vol. 194, no. 6 the american naturalist december 2019

Lifetime Fitness in Wild Female Baboons: Trade-Offs and Individual Heterogeneity in Quality

Emily M. McLean,[1,*] Elizabeth A. Archie,[2,3] and Susan C. Alberts[1,2,4]

1. University Program in Genetics and Genomics and Department of Biology, Duke University, Durham, North Carolina 27708; 2. Institute of Primate Research, National Museums of Kenya, Karen 00502, Nairobi, Kenya; 3. Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556; 4. Department of Evolutionary Anthropology, Duke University, Durham, North Carolina 27708

Submitted August 9, 2017; Accepted June 5, 2019; Electronically published October 11, 2019

Online enhancements: appendix. *Dryad data:* https://doi.org/10.5061/dryad.fv3t300.

abstract: Understanding the evolution of life histories requires information on how life histories vary among individuals and how such variation predicts individual fitness. Using complete life histories for females in a well-studied population of wild baboons, we tested two nonexclusive hypotheses about the relationships among survival, reproduction, and fitness: the quality hypothesis, which predicts positive correlations between life-history traits, mediated by variation in resource acquisition, and the trade-off hypothesis, which predicts negative correlations between life-history traits, mediated by trade-offs in resource allocation. In support of the quality hypothesis, we found that females with higher rates of offspring survival were themselves better at surviving. Further, after statistically controlling for variation in female quality, we found evidence for two types of trade-offs: females who produced surviving offspring at a slower rate had longer life spans than those who produced surviving offspring at a faster rate, and females who produced surviving offspring at a slower rate had a higher overall proportion of offspring survive infancy than females who produced surviving offspring at a faster rate. Importantly, these trade-offs were evident even when accounting for (i) the influence of offspring survival on maternal birth rate, (ii) the dependence of offspring survival on maternal survival, and (iii) potential age-related changes in birth rate and/or offspring survival. Our results shed light on why trade-offs are evident in some populations while variation in individual quality masks trade-offs in others.

Keywords: individual fitness, offspring survival, life-history trade-offs, quality, birth rate, interbirth interval.

Introduction

Measuring within-species variation in survival and reproduction is essential for understanding the selection pressures that influence phenotypic traits. Studies that measure how variation in behavioral phenotypes leads to differences in individual survival and reproduction have both confirmed and challenged assumptions about the evolution of many behavioral traits, including cooperation, foraging, and inbreeding avoidance (e.g., Altmann 1991; Krakauer 2005; Reid et al. 2015). At the same time, understanding the relationships between life-history traits and fitness itself sheds light on the evolutionary significance of within-species variation in life-history traits and other fitness components and on how such variation is maintained in natural populations (e.g., Gaillard et al. 2000; Weladji et al. 2006).

Trade-offs between fitness components are a fundamental assumption of life-history theory (Stearns 1989; Roff 2002). For instance, individuals who invest highly in reproduction are expected to face costs in terms of survival and/or future reproduction (Reznick 1985; Stearns 1989; Viallefont et al. 1995; Visser and Lessells 2001; Blomberg et al. 2013). However, interindividual variation in quality (e.g., in the ability to acquire or efficiently use resources) may mask variation in resource allocation strategies if high-quality individuals show both high birth rates and high survival (Cam et al. 1998; Cam and Monnat 2000; Beauplet et al. 2006; Sanz-Aguilar et al. 2008; Weladji et al. 2008; Hamel et al. 2009*a*, 2010*a*; Torres et al. 2011). Variation in individual quality may mask trade-offs or even produce positive correlations between traits that are expected to trade off (e.g., Weladji et al. 2008; Olijnyk and Nelson 2013).

The roles of both trade-offs and individual heterogeneity in life-history variation have been examined in a number of studies (for recent reviews, see Hamel et al. 2010*b*, 2017*a*; Vedder and Bouwhuis 2018), and methods have been developed for identifying trade-offs in the presence of significant individual heterogeneity (e.g., Hamel et al. 2014, 2017*b*; Descamps et al. 2016). This work has revealed that both the strength of trade-offs and the role of individual heterogeneity in modulating trade-offs vary across environmental conditions (e.g., Pilastro et al. 2003; Cubaynes et al. 2011; King et al. 2011), across the life course of individuals (e.g., Beauplet et al. 2006; Descamps et al. 2008), and between species and populations (e.g., Hamel et al. 2009*b*, 2010*b*).

---

[*] Corresponding author; email: erm22@duke.edu.

Am. Nat. 2019. Vol. 194, pp. 000–000. © 2019 by The University of Chicago. 0003-0147/2019/19406-57875$15.00. All rights reserved.
DOI: 10.1086/705810

However, why trade-offs are evident in some populations while variation in individual quality masks trade-offs in others is not yet completely understood (see Descamps et al. 2009). Answering this question will require extensive longitudinal, individual-based data on survival, reproduction, and fitness in natural populations of multiple taxa.

Here we examine trade-offs and individual heterogeneity using a large, long-term data set of complete life histories from the well-studied, wild Amboseli baboon population. This population lives in a natural savannah ecosystem with a full complement of predators and no food provisioning. Thus, the birth and death rates reflect natural processes of intraspecific competition and predation. Further, baboons breed nonseasonally, and females show considerable variation in birth rates both within and between individuals; this variation in birth rates is strongly linked to variation in the ability to acquire resources (Gesquiere et al. 2018). In addition, the 47-year study includes unusually detailed data not only on life span but also on every reproductive event of the female study subjects (fig. 1). Most relevant here are our data on pregnancy outcomes (live birth vs. fetal loss or stillbirth), survival status of offspring, and time to next conception and birth.

