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Early life drought predicts components of adult body size in wild female baboons

Emily J. Levy[1,2] | Anna Lee[2] | I. Long'ida Siodi[3] | Emma C. Helmich[2] |
Emily M. McLean[4] | Elise J. Malone[2] | Maggie J. Pickard[2] |
Riddhi Ranjithkumar[5] | Jenny Tung[2,6,7,8] | Elizabeth A. Archie[9] |
Susan C. Alberts[2,7]

[1]Department of Biology, Indiana University, Bloomington, Indiana, USA

[2]Department of Biology, Duke University, Durham, North Carolina, USA

[3]Amboseli Baboon Research Project, Amboseli National Park, Kajiado, Kenya

[4]Division of Natural Sciences, Oxford College of Emory University, Oxford, Georgia, USA

[5]Department of Biomedical Engineering, Duke University, Durham, North Carolina, USA

[6]Department of Primate Behavior and Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[7]Department of Evolutionary Anthropology, Duke University, Durham, North Carolina, USA

[8]Canadian Institute for Advanced Research, Toronto, Canada

[9]Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana, USA

Correspondence
Susan C. Alberts, Department of Biology, Duke University, Durham NC 27708, USA.
Email: alberts@duke.edu

Abstract

Objectives: In many taxa, adverse early-life environments are associated with reduced growth and smaller body size in adulthood. However, in wild primates, we know very little about whether, where, and to what degree trajectories are influenced by early adversity, or which types of early adversity matter most. Here, we use parallel-laser photogrammetry to assess inter-individual predictors of three measures of body size (leg length, forearm length, and shoulder-rump length) in a population of wild female baboons studied since birth.

Materials and Methods: Using >2000 photogrammetric measurements of 127 females, we present a cross-sectional growth curve of wild female baboons (*Papio cynocephalus*) from juvenescence through adulthood. We then test whether females exposed to several important sources of early-life adversity—drought, maternal loss, low maternal rank, or a cumulative measure of adversity—were smaller for their age than females who experienced less adversity. Using the "animal model," we also test whether body size is heritable in this study population.

Results: Prolonged early-life drought predicted shorter limbs but not shorter torsos (i.e., shoulder-rump lengths). Our other measures of early-life adversity did not predict variation in body size. Heritability estimates for body size measures were 36%–67%. Maternal effects accounted for 13%–17% of the variance in leg and forearm length, but no variance in torso length.

Discussion: Our results suggest that baboon limbs, but not torsos, grow plastically in response to maternal effects and energetic early-life stress. Our results also reveal considerable heritability for all three body size measures in this study population.

KEYWORDS
early-life adversity, environmental effects, growth, photogrammetry, primate

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1 | INTRODUCTION

1.1 | Effects of early-life adversity on body size across species

During development, all organisms must allocate energy toward the body's many developing systems, including sensory abilities, the immune system, and growth. When energy is limited, organisms cannot allocate adequate resources to all systems and must alter development to survive. Consequently, during early life, adverse environments affect phenotypes by forcing organisms to make developmental trade-offs.

In many taxa, adverse early-life environments, such as famine, drought, or social neglect, have been shown to predict wide-ranging and long-term effects (e.g., blue-footed boobies, *Sula nebouxii*: Ancona & Drummond, 2013; humans, *Homo sapiens*: Brown et al., 2009; Elo & Preston, 1992; Galobardes et al., 2008; Hayward et al., 2013; rhesus macaques, *Macaca mulatta*: Lewis et al., 2000; water pythons, *Liasis fuscus*: Madsen & Shine, 2000; banded mongoose, *Mungos mungo*: Marshall et al., 2017; baboons, *Papio anubis*: Patterson et al., 2021; baboons, *Papio cynocephalus*: Tung et al., 2016). One common effect is slowed growth, which leads to reduced adult body size. For example, in a longitudinal study of the 1958 British birth cohort, children raised in larger families or more crowded homes were shorter - both in childhood and adulthood - than those raised in smaller families or more spacious homes (Li et al., 2007). In another study, children raised in Ukrainian orphanages—a source of intense psychosocial stress, but not energetic stress—had stunted growth and low body mass compared to children raised by their families (Dobrova-Krol et al., 2008). Poor early-life environments have also been associated with slower growth and smaller adult body size in wild and captive non-human mammals (wild bighorn sheep, *Ovis canadensis*: Festa-Bianchet et al., 2000; wild roe deer, *Capreolus capreolus*: Pettorelli et al., 2002; captive squirrel monkeys, *Saimiri sciureus boliviensis*: Pucciarelli et al., 2000). For example, wild roe deer born during a time of high population density weighed approximately 15% less as adults than deer born during a time of low population density (Pettorelli et al., 2002).

Whereas body size in humans and ungulates is relatively well studied, analyses of adult body size or growth patterns in most wild mammals are scarce. This is especially true for wild primates: obtaining body size data have typically involved immobilization or provisioning, both of which present particular challenges for primates. To our knowledge, measures of growth or body size during both pre-adult and adult life stages have only been estimated for geladas, Assamese macaques, owl monkeys, black-and-white snub-nosed monkeys, anubis baboons, eastern chimpanzees, and mountain gorillas (Anzà et al., 2022; Galbany et al., 2017; Huck et al., 2011; Li et al., 2023; Lu et al., 2016; Pusey et al., 2005; Strum, 1991). Further, predictors of inter-individual differences in body size or mass have only been assessed for a handful of wild primate populations (Altmann & Alberts, 2005; Berghänel et al., 2015, 2016; Borg et al., 2014; Jarrett et al., 2020; Johnson, 2003; Pusey et al., 2005; Thompson

et al., 2016; Wright et al., 2019, 2020). In these studies, for example, higher social dominance rank was associated with larger body mass-for-age in juvenile and adult female chimpanzees and larger body size-for-age in adult male gorillas, respectively, but dominance rank did not predict these phenotypes in male chimpanzees or female gorillas (Pusey et al., 2005; Wright et al., 2019, 2020). Similarly, semi-free ranging mandrills with older or higher-ranking mothers were heavier-for-age than those with younger or lower-ranking mothers (though there was no difference in torso length; Setchell et al., 2001). Among wild baboons, social groups that fed on agricultural crops or human trash gained weight faster and/or reached maximum body mass at younger ages than baboons in naturally-foraging groups (Altmann & Alberts, 2005; Strum, 1991). Furthermore, among naturally foraging groups of wild anubis baboons, female weight gain slowed during a drought period with low food availability (Strum, 1991). Finally, Assamese macaques whose mothers had higher prenatal glucocorticoid levels grew more quickly and were larger-for-age than those whose mothers had lower prenatal glucocorticoids (Berghänel et al., 2016). This pattern of accelerated growth in response to prenatal stress—particularly during early gestation—is also seen in several captive and laboratory mammal species (Berghänel et al., 2017).

