Molecular Ecology (2008) **17**, 1998–2011 doi: 10.1111/j.1365-294X.2008.03723.x

Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population

J. TUNG,* M. J. E. CHARPENTIER,*† D. A. GARFIELD,* J. ALTMANN‡§ and S. C. ALBERTS*§
Department of Biology, Duke University, PO Box 90338, Durham, NC 27708, USA, †Centre d'Ecologie Fonctionnelle et Evolutive, Unite Mixte de Recherche 5175, Centre National de la Recherche Scientifique, 1919 Route de Mende, 34293 Montpellier Cedex 5, France, ‡Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08540, USA, §Institute of Primate Research, National Museums of Kenya, PO Box 24481, Nairobi, Kenya

Abstract

The process and consequences of hybridization are of interest to evolutionary biologists because of the importance of hybridization in understanding reproductive isolation, speciation, and the influence of introgression on population genetic structure. Recent studies of hybridization have been enhanced by the advent of sensitive, genetic marker-based techniques for inferring the degree of admixture occurring within individuals. Here we present a genetic marker-based analysis of hybridization in a large-bodied, long-lived mammal over multiple generations. We analysed patterns of hybridization between yellow baboons (*Papio cynocephalus*) and anubis baboons (*Papio anubis*) in a well-studied natural population in Amboseli National Park, Kenya, using genetic samples from 450 individuals born over the last 36 years. We assigned genetic hybrid scores based on genotypes at 14 microsatellite loci using the clustering algorithm implemented in STRUCTURE 2.0, and assessed the robustness of these scores by comparison to pedigree information and through simulation. The genetic hybrid scores showed generally good agreement with previous morphological assessments of hybridity, but suggest that genetic methods may be more sensitive for identification of low levels of hybridity. The results of our analysis indicate that the proportion of hybrids in the Amboseli population has grown over time, but that the average proportion of anubis ancestry within hybrids is gradually decreasing. We argue that these patterns are probably a result of both selective and nonselective processes, including differences in the timing of life-history events for hybrid males relative to yellow baboon males, and stochasticity in long-distance dispersal from the source anubis population into Amboseli.

Keywords: Amboseli baboons, gene flow, hybrid fitness, hybrids, microsatellites, population structure

Received 28 November 2007; revision received 20 January 2008; accepted 24 January 2008

Introduction

Naturally occurring interspecific hybrids have been of long-standing interest in evolutionary biology because of their importance in helping to understand the processes of introgression, speciation, and reproductive isolation (Mayr 1942; Anderson & Stebbins 1954; Barton & Hewitt 1985; Arnold 1992; Arnold & Hodges 1995). Depending on the adaptive consequences of hybridization, hybrids can reveal strong selective boundaries between species when hybrids are selected against, or can illustrate how increased heterozygosity and genetic diversity may lead to a hybrid fitness advantage. Additionally, hybridization is itself an important mechanism of evolutionary change. Through the introduction of new genetic variation and new allelic combinations, hybridization may influence the evolutionary trajectory of the hybrid population, the parental populations, or both (Anderson & Stebbins 1954; Lewontin & Birch 1966; Arnold 1992; Rieseberg 1997; Rieseberg *et al*. 2003).

The evolutionary consequences of hybridization are related to the frequency of interspecific mating, the genetic

Correspondence: Jenny Tung, Fax: +01 919-660-7293;
E-mail: jt5@duke.edu

distance between parental species, and the fitness effects of hybridity. Studies on hybridization, particularly within hybrid zones, have largely focused on this last component, especially on the classification of hybrids as either more or less fit than one or both of their parental species. Hybrids with relatively high fitness suggest hybrid advantage or hybrid superiority; this is often associated with hybridization that occurs in specialized ecological circumstances (e.g. temporal or clinal ecological transitions). In contrast, hybrids with relatively low fitness suggest that selection against hybrids in a 'tension zone' helps to maintain species boundaries and counteracts the effect of regular gene flow (Barton & Hewitt 1985; Grant & Grant 1992; Barton 2001; reviewed in Arnold & Hodges 1995). Alternatively, if hybrid fitness is equivalent to that of the parental species and independent of ecological context, hybrids may represent a snapshot of species fusion in process (Rhymer & Simberloff 1996; Salzburger *et al*. 2002). This framework provides three mutually exclusive predictions about the consequences of hybridization, differentiated by the direction of relative fitness differences between hybrids and the parental species (Moore 1977; Arnold & Hodges 1995). However, while these predictions suggest that the conditions surrounding hybridization and the fitness consequences of hybridization are static, the rate and consequences of hybridization within a population may in fact fluctuate over time.

Here, we describe a dynamically changing pattern of hybridity in a wild population of savannah baboons from the Amboseli basin of southern Kenya, a known baboon hybrid zone (Maples & McKern 1967; Samuels & Altmann 1986; Alberts & Altmann 2001). The focal population has been under continuous observation on a near-daily basis since 1971, resulting in a data set representing up to six generations of individually known animals. DNA samples are available for a large number of these individuals (Altmann *et al*. 1996; Alberts *et al*. 2006; Loisel *et al*. 2006). The Amboseli baboon population is comprised primarily of yellow baboons (*Papio cynocephalus*). It represents one of the type examples of the widespread 'ibean' morphotype of yellow baboons (Jolly 1993; see Supplementary material), which shares more morphological similarities with anubis baboons than do the two other yellow baboon morphotypes (the 'typical' and 'kinda' morphotypes), possibly because of anubis admixture that has occurred in the ibean lineage over the course of evolutionary history (Jolly 1993). In addition, hybrids are found in the population due to the occasional immigration of anubis (olive) baboons (*Papio anubis*) from outside the basin (Alberts & Altmann 2001). Specifically, six anubis males have immigrated into study groups in the basin over the course of the study (see Supplementary material), and one small (*c*. 18) mixed-sex group of anubis baboons also entered the basin in the early 1980s (Samuels & Altmann 1991). Hybrids now occur in both study groups and in nonstudy groups in the basin, and they have resulted not only from these anubis immigrations, but also from the movement and successful reproduction of hybrid males between and within study and nonstudy groups.

The status of Amboseli as a hybrid zone is consistent with the geographical distribution of baboon species: this population is situated on the boundary between the ranges of yellow and anubis baboons, with yellow baboons approximately to the south and east and anubis baboons to the north and west (Jolly 1993; Newman *et al*. 2004; see Fig. 1 in Alberts & Altmann 2001 for a fine-scale map of the study area). These two species represent two of the five commonly recognized baboon species (or subspecies: see discussion in Jolly 1993) within the genus *Papio* (also including *P. hamadryas*, *P. papio*, and *P. ursinus*), all of which exhibit moderate geographical separation, are readily distinguished morphologically, and represent a range of distinct patterns of social structure and behaviour (Jolly 1993, 2001; Henzi & Barrett 2003; Newman *et al*. 2004). Nevertheless, all baboon species can interbreed with their neighbouring congeners to produce viable, fertile hybrid offspring, and several naturally occurring hybrid zones have been described near the geographical boundaries between species (Maples & McKern 1967; Nagel 1973; Phillips-Conroy & Jolly 1986; Alberts & Altmann 2001; Jolly & Phillips-Conroy 2007). Hybrid anubis-yellow baboons have also been documented in captivity (e.g. Ackermann *et al*. 2006).

Intriguingly, in both the well-described anubis-hamadryas hybrid zone in Ethiopia and in the Amboseli anubis-yellow hybrid zone, morphological estimates of hybridity indicate that patterns of hybridization and introgression have changed over time (Phillips-Conroy & Jolly 1986; Alberts & Altmann 2001). In Ethiopia, the original pattern described by Nagel (1973) based on work in the late 1960s was characterized by spatially distinct anubis, hybrid, and hamadryas groups, with hybrids confined to a narrow intermediate zone between the two parent species. Between the late 1960s and 1973, the anubis-hamadryas hybrid zone expanded and gave way to a graded clinal pattern, suggesting that hybrids enjoyed success in backcrossing into both parent populations (Phillips-Conroy & Jolly 1986). Hybrids have also been reproductively successful within Amboseli. Based on morphological estimates of hybridity, the frequency of hybrid births in Amboseli increased from the 1960s and 1970s, when no anubis and few possible hybrid baboons were observed, to the 1990s, when hybrids made up an estimated 10% of births (Alberts & Altmann 2001). These changes may reflect either increasing anubis baboon gene flow into the predominantly yellow baboon-occupied basin, the selective outcome of fitness differences between hybrid baboons and yellow baboons, or a combination of both. Analyses based on morphological scoring of hybrids indicated that hybrid males tend to undergo natal dispersal earlier in life than do yellow males (Alberts & Altmann

2001). Dispersal represents a major life-history marker for male baboons, and variation in the timing of this event is correlated with the timing of other important social and reproductive milestones, including age at physical maturation and age at first mate-guarding episode, a proxy for first reproduction (Alberts & Altmann 1995; Charpentier *et al*. 2008). Therefore, if the benefits of earlier dispersal are not offset by costs later in life, earlier dispersal may result in a selective advantage. We hypothesized that a selective advantage would therefore accrue to hybrids, mediated by early maturation and dispersal in males, and that this advantage would be reflected in changes in the frequency of hybrid individuals in the population. This possibility motivates a more in-depth, genetically based analysis of hybridity within the Amboseli population.

