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Genetic structure in a dynamic baboon hybrid zone corroborates behavioural observations in a hybrid population

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Abstract

Behaviour and genetic structure are intimately related: mating patterns and patterns of movement between groups or populations influence the movement of genetic variation across the landscape and from one generation to the next. In hybrid zones, the behaviour of the hybridizing taxa can also impact the incidence and outcome of hybridization events. Hybridization between yellow baboons and anubis baboons has been well documented in the Amboseli basin of Kenya, where more anubis-like individuals tend to experience maturational and reproductive advantages. However, it is unknown whether these advantages are reflected in the genetic structure of populations surrounding this area. Here, we used microsatellite genotype data to evaluate the structure and composition of baboon populations in southern Kenya. Our results indicate that, unlike for mitochondrial DNA, microsatellite-based measures of genetic structure concord with phenotypically based taxonomic distinctions and that the currently active hybrid zone is relatively narrow. Isolation with migration analysis revealed asymmetric gene flow in this region from anubis populations into yellow populations, in support of the anubis-biased phenotypic advantages observed in Amboseli. Populations that are primarily yellow but that receive anubis gene flow exhibit higher levels of genetic diversity than yellow populations far from the introgression front. Our results support previous work that indicates a long history of hybridization and introgression among East African baboons. Specifically, it suggests that anubis baboons are in the process of gradual range expansion into the range of yellow baboons, a pattern potentially explained by behavioural and life history advantages that correlate with anubis ancestry.

Keywords: asymmetric migration, baboons, gene flow, hybrid zone, population structure, range expansion

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Introduction

Behaviour—particularly patterns of philopatry and dispersal, patterns of reproductive skew and the level of sex bias in these patterns—is a key determinant of genetic structure and particularly of the degree to which genetic structure departs from classical Wright–Fisher models (Chesser 1991; Sugg *et al.* 1996). Behavioural observations that capture when an individual leaves its natal group, how far it goes and whether, when and with whom it mates, can therefore predict

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broader patterns of population genetic structure and provide insight into its underlying causes (see, for example, Holekamp *et al.* 2011; Kerth & van Schaik 2011; Ribeiro *et al.* 2011). For example, endogamous marriage patterns among humans in India partially explain high levels of population structure on the Indian subcontinent (Reich *et al.* 2009), and practices of residency after marriage have been shown to yield contrasting patterns of structure in Y-chromosome and mitochondrial DNA in culturally diverse human populations (Oota *et al.* 2001; Wilder *et al.* 2004; Wilkins 2006; Hunley *et al.* 2008; Crubezy *et al.* 2010).

The relationship between behaviour and population genetic structure is of particular interest in hybrid zones. In particular, mate preferences can evolve rapidly within diverging taxa (Foltz 1981; Fuentes & Dewsbury 1984; Insel & Shapiro 1992; Bester-Meredith *et al.* 1999). In contact zones between such taxa, changes in mate preferences or in dispersal behaviours can play an important role in determining whether, how often, and who participates in hybridization events, which may in turn influence hybridization's long-term evolutionary impact. For instance, assortative mating has made an important contribution to divergence in the face of gene flow among sympatric cichlids in Lake Victoria (Seehausen & Schluter 2004; Seehausen *et al.* 2008), benthic and limnetic sticklebacks in British Columbia (Boughman 2001) and *Heliconius* butterflies in South America (Mavarez *et al.* 2006). Divergent mating behaviours can also favour hybridization. Female mate choice allows female *Spea bombifrons* spadefoot toads to choose heterospecific *Spea multiplicata* males under environmental conditions in which hybrid offspring would be favoured. No such advantage accrues to heterospecific matings for *S. multiplicata* females, and *S. multiplicata* females do not choose heterospecific mates—thus explaining asymmetric patterns of hybridization in regions where these species co-occur (Pfennig 2007). Behavioural patterns that govern how sister taxa interact within hybrid zones can therefore act as important predictors of genetic structure during the early stages of divergence.

Among primates, hybridization during divergence is extremely common (Arnold 1997; Arnold & Meyer 2006). Many primate species exhibit long-term, individually differentiated social relationships and a degree of mate choice by both sexes, both of which may be strongly influenced by social status and social hierarchy. In addition, primate dispersal patterns are diverse and may include male-only dispersal, female-only dispersal or dispersal by both sexes (Pusey & Packer 1987). These behavioural factors may be important in determining the incidence and outcome of hybridization events. As such, primate hybrid zones provide useful models for how complex social systems influence hybridization, potentially providing insight into the dynamics of proposed admixture events in our own ancient history (Green *et al.* 2010; Reich *et al.* 2010).

Baboons (genus *Papio*) are one of the most extensively studied primate taxa with respect to behavioural aspects of natural hybridization. The five commonly recognized species (or subspecies: see Jolly 1993) of baboons inhabit geographically distinct ranges and exhibit marked differences in social organization, mating system and morphology (Kingdon 1971; Jolly 1993; Henzi & Barrett 2003; Newman *et al.* 2004). In zones of contact between species ranges, however, baboon taxa hybridize readily, producing viable and fertile hybrid offspring (Maples & McKern 1967; Phillips-Conroy & Jolly 1986; Samuels & Altmann 1986; Jolly 1993). Phylogeographic evidence from mitochondrial DNA indicates that this process may reflect a long history of hybridization in this genus (Wildman *et al.* 2004; Zinner *et al.* 2009; Keller *et al.* 2010). Jolly and colleagues have proposed that several of the current contact zones may therefore represent snapshots of range expansions in progress, as a result of asymmetric fitness between hybridizing groups within hybrid populations (Jolly 2001; Jolly *et al.* 2011).

This phenomenon—range expansion accompanied by hybrid zone movement—has been reported in a number of other taxa (Buggs 2007) but has not been well documented in primates. The long-term evolutionary consequences of hybridization in the current baboon contact zones are not yet clear. However, changes in the structure of hybrid populations that have been observed over time suggest that baboon hybrid zones may be quite dynamic (Phillips-Conroy & Jolly 1986; Tung *et al.* 2008). Further, phylogeographic studies of baboons have revealed complex patterns of historical mitochondrial and Y-chromosome introgression that support the proposed pattern of range expansion. Specifically, mitochondrial DNA phylogenies from east African, southern African and continent-wide samples are consistently paraphyletic with respect to phenotypically based taxonomic designations (Newman *et al.* 2004; Wildman *et al.* 2004; Zinner *et al.* 2009; Keller *et al.* 2010). Several authors have attributed this signature to introgression and 'nuclear swamping' of one taxon by a second group in historic or current contact zones, mediated by sex-biased dispersal and highly directionally biased mating events (i.e. with the male in a pair consistently from the same species; Jolly 1993; Zinner *et al.* 2009; Keller *et al.* 2010; Jolly *et al.* 2011).

Modern-day baboon populations provide useful models in which to test these hypotheses. For instance, in the Kafue National Park of Zambia, Jolly *et al.* (2011) interpreted a 'tail' of phenotypic hybrids and Kinda

(*Papio cynocephalus kindae*) Y-chromosomes in a predominantly grey-footed chacma (*Papio ursinus griseipes*) region of the park as evidence for gradual expansion of the grey-footed chacma range into the historic range of Kinda baboons. Interestingly, their data also indicated asymmetry in cross-taxon matings that tended to be driven by male Kinda mating with female chacma baboons. Behavioural studies in the Awash National Park of Ethiopia, where hamadryas baboons (*P. hamadryas*) and anubis baboons (*Papio anubis*) hybridize, paint a more complicated picture. In some cases, hybrid males enjoyed high reproductive success (Bergman *et al.* 2008), which might favour further hybridization and, under some circumstances, range expansion. On the other hand, females also have been demonstrated to show a strong preference for males of a similar phenotype (Bergman & Beehner 2003; Beehner & Bergman 2006). If these phenotypic differences are reflected by genetic background, such preferences could also slow the process of introgression and expansion.