In analyzing the relationships among maternal rate, offspring survival, and maternal reproductive life span, our data set allowed us to address three potential complications. First, in baboons, like many species with extended periods of maternal care, maternal birth rate is accelerated when an offspring dies before being weaned, so that fast birth rates will generally be associated with poor offspring survival. Second, offspring survival depends on maternal survival; when a mother dies before an offspring is sufficiently weaned, that offspring almost certainly will not survive (Tung et al. 2016). Third, birth rate and/or offspring survival could vary

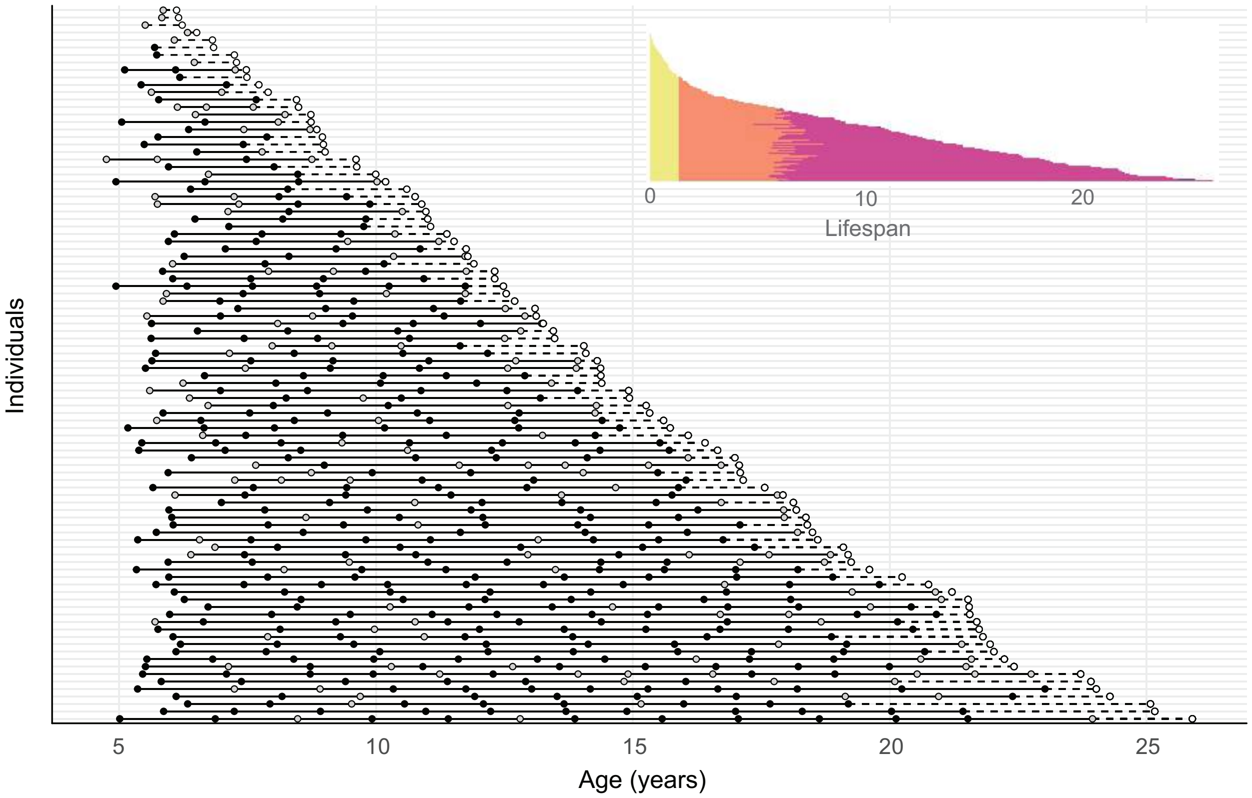


Figure 1: Visualization of complete female life histories. The main panel includes only females who experienced at least one live birth ($N = 96$). Each line represents a distinct female, and each filled circle represents a live birth; black circles represent offspring who survived to weaning age and gray circles offspring who died before the average age of weaning in our population. Solid black line segments represent interbirth intervals (some of which represent live interbirth intervals and some surviving interbirth intervals; see text and table A2). Open circles indicate the female's age at death and dashed lines the time between her last birth and death. The inset shows all females in the data set, including those who died without reproducing ($N = 199$). Infancy (to average weaning age) is shown in yellow, the juvenile period (between weaning and age at first reproduction) in orange, the reproductive period in magenta, and postreproductive life in dark purple (considered to begin 915 days after a female's last live birth; i.e., the mean live interbirth interval plus 2 SD).

systematically with maternal age (e.g., Descamps et al. 2008; Hayward et al. 2015), producing a phenotypic correlation between one or both of these reproductive phenotypes and reproductive life span. These potential complications reflect the fact that offspring survival is partly a function of maternal traits and behaviors. Thus, although we followed standard procedures for measuring fitness and did not consider offspring survival as a component of maternal fitness (Wolf and Wade 2001; Wilson et al. 2005), we nonetheless statistically controlled for the relationships between (i) offspring survival and maternal birth rate and (ii) offspring survival and maternal survival. We also (iii) included maternal age in our models to control for variation in offspring survival and maternal birth rate across the life span of the mother.

We evaluated two nonexclusive hypotheses regarding the nature of the phenotypic relationship between reproduction and survival. The trade-off hypothesis posits that environmentally or genetically mediated differences in individual resource allocation drive a negative relationship between reproduction and adult female survival. Under the trade-off hypothesis, individuals who allocate highly toward reproduction—via high birth rates or high offspring survival—will have shorter lives than individuals with lower allocation to reproduction. Similarly, individuals who allocate resources toward one component of reproduction will have reduced output in other reproductive traits. In contrast, the quality hypothesis posits that differences in individual quality, resulting from either genetic or environmental differences between individuals, drive a positive relationship between reproduction and survival. Under this hypothesis, individuals with high allocation to reproduction will have longer lives than individuals with low allocation to reproduction, because their high phenotypic quality allows them to maintain high levels of reproduction without compromising survival. These hypotheses are not mutually exclusive (Oli et al. 2002; Weladji et al. 2008; Hamel et al. 2009*a*, 2010*a*; Wilson and Nussey 2010; Théoret-Gosselin et al. 2015): the observed phenotypic relationships between reproductive phenotypes and survival reflect the contributions of both trade-offs and interindividual variation in quality.

Methods

Study Population

We studied a population of wild savannah baboons in the Amboseli ecosystem of southern Kenya that has been the subject of ongoing research for more than 4 decades (Alberts and Altmann 2012). This population is composed primarily of yellow baboons with some naturally occurring admixture from neighboring anubis baboon populations (Alberts and Altmann 2001; Tung et al. 2008). Savannah baboons live in stable social groups containing multiple adults and juveniles of both sexes, ranging in size from approximately 20 to 100 animals. The Amboseli Baboon Research Project monitors multiple such groups (study groups) in the Amboseli ecosystem (Alberts and Altmann 2012). All subjects are individually recognized based on unique morphological and facial features. All demographic and life-history events (births, maturation events, immigrations, deaths, and emigrations) are recorded on a routine basis as part of the near-daily monitoring of the study groups.