Towards that end, here we extend our previous analysis of hybridization patterns in Amboseli by assessing multilocus microsatellite genotypes for evidence of admixture in this population. This genetic analysis of hybridity is an important extension of our previous morphological analysis of hybridity. First, genetic marker-based analyses do not depend on observer-defined phenotypes (e.g. pelage colour or body size) identified a priori to differentiate the parental species. Second, relying on specific phenotypes can be misleading because phenotypic differences may reflect variation at only one or a few loci, whereas hybridization is a genome-wide phenomenon. In cases involving dominant and recessive variants, the degree of hybridization inferred from the trait is particularly vulnerable to overestimation or underestimation because heterozygotes may not express the mean parental phenotype. Third, credible intervals can readily be assigned to genetic marker-based hybridity estimates, permitting interpretation of these estimates in the light of quantitative uncertainty. Finally, genetic assignments of hybridity lend themselves directly to analyses of admixture-mediated changes in population genetic structure, which can help address questions about the possible fitness consequences of hybridity and introgression. We also compare our results to previously collated morphological hybridity estimates. Such comparisons help identify any systematic biases that differentiate the morphological and genetic hybrid scoring methods, and particularly increase confidence in those assignments for which morphological and genetic estimates are congruent.

We assigned genetic hybrid scores with data from 14 unlinked microsatellites typed in 450 Amboseli baboons born from 1968 to 2004, using the Bayesian clustering algorithm implemented in the program STRUCTURE 2.0 (Pritchard *et al*. 2000; Falush *et al*. 2003). These hybrid scores estimate the proportion of each individual's genome derived from *P. anubis* ancestry. Similar approaches have been previously applied towards the identification of introgression in European wildcats (Beaumont *et al*. 2001; Pierpaoli *et al*. 2003; Lecis *et al*. 2006), characterization of hybrid zone dynamics in Baltic fish (Nielsen *et al*. 2003, 2004), and confirmation of the genetic integrity of endangered species, such as the black-faced impala (Lorenzen & Siegismund 2004). We assessed the robustness of our results by checking for consistency of the hybrid score assignment in families using pedigree data, and through simulations that tested the sensitivity of our results to different conditions.

Our analyses suggest that, even with a modest number of genetic markers, we have good power to identify the signature of hybridity within individual baboons. Using these data, we describe how hybridization patterns within the Amboseli population — both changes in the abundance of hybrids and in the distribution of hybrid scores — have changed over time. We evaluate these results in the light of known and inferred patterns of anubis immigration into this population, and speculate on the resulting implications for the evolutionary dynamics of this hybrid zone.

Materials and methods

Samples and genotyping

We assigned genetic admixture scores to 450 Amboseli baboons born between 1968 and 2004. All subjects were born in or immigrated into groups subject to long-term monitoring by the Amboseli Baboon Research Project, with continuous observation starting in 1971 and continuing to the present (Altmann & Alberts 2003; Alberts *et al*. 2006). Those born into study groups had birth dates known to within a few days. Birth dates for immigrants were estimated using morphological and behavioural evidence and a set of criteria calibrated to baboons of known age, such as pelage condition and canine wear (Alberts & Altmann 1995; Alberts *et al*. 2003). One of the study groups began feeding at a refuse pit associated with a tourist lodge in the 1980s (Altmann & Muruthi 1988; Muruthi *et al*. 1991; Altmann & Alberts 2005). Because this alternative foraging pattern influenced immigration and emigration in this group, we excluded from our analysis all individuals born into this group after 1979.

In order to capture change in hybridity within the population over time, we partitioned the total data set into four nonoverlapping data partitions, or 'cohorts', corresponding to individuals born in the late 1960s or 1970s (the 1960s/1970s data partition: $n = 31$), the 1980s (1980s: $n = 117$), the 1990s (1990s: $n = 187$), and the 2000s (2000s: $n = 115$). The 10-year span of these partitions is somewhat arbitrary, but is a convenient method of dividing the data set and allows for one to two generations (~6 years in this population) to pass between re-evaluations of the data.

As part of previous analyses of paternity and relatedness, all 450 Amboseli baboons included in this analysis were genotyped at 14 polymorphic microsatellite loci. Genomic DNA was available for all individuals based on either

extractions from blood samples obtained during infrequent dartings or from noninvasively collected faecal samples (for details on faecal DNA extractions see Buchan *et al*. 2005; Alberts *et al*. 2006). The methods used for genotype assignments and data on the performance of the 14 microsatellite primer pairs have been reported by Buchan *et al*. (2005) and Alberts *et al*. (2006). Importantly for these analyses, no two loci were located on the same chromosome, ensuring that there was no physical linkage between any of the 14 markers (Rogers *et al*. 2000). Infrequent polymerase chain reaction (PCR) failure and inconsistent genotyping results, which may occur during noninvasive genotyping, led to missing data for 2.48% of the total Amboseli genotyping data set (i.e. for a small subset of individuals at a few loci).

In order to help generate estimates of yellow-anubis hybridity, we also produced genotypes from the same set of microsatellite markers for a total of 13 *Papio anubis* individuals. Three of these were anubis males that immigrated into Amboseli study groups from anubis source populations; they were designated as anubis based on their morphology and coat colour as assessed by experienced observers. The other 10 *P. anubis* samples were from Masai Mara National Reserve, Kenya, about 250 km to the northwest of Amboseli and far from the range of yellow baboons, as well as from any hybrid zone (Jolly 1993; Kingdon 1997). All Masai Mara samples were collected in August 2004 and were obtained as extracted DNA from the Integrated Primate Biomaterial and Information Resource (courtesy of R. Sapolsky; sample numbers are provided in Table S1, Supplementary material). Due to PCR failure or inconsistent genotyping, 2.14% of the total set of individual-by-locus genotypes for Masai Mara individuals was missing in this analysis.

Summary statistics on heterozygosity at the 14 microsatellite markers for the Amboseli population (including the three anubis males that immigrated into Amboseli) and for the Masai Mara population are provided in Table S2, Supplementary material.

Assignment of genetic hybrid scores

For the 450 Amboseli baboons included in this study, we generated an estimate of the proportion of each individual's genome attributable to anubis (as opposed to yellow) baboon heritage (i.e. a 'genetic hybrid score') using the admixture analysis implemented in the program STRUCTURE 2.0 (Pritchard *et al*. 2000; Falush *et al*. 2003). STRUCTURE uses a Bayesian model-based clustering algorithm to estimate the allele frequency distributions for each marker locus for each source population (K) that contributes to the admixed population. The program probabilistically assigns each genotyped allele for each individual to one of these populations. The result is an estimate of the amount of genetic material contributed from each source population to each individual. Importantly, this method allows individual-specific admixture estimates to be produced even when most alleles are shared between source populations, and does not require prior specification of allele frequencies in these populations. Rather, it draws on genotype data for all individuals in the data set ($n = 463$ total individuals, including 13 individuals of known genetic background) in order to assign estimates of admixture. The degree to which the assignments maximize linkage equilibrium and Hardy–Weinberg equilibrium within populations determines the likelihood of a particular set of assignments.