Together, this work indicates that primate body size is systematically related to aspects of the social and ecological environments. Furthermore, body size predicts individual fitness in a number of animal species (reviewed in Kingsolver & Pfennig, 2004), highlighting the importance of understanding the determinants of adult body size in diverse species.

1.2 | Testing associations between early-life adversity and body size in wild baboons

In this study, we use photogrammetry to estimate body size for 127 immature and adult female baboons in the Amboseli ecosystem of southern Kenya. We then test the hypothesis that the energetic and/or psychosocial stress associated with early-life adversity causes small-for-age body size in female baboons. If so, baboons who experienced more early-life adversity will be smaller than those who experienced less adversity. We also provide the first estimate of heritability of body size in a wild primate population.

First, using multiple linear regression, we test three sources of early life adversity as putative predictors of later-life body size: early-life drought, maternal loss, and low maternal rank. *Early-life drought* is a proxy for food availability, which in turn is a well-known predictor of growth, maturation, and body size in primates (Altmann et al., 1993; Altmann & Alberts, 2005; Lee et al., 1986; Leigh, 1994; Mori et al., 1997; Strum, 1991; Sugiyama & Ohsawa, 1982; Whitten & Turner, 2009). Our study population resides in a semi-arid savannah, in which seasonal rainfall patterns are a major predictor of food availability for baboons, who are primarily herbivores (Alberts et al., 2005; Byrne et al., 1993; Post, 1982). Prior studies of this baboon population suggest that baboon growth, fertility, and survival are sensitive to drought and

food availability in early life (Altmann, 1991; Altmann et al., 1993; Lea et al., 2015). Our second source of early-life adversity, *maternal loss* (after weaning but prior to adulthood) affects multiple outcomes later in life. In many mammals, including primates, mothers continue to provide social support, social learning opportunities, and protection against predators after the weaning period (van Noordwijk, 2012). As a result, maternal loss in early life is a strong predictor of shortened adult lifespan in several mammals (e.g., Andres et al., 2013; Foster et al., 2012; Stanton et al., 2020). In the baboon population we studied, offspring whose mothers died before adulthood exhibit higher juvenile and adult mortality (Tung et al., 2016; Zipple et al., 2019), and this effect extends to infants and juveniles whose grandmothers experienced early-life maternal loss (Zipple et al., 2019). Finally, *low maternal dominance rank* predicted smaller mass-for-age in two previous studies of immature baboons (Altmann & Alberts, 2005; Johnson, 2003). More broadly, studies of several baboon populations have revealed that low-ranking female baboons have decreased offspring survival, offspring with later age at sexual maturity, longer inter-birth intervals, more interruptions while feeding, or shorter lifespans (Altmann et al., 1988; Altmann & Alberts, 2003; Cheney et al., 2006; Post et al., 1980; Silk et al., 2003, 2010).

We then investigate whether body size is predicted by a cumulative early-life adversity index that combines six potential sources of adversity (Tung et al., 2016). The six sources include drought, maternal loss, and low maternal dominance rank, as well as three other aspects of a young baboon's physical and social environment: maternal social isolation, which may be associated with psychosocial or energetic stress (Silk et al., 2003); large group size, which may increase competition and therefore slow growth; and having a close-in-age younger sibling, which we hypothesize reduces maternal investment and consequently growth (Tung et al., 2016). Cumulative measures of early-life adversity, such as the Adverse Childhood Experiences index of stressful or traumatic experiences (Felitti et al., 1998), are commonly used in studies of humans. These measures capture a broad range of factors and provide a continuous and powerful measure of early-life conditions. In baboons, females who experience greater cumulative early-life adversity exhibit lower adult survival and higher fecal glucocorticoid levels, and their offspring are less likely to survive to adulthood (Patterson et al., 2021; Rosenbaum et al., 2020; Tung et al., 2016; Zipple et al., 2019). The present study thus sheds light on the possibility that reduced growth and smaller adult body size could link early adversity to fertility and survival later in life.

2 | METHODS

2.1 | Study population and subjects

The study population resides in the Amboseli basin (2°40′ S, 37°15′ E, 1100 m altitude), a semi-arid short-grass savannah ecosystem at the base of Mount Kilimanjaro. In this ecosystem, rainfall is limited and highly variable (Western & Maitumo, 2004). Food for baboons is most abundant in the rainier months of November–May; during the dry months of June through October, baboons rely on corms—the underground storage organs of grasses—which require considerable processing effort and thus represent a low-yield fallback food (Alberts et al., 2005; Altmann, 1998, 2009; Post, 1982). During droughts, even corms can become limited, sometimes creating extreme food shortages.

The study population consists of wild yellow baboons (*Papio cynocephalus*) with historic and recent admixture with anubis baboons (*Papio anubis*; Alberts & Altmann, 2001; Vilgalys et al., 2022; Wall et al., 2016). Study subjects were studied since birth by the Amboseli Baboon Research Project. Experienced observers (R. Mututua, S. Sayialel, K. Warutere, L. Siodi) recognize each study subject by sight, and they collect detailed behavioral, demographic, and developmental data from each subject several times a week. Female baboons in Amboseli reach sexual maturity in the study population at a median age of 4.5 years and experience their first live birth at a median age of 6.0 years (Onyango et al., 2013). Baboon infants are weaned at approximately 16 months, at which point they are nutritionally independent but still dependent on their mothers for protection, social support, and social learning opportunities (Altmann, 1998). The median lifespan for a female baboon who survives past age 4 is 18.5 years, with a maximum known age of 27.7 years (Tung, Archie et al., 2016).

The study subjects were 127 wild female savannah baboons living in six different social groups at the time of data collection (July–December 2019). Subjects were a mix of juvenile, adolescent, and adult females. Birth dates for all subjects were known to within a few days' error, and subjects ranged in age from 3.3 to 22.6 years, with mean and median ages of 9.9 and 8.7 years, respectively. Of the 127 females in our dataset, 110 had reached sexual maturity, and 89 had given birth to at least one live offspring. Age at menarche and first birth among the study subjects were similar to the population as a whole (4.7 and 6.3 years, respectively, for the study subjects, as compared to 4.5 and 6.0 years; Onyango et al., 2013).

