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Ecology and age, but not genetic ancestry, predict fetal loss in a wild baboon hybrid zone

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Abstract

Objectives: Pregnancy failure represents a major fitness cost for any mammal, particularly those with slow life histories such as primates. Here, we quantified the risk of fetal loss in wild hybrid baboons, including genetic, ecological, and demographic sources of variance. We were particularly interested in testing the hypothesis that hybridization increases fetal loss rates. Such an effect would help explain how baboons may maintain genetic and phenotypic integrity despite interspecific gene flow.

Materials and Methods: We analyzed outcomes for 1020 pregnancies observed over 46 years in a natural yellow baboon-anubis baboon hybrid zone. Fetal losses and live births were scored based on records of female reproductive state and the appearance of live neonates. We modeled the probability of fetal loss as a function of a female's genetic ancestry (the proportion of her genome estimated to be descended from anubis [vs. yellow] ancestors), age, number of previous fetal losses, dominance rank, group size, climate, and habitat quality using binomial mixed effects models.

Results: Female genetic ancestry did not predict fetal loss. Instead, the risk of fetal loss is elevated for very young and very old females. Fetal loss is most robustly predicted by ecological factors, including poor habitat quality prior to a home range shift and extreme heat during pregnancy.

Discussion: Our results suggest that gene flow between yellow and anubis baboons is not impeded by an increased risk of fetal loss for hybrid females. Instead, ecological conditions and female age are key determinants of this component of female reproductive success.

KEYWORDS
baboon, fetal loss, genetic ancestry, hybridization

Arielle S. Fogel and Peter O. Oduor contributed equally to this work.

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1 | INTRODUCTION

Hybridization (i.e., interbreeding between distinct genetic lineages) is a common feature of primate evolution. Historic or ongoing hybridization has been documented in all primate families, including in the genus *Homo* (reviewed in Arnold & Meyer, 2006; Dannemann & Racimo, 2018; Tung & Barreiro, 2017; Zinner et al., 2011). In many cases, however, hybridizing taxa remain phenotypically and genetically distinct, despite the expectation that hybridization should have a homogenizing effect and ultimately lead to the erosion of species differences. These observations strongly suggest that hybridization incurs fitness costs, but the nature of these costs is largely unknown in natural non-human primate hybrid zones (in contrast to well-documented cases in several non-primate hybrids: e.g., Ålund et al., 2013; Neubauer et al., 2014; Powell et al., 2020; Svedin et al., 2008; Turner et al., 2012; Walsh et al., 2016). Thus, the mechanisms that limit gene flow between primate lineages remain a major unresolved puzzle in the study of primate biodiversity and evolution.

Costs to fertility are a likely candidate, given the apparent viability of many natural primate hybrids and the potential subtlety of effects on fecundability or miscarriage rates. Indeed, in captivity, crosses among lemur, tamarin, and macaque species produce hybrid offspring with compromised fertility (Bernstein & Gordon, 1980; Rumpler & Dutrillaux, 1980; Soto-Calderón et al., 2018; Tattersall, 1993). A few studies of naturally occurring admixture also provide preliminary support for fertility-related isolating barriers. For example, in a hybrid zone in Mexico between two distantly related howler monkey species, crosses between mantled howler females (*Alouatta palliata*) and black howler males (*A. pigra*) do not appear to produce fertile offspring (Cortés-Ortiz et al., 2007). In more recently diverged chacma baboons (*Papio ursinus*) and Kinda baboons (*P. kindae*) in Zambia, the rarity of offspring from crosses between small female Kindas and large male chacmas may be a result of gestational and obstetric challenges that limit gene flow, at least in one direction (Jolly et al., 2011). Finally, in the human lineage, reduced fertility has been hypothesized to have limited admixture between the ancestors of modern humans and Neanderthals and Denisovans (Jégou et al., 2017; Sankararaman et al., 2014; Sankararaman et al., 2016). However, in all three of these cases, evidence for compromised fertility in hybrids is indirect because no phenotypic data on fertility-related traits is available.

Baboons, members of the genus *Papio*, are well-suited for assessing fertility-related costs to hybrids as they are intensively studied in the wild, have external indicators of reproductive state that facilitate data collection on mating and pregnancy outcomes, and frequently hybridize in nature (Altmann, 1973; Fischer et al., 2019). Originating in southern Africa, baboons subsequently expanded across the continent 1–2 million years ago to form two distinct lineages: the northern clade, including the anubis (or olive) baboon (*P. anubis*), the hamadryas baboon (*P. hamadryas*), and the Guinea baboon (*P. papio*); and the southern clade, including the chacma baboon (*P. ursinus*), the Kinda baboon (*P. kindae*), and the yellow baboon (*P. cynocephalus*) (Rogers et al., 2019). Today, these species occupy largely non-overlapping geographic ranges across Africa and the Arabian peninsula and are distinguishable based on morphological and behavioral features (Fischer et al., 2019). However, although current scientific consensus recognizes them as distinct species (Fischer et al., 2019; Rogers et al., 2019), they interbreed to produce hybrids at the boundaries between their current geographic ranges (Charpentier et al., 2012; Jolly et al., 2011; Phillips-Conroy & Jolly, 1986). This process of interspecific exchange appears to be part of a long, complex history of independent evolution interspersed with repeated episodes of gene flow among baboon species (Rogers et al., 2019; Vilgalys et al., 2022; Wall et al., 2016; Zinner et al., 2009).

What keeps baboon species distinct? Studies of natural hybrid zones—between anubis and hamadryas baboons in Ethiopia, chacma and Kinda baboons in Zambia, and yellow and anubis baboons in Kenya—have not yet produced clear answers. In Ethiopia, anubis baboons hybridize with hamadryas baboons despite major differences in their social and mating structures: multilevel societies featuring one-male, multifemale units and female dispersal in hamadryas baboons, versus polygynandrous, multimale, multifemale social groups with male dispersal in anubis baboons (Bergman & Beehner, 2004; Kummer, 1968; Kummer et al., 1970). Some reports suggest that hybrids fare well near the center of the hybrid zone, where social groups are highly admixed (Beehner & Bergman, 2006; Bergman et al., 2008; Bergman & Beehner, 2003; Phillips-Conroy et al., 1991). However, species differences in behavior may also impose costs on anubis-hamadryas hybrids, potentially explaining the narrowness of this hybrid zone (Nagel, 1973; Nystrom, 1992). Meanwhile, in the Zambian hybrid zone between Kinda baboons and chacma baboons, asymmetric hybridization also suggests potential costs of hybridization (Jolly et al., 2011). Both hmorphological and behavioral mechanisms have been hypothesized, but their roles in mediating reproductive isolation-associated costs have not been quantified.