We ran STRUCTURE under the F model, which allows allele frequency spectra between the source populations to be correlated and allows admixture within individuals (Falush *et al*. 2003). All individuals were analysed in a pooled analysis (see Supplementary material and Table S3 for justification of this decision). We flagged the 13 anubis baboons (10 Masai Mara baboons and three anubis immigrants into Amboseli) as members of a single identified population and flagged the 450 Amboseli baboons as unassigned to a population. We set the total number of populations, K, equal to 2. Thus, the 450 Amboseli individuals could have been assigned to the anubis cluster (made up of the Masai Mara baboons and the three anubis immigrants), to an alternative cluster distinct from the anubis cluster, which we interpret as characteristic of a yellow baboon genetic make-up, or as hybrids between the two clusters. Ideally, we would have drawn more of the anubis sample from the population of origin for anubis immigrants into Amboseli, but sampling constraints prevented us from pursuing this strategy both because the identity of this population is uncertain, and because sampling from unhabituated baboons is logistically difficult. Hence, we also examined the effects of our small anubis sample size using three different sets of simulations, described below.

Each analysis was run with a burn-in length of 100 000 Markov chain Monte Carlo iterations and a run length of 1 million iterations (see Supplementary material for parameter settings). To obtain a final genetic hybrid score for each individual, we reran the entire analysis three times and averaged the proportion of each Amboseli individual's genome assigned to the anubis population over these three runs.

Comparison with morphological hybrid scores

Morphological hybrid scores were assigned prior to genetic analysis, based on observation and scoring of seven phenotypic characteristics that distinguish anubis and yellow baboons: coat colour, body shape, hair length, head shape, tail length and thickness, tail bend, and muzzle skin appearance (see Alberts & Altmann 2001). Three to four experienced observers independently assigned separate morphological hybrid scores, which were then averaged into one composite hybrid score (Alberts & Altmann 2001).

We rescaled these morphological hybrid scores to correspond to the scale of the genetic hybrid scores, with 0 representing pure yellow and 1 representing pure anubis. Interobserver agreement and agreement between morphological scores assigned at different life stages were both high (Supplementary material). In all comparisons of morphological hybrid scores and genetic hybrid scores, we used the average of the composite scores assigned during adulthood as the morphological point estimate of hybridity. For those individuals that had yet to reach adulthood by the end of data collection or that died before reaching adulthood, we used the average of composite scores assigned as juveniles instead ($n = 84$). In all, morphological hybrid scores were available for 315 of the 450 Amboseli baboons used in the genetic analysis.

In order to assess agreement between the morphological scores and the genetic hybrid scores assigned in this study, we calculated the Pearson correlation between the two scores for the same individuals ($n = 315$). However, because the Amboseli population is predominantly yellow, a large proportion of these scores fall at or near 0. We therefore calculated a *P* value for this correlation using a nonparametric approach. We randomly permuted the genetic hybrid scores 10 000 times against constant morphological hybrid scores, using the R statistical package (R Development Core Team 2006). We ranked the observed correlation coefficient, *r*, from the actual data among the 10 000 *r*-values calculated from these permutations. The significance of the observed correlation was defined as the proportion of larger *r*-values observed in the random permutations.

Assessment of the consistency of genetic hybrid scores using pedigree data

In order to test whether our method of assigning genetic hybridity was consistent across individuals, we correlated the genetic hybrid score for individuals with the midpoint value for their parents, when all three baboons were included in the study ($n = 272$ offspring–parent triads, including the offspring–parent triads that included anubis immigrants). Because STRUCTURE infers the population of origin for each allele copy for each individual (not the probability of population of origin for each allele across individuals) and has no prior information on pedigree relatedness, a strong correlation between the parental mean and the offspring hybrid score is not a necessary outcome of the program, and should occur only when it is performing consistently for the whole data set. For comparison, we conducted the same analysis using morphological hybrid scores ($n = 151$ offspring–parent triads). Because of the large number of zero or near-zero values in both data sets, significance values for these analyses were assigned by repeated permutations of parental midpoint values on constant individual hybrid scores; this approach was identical to the method we used to assign significance in the morphological hybrid score–genetic hybrid score comparison. A high correlation between parents and offspring for the genetic hybrid scores would indicate that assignments were made in a consistent manner; it would not independently validate these scores, because paternity assignments were made using the same microsatellite loci used for the hybridity analysis. However, this method does act as an independent measure of the validity of the morphological scores, because the morphological hybrid scores were assigned using a completely different data set than that used to generate pedigrees.

Assessment of the robustness and replicability of genetic hybrid scores using simulation

We used three sets of simulations to assess whether the genetic hybrid scores we assigned were robust to replication and/or different estimates of the allele frequency spectra for the known anubis baboons. Because we use a relatively small number of known anubis in the analysis, the estimated allele frequencies based solely on the known anubis will approximate the 'true' allele frequency spectra in the anubis source population, but are almost certainly inexact. The purpose of these simulations is to test whether the genetic hybrid score assignments remain stable within a realistic range of uncertainty surrounding these allele frequency estimates.

Simulation 1: replicability of hybrid scores given observed allele frequencies. We generated 100 simulated baboon data sets that were of the same size (450 individuals) as the empirical data set and that exhibited a similar distribution of genetic hybrid scores as inferred from the observed genetic data. We asked how well the inferred hybrid score for a simulated individual matched with the known degree of hybridity for the same individual, given (i) the observed degree of genetic differentiation between yellow and anubis baboons, (ii) the number of markers used in this study and the observed allelic diversity for each marker, and (iii) the number of individuals in the data set. This analysis assessed the replicability of our results, given the same model of allele frequency distributions for both source populations.

First, we created a 'yellow' pool of alleles from the genotypes of 120 Amboseli individuals with the lowest genetic hybrid scores (range = 0.029–0.058 in the empirical data set), and an 'anubis' pool of alleles from the 10 Masai Mara baboons and the three anubis immigrants into Amboseli, for all 14 markers. These pools of alleles were used to create all 450 simulated individuals in the 100 simulated data sets in Simulation 1. Second, to create each individual within a simulated data set, we randomly drew a genetic hybrid score from the 450 actual (i.e. not simulated) genetic hybrid

scores in the empirical data set. Third, simulated genotypes were created for each of these simulated individuals by sampling twice from the anubis pool of alleles at a probability equal to the value of the genetic hybrid score previously assigned for that individual, or else from the yellow pool of alleles, for each of the 14 marker loci. For example, if a genetic hybrid score of 0.60 was randomly drawn from the observed data set, then for each of the two alleles at each of the 14 marker loci, the simulated individual would have a 60% probability of being assigned an allele from the anubis pool of alleles, and a 40% chance of being assigned an allele from the yellow baboon pool of alleles. The proportion of the total genotypes drawn from the anubis baboon pool of alleles following this step represented the 'known' hybrid score for that simulated individual. All samplings were conducted with replacement, so that for each draw of a genetic hybrid score for each new individual in the simulated population, and for each draw of an allele from the anubis or yellow baboon pools, the original probabilities still obtained. We repeated this procedure 100 times to create 100 simulated data sets, each containing 450 individuals. The resulting data sets were run in STRUCTURE using the parameter set chosen for the original assignment of genetic hybrid scores (see Supplementary material) to produce the 'inferred' genetic hybrid scores for the simulated individuals. In order to assess the accuracy of hybrid score assignment, we evaluated the difference between this inferred genetic hybrid score and the known genetic hybrid score for each simulated individual (n = 45 000).

Simulation 2: sensitivity of hybrid scores to incorrect estimates of anubis allele frequency distributions. Assignment of individual genetic hybrid scores depends in part upon the inferred allele frequency distributions for the 14 marker loci in the two source populations; these are drawn from a large sample in the case of the Amboseli population, but from a small sample in the case of anubis baboons. This small sample size could potentially affect the accuracy of our inferences due to incorrect estimation of the anubis allele frequency distributions for the marker loci.

In Simulation 2, we investigated this possibility by randomly simulating 10 individuals from the genotype pool of the 13 anubis baboons, as in Simulation 1. We used this subset of 10 individuals as the full set of anubis baboons in the analysis, in combination with the actual empirical genotype data for the 450 Amboseli baboons, which we designated of unknown ancestry for the simulation. Each run therefore drew on true genotype data for 450 unknown Amboseli individuals and simulated data for 10 anubis baboons instead of 13 known anubis baboons. We then produced genetic hybrid scores in STRUCTURE using the same parameter set chosen for the original assignment of genetic hybrid scores. This subsampling routine created modest run-to-run fluctuations in allele frequencies within the pool of anubis. We also repeated this set of simulations using a sample of only five anubis baboons, which created much larger fluctuations in the allele frequencies for the anubis. We repeated both sets of simulations 100 times each and then analysed the difference between the hybrid scores assigned to individuals in the subsampled, simulated data sets and the hybrid scores assigned to the corresponding individuals in the actual data set. The results of these simulations provide an estimate of the threshold at which small sample sizes of anubis will cause large errors in the inferred allele frequency distributions for the anubis source population, which would also affect hybrid score assignment.