Our understanding of admixture-related genetic structure and gene flow can therefore be greatly enriched when investigated in the context of behavioural patterns associated with hybridization. To do so, we turned to another known hybrid zone in baboons, that between yellow baboons (*P. cynocephalus*) and anubis baboons in East Africa and specifically in southern Kenya (throughout, we use the term 'hybrid zone' to refer to the region in which the ranges of yellow and anubis baboons overlap and interbreeding occurs). As a result of forty years of long-term observations near the centre of this region, in the Amboseli basin of Kenya, this hybrid zone has been unusually well characterized from a phenotypic and demographic perspective. Because of these observations, the origins of the current phase of hybridization in Amboseli—a predominantly yellow baboon population—can be precisely dated to the early 1980s (Samuels & Altmann 1986), and expansion of the anubis genetic background in Amboseli has been closely tracked over time since then (Tung *et al.* 2008).

Our goal was not only to describe the pattern of genetic structure in this region with respect to admixture, but also to place these findings in the context of known demographic, behavioural and life history patterns associated with hybridization. In particular, analyses of intrapopulational variation within Amboseli have revealed that more anubis-like hybrids of both sexes reach maturation faster (Charpentier *et al.* 2008), and males (the dispersing sex in both yellow baboons and anubis baboons) also disperse significantly earlier than their yellow baboon counterparts (Alberts & Altmann 2001; Charpentier *et al.* 2008). As adults, more anubis-like males also participate in significantly higher rates of consortship (mate guarding) events (J. Tung, M.J.E. Charpentier, S. Mukherjee, J. Altmann, S.C. Alberts, submitted). Given that most mating in Amboseli takes place in the context of consortships (particularly mating that results in conception), these advantages suggest that differences in life history and mating behaviour between yellow and anubis baboons may provide a plausible mechanism for possible anubis range expansion in east Africa, a process that would leave a signature in population genetic data.

Testing this possibility on a genetic level, however, requires context from the populations surrounding Amboseli. If the anubis advantages observed in Amboseli are either transient or specific to Amboseli (for example, because of local ecological context), or opposed by other factors (consortships in Amboseli also appear to be shaped by assortative mating for genetic background; Tung *et al.*, submitted), they may not be reflected in the pattern of population structure in other regions of the hybrid zone that we have not studied intensively. Additionally, if anubis immigration into Amboseli is mirrored by yellow immigration into anubis populations, a general breakdown in geographic barriers to dispersal may better account for the increased admixture observed in Amboseli than anubis range expansion.

We evaluated the evidence for these disparate explanations using nuclear microsatellite data from 15 baboon populations across the anubis–yellow contact zone (Fig. 1). We asked whether analyses of genetic structure in this region, based on nuclear markers, support the hypothesis that the anubis phenotypic advantages identified in Amboseli contribute to anubis baboon range expansion. We were particularly interested in the extent and composition of the hybrid zone in the sampled region and whether we could identify higher rates of gene flow from anubis baboon populations into yellow baboon populations than in the opposing direction. These results shed initial light onto the complex patterns of introgression and change in the yellow–anubis hybrid zone of east Africa, thus highlighting how behavioural data and genetic data can be mutually informative in understanding the causes and consequences of hybridization.

Methods

Study populations and sample collection

In total, we obtained data from 658 east African yellow baboons, anubis baboons and yellow–anubis hybrids in this study, representing a total of 15 populations (Fig. 1, Table S1, Supporting information). Genotype data for three of these populations were available from earlier published studies: specifically, we drew

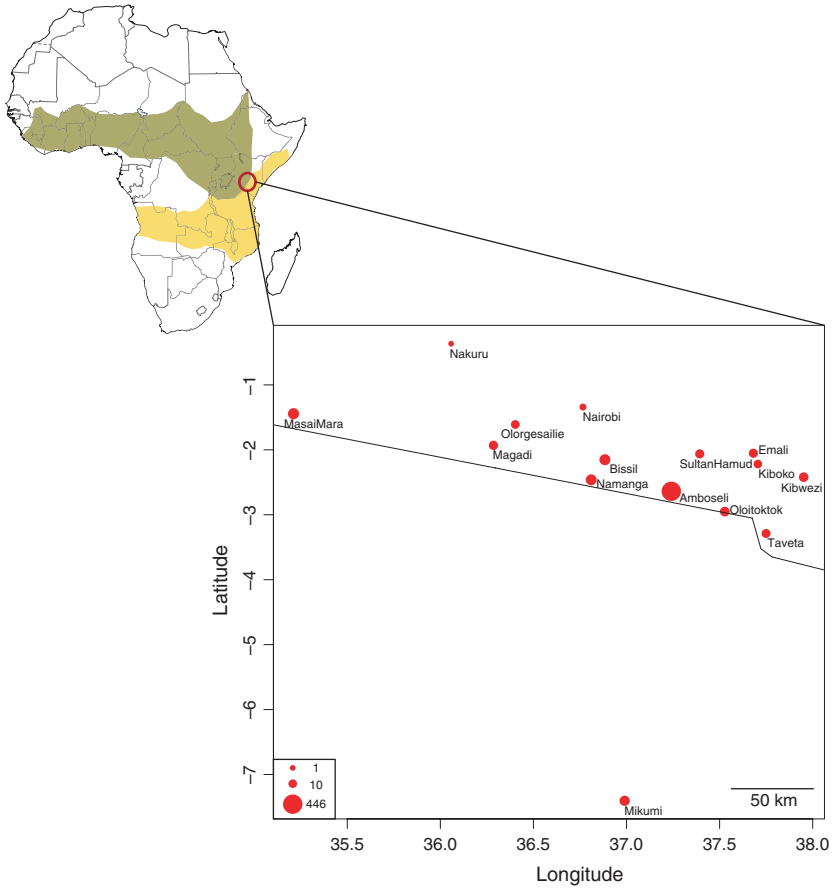

Fig. 1 Geographic distribution of samples included in this study. The diameter of each circle is proportional to the sample size for the corresponding population. Map of Africa to the left shows the geographic distribution of anubis baboons (green) and yellow baboons (yellow) and the location of the contact zone (red circle) that is the focus of this study.

genotype data from 20 baboons from a known yellow baboon population in Mikumi National Park, Tanzania, and genotype data from 10 baboons from a known anubis baboon population in the Maasai Mara National Reserve, Kenya (from Tung *et al.* 2009). We also integrated genotype data from 446 baboons from the Amboseli basin, as previously described (Buchan *et al.* 2003; Alberts *et al.* 2006; Tung *et al.* 2008).

We augmented these data with genotype information from 182 new, geographically dispersed samples, collected in June and July of 2008. Specifically, we conducted noninvasive sampling of baboon faeces from 12 new populations (and collected additional samples in the Maasai Mara area) within or close to the known hybrid baboon population around Amboseli and around a second previously reported hybrid population near the town of Simba (close to our 'Emali' population) (Maples & McKern 1967; Alberts & Altmann 2001). Our sampling strategy thus covered a rough transect from the northwest to southeast regions of southern Kenya (Fig. 1), plus the samples from Mikumi in central Tanzania. Samples were collected in as fresh a condition as possible. We either located baboon groups at their sleeping sites before dusk and returned in the early morning to collect fresh samples (baboons often defecate before moving away from their sleeping site) or collected samples opportunistically by following baboon groups during their daytime movements. On rare occasions, we sampled baboon faeces at sites in which they were known to spend time: in these cases, faecal samples were likely one to several days old. For all samples, we collected approximately 2–5 g of faecal material in 15–20 mL of 95% ethanol. Samples were stored for up to a month and a half in the field in an evaporatively cooled charcoal structure before being placed in long-term storage at −80 °C.