Our study subjects encompassed all of the female baboons born into study groups between 1971 (the start of continuous observation on this population) and 1996 (the latest year from which no females born were still alive at the time of analysis), yielding 205 complete female life histories. We excluded females born after 1996 because including them would bias our data set against individuals with long life spans. We knew the birth and death dates for all 205 subjects to within a few days. For the study subjects who reproduced, we also knew the birth dates of all of their offspring to within a few days, with a few exceptions ($n = 7$) where the uncertainty in birth date was ≥ 1 month. We ran all analyses of interbirth intervals with and without these uncertain cases and found no difference in magnitude, direction, or significance of results. Death dates were known for all offspring who died before the study ended. We also excluded six outliers from all analyses presented in the main text: three with early cessation of reproduction, one with late age at first birth (associated with a near-fatal injury sustained in late puberty), and two with exceedingly slow birth rates (table A1; tables A1–A8 are available in the online appendix). These outliers had phenotypes that were >3 SD from the mean and/or exerted a disproportionate influence on the results of a regression model (Cook's distance > 0.5; details in table A1). See the supplement for analyses that include these outliers, leading to some minor changes in the significance of some tests (tables A3–A5, "Results," and "Discussion"). Our final data set included 199 individuals.

In baboons, births are nonseasonal, occurring frequently in all months of the year. Female baboons remain in their natal group throughout their lives, and our study subjects were observed several times each week for their entire lives, with occasional exceptions. It is very unlikely that any pregnancies were missed; female baboons exhibit external indicators of reproductive state that make it easy for observers to detect cycling, conception, and pregnancies (for details, see Altmann 1973; Beehner et al. 2006; Gesquiere et al. 2007). The onset dates for all pregnancies are assigned using visual assessment of these reproductive indicators. Endocrinological analyses in our study population combined with decades of close observation confirm that these visual methods are greater than 97% accurate for identifying the timing of the onset of pregnancy and, in turn, pregnancy due dates (Beehner et al. 2006).

Life-History Traits

Age at Death (AD). Death is assigned when a carcass is found or at the time a female disappears from the study population, as no female has ever permanently dispersed to a new group during the 47-year study (table A2). Our study population represents approximately half of the baboon population in the Amboseli ecosystem, suggesting that we would be very likely to detect even rare cases of permanent female movement between groups.

Age at First Live Birth (AFLB). During each observation day, all members of a study group are registered as present or not, and the reproductive state of all adult females is assessed based on external indicators (see Beehner et al. 2006; Gesquiere et al. 2007). New infants are identified on the first observation day on which they are seen, typically within 0–3 days of birth. We mark the start of a female's reproductive life as the age at which she first gives birth to a live offspring (table A2).

Reproductive Life Span (RL). We define reproductive life span as AD − AFLB (table A2). We use age at death as the endpoint instead of age at last birth because nearly all baboon females (94.75% of our data set; fig. 1) are reproductively active (cycling, pregnant, or lactating) at the time of their death and baboon females do not experience systematic reproductive cessation toward the end of life (fig. 1; Altmann et al. 2010; Alberts et al. 2013*b*). We reran the analyses presented here with an alternative definition of RL (age at last live birth minus age at first live birth) and found only small differences in effect sizes, with no differences in the direction or significance of any of our results (tables A3–A5).

Offspring Survival (OS). We measured offspring survival as the proportion of a female's liveborn offspring who survived to 70 weeks of age, the estimated age at weaning in our population (Altmann 1998; table A2). We refer to individuals that are between birth and 70 weeks of age as infants.

Live Interbirth Interval (IBI_L). To estimate birth rate, we counted the number of days between live births (the live interbirth interval) for each female that had at least two live births in our data set ($n = 87$). The time between two live births is strongly influenced by offspring survival: mothers experience much shorter postpartum amenorrhea when their offspring dies before weaning and resume cycling, conceive, and give birth again more quickly after the death of an unweaned infant (Altmann et al. 1978).

Surviving Interbirth Interval (IBI_S). Because the interval between live births is heavily determined by offspring survival, we also calculated the average duration (in days) of the interval between the birth of an infant who survived at least 70 weeks (the entire period of infant dependence, hereafter the infancy period) and the next birth for all mothers with at least one such interval ($n = 82$). This interval, termed the surviving interbirth interval, represents the average time required by each mother to raise an infant successfully to weaning and subsequently conceive, gestate, and birth another live infant. This metric is correlated with IBI_L ($R = 0.81$, $p < .0001$), but the two metrics are distinct; we interpret IBI_S as a direct reflection of a female's ability to recover from a reproductive event (production of an offspring who survives infancy). Therefore, we used IBI_S when considering heterogeneity in individual quality and investigating trade-offs between allocation to reproduction and allocation to survival (table A2).

Measures of Individual Fitness

Lifetime Reproductive Success (LRS). Lifetime reproductive success for each female was defined as the total number of live offspring born to her, regardless of the offspring's subsequent survival. The ability of a mother to raise an offspring to independence can be treated as a component of maternal fitness (e.g., Clutton-Brock 1988), but we removed OS—a phenotype that combines maternal and offspring characteristics—entirely from our measure of a mother's LRS. This allowed us to investigate the relationship between offspring survival and individual fitness and follows the strict bookkeeping practices suggested by quantitative evolutionary biologists for estimating measures of selection (Arnold 1983; Lande and Arnold 1983; Cheverud 1984; Wolf and Wade 2001).

λ_{ind}. The measure λ_{ind} is the individual-level analogue to λ_{pop}, the population rate of increase, and incorporates two fitness components—the number of liveborn offspring produced by an individual and the year of life during which these offspring are produced—to estimate each individual's rate of increase. The value λ_{ind} is calculated separately for each observed individual life history. Specifically, λ_{ind} is the dominant eigenvalue of each individual's age-structured population projection matrix (for details, see McGraw and Caswell 1996). We constructed these matrices from our longitudinal individual-level data on births and deaths and calculated λ_{ind} using the popbio package in R, version 3.3.1. The individual with the highest λ_{ind} (i.e., fastest growth rate) is considered to have the highest fitness.

Variance in LRS Explained by Survival to AFLB. We had two classes of individuals in our data set: females who died without reproducing (nonbreeders, $n = 103$) and females who gave birth to at least one live offspring (breeders, $n = 96$). We followed the methods detailed by Brown (1988) and calculated the contribution to variance in LRS of females who reproduced successfully as $p(\sigma^2_{\mathrm{LRS}})$ and the contribution of females who failed to reproduce as $p(1-p)(\bar{x}^2_{\mathrm{LRS}})$, where p is the proportion of individuals who gave birth to at least one live offspring ($p = .49$), and σ^2_{LRS} and $\bar{x}^2_{\mathrm{LRS}}$ are the variance and squared mean of those breeders' LRS, respectively.

