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Climate and Land Cover Analysis Suggest No Strong Ecological Barriers to Gene Flow in a Natural Baboon Hybrid Zone

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Abstract Admixture between diverging taxa has made, and continues to make, an important contribution to primate diversity and evolution. However, although naturally occurring hybrids have now been documented in all major primate lineages, we still know relatively little about the factors that shape when and where admixture occurs. Baboons (genus *Papio*), in which multiple natural hybrid zones are well described, provide a valuable system to investigate these factors. Here, we combined Geographic Information Systems and weather station data with information on genetically

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characterized populations in southern Kenya to investigate if ecological variables present a potential barrier to gene flow between anubis baboons and yellow baboons in the region. Specifically, we asked if altitude, seasonal temperature, or seasonal precipitation differ for weather stations in anubis, yellow, or hybrid ranges in southern Kenya, and if land cover or altitude covary with population ancestry near the hybrid zone. Our analyses suggest that the range of yellow baboons in Kenya is climatically distinct from the range of anubis baboons, with hybrids in intermediate regions. However, we identified no clear pattern of climate or land cover differentiation near the hybrid zone itself. Thus, when yellow baboons and anubis baboons come into contact, our data suggest that the resulting population composition is not consistently predicted by the ecological variables we considered. Our results support the designation of baboons as highly flexible "generalists," and suggest that more fine-grained analyses (e.g., relative success in ecologically stressful years) may be necessary to detect clear signals of ecological barriers to gene flow.

Keywords Admixture · Gene flow · Geographic Information Systems · Hybrid zone · *Papio*

Introduction

The process of admixture has long been of interest in evolutionary biology because of its importance in understanding divergence, speciation, and adaptation (Anderson and Stebbins 1954; Arnold 1992; Barton 1989, 2001; Lewontin and Birch 1966). Within primates, its importance has been reemphasized in recent years by the revelation that admixture with other archaic humans has significantly contributed to our own evolutionary history (Green *et al.* 2010; Kuhlwilm *et al.* 2016; Prüfer *et al.* 2014; Sankararaman *et al.* 2012; Ségurel and Quintana-Murci 2014; Wall and Brandt 2016). Comparative genomic analyses also point to long histories of admixture in other primate genera, including *Pan*, *Macaca*, *Papio*, and *Chlorocebus* (de Manuel *et al.* 2016; Osada *et al.* 2010; Rogers *et al.* unpubl. data; Svardal *et al.* 2016; Wall *et al.* 2016). Combined with field observations of hybrid populations, these findings establish admixture as a key factor in primate evolution, with evidence for a contribution to all of the major primate lineages (Arnold and Meyer 2006; Zinner *et al.* 2011a). However, they also raise an important question: given that closely related primates often produce viable, fertile offspring, what forces act to maintain taxonomic integrity in the face of admixture?

Ecological factors, such as temperature, rainfall, vegetation, predator complement, can function as barriers to gene flow if the parent taxa are adapted to distinct ecological niches (as defined by Hutchinson 1957) and hybridization compromises these adaptations (Jiggins and Mallet 2000; Rundle and Nosil 2005; Schluter 2009). For example, three-spined sticklebacks (*Gasterosteus aculeatus*) have repeatedly diverged into benthic and limnetic forms with distinct morphology, predator avoidance strategies, and feeding ecology (McKinnon and Rundle 2002). Although they experience no major fitness costs in the lab, benthic-limnetic F1 hybrids experience a growth disadvantage when transplanted to the habitat of either parental form, suggesting that ecological pressures have contributed to divergence between these interfertile taxa (Hatfield and Schluter 1999). Support for ecological selection against hybrids also comes from

studies of small mammals. In the western United States, for example, two closely related species of woodrat (*Neotoma bryanti* and *N. lepida*) are adapted to mesic and xeric habitats, respectively. Although hybrids are regularly produced at the boundary between the two species' distributions, they exhibit poorer survival to adulthood than unadmixed individuals, likely due to ecological selection (Shurtliff *et al.* 2014). Similar dynamics may occur in primate hybrid zones. To date, however, the role of ecological factors in shaping primate hybrid zones has not been extensively explored. Importantly, understanding the role of climatic factors in species range distributions may also reveal whether future climate change will influence admixture rates in primates, as has been suggested for other taxonomic groups (Seehausen *et al.* 2008; Taylor *et al.* 2014).

African baboons (genus *Papio*) are one of the best-studied primate taxa in the context of natural hybridization and are well positioned as a model for investigating these forces (Alberts and Altmann 2001; Beehner and Bergman 2006; Charpentier *et al.* 2012; Jolly *et al.* 2011; Keller *et al.* 2010; Phillips-Conroy and Jolly 1986; Tung *et al.* 2008; Zinner *et al.* 2009, 2013). The six currently recognized species within *Papio* reside largely in allopatry, are easily distinguished morphologically (Jolly 1993), and some of the species are also behaviorally distinct. Specifically, anubis (*P. anubis*, also known as the olive baboon), yellow (*P. cynocephalus*), Kinda (*P. kindae*), and chacma (*P. ursinus*) baboons live in multimale, multifemale social groups and show male-biased dispersal, while the more derived hamadryas (*P. hamadryas*) and Guinea (*P. papio*) baboons live in one-male, multifemale groups (hamadryas) or nested multilevel social groups (Guinea) with predominantly female dispersal (Fischer *et al.* 2017). In addition, the three most well-studied taxa (anubis, yellow, and chacma baboons) exhibit striking variation in the tendency for males to form coalitions against higher ranking males: this behavior is common in yellow and anubis males, but has not been observed in chacma (Alberts *et al.* 2003).