DNA extraction

DNA extracted from faecal samples is degraded and low in quantity. Additionally, because the loci we targeted in this study also cross-amplify in humans, the risk of contamination of our samples was high. All DNA extractions were therefore performed in a DNA

clean room specifically designed to extract DNA from highly sensitive samples. Extractions were performed from the 13 populations sampled *de novo* for this study (including Maasai Mara), using the QIAamp DNA Stool Mini Kit (Qiagen, Courtabœuf, France) with modifications to the protocol as described by Buchan *et al.* (2003). We further modified the protocol by adding 1.2 mL of buffer ASL instead of 1.6 mL during the lysis step and by incubating the samples overnight at 70 °C (C. Poillot and C. Miquel, personal cummunication). DNA samples were eluted in 200 μL of buffer AE.

Microsatellite amplification and genotyping

Baboons were genotyped at 10 tetranucleotide (AGAT006, D1S1656, D3s1768, D4s243, D6s501, D8s1106, D10s611, D11s2002, D14s306 and D18s851) and two dinucleotide (D7s503 and D13s159B) microsatellite loci, as described by Buchan *et al.* (2005). Each reaction was performed using a modified version of the multitubes approach (Taberlet *et al.* 1996; Table S2, Supporting information) in a final volume of 10 μL (per sample per locus) containing 5 μL of a 2× Qiagen Multiplex PCR Master Mix, 0.5 μL of primers at 2 μM, 1 μL of Qsolution 5×, 2.5 μL of ultrapure water and 1 μL of template DNA (for marker D18s851, we increased the primer concentration to 1 μL and decreased the amount of water accordingly). All loci were amplified using an initial denaturation of 95 °C for 10 min, 45 cycles of 94 °C for 30 s, 58 °C for 90 s, and 72 °C for 90 s, and a final 10-min extension step at 72 °C. PCRs were carried out in a 96-well block Eppendorf Mastercycler Gradient S.

We used the software GeneMapper v 4.0 to analyse the genotyping data. To facilitate genotype assignment given the large amount of raw data we collected, we developed a PHP script based on scoring rules that allowed automated (to overcome human error) and fast processing of all individuals' genotypes. We used the identity analysis implemented in the program Cervus 3.0 to remove samples that likely represented duplicate genotypes from the same individual (because we were sampling from unhabituated animals, we were unable to attribute each faecal sample to a unique individual, and in some cases, repeated sampling occurred). We attributed samples to the same source when genotypes matched perfectly, or only one mismatched allele occurred (one case). This mismatch involved a heterozygous genotype and one of the two homozygous corresponding forms. In this unique case, we considered the heterozygous genotype as more reliable and retained it for downstream analyses. For the newly genotyped individuals ($n = 182$), estimates of genotyping error rates (allelic dropout and contamination) are provided in Table S3 (Supporting information; see also Buchan *et al.* 2005, for details on genotyping errors of earlier genetic analyses performed on Amboseli baboons).

Merging external genotype data into the data set

We completed the data set using genotypes from the same 12 loci described above, obtained from baboons previously genotyped at Duke University (NC, USA) [446 individuals from Amboseli: (Buchan *et al.* 2003; Alberts *et al.* 2006; Tung *et al.* 2008), 10 individuals from the Maasai Mara National Reserve (Tung *et al.* 2009) and 20 individuals from Mikumi National Park in Tanzania (Tung *et al.* 2009)]. We combined genotypes for the individuals from Maasai Mara with those obtained from Maasai Mara as part of sampling for this study. Because these samples were genotyped in a different laboratory, possible allelic shifts may have occurred owing to differences in technical methods or genotype assignment. Consequently, we regenotyped 30 Amboseli individuals with previously assigned genotypes in conjunction with our novel genotyping efforts described earlier. Based on this information, we were able to identify all shifts that occurred between laboratories and update the previously published genotype data to correspond with the novel data produced for this study. Very few cases were ambiguous (<0.5% of all alleles); in these cases, we removed the ambiguous genotypes.

Population genetic structure analysis

To delineate the extent of the yellow–anubis hybrid zone in the part of east Africa we sampled, we employed a Bayesian individual-based clustering algorithm implemented in the program Tess 2.3.1 (Durand *et al.* 2009). Like other such algorithms (e.g. Structure 2.3: Pritchard *et al.* 2000; Falush *et al.* 2003), Tess simultaneously performs inference of allele frequency spectra for each cluster, given an assumed number of population clusters K and the proportion of ancestry for each individual in each cluster (q). In contrast to other approaches, Tess includes a spatially explicit model that incorporates information on the sampling locations for each individual (Durand *et al.* 2009; François & Durand 2010). Thus, clusters correspond to spatially as well as genetically continuous units, which may be separated by small discontinuities where genetic barriers are crossed. We chose to use this approach because incorporation of a spatial component into the clustering model can help illuminate clustering vs. clinal tendencies in the data (François & Durand 2010).

We ran the Tess algorithm using the conditional autoregressive (CAR) Gaussian model of admixture, with a linear trend surface (Durand *et al.* 2009). The admixture parameter, α, was initially set to $\alpha = 1$ and the initial

interaction parameter, ρ, was initially set to $\rho = 0.6$. We set a burn-in period of 5×10^4 Markov chain Monte Carlo (MCMC) iterations and used 5×10^5 additional iterations to perform parameter estimations. Although we were most interested in distinguishing between anubis and yellow genetic backgrounds (which corresponds well to $K_{max} = 2$), we explored a range of K_{max} from 2 to 5 to assess the extent of within-species population structure as well (Figs S1 and S2, Supporting information). For each value of K_{max}, we performed 10 replicate runs and used the software CLUMPP 1.1 (Jakobsson & Rosenberg 2007) to allow for label switching and test for convergence (using a greedy algorithm with 100 random input sequences; convergence was assessed via a G' statistic). Barplots of individual ancestries in each cluster were generated using custom R code (R Development Core Team 2011), available upon request. A map of spatially interpolated levels of admixture coefficients was generated using the kriging method in R (plot.membership.r function available at http://membres-timc.imag.fr/Olivier.Francois/admix_display.html). Finally, to corroborate the clustering results obtained from TESS, we also performed a mean-centred principal component analysis (PCA) on the microsatellite individual-genotype matrix using the R package *ADEgenet* (Jombart 2008), an approach that identifies the major contributors to overall genetic variation in the sample (via eigendecomposition) but which does not rely on any model assumptions.

For all downstream analyses in which we assigned individuals as anubis or yellow, we used the q value for these individuals inferred from TESS analysis. Specifically, we considered unadmixed individuals as those with a $q \geq 0.98$ in the anubis baboon cluster or the yellow baboon cluster identified at $K_{max} = 2$.

Genetic diversity and genetic differentiation within and between populations

To understand and compare the population genetic patterns that characterize yellow baboons and anubis baboons in this region, we investigated genetic diversity and genetic structure within and between the 15 populations we sampled.

As measures of genetic diversity, we calculated allelic richness and private allelic richness using the program ADZE 1.0 (Szpiech *et al.* 2008) and the number of alleles and expected heterozygosity (Nei's genetic diversity) for each locus using FSTAT 2.9.3 (Goudet 1995, 2001). We tested for differences between anubis and yellow baboons in allelic richness and genetic diversity using Wilcoxon signed-ranks tests. Additionally, we analysed the entire set of individuals ($n = 658$) together and the entire set of individuals excluding hybrids together ($n = 458$) to investigate the possibility of Wahlund effects, which are expected if anubis and yellow populations do not freely interbreed. Deviations from Hardy–Weinberg expectations (across all samples, within species and within populations) were assessed using permutation tests.

As measures of genetic structure, we calculated F_{ST} between populations and species and F_{IS} within populations and species (Weir & Cockerham 1984) using FSTAT 2.9.3 (Goudet 1995, 2001) (using the definition of pure yellow or pure anubis individuals described earlier for the species comparisons). We also performed a decomposition of overall genetic variance in the sample by region (anubis, hybrid and yellow, as defined by TESS) and population using the analysis of molecular variance (AMOVA) tool implemented in POPGRAPH (Dyer & Nason 2004), testing for the significance of genetic variance partitions via 1000 permutations. Finally, we calculated mean relatedness within each population using COANCESTRY (Wang 2010) and the likelihood estimator of Wang (2002), excluding the individuals from Amboseli that were not sampled explicitly for this study. We chose to exclude these individuals because they were sampled as part of intensive behavioural observations, and it is therefore likely that they were members of groups that were more completely sampled (including more close kin) than is the case for groups sampled via the protocol described earlier.