Relationships among OS, RL, IBI_L, and Fitness

We constructed a path analysis to examine the pairwise relationships between the proportion of offspring surviving, reproductive life span, live interbirth interval, and lifetime reproductive success. This analysis produced partial correlation coefficients between all pairs of our variables of interest while simultaneously controlling for effects of the other variables in the model. Given the biological constraints of this model (i.e., one cannot continue producing offspring after death), we view these path coefficients as simply partial correlation coefficients, and we caution against interpreting them as indicative of causal relationships per se.

We calculated the variance-covariance matrix between all standardized predictor and response variables and performed path analysis in the structural equation modeling package (sem) in R, version 3.3.1. We used variance-standardized variables, including variance-standardized LRS, so that we could directly compare path coefficients between variables. We modeled the proportion of offspring surviving a priori as an exogenous variable (with no prior links in the causal pathway) because of its known effects on $\mathrm{IBI_L}$. In contrast, we modeled RL, $\mathrm{IBI_L}$, and LRS as endogenous variables (i.e., with prior links in the causal pathway). Because the large majority of infant deaths occur in the first few months of life and shorten the interbirth interval by more than a year, we only modeled an effect of offspring survival on interbirth interval and did not model the reverse effect of interbirth interval on offspring survival (Altmann et al. 1978). We present the results for the model with the lowest Bayesian information criterion, as determined by backward stepwise model selection.

Addressing Effects of Maternal Age, Maternal Survival, and OS on Life-History Traits

Our path analysis supported the quality hypothesis (i.e., we found a positive correlation between offspring survival and maternal survival). However, as discussed in the introduction, three complications plague analyses of the relationship between lifetime reproduction and survival in baboons and any other long-lived, nonseasonally breeding mammal (including humans): (i) offspring survival influences maternal birth rate, (ii) offspring survival depends on maternal survival, and (iii) birth rate and/or offspring survival could vary systematically with maternal age.

To address these concerns and their potential effects in the path analysis, we constructed two linear mixed models to examine the relationship between maternal reproductive life span (which represents survival) and the two reproductive traits in our path analysis: offspring survival and the live interbirth interval. The first linear model, the OS model, was a generalized linear mixed model (GLMM) with the survival status of each offspring in our data set as the response variable (table A4). The second linear model, the $\mathrm{IBI_L}$ model, was a linear mixed model with the length of each live birth interval (IBI) in our data set as the response variable (table A4). Maternal age at offspring birth and maternal RL were continuous predictors in both models. Because the relationship between maternal age and reproductive phenotypes may not be linear in our population (Gesquiere et al. 2018), we added an additional categorical predictor of maternal parity (nulliparous or not) to both models. We did not include a quadratic effect of maternal age, because quadratic models are often not the most appropriate way to model age dependence in traits (for a discussion, see Berman et. al 2009). However, by modeling the effects of maternal parity, we allow for the outcome that inexperienced (and generally young) mothers may have reproductive phenotypes similar to old, senescent mothers. Because offspring will generally not survive infancy if their mother dies, we included an additional categorical predictor in the OS model indicating whether the mother died before the offspring during the 70-week infancy period. Because offspring survival greatly influences the duration of postpartum amenorrhea, we included an additional categorical predictor in the $\mathrm{IBI_L}$ model indicating whether the offspring was alive for the entire 70-week infancy period. Both models included random effects of maternal identity and year the offspring was born. The OS model allowed us to measure the relationship between OS and RL controlling for the effects of maternal death during infancy. The $\mathrm{IBI_L}$ model allowed us to measure the relationship between $\mathrm{IBI_L}$ and RL, controlling for the effect of offspring death during infancy.

The results of the OS model indicated that the relationship between OS and RL resulted from the selective disappearance (i.e., early mortality) of females with low OS (Van de Pol and Verhulst 2006) rather than from a positive correlation between maternal age and OS. Similarly, the results of the $\mathrm{IBI_L}$ model confirmed that the relationship between $\mathrm{IBI_L}$ and RL was not statistically significant, even after considering effects of maternal age and parity (table A4). The results of these two linear mixed models also allowed us to rule out the possibility that changes with age in OS and IBI could produce spurious correlations between RL and these two phenotypes in our path analysis. We ran these models in R, version

3.3.1, using the lme4 package (Bates et al. 2015); we ran the OS model with a binomial distribution and a logit link.

Detecting Survival Costs and Reproductive Costs of Reproduction by Considering Heterogeneity in Female Quality

Both our path analysis and the mixed effects models of OS and IBI_L failed to detect trade-offs between survival and reproduction, suggesting marked differences in female quality. Consequently, we hypothesized that the relationship between survival and reproduction might be influenced by individual quality. To test this hypothesis, we used a multivariate index of phenotypic quality (Hamel et. al 2009*a*; Wilson and Nussey 2010). We used four fitness-associated phenotypes as indicators of quality: AFLB, IBI_S, OS, and RL. Specifically, we used principal component analysis (PCA) to identify independent axes of covariation among these fitness-associated phenotypes. A principal component (PC) of trait covariation can be interpreted as reflecting substantial variance in individual quality if each trait loads onto the PC in a direction consistent with increasing fitness, if the PC accounts for a large part of observed variation in traits, and if it is positively correlated with variance in individual fitness (Hamel et al. 2009*b*). Alternatively, a principal component of trait covariation may reflect trade-offs if some traits load onto the PC in a direction that reflects increasing fitness, while others load in a direction that reflects decreasing fitness or if the PC is not strongly correlated with individual fitness (Hamel et al. 2009*b*).

Our results indicated that the covariance between AFLB, IBI_S, OS, and RL was consistent with variation in quality (see below), and we subsequently designated the first principal component (PC1) of the PCA as our quality index (table 1). In contrast, we found that the second principal component (PC2) of covariation captured negative covariation among several of our traits, consistent with the idea that it reflects trade-offs (table 1; Hamel et al. 2009*b*).