Hybrids are frequently observed on the boundaries between *Papio* species ranges, including in three well-studied natural hybrid zones (Charpentier *et al.* 2012; Jolly *et al.* 2011; Phillips-Conroy and Jolly 1986). Possible behavioral and morphological barriers to gene flow have been identified in at least two of these hybrid zones. In Ethiopia, the differences in social behavior described in the preceding text between hamadryas baboons and anubis baboons have been hypothesized to decrease the fitness of hybrids in predominantly unadmixed social groups, with some empirical support. Specifically, hybrid hamadryas–anubis males exhibit ineffective mating strategies relative to unadmixed males, intermediate between the intense vigilance and female herding behavior exhibited by hamadryas males and the mostly loose associations (outside of female estrus periods) between anubis males and females (Bergman *et al.* 2008; Nagel 1973; Phillips-Conroy and Jolly 1981; Phillips-Conroy *et al.* 1991). Hybrid hamadryas–anubis males have also been reported to direct neck-biting behavior—a ritualized strategy used in hamadryas one-male units to control female movement—toward anubis females, with little success (Phillips-Conroy *et al.* 1991). Meanwhile, in a chacma baboon–Kinda baboon hybrid zone in Zambia, both behavioral barriers and obstetric complications are thought to limit successful pairings between Kinda females and much larger chacma baboon males (but not pairings in the opposite direction) (Jolly *et al.* 2011).

Less is known about potential barriers to admixture in yellow baboons and anubis baboons. After the initial expansion of *Papio* from its origins in southern Africa, yellow baboons and anubis baboons are thought to have evolved separately, such that anubis baboons are most closely related to the other "northern" lineages (hamadryas baboons and Guinea baboons) and yellow baboons are most closely related to the other "southern" lineages (Kinda baboons and chacma baboons) (Zinner *et al.* 2011b). Of the southern lineages, yellow baboons expanded the furthest north along the eastern side of the continent, presumably after the retreat of densely forested habits that are inhospitable to baboons. There, the northernmost populations are believed to have experienced secondary contact with anubis baboons (Zinner *et al.* 2011b, 2015). Thus, the yellow and anubis baboon lineages diverged earlier (ca. 1.4 million years ago) than either hamadryas and anubis (ca. 733 kya) or chacma and Kinda (ca. 578 kya), the parent taxa in other well-studied baboon hybrid zones (Rogers *et al.* in review). However, yellow and anubis baboons are similarly sized: mean body mass for anubis baboon males is 23.6 kg and mean body mass for yellow baboon males is 24.4 kg; comparable numbers for females are 12.7 kg and 12.3 kg, respectively, based on the mean of average body masses across multiple populations (Altmann *et al.* 2013; Palombit 2013). They also have similar social organizations: both live in multimale, multifemale social groups with male dispersal and a polygynandrous mating system. Further, naturally occurring hybrids do not suffer from obvious developmental defects, suggesting few intrinsic barriers to hybridization. Indeed, while unusual dentition and skull suture patterns have been reported in captive yellow–anubis hybrids (Ackermann *et al.* 2006, 2014), to our knowledge, the dentition and skeletal phenotypes associated with captive hybrids have no known fitness consequences. In addition, male yellow–anubis hybrids in the wild appear to experience phenotypic advantages over yellow baboon males in a majority yellow population. These advantages include accelerated maturation and higher male mating success (Charpentier *et al.* 2008; Tung *et al.* 2012) (similar studies in majority anubis populations have not been done).

These observations suggest that there may be relatively free gene flow between yellow baboons and anubis baboons. Alternatively, or in addition, anubis baboons may be expanding into the historic range of yellow baboons (Charpentier *et al.* 2012; Jolly 1993). However, two pieces of genetic evidence indicate that gene flow is in fact restricted. First, where the yellow–anubis hybrid zone has been genetically characterized, i.e., based on the populations included in Charpentier *et al.* (2012), it is geographically narrow (<100 km) relative to the range sizes of the parent species (Fig. 1), with a sharp transition between phenotypically and genetically yellow populations and phenotypically and genetically anubis populations (Charpentier *et al.* 2012). This pattern contrasts to the gradual, clinal pattern expected under unrestricted gene flow. Second, genomic analysis rejects a simple secondary contact or isolation–migration model, including a simple model of anubis expansion relative to yellow baboons (Wall *et al.* 2016). Thus, although recent gene flow appears to be biased from anubis baboons to yellow baboons, this hybrid zone does not appear to be a consequence of straightforward anubis expansion relative to yellow baboons, as has been hypothesized in previous work (Charpentier *et al.* 2012; Jolly 2001). Instead, there appears to have been intermittent admixture in this region for hundreds to thousands of generations (Wall *et al.* 2016), indicating that taxonomic integrity has been maintained in the face of gene flow for a long time.