In the well-characterized baboon hybrid zone between yellow baboons and anubis baboons in East Africa, hybrids are viable and reproduce readily with both parent species and with other hybrids, even though their parent species are as distantly related as possible among extant baboons (~1.4 million years diverged vs. ~750 thousand years for anubis-hamadryas and ~ 600 thousand years for chacma-Kinda) (Rogers et al., 2019). Yellow and anubis baboons have similar social systems and are similar in size, so neither fundamental differences in mating behavior nor gestational and obstetric considerations likely pose a barrier to hybridization (Fischer et al., 2019; Rogers et al., 2019). Indeed, yellow-anubis hybrids may sometimes experience phenotypic advantages. In the Amboseli region of Kenya, near the center of the hybrid zone, greater anubis ancestry in this majority yellow ancestry population is associated with accelerated maturation and an increased rate of opposite-sex affiliation, an important predictor of lifespan in this population (Archie et al., 2014; Campos et al., 2020; Charpentier et al., 2008; Fogel et al., 2021). In males, more anubis ancestry also predicts earlier natal dispersal and increased mating success (Charpentier et al., 2008; Tung et al., 2012). Nevertheless, the hybrid zone is narrow relative to the large geographic ranges of the two parent species (Charpentier et al., 2012) and genomic analyses reveal selection against admixture in Amboseli

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(Vilgalys et al., 2022). Together with evidence that gene flow between yellow baboons and anubis baboons is a repeated occurrence in baboon evolutionary history (Rogers et al., 2019; Vilgalys et al., 2022; Wall et al., 2016), these observations suggest that fitness costs to admixture must exist, but are likely subtle and/or temporally or spatially variable.

Here, we investigated whether fertility-related costs, measured in terms of fetal loss (miscarriage or stillbirth), act as a mechanism to restrict interspecific gene flow in the Amboseli baboon hybrid zone. To do so, we combined the most comprehensive data set yet compiled for cases of fetal loss in wild non-human primates ($n = 1020$ pregnancies in 175 baboon females) with recent estimates of genetic ancestry derived from whole-genome resequencing data (Vilgalys et al., 2022). We tested whether higher levels of introgressed (anubis) ancestry, intermediate ancestry, or recent (relative to historic) hybridity predicted negative pregnancy outcomes, consistent with fetal loss-related barriers to admixture. We also placed these genetic ancestry effects in the context of other variables known or suspected to contribute to fetal loss in primates, including age, dominance rank, group size, ecological conditions (e.g., rainfall, temperature, and overall habitat quality), and individual history of miscarriage (e.g., Bailey et al., 2021; Beehner, Onderdonk, et al., 2006; Dezeure et al., 2022; Kolte et al., 2021; Nybo Andersen et al., 2000; Packer et al., 1995; Robbins et al., 2006; Roof et al., 2005; Schlabritz-Loutsevitch et al., 2008; Wasser, 1995).

2 | MATERIALS AND METHODS

2.1 | Study site and subjects

The Amboseli basin of southern Kenya is a semi-arid, savanna environment situated within a dry Pleistocene lakebed near the northern base of Mt. Kilimanjaro. Animals in this ecosystem contend with "a place of extremes" (Alberts, 2019). Temperatures vary from extreme midday heat, which can reach 45°C during the hottest months of the year, to nighttime lows of 5°C during the coldest months. Rainfall is generally absent during the predictable long dry season from June to October and is extremely variable and unpredictable during the long wet season from November to May. On average, total annual rainfall equals approximately 350 mm, but rainfall is also highly variable across years (Alberts, 2019).

Subjects in this study were pregnant females from multiple social groups of wild baboons living in the Amboseli ecosystem. This baboon population has been intensively studied for over five decades, revealing both substantial variation in pregnancy outcomes and a complex history of admixture (Alberts & Altmann, 2001; Alberts & Altmann, 2012; Beehner, Onderdonk, et al., 2006; Samuels & Altmann, 1986; Tung et al., 2008; Vilgalys et al., 2022; Wall et al., 2016). All animals in this majority yellow baboon population are multigenerational hybrids: some individuals harbor anubis ancestry from hybridization events that predate long-term observations (hereafter, historic hybrids), while others are products of both historic gene flow and a recent wave of admixture dating from the 1980s (hereafter, recent hybrids) (Samuels & Altmann, 1986; Tung et al., 2008; Vilgalys et al., 2022; Wall et al., 2016). The Amboseli hybrid population is located close to the center of a narrow yellow-anubis hybrid zone in southern Kenya that minimally extends into central Kenya and likely occurs wherever anubis and yellow baboon ranges meet (Charpentier et al., 2012; Maples & McKern, 1967). Males who immigrate into the study population tend to be more anubis-like than the study population as a whole, partly explaining an increase in anubis ancestry in Amboseli over the past four decades (Vilgalys et al., 2022). However, some immigrant males are more yellow-like than the study population as a whole, indicating that male immigration from both parental taxa contributes to admixture in this population (Vilgalys et al., 2022).

Members of the study population are individually recognizable and followed on a near-daily basis. During these follows, data are collected on individual-level behavior and reproductive status as well as group demography (Alberts et al., 2020). Study subjects for this analysis were pregnant females followed between November 1976 and December 2021 as members of 23 different social groups, representing two original study groups and their subsequent fission and fusion products. A minority of these groups (3 out of 23) were semi-provisioned because of their close proximity to a tourist lodge. While these three groups differ demographically and behaviorally from wild-feeding groups (e.g., they exhibit reduced male dispersal, higher rates of inbreeding, and shorter interbirth intervals: Altmann & Alberts, 2003; Galezo et al., 2022), our model results were similar whether we included or excluded them. Therefore, we included pregnancies from all social groups in our main analysis and we report results that exclude subjects in food-supplemented groups in the Supplementary Information (Table S1).

We restricted the data set to females for whom genetic ancestry estimates from whole-genome resequencing data were available (Vilgalys et al., 2022) and whose birthdates were known within ±6 months' error. We also excluded one female who was a known reproductive outlier in the study population (i.e., she experienced continuous cycling and failed to conceive over many years). The resulting sample contained 175 unique females, who together were observed during 1020 pregnancies (see below).

The research in this study was approved by the Institutional Animal Care and Use Committee (IACUC) at Duke University (#A273-17-12). In Kenya, our research was approved by the Wildlife Research Training Institute (WRTI), the Kenya Wildlife Service (KWS), the National Environment Management Authority (NEMA), and the National Council for Science, Technology, and Innovation (NACOSTI).