2.2 | Measuring early-life adversity

Each type of adversity that we included in one or more of our growth models is described below; see Section 2.6 for a description of the statistical models.

2.2.1 | Drought

Guided by prior studies in the Amboseli baboons, we measured both cumulative rainfall and drought (e.g., Beehner et al., 2006; Gesquiere et al., 2008; Tung et al., 2016). We assessed two measures of drought: the proportion of "drought days" during (1) the first year and (2) the first 4 years of a subject's life. We defined a drought day as a day on which less than 50 mm of rain had fallen in the previous 30 days (Beehner et al., 2006; Bronikowski & Altmann, 1996; Le Houérou, 1989) (Supplement S1: Measuring drought days). We express these two drought variables as a proportion of drought days—rather than absolute number

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of drought days—within the first year or first 4 years of life to accommodate the fact that eight females were slightly younger than 4 years old at the time of data collection, and therefore did not have as many possible days to experience drought. For these eight females, we calculated the proportion of drought days in the first 4 years from birth until the mean age at which each female's photogrammetry data were collected. Because cumulative rainfall and drought overlap in what they measure and produced similar results in our study, we focus on drought in the main text; parallel results for cumulative rainfall are provided in Supplement S1: Final dataset and model results.

2.2.2 | Maternal loss

Maternal loss was measured as a binary variable indicating whether the subject's mother died before the subject reached 4 years of age. Of the eight study subjects who were younger than 4 years at the time of data collection, one lost her mother before data collection; mothers of the other seven subjects survived past data collection and past their daughters' fourth birthdays.

2.2.3 | Maternal rank

Because two common measures of dominance rank—ordinal and proportional—differ in their ability to predict phenotypes in this population (Levy, Zipple et al., 2020), we assessed model fit with both measures of maternal rank using one representative model (leg length as a function of maternal loss, maternal rank, and proportion of drought days in the first 4 years of life). The model with maternal proportional rank was preferred and was thus used in all of our other analyses ($\Delta AIC = 6.46$). Proportional rank was calculated at the time of the study subject's birth.

2.2.4 | Cumulative early-life adversity score

The cumulative early-life adversity score was calculated using the six factors identified by Tung, Archie et al. (2016) as predictors of adult mortality in female Amboseli baboons. These factors are: (1) experiencing maternal loss before age 4 years; (2) having a close-in-age younger sibling (sibling born <1.5 years after subject, approximately the lowest quartile of inter-birth intervals in the population); (3) experiencing high group density at birth (adult group size >35 at birth, highest quartile for group size in the population); (4) having a low-ranking mother (mother's ordinal rank >11 at study subject's birth, the lowest quartile of ordinal ranks in the population); (5) having a mother with low social connectedness to other females in the first 2 years of subject's life (lowest quartile in the population); and (6) being born during a drought year (<200 mm rain during the first year of life). For each subject we created a cumulative early-life adversity score, which was the total number of adverse events experienced in early life (observed range = 0–4). Because very few individuals had scores greater than three, we grouped all individuals with an adversity score of three or more into a single category. We coded cumulative early-life adversity score as a continuous variable. Note that cumulative early-life adversity score was never used in a model that included one of the three sources described above (drought, maternal loss, or maternal rank).

2.3 | Measuring body size via parallel-laser photogrammetry

To measure baboon body size, we used parallel-laser photogrammetry, a non-invasive technique that enables repeated measures of body parts (Galbany et al., 2016; Lu et al., 2016; Wong & Auger-Méthé, 2018; Wright et al., 2019, 2020). We collected three body size measures: shoulder-rump length (Lu et al., 2016), leg length, and forearm length (Figure 1). All images were taken using an Olympus OM-D EM-5 Mark II mirrorless camera (15.9 megapixel, 3.75 μ pixel size) with an M. Zuiko 12–100 mm f/4 IS Pro Digital lens. The lens was fully extended to 100 mm during data collection (see Supplement S1: Specifications and calibration of the parallel laser unit). Our validation of this method with inanimate objects demonstrates that the parallel-laser apparatus is highly accurate when compared to manual measurements (Supplement S1: Inanimate object validation).

Images were taken at a distance of 5–15 m from the study subjects, between July and December 2019. To minimize pseudoreplication, measurements of the same subject and same body part were only included if the study subject moved (e.g., took at least one step) between images (see Supplement S1: Collecting images). Images were assessed for inclusion based on the estimated accuracy and precision of a body measurement, given the image characteristics (e.g., focus, distance) and the position of the study subject (e.g., parallax, body part obscured by another baboon; Figure 2; Supplement S1: Exclusion criteria). Photographers and researchers performing the measurements were blind to the early-life conditions of the study subjects.

2.3.1 | Measuring images

Landmarks were chosen based on baboon skeletal morphology in an attempt to measure skeletal size alone instead of skeletal size along with muscle and fat (Figure 1; Supplement S1: Measuring images and Protocol for measuring photogrammetry images).

To measure the inter-laser distance, we used an automated system that identifies laser spots via brightness and color (Richardson, Levy et al., 2022). Of the 2172 images in our dataset, 1975 were measured using this automated system. The remaining 197 did not yield inter-laser distance outputs with the automated system so were measured manually in ImageJ. We only measured the distance between the two outer-most laser beams. All hand-measured distances (body measurements and some inter-laser distances) were taken twice and averaged. We waited at least one day between making the two measurements.

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After collecting the inter-laser distance and body size measurements in pixels, we converted the body size measurements to centimeters. First, we used the inter-laser distance to calculate the number of pixels per 4 cm, and then obtained body size measurements in centimeters by using the following standard equation (see Supplement S1: Calibrating the parallel lasers):

$$\text{Body size in cm} = 4 \times \frac{\text{Body size in pixels}}{\text{\#Pixels in 4 cm}}$$

2.3.2 | Dataset and variability

Of the 2172 images used in the analysis, 1082 yielded shoulder-rump measures for 121 baboons, 1417 yielded leg measures for 124 baboons, and 1515 yielded forearm measures for 125 baboons (Table S3, Figure 2; numbers do not sum to 2172 because some photos yielded measures of multiple body parts). Cumulative early-life adversity score was not available for several study subjects, so the datasets used to test the association between cumulative early-life adversity score and body size were slightly smaller than those for drought, maternal loss, and maternal rank (Table S3). Measurement variability was comparable to or lower than those reported in prior studies: within-image percent difference (i.e., difference between two measurements of the same image) was 0.4%–1.3%, and within-subject coefficient of variation was 1.9%–3.8% (see Supplement S1: Image variability and the importance of sample size).

