africa} \pm SD = 0.983 \pm 0.003$, $Hd_{Arabia} \pm SD = 0.871 \pm 0.026$, $p < 0.001$; $\pi_{Africa} \pm SD = 0.04251 \pm 0.00088$, $\pi_{Arabia} \pm SD = 0.01920 \pm 0.00243$, $p < 0.001$). Haplotype diversity and nucleotide diversity are both significantly higher ($p < 0.001$) in Clade Arab_Z ($n = 61$) than in Clade Arab_Y ($n = 16$): ($Hd_Z \pm SD = 0.825 \pm 0.040$, $Hd_Y \pm SD = 0.533 \pm 0.142$) and ($\pi_Z \pm SD = 0.00431 \pm 0.00046$, $\pi_Y \pm SD = 0.00218 \pm 0.00076$).

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). Both Arabian clades probably underwent a population expansion, as neither the demographic nor the spatial expansion model is rejected at $\alpha = 5\%$ (Table 2). 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 2).

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

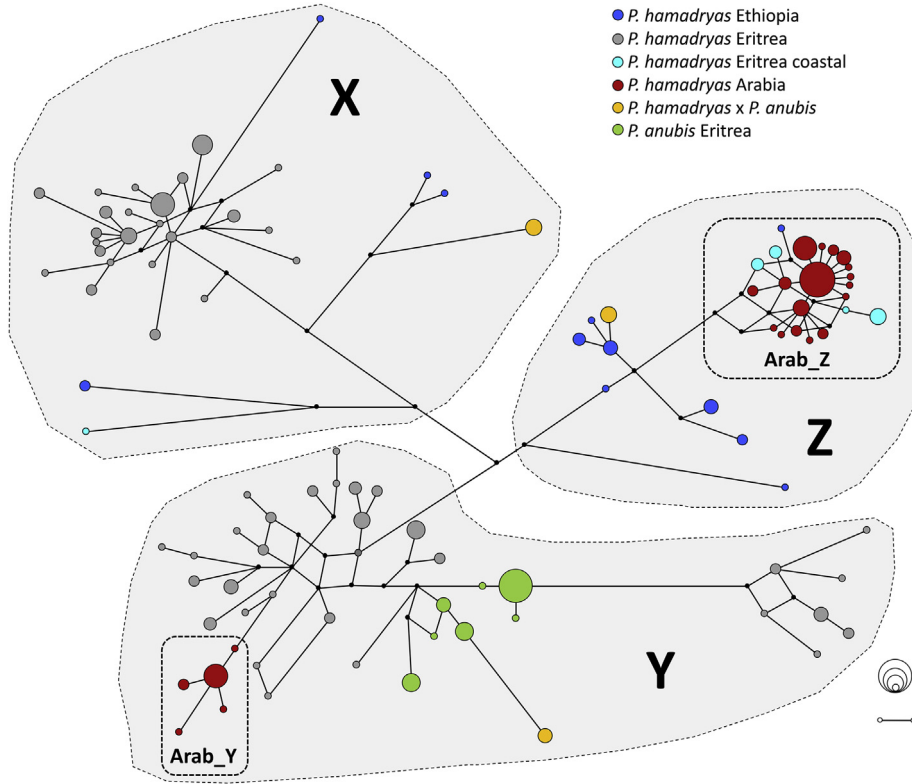


Figure 3. Median-joining HVRI haplotype network of hamadryas baboons with the three major clades X, Y, and Z indicated by grey shading and the two Arabian clades Arab_Y and Arab_Z indicated by dashed boxes ($n = 280, 338$ bp). Scale bar = 1 pairwise difference; node sizes are proportional to haplotype frequencies (scale indicates 1, 5, 10 and 20). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hamadryas baboons (Fig. 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.

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. 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., between 150 and 31 kya). This time period includes sea level lowstands around 130 kya and 65 kya (Fig. 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. 7).