2.2 | Fetal losses

To track pregnancy outcomes, we relied on an established method regularly used during long-term monitoring of this population (Alberts et al., 2020; Altmann, 1973; Beehner, Nguyen, et al., 2006). Briefly, pregnancy is detectable when a female (i) ceases sexual cycling

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(i.e., ceases to exhibit sex skin swellings and does not menstruate) and (ii) her paracallosal skin gradually changes from black to pinkish red (the "pregnancy sign" in baboons: Altmann, 1973). A conception date is then estimated *a posteriori* as the first day of deturgescence of her sexual swelling during the cycle in which conception occurred (i.e., the conceptive cycle). Analyses of steroid hormone profiles from reproductive females in our study population confirm that this visual assessment method identifies 97% of endocrinologically-identified pregnancies (Beehner, Nguyen, et al., 2006). However, we are likely to miss pregnancies that terminate early in gestation (e.g., in the first trimester, especially early in the first trimester).

A pregnancy ends with either a live birth—when a previously pregnant female is seen with a new infant—or a fetal loss. Fetal losses are recorded when a female who has been scored as pregnant on the basis of the above criteria resumes cycling without producing a live infant, and also shows signs of fetal loss that may include vaginal bleeding, production of a dead fetus, and/or hormonal signatures of fetal loss (see Beehner, Nguyen, et al. (2006) for a detailed description and validation of these methods).

We excluded pregnancies that ended due to the pregnant female's death. We included all pregnancies that overlapped periods when social groups were fissioning or fusing, as well as all pregnancies that occurred during several periods of reduced data collection. We also included pregnancies that occurred during the 2009 hydrological year (November 1st, 2008 to October 31st, 2009), which included the most severe drought ever recorded in the Amboseli ecosystem and led to reduced conception rates (Carabine et al., 2014; Lea et al., 2015; Okello et al., 2016; Tuqa et al., 2014). Models that excluded these time periods produced similar results, however, as reported in Table S1.

2.3 | Genetic ancestry

Genome-wide estimates of admixture—here, the estimated proportion of a study subject's genome derived from anubis ancestry—were included for all females. These estimates can range from 0 (unadmixed yellow) to 1 (unadmixed anubis) and were based on low coverage whole-genome resequencing data generated in a previous study (median = 1.08× coverage, mean = 2.00× coverage) (Vilgalys et al., 2022). To estimate genome-wide ancestry, we first assigned local ancestry states to sequenced sites across the genome: each site was assigned a state of homozygous yellow, homozygous anubis, or heterozygous. To do so, we used a composite likelihood method suitable for low coverage data (*LCLAE*: Wall et al., 2016) and parental species allele frequencies for putatively unadmixed yellow and anubis baboons (Robinson et al., 2019; see Vilgalys et al., 2022). We then averaged local ancestry states across the autosomes for each female to produce a global, genome-wide estimate of ancestry. Females in this study varied in their genome-wide ancestry estimates from 0.23 to 0.60 (mean ± SD: 0.36 ± 0.08; Figure 1).

To assess genetic ancestry effects on fetal loss, we included both linear and quadratic effects of genome-wide ancestry in our model. The linear effect tests the hypothesis that females with more anubis ancestry in this majority yellow population have an increased likelihood of fetal loss. The quadratic effect tests the hypothesis that intermediate hybrids are more likely to experience fetal loss than animals near the extremes of yellow-like and anubis-like ancestry observed in Amboseli, as might be expected if F1-like animals incur the greatest costs of admixture. We also reasoned that admixture-related costs might not be detectable in historically admixed animals if selection has had sufficient time to remove deleterious variants. Therefore, we ran an alternative model in which we replaced the continuous estimates of ancestry with a binary variable corresponding to whether a female was a recent ($n = 89$) or historic ($n = 75$) hybrid (see Vilgalys et al., 2022). Because we could not assign historic versus recent hybrid status for 11 females in our sample, this model was fit to a reduced data set (164 females, 944 pregnancies, 136 fetal losses).

2.4 | Ecological effects

Even in non-seasonal breeders like baboons, ecological conditions can still influence female reproductive timing and pregnancy outcomes (Altmann & Alberts, 2003; Beehner, Onderdonk, et al., 2006; Bercovitch & Harding, 1993; Gesquiere et al., 2018; Hill et al., 2000; Lea et al., 2015; Lycett et al., 1999). We therefore evaluated the effects of three key aspects of baboon ecology on the probability of fetal loss: temperature, rainfall, and habitat quality.

2.4.1 | Temperature

Heat stress, when the environment drives core body temperature above its optimum, can have deleterious effects on sperm production, oocyte maturation, and fetal and placental growth (reviewed in Boni, 2019; Hansen, 2009; Walsh et al., 2019). To assess the potential effects of heat stress on fetal loss, we followed Beehner, Onderdonk, et al. (2006) by assessing the effects of temperature in two time periods: the 2 months prior to conception and the 2 months prior to the live birth or fetal loss. Temperature (°C) was measured daily using a min-max thermometer. We calculated the average daily maximum temperature for both time periods, which were weakly negatively correlated, indicating that females who conceived during the cooler months of the year tended to experience pregnancy outcomes in the warmer months of the year and vice versa (Pearson's $r = -0.157$, $p < 10^{-6}$; Table S2). This is expected given patterns of seasonality in Amboseli and the 6-month gestation period of baboons. We included temperature in both time periods as continuous predictors in our models (note that this choice differs from Beehner, Onderdonk, et al. (2006), who used a binary variable to differentiate "normal" periods from those with extreme heat).

For daily maximum temperature data collected from June 1992 to 1997, the thermometer was located close to the research camp's kitchen, producing systematically high temperature measurements. Before and after that time period, the thermometer was placed in