IMa2 analysis: migration rates, effective population sizes and divergence times

We used the 'isolation with migration' (IM) model (Hey & Nielsen 2004) implemented in the computer program IMa2 (Hey 2010b) to analyse the pattern of divergence and gene flow between anubis and yellow baboons. IMa2 uses coalescent simulations within a Bayesian inference framework to estimate the posterior probability distributions for six demographic parameters scaled by the mutation rate μ: the time since the split between two species or populations ($t = T\mu$); neutral population genetic diversity of the ancestral (presplit) population (θ_A) and the two contemporary (postsplit) populations (θ_1 and θ_2), proportional to their respective effective population sizes N_e ($\theta = 4N_e\mu$); and the bidirectional migration rates between populations (from population 1 into population 2: $M_{1 \to 2} = m_{1 \to 2}/\mu$; from population 2 into population 1: $M_{2 \to 1} = m_{2 \to 1}/\mu$). Based on the two estimates of migration rates, the posterior distributions of the effective number of migrant gene copies per generation (i.e. the population migration rate, $2N_1M_{2 \to 1} = (4N_1u \times M_{2 \to 1}/u)/2$ and $2N_2M_{1 \to 2} = (4N_2u \times M_{1 \to 2}/u)/2$) can be calculated (Hey 2010b).

To understand the relationships between migration rate, genetic diversity and proximity to the hybrid zone

identified using TESS, we conducted IMa2 analyses on three sets of comparisons in which the focal populations differed with respect to their distance from the centre of the hybrid zone: (i) individuals from the Maasai Mara (anubis) and Mikumi (yellow) at the extreme ends of our sampling distribution, furthest from the known hybrid populations of Amboseli and Emali-Kiboko (equivalent to the population near Simba described in (Maples & McKern 1967); (ii) individuals from the Maasai Mara (anubis) and Taveta (yellow), which represented an intermediate distance from the known hybrid populations; and (iii) individuals from Namanga, Bissil and Sultan Hamud and individuals from Kibwezi and Oloitoktok, located very near the previously known hybrid populations; our TESS analysis also indicated these populations contained hybrids. We included individuals from Amboseli (primarily yellow but with well-characterized hybrid individuals) in this third comparison set. Because of the large number of individuals sampled in Amboseli, we chose a random sample of 20 yellow baboons from the Amboseli data set for the purposes of this analysis.

We conducted MCMC simulations using the IMa2 program (Hey & Nielsen 2004), assuming a stepwise-mutation model of microsatellite evolution and uniform prior distributions over the prespecified parameter ranges. These ranges were empirically determined via multiple preliminary runs of the simulations to ensure that the posterior distributions fell completely within the prior range. The mode of the posterior probability distribution was taken as the maximum likelihood estimate (MLE) for each of the six parameters, and we used the 95 per cent highest probability density intervals (HPD interval: the narrowest range of parameter values that includes 95% of the probability density in the posterior distribution for that parameter) as a measure of uncertainty in the estimate.

Ensuring that the Markov chain adequately mixes is a challenging issue for microsatellite data sets and particularly for histories that include gene flow (Hey 2010b). For the analyses reported here, we ensured adequate mixing by using a large number of heated Metropolis-coupled Markov chains (Hey & Nielsen 2004) for each run (100 heated chains per run). We also allowed runs to proceed until they appeared to achieve stationarity and until they produced highly consistent results across multiple independent runs. Within runs, stationarity was assessed by (i) checking for the absence of autocorrelation in the splitting time estimate over the course of the run; (ii) checking that the parameter estimates generated using genealogies sampled in the first and second halves of the run were highly similar; and (iii) visually inspecting trend plots for splitting time terms to check for poor mixing of the MCMC. The results for each comparison are based on genealogies sampled from multiple (two to three) independent runs. Table S4 (Supporting information) shows the burn-in duration, heating parameters used, and runtimes for each of the analyses, and the number of genealogies used for parameter estimation.

To convert the posterior estimates from the IMa2 analyses, which are scaled by the mutation rate μ, into more interpretable demographic units (i.e. t into estimated calendar years since the split and θ in terms of effective population size, N_e: Hey & Nielsen 2004), we assumed a mutation rate of 5.0×10^{-4} mutations per generation (often treated as the mean microsatellite mutation rate for many species: Brinkmann *et al.* 1998; Estoup & Angers 1998; Ellegren 2000; Estoup *et al.* 2002; Sun *et al.* 2009) and a generation time (G) of 8 years.

Results

The hybrid zone between yellow baboons and anubis baboons in this region is restricted to a narrow corridor

Our two-cluster TESS analysis revealed a strong pattern of structure in the genetic data that correlates well with known geographic information about the ranges of anubis baboons and yellow baboons in east Africa (Fig. 2). Specifically, we identified one cluster as dominant in the north and west of our sampling transect and a second cluster as dominant in the southern and eastern extremes of the same region. The northern and western cluster probably corresponds to an anubis genetic background, whereas the southern and eastern cluster probably corresponds to a yellow baboon genetic background. In support of this pattern, individuals in the Mikumi population in Tanzania, which is well within the geographic range of yellow baboons, were entirely assigned to the 'yellow' cluster at $K = 2$; similarly, individuals in the Maasai Mara population at the western extreme were entirely assigned to the 'anubis' cluster. Both of these groups represent well-studied baboon populations that have been previously characterized as yellow and anubis, respectively (e.g. Sapolsky 1986; Rhine *et al.* 1992). Thus, the dominant pattern of population structure at $K = 2$ reflects the differences between anubis baboons and yellow baboons, as anticipated.

This analysis also confirmed the presence of previously reported hybrid populations in Amboseli (Samuels & Altmann 1986; Alberts & Altmann 2001; Tung *et al.* 2008) and at Simba in the vicinity of our Emali and Kiboko sampling locations (Maples & McKern 1967) (Fig. 2b). The majority of the samples from Amboseli represent yellow baboons, in agreement with

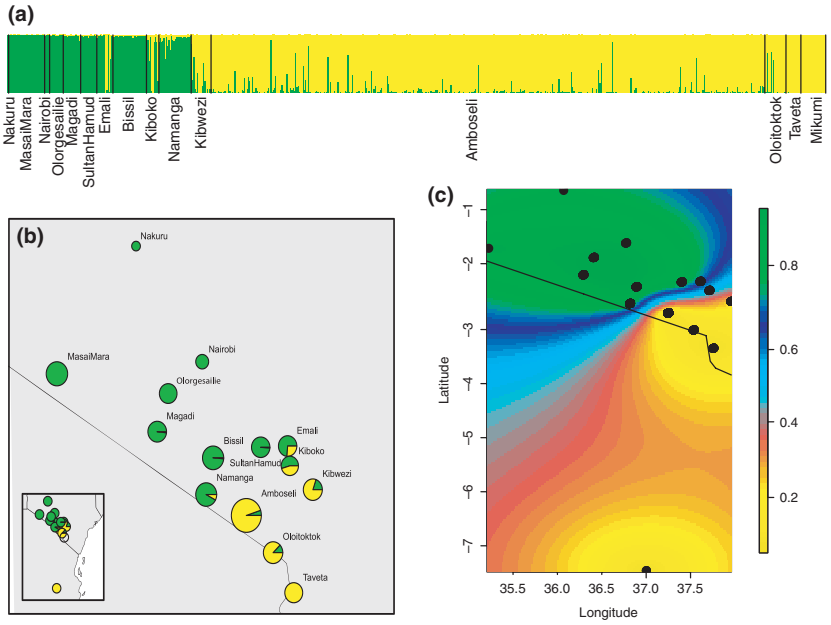

Fig. 2 Genetic structure of the anubis baboon–yellow baboon hybrid zone and surroundings. The results of the TESS analysis at $K_{max} = 2$ are shown as (a) a barplot of the individual ancestry fraction for each individual. Each individual is represented by a thin vertical line divided into two coloured segments that represent the proportion of membership in each cluster. Green reflects ancestry in the anubis baboon cluster, yellow reflects ancestry in the yellow baboon cluster, and black lines separate individuals from different populations. (b) Ancestry fractions for the two different clusters for each population (inset includes Mikumi); green reflects anubis baboon ancestry and yellow reflects yellow baboon ancestry. Sizes of each circle are proportional to the number of samples obtained from that population. (c) Spatial interpolation map showing the expected proportion of anubis ancestry (0 corresponds to an unadmixed yellow baboon; 1 corresponds to an unadmixed anubis baboon) in hypothetical populations across the sampled geographic region. Black dots show the location of populations sampled in this study.