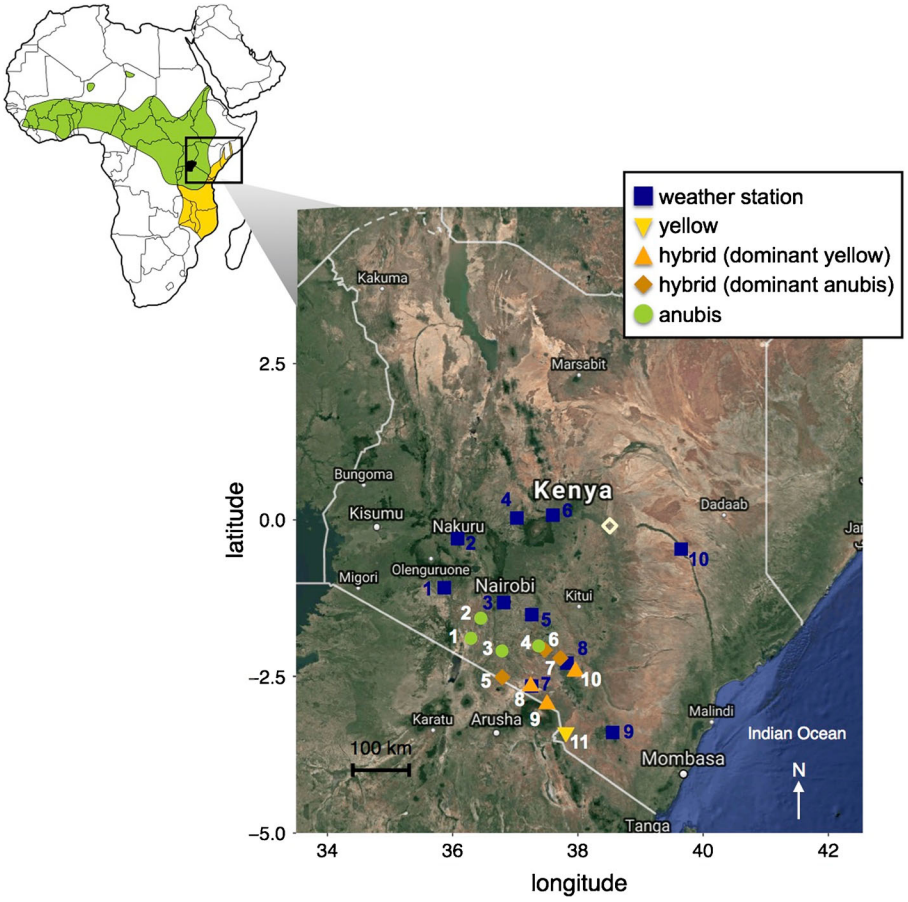

Fig. 1 Study populations and weather station map. Map of Kenya generated using *ggmap* (Kahle and Wickham 2013), relative to the ranges of anubis baboons and yellow baboons in Africa. In the map of Africa, the range of anubis baboons is shown in green and the range of yellow baboons is shown in yellow (map of species ranges in Africa is modified from a map created by Kenneth Chiou under a CC BY 3.0 license). For more details on geo-referenced anubis and yellow baboon populations in Kenya, see http://wildsolutions.nl/photomaps/Papio/. Numbers for weather stations (blue squares) and study populations (all other filled markers) in the map of Kenya correspond to the numbers in Table I. Unfilled diamond shows the approximate location of a putative additional yellow-anubis hybrid zone near Kora National Reserve. Note that the Amboseli dominant yellow population (population 8) is colocalized with the Amboseli weather station.

Ecological specialization could help resolve this puzzle. In support of such an argument, taxonomic guide books for African primates associate anubis baboons with higher altitude environments than yellow baboons. They further indicate that anubis baboons occur across a wider range of habitats including forest, which is not typical of savannah grassland–associated yellow baboons (Altmann *et al.* 2013; Kingdon 1997; Palombit 2013). Yellow baboons also have lighter pelage, perhaps reflecting adaptation to a hotter environment: extreme heat produces elevated glucocorticoid levels and has potential effects on fertility in both female and male baboons, including in social groups within the yellow–anubis hybrid zone (Beehner *et al.* 2006; Gesquiere *et al.* 2008, 2011).

In opposition to an ecological argument, however, both anubis baboons and yellow baboons are considered generalist species that are not highly constrained by ecological variation in climate or vegetation. Indeed, in a continent-wide analysis of ecological variation across the ranges of *Papio* species, Winder (2015) showed that variation in temperature, rainfall, vegetation cover, and altitude is consistently greater within the ranges of individual species than between species, suggesting no strong overall niche differentiation between baboon species. In support, skull size and shape—morphological features expected to covary with climate—show no consistent relationship to geography in this genus (Dunn *et al.* 2013).

Assessing whether ecological factors play a role in restricting gene flow in the East African yellow–anubis hybrid zone demands a closer analysis of whether yellow and anubis baboons are ecologically differentiated to begin with. Although continent-wide analyses suggest weak differentiation, if any, such large-scale analyses may fail to capture subtle differences between species that influence their relative fitness in the same environment, i.e., within a hybrid zone. To address this possibility, here we assess the potential role of ecology in determining the dynamics of a yellow baboon–anubis baboon hybrid zone in East Africa. We first performed an analysis of ecological differentiation as a function of yellow and anubis ancestry in the genetically characterized Kenyan yellow–anubis hybrid zone. Specifically, we combined information on the known genetic ancestry of 11 previously characterized populations located in southern Kenya (Charpentier *et al.* 2012) with Geographic Information Systems (GIS) data on land cover and altitude, which is a reasonable proxy for temperature and for rainfall during the "long wet season" that typifies this region. Second, we drew on temperature, rainfall, and altitude data from weather stations scattered throughout southern and central Kenya, representing a larger portion of the yellow baboon and anubis baboon ranges in Kenya, to investigate patterns of ancestry on a broader geographic scale (see Fig. 1). Using these data, we asked whether these ecological variables systematically covary with the ranges of the parent species and their hybrids. Although nonexhaustive, our analysis thus focused on ecological variables that could be reliably measured and could be colocalized with the populations we studied or could be collected from weather stations. These variables have been either linked to fitness-related traits in baboons (precipitation, temperature) or associated with different baboon species in taxonomic guidebooks.