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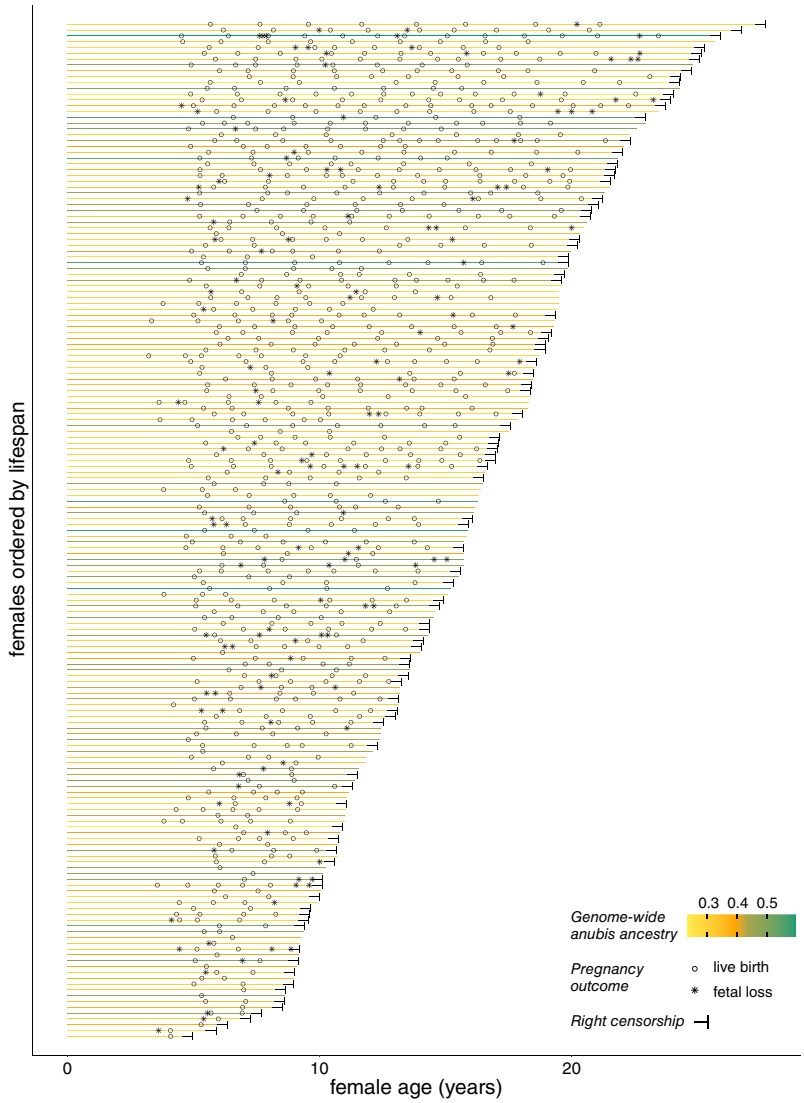

FIGURE 1 Live birth and fetal loss patterns in Amboseli baboon females. Each horizontal line represents the observed lifespan of a single female. The right end of each line corresponds to either the female's age at last observation (right censorship; denoted by a horizontal T) or age at death. Horizontal lines are organized from bottom to top based on lifespan and are colored by genetic ancestry. Open circles show live births and asterisks show fetal losses.

several other locations in the research camp that were far from any building structure. To correct the data from June 1992 to 1997, we subtracted 4.2°C from all maximum daily temperature values recorded during this time period. This adjustment factor was calculated based on modeling daily maximum temperature as a function of the day of the year and a random effect of thermometer (instrument used from 1992–1997 vs. the four other thermometers). Importantly, a model excluding pregnancy records from this time period produced qualitatively unchanged results.

2.4.2 | Rainfall

In the semi-arid Amboseli ecosystem, rainfall mediates female fertility by affecting food availability and thus female nutritional condition. Following Beehner, Onderdonk, et al. (2006), we evaluated the effects of rainfall conditions in the 5 months prior to conception as well as the 5 months prior to the pregnancy outcome (either live birth or fetal loss). Daily rainfall (millimeters) was measured every morning using a rain gauge. For both the 5 months preceding conception and the end of the pregnancy, we calculated the mean daily rainfall across each time period. These two predictors were moderately negatively correlated in our data set, again consistent with seasonal rainfall patterns in Amboseli (Pearson's $r = -0.385$, $p < 10^{-36}$; Table S2). We modeled rainfall in both time periods as continuous predictors (in contrast to the binary variable distinguishing unusually dry periods—that is, droughts—from non-drought periods in Beehner, Onderdonk, et al. (2006)).

2.4.3 | Habitat quality

In the central part of the Amboseli basin, the mid-1960s to the mid-1980s saw a precipitous decline in *Acacia* woodlands (Altmann et al., 1985; Western & Van Praet, 1973). Because baboons in Amboseli rely on *Acacia* trees as an important food source and for sleeping sites, this change led to substantially degraded habitat quality for them (Altmann et al., 1985). Subsequently, in the late 1980s and early

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1990s, the two study groups then monitored by the Amboseli Baboon Research Project shifted their home ranges ~5–6 km from the central part of the basin to its south-western perimeter, where food was more readily available (Altmann & Alberts, 2003; Bronikowski & Altmann, 1996). After the home range shift, the baboons spent more time resting and socializing and less time foraging, and females experienced earlier maturation, increased offspring survival, and shorter interbirth intervals (Alberts et al., 2005; Altmann & Alberts, 2003; Bronikowski & Altmann, 1996; Gesquiere et al., 2018). We therefore modeled habitat quality as a binary variable in our model, indicating whether a pregnancy was conceived pre- or post-home range shift (i.e., in low or high habitat quality, respectively).

2.5 | Other potential sources of variance in fetal loss rates

2.5.1 | Age

Female age is a known predictor of fertility in a diverse set of species (e.g., Campos et al., 2022; Ericsson et al., 2001; Froy et al., 2013; Gruhn et al., 2019; Hayward et al., 2013; Jones et al., 2014; Nussey et al., 2009; Reid et al., 2003). In the Amboseli baboons, conception probabilities peak in mid-adulthood, and younger and older females experience the longest periods of cycling before conceiving and the shortest pregnancy lengths (Beehner, Onderdonk, et al., 2006; Campos et al., 2022; Gesquiere et al., 2018). We therefore included linear and quadratic effects of female age at conception in our model (following Beehner, Onderdonk, et al., 2006; Campos et al., 2022; Gesquiere et al., 2018). Because female age was highly correlated with parity (primiparous vs. multiparous) (Pearson's $r = 0.515$, $p < 10^{-69}$), we included female age but not parity in the model (we note, however, that we identified no effect of primiparity/multiparity in a *post hoc* analysis: $\beta = -0.203$, $p = 0.559$). For 92% (161 out of 175) of the females in the data set, birthdates were known to within a few days' error. For the remaining female subjects, 12 females had birthdates that were estimated to within ±3 months' error and 2 females had birthdates that were estimated to within ±6 months' error (see Table S1 for results of a model excluding females with birthdates estimated with greater than a few days' error, which were similar to the main analysis). Female age in our data set ranged from 3.2 to 23.4 years of age, with a mean female age of 10.4 years.

2.5.2 | Social status

In social animals, dominance rank can dictate a female's access to a variety of crucial resources including food, mates, and social partners, which may then affect her reproductive success (e.g., Holekamp et al., 1996; Pusey et al., 1997; Setchell et al., 2002; von Holst et al., 2002; Wasser et al., 2004; Wright et al., 2020; reviewed in Stockley & Bro-Jørgensen, 2011). We therefore modeled a female's rank at the time of conception as a fixed effect in the model. Ordinal ranks were assigned on a monthly basis using observed wins and losses in agonistic interactions between all pairs of adult females living in the same social group in a given month: the top-ranking female in the hierarchy in each month was assigned rank 1 and lower-ranking individuals were assigned successively higher numbers (i.e., ranks 2, 3, 4 … x, where x is the total number of adult females in the social group) (Alberts et al., 2020; Alberts & Gordon, 2018).