## 2.4 | Assessing the shape of cross-sectional growth

To determine the best-fitting cross-sectional growth curve model for shoulder-rump, leg, and forearm lengths of the female baboons in our dataset, we assessed the model fit of three different models of body size as a function of age while accounting for genetic effects (see Section 2.6). We tested a piecewise linear-linear model with one knot similar to Pusey et al., (2005), a piecewise quadratic threshold model following Lu et al., (2016), and a quadratic log–log model that approximates logistic growth (see Supplement S1: Testing the fit of growth models for details about these models and how we tested them). Among these three methods, the quadratic log–log model provided the best fit based on R^2 values (Table S4). As a result, we used the quadratic log–log method to both model a cross-sectional growth curve and to analyze the relationship between early-life adversity and body size. We also used the quadratic log–log method to estimate the ages at which female shoulder-rump, leg, and forearm lengths were at a maximum (i.e., approximating maximum adult body size). To do so, we used the coefficients from the model outcomes to calculate the age at which the three models had a slope of 0 (i.e., the apex in the quadratic equations).

FIGURE 1 Overview of parallel-laser photogrammetry method. Top: Schematic of image capture and measurement. Parallel laser beams of known inter-beam distance, described in Figure S1, were projected onto the study subject while the subject was photographed. Using ImageJ, we then measured the shoulder-rump length (orange), leg length (pink), forearm length (red), and inter-laser distance (green) in pixels. Bottom: We used this equation to calculate body size in centimeters using the inter-beam distance (in centimeters) between the outer-most laser beams, the inter-laser distance (in pixels) between the two outer-most laser spots projecting onto the study subject, and the body measurement (shoulder-rump, leg, or forearm, in pixels). *Source*: Adapted from Richardson, Levy et al. (2022). Created in BioRender.
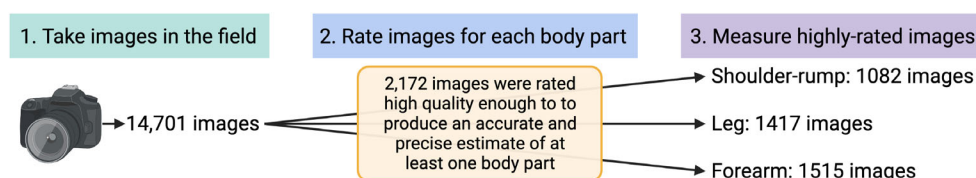
FIGURE 2 Workflow from image collection (step 1) to image rating (step 2) to image measurement (step 3). For full details of the rating process, see Supplement S1. Created in BioRender.

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2.5 | Testing environmental and genetic predictors of body size

We fit 15 "animal models" (see next section) using the quadratic log–log model described above to assess whether early-life environments predict adult female body size. Each model had one of three outcome measures: (1) shoulder-rump length, (2) leg length, or (3) forearm length. For each body part, we ran three multiple linear regression models to test our early-life environment predictors: (1) a model that included maternal loss, maternal rank, and proportion of drought days in the first year of life; (2) a model that included maternal loss, maternal rank, and proportion of drought days in the first 4 years of life; and (3) a model that included only one type of early-life adversity, the cumulative early-life adversity score. These nine models are reported in the main text. In addition, six parallel models using cumulative rainfall instead of drought days are reported in the Supplement S1.

Every model included fixed effects of log(age) and log(age)^2. In the leg length models, we also included a predictor of leg position (slightly bent vs. straight), as measurements with the leg slightly bent tended to be shorter than measurements with the leg straight.

Because Amboseli is a hybrid zone between yellow and anubis baboons, we also tested whether level of yellow versus anubis ancestry (i.e., "hybrid score") predicted body size, but the structure of our dataset limited our ability to draw conclusions from this analysis (see Supplement S1: Testing whether hybrid score improves model fit).

2.6 | Using the animal model to assess predictors of body size

Body size is highly heritable in many animal taxa (Hallgrímsson et al., 2002; Mousseau & Roff, 1987; Visscher et al., 2008). To account for genetic effects on body size in our dataset, we ran all our models using the quantitative genetic "animal model," which accounts for relatedness among study subjects. Models were fit in R version 4.1.1 using ASReml-R software version 4, a statistical software package that uses residual maximum likelihood to fit general linear mixed models (Butler et al., 2009).

In all statistical models, we included a random effect that accounts for additive genetic effects, which incorporates the inverse pedigree matrix to represent genetic similarity between individuals in the data set. This approach both allowed us to estimate heritability and controlled for the potential confound of relatedness in our estimates of the fixed effects. Our pedigree included body size for 54 daughters of 31 unique mothers, and 88 (69%) of study subjects had at least one maternal half- or full sister in the dataset. However, the pedigree was incomplete with respect to paternal identity (30 of 127 study subjects had unassigned paternities), limiting our power to fully calculate and control for genetic effects.

All our models also included a random effect of maternal identity to estimate combined environmental and genetic maternal effects and to control for the fact that sharing a maternal environment may result in more similar body size above and beyond the similarities arising from relatedness between maternal sisters (Wilson et al., 2010). Finally, to account for the fact that nearly all study subjects were represented by multiple images in the dataset, we included individual identity as a random effect. This random effect estimates repeatability within individuals (Wilson et al., 2010). These three random effects improved the fit of our model (Supplement S1: Animal model construction).

