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Original Article

Lifetime fitness and annual survival are heritable and highly genetically correlated in a wild primate population

Beniamino Tuliozi[1], Elizabeth A. Archie[2], Jenny Tung[1,3,4,5], Susan C. Alberts[1,3,6]

[1]Department of Biology, Duke University, Durham, United States
[2]Department of Biological Sciences, University of Notre Dame, Notre Dame, United States
[3]Department of Evolutionary Anthropology, Duke University, Durham, United States
[4]Department of Primate Behavior and Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[5]Faculty of Life Sciences, Institute of Biology, Leipzig University, Leipzig, Germany
[6]Duke University Population Research Institute, Duke University, Durham, United States

Corresponding author: Department of Biology, Duke University, Box 90383, Durham, NC 27708, United States. Email: beniamino.tuliozi@duke.edu

Abstract

The additive genetic variance (V_A) of fitness quantifies the expected response to selection. Lifetime reproductive success (LRS) is an effective metric of lifetime fitness in animal population, while time-limited fitness metrics such as annual survival or fertility can help to identify which fitness component—e.g., annual survival or fertility—harbors the most V_A in fitness. Here, we estimated the V_A and heritability (h^2) of LRS and 3 time-limited fitness metrics in a wild female baboon population in Kenya. The most heritable metrics were LRS ($h^2 = 0.25$ [0.18, 0.34]) and annual survival ($h^2 = 0.23$ [0.15, 0.33]). By further partitioning LRS, we were able to show that nearly all the V_A for LRS was attributable to survival to first successful reproduction. Furthermore, all fitness metrics examined were highly genetically correlated with each other, supporting the use of time-limited metrics when LRS data are limited. Our analyses predicted faster phenotypic evolution than we have observed, raising the possibility that environmental or social variables masked responses to selection or inflated estimated V_A. Overall, our findings reveal a substantial genetic contribution to variation in survival, and in turn, to fitness and contemporary evolution in a long-lived animal.

Keywords: quantitative genetics, genetic variance, fitness, lifetime reproductive success, evolution, selection

Introduction

Individual fitness is the complex outcome of multiple influences, external and internal to the organism. Environmental, social, and maternal effects, as well as random chance, can all greatly influence fitness (Sæther & Engen, 2015; Schroeder et al., 2012; Snyder & Ellner, 2018; Snyder-Mackler et al., 2020). At the same time, fitness is also the emergent outcome of individual traits that contribute to fertility and survival, and whose variation often has a genetic basis (Warrington et al., 2024; Wolak et al., 2018). The heritable component of these traits constitutes the genetic basis of fitness variation, which in turn determines if, and at what rate, evolutionary change can occur in natural populations (Bonnet et al., 2019a; Fisher, 1930; Hendry et al., 2018; Price, 1970, 1972). Quantifying the genetic basis of fitness variation is essential for assessing a population's potential for adaptive evolution in the face of natural selection, and for understanding how evolution has shaped a species' life history and behavior.

In recent years, interest in the additive genetic variance (V_A) of fitness has soared, thanks to the emerging availability of datasets from long-term studies that enable the V_A of fitness to be estimated in nature (Sheldon et al., 2022). At the same time, the quantitative genetic techniques used in the analysis of such datasets have continued to be refined (Bonnet et al., 2019a; de Villemereuil et al., 2016, 2018; Postma, 2014). Because individual fitness is an emergent property of many traits, it is amenable to analysis as a highly polygenic trait using mixed effect models, which partition trait variance by attributing variance to genetic effects via an additive genetic relationship matrix ("animal model"; Kruuk, 2004; Wilson et al., 2010).

Lifetime reproductive success (LRS), frequently defined as the number of progeny produced over the course of an individual lifetime that survive to a specific age (Clutton-Brock, 1988), is a common metric of individual lifetime fitness (Hendry et al., 2018; Young et al., 2023). However, for a precise and unbiased measure of LRS, the entire life history of most individuals in all considered cohorts should be recorded—data that are difficult to obtain, especially for long-lived species in the wild. Furthermore, both the physical and the social environment have the potential to affect fitness metrics, but their influence is difficult to capture accurately when LRS reflects the composite contribution of many years. Thus, LRS—while an essential metric for understanding variance in total fitness—is less appropriate for investigating selective pressures that vary on timescales shorter than an adult's lifespan, because LRS can be too coarse to capture fine-scale variation in the selective environment

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(Coulson et al., 2006; Scranton et al., 2016). In addition, measuring the V_A of LRS by itself does not provide information on which fitness components (e.g., survival versus fertility) underlie genetic variation in fitness, and when in the life course they operate. While a handful of studies have investigated how different life-history traits contribute to the genetic basis of variation in lifetime fitness, the results vary with the life history of the study species (Walling et al., 2014; Wolak et al., 2018).

Studies on natural populations of long-lived animals have thus often employed alternatives to LRS. One set of alternatives involves using proxy traits thought to be correlated with LRS, such as age at first reproduction, birth weight, adult body size, or foraging rate (Alif et al., 2022; Hendry et al., 2018). However, such proxy traits are indirect measures of fitness that are usually highly system-specific and thus difficult to generalize. Moreover, the strength of their actual correlation with fitness is often untested (Hendry et al., 2018). A second set of alternatives involves using time-limited fitness metrics measured over specific intervals of the individual lifetime, such as annual survival or annual fertility (Postma, 2014; Qvarnström et al., 2006). These metrics directly measure fitness components while also capturing influences on fitness and selection that operate on timescales shorter than the full life course, which may include variation in the social environment, habitat quality, and annual environmental variation (Viblanc et al., 2022). Hence, using these metrics has the potential advantage to improve our understanding of the genetic components of fitness in the wild by revealing which fitness components drive variation in lifetime fitness (de Villemereuil et al., 2018; Wilson, 2008).

Genetic correlations between different life-history traits have been investigated in several taxa, especially invertebrates (see the meta-analysis by Chang et al., 2024), usually with the purpose of determining the presence of trade-offs or life-history constraints (Chang et al., 2024; Morrissey et al., 2012; Teplitsky et al., 2014). However, few studies have estimated the genetic correlations between time-limited and lifetime fitness metrics (Schroeder et al., 2012; Walling et al., 2014; Wolak et al., 2018). While several recent studies have compared different fitness metrics with the specific purpose of determining their interchangeability, their respective biological relevance, and their relative merits (Alif et al., 2022; Dobson et al., 2020; Van de Walle et al., 2022; Viblanc et al., 2022; Young et al., 2023), to date no comprehensive estimates of genetic correlations between lifetime fitness and time-limited fitness metrics have been conducted. Estimating these genetic correlations is important because they reveal whether different fitness metrics behave similarly when used to quantify selection and evolutionary change (although V_A of lifetime fitness should be used to quantify rates of adaptative evolution, whenever available). Moreover, when LRS and fitness components are both available, their genetic (co)variances can detail the relative importance of each component for the overall V_A of fitness, including the component's predicted evolutionary response to selection.