Simulation 3: sensitivity of hybrid scores to the detection of rare alleles. A small sample size of anubis baboons may also impact genetic hybrid score assignment due to a failure to sample rare alleles in the anubis population. In such cases, allele frequency distributions will not be greatly affected, but rare alleles that are actually shared between both anubis and yellow populations will then look like private alleles found only in yellow baboon populations. Individuals that carried these alleles would therefore be assigned genetic hybrid scores that are biased towards lower values.

In Simulation 3, we asked how the small sample size of anubis individuals may have impacted our results due to a failure to sample rare anubis alleles. First, we randomly selected one of the 14 marker loci. Then, we randomly removed one of the three rarest alleles for that locus from the data set. Designation of rare alleles was based on observed allele frequencies among the pool of 13 anubis baboons. We readjusted the frequencies of the other alleles upwards to compensate for the missing allele by uniformly allocating the number of times the missing allele was originally observed across the remaining set of alleles. This process simulated the resulting genotype data if we had failed to sample one rare allele at one of the 14 marker loci. We then produced genetic hybrid scores in STRUCTURE using this altered data set. After 100 iterations of this simulation, we asked how well the resulting hybrid scores correlated with the hybrid scores produced in the full analysis. We repeated the same procedure in two additional sets of simulations, in which we simulated a failure to sample one rare allele at each of five marker loci and one rare allele at all of the marker loci, respectively. If the differences between the results of these simulations and the results from the whole data set are small, then the genetic hybrid scores we have assigned are robust to missing rare alleles within the anubis data set. This test is in fact conservative, because the definition of 'rare allele' we use here encompasses alleles that actually were sampled in the anubis data set, and are therefore unlikely to be extremely rare among true anubis populations.

Analysis of temporal changes in hybridization patterns

We used three metrics to assess potential changes in hybridization patterns over time. First, we asked about increase, decrease, or stability in the percentage of hybrid baboons born in the population from the late 1960s/1970s to the present. We defined hybrid individuals as all Amboseli baboons in the data set for which the lower bound of the 90% credible interval for their genetic hybrid score was greater than or equal to 0.05. This cut-off is a conservative threshold that assures that we have counted as hybrids only the individuals for which a genetic hybrid score of 0, corresponding to a pure yellow genomic composition, could be ruled out with high confidence. We calculated the percentage of hybrids born into the population separately for the 1960s/1970s, 1980s, 1990s, and 2000s data partitions.

Second, we asked whether the degree of hybridization among hybrids showed any trend up or down over time. We defined degree of hybridization as the average of genetic hybrid scores in a data partition, considering only hybrids. Changes in the degree of hybridization reveal information about introgression, gene flow, and the success of anubis and/or hybrid baboons in reproducing within the Amboseli population. For example, if all hybrids in every data partition had hybrid scores around 0.50, with no change over time, we would infer that although anubis baboons could successfully mate within Amboseli, F_1 hybrids generally suffered from poor reproductive success. In contrast, if the degree of hybridization among hybrids decreased over time but the number of hybrids (as revealed by the categorical analysis described above) did not, we would infer that backcrosses and hybrid–hybrid matings were common in the population due to hybrids reproducing in the population.

Third, we examined the frequency distribution of hybrid scores of individuals born in different decades to ask whether the frequency distribution of hybrid scores shifted down over time; this analysis included both hybrid and nonhybrid individuals (i.e. the full set of individuals in the study). We conducted two-sample one-tailed Kolmogorov–Smirnov tests comparing the distribution of hybrid scores among the cohorts represented by each pair of temporal data partitions. A significant result would indicate that a random draw from the more recent cohort would be significantly more likely to correspond to a lower hybrid score than would a random draw from the earlier cohort. This third metric is closely related to the above analysis of changes in hybridization among hybrids, but also tests whether the patterns of change among individuals with high genetic hybrid scores (those for whom anubis ancestry can be inferred with very high confidence) are reflected in the hybrid dynamics in the population as a whole. Because we did not identify any hybrids in the 1960s/1970s data set, we excluded those individuals from this component of our analysis.

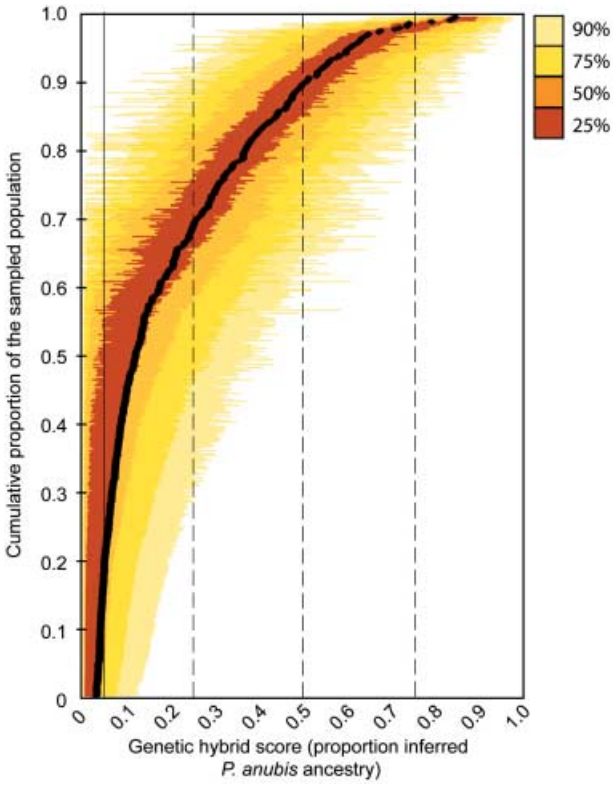

Fig. 1 Genetic hybrid scores (i.e. proportion anubis ancestry) for each of the 450 individuals in the analysis, averaged over three STRUCTURE runs and shown as the cumulative proportion of the sampled population. Each black point represents the mean hybrid score for one individual. Individuals are ordered along the *y* axis from lowest (least anubis ancestry) to highest (most anubis ancestry) genetic hybrid scores. Flanking lines show 25%, 50%, 75%, and 90% credible intervals. Individuals with lower 90% credible intervals > 0.05 (boundary indicated by solid vertical line) were considered hybrids for the purposes of this analysis.

Results

Genetic hybrid score assignments in Structure

Our analysis generated a mean hybrid score (±90% credible interval) for each of the 450 Amboseli baboons. Individual hybrid scores showed very close run-to-run agreement (mean standard deviation across runs for the same individual = 0.0025). Figure 1 shows the cumulative distribution of genetic hybrid scores for all Amboseli individuals. Ninety per cent credible intervals were largest for baboons with mean hybrid scores in the midrange values, as has also been the case for similar analyses of admixture in other systems (Beaumont *et al*. 2001; Pierpaoli *et al*. 2003). Ninety-nine of 450 individuals were deemed to have anubis ancestry based on their genetic hybrid scores, using the criterion of credible intervals with a lower bound > 0.05.

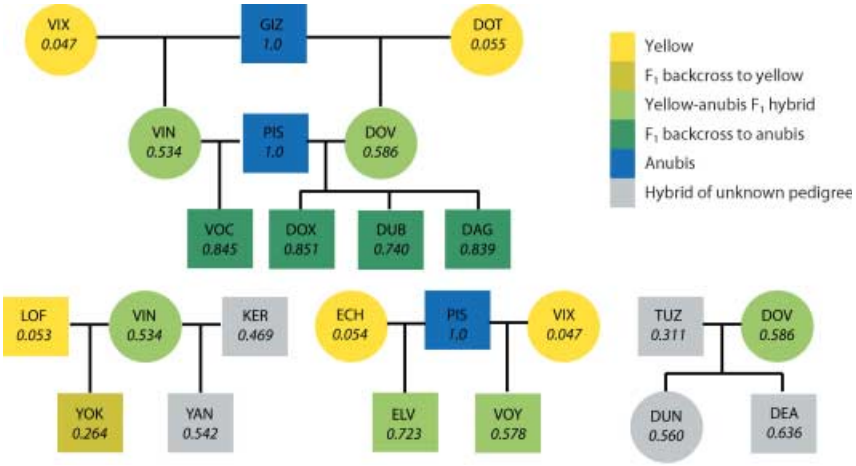

Fig. 2 Pedigrees showing a subset of the hybrid crosses and backcrosses that we have observed in the Amboseli population. All genotyped offspring and some grand-offspring of two anubis male immigrants (GIZ and PIS) are shown, as well as crosses between other hybrids in the population. Note that four of PIS's offspring are GIZ's grandoffspring. The genetic hybrid score for each individual is shown in italics below the three-letter ID. Circles represent females and squares represent males; yellow, F_1 hybrid, anubis, and backcrossed individuals (based on pedigree relationships and genetic hybrid score) are represented as different colours.