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

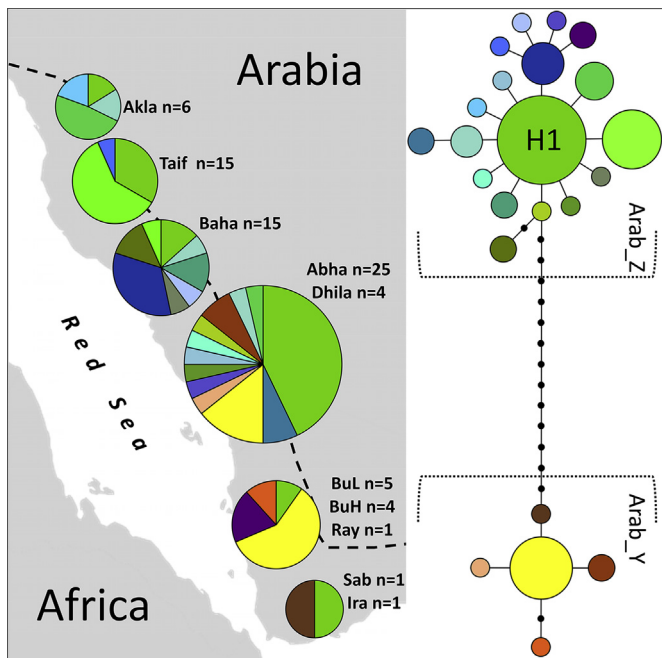


Figure 4. HVRI haplotypes network of Arabian hamadryas baboons showing the spatial distribution and frequency of haplotypes.

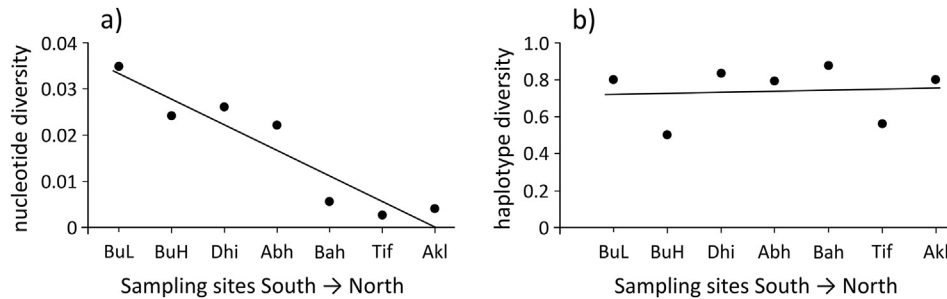


Figure 5. South-north gradients in Arabian hamadryas baboons in (a) nucleotide diversity and (b) haplotype diversity.

structuring. This is in support of a recent study that discusses this topic in detail (Kopp et al., 2014). 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. First, 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 and Geraads, 2000). Second, 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. (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 mitochondrially structured. Two factors support the first alternative. First, 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. Second, 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.,

Table 2
Analysis of mismatch distribution to test for population expansion for both Arabian hamadryas baboon lineages.

HVRI clade	Demographic expansion		Spatial expansion		Time since expansion (ka)	
	τ (confidence interval)	<i>p</i> -value	τ (confidence interval)	<i>p</i> -value	15% [$\mu = 5.07 \times 10^{-5}$]	20% [$\mu = 6.76 \times 10^{-5}$]
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)

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.