We examined the relationship between our quality index (PC1) and fitness in two ways. First, we calculated a simple correlation between quality and individual fitness (measured as both LRS and λ_{ind}). Second, we calculated selection differentials and selection gradients (partial regression coefficients) for each phenotype in the quality index (see the appendix; table A6). We then used these selection gradients (i.e., multivariate vectors of selection) to determine Θ, the angle between the vector of multivariate selection and the principal component representing our quality index; we report the values of Θ in the appendix (table A7; for details, see Wilson and Nussey 2010). Small values of Θ (representing a close alignment between the vector of multivariate selection and the quality index) are characteristic of populations in which selection may act on variation in phenotypic quality (Wilson and Nussey 2010).

Finally, to test the hypothesis that the relationship between survival and reproduction is influenced by individual quality, we constructed two sets of linear models, designated the trade-off models, both of which had individual quality and IBI_S as the sole predictors. The first trade-off model had RL as the response variable; the second trade-off model had OS as the response variable. We note that these two response variables were also among the measures that contributed to individual quality (i.e., to PC1 of our PCA). Thus, we expect a positive relationship between quality

Table 1: Summary of putative indicators of multivariate female quality from principal component analysis

Component	Variable loadings	Variance explained	Description	Correlation with measures of fitness	
				LRS (p)	λ_{ind} (p)
PC1	AFLB: −.87 IBI_S: −.79 RL: .20 OS: .27	38%	Females with early ages at first reproduction and short interbirth intervals (fast birth rates) vs. females with late ages at first reproduction and long interbirth intervals (slow birth rates); this axis represents a quality axis	.31 (.005)	.36 (.0008)
PC2	AFLB: −.03 IBI_S: −.39 RL: −.70 OS: −.69	28%	Females with short lives and low OS but short interbirth intervals (fast reproduction) vs. females with long lives and high OS but long interbirth intervals (slow reproduction); this axis thus describes both trade-offs with interbirth interval length and evidence of quality differences (seen in the covariation between OS and RL)	.54 (.001)	.33 (.003)

Note: AFLB = age at first live birth; IBI_S = surviving interbirth interval; RL = reproductive life span; OS = offspring survival; LRS = lifetime reproductive success; λ_{ind} = individual fitness.

and RL and between quality and OS. However, such a positive relationship still allows for trade-offs between RL and IBI_S and between OS and IBI_S, as demonstrated by the loadings onto PC2 (table 1).

Our trade-off models explicitly test for the relationship between IBI_S and RL (first set of trade-off models) and between IBI_S and OS (second set of trade-off models) while controlling for variation in quality (i.e., for PC1). This approach is conceptually related to the PCA itself, which describes multiple axes of covariation among variables. Specifically, PC1 in our PCA describes significant covariation among our four life-history traits in a direction consistent with increasing fitness (with a considerable range of values in the loadings for each trait; table 1), and PC2 describes some negative covariation among some of the variables, once PC1 is accounted for, reflecting likely trade-offs (again, with a range of values for trait loadings; table 1). In our trade-off models, we seek to explicitly examine the trade-offs that are suggested in the PCA by asking whether individuals with long reproductive life spans for their quality (first trade-off model) or high OS for their quality (second trade-off model) also tend to have relatively long birth intervals after a surviving birth.

To confirm the statistical validity of our regressions, we examined the variance inflation factors of the trade-off models and found that collinearity between predictors was low (all variance inflation factors < 5), indicating that these models are stable. In addition, we designed a permutation test to examine the possibility that the covariation between our response variables (RL or OS) and our predictor variable (IBI_S) may have influenced our quality metric in such a way as to bias our trade-off models in favor of detecting trade-offs. Specifically, we assigned a second p value to each model via a permutation test in which we retained the actual pattern of IBI_S and RL values (for trade-off model 1) and IBI_S and OS values (for trade-off model 2) but in which other relationships among the life-history variables occurred at random. This procedure removed evidence of any trade-offs, indicating that the trade-off outcome was not an inevitable outcome of the existing data structure (see the appendix for more details).

Results

Females Vary Considerably in Life-History Phenotypes and Fitness

AD, AFLB, RL, IBI, and OS. The median age at death in the full data set ($n = 199$) was 5.41 years (range 0.01–25.89 years; fig. A1*A*). Ninety-six of these 199 females gave birth to at least one live offspring (fig. 1). The data used to construct figure 1 and for all subsequent analyses are deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.fv3t300; McLean et al. 2019). The median age at death for these 96 breeders was 14.31 years (range 6.12–25.89 years; fig. A1*A*), and the median reproductive life span was 8.27 years (range 0.18–20.88 years; fig. A1*E*). The median age at first live birth was 5.9 years; this trait was the least variable of all of our life-history phenotypes, ranging from just 4.75 to 7.98 years (fig. A1*C*). The median interval between live births in our data set was 1.67 years (608.6 days; range 269.5–959 days; fig. A1*B*). The median interval between surviving births in our data set was 1.75 years (638.5 days; range 392–960 days; fig. A1*D*). The median proportion of offspring who survived to 70 weeks was 0.75 (range 0–1; fig. A1*F*). The generation time, estimated from our empirical data and defined as the average age of a mother at the birth of a daughter (Coale 1972), was 11.41 years.

Measures of Fitness. The mean lifetime reproductive success considering all 199 females was 2.71 ± 3.59 (mean ± SD) live offspring (range 0–14). For the 96 breeders, the mean LRS was 5.61 ± 3.21 live offspring (range 1–14; fig. A2*A*). The mean value of λ_{ind} for the 199 females in our data set was 0.52 ± 0.55 (mean + SD; range 0–1.18). For the 96 breeders, the mean λ_{ind} was 1.09 ± 0.08 (range 0.87–1.18; fig. A2*B*). Note that the population average of λ_{ind} is not the same as the population rate of increase (λ_{pop}) because the mean of a set of eigenvalues (in this case, a set of λ_{ind}) is not the same as the eigenvalue of the mean matrix (λ_{pop}; Lenski and Service 1982). The fitness measures LRS and λ_{ind} were positively associated ($R^2 = 0.68, p < .001$), and the relationship between the two was curvilinear (fig. A3), consistent with findings in other species (Brommer et al. 2002, 2004; Robbins et al. 2011).

Following Brown (1988), we partitioned the variance in LRS among females of different classes (nonbreeders and breeders) and found that 61.3% of the variance in LRS among all females was attributable to females who never reproduced. Consistent with previous work in our population (Alberts and Altmann 2003) and expectations for a long-lived species, survival also explained the majority of the variance in LRS among the individuals who did survive to reproduce. The parameter estimate in the path analysis indicates that an increase of 1 SD in RL increases LRS by 2.90 live births (i.e., by 0.97 SD for LRS). In contrast, an increase of 1 SD in IBI_L increases LRS by only 0.63 births (less than 1/4 SD for LRS).