In this study, we estimated additive genetic variance (V_A) and genetic covariance for lifetime and time-limited fitness metrics in the wild baboons of the Amboseli basin of southern Kenya. The Amboseli baboons are ideally suited to compare time-limited and lifetime fitness metrics because multiple generations of individuals have been followed continuously for five decades, producing numerous complete cohorts for unbiased estimates of female LRS. Notably, in a comparison of multiple mammal and bird studies, the Amboseli baboons were found to have one of the highest estimates of additive genetic variance in relative lifetime fitness ($V_A(w)$, Bonnet et al., 2022). Here, we focus on females because male dispersal makes estimates of male LRS considerably more difficult to obtain. Although this decision was determined by field study limitations, it has consequences for the interpretation of evolutionary parameters that we address in the *Discussion* section. In addition, the wealth of detailed complementary information available on this population gives us the rare opportunity to estimate the effects of time-varying social variables (group identity, group size) and environmental conditions (rainfall, habitat quality) on time-limited fitness metrics.

Our first aim was to estimate the magnitude of V_A for both time-limited and lifetime fitness metrics for female baboons in this population. To achieve this aim, we fitted univariate animal models for both LRS and three time-limited measures of fitness: annual survival, annual reproductive success, and triannual reproductive success. Our second aim was to calculate genetic correlations between these fitness metrics, with the ultimate objective of investigating how the V_A of fitness was associated with different fitness components and determining the interchangeability of time-limited and lifetime fitness metrics in Amboseli baboons. To achieve this aim, we fitted bivariate animal models for all pairwise combinations of the above-mentioned fitness metric. These models allowed us to estimate the genetic covariance(s) between each pair of traits (i.e., the degree to which different fitness components have a shared genetic basis), and to identify the largest source(s) of genetic variance in fitness in this population, while also accounting for major components of the social and physical environment (maternal and group effects or year effects, respectively). We predicted either zero or positive genetic correlations between the measures we considered, as meta-analytic findings show weak to mixed evidence for antagonistic trade-offs between reproduction and survival across a wide range of animal taxa (Chang et al., 2024; Winder et al., 2025) and both reproductive success and survival are expected to contribute positively to LRS (Dobson et al., 2020; Walling et al., 2014).

Methods

Study population and subjects

The baboon population in the Amboseli basin of southern Kenya has been the subject of ongoing longitudinal data collection since 1971 (Alberts & Altmann, 2012). All baboons in Amboseli are admixed as a result of both historical and recent admixture events; most individuals show a majority of yellow baboon ancestry (*Papio cynocephalus*) with varying amounts of admixed anubis baboon ancestry (*P. anubis*) (Vilgalys et al., 2022; Wall et al., 2016). The Amboseli ecosystem is a highly seasonal semi-arid savanna: the "hydrological year" in Amboseli (the "hydroyear") starts on November 1 each year with the onset of the rainy season and ends on October 31 of the following calendar year. Females conceive and give birth throughout the year, with only mild seasonal variation (Gesquiere et al., 2024).

Table 1. Fitness metrics used in our study: definitions, sample sizes, data distributions, and pedigree.

	Fitness metric	Definition	Sample size	Distribution	Trimmed pedigree
Time-limited metrics	Annual reproductive success[a]	Number of offspring born during each hydroyear of a female's life that survived to at least 365 days; binary (0 or 1 for each female-hydroyear)	806 females, 5896 female-hydroyears	Binomial distribution analyzed with threshold GLMM	• 932 individuals • 828 known mothers, 354 known fathers • 47 full sib pairs • 658 paternal half sib pairs • 1271 maternal half sib pairs
	Annual survival	Binary variable, with 1 for every female-hydroyear when the individual was alive, and 0 for the female-hydroyear of its death	806 females, 5896 female-hydroyears	Binomial distribution analyzed with threshold GLMM	Same as for annual breeding success
	Triannual[b] reproductive success	Number of offspring born during each three-year interval (triennium) of a female's life that survived to at least 365 days; ordinal values of 0, 1, 2, 3 for each female-triennium	790 females[c], 2036 female-triennia	Ordinal distribution analyzed with ordinal GLMM	• 918 individuals, • 817 known mothers, 354 known fathers, • 47 full sib pairs, • 658 paternal half sib pairs, • 1268 maternal half sib pairs
Lifetime metrics	LRS[d]	Total number of offspring produced during the lifetime of a female, counting only infants that survived at least 365 days	265 females	Zero-inflated Poisson distribution analyzed with zero-inflated Poisson GLMM	• 345 individuals, • 293 known mothers, 107 known fathers, • 3 full sib pairs, • 131 paternal half sib pairs, • 363 maternal half sib pairs
	Binary LRS	Whether or not the female ever produced an offspring that survived to 365 days	265 females	Binomial distribution analyzed with threshold GLMM	Same as for total LRS

[a] The same dataset is used for annual breeding success.
[b] The same dataset is used for triannual breeding success.
[c] The triennial dataset is smaller than the annual one because more individuals are censored because the triennium is longer than the hydroyear: it is thus more common for a triennium to be censored at the endpoint of this study.
[d] The same dataset is used for lifetime breeding success and binary LBS.

Baboons in Amboseli live in stable social groups, ranging from 15 to 130 individuals. Several social groups, hereafter "study groups," are each observed two to five times each week. Data are collected on demographic and life-history events (births, deaths, maturations, and dispersals) and social behavior. Because female baboons are philopatric, females in study groups are followed from birth until death, unless they were alive before the study groups were established (left-truncated) or belonged to a group where monitoring stopped (right-censored). Our analyses included all life-history events that occurred for all subjects when they were in a study group. The pedigree was based on observations of pregnancies and births, augmented by genetic analysis (Galezo et al., 2022; McLean et al., 2023). The full pedigree consists of 1,918 individuals, including 1,789 individuals with known mothers and 651 individuals with known fathers: "trimmed" pedigrees (without individuals unrelated to the study subjects) are described in Table 1. The research in this study was approved by the Institutional Animal Care and Use Committee (IACUC) at Duke University (current protocol no. A003-24-01) and adhered to the laws and guidelines of the Kenyan government.

Quantitative genetic analyses of fitness metrics

Response variables and datasets

To estimate the genetic variance associated with fitness metrics, we used a variance-partitioning approach called the animal model (Wilson et al., 2010). The response variables in the animal model are vectors of trait values (in this case, fitness metrics). The model estimates the fraction of trait variance (phenotypic variance) that can be explained by pedigree-based genetic relationships between individuals (Kruuk, 2004). We fitted five univariate animal models, each with one of the following response variables: *i*) *annual reproductive success*, *ii) annual survival*, *iii) triannual reproductive success* (i.e., reproductive success across three consecutive years), *iv) lifetime reproductive success* (*LRS*), and *v*) *binary lifetime reproductive success* (*binary LRS*; see below and Table 1 for definitions).