2.7 | Study ethics and data availability

This research was approved by the IACUCs at Duke University and the University of Notre Dame and adhered to all the laws and guidelines of Kenya. Data and are available at the Duke Data Repository (https://doi.org/10.7924/r43r11g2m) and code is available on github (https://github.com/ejlevy/Female-baboon-body-size).
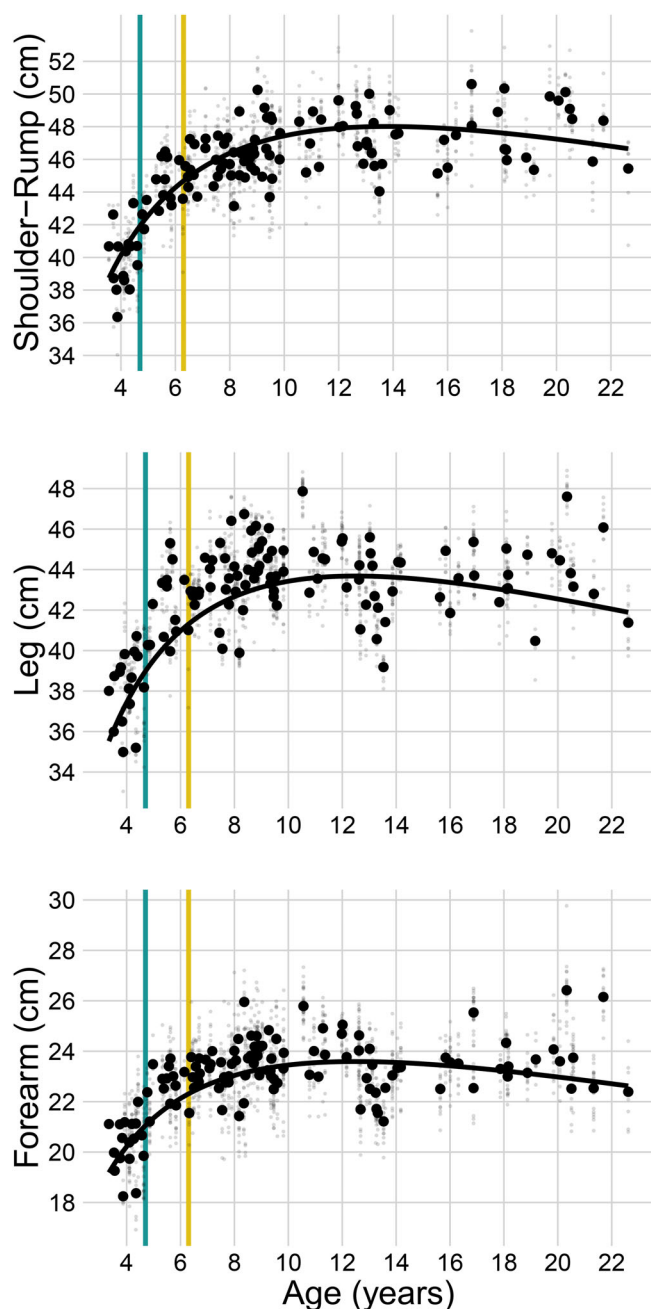
3 | RESULTS

3.1 | Cross-sectional growth curves

Based on our quadratic log–log models of cross-sectional growth, females who were 6 years old (median age at first live birth; Onyango et al., 2013) had shoulder-rump, forearm, and leg lengths that were approximately 92%–94% as long as the maximum sizes estimated by the apexes of the curves in our models (Figure 3). At their maximum points, our models indicate that shoulder-rump, leg, and forearm lengths were 47.9, 41.9, and 23.9 cm, respectively.

3.2 | Early-life adversity and later-life body size: Drought predicts limb length

Both leg and forearm length were predicted by the proportion of drought days in the first 4 years of life (leg: $p = 0.001$; forearm: $p = 0.001$; Table 1). In these models, each additional day of drought predicted leg and forearm lengths that were shorter by 0.018% and 0.021%, respectively. Put another way, a female who experienced drought days in 82.3% of her first 4 years, which corresponds to 1 SD above the mean of 78.7%, is predicted to have legs and forearms that are 0.94% and 1.08% shorter, respectively, than if she had experienced the mean proportion of drought days (Figure 4, orange and teal lines). Using our body size maxima, this effect equates to 0.4 and 0.3 cm shorter leg and forearm lengths, respectively. For our study subjects, the proportion of drought days experienced in the first 4 years of life ranged from 69.1% to 88.2%, indicating a predicted 5.0% (2.2 cm) difference in leg length and 5.7% (1.4 cm) difference in forearm length from the most- to least-affected female (Figure 4, dark blue and red lines). Drought during the first year of life alone had no detectable effect on leg or forearm length (leg: $p = 0.33$; forearm: $p = 0.63$; Table S7).

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FIGURE 3 Cross-sectional body size-for-age for shoulder-rump length (top), leg length (middle), and forearm length (bottom) in female Amboseli baboons. Each large point shows mean body size for a unique female, situated along the x-axis at the mean age at which her data were collected. Each small transparent point is a body size measurement from a single photograph, which is the unit of analysis in our statistical models. Black lines are the model fits from the quadratic log–log animal models of body size as a function of proportion of drought days in the first 4 years of life, maternal rank, and maternal loss. For these lines, we used coefficients corresponding to no maternal loss, the mean amount of drought experienced by our study subjects, maternal proportional rank of 0.5, and the mean leg rating. The vertical lines show median ages at the attainment of two key life-history milestones for females in this data set: menarche (teal; 4.7 years) and first live birth (yellow; 6.3 years).

Shoulder-rump length was not predicted by drought in the first year or the first 4 years of life (1st year: $p = 0.84$; 4 years: $p = 0.58$; Table S7). Furthermore, none of our body-size measures—shoulder-rump, leg, or forearm length—were predicted by cumulative early-life adversity score (all $p > 0.40$, Table S7).

3.3 | Maternal dominance rank, maternal loss, and later-life limb length

Forearm length was weakly predicted by maternal rank in all models, but the effect did not reach statistical significance. Specifically, the daughter of the highest-ranking mother was predicted to have forearms 2.6%–2.8% longer than the daughter of the lowest-ranking mother (p-values = 0.08–0.11, Table 1, Table S7). Leg length and shoulder-rump length were not predicted by maternal rank (leg: $p > 0.13$; shoulder-rump: $p > 0.91$; Table 1; Table S7).

In one model, forearm length was weakly predicted by maternal loss, but this effect did not reach statistical significance; in this model, baboons who experienced maternal loss were predicted to have forearms 1.7% shorter than those who did not ($p = 0.075$, Table 1). Forearm length in all other models, and leg length and shoulder-rump length in all models, were not predicted by maternal loss (forearm $p > 0.32$; leg $p > 0.38$; shoulder-rump $p > 0.28$; Table S7).

3.4 | Body size is highly heritable

Additive genetic variance explained a large proportion of total variance in all three measures of body size, indicating substantial narrow sense heritability of body size in female baboons. Heritability estimates varied slightly across models and body parts. Heritability of shoulder-rump length was 58%, heritability of leg length was 62%–67%, and heritability of forearm length was 36%–41% (Table 2, Figure S6, Table S8). Maternal effects also explained a relatively large proportion of variance in limb length, with variance between mothers accounting for 13%–17% and 13%–16% of variance in leg and forearm length, respectively. In contrast, maternal effects explained almost no variance in shoulder-rump length. The random effect of individual identity, which measures within-individual repeatability of non-genetic sources of variance, also explained almost no variance in any body size measures, indicating high repeatability of our photogrammetric measures of body size, and therefore, relatively small within-individual variation in body size. Finally, residual variance accounted for 42% of the total variance in shoulder-rump length, 46%–48% of the total variance in forearm length, and only 19%–22% of the total variance in leg length. The higher residual variances for shoulder-rump and forearm lengths may reflect the fact that the shoulder-rump and forearm measures were noisier than the leg measure (Table S3). See Table 2 and Figure S5 for the random effects estimates from representative models and Table S8 for the random effects estimates from all 15 models.