The ordinal ranking approach assumes that rank-based competition for resources is density-dependent, such that the resources over which females compete do not scale with changes in group size (Levy et al., 2020). However, females may also compete for density-independent resources, which is better captured by proportional rank (Levy et al., 2020). Therefore, we also assessed the robustness of our models to substituting proportional rank for ordinal rank. Proportional rank was calculated using ordinal rank values and hierarchy size, such that values range from 0 to 1 and represent the proportion of females in the hierarchy that a given female outranks (e.g., the highest-ranking female is assigned a value of 1 because she outranks 100% of other individuals in the hierarchy). Using ordinal or proportional ranks as the rank-related predictor in our model did not qualitatively change our results so we report results using ordinal rank in the main text (see Table S3 for results using proportional rank).

2.5.3 | Group size

To measure group size, which indexes experienced density and resource competition, we included the number of adult females in the social group at the time of conception as a continuous predictor in our model. We used the number of adult female group members instead of the total number of group members because the number of adult females in the social group is the stronger predictor of female fertility traits, such as interbirth intervals, in the Amboseli baboons (Altmann & Alberts, 2003).

2.5.4 | Previous fetal losses

The number of previous fetal losses is one of the two strongest predictors of miscarriage rates in humans (in addition to maternal age) (Brosens et al., 2022). We therefore included the number of previous fetal losses as a fixed effect predictor when modeling pregnancy outcome. Primiparous mothers were assigned a value of 0 (no previous fetal losses).

2.6 | Statistical analysis

We analyzed the probability of fetal loss using a mixed effects logistic regression approach. Each row of data corresponded to a unique pregnancy and was assigned a value of 1 if the pregnancy resulted in a fetal loss and a 0 if the pregnancy resulted in a live birth. We fit the model using the R package *glmmTMB* (Brooks et al., 2017):

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$$y_{ij} \sim \text{Bin}(1, p_{ij}),$$

$$p_{ij} = \text{logit}(\beta_0 + \boldsymbol{X_{ij}\beta} + f_i + \varepsilon_{ij}),$$

where y_{ij} is 0 or 1, corresponding to whether female i experienced a live birth (0) or fetal loss (1) during pregnancy j. y_{ij} is drawn from a binomial distribution, where the probability of fetal loss (p_{ij}) is modeled as the function of the logit-transformed sum of (i) the intercept, β_0; (ii) the fixed effects ($\boldsymbol{X_{ij}\beta}$) of female genome-wide ancestry (or recent vs. historic hybrid status), female genome-wide ancestry squared, female age at conception, female age at conception squared, number of previous fetal losses, female ordinal dominance rank, group size, average daily maximum temperature 2 months prior to conception, average daily maximum temperature 2 months prior to live birth/fetal loss, average daily rainfall 5 months prior to conception, average daily rainfall 5 months prior to live birth/fetal loss, and habitat quality ($\boldsymbol{X_{ij}}$ represents all of these data using standard matrix notation and $\boldsymbol{\beta}$ refers to the vector of all fixed effect estimates); and (iii) the random effect of female identity, f_i. ε_{ij} represents model error. All analyses were run and figures were made in R (v.3.6.1; R Core Team, 2019).

3 | RESULTS

3.1 | Fetal loss rates in the Amboseli baboon population

The resulting data set consisted of 1020 pregnancies (minimum number of pregnancies per female = 1, maximum = 18, mean = 6). For 98% of pregnancies, the dates of conception (1002 out of 1020) and end of the pregnancy (1005 out of 1020) were known to within a few days' error. Inclusion or exclusion of pregnancies with less certain conception or pregnancy end dates did not qualitatively change our model results (Table S1). Of the 1020 pregnancies in our data set, 143 (14%) resulted in fetal loss (see Beehner, Onderdonk, et al. (2006) for similar results in a smaller, earlier dataset for this population). Thus, the rate of fetal losses in our population has been relatively stable over the course of our long-term study, and is similar to the rate reported in human females following clinical recognition of pregnancy (i.e., usually after 4–6 weeks gestational age) (Dimitriadis et al., 2020; Pinar et al., 2018). It is slightly higher than miscarriage estimates for anubis baboons from Gombe National Park, Tanzania (9.6%–10.7%: Bailey et al., 2021; Packer et al., 1995) and for yellow baboons from Mikumi National Park, Tanzania (10%: Wasser, 1995), although differences in population ecology and inclusion criteria for fetal losses (e.g., we include stillbirths but Bailey et al. (2021) exclude them) make direct comparisons difficult.

Exactly half of the females in our sample never experienced a fetal loss, and both the number of fetal losses and number of live births per female tracked their total number of pregnancies (linear model estimate for live births: $\beta = 0.824$, $p < 10^{-89}$, Figure S1A; linear model estimate for fetal losses: $\beta = 0.176$, $p < 10^{-14}$, Figure S1B). Fetal losses were recorded during all three trimesters, although almost half were documented during the third trimester (Figure 2). Very few fetal losses were related to the immigration of feticidal males, an important source of social stress for pregnant females ($n = 4$–8 of the 113 fetal losses in our data set overlapped the data set of Zipple et al. (2017); minimum value corresponds to high confidence feticides and maximum value includes additional possible feticides), so we included these cases in our main data set. A model excluding feticides is consistent with the results from the main model (Table S4).