For all fitness metrics that included the number of offspring produced by a female (i.e., all but annual survival), we counted infants that survived at least 365 days (hereafter "surviving offspring") to represent "reproductive success." This age corresponds closely to near-complete weaning and the earliest age at which offspring can survive the death of their mother in this population (Alberts & Altmann, 2003; Altmann, 1998; Altmann & Alberts, 2003). Using this age as our metric of offspring production is analogous to using counts of offspring that survive to various post-zygotic stages in other species (e.g., Dunning et al., 2023; Moiron et al., 2022; Viblanc et al., 2022). While zygote-to-zygote measures are theoretically preferred (Arnold & Wade, 1984), they are not commonly used because of practical issues in recording zygote-to-zygote life histories (Hendry et al., 2018; Wolak et al., 2018). Moreover, lifetime fitness metrics are better predictors of individual genetic contributions to the future population when measured at later stages (Alif et al., 2022). However, for completeness, we also fitted an additional set of models that counted all live-born infants, not only those that survived to 365 days (see the *Additional metrics of fitness* section below). For all time-limited fitness metrics, we excluded female-hydroyears (or female triennia)

in which a hydroyear included less than 90 days of data, unless it represented the hydroyear in which the female was born or died.

Annual reproductive success (ARS). For ARS, our dataset included 5,896 female-hydroyears belonging to 806 baboons that lived in wild-feeding (i.e., non-provisioned) study groups between 1971 and 2022 (see Table 1 for dataset descriptions). We modeled ARS as the number of surviving offspring born during each hydroyear of a female's life. No females in the dataset produced two surviving offspring during the same hydroyear. Consequently, ARS defaults to a binary trait, corresponding to a value of 1 for female-hydroyears in which an offspring that survived to 365 days was produced, and 0 for female-hydroyears in which no surviving offspring was produced. Note that we measured a female's ARS in all years of her life, including years in which she was immature; females that died before adulthood therefore only had ARS values of 0. This approach ensured that we produced an unbiased fitness metric that includes a crucial component of the true variance in ARS, as 47.55% of females in the dataset did not reach reproductive age.

Annual survival. For annual survival, we used the same dataset as for ARS (Table 1). We modeled annual survival as a binary variable: 1 for every full hydroyear that a female survived, including her birth hydroyear, and 0 for the hydroyear of death.

Triannual reproductive success (TRS). We included a triannual metric of reproductive success because an annual period is short relative to the reproductive cycle of female baboons (interbirth intervals are almost 2 years long) and therefore might not adequately capture differences in female fertility (Gesquiere et al., 2018). For TRS, the dataset is somewhat smaller than the dataset for the annual metrics because incomplete intervals occur more frequently for 3-year than 1-year intervals (Table 1). We modeled TRS as the number of surviving offspring that a female produced within each 3-year interval. Each female baboon was assigned one of four ordinal values during each triennium of her life: 0, 1, 2, or 3 depending upon how many surviving offspring she produced in that triennium. The first 3-year interval began at birth, the second at 3 years of age, the third at 6 years of age, and so on, including triennia in which the female died. While the annual metrics refer to hydroyears and thus have the same timeframe for all individuals, TRS was individually calculated, starting on the day of each female's birth; the last interval ended on the individual's death.

Lifetime reproductive success (LRS). We modeled LRS as the total number of surviving offspring produced during the lifetime of an individual. For LRS, our dataset comprised 265 female baboons (Table 1). This dataset is smaller than the datasets for annual and triannual metrics because, to provide accurate, unbiased, and comparable measures of LRS, we required that both each subject's life-history records and those of her age cohort be complete. We therefore included only female baboons i) who were followed from birth to death, ii) for whom the birth dates and survival status of all her offspring were known, and iii) who were born before hydroyear 2002, because all but one female born prior to 2002 had died by the time of this analysis. We also excluded all baboons born before systematic observations began in 1971, and all individuals that were not followed throughout their entire life (e.g., because their study groups were dropped).

Binary lifetime reproductive success (binary LRS). Our preliminary analysis revealed that most of the genetic variance in LRS was linked to whether a female produced at least one surviving infant during her life (which in turn was almost entirely predicted by whether she survived to adulthood; see the *Univariate models* section below). Therefore, we modeled LRS a second time as a binary outcome (binary LRS), using the same dataset as the LRS analysis (Table 1). We assigned 1 to all females who produced at least one surviving infant, and 0 to all females that did not.

Fixed and random effects

We included several biologically relevant non-genetic random and fixed effects in our models based on previous evidence that they influence fitness-related outcomes (Campos et al., 2020; McLean et al., 2019). We z-score transformed all continuous covariates to make comparisons between estimates more intuitive (see Supplementary Methods S1). Because missing pedigree links and admixture-related variation in genetic ancestry could also affect our estimates of V_A but are documented only for a subset of genetically well-characterized individuals, we also explored their potential impact in similar models with smaller datasets (see Supplementary Methods S2 and S3 and Supplementary Table S1).

Annual reproductive success and *annual survival*. The annual fitness metrics were modeled using the following fixed effects (see Supplementary Methods S1 for details on each fixed effect): i) the subject's age and ii) age squared; iii) average social group size (count of adult females) during that hydroyear and iv) average group size squared; v) habitat quality during the hydroyear, and vi) rainfall anomaly for the previous hydroyear. We also included random effects of i) permanent environment, representing individual non-genetic repeatability; ii) maternal identity (some values were missing as the mothers of 32 females were unknown); iii) hydroyear, to account for random differences in environmental conditions between hydroyears; and iv) hydroyear-group, to capture variance associated with random variation between different social groups.

Triannual reproductive success. TRS was modeled with fixed effects averaged over 3-year intervals (triennia) in the life of each female baboon (see Supplementary Methods S1): i) triennium, as a measure of age; ii) triennium squared; iii) group size; iv) group size squared; v) habitat quality where the majority of the triennium was spent; and vi) rainfall anomaly over a 3-year period starting 365 days before the start of the triennium. Additional random effects included i) permanent environment (individual non-genetic repeatability) and ii) maternal identity. Because each sequence of triennia was calculated uniquely for every individual, it was not possible to fit random effects associated with specific time units, like hydroyear or group-hydroyear.

LRS and binary LRS. Many dramatic changes can occur in the physical and social environment of a female baboon during her long life; averaging these effects over her entire lifespan is potentially meaningless. Therefore, we limited the fixed effects for LRS to environmental influences that could be compared across individuals of any age. We did not include measures of early life adversity associated with individual characteristics (e.g., dominance rank and social connectedness) because such characteristics can be influenced by genotype, which could therefore bias our fitness es-

timates (Wilson, 2008). Our fixed effects therefore included i) rainfall anomaly a year before birth; ii) habitat quality at birth; and iii) hydroyear of birth as a linear covariate. Additional random effects included i) maternal identity and ii) hydroyear of birth. Following Bonnet et al. (2022), hydroyear of birth was fitted both as a fixed and a random effect, to account for both linear and random time-linked variation during the study period.

Implementation of animal models

We ran all our mixed-effects animal models in a Bayesian framework using the MCMCglmm package (Hadfield, 2010) within the R environment (R Core Team, 2013). We tested convergence by visually assessing the posterior density distributions and chains, and by using the Heidelberger and Welch convergence test implemented in the coda package in R (Plummer et al., 2007). To obtain an appropriate effective sample size for characterizing the posterior distribution, we ran our models with different combinations of thinning, number of iterations, and burn-in (reported in Supplementary Table S2). In models involving LRS and bivariate models involving binary LRS, we detected under-/overflow and constrained the latent values accordingly (models with non-truncated latent variables returned almost identical results) (Hadfield, 2010; Hadfield et al., 2013; Regan et al., 2019).