observational and historical data from this population (Altmann & Altmann 1970; Alberts & Altmann 2001). In addition to Amboseli and Simba/Emali-Kiboko, however, we also identified one additional hybrid population (in a population composed mostly of anubis baboons) to the northwest of Amboseli at Namanga and two additional hybrid populations to the southeast of Simba/Emali-Kiboko and Amboseli, in Kibwezi and Oloitoktok (populations composed mostly of yellow baboons). Although a very small proportion of yellow genetic background was inferred for the (mostly anubis) populations at Magadi, Bissil and Sultan Hamud when the populations were considered as a whole, no single individual in any of these populations exhibited strong evidence for hybrid ancestry.

The locations of these three newly identified hybrid populations (close to the previously reported hybrid populations in Amboseli and Simba) suggest a rapid transition between populations dominated by an anubis genetic background and populations dominated by a yellow genetic background. A rapid transition was also suggested by an analysis using TESS to interpolate between the populations we sampled directly, providing estimates of the likely genetic composition of baboon populations elsewhere in east Africa, as well as probable locations in which other hybrid populations may be likely to occur (Fig. 2c). Finally, more evidence of a rapid transition comes from the fact that the heavily anubis population in Namanga and the mostly yellow baboon population in Amboseli are separated by only 52 km; for comparison, males in Amboseli have been known to move as much as 30 km from their natal group during their natal dispersal (S.C. Alberts and J. Altmann, unpublished). Consequently, the Amboseli–Namanga distance could potentially be traversed by a single male in his lifetime (if he dispersed repeatedly) or by multiple dispersing males over several generations. However, Namanga is separated from Amboseli by a stretch of waterless and treeless habitat inhospitable to baboons, and such a physical barrier could contribute greatly to the rapid anubis–yellow transition between Namanga and Amboseli; the extent to which such physical barriers might occur elsewhere in the putative hybrid zone is not well known.

Genetic diversity and relatedness in anubis baboons and yellow baboons

The estimates of individual admixture proportions provided by the TESS analysis allowed us to identify a

subset of the baboons in the data set as *P. anubis* or *P. cynocephalus* with high confidence (100 anubis individuals and 358 yellow individuals in total, based on assigned membership in the corresponding cluster at $q \geq 0.98$). To compare levels of genetic diversity between these species, we therefore calculated allelic richness and heterozygosity levels using these individuals as unadmixed representatives of their respective group.

Anubis baboons exhibited significantly greater genetic diversity than yellow baboons with respect to allelic richness and private allelic richness (Table 1; $P = 0.019$ for allelic richness and $P = 0.005$ for private allelic richness). For allelic richness, this pattern was observed at all but three of the microsatellite loci we investigated and all but two of the loci we investigated when considering only private alleles. In contrast, heterozygosity levels for anubis individuals did not significantly differ from heterozygosity levels for yellow baboons ($P = 0.138$).

When all individuals were analysed together ($n = 658$), we identified significantly positive F_{IS} values (e.g. a Wahlund effect) for half of our loci (at $P < 0.05$), as expected if the genetic distance between anubis baboon populations and yellow baboon populations is greater than within populations and if anubis and yellow baboons do not exhibit random mating. This pattern was strengthened when we considered only those individuals that were unlikely to be admixed ($n = 458$) (Table 1).

All populations we investigated exhibited a distribution of pairwise relatedness variables centred near 0, with the exception of Oloitoktok (Fig. S3, Supporting information). In this population, we identified a bimodal distribution of relatedness, with one mode near 0 and one mode shifted to approximately $r = -0.5$, reflecting individuals that were more genetically distant than expected given the genetic composition of the Oloitoktok baboon population as a whole. This result suggests that we sampled multiple social groups in this region that have not historically exchanged immigrants via dispersal, which is highly unusual for nearby social groups. Further examination of this pattern indicated that all genetically distant dyads reflected dyads composed of a hybrid individual and a likely unadmixed yellow individual, whereas all dyads in the distribution near zero represented hybrid–hybrid or yellow–yellow dyads. This finding suggests that unadmixed yellow baboon groups in this region may reside very close to social groups in which introgression has already taken place and that Oloitoktok is a region of active population genetic change. Overall, however, we identified no significant differences in the distribution of r values between any pair of populations in our analysis (Tukey's HSD: all $P > 0.05$).

Low level of population differentiation between anubis and yellow baboons in this region

Although genetic differentiation between anubis baboons and yellow baboons constituted the main axis of genetic variation in our sample (Fig. S4, Supporting information), the absolute levels of differentiation between these two taxa were relatively low. When considering only individuals that the TESS analysis categorized as anubis and yellow, F_{ST} between anubis baboons and yellow baboons was significant ($P < 0.001$), but only 0.083 (CI 95%: 0.054–0.112), consis-

Table 1 Descriptive statistics for all individuals in the sample and for unadmixed anubis baboons and yellow baboons

	All (n = 658)				Anubis (n = 100)					Yellow (n = 358)					Anubis+Yellow (n = 458)			
Locus	#A	Ar	H_e	F_{IS}	#A	Ar	pAr	H_e	F_{IS}	#A	Ar	pAr	H_e	F_{IS}	#A	Ar	H_e	F_{IS}
AGA	12	10.2	0.85	0.03*	11	10.3	1.0	0.81	0.07	11	9.2	0.2	0.82	−0.03	12	10.2	0.85	0.03*
D1	17	9.6	0.83	0.00	10	8.4	0.3	0.80	0.05	11	8.6	0.2	0.80	−0.04	12	9.0	0.81	−0.01
D3	13	9.6	0.82	0.02	12	11.7	2.0	0.79	0.02	10	7.2	0.3	0.81	−0.01	13	9.4	0.82	0.02
D4	11	8.1	0.82	0.02	7	7.0	0.3	0.82	0.07	10	7.9	1.0	0.82	0.02	10	8.2	0.82	0.04*
D6	19	14.5	0.85	0.04***	16	14.3	2.9	0.87	0.02	15	12.3	0.3	0.80	0.00	18	14.5	0.84	0.04**
D7	15	10.8	0.84	0.03*	9	8.4	2.6	0.80	0.09	11	9.4	1.2	0.80	−0.03	15	11.2	0.84	0.04**
D8	13	8.9	0.81	0.07***	13	11.1	2.7	0.80	0.07	10	8.2	0.0	0.73	0.02	13	9.1	0.79	0.10***
D10	17	13.4	0.86	0.05***	16	15.6	2.4	0.92	0.04	14	9.9	0.0	0.79	0.04	16	13.2	0.84	0.06***
D11	11	7.3	0.84	−0.04	9	8.3	1.5	0.83	0.02	7	7.0	0.0	0.84	−0.04	9	7.2	0.84	−0.03
D13	13	8.4	0.82	0.01	9	8.7	3.0	0.77	0.03	7	6.1	0.0	0.79	−0.04	11	7.9	0.82	0.02
D14	14	7.9	0.78	−0.03	10	8.9	2.4	0.81	−0.03	8	6.5	0.2	0.76	−0.02	11	7.6	0.77	−0.02
D18	14	7.8	0.78	0.02	7	7.0	1.0	0.83	0.29	8	6.3	0.4	0.72	−0.05	10	7.3	0.75	0.02
All	14	9.7	0.83	0.02***	11	10.0	1.8	0.82	0.06	10	8.2	0.3	0.79	−0.02	13	9.6	0.82	0.03***

#A, number of alleles; Ar and pAr, allelic and private richness calculated using ADZE; H_e, expected heterozygosity (or Nei's genetic diversity); F_{IS}, inbreeding coefficient. P-values for F_{IS} were derived via permutation tests to test for departure from Hardy–Weinberg expectations: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$. Locus names are abbreviated to chromosome number or the first three letters.

tent with estimates based on Mikumi, Maasai Mara and Amboseli data reported elsewhere (Tung *et al.* 2009; see Table S5, Supporting information) for pairwise F_{ST} values between all populations and Table S6 (Supporting information) for summary statistics by population).