Methods

Analysis 1: Ecological Differentiation in and Near the Hybrid Zone

Genetically Characterized Study Populations For our first analysis of ecological differentiation in and near the hybrid zone, we focused on 11 populations in southern Kenya. Here, we define "population" as individuals sampled in the same geographic location, which may represent multiple social groups: with the exception of Amboseli, the fecal samples for genetic analysis came from unhabituated, unmonitored individuals, precluding collection of more detailed data on social structure or population demography. Charpentier and colleagues previously characterized the geographic and genetic structure of these populations (Alberts and Altmann 2001;

Charpentier *et al.* 2012; Tung *et al.* 2008) (Fig. 1; Table I). Although a relatively small set, to our knowledge these represent the only populations in which genetic ancestry has been assessed with reference to anubis baboon and yellow baboon admixture. These populations fall along a rough transect (ca. 300 km in length) from unadmixed or majority yellow populations to the south and east toward unadmixed or majority anubis populations to the west and north, ranging across the Great Rift Valley. Based on the genetic analysis in (Charpentier *et al.* 2012), we scored four populations as unadmixed anubis (Olorgesailie, Magadi, Bissil, and Sultan Hamud), one population as unadmixed yellow (Taita Taveta), and five populations as admixed (Namanga, Emali, Kiboko, Kibwezi, Oloitoktok, and Amboseli). Based on the ancestry proportions for each admixed population, we further distinguished between admixed populations that are majority (>50%) anubis (Namanga, Emali, Kiboko) and those that are majority (>50%) yellow (Kibwezi, Oloitoktok, and Amboseli). This classification scheme resulted in an ordinal scoring of populations from 1 (anubis) to 4 (yellow). For location information, we used GPS coordinate data collected concurrently with the original sample collection in 2008.

Table I Weather station and population coordinates and ancestry designation

	Latitude	Longitude	Ancestry
Weather station			
1. Narok	−1.082947	35.866728	Anubis
2. Nakuru	−0.295256	36.079674	Anubis
3. Wilson[a]	−1.320517	36.814706	Anubis
4. Laikipia	0.030041	37.025442	Anubis
5. Machakos	−1.514735	37.263193	Anubis
6. Meru	0.075874	37.599621	Anubis
7. Amboseli	−2.652251	37.261391	Hybrid
8. Makindu	−2.290554	37.824626	Hybrid
9. Voi	−3.397118	38.555782	Yellow
10. Garissa	−0.463352	39.648364	Yellow
Baboon population			
1. Magadi	−1.893252	36.292034	Anubis
2. Olorgesailie	−1.571534	36.45018	Anubis
3. Bissil	−2.094703	36.787713	Anubis
4. Sultan Hamud	−2.016304	37.37295	Anubis
5. Namanga	−2.515061	36.792784	Hyb–anu
6. Emali	−2.078964	37.472667	Hyb–anu
7. Kiboko	−2.209935	37.721802	Hyb–anu
8. Amboseli	−2.657	37.247	Hyb–yel
9. Oloitokitok	−2.944	37.507	Hyb–yel
10. Kibwezi	−2.422	37.961	Hyb–yel
11. Taita	−3.396	37.809	Yellow

[a] Only precipitation data were available for the Wilson weather station

Land Cover Classification To evaluate variation in land cover for each of these 11 study populations, we imported LandSat satellite imagery overlapping their locations from the United States Geological Survey into the program ArcGIS (https://earthexplorer.usgs.gov; Electronic Supplementary Material [ESM] Table SI; satellite images cover the Kajiado, Machakos, and Taita-Taveta districts in Kenya, based on 1998 boundaries). We refer to the area contained within these images as the study area (46,411 km^2). We considered seven possible land use–land cover (LULC) types: 1) forest: closed stands of trees with at least 80% closed canopy; 2) woodland: open stands of trees with 40–80% canopy cover; 3) bushes: shrub cover of >40% of the landscape; 4) grasslands: open grass cover of >60% of the landscape; 5) bare ground: land devoid of vegetation; 6) swamp land; and 7) agricultural land: land used for crop cultivation. To assign LULCs to pixels in the satellite images (each pixel = 28 m per side), we generated a stratified random sample of 600 sites from the study area (each site represents ca. 20–100 pixels). We then thinned this set to a subset of 318 sites that fell in homogeneous patches of vegetation, based on visual inspection of the LandSat imagery and corresponding Google Maps images for the same region. We manually assigned LULC classes to all 318 sites and chose a further subset from these 318 (N = 123 sites, located in accessible regions covered by the satellite images), all of which were ground-truthed through site visits by the first author. We treated the other 195 sites (318 minus the ground-truthed set) as the "reference site" set.