Since all of our fitness metrics produced non-Gaussian data distributions, we reported our results on both the liability and the observed scale. The liability scale represents the phenotype as a normally distributed "latent trait" (de Villemereuil et al., 2016, 2018); we also back-transformed the results to the observed scale, i.e., the scale of the original data including the stochastic process generated by sampling phenotypic values around the expectation, using the *QGparams* and *QGmvparams* functions in the QGglmm package (de Villemereuil et al., 2016). Back-transformation allows us to draw evolutionary inferences and to include fixed effects in the estimate of genetic parameters, as it considers the true distribution of the trait (Bonnet et al., 2019a; de Villemereuil et al., 2018). For more information on data distribution scales see Supplementary Methods S4 ("Glossary").

We provide the 95% credible intervals (CI) built on model iterations after burn-in for both fixed and random effects. Fixed effects were highlighted if the 95% CI did not include zero. We considered variances attributed to random effects to be non-zero if the lower end of their 95% CI exceeded 0.001 (Bonnet et al., 2022; Dobson et al., 2023). We highlighted genetic correlations for which the 95% CI for the correlation coefficient did not overlap zero.

Univariate models

Our first aim was to fit univariate animal models to estimate the additive genetic variance (V_A) of each fitness metric alone. We implemented models for binomially distributed fitness metrics (ARS, annual survival, and binary LRS) using the "threshold" family specification in MCMCglmm; our models for ordinal fitness metric (TRS) employed MCMCglmm's "ordinal" family specification; and our zero-inflated Poisson distributed metric (LRS) used the "zipoisson" family specification. We used weakly informative, parameter expanded Fisher's priors for all models (de Villemereuil et al. 2013: variance $V = 1$, degree-of-beliefs nu = 1,000; alpha.mu = 0 and alpha.V = 1), except for LRS (priors: $V = 1$, nu = 3, alpha.mu = 0, and alpha.V = 1,000, for each component). Residual variances for all binarily distributed responses (threshold, multi-threshold—i.e., ordinal—models, and the Bernoulli component of the zero-inflated Poisson) were fixed to 1. We ran the models to obtain minimum effective sample sizes from the posterior distribution of >9,000 for all fixed effects and >6,800 for all random effects, with autocorrelation below 0.1 for all variances. To back-transform variance estimates to the observed scale, we used the "binom1.probit" model specification from *QGparams* for binomially distributed variables (results did not change when using the "logit" link) and the "ordinal" specification for ordinal metrics. For ordinal variables, however, we discuss the liability scale results because they produce a single estimate of genetic variance, rather than the variance–covariance matrix generated by back-transformed values, and are generally the preferred ones for interpretation (de Villemereuil, 2018). For LRS, we first back-transformed estimates of variance components separately for the zero-inflated and the Poisson components, which is useful since they have distinct biological meaning (Moiron et al., 2022). The Poisson component represents the number of offspring produced (i.e., overall reproductive success) while the zero-inflated component represents excess zeroes in the distribution, which is strongly shaped by whether or not the subject survived the juvenile period. We also obtained a combined, meaningful estimate of the total observed genetic variance and total heritability for the LRS trait (including both components together) using the "ZIPoisson.log.logit" specification for the *QGmvparams* function (kindly provided by P. de Villemereuil) within the "compound" branch of the QGglmm package.

Bivariate models: response variables, effects structure, and implementation

To estimate genetic correlations between our fitness metrics, we fitted 10 bivariate animal models, featuring all possible pairs of fitness metrics as bivariate response variables (convergence issues precluded us from fitting a single multivariate model including all fitness metrics). We used the same datasets, response variables, and suites of fixed effects for the bivariate analyses as for the univariate analyses. In the bivariate analyses, however, the random effect structures included both the random effects and, when appropriate, their covariances (see Supplementary Methods S5–S6). All bivariate models were implemented in MCMCglmm using the families and priors of the univariate models that composed them: for a list of all priors used in bivariate analyses, see Supplementary Methods S7. Back-transformation for bivariate models was performed in the same way as for univariate models but with the *QGmvparams* function from QGglmm package; we used 120–500 iterations per bivariate model (Biquet et al., 2022). For models of the "ordinal" family, no specification is currently available for *QGmvparams*, so we used "binom1.probit." We iterated all bivariate models enough times to obtain minimum effective sample sizes of 1,114 for random effects and 1,691 for fixed effects (see Supplementary Methods S6 and Table S2). To further test the robustness of our parameter estimates, we ran a subset of bivariate models with a permuted dataset (see Supplementary Methods S8).

Additional metrics of fitness

Our main analyses of reproductive success focused on counts of infants that survived to 365 days. To test how that choice may have influenced our results, we fitted four additional univariate animal models of fitness metrics based on live births rather than surviving offspring (i.e., breeding success sensu Clutton-Brock, 1988). These fitness metrics were annual breeding success (ABS), triannual breeding success (TBS), lifetime breeding success (LBS), and binary LBS. We performed these analyses using datasets and models identical to the corresponding "reproductive success" metrics. We also fitted bivariate animal models between all combinations of ABS, TBS, LBS, binary LBS, and annual survival. Finally, because our primary analyses suggest that most V_A in fitness is explained by whether females survived to produce offspring at all, we analyzed "survival to maturity" as an additional binary fitness metric, using the same dataset and model specification described above for binary LBS. For more information about these analyses see Supplementary Methods S9.

Estimate of genetic parameters

For each of our fitness metrics, we report the additive genetic variance V_A and the narrow-sense heritability, h^2 (Bonnet et al., 2019a; Hendry et al., 2018), on both the liability and the observed scales (de Villemereuil et al., 2016); see Supplementary Methods S4, "Glossary." Narrow-sense heritability was calculated as V_A/V_P (additive genetic variance divided by total phenotypic variance). On the observed scale, h^2 was adjusted to account for the fixed effects using the QGglmm R package; accounting for fixed effects is not straightforward on the liability scale (de Villemereuil et al., 2018). Genetic correlations (r_a) were calculated as $r_a = \sigma_{a_{12}}/(\sigma^2_{a_1} \times \sigma^2_{a_2})^{0.5}$. Phenotypic correlations (r_p) were calculated as $r_p = \sigma_{P_{12}}/(\sigma^2_{P_1} \times \sigma^2_{P_2})^{0.5}$, where $\sigma_{P_{12}}$ represents the phenotypic covariance and $\sigma^2_{P_1}$ and $\sigma^2_{P_2}$ represent the phenotypic variances of the fitness metrics 1 and 2. Genetic and phenotypic correlations were calculated on the observed scale, which includes not only the expected value of the trait, but also the stochastic process linked to the non-Gaussian data distribution (de Villemereuil et al., 2016). Furthermore, we obtained an estimate of $V_A(w)$ (additive genetic variance of relative fitness) by back-transforming the liability-scale estimates using the protocol detailed in Bonnet et al. (2022) (Supplementary Results S10 and S11). For the heritability of relative individual fitness, we divided $V_A(w)$ by the total variance in relative fitness (Lynch & Walsh, 1998).