Agreement between genetic hybrid scores and morphological hybrid scores

In general, we observed good agreement between morphological hybrid scores and the genetic hybrid scores assigned in this study ($n = 315$, $r = 0.484$, $P < 0.0001$). Permutation tests yielded $P < 0.0001$ in 10 000 permutations, demonstrating that the observed correlation was not a product of the structure of the data set but actually reflected significant concordance between these two metrics. However, the cumulative distribution of genetic hybrid scores was right-shifted (towards more anubis ancestry) relative to the cumulative distribution of morphological scores (compare Fig. 1 with Fig. 3 in Alberts & Altmann 2001). Discrepancies in the scores originated primarily from individuals who were assigned higher genetic hybrid scores than morphological hybrid scores. This bias is clear when the two metrics are compared in subsets. Individuals with low genetic scores (< 0.25) almost invariably had morphological scores that were also lower than 0.25 and similar to the genetic scores (only five of 200 animals in this category violated this pattern). However, individuals with genetic hybrid scores above 0.25 generally had morphological scores that were lower (more yellow) than their genetic scores: specifically, 68 of the 77 individuals with genetic scores between 0.25 and 0.5 and for whom we had both scores had morphological hybrid scores lower than their genetic scores. Only nine had morphological scores higher than their genetic scores. Similarly, 28 of the 36 individuals with genetic hybrid scores between 0.5 and 0.75 had morphological hybrid scores lower than their genetic scores, whereas only eight had morphological hybrid scores higher than their genetic scores.

These comparisons suggest that differences between the two metrics were not random, but were caused almost entirely by cases in which genetic estimates indicated some anubis admixture, but morphological assessments did not. In other words, the individuals inferred as predominantly yellow by the genetic analysis were almost always assessed as predominantly yellow in morphological analyses, and individuals assessed as hybrids in the morphological analyses were almost always assessed as hybrids in the genetic analyses, but individuals assessed as hybrids in the genetic analyses were frequently assigned morphological scores that suggested lower levels of anubis ancestry.

Consistency within the data set

Comparisons of individual genetic hybrid scores with the midpoint values of the parents showed that the assignment of genetic hybrid scores was extremely consistent with predictions from previously constructed pedigrees, such that the distance between the scores of parents and the scores of offspring were in agreement with Mendelian inheritance at the 14 microsatellite markers ($n = 272$, $r = 0.905$; $P < 0.0001$). As an example, Fig. 2 shows the genetic hybrid scores of offspring of several different types of crosses that we observed in the study population, including yellow × anubis crosses, both types of backcrosses, and hybrid–hybrid crosses. These results suggest that an individual's genetic hybrid score is a good representation of genome-wide hybridization. The same analysis conducted on a distinct data set, the morphological hybrid scores, yielded $r = 0.588$ ($n = 151$, $P < 0.0001$). Parent–offspring resemblance in hybrid scores based on morphological traits, although high, is apparently not as consistent a metric as one based on genetic markers. Both measures indicate a general ability to assign hybrid scores across a wide range of degrees of admixture.

Simulation results

The results of all three simulations are summarized in Fig. 3. Together, they showed that the genetic hybrid scores we assigned were (i) highly repeatable given the parameters

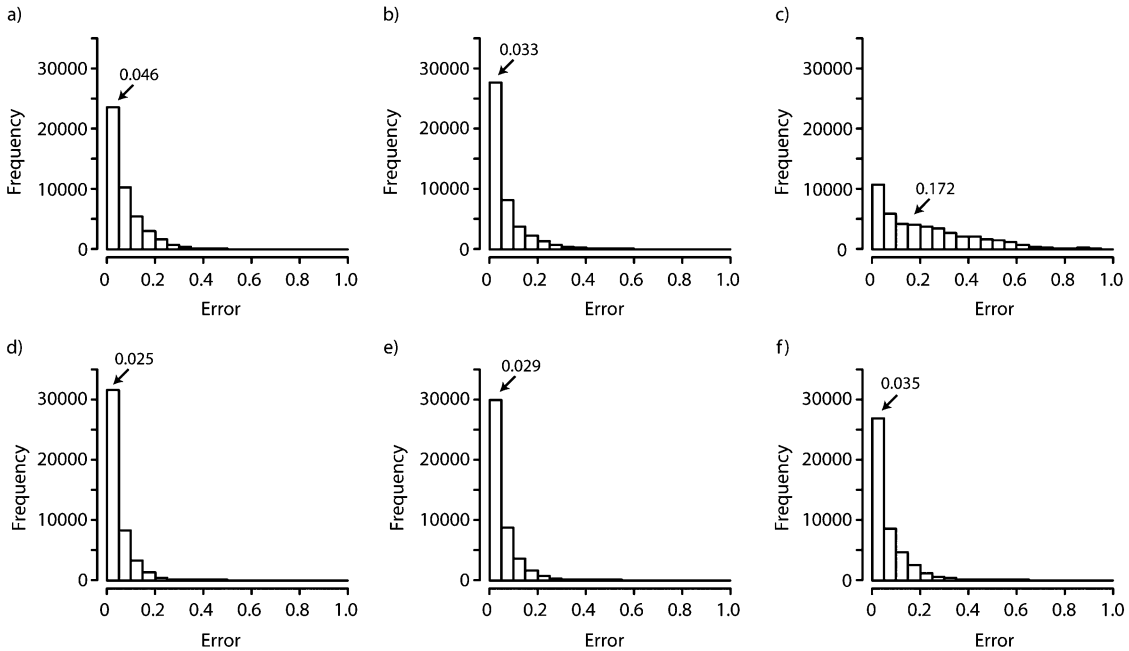

Fig. 3 Simulation results. Arrows show the value of the median error for each simulation. (a) Results from Simulation 1, showing the distribution of the margin of error between inferred genetic hybrid scores and known, simulated admixture proportions for each of 450 individuals in 100 simulated data sets (n = 45 000). Margins of error were calculated as the absolute value of the difference between the inferred hybrid score from STRUCTURE runs and the actual simulated degree of anubis ancestry for each individual. (b) and (c) Results from Simulation 2, showing the distribution of the absolute value of the difference between inferred genetic hybrid scores for runs in which 10 anubis individuals were included and for runs in which five anubis individuals were included, respectively, and corresponding hybrid scores assigned to the same individuals in the full analysis. (d), (e), and (f) Results from Simulation 3, showing the distribution of the absolute value of the difference between inferred genetic hybrid scores for runs in which a rare allele was not sampled at 1, 5, and all 14 loci, respectively, and corresponding hybrid scores assigned to the same individuals in the full analysis. All STRUCTURE runs were conducted using the same parameters we applied to the observed data.

of the observed data (Fig. 3a); (ii) robust to modest errors in measuring allele frequencies (but less so to the more extreme errors that would result if, for example, we had sampled only five individuals; Fig. 3b, c); and (iii) robust to cases in which rare alleles were not sampled (Fig. 3d–f). In particular, the results of Simulation 2 suggest that increasing the number of anubis individuals in the analysis tends to stabilize the point estimates of genetic hybridity, but that we have achieved much of this stability already by sampling 13 individuals. Interestingly, Simulation 3 suggests that rare alleles in the anubis population provide very little information about hybridity in the Amboseli population.

Changes in patterns of hybridization over time

The percentage of individuals born into the Amboseli population with hybrid ancestry increased in the study groups over the time period we considered (Fig. 4a). Whereas none of the baboons in the sample born from 1968 to 1979 had anubis ancestry based on our criterion, 12.8% of the genotyped individuals born during the 1980s (15 of 117 animals), 25.1% of animals born during the 1990s (47 of 187), and 31.3% of those born from 2000 to 2004 (36 of 115) had anubis ancestry based on our criterion. This suggests that the proportion of individuals with anubis ancestry increased in the Amboseli population throughout the study, but that the rate of increase slowed after the year 2000.