Evidence for the Quality Hypothesis: The Longest-Lived Females Had the Highest OS

Our path analysis revealed a positive relationship between offspring survival and reproductive life span (fig. 2; table A3): females with higher rates of OS were themselves more successful at surviving. The results from our GLMM of offspring

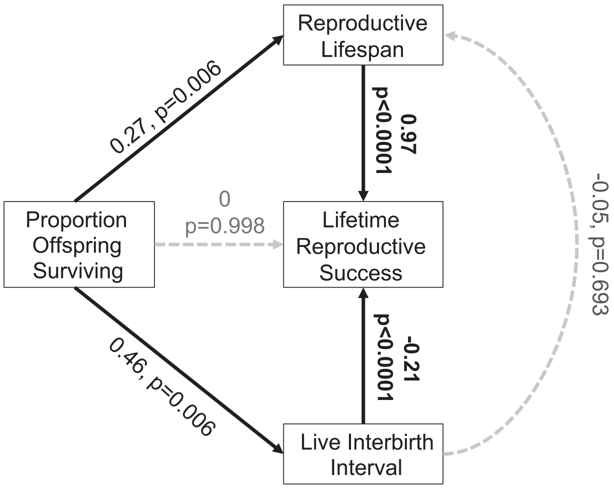


Figure 2: Path analysis with standardized pairwise partial correlation coefficients between life-history traits and fitness. Significant partial correlation coefficients are in boldface. Paths that are included in the full model but not in the best-supported model (as determined by backward stepwise selection) are shown in light gray with dashed lines. Longer live interbirth interval (slower production of live offspring) is associated with higher offspring survival and lower lifetime reproductive success (LRS). Longer reproductive life span is associated with higher offspring survival and higher LRS.

survival (the OS model; see "Methods" and table A4) also support this finding. Specifically, even while controlling for other important effects—including maternal loss ($\beta = -1.42$, $p < .001$), maternal parity ($\beta = -0.62$, $p = .056$), and maternal age ($\beta = -0.37$, $p = .018$) on offspring survival—females who would ultimately lead long reproductive lives produced offspring with a higher probability of surviving than females who would ultimately lead shorter reproductive lives ($\beta = 0.35$, $p = .017$; fig. 3*A*; table A4). This result suggests that quality differences among females may have contributed to differences both in reproductive life span and offspring survival.

Our path analysis also revealed the negative relationship between offspring survival and live interbirth interval that one expects for nonseasonal breeders (fig. 2). Our LMM of live interbirth interval (the IBI_L model; see "Methods" and table A4) confirmed that this relationship was caused by females' immediate responses to offspring death. Specifically, if their current offspring died in infancy, females reproduced again quickly: live birth intervals in which the offspring survived to weaning were 171 ± 15 days longer ($p < .0001$) than live birth intervals in which the offspring died before 70 weeks of age (table A4). The IBI_L model also confirmed that interbirth interval was unrelated to other life-history variables, although nulliparous females showed a trend toward longer

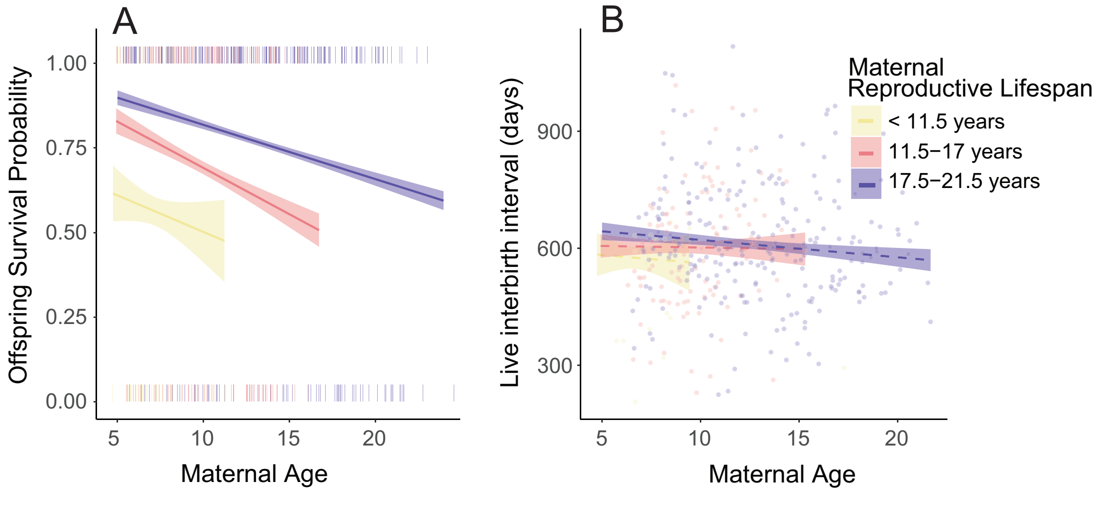


Figure 3: Reproductive life span (RL) is correlated with offspring survival (OS; *A*) but not with live interbirth interval (IBI_L; *B*). The regression lines in both panels represent visualizations of (generalized) linear mixed models. *A*, Probability of OS as a function of mother's age at birth and RL. The trendlines show predicted values with 95% confidence intervals (CIs) from a model that also includes maternal parity, maternal death in the weaning period, and random effects of maternal identity and offspring birth year. The model indicates a statistically significant relationship between OS and maternal age, as well as between OS and maternal RL (depicted as categorical but modeled as continuous). The small vertical lines show our actual OS data. *B*, Live interbirth interval as a function of mother's age and RL. The trend lines show predicted values with 95% CIs from a model that also includes maternal parity, offspring death in the weaning period, and random effects of maternal identity and offspring birth year; the model indicates no statistically significant relationship between IBI_L and maternal age or between IBI_L and RL. The points show our observed interbirth interval data.

intervals (especially when including outliers; see table A4). The IBI model also revealed considerable heterogeneity among females in interbirth interval lengths (table A4).