Results

Univariate analyses of fitness metrics

Among the time-limited fitness metrics, we found measurable, non-zero V_A only for annual survival and TRS (Figure 1 and Table 2). We estimated the heritability for annual survival to be $h^2_{observed} = 0.23$ (Table 3). We also found high additive genetic variance for lifetime fitness in female Amboseli baboons (Figure 1 and Table 2). Binary LRS, the zero-inflated component of LRS, and survival to maturity all produced similar heritability estimates, as expected, given that they capture a similar biological phenomenon: survival to reproductive age (Table 3). In contrast, the CI for estimates of V_A for the Poisson component of LRS, which reflects the count of surviving offspring, overlapped 0 (Table 2). Consequently, the heritability for LRS overall was intermediate between the heritabilities of its two components (Table 3). Our breeding success-based measures of lifetime fitness, LBS and binary LBS, had heritability estimates very similar to LRS and binary LRS (Table 3). Following Bonnet et al. (2022), we obtained an estimate of $V_A(w)$ (additive genetic variance for relative LRS on the observed scale) that was also very high ($V_A(w) = 0.9023$). For a discussion of this value in comparison with that obtained by Bonnet et al. (2022), see Supplementary Results S10.

We found hydroyear effects for ARS, indicating non-genetic variance associated with random year-to-year variation in the environment (Figure 2 and Table 2). We also found effects of group-hydroyear for both ARS and annual survival, indicating non-genetic variance associated with differences among social groups specific to different hydroyears (Figure 2 and Table 2). In contrast, 95% CIs overlapped zero for permanent environment and maternal effects in the annual and triannual models (Table 2). For the influence of fixed effects and non-genetic sources of variance on fitness metrics, see Supplementary Results S12, Supplementary Table S3 and Supplementary Figures S1 and S2.

Bivariate analysis of fitness metrics

We found very high positive genetic correlations (r_a) between all fitness metrics (Supplementary Table S4). Genetic correlations between the three annual metrics, and between the annual metrics and TRS, were particularly high ($r_a > 0.98$; Table 4). Genetic correlations were also high between the time-limited fitness metrics and binary LRS (range $r_a = 0.89$–0.99). The correlation between ARS and binary LRS was the lowest of this set, albeit still substantial ($r_a = 0.89$), and all correlations with ARS produced relatively wide credible intervals (Table 4). Genetic correlations between time-limited fitness metrics and LRS were weaker in comparison (despite being still relatively high; Table 4). Models run with permuted datasets showed much lower, non-significant genetic correlations, indicating that these results were not driven by the model structure and implementation (see Supplementary Methods S8). Genetic correlations between breeding success-based metrics were generally similar to genetic correlations between reproductive success metrics, but tended to be lower, and genetic correlations with ABS often overlapped zero (Supplementary Table S4).

Phenotypic correlations (r_p) were all positive but lower and more variable (Table 4). For the bivariate model estimates of heritability and non-genetic variances, see Supplementary Results S13, and Supplementary Table S5.

Discussion

Our results show that genotype plays a substantial role in explaining variance in lifetime fitness and annual survival in female Amboseli baboons. We also show that the bulk of the genetic contribution to survival occurs during the infant and juvenile stages, prior to first reproduction, reflecting variation in the ability to survive through the infant and juvenile period. However, all our fitness metrics exhibited high positive genetic correlations, indicating that, whether fitness is measured over the full life course or on shorter time scales,

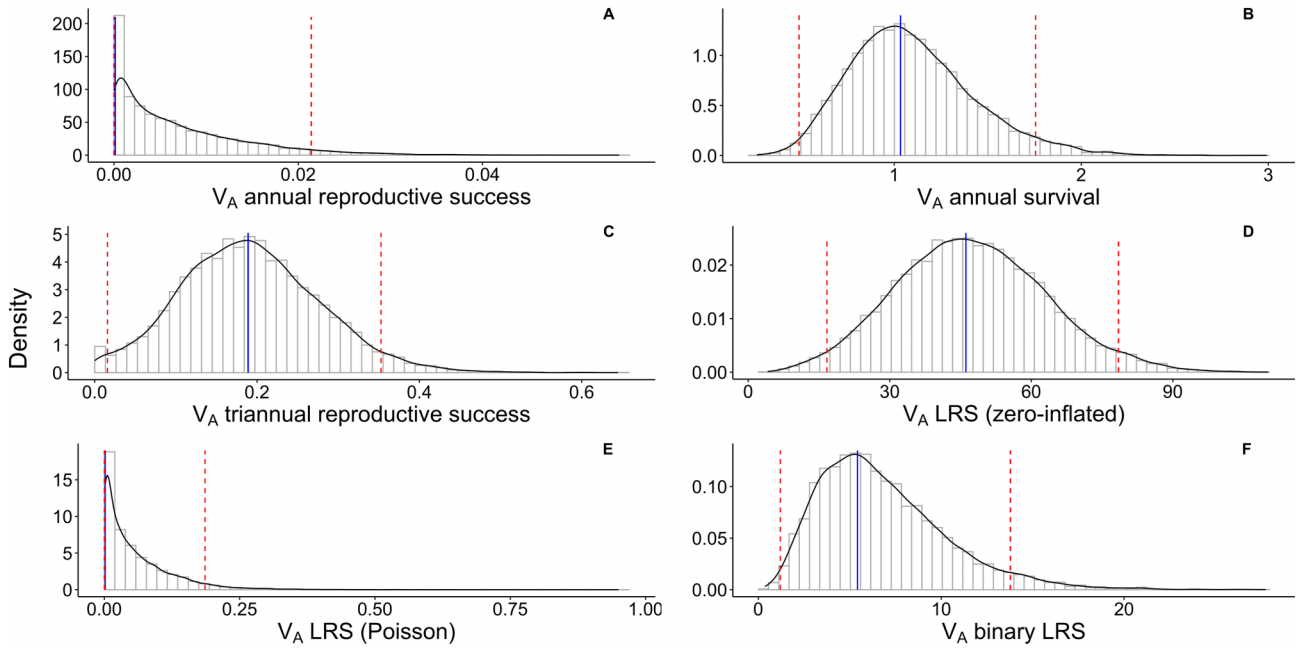


Figure 1. V_A on the liability scale of (A) *annual reproductive success*, (B) *annual survival*, (C) *triannual reproductive success*, (D) lifetime reproductive success (*LRS*) (zero-inflated component), (E) *LRS* (Poisson component), and (F) *binary LRS*; estimated with univariate animal models and represented by their posterior MCMC distribution (bars), overlapped with their kernel density (solid black line). 95% credible intervals are indicated by red dashed lines; posterior mode is indicated by solid blue line.

Table 2. Univariate animal models: posterior modes (and 95% credible intervals, CI) of all variances associated with random effects estimated for all different fitness metrics.