In contrast to the increase in the percentage of hybrids born over time, our results suggest that the mean genetic hybrid score assigned to hybrid individuals actually decreased in the population over time (Fig. 4b). The mean hybrid score among hybrids decreased by 0.055 between animals born in the 1980s (0.522 ± 0.099 SD) and those born in the 2000s (0.467 ± 0.131 SD), and the variance in hybrid scores within data partitions increased. This suggests that the hybrids we detected were increasingly offspring of backcrosses and crosses between hybrids (see Fig. 2 for examples), and not F_1 hybrids.

This trend was further supported by the results of pairwise Kolmogorov–Smirnov tests (Table 1) comparing the frequency distributions of all hybrid scores (including both hybrids and nonhybrids) across the sequential data sets. We observed a subtle but significant decrease in the distribution of hybrid scores among individuals born in the 1980s and the 2000s, but no significant differences between sequential decades, which was unsurprising given

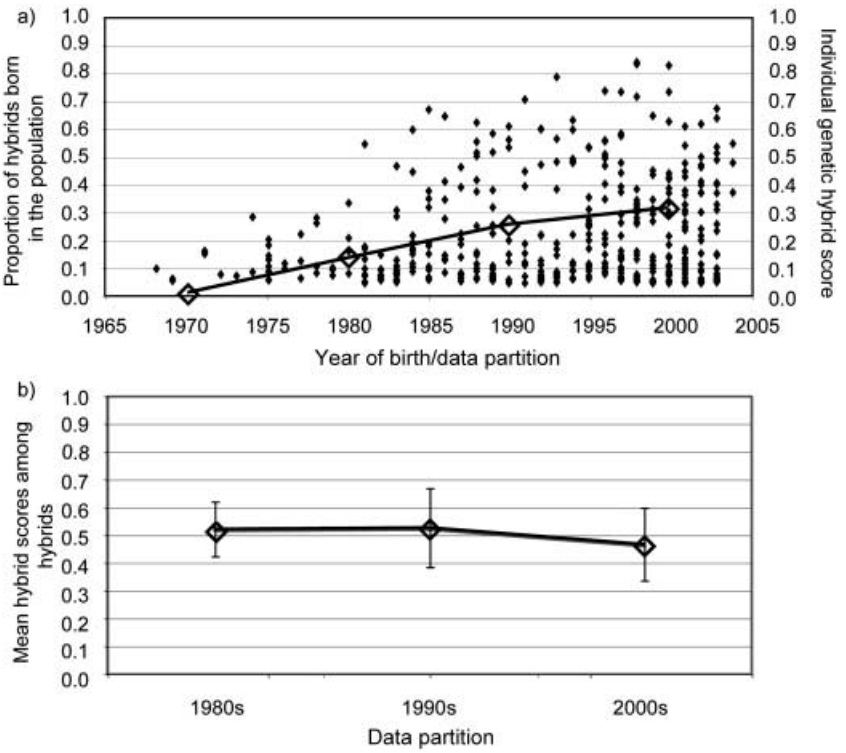

Fig. 4 (a) Broken line showing the proportion of hybrid baboons born in the Amboseli population during different decades, based on genetic hybrid scores (left *y* axis; hybrids are defined as individuals for whom the lower bound of the 90% credible interval on the genetic hybrid score is > 0.05), and scatterplot of the genetic hybrid scores of all 450 Amboseli individuals used in the analysis (right *y* axis), plotted against year of birth. The number of hybrid individuals has increased over time, as has variation in the amount of anubis admixture among hybrids. (b) Mean genetic hybrid score among hybrids born in Amboseli over the same period of time.

Table 1 *D* values for pairwise one-tailed Kolmogorov–Smirnov tests comparing the distribution of hybrid scores across temporal data sets within Amboseli. Significance values are given in parentheses; significant values ($P < 0.05$) are indicated in bold. Comparisons against the 1960s/1970s were not conducted due to the small sample size of individuals in that data partition, which included a single anubis individual and no apparent hybrids

	1980s	1990s	2000s
1980s	*		
1990s	0.130 (0.089)	*	
2000s	**0.196 (0.012)**	0.082 (0.386)	*

that the decrease in average hybrid score among hybrids was also only detectable on this scale. The overall pattern suggests that, while the representation of hybrids in the population has increased, hybrids born today are likely to have a smaller proportion of anubis ancestry relative to hybrids born 15–20 years ago. This trend has changed the distribution of hybrid scores in the population as a whole.

Discussion

Robustness in the genetic hybrid score assignments

Using the clustering method implemented in STRUCTURE, we were able to assign estimates of anubis ancestry to 450 individuals in the Amboseli baboon population, and to identify 99 of the 450 individuals as highly probable hybrids. Although we used only a modest number of markers and a small number of anubis individuals for this analysis, the results of the simulations suggest that our scores are robust and reliable measures of genetic hybridity. Additionally, the agreement we observed within parent–offspring triads shows that the genetic hybrid score assignments are consistent with expectations from pedigree data. Most importantly, although the 90% credible intervals surrounding many of the genetic hybrid score estimates are large (but comparable to those in other similar studies: see Beaumont *et al*. 2001; Pierpaoli *et al*. 2003), the lack of strong genetic differentiation between temporal data sets (Table S4, Supplementary material) suggests that year of birth and error in genetic hybrid score assignment are unlikely to be correlated. Thus, while this uncertainty adds noise to the data set, it is unlikely to have created or significantly altered the trends over time we have identified.

We also observed good agreement between the genetic hybrid scores assigned here and previous morphologically based estimates of hybridity, especially given the complete independence of the two metrics and the subjectivity inherent in assigning morphological hybrid scores. Our results are comparable to the results of Beaumont *et al*. (2001), who also compared morphological methods and genetic methods of assessing hybridity in wildcat–domestic cat hybrids. They report a 'strong correlation' between these methods based

on a significant Spearman rank correlation (Spearman's $\rho = 0.372$, $P < 0.01$); this is similar to the significant correlation we report of $r = 0.484$. Because genetic and morphological scores represent two completely independent methods of assessing yellow-anubis ancestry, this result provides strong support for the assertion that we are accurately identifying hybridity in our study population. Much of the discrepancy between the two scores occurred when genetic estimates indicated a hybrid background but morphological scores suggested these individuals were yellow. Such results are similar to those of Pierpaoli *et al*. (2003) in wildcats and to those of Noren *et al*. (2005) in foxes, in that they also identified probable hybrids that show no clear morphological signature of hybridity ('cryptic hybrids').

These differences may reflect a greater sensitivity to detecting hybridity using genetic markers than with phenotypic traits in some cases. However, because of the modest number of loci used here and the conservative threshold we used to classify hybrids, it is also likely that genetic assignments will produce some false negatives and false positives. Increased confidence in a genetic hybrid score can be conferred when independent assessments of hybridity, such as morphologically based hybrid scores, corroborate the genetic hybrid score. Overall, the results of our simulations, comparisons with morphological scores, and pedigree analysis suggest that, in general, the majority of individual estimates do not strongly differ from the 'true' proportion of anubis ancestry for those individuals.

Dynamic patterns of hybridization among the Amboseli baboons

The results of our analyses suggest that patterns of hybridization are changing in Amboseli over time. Specifically, the number of hybrids born into the population increased from the late 1960s and 1970s through the early 2000s, although the rate of increase seems to have slowed in the final decade of the analysis. While individuals with anubis ancestry were rare in the 1960s and 1970s, hybrids were born with increasing frequency in Amboseli beginning in the 1980s, and individuals with some degree of anubis ancestry comprised more than one-quarter of the baboons born into the study population by the 2000s. At the same time, the level of anubis ancestry among hybrids born into the population appears to have gradually decreased within this period, reflecting gradual introgression of 'anubis-like' genetic material into the still predominantly yellow baboon population. This pattern was also apparent in the shift of the distribution of genetic hybrid scores towards lower values over the last two and a half decades.

These results indicate that the pattern of hybridization in Amboseli has been dynamic over time. This argues for the importance of observing hybrid zones over multiple time points, either by repeated sampling or by assigning individuals observed together to different age cohorts (Albert *et al*. 2006), in order to capture the magnitude and direction of these changes (see also Lecis *et al*. 2006; Verardi *et al*. 2006 for alternative approaches). Understanding the dynamics of hybridization is critical because hybridization can alter population genetic patterns over time, thus impacting related evolutionary processes such as adaptation and speciation (Moore 1977; Arnold 1992; Rieseberg *et al*. 2003).