The AMOVA results for the entire sample set also suggest low levels of genetic differentiation. Reflecting the large number of shared alleles between yellow and anubis baboons, only 2.8% ($P = 0.046$) of overall genetic variance could be explained by categorization of populations as anubis, yellow or hybrid, whereas 9.9% ($P = 0.001$) and 87.4% ($P = 0.001$) of genetic variance could be explained by variation between populations within these designated sets or between individuals within populations, respectively. However, inclusion of the hybrid populations, which are by definition composed of mixed ancestry individuals, probably depresses the genetic variance explained by anubis–yellow differentiation. Indeed, when populations containing hybrids were excluded (Namanga, Amboseli, Emali, Kiboko, Kibwezi and Oloitoktok), 10.1% of overall genetic variance distinguished anubis populations from yellow populations ($P = 0.001$), while the percentage of variance explained by population differentiation within regions (9.2%, $P = 0.001$) remained consistent. This result emphasizes that genetic distance between yellow baboons and anubis baboons in and around a hybrid zone is likely to be reduced relative to estimates derived from samples that might be obtained further away from the hybrid zone.

Migration is asymmetrically biased towards anubis migration into yellow populations

We obtained repeatable and well-resolved posterior probability distributions for all six IMa2 parameters, for all three of our comparisons (Fig. 3 and Figs. S5–S7, Supporting information). Interestingly, the resulting population genetic diversity ($\theta = 4Ne\mu$) and migration rate estimates revealed a pattern of change related to distance from centre of the hybrid zone.

Specifically, estimated population genetic diversity was slightly lower in yellow baboons than in anubis baboons when comparing Maasai Mara anubis baboons with Mikumi yellow baboons, the two populations farthest away from the hybrid zone. However, in both comparisons involving yellow baboons closer to the hybrid zone, this difference was reversed: at an intermediate distance from the hybrid zone, yellow baboons exhibited slightly higher population genetic diversity than anubis baboons, and on the border of the hybrid zone, yellow baboons exhibited substantially higher population genetic diversity than anubis baboons on the other side of the hybrid zone border (Fig. 3 and Table 2). This change in relative effective population size was accompanied by a change in estimated migration rates. Estimates of migration rates from anubis populations into yellow populations were significantly nonzero for both the comparison focused on populations distant from the current contact zone (Maasai Mara vs. Mikumi: 2Nm = 0.94, 95% HPD interval: 0.12–1.84) and the comparison of populations close to the hybrid zone (Namanga, Bissil and Sultan Hamud vs. Amboseli, Kibwezi and Oloitoktok: 2Nm = 2.94: 95% HPD interval: 0.45–5.44). This rate increased with decreasing distance between populations (Fig. 3 and Table 2). In contrast, migration in the reverse direction, from yellow populations into anubis populations, was significantly different from zero only close to the hybrid zone (2Nm = 1.37; 95% HPD: 0.07–2.84). In all cases, migration rates from anubis populations into yellow populations were larger than migration rates in the other direction, although credible intervals for migration rates in both directions overlapped zero for the intermediate distance Maasai Mara–Taveta comparison. Thus, the observed increase in the value of θ for yellow baboons with decreased distance from the hybrid zone may reflect the higher rate of introgression of anubis baboons into yellow baboon populations.

In contrast to the migration rate and population genetic diversity estimates, estimates of the mutation-scaled divergence time between anubis and yellow baboons were comparable whether considering populations distant from or close to the contact zone. For microsatellite data, unscaled estimates of divergence time are highly sensitive to assumptions about microsatellite mutation rate, which range across several orders of magnitude based on data from humans (10^{-3} and 10^{-5}) (Brinkmann *et al.* 1998; Estoup & Angers 1998; Ellegren 2000; Sun *et al.* 2009). When translated into years, therefore, our divergence time estimates cover a substantial range. Assuming a microsatellite mutation rate of 5×10^{-4} and a generation time of 8 years, we estimate a split time of yellow baboons and anubis baboons between 627 and 15 427 years ago (average mode across the three population comparisons: 3773; Table S7, Supporting information), much more recent than the 150 000–172 000 year estimates from mitochondrial DNA (Newman *et al.* 2004). However, a single order of magnitude change to a lower mutation rate (5×10^{-5}), within the range of possible mutation rates for microsatellite DNA, would place our estimates at a similar number (up to 154 000 years ago). Moreover, if the population history of this region has involved past discrete waves of introgression, divergence times may be diffi-