Trait	Variable	Posterior mode of the variance	95% CI
Annual reproductive success	Additive genetic effect (V_A)	0.0001	[0, 0.0214]
	Permanent environment	0	[0, 0.0088]
	Maternal effect	0.0001	[0, 0.0131]
	Hydroyear	**0.0262**	**[0.0019, 0.0641]**
	Group-hydroyear	**0.0323**	**[0.0051, 0.0766]**
Annual survival	**Additive genetic effect (V_A)**	**1.0336**	**[0.4913, 1.7559]**
	Permanent environment	0.0005	[0, 0.1906]
	Maternal effect	0.0004	[0, 0.1580]
	Hydroyear	0.0002	[0, 0.0843]
	Group-hydroyear	**0.1455**	**[0.0595, 0.2541]**
Triannual reproductive success	**Additive genetic effect (V_A)**	**0.0189**	**[0.0157, 0.3527]**
	Permanent environment	0.0006	[0, 0.1063]
	Maternal effect	0.0009	[0, 0.1533]
LRS, zero-inflated component	**Additive genetic effect (V_A)**	**46.1429**	**[16.6974, 78.4829]**
	Maternal effect	0.1286	[0, 16.9133]
	Hydroyear of birth	0.0084	[0, 5.9133]
LRS, Poisson component	Additive genetic effect	0.0015	[0, 0.1858]
	Maternal effect	0.0005	[0, 0.1407]
	Hydroyear of birth	0.0009	[0, 0.1227]
Binary LRS	**Additive genetic effect (V_A)**	**5.4168**	**[1.1961, 13.7798]**
	Maternal effect	0.0039	[0, 2.1083]
	Hydroyear of birth	0.0069	[0, 0.8008]

Note. LRS = lifetime reproductive success. Variances are on the latent scale and are marked in bold when the lower bound of the 95% credible interval is >0.001[a]. Values below 10^{-4} are marked 0.
[a]Note that since these are variance estimates, they cannot be lower than 0.

it involves a consistent underlying genetic architecture. Below, we discuss both the evolutionary and methodological implications of these findings for understanding evolution in natural populations, including the surprisingly high levels of additive genetic variance for several of the fitness measures we considered.

Table 3. Univariate animal models: posterior modes (and 95% credible intervals, CI) for the heritability of different fitness metrics.

Fitness metric	h^2 on the liability scale[a]		h^2 on the observed scale	
	Posterior mode	95% CI	Posterior mode	95% CI
Annual reproductive success	0.0001	[0, 0.0196]	0	[0, 0.0048]
Annual breeding success	0	[0, 0.0108]	0	[0, 0.0025]
Annual survival	**0.4485**	**[0.3908, 0.5837]**	**0.2317**	**[0.1498, 0.3309]**
Triannual reproductive success[b]	**0.0807**	**[0.0156, 0.1543]**	≪0≫ **0.0134** ≪1≫ 0.0011 ≪2≫ **0.0134** ≪3≫ 0.0012	**[0.0014, 0.0247]** [0, 0.0031 **[0.0025, 0.0254]** [0, 0.0029
Triannual breeding success[b]	0.0002	[0, 0.0903]	≪0≫ 0 ≪1≫ 0 ≪2≫ 0 ≪3≫ 0	[0, 0.0099] [0, 0] [0, 0.0109] [0, 0.0059]
LRS				
• **Zero-inflated component**	**0.8928**	**[0.6062, 0.9460]**	**0.5097**	**[0.3605, 0.5674]**
• Poisson component	0.0019	[0, 0.4466]	0.0007	[0, 0.1311
Total	NA[c]	NA	**0.2511**	**[0.1768, 0.3353]**
Binary LRS	**0.8385**	**[0.5593, 0.9289]**	**0.4480**	**[0.3114, 0.5167]**
LBS				
• **Zero-inflated component**	**0.8550**	**[0.6159, 0.9430]**	**0.4863**	**[0.3666, 0.5630]**
• Poisson component	0.0019	[0, 0.4014]	0.0006	[0, 0.1112]
Total	NA[c]	NA	**0.2765**	**[0.1789, 0.3397]**
Binary LBS	**0.7819**	**[0.5092, 0.9235]**	**0.4321**	**[0.2842, 0.5164]**
Survival to maturity	**0.7877**	**[0.4866, 0.9158]**	**0.4437**	**[0.2876, 0.5314]**

Note. LBS = lifetime breeding success; LRS = lifetime reproductive success. Fitness metrics are marked in bold when the lower bound for the 95% credible interval for additive genetic variance (V_A) is >0.001 (on the liability scale). Values below 10^{-4} are marked 0.
[a]To estimate heritability on the liability scale, we added the link variance to the total phenotypic variance (V_P).
[b]For triannual breeding success, we back-transformed from an ordinal (multiple threshold) model to the observed scale. This procedure results in separate values of h2 on the observed scale for each trait value (0, 1, 2 or 3 in our model).
[c]Total h2 on the liability scale is not provided because it is not easily interpretable for zero-inflated Poisson models.

The genetic components of fitness metrics in female Amboseli baboons

Our results identify survival to the first production of a surviving offspring as the life-history trait for which genetic differences among females are most influential. In contrast, the total number of offspring produced beyond the first is much less affected by genotype and is better explained by environmental and stochastic effects on female fertility in her reproductive years. These conclusions stem from the observation that the additive genetic variance (V_A) of LRS was entirely associated with the zero-inflated component of the LRS distribution (Table 3), which essentially corresponds to survival to the first successful reproduction (Moiron et al., 2022). In contrast, the overall number of infants produced (Poisson component) did not appear to possess measurable V_A. Accordingly, while the genetic correlation between the LRS and binary LRS—i.e., survival to first reproduction—indicates an almost complete genetic correspondence, the phenotypic correlation is much lower, indicating that binary LRS captures all the genetic variance of LRS, but it does not capture all the variance in LRS that is not genetic (Table 4). In other words, the additive genetic effects on binary LRS and LRS are nearly identical, but the environmental effects on binary LRS and LRS differ in kind, magnitude, or both. Accordingly, the heritability of binary LRS is higher than that of LRS, because while the two metrics share the same genetic variance, LRS exhibits greater phenotypic variance than binary LRS, as it includes the non-genetic variances of both zero-inflated and Poisson components.

Correspondingly, among the time-limited fitness metrics, annual survival is relatively highly heritable (Table 3). However, ARS does not appear to harbor appreciable genetic variance, a result in line with some other studies of time-limited fitness metrics (McFarlane et al., 2014; Moiron et al., 2022; Wolak et al., 2018). That is, whether a female baboon can produce a live offspring consistently on an annual basis does not appear to be measurably influenced by an individual's genotype, but only by environmental and social factors (partially captured by hydroyear and group-hydroyear: see Supplementary Results S12). The heritability of TRS, i.e., reproductive success measured over 3-year intervals, was low but bounded away from zero. This difference likely reflects the fact that for long-lived, non-seasonal reproducers like baboons, longer time intervals will allow small differences