Detecting Trade-offs Depends on Measuring Individual Quality

Our finding that the longest-lived females had the highest offspring survival suggests that variation in female quality is a salient feature in this population and that it may obscure trade-offs between reproduction and survival. To test for evidence of trade-offs between reproduction and survival while controlling for variation in female quality, we developed a multivariate index of female quality, PC1, from a PCA of covariation among life-history traits (see "Methods"). The variables that loaded most heavily on PC1 were AFLB and IBI_S (for more details, see tables 1, A8; fig. A4). Both AFLB and IBI_S had negative loadings on our quality index, because early ages at first live birth and short surviving birth intervals are consistent with features of high-quality females. Our quality index, PC1, showed a statistically significant positive correlation with individual fitness measured both by LRS and λ_ind ($R = 0.31$, $p = .005$ and $R = 0.36$, $p = .0008$, respectively).

After controlling for variation in female quality (i.e., after including PC1 as a predictor in a multiple regression), our trade-off model of reproductive life span revealed a negative relationship between IBI_S and RL. That is, females with long life spans had longer surviving birth intervals than those with short life spans, a trade-off that was evident only when accounting for variation in female quality (fig. 4*A*, 4*B*; table 2). Our permutation tests revealed that this trade-off was not an inevitable outcome of the existing data structure (fig. A5). However, this trade-off was not statistically significant when we included outliers (see tables A1, A5).

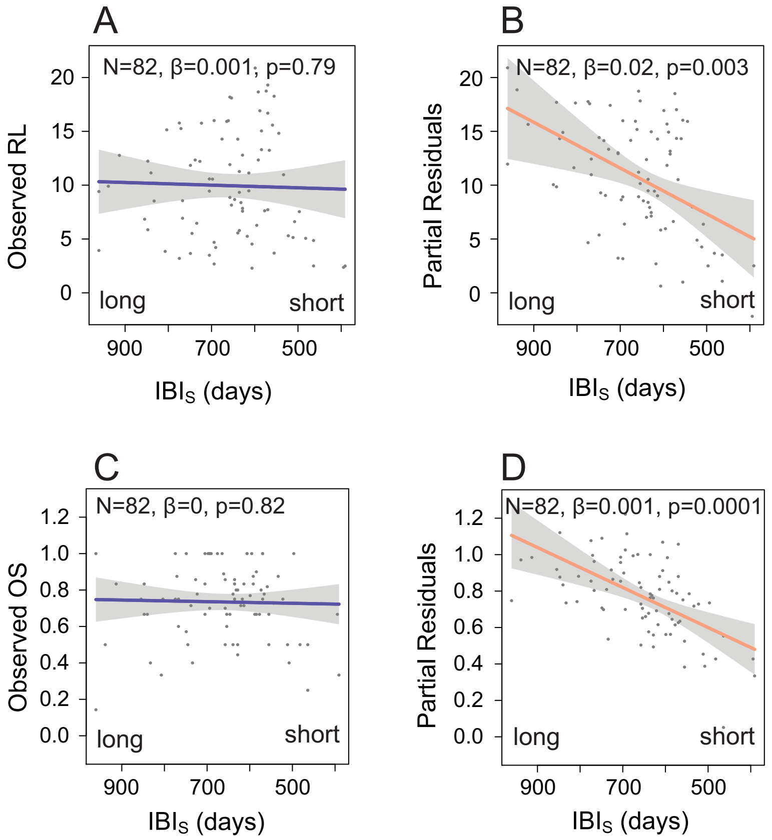


Figure 4: Survival and reproductive costs are apparent after accounting for individual heterogeneity in quality. *A*, Observed population-level relationship between surviving interbirth interval (IBI_S) and reproductive life span (RL). *B*, Population-level relationship between IBI_S and RL after accounting for variation in phenotypic quality. The points in *B* represent the partial residuals from a regression of our quality metric (i.e., first principal component, PC1) against RL, plotted as a function of IBI_S (i.e., average time between birth of an offspring who survived infancy and mother's next live birth). *C*, Observed population-level relationship between IBI_S and proportion of offspring surviving (OS). *D*, Population-level relationship between IBI_S and OS after accounting for variation in quality. The points in *D* represent the partial residuals from a regression of our quality metric (i.e., PC1) against OS, plotted as a function of IBI_S.

Table 2: Results of four trade-off models of the relationships between surviving interbirth interval (IBI_S) and reproductive life span (RL) and between IBI_S and offspring survival (OS), controlling for individual quality

Model, predictor	Effect size (SE)	p
1. RL ~ IBI_S (fig. 4*A*):		
IBI_S	.001 (.004)	.791
2. RL ~ IBI_S + quality score (fig. 4*B*):		
IBI_S	.02 (.007)	.003
Quality score	2.47 (.69)	.0006
3. OS ~ IBI_S (fig. 4*C*):		
IBI_S	0 (1.89e−04)	.815
4. OS ~ IBI_S + quality score (fig. 4*D*):		
IBI_S	.001 (2.67e−04)	.0001
Quality score	.13 (.03)	5.4e−06

Note: The tilde in each model description indicates that the model tests the dependence of the response variable on the predictor variables (listed after the tilde). See table A5 for trade-off models including outliers and using an alternative definition of RL.

Similarly, after controlling for variation in female quality, our trade-off model of offspring survival revealed a negative relationship between IBI_S and OS. That is, females with long intervals after a surviving birth had higher overall rates of offspring survival than those with shorter intervals after a surviving birth (fig. 4*C*, 4*D*; table 2; for results with outliers, see table A5). Again, our permutation test revealed that this trade-off was not an inevitable outcome of the existing data structure (fig. A5).

Maternal Age Affects OS but Not IBI_L

Finally, our GLMM of offspring survival revealed that maternal age strongly influenced offspring survival: older mothers were less successful at producing surviving offspring ($\beta = -0.37$, $p = .018$; fig. 3*A*), as were first time mothers ($\beta = -0.62$, $p = .056$; table A4). In contrast, females showed no statistically significant change in live interbirth intervals with age.

Discussion

We demonstrated considerable variance in lifetime fitness among wild female baboons. As expected for long-lived organisms, individual survival (measured both as survival to first reproduction and length of reproductive life span) was the primary determinant of individual fitness (see also Clutton-Brock 1988; Newton 1989). We also found evidence that both heterogeneity in female quality and trade-offs drive the phenotypic relationships between reproduction and survival in wild baboons. Specifically, female baboons who led long reproductive lives also achieved high rates of offspring survival, indicating early mortality of lower-quality females and suggesting the existence of a quality syndrome among female baboons that promotes the survival of both high-quality females and their offspring. Similar selective disappearance of individuals with lower reproductive success has been documented in other long-term studies (e.g., Weladji et al. 2006; McCleery et al. 2008; Bouwhuis et al. 2009; Hayward et al. 2013). By accounting for individual heterogeneity in phenotypic quality, we also found evidence for two trade-offs that females experience if they produce surviving offspring (as opposed to simply live births) at a relatively high rate: such females (i) die younger and (ii) produce fewer surviving offspring overall. We discuss each of these results in more detail below.