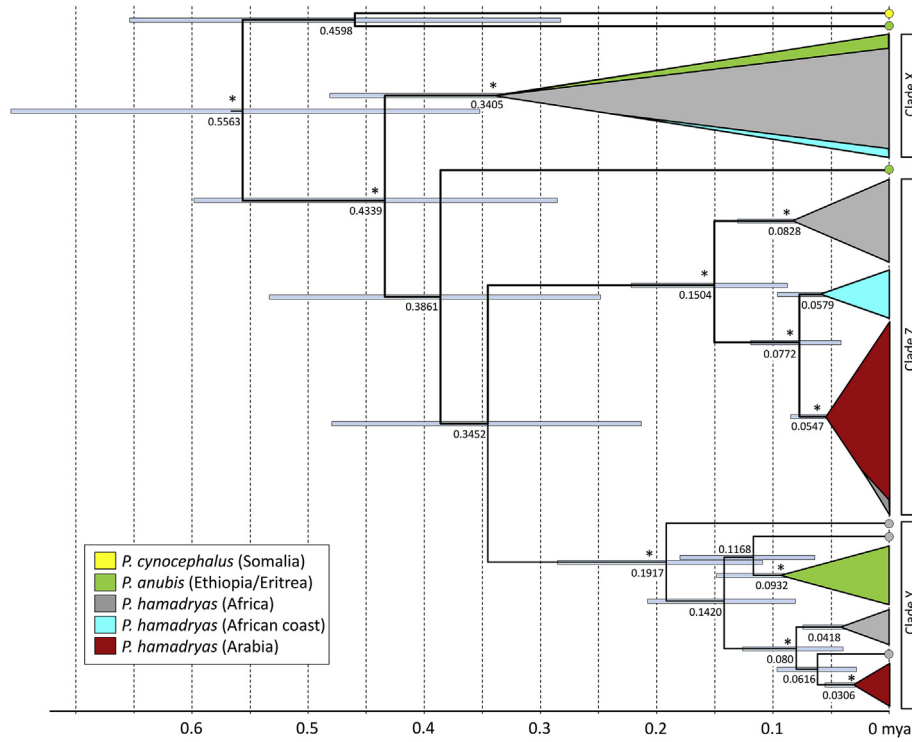


Figure 6. Bayesian divergence time estimations of Northeast African and Arabian baboon mtDNA lineages (concatenated Brown region + cyt b + HVRI, 2373 bp) based on 52 unique Northeast African and Arabian hamadryas baboon haplotypes, 17 other *Papio*, and one *Theropithecus* haplotype. In order to conserve 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). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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

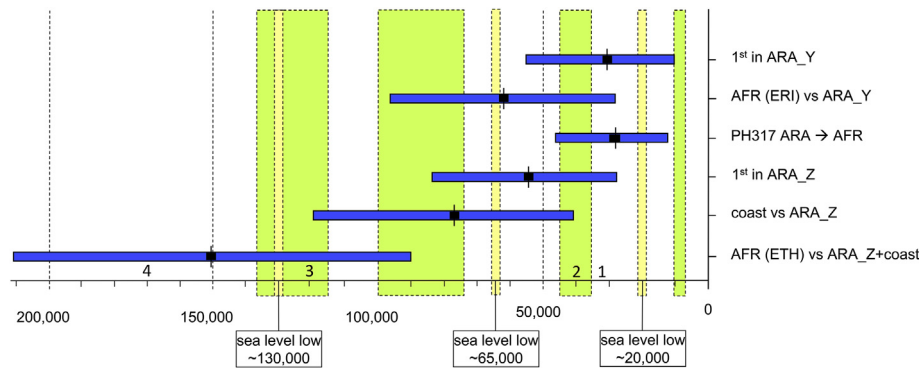


Figure 7. Divergence ages between African and Arabian hamadryas baboon mtDNA clades in relation to Red Sea sea level lowstands (yellow; Rohling, 1994; Rohling et al., 1998, 2009) and Green Sahara Periods (green; Blome et al., 2012; Drake et al., 2013). Numbers 1 to 4 refer to estimated colonization times 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). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 low-stand 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. 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. 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; Drake et al., 2013; Larrasoana 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; Arnold, 1995 cited in; Masseti and 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 also 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 and Petit-Maire, 1994; Groucutt and Petraglia, 2012; Rosenberg et al., 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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Appendix A. Supplementary online material

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2014.08.003>.

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