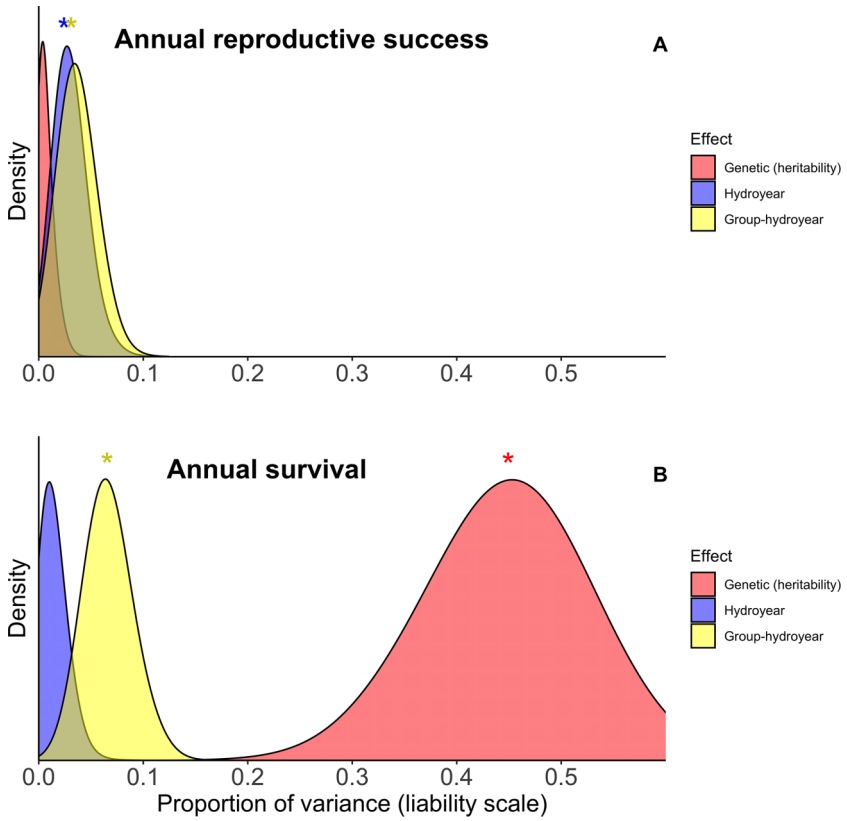


Figure 2. Variance components (proportion of phenotypic variance) for (A) *annual reproductive success*, (B) *annual survival*, estimated with univariate animal models and represented by the density of their posterior MCMC distribution on the liability scale. Heritability (h^2) is shown in red, hydroyear effects in blue, and group-hydroyear effects in yellow: asterisk indicates that the lower bound of the 95% credible interval is greater than 0.001. Permanent environment and maternal effects are not presented as the posterior density was heavily weighted toward zero. Distributions are scaled to aid comparisons.

Table 4. Bivariate analyses of fitness metrics.

	Annual reproductive success	Annual survival	Triannual reproductive success	LRS	Binary LRS
Annual reproductive success		**0.9866** [0.8228, 0.9974]	**0.9854** [0.8426, 0.9992]	**0.7299** [0.6134, 0.8829]	**0.8908** [0.2090, 0.9988]
Annual survival	**0.0450** [0.0187, 0.0599]		**0.9977** [0.9030, 0.9997]	**0.8529** [0.7527, 0.9166]	**0.9955** [0.9757, 0.9997]
Triannual reproductive success	0.0011 [-0.0043, 0.0095]	**0.0768** [0.0489, 0.1028]		**0.7884** [0.6795, 0.8641]	**0.9626** [0.6236; 0.9971]
LRS	**0.0320** [0.0166, 0.1095]	**0.1455** [0.0914, 0.1822]	**0.1754** [0.1150, 0.2419]		**0.9822** [0.9547; 0.9969]
Binary LRS	**0.0201** [0.0031, 0.0448]	**0.3366** [0.2934, 0.3803]	**0.0680** [0.0301, 0.0971]	**0.4984** [0.4351, 0.5477]	

Note. Posterior modes and 95% credible intervals for correlations between fitness metrics on the observed scale. Additive genetic correlations are shown above the diagonal (boxes are shaded light gray); phenotypic correlations are shown below the diagonal (boxes are shaded dark gray). Correlations marked in bold are different than 0 (credible intervals do not contain zero).

in reproductive success to accumulate, making a signal more detectable over fewer total intervals. Overall, the low heritability of time-limited metrics of reproductive success aligns with the lack of V_A in the Poisson component of LRS, as both indicate that the realized rate of infant production is less influenced by genotype than survival (especially survival to first reproduction).

Implications of the high V_A and h^2 of fitness in our population

The heritability of LRS in female baboons in Amboseli ($h^2_{observed} = 0.2511$) is high for a lifetime fitness metric (the estimated mean for wild and semi-wild populations of birds and non-human mammals < 0.1; Bonnet et al., 2022; Hendry et al., 2018). Fitness measured in other long-term studies of animal populations sometimes reveals measurable additive genetic variance, but heritability is usually much smaller (Hendry et al., 2018). The additive genetic variance in fitness corresponds to the upper limit of phenotypic change that can happen in a population: based on females, at least, this population therefore shows considerable genetic evolutionary potential. However, high V_A does not necessarily imply the same potential for phenotypic change, even when a trait is under selection (Gauzere et al., 2022; Pemberton et al., 2022) or if the trait is fitness itself (Bonnet et al., 2022). The high heritability of fitness implies, for example, that mean absolute fitness (i.e., LRS) in this population has the genetic capacity to increase over time. If the V_A and heritability we report for LRS were extrapolated to a predicted phenotypic response to selection, population sizes should have grown exponentially. Indeed, based on our estimates, mean LRS is expected to have quintupled in two generations, something that is clearly not occurring in the Amboseli baboons, where the population has grown modestly since the 1970s (Supplementary Results S9; Bonnet et al., 2022).

One explanation for this phenotypic stasis might be environmental change. Amboseli is a highly dynamic, changing environment (Alberts & Altmann, 2012; Okello et al., 2016; Western & Behrensmeyer, 2009; Western & Van Praet, 1973). If the environment deteriorates, organisms may experience phenotypic plasticity (non-genetic) that translates to lowered LRS, despite selection for higher LRS. Under this scenario, environmentally induced changes in phenotype can overshadow genetic evolution, so that genetic change is counterbalanced by environmental shifts (Bonnet et al., 2017; Hunter et al., 2022). Note that while fluctuating selection could have a role in maintaining genetic variance in fitness over longer timescales in Amboseli, it is unlikely to explain the results we present here (see Supplementary Results S14).

Our estimate of the evolutionary potential of the population could change if we included males in our analysis. The challenges that females and males experience in this population are very different: philopatric females remain with their female relatives throughout life while males disperse to find different groups, where they fight to establish rank and gain access to mates. Given the divergence in male and female life history, genotypes that are beneficial for females might not be beneficial for males, creating negative genetic covariance between the genetic components of female and male LRS (i.e., sexual antagonistic pleiotropy, Brommer et al., 2007). Alternatively, even in the absence of sexually antagonistic pleiotropy, if V_A for fitness was lower in males than in females, the genetic variance for fitness in both sexes would be reduced, a prediction consistent with previous, lower estimates of $V_A(w)$ when males and females were considered together (Bonnet et al., 2022: Supplementary Results S8). Understanding differences between the sexes in the genetic component of fitness—whether due to changes in sign or magnitude—is another important goal for assessing the potential for responses to natural selection in the wild (Wolak et al., 2018).