TABLE 1 Results of models predicting leg length (top) and forearm length (bottom) as a function of maternal loss, maternal rank, and drought in the first 4 years of life (SE = standard error).

Body part	Predictor	Coefficient	$e^{\text{Coefficient}}$ [a]	e^{SE} [a]	p-Value	Interpretation
Leg	Intercept	3.221	25.058	1.093	<2.22E−16	Leg length is predicted to be 25.1 cm at 1 year.
	log (Age)	0.601	1.823	1.058	<2.22E−16	Leg length is strongly predicted by age.
	log (Age^2)	−0.119	0.888	1.013	<2.22E−16	
	Leg bent vs. straight	0.017	1.017	1.001	<2.22E−16	Leg lengths are estimated to be 1.7% longer when photos are taken with straight legs than when slightly bent.
	Maternal proportional rank[b]	0.019	1.019	1.013	0.150	Leg length is not predicted by maternal rank.
	Proportion drought days in 4 years[c]	−0.307	0.736	1.100	0.001	Leg length is 0.26% shorter with each 1% increase in the proportion of drought days, and 0.018% shorter with each additional day of drought.[d]
	Maternal loss	0.009	1.009	1.009	0.308	Leg length is not predicted by maternal loss.
Forearm	Intercept	2.670	14.444	1.107	<2.22E−16	Forearm length is predicted to be 14.4 cm at 1 year.
	log (Age)	0.601	1.824	1.067	<2.22E−16	Forearm length is strongly predicted by age.
	log (Age^2)	−0.118	0.889	1.015	1.33E−15	
	Maternal proportional rank[b]	0.026	1.027	1.015	0.084	Forearm length is 2.7% longer for the daughter of the highest-ranking mother than for the daughter of the lowest-ranking mother, but this effect is not statistically significant.
	Proportion drought days in 4 years[c]	−0.357	0.700	1.112	0.001	Forearm length is 0.30% shorter with each 1% increase in proportion of drought days, and 0.021% shorter with each additional day of drought.[d]
	Maternal loss	0.017	1.017	1.010	0.075	Forearm length is 1.7% shorter for baboons whose mothers died before age 4 than baboons whose mothers did not die, but this effect is not statistically significant and not present in any other models.

[a]Every one-unit increase in the predictor is associated with the percent change equivalent to the value in these columns, with the exception of intercept and proportion of drought days.

[b]Maternal proportional rank at study subject's birth.

[c]The proportion of days, in the study subject's first four years of life, in which <50 mm rain had fallen over the preceding 30 days.

[d]A one-unit change in proportion of drought days (i.e., from 0% to 100% drought days) is not biologically relevant, so in our interpretation we state how limb length is predicted to change in response to a 1% change in proportion of drought days and to each additional day of drought.

4 | DISCUSSION

4.1 | Summary of findings

Using cross-sectional body size data from wild female baboons, we found that prolonged early-life drought, which is a proxy for low food abundance, is correlated with stunted limb length later in life. Specifically, more exposure to drought in the first 4 years of life was associated with statistically significantly shorter limbs, with a predicted 5%–6% difference in limb length between the most-affected and least-affected females. In contrast, no measure of female body size was significantly predicted by the three measures of early-life adversity that represent combined energetic and psychosocial stressors: cumulative early-life adversity score, maternal loss, and low maternal dominance rank. Notably, shoulder-rump (i.e., torso) length showed no relationship to any of the early life conditions we examined; only

limb length seemed to respond to environmental variation (see Limb growth vs. torso growth below). These differences between shoulder-rump and limb lengths do not seem driven by differences in measurement error across our three body part measurements, as forearm length had the highest within-subject variation, followed by shoulder-rump length and then leg length.

Our findings are best interpreted in the context of the evolution of developmental plasticity. Females may reduce long bone growth in response to early-life energetic stress to allocate limited energy to biological systems that are more crucial for short-term survival and long-term fitness. The effects of drought on limb length in this study are of similar magnitude to a study of British children in the 1930s, in which girls whose families were above the median food expenditure had 3.4% longer legs and 2.4% longer trunks than girls whose families were below the median for food expenditure (data extracted from Gunnell et al., 1998 using WebPlotDigitizer). Further, effects of this
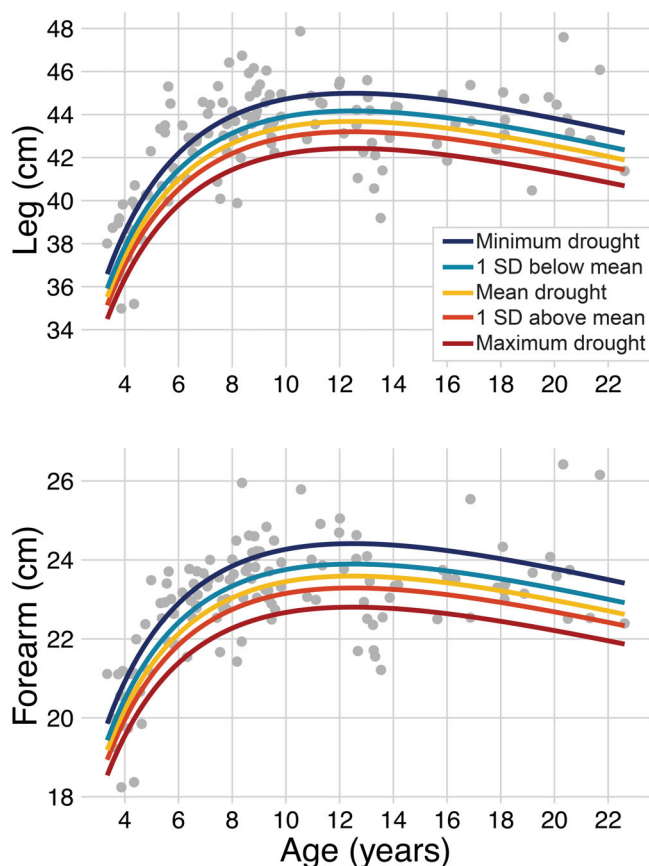
FIGURE 4 Predicted body size-for-age for leg length (top) and forearm length (bottom) as a function of the proportion of drought days experienced in the first 4 years of life. Each line was drawn from the model fits of the quadratic log–log animal models of body size as a function of proportion of drought days in the first 4 years of life, maternal rank, and maternal loss. Colors vary by the amount of drought, from the minimum amount experienced by our study subjects (dark blue; 69.1%) to the maximum (dark red; 88.2%). For these lines, we also used coefficients corresponding to no maternal loss, maternal proportional rank of 0.5, and the mean leg rating. Each point shows mean body size for a unique female, situated along the x-axis at the mean age at which her data were collected.