The most commonly described hybrid zone patterns do not appear to pertain to Amboseli. The rapid increase over time in the abundance of hybrids within Amboseli, despite the low level of observed *Papio anubis* immigration, suggests that hybrids were not selected against, as would be the case if hybrids exhibited reduced fitness relative to the yellow baboon parental species. Instead, hybrid individuals have clearly reproduced successfully within the Amboseli population, and have done so over multiple generations to create descendant crosses and backcrosses, as the broad distribution of the genetic hybrid scores indicates (Fig. 1). In fact, both previous and current analyses suggest that hybrid males in this population mature and disperse at an earlier age than yellow males (Alberts & Altmann 2001; Charpentier *et al*. accepted) and this may confer a selective advantage on hybrid males (see discussion in Charpentier *et al*. accepted).

However, the possibility of hybrid advantage runs counter to our observation that the distribution of hybrid scores has shifted downwards through time. A simple pattern of consistent anubis immigration and subsequent anubis and hybrid advantage over yellow baboons would lead one to predict higher rather than lower average anubis ancestry in the population over time, while an alternative pattern of hybrid superiority over both parental types would predict the maintenance of a steady intermediate level of anubis ancestry. These two conflicting pieces of evidence lead us to hypothesize that the dynamics of the Amboseli hybrid zone are driven by both nonselective processes (specifically, stochasticity in the immigration rate of anubis males into Amboseli) and selective processes (specifically, an advantage experienced by hybrids relative to yellow males). Such an advantage, coupled with a low rate of anubis immigration, would account for the increase over time in the number of hybrids in the population and the simultaneous decrease in anubis ancestry among hybrids, as well as the unchanged genetic distance between Amboseli and the Masai Mara anubis population during the study period.

Nonselective processes

With respect to stochasticity in the rate of anubis immigration, we envision a scenario in which chance plays a large role in whether anubis males immigrate into Amboseli. All of the nearest possible anubis source populations are moderately

far from Amboseli, and are separated from it by physical obstacles, particularly a large stretch of waterless land inhospitable to baboons. The severity of these physical obstacles will presumably fluctuate over time due to local changes in habitat or weather, resulting in a low rate of anubis male immigration that varies stochastically over time. These barriers create a moderate degree of geographically mediated prezygotic isolation between these populations.

Existing data on the Amboseli baboon population indicate that anubis male baboons have immigrated into the population at a mean rate of about once every 6 years (Alberts & Altmann 2001). How far do they have to travel to do this, and is this within the typical range of dispersal distances for male baboons? If the necessary travel distance is on the extreme end of dispersal distances, then this would account for the low and variable rate of anubis immigration into Amboseli. Although most male baboons disperse to neighbouring baboon groups during both natal and secondary dispersal (Samuels & Altmann 1986; Alberts & Altmann 1995), males occasionally disperse much farther: currently, several males natal to the Amboseli study groups are resident in groups up to 30 km from their natal home range (Alberts and Altmann, unpublished data). Rogers & Kidd (1996) used Wright's isolation-by-distance model (Wright 1946) to estimate that two-thirds of male yellow baboons in the Mikumi region of Tanzania dispersed less than 15–22 km from their natal groups, based on the effective population size of the Mikumi population and estimates of population density. We applied Wright's model to the Amboseli data in a similar manner, using an effective population size of 1037–3456 (estimated from genotype data presented in Storz *et al*. 2002) and a population density of 1.5 baboons/km^2 in the late 1980s and early 1990s (Samuels & Altmann 1991). The resulting estimate suggests that about two-thirds of Amboseli males dispersed less than 10.5–19.1 km from their natal groups during this time. If members of the source *P. anubis* population show a similar pattern of dispersal, and if the proportion of anubis immigrants into the Amboseli population is approximately 0.025 (~6 immigrant males over the 30-year study period were anubis), then these individuals would potentially have to travel some 20.6–37.5 km to reach the Amboseli basin. As noted above, the degree to which the physical environment in this stretch of land operates as a barrier to crossing this distance would introduce an additional degree of stochasticity to these events.

Selective processes

However, those anubis males that immigrate successfully into Amboseli do successfully reproduce (Samuels & Altmann 1991; Alberts & Altmann 2001), and the number of hybrids in the population has in fact increased over time. These observations support the hypothesis, posed above, that selective processes might be acting alongside stochastically varying rates of gene flow to influence the dynamics of this hybrid zone. Specifically, we hypothesize that early hybrid male maturation relative to yellow males reflects a selective advantage that has contributed to the increase over time in the number of animals with anubis ancestry (see discussion in Charpentier *et al*. 2008).

The hypothesis that hybrids are advantaged relative to yellow baboons is also supported by the geographical patterning of genetic variation in *Papio* in the wild (Newman *et al*. 2004; Wildman *et al*. 2004), which has led C.J. Jolly (personal communication) to argue that anubis baboons represent an 'invasive' phenotype relative to other members of the genus *Papio*. According to this hypothesis, the anubis phenotype is engaged in a gradual process of range expansion driven by dispersal of anubis males into other *Papio* populations. The patterns of earlier dispersal and earlier maturation observed among hybrid males (Alberts & Altmann 2001; Charpentier *et al*. 2008) may represent one mechanism by which this invasive tendency is manifested.

Conclusions

We report changing patterns of hybridization in the Amboseli baboon population over the past three and a half decades. Specifically, we observed an increased abundance of hybrids during this time, coupled with a shift in the population to a decreased level of hybrid ancestry among hybrid individuals. These patterns emphasize the utility of long-term observations on hybrid zone dynamics; we would not have been able to identify these trends using samples from any single point in time. By utilizing longitudinal data, we not only identified the presence of trends over time, but also began to identify the evolutionary and demographic influences that have shaped the particular hybrid zone dynamics within this population. Our results suggest that some selective advantage among hybrids may combine with low gene flow and stochastic variance in dispersal to produce the patterns we have observed. These hypotheses are amenable to additional testing, using both empirical data on life-history markers and reproductive success within the study population, and detailed theoretical population genetic models.

Acknowledgements

This work was supported by the National Science Foundation (BCS-0323553, IOB-0322613, IOB-0322781 and BCS-0323596), the Chicago Zoological Society, and Duke University. J.T. is supported by an NSF Graduate Research Fellowship; M.J.E.C. is supported by a Marie-Curie Outgoing Fellowship. We thank the Office of the President, Republic of Kenya, the Kenya Wildlife Services, its Amboseli staff and Wardens, the Institute of Primate Research, the National Museums of Kenya, and the members of the Amboseli-Longido pastoralist communities. Particular thanks go the Amboseli

fieldworkers who contributed to genetic sampling and morphological hybrid score assignments, especially R.S. Mututua, S. Sayialel, and J.K. Warutere. Additionally, we are grateful to Jason Buchan and Russ Van Horn for their extensive contributions to the genotyping effort; Sayan Mukherjee and Franck Prugnolle for help with the data analysis; and the Coriell Institute, the Integrated Primate Biomaterial and Information Resource, and Robert Sapolsky for providing samples from the Masai Mara. Finally, we thank Cliff Jolly for important discussions about his invasive anubis hypothesis and permission to discuss it in the manuscript.

References

Ackermann RR, Rogers J, Cheverud JM (2006) Identifying the morphological signatures of hybridization in primate and human evolution. *Journal of Human Evolution*, **51**, 632–645.

Albert V, Jonsson B, Bernatchez L (2006) Natural hybrids in Atlantic eels (*Anguilla anguilla*, *A. rostrata*): evidence for successful reproduction and fluctuating abundance in space and time. *Molecular Ecology*, **15**, 1903–1916.

Alberts SC, Altmann J (1995) Balancing costs and opportunities: dispersal in male baboons. *American Naturalist*, **145**, 279–306.

Alberts SC, Altmann J (2001) Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *American Journal of Primatology*, **53**, 139–154.

Alberts SC, Watts HE, Altmann J (2003) Queuing and queue-jumping: long term patterns of reproductive skew among male savannah baboons. *Animal Behaviour*, **65**, 821–840.

Alberts SC, Buchan JC, Altmann J (2006) Sexual selection in wild baboons: from mating opportunities to paternity success. *Animal Behaviour*, **72**, 1177–1196.