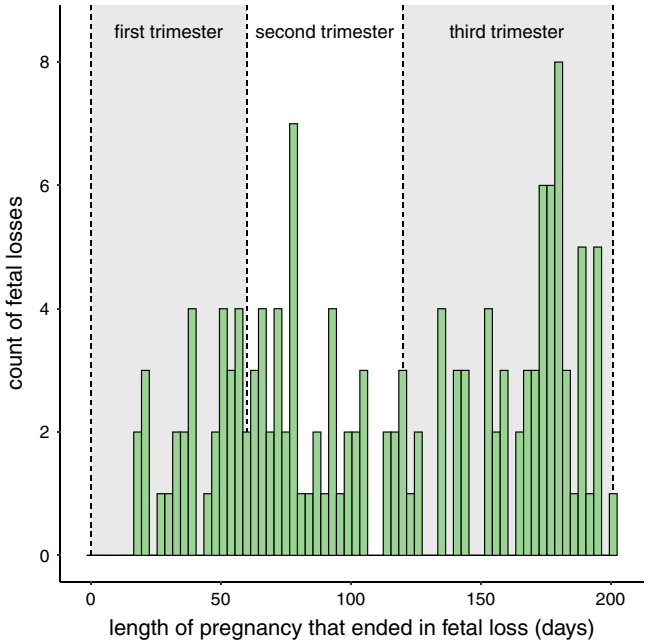

FIGURE 2 Records of fetal loss by trimester in the data set ($n = 143$). Approximately half of observed fetal losses (67 out of 143) occurred in the third trimester. Mean gestation length for live births in Amboseli baboons is 178 days (Gesquiere et al., 2018), but stillbirths sometimes occurred several weeks beyond this mean value; thus, the third trimester losses in this dataset occurred from days 121–202 post-conception (where 202 is the maximum number of days at which fetal loss was documented). Second and first trimester losses represented 32.9% (47 out of 143) and 20.3% (29 out of 143) of fetal losses, respectively. Data are binned in three-day increments and include 3 cases where the dates of conception or end of the pregnancy were known to greater than a few days' error.

3.2 | Genetic ancestry and hybrid status are not associated with fetal loss

The results of our main model indicate that a female's genome-wide ancestry did not predict her likelihood of fetal loss (linear effect: $\beta = -8.492$, $p = 0.506$; quadratic effect: $\beta = 11.454$, $p = 0.471$; Table 1, Figure 1, Figure 3a). Substituting a binary variable corresponding to a female's hybrid status (i.e., recent or historic) in place of the linear and quadratic genetic ancestry predictors also did not reveal any effect of admixture on pregnancy outcome ($\beta = 0.201$, $p = 0.408$; Table S5). Both models produced qualitatively similar results and while

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TABLE 1 Results from the main logistic regression model predicting fetal loss

		Effect estimate	SE	Z	p†	Effect direction‡
	Intercept	−9.293	4.063	−2.287	0.022	-
Individual-level	Genetic ancestry	−8.492	12.782	−0.664	0.506	-
	(Genetic ancestry)^2	11.454	15.903	0.720	0.471	
	Age at conception	−0.203	0.108	−1.889	0.059	**Younger and older mothers → ↑ Pr(fetal loss)**
	(Age at conception)^2	**0.010**	**0.004**	**2.382**	**0.017**	
	Number of previous fetal losses	−0.235	0.275	−0.855	0.392	-
Social and Demographic	Dominance rank at conception	0.016	0.020	0.772	0.440	-
	Group size	−0.019	0.021	−0.901	0.367	-
Ecological	Temperature 2 months pre-conception	0.099	0.057	1.738	0.082	-
	Temperature 2 months pre-live birth or fetal loss	**0.195**	**0.066**	**2.973**	**0.003**	**Higher temperatures before end of pregnancy → ↑ Pr(fetal loss)**
	Rainfall 5 months pre-conception	0.089	0.130	0.684	0.494	-
	Rainfall 5 months pre-live birth or fetal loss	0.070	0.122	0.571	0.568	-
	Habitat quality (high = 0, low = 1)	**0.888**	**0.433**	**2.051**	**0.040**	**Low habitat quality at time of conception → ↑ Pr(fetal loss)**

†Predictor variables for which $p < 0.05$ are bolded.
‡Pr(fetal loss) = probability of fetal loss.

we focus on the main model below, we note when results differed between models.

3.3 | Maternal age predicts fetal loss

Our main model identified female age as the only individual-level characteristic that predicted fetal loss (Table 1, Figure 3a). Younger and older pregnant females were more likely to experience fetal loss than middle aged females (quadratic effect of age: $\beta = 0.010$, $p = 0.017$; Table 1, Figure 3b). Based on model predictions, females at the oldest age included in our data set (23.2 years) are the most likely to suffer fetal loss (38.6% probability of fetal loss vs. 13.9% for females at the youngest age; Figure 3b), while females at approximately the median age in the data set (9.73 vs. median 9.49 years) are the least likely to suffer fetal loss (9.3%).

3.4 | Ecological factors, but not social status or group size, contribute to variance in pregnancy outcomes

Beyond age effects, which are common in humans and other animals, the primary predictors we identified for fetal loss were related to heat stress and overall habitat quality. Increasing mean maximum temperatures prior to the end of pregnancy predicted an increased chance of fetal loss ($\beta = 0.195$, $p = 0.003$, Table 1, Figure 3a,c; see Beehner, Onderdonk, et al. (2006) for a similar result for first trimester losses). Elevated mean maximum temperatures prior to conception may also weakly contribute to the probability of fetal loss, although this effect was not statistically significant ($\beta = 0.099$, $p = 0.082$, Table 1, Figure 3a; see also Tables S1, S3, S4, and S5 for alternative model specifications with similar results). Additionally, pregnancies when females lived in low habitat quality were more likely to end in fetal loss relative to those occurring in high habitat quality ($\beta = 0.888$, $p = 0.040$; Table 1, Figure 3d), although this effect was not statistically significant under several alternative model specifications ($\beta = 0.857$–1.039, $p = 0.053$–0.103, Tables S1, S4, and S5). In contrast, social rank, group size, and rainfall levels pre-conception and before the end of pregnancy did not predict fetal loss rates in any version of our models (all $p > 0.20$; Table 1, Figure 3a, Tables S1, S3, S4, and S5).

4 | DISCUSSION

Together, our analysis combines long-term data on behavior, demography, and ecology with the ability to track fetal loss to produce the largest study of fetal loss rates in wild primates to date. We found no support for the hypothesis that fetal loss acts to counter free gene flow between yellow baboons and anubis baboons in Amboseli. Instead, our findings show that a female's genetic ancestry in this