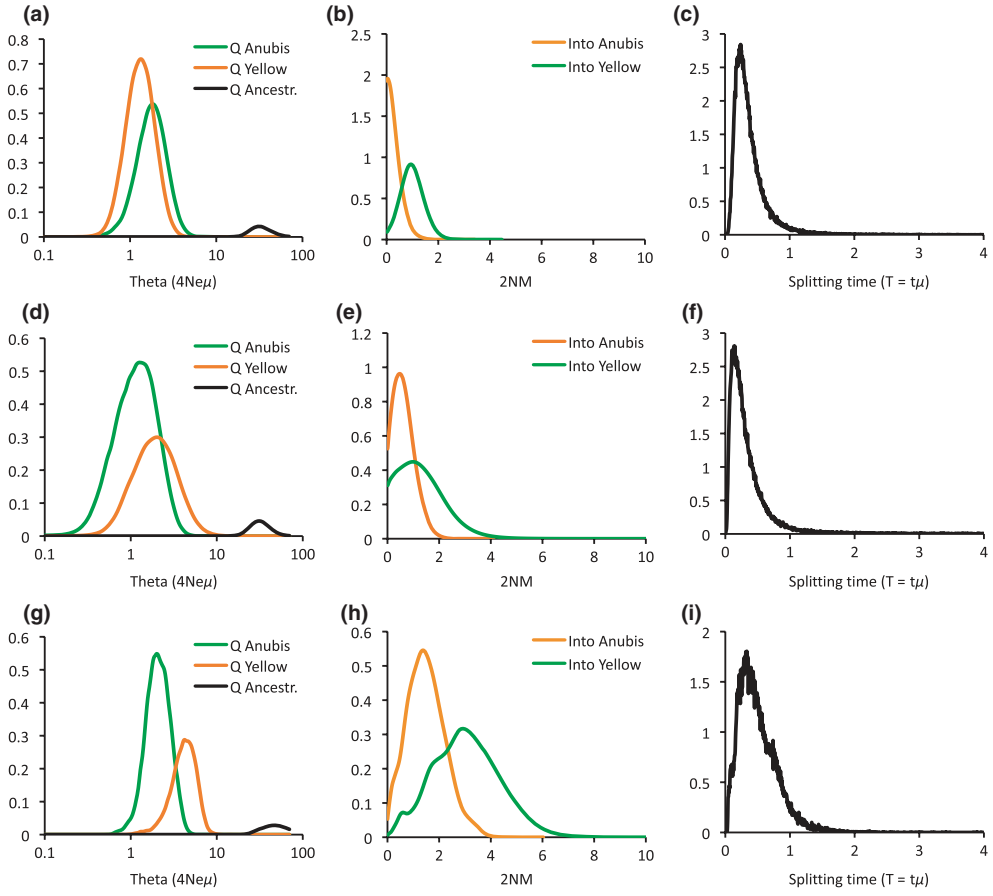

Fig. 3 Marginal posterior probability densities for each parameter of the IM model. Density curves are shown for the analyses comparing anubis and yellow baboons sampled far from the hybrid zones (Maasai Mara anubis baboons and Mikumi yellow baboons: a–f); at intermediate distance from the hybrid zone (Maasai Mara anubis baboons and Taveta yellow baboons: d, e, f); and at the border of the hybrid zone (Namanga, Bissil and Sultan Hamud anubis baboons and Amboseli, Kibwezi and Oloitoktok yellow baboons: g, h i). Scaled effective population sizes are shown in a, d and g; migration rates (2NM in number of migrating individuals per generation) are shown in b, e and h; and split time estimates are shown in c, f and i.

Table 2 Point estimates and 95% highest probability density (HPD) intervals of parameter estimates under the IM model*

	Far from the hybrid zone†			Intermediate distance from the hybrid zone‡			Bordering the hybrid zone§		
	Mode	HPD95Low	HPD95High	Mode	HPD95Low	HPD95High	Mode	HPD95Low	HPD95High
$t = T\mu$	0.2425	0.0575	0.8625	0.1325	0.0175	0.9875	0.3325	0.0425	1.042
$\theta_{Anubis} = 4N_e\mu$	1.855	0.735	3.955	1.295	0.385	3.325	1.995	0.945	3.955
$\theta_{Yellow} = 4N_e\mu$	1.365	0.525	2.905	1.995	0.525	6.475	4.235	2.065	7.455
$\theta_{Ancestral} = 4N_e\mu$	31.54	19.14	58.7	31.05	18.52	55.69	46.45	28.88	69.97
$m = M/\mu$ into anubis	0.0125	0	1.1270	0.3225	0	3.0130	0.8675	0	3.4730
$m = M/\mu$ into yellow	0.9175	0	3.3330	0.3025	0	3.5830	1.1430	0.1075	2.9380
2NM into anubis	0.04	0	0.87	0.48	0	1.40	1.37	0.07	2.84
2NM into yellow	0.94	0.12	1.84	0.98	0	2.99	2.94	0.45	5.44

*Values are provided for the three pairs of populations from each baboon species and scaled by the mutation rate.
†Results from the comparison of Masai Mara anubis baboons and Mikumi yellow baboons, the two populations furthest from one another.
‡Results from the comparison of Masai Mara anubis baboons and Taveta yellow baboons.
§Results from the comparison of Namanga, Bissil and Sultan Hamud anubis baboons and Amboseli, Kibwezi and Oloitoktok yellow baboons.

cult to accurately assess and could produce a more recently biased date.

Discussion

These results provide the first report of genetic structure in anubis baboons and yellow baboons based on nuclear markers, complementing the continent-wide (Newman *et al.* 2004; Zinner *et al.* 2009) and regional studies (Keller *et al.* 2010; Jolly *et al.* 2011) of mitochondrial and Y-chromosome variation in baboons elsewhere in Africa. Unlike mtDNA haplotypes, however, the nuclear markers we used here were in strong concordance with phenotypic and morphologically based taxon assignments within *Papio*. Indeed, the most prominent axis of genetic structure in this region is that which discriminates anubis baboons from yellow baboons, a pattern consistent with the motivating evidence for this study: phenotypic divergence by genetic background detectable in hybrids within the Amboseli population. Interestingly, although anubis baboons and yellow baboons readily mix within the hybrid zone as well as in captivity (Ackermann *et al.* 2006), we also found that the geographic transition between anubis baboon populations and yellow baboon populations was relatively rapid. The geographic extent of the zone of ongoing hybridization (including relatively unadmixed populations such as those at Namanga and Oloitoktok) covers only about a quarter of the northwest–southeast range of our transect and a minuscule amount compared with the entire geographic ranges of anubis baboons and yellow baboons, respectively (Fig. 1). This result implies that the vast majority of anubis baboon and yellow baboon populations in Africa have nuclear genomes that are not currently being influenced by hybridization between these two groups.

This result can be reconciled with the data from mitochondrial DNA, which indicates substantial hybridization across Africa, because mtDNA retains much more ancient signatures of introgression than do dispersed nuclear markers: mtDNA does not recombine, whereas recombination both breaks up associations among introgressed nuclear regions, and can contribute to purging introgressed loci linked to regions under negative selection (Harrison 1990; Funk & Omland 2003). Our results therefore model the process of hybridization-mediated genetic change during periods of active admixture, while previous mtDNA studies indicate the broader historical importance of this process in the baboon lineage.

Within the immediate region around the hybrid zone, anubis–yellow admixture appears to be the cause of interesting and potentially important patterns of evolutionary genetic change. In particular, the IMa2 analysis of our data suggests that hybridization in this region is asymmetric: more anubis individuals disperse into and are reproductively successful within yellow baboon populations than vice versa. This pattern is not uncommon within hybrid zones (Buggs 2007), including within primates. For example, higher rates of gene flow are observed in Indochina from rhesus macaques (*Macaca mulatta*) into cynomolgus (long-tailed) macaques (*Macaca fascicularis*) than from cynomolgus macaques into rhesus (Bonhomme *et al.* 2009; Stevison & Kohn 2009). Similarly, historical gene flow among chimpanzee subspecies appears to have been greater from western chimpanzees (*Pan troglodytes verus*) into central (*P. t. troglodytes*) and eastern (*P. t. schweinfurthii*) chimpanzees than vice versa (Hey 2010a). However, in most cases, the behavioural explanations for these differences in gene flow are speculative, relying on size differences among males (Stevison & Kohn 2009), for example, that could be misleading (Jolly *et al.* 2011). In contrast, here the genetic data in favour of asymmetric hybridization corroborate the direction predicted by phenotypic observations in a hybridizing population. Specifically, observations in Amboseli have previously indicated that (i) anubis introgression into Amboseli, at least in recent years, is rare but regular, suggestive of directional anubis population movement into this historically yellow baboon population (Tung *et al.* 2008); (ii) anubis-like individuals in Amboseli reach social and reproductive maturation earlier than yellow baboons (Charpentier *et al.* 2008); and (iii) male anubis-like individuals in Amboseli also have an advantage in gaining consortships (Tung *et al.* submitted), a key component of winning paternities (Alberts *et al.* 2006). These results suggested that individuals with more anubis ancestry tend to have an adaptive advantage over unadmixed yellow baboons, thereby providing a set of behavioural mechanisms that may explain the patterns of genetic structure and gene flow we describe here.

Our data also indicate that the anubis migration rate into yellow baboon populations is higher than the rate of yellow migration into anubis populations, a pattern that is most marked close to the anubis–yellow contact zone, but which also is apparent farther away from the contact zone. Although yellow baboons do enter into anubis baboon populations near the zone of contact, the genetic effects of this introgression dissipate much more rapidly than the effects of anubis introgression across the hybrid zone into yellow populations. Indeed, the estimated migration rates around the contact zone suggest a relatively regular rate of movement by anubis into nearby yellow baboon social groups, with the range of likely values encompassing the estimate of about 1.33 anubis immigrants per generation obtained from observational field data in Amboseli (Tung *et al.* 2008). Interestingly, we also observed an atypical bimodal pattern of relatedness in samples from the (likely recent) hybrid

population in Oloitoktok, at the southeastern extent of anubis introgression. Oloitoktok may therefore represent the easternmost wavefront of the previously proposed anubis baboon range expansion (Jolly 2001; Jolly *et al.* 2011), with hybrids detectable in some groups, but not yet all groups, in this population. Alternatively, an admixed social group may recently have moved near Oloitoktok, as occurred in Amboseli 26 years earlier around the onset of the recent wave of hybridization (Samuels & Altmann 1986)—an event that almost certainly contributed to the rapid increase in hybrid individuals within that population.