To classify the entire study area into LULC types, we used a two-step process. First, we performed unsupervised classification for the full study area using the algorithm ISOCLUST, run in IDRISI Kilimanjaro, set to recognize 35 distinct spectral classes (Eastman 2003). We compared each spectral class to the reference site set to identify the subset of spectral classes that were consistently associated with one of the six LULC types. This procedure allowed us to classify ca. 65% of the study area. Second, we used the maximum likelihood algorithm MAXLIKE in IDRISI to perform supervised classification of the remaining area based on the spectral class–LULC associations (Eastman 2003). To assess the sensitivity and specificity of our results for each LULC class, we compared the resulting assignments to the 123 sites in the ground-truthed data set.

Finally, to determine LULC proportions for each of our 11 study populations, we drew a circle with a 10-km radius centered on the GPS coordinates for each population. We chose 10 km because, in a given year, a wild baboon group in this area of Kenya can range over an area of more than 40 km^2 (Altmann and Muruthi 1988), with varying levels of home range overlap (Markham *et al.* 2013). A 10-km radius thus captures a reasonable sample of land covers that baboons in each study population might encounter in typical ranging and dispersal patterns. We then calculated the proportion of pixels within that circle representative of each LULC type. Swamp land was found only in the 10-km radius surrounding the Amboseli study population, so we excluded this LULC class in our downstream analyses.

Altitude and Climate To investigate the possibility that climate is associated with genetic ancestry in our 11 study populations, we used altitude (range 645–1606 m.a.s.l. across these populations) as a proxy for climate. Altitude is a variable that can be accurately obtained for each study population, whereas temperature and rainfall data cannot be accurately obtained (except for Amboseli) without a weather station. To assess the suitability of altitude as a climate proxy, we therefore first analyzed detailed

data on temperature and rainfall obtained from nine inland weather stations across southern and central Kenya (Fig. 1). We collected precipitation, minimum daily temperature, and maximum daily temperature values averaged per month (using the mean) between 1980 and 2011 (with the exception of Nakuru and Narok, where data collection began in 1984 and extended into January 2012; ESM Tables SII–SIV), roughly coinciding with the onset of recent admixture described in the Amboseli region (Samuels and Altmann 1986). We then used the weather station data to test whether altitude could be used as a proxy for temperature and rainfall in this region. As is typical for this region of Africa, monthly means across years revealed two distinct wet seasons and two distinct dry seasons in this region: Wet Season 1 (WS1: October–December), Dry Season 1 (DS1: January–February), Wet Season 2 (WS2: March–May; the "long wet season"); and Dry Season 2 (June–September) (Fig. 2a). We therefore considered mean monthly precipitation, mean minimum temperature, and mean maximum temperature for each of these four seasons, for each weather station, in our subsequent analyses.

We then extracted altitude information for the weather stations and for the baboon study populations from the United States Geological Survey (http://earthexplorer.usgs.gov: ESM Fig. S1). These data revealed that weather station altitude is very strongly correlated with minimum temperature for all four seasons (Pearson's R^2 ranges from 0.907 to 0.960, all $P < 10^{-4}$, $N = 9$), strongly

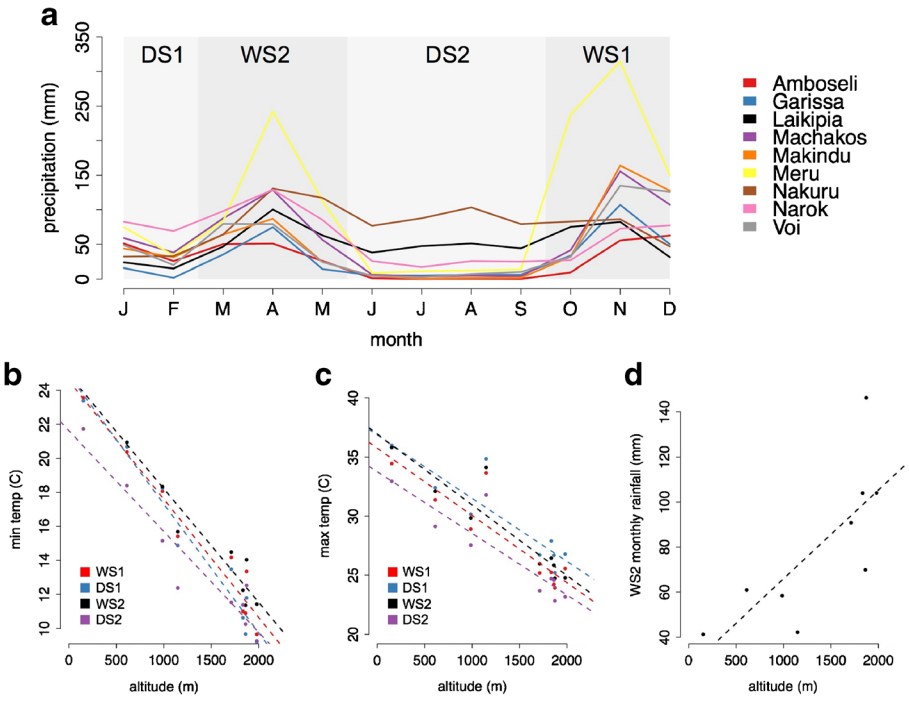

Fig. 2 Weather station climate patterns. **a** At the nine weather stations included in our analysis, two wet seasons and two dry seasons characterize southern Kenya. **b** Altitude is negatively correlated with minimum temperature across all four seasons and (**c**) negatively correlated with maximum temperature across all four seasons. **d** Altitude is positively correlated with mean monthly rainfall in WS2. Dashed lines show the best fit slope and intercept for a linear model relating altitude to the climate variable, separated by season for (**b**) and (**c**).