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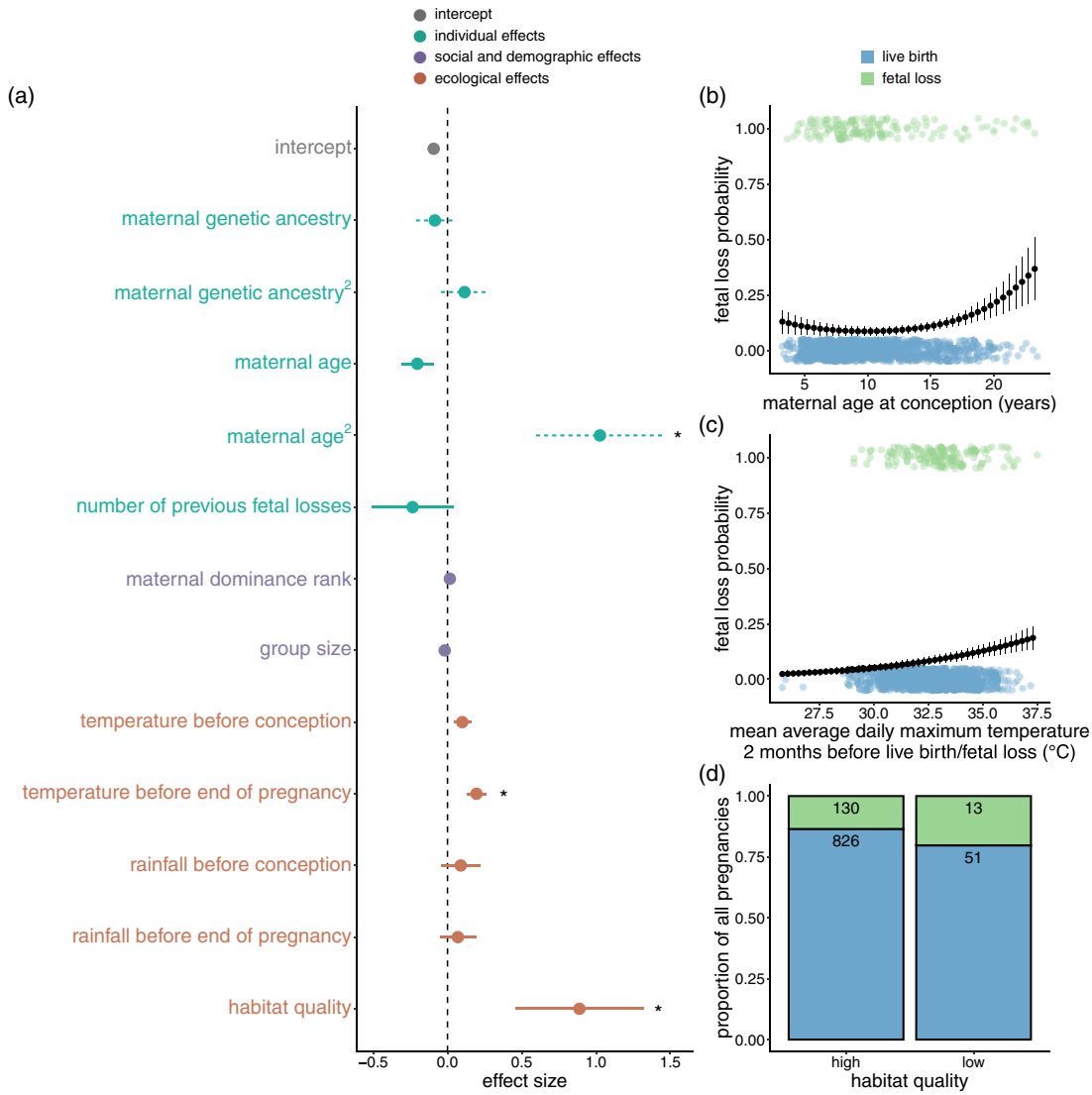

FIGURE 3 Predictors of fetal loss in wild baboons. (a) Effect estimates for the intercept and fixed effects in the main logistic regression model predicting fetal loss. Dots correspond to effect sizes and horizontal lines correspond to effect sizes ±1 standard error. Dashed horizontal lines correspond to the intercept and genetic ancestry-related predictors (which were divided by 100 to place them on a similar scale as the other predictors, to facilitate visualization) and maternal age^2 (multiplied by 100 for scaling, for the same reason). Solid horizontal lines correspond to unscaled effect sizes and standard errors. Asterisks denote predictor variables for which $p < 0.05$. (b) The probability of fetal loss as a function of a female's age at conception. Black dots and vertical lines correspond to the predicted relationship (±1 standard error for each female age) based on model estimates, assuming average values for all other covariates. Colored dots show fetal loss ($y = 1$; green) or live birth ($y = 0$; blue) for all 1020 pregnancies (dots are jittered vertically for visibility). (c) As in (b), with the probability of fetal loss as a function of temperature 2 months prior to the end of pregnancy. (d) The proportion of all pregnancies that were fetal losses (colored green) or live births (colored blue) as a function of habitat quality. Counts per pregnancy outcome for each type of habitat quality are shown as numbers within each bar.

admixed population does not predict fetal loss, despite substantial variation in pregnancy outcomes overall. Thus, this aspect of female fertility is unlikely to play a substantial role in maintaining species boundaries in baboons, unless the effects of maternal genetic ancestry are concentrated during the first few weeks of gestation, when we are unable to accurately detect pregnancy. In our data set, the earliest fetal losses occurred at approximately 3 weeks gestational age, which roughly equates to the first 5 weeks of pregnancy in humans. In human women, losses during this time are thought to be associated with spontaneous chromosomal abnormalities, primarily aneuploidies, in the embryo (Larsen et al., 2013; Pinar et al., 2018; but see Brosens et al., 2022). Hybridization can increase aneuploidy rates in some animal systems (Dion-Côté et al., 2015; Fujiwara et al., 1997; Hauffe et al., 2012; Hu et al., 2013; Sakai et al., 2007). However, hybridization-driven chromosomal abnormalities are not an obvious expectation in baboons, where chromosome numbers are identical in all extant taxa and synteny is thought to be very high (Stanyon et al., 2008).

Our results indicate that the ability of hybrid females to carry a pregnancy to term is unlikely to explain reproductive isolation

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between baboon species. A caveat to our findings is that all animals in our study population are hybrid: if the effect of ancestry on fetal loss only appears in comparisons between unadmixed females and hybrids of any degree, we would not observe it. Although we cannot rule out this possibility, we view it as unlikely given that the range of ancestry values in the Amboseli population has been sufficient to both detect genetic ancestry effects on other life history and behavioral traits (Charpentier et al., 2008; Fogel et al., 2021; Franz et al., 2015; Tung et al., 2012) and to identify genetic evidence for selection against introgression (Vilgalys et al., 2022). Additionally, other aspects of conception or pregnancy may contribute to reproductive isolation. For instance, we were unable to investigate effects of paternal ancestry in this study because, in a multiply mating species like baboons, paternal identity cannot be confirmed without genetic data, which are not available for miscarried or stillborn fetuses. Thus, it remains possible that genetic ancestry affects fetal loss as a function of the father's ancestry. This possibility would be consistent with Haldane's rule, which posits that when species interbreed, hybrids of the heterogametic sex (e.g., fathers) are more likely to suffer fitness costs relative to hybrids of the homogametic sex (e.g., mothers) (Haldane, 1922). Notably, costs to hybrid male fertility need not be complete for Haldane's Rule to be satisfied. Further, even if hybrid males suffered fertility-related costs, hybrid females could mate with yellow-like males to produce backcrossed offspring and perpetuate the hybrid zone. Finally, the interaction between maternal and paternal genetic ancestries could play a role if ancestry combinations at specific regions of the genome negatively interact in the developing fetus (i.e., Bateson-Dobzhansky-Muller incompatibilities, or BDMIs: Bateson, 1909; Dobzhansky, 1936; Muller, 1942). The locations of putative BDMIs can be inferred via genetic scans for local ancestry combinations that are underrepresented in hybrid populations (Payseur & Hoekstra, 2005; Pool, 2015; Schumer et al., 2014), suggesting a potential path forward for testing this hypothesis in hybrid populations where fetal loss and genetic ancestry data are available.