magnitude may have consequences for health and survival. In a study of over one million Norwegian women born throughout the 1900s, those who were 3% shorter than the height associated with lowest mortality were 1% to 3% more likely to die at any given time, even after controlling for body mass index, age, and cohort effects (Engeland et al., 2003). In nonhuman animals, too, relatively small differences in morphology can be linked to important fitness differences. During an intense drought in the Galapagos Islands, a population of finches (*Geospiza fortis*) experienced a population decline of 85%, with natural selection favoring the largest birds. In this canonical example of natural selection, the differences in body mass and beak size between the pre-drought and post-drought populations were 3.5%–5.5% (Boag & Grant, 1981). As Charles Darwin wrote, "What a trifling difference must often determine which shall survive, and which perish!" (Darwin & Wallace, 1858).

Contrary to our expectation, we found that maternal dominance rank did not predict any body size measure (with the exception of a relationship to forearm length that did not reach statistical significance). In two prior studies of infant and juvenile wild baboons, higher maternal rank predicted larger body mass-for-age (Altmann & Alberts, 2005; Johnson, 2003), a result that aligns with other evidence that higher ranking female baboons have increased access to food resources (Charpentier et al., 2008; Gesquiere et al., 2018; Post et al., 1980).

Finally, in the first estimates of body size heritability in wild primates, we found that all three measures of body size were highly heritable, in line with estimates of heritability for morphological traits in many other species (Hallgrímsson et al., 2002; Visscher et al., 2008). Further, we found that maternal effects explained variation in limb length but not torso length. The presence of both maternal effects and drought effects for limb lengths, but not for torso length, suggests that limb growth is more plastic in response to early-life environments than growth in the torso.

4.2 | Limb length versus torso length

Our evidence that limb length (i.e., leg and forearm length), but not torso length (i.e., shoulder-rump length), is plastic in response to environmental variation agrees with prior literature on humans suggesting that limb length tends to be more affected than torso length in the face of early-life adversity (Billewicz et al., 1983; Bogin et al., 2002; Bogin & Varela-Silva, 2010; Gunnell et al., 1998; Wadsworth et al., 2002). For example, a longitudinal study of British men born in 1946 found that several early-life factors, such as not being breastfed and having limited energy intake, were associated with shorter adult leg length, whereas fewer of these factors were associated with torso length, and to a smaller degree (Wadsworth et al., 2002). Shorter leg length, but not shorter overall height, has also been associated with lower offspring birth weight and higher incidence of cardiovascular disease and type II diabetes (Chung & Kuzawa, 2014; Gunnell et al., 2003; Lawlor et al., 2004; Smith et al., 2001; Weitzman et al., 2010). During the early-life period, humans undergo proportionally more leg growth than torso growth, which may explain why researchers have observed greater developmental plasticity in leg length than in torso length (Gunnell, 2002; Gunnell et al., 1998; Lawlor et al., 2004). Growth plates in the human spine also fuse at later ages than growth plates in the limbs (Albert & Maples, 1995; Buikstra & Ubelaker, 1994; White et al., 2011). If the same growth pattern and timing of growth plate fusion holds for baboons, such that the limbs grow proportionally more than the torso at early ages and that the growth plates in the spine fuse at later ages than those in the limbs, early-life effects may exhibit larger effects on the limbs than the torso during the period of adversity. There may also be more opportunity for compensatory skeletal growth of the torso than of the limbs.

In non-human primates, the relatively few prior studies of skeletal plasticity provide mixed evidence for whether limb length is more

TABLE 2 Estimates of random effects for the three models that assessed whether maternal loss, maternal rank, and the number of drought months a female baboon experienced in her first 4 years of life (i.e., same models as Table 1) predicted shoulder-rump, leg, and forearm lengths (ID = identity).

Body part	Random effect	Coefficient	Proportion of variance	Interpretation
Shoulder-rump	Additive genetic effect	1.28E−03	0.58	Additive genetic variance in the population explains 58% of total variation in shoulder-rump length.
	Maternal effect	5.45E−10	2.47E−07	Variance between mothers explains <0.01% of total variation in shoulder-rump length.
	ID (within-individual repeatability)	1.50E−10	6.82E−08	Variance within individuals explains <0.01% of total variation in shoulder-rump length.
	Residual variance	9.29E−04	0.42	42% of variation in shoulder-rump length is unexplained.
Leg	Additive genetic effect	1.23E−03	0.62	Additive genetic variance in the population explains 62% of total variation in leg length.
	Maternal effect	3.06E−04	0.16	Variance between mothers explains 16% of total variation in leg length.
	ID (within-individual repeatability)	3.99E−06	2.02E−03	Variance within individuals explains 0.202% of total variation in leg length.
	Residual variance	4.30E−04	0.22	22% of variation in leg length is unexplained.
Forearm	Additive genetic effect	1.27E−03	0.36	Additive genetic variance in the population explains 36% of total variation in forearm length.
	Maternal effect	5.68E−04	0.16	Variance between mothers explains 16% of total variation in forearm length.
	ID (within-individual repeatability)	5.87E−07	1.67E−04	Variance within individuals explains 0.02% of total variation in forearm length.
	Residual variance	1.69E−03	0.48	48% of variation in forearm length is unexplained.

plastic than torso length. Japanese macaques (*Macaca fuscata*) living on a small island had shorter limbs relative to their body size than those living on larger islands in Japan, possibly because the population on the small island was near its carrying capacity and had limited food availability (Buck et al., 2018). However, a study of captive capuchin monkeys (*Cebus albifrons*) found no difference between limb and torso growth between individuals raised with and without food restrictions (Fleagle et al., 1975). Much work remains to understand differences between limb growth and torso growth in nonhuman primates.

4.3 | Heritability and maternal effects

In this study, we estimated additive genetic effects (i.e., narrow-sense heritability) and maternal effects on body size. To our knowledge, this study is the first to do so in a wild primate population. We estimated heritability values of approximately 62%–67% for leg length, 36%–41% for forearm length, and 58% for shoulder-rump length. These values are within the range reported for the heritability of body size in other non-human animals, which tend to fall between 30% and 70% (Hallgrímsson et al., 2002; Mousseau & Roff, 1987; Visscher et al., 2008). The high heritability of our body size measures suggests segregating genetic variation for these traits and the potential for the population to respond to natural selection.