correlated with maximum temperature for all four seasons (Pearson's R^2 ranges from 0.796 to 0.854, all $P < 2 \times 10^{-3}$, $N = 9$), and moderately correlated with rainfall in Wet Season 2 (the "long rains:" Pearson's $R^2 = 0.564$, $P = 0.020$, $N = 9$) (Fig. 2b; ESM Table SV). Rainfall in Wet Season 2 in turn is the best predictor, across all four seasons, of cumulative rainfall patterns summed across the hydrological year (Pearson's $R^2 = 0.947$, $P = 1.03 \times 10^{-5}$, $N = 9$). Thus, the altitude and climate data at the weather stations indicate that altitude data alone provides considerable information about the climate experienced by baboons living in southern Kenya. Specifically, the genetically characterized study populations that live at higher altitude will generally experience colder and wetter climates. Although explicit spatial interpolation of climate data is an attractive alternative to using altitude as a proxy for climate, our exploratory analyses indicated that we had insufficient data to perform accurate interpolation in our study area.

Analysis 2: Climate Variables and Baboon Species Ranges

To investigate how climate variables are related to the known ranges of yellow and anubis baboons, we analyzed altitude, temperature, and rainfall data obtained from the nine inland weather stations, as shown in Fig. 1. Two of these weather stations are located in the known range of yellow baboons (Voi and Garissa), five in the known range of anubis baboons (Laikipia, Machakos, Meru, Nakuru, and Narok), and two are within the genetically characterized hybrid zone (Amboseli and Makindu, which lies between the Kiboko and Kibwezi study populations) (Charpentier *et al.* 2012; de Jong and Butynski 2010). We therefore used data from these weather stations to test the general pattern suggested by taxonomic guides for African primates: that yellow baboons are found in lower altitude, less forested, and hence hotter and dryer climates than anubis baboons (Altmann *et al.* 2013; Kingdon 1997; Palombit 2013). To do so, we analyzed the altitude data and mean monthly precipitation, mean minimum temperature, and mean maximum temperature for the two wet and two dry seasons, for each weather station, as described earlier.

Statistical Analysis of Ancestry, Land Cover, and Climate

To investigate the relationship between land cover, altitude, and ancestry specifically at the 11 genetically characterized baboon populations in and near the hybrid zone, we used a series of linear models with population ancestry assignment (1–4) as the predictor variable and proportional land cover (grassland, woodland, bushes, agriculture, bare ground, forest) or altitude as the response variable.

To investigate the relationship between climate patterns and baboon ancestry using data from the nine weather stations in southern and central Kenya, we performed principal components analysis on the altitude, seasonal precipitation data, seasonal minimum temperature, and seasonal maximum temperature data (based on Pearson's correlation analysis between values collected for each weather station, many of these variables were correlated: ESM Table SV) using the *prcomp* function in R (R Core Team 2015). Before PCA, we scaled and centered each variable and calculated the weather stationwise covariance matrix as the input data. We then asked whether the top resulting principal components differentiated weather stations located in the range of

yellow baboons, in the hybrid zone, and in the range of anubis baboons. Because we found that the top PC was strongly associated with longitude, we also compared the explanatory power of a model based on climate as a predictor of range to a model based simply on latitude and longitude as a predictor of range.

Ethical Note

The current study required no direct work with any animals; research involved only assessment of landscape and climate vis-à-vis previously determined species range distributions and population-level ancestry measurements. All research adhered to the ethical and legal requirements of the government of Kenya. The authors declare no conflict of interest.

Results

Ancestry is Uncorrelated with Land Cover and Climate in and Near the Hybrid Zone

LULC type classification accuracy was generally high for the study area covered by our satellite images (Table II; ESM Fig. S1). Specifically, producer's accuracy (defined as the percentage of ground-truthed pixels in a given LULC type actually assigned to that LULC type) ranged from 65.7% for bare ground to 87.6% for grassland in the held-out, ground-truthed data (N = 123 sites). Notably, values were all in the higher part of this range for the four dominant land cover classes near our study populations (73.9% –87.6% for bushes, grassland, woodland, and agriculture; ESM Table SVI). User's accuracy (defined as the percentage of pixels assigned to a LULC type that were confirmed to be of that type in the ground-truthed data) was also high for these classes, ranging from 72.2% for agriculture to 89.0% for bushes (Table II).

Table II Accuracy of land cover assignment

	Producer's[a] (%)	User's[b] (%)
Agriculture	73.9	72.2
Bare ground	65.7	61.1
Bushes	76.6	89.0
Forest	76.9	81.8
Grassland	87.6	87.0
Swampland	75.7	60.5
Woodland	86.6	68.3

[a] Percentage of 123 ground-truthed pixels that truly belong to the land cover class that were assigned to that class by our classification procedure

[b] Percentage of pixels assigned to a land cover class that were confirmed to actually be of that class in the ground-truthed data

Of the six common LULC types near our study populations, five (woodland, bushes, grassland, bare ground, forest) were not significantly associated with population ancestry assignment (linear model: $t = -1.85$, $P = 0.097$, $N = 11$; $t = 0.225$, $P = 0.827$, $N = 11$; $t = -0.637$, $P = 0.540$, $N = 11$; $t = -0.294$, $P = 0.776$, $N = 11$; $t = 0.900$, $P = 0.391$, $N = 11$, respectively). Population ancestry did appear to predict the proportion of land use devoted to agriculture ($t = 2.33$, $P = 0.044$, $N = 11$). However, visual inspection suggests that this pattern is entirely driven by the Taita (yellow baboon) study population, where agricultural land use is very high. Removing this outlier resulted in no detectable relationship between agricultural land use and population ancestry ($t = 0.722$, $P = 0.491$, $N = 10$).