These results and the behavioural data from Amboseli suggest that, at least at the moment, east African anubis populations are indeed expanding at the expense of yellow baboon populations, that the contact zone stretching southwest to northeast through Amboseli probably represents an introgression front, and that this effect is probably mediated by reproductive and life history advantages in mixed populations that are related to the anubis genetic background. Importantly, the observational field data available for this region not only allow us to posit a mechanism that accounts for the inferred asymmetry in migration rates, but also allow us to rule out the possibility that the narrowness of the hybrid zone is because of a classic tension zone scenario in the region around Amboseli (in which selection against hybrids counterbalances dispersal and reproduction across species boundaries: Barton & Hewitt 1985; Barton 1989). Indeed, while additional work will be necessary to account for the rapid transition between anubis baboons and yellow baboons in this region—which could potentially include ecological selection against hybrids on the edges of the hybrid zone that we have described—the behavioural data strongly indicate that, in at least part of this contact zone, depressed hybrid fitness is not sufficient to explain this pattern.

In addition to asymmetric gene flow and possible local anubis range expansion, our data also indicate that hybridization in this region is the underlying cause of a second pattern: increased genetic diversity among yellow baboon populations close to the hybrid zone boundary. Specifically, based on the three IMa2 comparisons we pursued, yellow baboon populations that receive more anubis immigrants also exhibit higher levels of population genetic diversity. Thus, our estimates of θ for yellow baboons increased with decreasing distance from, and increasing migration across, the yellow–anubis contact zone. In contrast, genetic diversity in anubis baboon populations, which apparently receive relatively few yellow baboon immigrants, does not benefit from proximity to the contact zone. These observations indicate that immigration and admixture rates may be one of the primary determinants of variation in the levels of population genetic diversity in this region and that populations near the contact zone may exhibit unusually high levels of genetic diversity relative to other baboon populations in general. Given that anubis–yellow genetic background is already known to be correlated with several adaptively relevant traits (Alberts & Altmann 2001; Charpentier *et al.* 2008; Tung *et al.* submitted), the relationship between this increased genetic diversity, phenotypic diversity, and heritability and selection on such traits in response to hybridization represents a fascinating topic for further exploration, especially if anubis baboons continue to expand eastwards and new populations begin receiving an influx of novel genetic variation.

Both additional behavioural data and additional genetic data will be necessary to address further questions about the future evolutionary trajectory of these species. Our results indicate that although nuclear markers support traditional morphology-based taxonomic distinctions among baboons, levels of genetic differentiation between anubis baboons and yellow baboons are relatively low. In comparison with microsatellite-based analyses of bonobos (*Pan paniscus*) and three chimpanzee subspecies (western: *P. troglodytes verus*; central: *P. t. troglodytes*; and eastern: *P. t. schweinfurthii*), for example, the level of genetic divergence between anubis and yellow baboons (generally given taxonomic species status) is in fact similar only to the most recent split among chimpanzees, between central and eastern subspecies (Becquet *et al.* 2007) (note, however, that other primate taxa given species status also exhibit surprisingly low levels of genetic distance: e.g. in gibbons between *Hylobates moloch* and *Hylobates muelleri*: Kim *et al.* 2011). The low level of nuclear genetic differentiation is somewhat surprising given the more ancient divergence times identified for the major baboon mitochondrial lineages (Zinner *et al.* 2009). However, historical admixture and anubis range expansion may have erased many of the nuclear genetic differences that have accumulated thus far, particularly in the geographic region that was the focus of this study. Indeed, admixture may have extensively shaped the baboon populations in this region in the past: several investigators have hypothesized that the 'ibean' morphotype of yellow baboons, which typifies yellow baboons in and around Amboseli, resulted from a past wave of anubis admixture into yellow baboon populations (Jolly 1993; Zinner *et al.* 2008, 2009) or from yellow baboon hybridization with hamadryas baboons (Zinner *et al.* 2009). Anubis baboons in this region may also have hybridized with hamadryas baboons in the past (Zinner *et al.* 2009). Such high rates of admixture are likely to act as a major barrier to complete separation of anubis and yellow baboons into reproductively isolated, 'good' species.

Taken together, our results illustrate how complementary information on population genetic structure and fine-scale behaviour and mating structure provides evolutionary insight into the dynamics of an active primate hybrid zone. However, these results also reinforce the need for data on additional dimensions of this puzzle. First, they highlight the importance of more extensive sampling of autosomal nuclear markers across the ranges of anubis baboons and yellow baboons. Genetic data from such samples will be necessary to obtain better divergence time estimates for the initial split between these two lineages and to explore more elaborate models of population history (for example, using approximate Bayesian computation: Beaumont *et al.* 2002; Csillery *et al.* 2010) which could shed light on the history of divergence between morphotypes in baboons as well as divergence between species/subspecies. In particular, such approaches could explicitly model the possibility of repeated bouts of divergence followed by gene flow, a scenario that may have complicated our estimates of the initial anubis–yellow split time, which were based on a relatively simple model of isolation with migration. Second, they emphasize the need for an ecological perspective on the hybrid zone and its surroundings. One plausible explanation for the phenotypic distinctiveness of anubis and yellow baboons, as well as the sharp phenotypic and genetic transition zone between their respective ranges, is that the divergence between yellow baboons and anubis baboons is a result of ecological selection in favour of divergence (Nosil *et al.* 2009)—a process that would oppose the homogenizing influence of hybridization. However, although circumstantial evidence indicates differences in the ecological regimes of anubis and yellow baboons (Kingdon 1971), no formal analyses of ecological niches or ecological adaptation in these groups have yet been conducted. Such work should be part of the next step in understanding the dynamics of evolutionary change in this hybrid zone, by providing a perspective on ecological structure that complements our growing sense of the impact of admixture on social organization, mating system and genetic structure.

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M.J.E.C. is interested in the study of mating systems, kin relationships and social structure in primates. M.C.F. studies demographic and selective processes associated with population adaptation and divergence. He is interested in methodological and statistical issues involved in the study of species diversification and phylogeography. E.C. is an evolutionary biology student. J.P.R. is interested in phylogenetics, phylogeography, and visual communication. T.J. and L.B. are laboratory assistants in genetics labs. N.B. is a research associate with a

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Data accessibility

Genotype data from this project are deposited at Dryad: doi:10.5061/dryad.sk013.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Genetic structure inferred by TESS for K_{max} = 2 to 5.

Fig. S2 Ancestry fractions for each sampled population.

Fig. S3 Distribution of pairwise relatedness values for 11 populations.

Fig. S4 Principal component plot of genetic variation in the data set.

Fig. S5 Marginal posterior distributions for each of three IMa2 runs for the Masai Mara-Mikumi comparison.

Fig. S6 Marginal posterior distributions for each of two IMa2 runs for the Masai Mara-Taveta comparison.

Fig. S7 Marginal posterior distributions for each of two IMa2 runs for the Namanga/Bissil/Sultan Hamud-Amboseli/Kibwezi/Oloitoktok comparison.

Table S1 Sample size and location by population.

Table S2 Scoring rules for microsatellite genotypes using the multitube approach.

Table S3 Proportion of allelic dropout and contamination per locus analyzed.

Table S4 Parameters, settings, run times, and number of genealogies saved and used for parameter estimations in IMa2.

Table S5 Pairwise F_{ST} values between populations (below the diagonal) and *P*-value for F_{ST} estimates (above the diagonal).

Table S6 Descriptive statistics by population.

Table S7 Point estimates and 95% HPD intervals of parameter estimates under the IM model, converted to demographic units.

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