Maternal effects explained variation in limb lengths (13%–16% of the variation) but not shoulder-rump length (Table 2). This difference

aligns with our finding of greater plasticity in limb length than in shoulder-rump length in response to drought. In the case of baboons and many other primates, maternal effects can act on energy availability through their effects on learning to forage. Baboons are highly selective omnivores for whom learning to forage requires the presence of tolerant and knowledgeable adults, and mothers commonly fill this role (e.g., Altmann, 1998; Coussi-Korbel & Fragaszy, 1995; King, 1994). While our estimates of heritability and maternal effects are comparable to values seen in other mammals (Maestripieri & Mateo, 2009), we still interpret these values with caution because we were missing paternities in 30 out of 127 study subjects. Where paternity data was missing, our model assumed each unidentified father was unrelated to every other individual in the population. This assumption may bias our estimates because the ability of our model to partition between additive genetic effects and maternal effects depends on pedigree structure. However, we were still able to differentiate the effects of sharing genes (additive genetic effects) and the effect of sharing a mother (maternal effects) on variance in phenotypes, because our pedigree includes maternal siblings who vary in their relatedness to each other (e.g., a pedigree must include both half and full siblings: see Lynch & Walsh, 1998, Kruuk, 2004 and Wilson et al., 2010 for further details). This happens commonly in this study population; while females primarily produce half-siblings, they sometimes produce full-siblings and their male mates are occasionally related to each other.

Further investigation into the source of these maternal effects will be necessary to understand how they may alter the evolutionary

potential of the body size traits we investigated. The maternal effects we detected could have a genetic basis, in that the particular alleles a mother carries could influence the way she impacts offspring growth, above and beyond the effect of any alleles her offspring inherit from her (a type of "indirect" genetic effect). It is also possible that these maternal effects could have an environmental basis; in other words, something about the environment a mother experienced could influence the way her offspring grow.

4.4 | Growth after sexual maturation

Our data suggest that female baboons may continue to grow for several years after reaching sexual maturity, although the majority of—but not all—growth has likely been completed by first live birth. While the cross-sectional nature of our data limits our ability to confirm this pattern, growth past sexual maturity is common in vertebrates: the growth plates of the long bones commonly fuse well after sexual maturity in rodents, ungulates, carnivores, and primates, including humans (Kilborn et al., 2002). For instance, body length in captive chimpanzees and body mass in wild chimpanzees continues to increase for several years past menarche (Hamada & Udono, 2002; Pusey et al., 2005; Walker et al., 2018). Thus, in spite of the limitations of our cross-sectional data, the idea that female baboons continue to grow after sexual maturity is consistent with data from other primates.

If females do continue to grow after they mature sexually, females in energy-limited environments probably face a trade-off between these two energy-intensive processes (Thompson et al., 2016; Whitten & Turner, 2009). In agreement with this idea, Leigh and Bernstein (2006) posited that baboons in particular experience a more stringent trade-off between growth and reproduction than other papionins. This potential tradeoff may explain why the youngest adult females in our study population exhibit relatively low fertility, poor infant growth, and reduced infant survival compared to prime-aged females (Altmann & Alberts, 2005; Beehner et al., 2006; Campos et al., 2022; Gesquiere et al., 2018). Relatively poor reproductive performance among young adult females is a common phenomenon in primates (reviewed in Pusey, 2012), suggesting that a growth-reproduction tradeoff for females may occur in multiple species. Whether it is more extreme for baboons than others is an interesting topic for future research.

Our models suggest that the oldest females may be smaller than middle-aged females, but we interpret this apparent pattern with caution. The cross-sectional nature of our dataset means that either cohort effects (which may not be completely controlled for by the fixed and random effects in our models) or differential mortality as a function of size could play a role in the apparently smaller size of older females compared to middle-aged ones. While previous work in this population has demonstrated that body mass index—mass for length—declines with age, that effect could be accounted for by declines in mass alone (Altmann et al., 2010). Furthermore, the quadratic nature of our growth model will impose some curvature on the fitted lines.

All of these issues can be exacerbated when older subjects represent a relatively small portion of the dataset, as in our case. In order to determine whether individual females decrease in size with age, longitudinal data on female body size will be needed.

4.5 | Limitations and future directions

Several aspects of our study limit the conclusions that we can draw from our findings. First, our data are cross-sectional. Collecting longitudinal growth curves for individual baboons will increase our ability to study predictors of inter-individual differences in body size, identify when growth stops, ask whether female baboons experience a trade-off between growth and reproduction, and test for compensatory growth following the cessation of adversity.

Second, although genetic ancestry (i.e., hybrid score) predicts several behavioral and life history phenotypes in this baboon population (Charpentier et al., 2008; Fogel et al., 2021), we were unable to include this predictor in our main models because of limitations on our dataset. Future work expanding the dataset will allow us to learn whether genetic admixture contributes to variation in body size.

Third, we measured three components of skeletal body size, but other components of body size may also be affected by early-life adversity. We did not measure body mass which, in conjunction with body size (i.e., body mass index or body condition) may be more important for female baboon survival and reproduction than body size alone (Gesquiere et al., 2018; Guinet et al., 1998).

And finally, our study is unable to determine whether the magnitude of effects we found are consequential for female baboon foraging efficiency, dominance rank, energy expenditure, and ultimately fitness. Future work will help us resolve how female baboons allocate limited resources to growth versus all other developing systems in response to early-life adversity.

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OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at [(https://research.repository.duke.edu/concern/datasets/vd66w0912?locale=en), (https://github.com/ejlevy/Female-baboon-body-size)].

DATA AVAILABILITY STATEMENT

This research was approved by the IACUCs at Duke University and the University of Notre Dame and adhered to all the laws and guidelines of Kenya. Data are available at the Duke Data Repository (https://doi.org/10.7924/r43r11g2m) and code is available on github (https://github.com/ejlevy/Female-baboon-body-size).

ORCID

Emily J. Levy 🔸 https://orcid.org/0000-0002-8182-9456
Jenny Tung 🔸 https://orcid.org/0000-0003-0416-2958
Elizabeth A. Archie 🔸 https://orcid.org/0000-0002-1187-0998
Susan C. Alberts 🔸 https://orcid.org/0000-0002-1313-488X

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