Analysis of the genetically characterized study populations close to the hybrid zone itself also revealed no relationship between population ancestry and altitude, a proxy for temperature and for precipitation levels in Wet Season 2 (linear model: $t = -0.211$, $P = 0.838$, $N = 11$; Fig. 3a).

Climate Variables Broadly Separate Baboon Species Ranges

The first principal component from a PCA decomposition of altitude, temperature, and climate variables measured at the nine weather stations strongly differentiated stations in the anubis, hybrid, and yellow ranges (coded as 1, 2, or 3 respectively; linear model: $t = -7.72$, $P = 1.14 \times 10^{-4}$, $N = 9$; Fig. 3b), in striking contrast to the lack of a relationship between climate and ancestry in the hybrid zone. However, variation in PC1 was also strongly associated with weather station longitude ($t = -3.99$, $P = 5.27 \times 10^{-3}$, $N = 9$). Thus, the association between species range and weather station data could simply reflect a biogeographic history in which yellow baboons occur closer to the Indian Ocean and anubis baboons further from it. Under this hypothesis, the correlation between species ranges and climate is a byproduct of

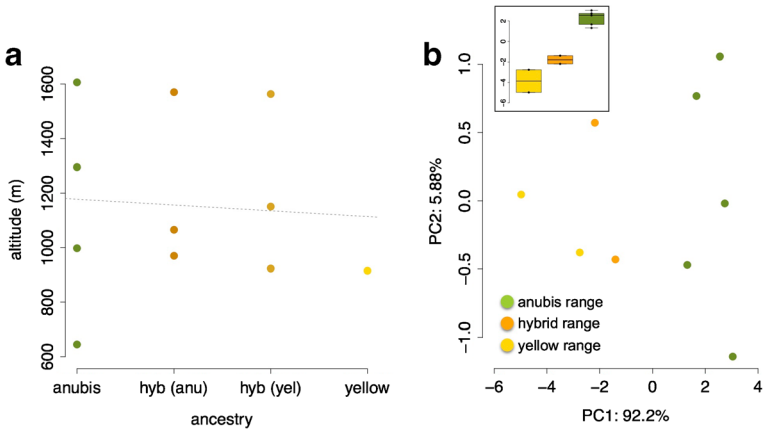

Fig. 3 Relationship between range, population ancestry, and climate variables. **a** Altitude (our best proxy for temperature and Wet Season 2 rainfall based on correlations from directly measured variables at weather stations) does not explain yellow baboon, anubis baboon, and hybrid population ancestry within and abutting the yellow–anubis hybrid zone in Kenya. **b** However, PC1 of altitude, temperature, and precipitation climate variables at more broadly distributed southern Kenyan weather stations separates those stations by species range. Inset shows the distribution of PC1 values (*y*-axis) by range classification.

independent correlations between climate and distance from the Indian Ocean (Schott *et al.* 2009) and baboon species distribution and distance from the Indian Ocean, such that climate does not causally affect the distribution of yellow baboons, anubis baboons, and their hybrids. This possibility cannot be fully excluded in the current analysis. However, a linear model based on species range explained more variance in PC1 ($R^2_{adj} = 0.880$) than a linear model including longitude and latitude ($R^2_{adj} = 0.744$) or longitude alone ($R^2_{adj} = 0.651$), provisionally supporting the hypothesis that species ranges are indeed influenced by climate.

Discussion

Together, our analyses indicate that ecological variables show some separation between the ranges of anubis baboons and yellow baboons in Kenya, but that they do not clearly predict the occurrence of anubis baboons, yellow baboons, and their hybrids in a known hybrid zone. Consistent with previous studies on a pan-African scale (Dunn *et al.* 2013; Winder 2015), our results support the idea that baboons are generalists and that they may be buffered from environmental variation relative to other mammals, perhaps owing to high cognitive ability and dietary flexibility (Morris *et al.* 2010). Clearly, both anubis baboons and yellow baboons in Kenya can cope successfully with a wide spectrum of temperature, rainfall, and land cover properties. Combined with their large size and terrestrial nature, which allow them to move freely over relatively large distances, this flexibility may mean that no part of the landscape will be divided up between them at a fine scale, even if some climates are more favorable to one species than the other.

We did find evidence that climate variables broadly distinguish weather stations located in the ranges of anubis baboons, yellow baboons, and their hybrids. This pattern suggests that, consistent with taxonomic guide books for African primates (Altmann *et al.* 2013; Kingdon 1997; Palombit 2013), anubis baboons are generally found in higher altitude environments, with higher rainfall and cooler temperatures, than yellow baboons; weather stations in the hybrid zone report intermediate climate patterns. However, it is difficult to cleanly distinguish the possibility that climate predicts species ranges from the possibility that historic biogeographic patterns alone explain species distributions. Proximity to the Indian Ocean strongly influences climate patterns in adjacent landmasses (Schott *et al.* 2009), and therefore the association between the weather station data and current baboon ranges could be, at least in part, an artifact of historical species range patterns. Given the importance of temperature and rainfall to baboons, though, we note that such an explanation still does not preclude some level of ecological adaptation (albeit subtle), in these highly generalist species.