Altmann J, Alberts SC (2003) Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, **15**, 401–409.

Altmann J, Alberts SC (2005) Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, **57**, 490–501.

Altmann J, Muruthi P (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. *American Journal of Primatology*, **15**, 213–221.

Altmann J, Alberts SC, Haines SA *et al.* (1996) Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences, USA*, **93**, 5797–5801.

Anderson E, Stebbins GL (1954) Hybridization as an evolutionary stimulus. *Evolution*, **8**, 378–388.

Arnold ML (1992) Natural hybridization as an evolutionary process. *Annual Review of Ecology and Systematics*, **23**, 237–261.

Arnold ML, Hodges SA (1995) Are natural hybrids fit or unfit relative to their parents? *Trends in Ecology & Evolution*, **10**, 67–71.

Barton NH (2001) The role of hybridization in evolution. *Molecular Ecology*, **10**, 551–568.

Barton NH, Hewitt GM (1985) Analysis of hybrid zones. *Annual Review of Ecology and Systematics*, **16**, 113–148.

Beaumont M, Barratt EM, Gottelli D *et al.* (2001) Genetic diversity and introgression in the Scottish wildcat. *Molecular Ecology*, **10**, 319–336.

Buchan JC, Archie EA, Van Horn RC, Moss CJ, Alberts SC (2005) Locus effects and sources of error in noninvasive genotyping. *Molecular Ecology Notes*, **5**, 680–683.

Charpentier MJE, Tung J, Altmann J, Alberts SC (2008) Age at maturity in wild baboons: genetic, environmental, and demographic influences. *Molecular Ecology*, doi: 10.1111/j.1365-294X.2008.03724.x

Falush D, Stephens M, Pritchard JK (2003) Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, **164**, 1567–1587.

Grant PR, Grant BR (1992) Hybridization of bird species. *Science*, **256**, 193–197.

Henzi P, Barrett L (2003) Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. *Evolutionary Anthropology*, **12**, 217–230.

Jolly CJ (1993) Species, subspecies, and baboon systematics. In: *Species, Species Concepts, and Primate Evolution* (eds Kimbel WH, Martin LB), pp. 67–107. Plenum Press, New York.

Jolly CJ (2001) A proper study for mankind: analogies from the papionin monkeys and their implications for human evolution. *Yearbook of Physical Anthropology*, **116**, 177–204.

Jolly CJ, Phillips-Conroy JE (2007) Ecology, history and society as determinants of hybrid zone structure in baboons. *American Journal of Physical Anthropology*, **132**, 138.

Kingdon J (1997) *The Kingdon Field Guide to African Mammals*. Plenum Press, San Diego, California.

Lecis R, Pierpaoli M, Birò S *et al.* (2006) Bayesian analysis of admixture in wild and domestic cats (*Felis silvestris*) using linked microsatellite loci. *Molecular Ecology*, **15**, 119–131.

Lewontin RC, Birch LC (1966) Hybridization as a source of variation for adaptation to new environments. *Evolution*, **20**, 315–336.

Loisel DA, Rockman MV, Wray GA, Altmann J, Alberts SC (2006) Ancient polymorphism and functional variation in the primate MHC-DQA1 5'cis-regulatory region. *Proceedings of the National Academy of Sciences, USA*, **103**, 16331–16336.

Lorenzen ED, Siegismund HR (2004) No suggestion of hybridization between the vulnerable black-faced impala (*Aepyceros melampus petersi*) and the common impala (*A. m. melampus*) in Etosha National Park, Namibia. *Molecular Ecology*, **13**, 3007–3019.

Maples W, McKern T (1967) A preliminary report on classification of the Kenya baboon. In: *The Baboon in Medical Research* (ed. Vagtborg H), pp. 13–22. University of Texas Press, Austin, Texas.

Mayr E (1942) *Systematics and the Origin of Species*. Columbia University, New York.

Moore WS (1977) An evaluation of narrow hybrid zones in vertebrates. *Quarterly Review of Biology*, **52**, 263–277.

Muruthi P, Altmann J, Altmann S (1991) Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia*, **87**, 467–472.

Nagel U (1973) A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatologica*, **19**, 104–165.

Newman TK, Jolly CJ, Rogers J (2004) Mitochondrial phylogeny and systematics of baboons (*Papio*). *American Journal of Physical Anthropology*, **124**, 17–27.

Nielsen EE, Hansen MM, Ruzzante DE, Meldrup D, Gronkjaer P (2003) Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Molecular Ecology*, **12**, 1497–1508.

Nielsen EE, Nielsen PH, Meldrup D, Hansen MM (2004) Genetic population structure of turbot (*Scophthalmus maximus* L.) supports the presence of multiple hybrid zones for marine fishes in the transition zone between the Baltic Sea and the North Sea. *Molecular Ecology*, **13**, 585–595.

Noren K, Dalen L, Kvaloy K, Angerbjorn A (2005) Detection of

farm fox and hybrid genotypes among wild arctic foxes in Scandinavia. *Conservation Genetics*, **6**, 885–894.
Phillips-Conroy JE, Jolly CJ (1986) Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. *American Journal of Physical Anthropology*, **71**, 337–350.
Pierpaoli M, Biro ZS, Herrmann M *et al*. (2003) Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridization with domestic cats in Hungary. *Molecular Ecology*, **12**, 2585–2598.
Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.
R Development Core Team (2006) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rhymer JM, Simberloff D (1996) Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, **27**, 83–109.
Rieseberg LH (1997) Hybrid origins of plant species. *Annual Review of Ecology and Systematics*, **28**, 359–389.
Rieseberg LH, Raymond O, Rosenthal DM *et al*. (2003) Major ecological transitions in wild sunflowers facilitated by hybridization. *Science*, **301**, 1211–1216.
Rogers J, Kidd KK (1996) Nucleotide polymorphism, effective population size, and dispersal distances in the yellow baboons (*Papio hamadryas cynocephalus*) of Mikumi National Park, Tanzania. *American Journal of Primatology*, **38**, 157–168.
Rogers J, Mahaney MC, Witte SM *et al*. (2000) A genetic linkage map of the baboon (*Papio hamadryas*) genome based on human microsatellite polymorphisms. *Genomics*, **67**, 237–247.
Salzburger W, Baric S, Sturmbauer C (2002) Speciation via introgressive hybridization in East African cichlids? *Molecular Ecology*, **11**, 619–625.
Samuels A, Altmann J (1986) Immigration of a *Papio anubis* male into a group of *Papio cynocephalus* baboons and evidence for an *anubis-cynocephalus* hybrid zone in Amboseli, Kenya. *International Journal of Primatology*, **7**, 131–138.
Samuels A, Altmann J (1991) Baboons of the Amboseli Basin — demographic stability and change. *International Journal of Primatology*, **12**, 1–19.
Storz JF, Ramakrishnan U, Alberts SC (2002) Genetic effective size of a wild primate population: influence of current and historical demography. *Evolution*, **56**, 817–829.
Verardi A, Lucchini V, Randi E (2006) Detecting introgressive hybridization between free-ranging domestic dogs and wild wolves (*Canis lupus*) by admixture linkage disequilibrium analysis. *Molecular Ecology*, **15**, 2845–2855.
Wildman DE, Bergman TJ, al-Aghbari A *et al*. (2004) Mitochondrial evidence for the origin of hamadryas baboons. *Molecular Phylogenetics and Evolution*, **32**, 287–296.
Wright S (1946) Isolation by distance under diverse systems of mating. *Genetics*, **31**, 39–59.

Jenny Tung is interested in the evolutionary genetics of wild populations, particularly the functional effects of genetic variation on fitness-related traits. Marie Charpentier is interested in the study of mating systems, kin relationships and social structure in primates. David Garfield is interested in the effects of genetic and ecological variation on embryonic development, and in how this variation can contribute to interspecific differences. Susan C. Alberts and Jeanne Altmann are co-directors of the Amboseli Baboon Research Project. Their research program seeks to identify demographic, environmental, endocrine and genetic correlates of and sources of variance in fitness components in a natural population of mammals.

Supplementary material

The following supplementary material is available for this article:

Table S1 Masai Mara sample information

Table S2 Summary statistics for microsatellite genotyping data

Table S3 Sources of variance explaining overall variation in the Amboseli and Masai Mara data set

Table S4 Pairwise F_{ST} values between temporal data sets within Amboseli and between these temporal data sets and the Masai Mara 2004 sample

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-294X.2008.03723.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.