While we found no evidence for genetic ancestry effects, our results do highlight several other sources of variance in pregnancy outcomes in this population. Female age predicted fetal loss, such that the youngest and oldest females experienced the highest rates of fetal loss. In a previous analysis in this population, Beehner, Onderdonk, et al., 2006 found no linear effect of age but did not examine a quadratic effect of age, which may explain the difference between this analysis and the earlier one. However, our results are similar to those described in captive baboons (Schlabritz-Loutsevitch et al., 2008). Indeed, even though captive baboons have much longer life expectancies (Bronikowski et al., 2002), fetal loss rates increase exponentially at ~14–15 years of age in both Amboseli and in the breeding colony at the Southwest National Primate Research Center (Schlabritz-Loutsevitch et al., 2008), suggesting that the onset of reproductive senescence in female baboons may be relatively insensitive to environmental differences.

Ecological stressors also predicted fetal loss: females living in low habitat quality and exposed to heat stress during pregnancy experienced elevated fetal loss rates. Here again, our findings expand on the work of Beehner, Onderdonk, et al. (2006), who also identified a possible effect of heat stress on fetal loss rates. However, this relationship did not reach statistical significance ($p = 0.07$ in Beehner, Onderdonk, et al. (2006)) and was detectable only in first trimester pregnancies. Further, their results could have been affected by the systematically elevated maximum daily temperature records during 5 years of the long-term study (1992–1997; see Methods). Our results, which include a substantially larger sample size ($n = 1020$ pregnancies vs. 656 in Beehner, Onderdonk, et al. (2006)) and corrected temperature data (see Methods), therefore confirm the importance of heat stress for pregnancy outcomes across gestation. Our results also dovetail with evidence from a wide variety of animal taxa on the relationship between heat stress and compromised fertility, starting from germ cell generation through gestation (reviewed in Boni, 2019; Hansen, 2009; Walsh et al., 2019).

In contrast to Beehner, Onderdonk, et al. (2006), who identified an effect of severe drought on pregnancy outcomes, we did not identify an effect of rainfall on fetal losses versus live births. This difference between our results and theirs may be partly attributable to the fact that we used a continuous rainfall measure, while they categorized 5-month periods as "drought" versus normal periods. Furthermore, our finding that overall habitat quality (not included in Beehner, Onderdonk, et al. (2006)) predicts fetal loss may capture a similar mechanism: a degraded resource base with inadequate food to support successful female reproduction. Notably, exposure to heat stress and drought conditions are expected to become more common in many animal populations due to accelerating climate change (Fuller et al., 2021; Walsh et al., 2019). Our results suggest that these changes may not only compromise habitat quality, but also alter vital rates for primate populations to decrease mean population fitness.

Our findings also reinforce the value of baboons as models for human reproduction (Bauer, 2015; D'Hooghe et al., 2009; Hendrickx & Peterson, 2009; Honoré & Tardif, 2009; Nathanielsz et al., 2009). Specifically, in addition to sharing slow life histories, little to no reproductive seasonality, and similarities in reproductive biology (e.g., size and anatomy of the internal reproductive tract, morphology of the placenta, incidence of gynecological diseases; reviewed in VandeBerg et al., 2009), our study suggests that fetal loss in baboons exhibits parallels to fetal loss in humans (Schlabritz-Loutsevitch et al., 2008). The rate of fetal loss in Amboseli—approximately 1.4 out of 10 pregnancies (Beehner, Onderdonk, et al. (2006) and this study)—is similar to some estimates of miscarriage rates for clinically recognized pregnancies in humans (e.g., ~10%–20% after implantation: Dimitriadis et al., 2020; Pinar et al., 2018). Moreover, abiotic environmental stressors, including high temperatures during pregnancy, have recently gained attention in potentially explaining adverse birth outcomes in humans, such as fetal loss (e.g., Hajdu & Hajdu, 2021; Kanner et al., 2020; Strand et al., 2012; Syed et al., 2022; but see Asamoah et al., 2018). For example, in low-risk pregnant women in Utah, extreme heat exposure (>90th temperature percentile) increased the odds of stillbirth by ~5-fold compared to exposure to moderate temperatures (Kanner et al., 2020). Further, age-related miscarriage risk in human women is thought to also follow a "J-shaped

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curve," with higher rates in very young women and increasing rates as women age (Brosens et al., 2022). However, in humans, age-related patterns of miscarriage also suffer from sociocultural biases that influence both pregnancy outcomes and the age of first pregnancy (Cohen, 2014; Santelli et al., 2017). Our novel observation that a similar "J-shaped curve" occurs in wild baboons therefore provides preliminary evidence that the pattern observed in humans may be in part due to evolutionarily conserved reproductive biology. Importantly, in humans, the causes of a large fraction of pregnancy failures remain unclear despite decades of biomedical research (Pinar et al., 2018). Thus, studies in wild non-human primates may therefore present valuable systems for understanding biological drivers of adverse pregnancy outcomes in humans.

AUTHOR CONTRIBUTIONS

Arielle S. Fogel: Formal analysis (equal); funding acquisition (supporting); investigation (equal); methodology (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Peter O. Oduor:** Formal analysis (equal); investigation (equal); methodology (equal); writing – review and editing (equal). **Albert W. Nyongesa:** Project administration (supporting); resources (supporting); supervision (supporting); writing – review and editing (equal). **Charles N. Kimwele:** Project administration (supporting); resources (supporting); supervision (supporting); writing – review and editing (equal). **Susan C. Alberts:** Conceptualization (equal); data curation (equal); funding acquisition (lead); project administration (lead); resources (lead); supervision (supporting); writing – review and editing (equal). **Elizabeth A. Archie:** Conceptualization (equal); data curation (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); writing – review and editing (equal). **Jenny Tung:** Conceptualization (equal); data curation (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at [https://github.com/ArielleF/Fetal-Loss].

DATA AVAILABILITY STATEMENT

Data on pregnancy outcomes and all predictor variables tested in our models are available in Table S6. R code for recreating the analyses and figures in the manuscript is available at https://github.com/ArielleF/Fetal-Loss.

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