In contrast to the weather station comparison across southern Kenya, none of the ecological variables we considered predicted the location of genetically characterized populations in the region immediately within the hybrid zone and its surroundings. Thus, when anubis baboons, yellow baboons, and their hybrids experience direct competition (i.e., when they forage and reproduce in the same habitat, so that one form could replace another if it had advantages in that habitat), ecological factors do not predict a clear "winner," at least when measured based on overall population composition. Several explanations could account for this observation. First, although we

analyzed all genetically characterized baboon populations in and near the yellow–anubis hybrid zone to date, we were able to include only one population comprised of unadmixed yellow baboons (two additional populations were scored as majority yellow). Along with the relatively small number of populations we sampled, we may therefore have failed to capture the full spectrum of ecological variation in and near the hybrid zone, particularly for yellow baboons. Thus, our analysis could have missed true differences in mean values for ecological variables due to sampling error. Conducting new sampling and genetic analysis for currently uncharacterized baboon populations was outside the scope of this study, but should be a priority for future work. Given a previous report of yellow–anubis hybrids near the Kora National Reserve northeast of Nairobi, this region of Kenya would be particularly interesting to sample (de Jong and Butynski 2010; Detwiler *et al.* 2005). However, we also note that the statistical evidence for a relationship between population ancestry and any of the measures in our current analysis is very weak ($P > 0.35$, with the exception of woodland). Our results thus suggest that if we missed true effect sizes owing to limited power, they are likely small.

Second, Alberts and Altmann (2001) suggested that the recent wave of hybridization in Amboseli may be a consequence of anthropogenic land use change in the Amboseli ecosystem (Alberts and Altmann 2001). Human-mediated changes in land use, e.g., the expansion of agriculture, and human population pressure are known to influence admixture rates in other primates. For example, in Brazil, human elimination of physical barriers to admixture has led to formation of a hybrid swarm between two marmoset species, *Callithrix jacchus* and *C. penicillata*, that are otherwise separated by the São Francisco River (Malukiewicz *et al.* 2015). In addition to affecting rates of admixture itself, anthropogenic pressures could therefore obscure a historical signal of ecological adaptation.

Third, climate variables may be most important when rainfall or temperature patterns reach extreme values; i.e., in addition to spatial structuring of ecological variables, there may also be temporal variability at play. Data from a long-term study population indicate that very dry conditions result in increased glucocorticoid concentrations in both males and females, while extreme heat depresses testosterone concentrations in males and increases glucocorticoid concentrations in females (Gesquiere *et al.* 2008, 2011). If ancestry predicts how well baboons do in extreme ecological conditions, ecological variability across years, and particularly the occurrence of recent extreme events, may be more important in predicting competitive outcomes than the mean climate patterns we examined here. In climatically "normal" periods, other factors, such as ancestry-related maturation time and mating success, may take precedence in driving hybrid zone dynamics.

Fourth, while we used high-quality data on directly measured temperature and rainfall from the weather stations, we only had an imperfect proxy (altitude) for temperature and rainfall in the hybrid zone. More fine-grained, direct measures of climate variables for these populations could reveal a relationship between ancestry and climate that is otherwise too subtle to detect. Alternatively, spatial interpolation methods, e.g., kriging or co-kriging, which impute missing values for spatially autocorrelated data, could be used to study the larger East African range of yellow and anubis baboons, especially if the north–south extent of the hybrid zone could also be genetically characterized (as noted above, yellow–anubis hybrids may also occur

northeast of Nairobi). Finally, other unmeasured variables could also be important. Kingdon argues, for example, that yellow baboons may be moderately specialized to feed on leguminous trees, such as *Acacia* (Kingdon 1997). If these resources are primarily correlated with other ecological factors, e.g., soil type or herbivore community, then temperature and rainfall may not be the most important variables to consider.

In conclusion, our analysis provides inconclusive support for the hypothesis that ecological barriers prevent protracted gene flow between species in this well-studied hybrid zone. The broader weather station analysis indicates that yellow baboons and anubis baboons may indeed have evolved in climatically distinct environments, but the impact of this history on competition within the hybrid zone itself remains unclear. Resolving this puzzle will likely require complementary insight from other approaches and a combination of intra- and interpopulation analyses. For example, it should be possible to use remote sensing methods to test if relative activity rates and space use (Markham and Altmann 2008; Strandburg-Peshkin *et al.* 2017) or the outcome of competitive interactions depends on ancestry, and whether these differences are larger in periods of ecological stress. Additionally, differences in pelage color and thickness between yellow and anubis baboons—perhaps the most visually apparent trait to distinguish these species—could be investigated to test for a relationship with surface body temperature and/or shade-seeking behavior. Notably, pelage color characteristics are some of the best studied traits in mammalian genetics (Hoekstra 2006; Hubbard *et al.* 2010), raising the possibility that an ecological study of its role in heat stress could be integrated with evolutionary analysis of its impact on the hybrid zone and a genetic analysis of its underlying basis.

Data Availability

All data analyzed in this study are included in the article and supporting Electronic Supplementary Material (Tables SI–SVI, Fig. S1).

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