The effect of social environment on the V_A of fitness

To account for the potential influence of the social environment on the V_A of fitness metrics, we included a fixed effect of group size and random effects of group-hydroyear and mother's identity. Neither mother's identity nor group size affected fitness metrics, but we found variance associated with group-hydroyear effects for both annual survival and ARS. Group-hydroyear effects provide a snapshot of the individual's social environment independently of population-wide annual variation, which is captured by the effect of hydroyear. Our results show that survival and ARS were influenced by group-level characteristics, which are affected by the social composition of a group and its home range during a given hydroyear (Markham et al., 2013, 2015).

Our findings for group-hydroyear suggest that social environmental variation matters to V_A for fitness, consistent with non-quantitative genetic analyses of fitness-associated traits in this and other primate populations (Campos et al., 2020). However, other possible, finer-grained sources of social non-genetic covariance might affect our estimates of the V_A of fitness at different life stages. We discuss three additional mechanisms through which the social environment could have influenced our estimates of V_A.

First, maternal social rank influences infant survival in the study population (Creighton et al., 2025; Silk et al., 2003), and female rank in baboons is socially inherited along matrilines (Lea et al., 2014). The extent to which social environments and maternal effects—including nepotistic patterns of social inheritance—affect estimates of variance components in fitness-related traits is largely unknown in social animals (Holekamp et al., 2012). An important future direction for our research is to disentangle the confounding effect of social inheritance on juvenile survival, by explicitly modeling it alongside genetic inheritance (Thomson et al., 2018).

Second, in the Amboseli baboon population, the death of the mother during the first year of an infant's life is usually fatal to the infant, and the death of the mother during the first 4 years of a female's life predicts shortened lifespan even if she survives to adulthood (Tung et al., 2023). Because maternal survival is correlated with offspring survival and mothers share genes with their offspring, V_A estimates will be inflated if the correlation stems from non-genetic covariance but is attributed to genotype.

Finally, indirect genetic effects, either maternal or from group-mates, may have affected our estimates of V_A and heritability (Fisher & McAdam, 2019; McGlothlin & Fisher, 2021; Pick et al., 2025; Pujol et al., 2018). Whereas a positive covariance between the survival of an individual and the survival of her kin might increase the V_A for survival, a negative covariance between direct and indirect genetic effects of fitness—e.g., that generated via competition in an environment with limited resources—would reduce the to-

tal response to selection of the trait (Hadfield et al., 2011; Wilson, 2014). Modeling social effects (both genetic and non-genetic) falls outside of the scope of this study, but quantifying indirect genetic effects on fitness and disentangling social and genetic effects remains an important frontier for studies of contemporary evolution in natural populations (Young et al., 2019).

Genetic parameters of breeding success metrics

The heritabilities of breeding success-based metrics of lifetime fitness, and their correlations with each other and with annual survival, were similar to those obtained with LRS and binary LRS. These outcomes corroborate our result that the bulk of V_A lies in survival to maturity. However, TBS—unlike TRS—does not appear to harbor measurable genetic variance, suggesting that the genetic variance found in TRS is linked to the survival of the infant to 365 days. In addition, the genetic correlations between annual survival and both TBS and ABS had very wide credible intervals overlapping zero, unlike their counterparts with TRS and ARS. This difference suggests that the genetic correlations between annual survival and TRS and ARS metrics hinge on the survival of an individual during the first year. Notably, in reproductive success metrics, genetic variance linked to the survival of an infant in its first hydroyear is attributed to the mother's genotype (i.e., to the individual reproducing), while in annual survival it is attributed to the infant's genotype (i.e., to the individual surviving). Our current analysis cannot disentangle the V_A in first-year survival that is due to the genotype of the mother from the V_A that is due to the genotype of the infant. Indeed, first-year survival in a highly altricial species like baboons likely depends on a complex combination of the genotypes of both mother and infant (Hadfield & Thomson, 2017), and represents an important topic for future research.

Genetic correlations between fitness metrics

Genetic correlations were positive and high between virtually all lifetime and annual fitness metrics, reinforcing the growing consensus that survival and reproduction often do not exhibit genetic trade-offs (Chang et al., 2024). We caution, however, that because survival has a causal effect on reproductive success (i.e., reproduction ceases with death; see discussion in Tuliozi et al., 2022), a subtle genetic trade-off could still be present but masked. Interestingly, a phenotypic trade-off between adult female reproduction and survival was identified in this population after adjusting for female phenotypic quality (McLean et al., 2019). In light of the genetic correlations we report here, this phenotypic trade-off is likely to be unlinked to genotype, and possibly explained by the finite resources available to adult females (Van Noordwijk & De Jong, 1986). Together, these observations underscore the importance of investigating sources of variance in fitness at both the genetic and the phenotypic levels, as they provide distinct but complementary information on how natural populations evolve.

Our finding that time-limited and lifetime fitness metrics are strongly genetically correlated in female baboons, despite having very different heritability values, has practical implications. Our results suggest that, for quantitative genetics purposes, time-limited metrics are an accurate proxy of LRS and may provide information on the genetic basis of individual variation in fitness when LRS is not available. In the Amboseli baboons, a metric based on the first successful reproduction (binary LRS) would serve as a similarly reliable proxy that is measurable on a much shorter timescale. Whether this result generalizes to other systems remains an important question; we speculate that it is most likely to hold in long-lived species with slow development.

Notably, longevity is the main contributor to variation in phenotypic fitness in long-lived female mammals: variation in how long females live is much more important for female LRS than variation in the relative frequency of offspring production. Here, we show that both annual and TRS are nevertheless genetically correlated with LRS and annual survival, likely because living longer results in more opportunities to reproduce, and thus more offspring. By itself, however, consistency in the production of offspring is not measurably heritable—and our results indirectly indicate that the small amount of V_A we were able to measure for TRS is linked to offspring survival during the first year.

Because of the strong correlation between short-term fitness components and LRS, we examined the possibility that annual survival (which has the highest V_A) could indeed be evolving (sensu Bonnet et al., 2017, 2019b; Gauzere et al., 2022). In support of this idea, the estimated breeding values (EBVs) for annual survival increased at a rate of 0.013 [0.006, 0.022] per hydroyear over the course of the study (see Supplementary Results S14 and Supplementary Figures S3–S4; Bonnet et al., 2019b; Hadfield et al., 2010; Tuliozi et al., 2023). At face value, this change is predicted to translate into a 14.8% higher probability of annual survival for an individual born in 2022 compared to one born in 1971 (Supplementary Figure S4), but no change of this magnitude is readily apparent at the phenotypic level. Nevertheless, the increase in EBVs that we observed for annual survival is consistent with a successful evolutionary response to directional selection.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

The data underlying this article are available at Dryad: https://doi.org/10.5061/dryad.pzgmsbd22

Author contributions

B.T.: conceptualization, methodology, formal analysis, and writing (original draft and review/editing). E.A.A.: resources, data curation, writing (review/editing), and funding acquisition. J.T.: resources, data curation, writing (review/editing), and funding acquisition. S.C.A.: conceptualization, resources, data curation, writing (review/editing), and funding acquisition.

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Conflict of interest

Editorial processing of the manuscript was conducted independently of S.C.A., who is an Associate Editor of *Evolution*. The other authors declare no conflict of interest.

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