Survival, Reproduction, and Fitness

Sixty-one percent of the variance in LRS in the study population was attributable to individuals who died at or before the average age of first reproduction. We attributed variance in LRS due to these individuals as variance in LRS explained by survival. However, it is possible that some of this variance in LRS is linked to the reproductive potential of an individual. For instance, individuals with below-average reproductive systems, destined to have low fertility, may also tend to be below average in other physiological functions and less likely to survive to reproductive age. Our evidence that variation in female quality drives the relationship between survival and reproduction in adult females lends support to this idea. However, no reproductive phenotypes can be measured for individuals who die before reproducing; they thus represent an invisible fraction of the population with regards to reproductive phenotypes (Grafen 1988).

Among the visible fraction of reproductive phenotypes, survival again explains the majority of the variance in individual fitness. That is, little of the population-wide variance in fitness is explained by differences among individuals in live interbirth interval, even though individuals with shorter live interbirth intervals tend to have higher fitness (fig. 2). Thus, using live interbirth interval (or other similar measures) as proxies for fitness may fail to accurately reflect the ways in which selection is acting on this system. Though these results are consistent with our expectations and the findings of prior studies, we highlight them here because studies in natural populations (including ours) sometimes use reproductive variables as proxies for fitness when investigating environmental and/or genetic sources of variance in fitness (reviewed in Altmann et al. 1988; Kingsolver et al. 2001 [see their table 3]; Altmann and Alberts 2003; Hereford et al. 2004 [see their table 1]; Siepielski et al. 2009 [see their app. S1]; but for illustrative counterexamples, see Tinbergen and Sanz 2004; Morrissey et al. 2012; Bonnet et al. 2017).

Variation in Quality Masks Trade-Offs at the Population Level

In contrast with the predictions of the trade-off hypothesis, we found that females with long reproductive lives had high offspring survival, suggesting that these females were of higher phenotypic quality than the females with short lives and poor offspring survival. We also found statistically significant interindividual variance in live interbirth intervals that was not associated with reproductive life span, suggesting that the best metric of female quality may involve multiple phenotypes. Indeed, using a multivariate index of female quality, we found that higher-quality females performed better in both survival and reproduction than females of lower quality but that females did indeed face survival and reproductive costs of reproduction. Specifically, a 4-month increase in the duration of the surviving interbirth interval (i.e., a slower surviving birth rate by 1 SD of the mean $\mathrm{IBI_S}$; table A2) corresponded to an additional 2.5 years of reproductive life and to an increase in overall offspring survival of about 13% (fig. 4; table A5).

Our study adds to the growing number of mammalian populations in which the effects of individual heterogeneity have been documented to modulate the effects of life-history trade-offs (e.g., Beauplet et al. 2006; Weladji et al. 2008; Hamel et al. 2009*a*; Vedder and Bouwhuis 2018). The multivariate approach we employed here is useful for identifying variation in quality, but as our analysis considered only life-history traits that are generally directly associated with fitness, they do not shed light on the sources of this variation in quality. These observations raise the question, What causes differences in female quality? In cercopithecine primates, female dominance rank is an intuitively appealing explanation for variance in female quality; however, given the system of nepotistic maternal rank inheritance (Lea et al. 2014) and limited evidence of a relationship between dominance rank and life span in our population (Archie et al. 2014), we suggest that while dominance rank may influence female quality (perhaps by providing access to higher value resources), dominance rank alone is not a sufficient causal explanation for variance in female quality.

Another intriguing possible driver of variation in female quality is the early-life environment. Conditions in early life affect life span and/or reproduction in a range of other taxa (e.g., in red-billed choughs: Reid et al. 2003; red deer: Nussey et al. 2007; Mauritius kestrels: Cartwright et al. 2014; humans: Hayward et al. 2014; goshawks: Herfindal et al. 2015; bighorn sheep: Pigeon et al. 2017). In Amboseli baboons, we have shown that early-life conditions affect both survival and reproduction in females (Lea et al. 2015; Tung et al. 2016). We also know from previous analyses that early-life adversity influences adult social connectedness: females with higher levels of early adversity show lower levels of social connectedness to other adult females (Tung et al. 2016). Low social connectedness, in turn, is linked to poor offspring survival and poor maternal survival (Silk et al. 2003; Archie et al. 2014). This set of results suggests that early-life adversity may influence female quality. More work is needed to investigate these and other potential sources of variance in female quality and how they may interact with dominance rank to influence life-history traits.

Stronger Evidence for Senescence in Maternal Competence than in Birth Rate

Our results provide evidence of maternal age-dependent variation in offspring survival, a finding demonstrated in a range of other taxa (e.g., see Kern et al. 2001; Torres et al. 2011; Hayward et al. 2014). However, the dynamics of the relationship between maternal age and offspring survival depend on the biology of the species considered, with evidence in some species suggesting a role for maternal experience in increasing offspring survival with age (e.g., Hastings and Testa 1998) and in other species a role of maternal senescence in decreasing offspring survival with age (e.g., Descamps et al. 2008). The cognitive complexity of baboons combined with the ecological complexity of the environment in which they live strongly suggests a role for maternal experience in promoting offspring survival (Pusey 2012; see also Muller et al. 2006). The current study is consistent with these results, as nulliparous mothers have lower offspring survival than more experienced mothers. However, the current study also suggests that maternal competence declines as females age, resulting in lower offspring survival among older mothers. Notably, offspring survival in our study decreases at a similar rate for mothers of both short and long life spans, indicating that maternal competence declines as the probability of maternal survival declines (fig. 3).

In contrast with the results for offspring survival, we found no evidence of a linear decline in live birth rate with maternal age (table A4), although reproductive senescence has been widely documented in a range of other taxa (for recent reviews, see Nussey et al. 2013; Lemaitre and Gaillard 2017; Gesquiere et al. 2018). Our evidence for reproductive senescence in the Amboseli baboons is ambiguous, as other work in the population has detected evidence of linear and/or quadratic age effects on some reproductive phenotypes (Beehner et al. 2006; Altmann et al. 2010; Alberts et al. 2013; Gesquiere et al. 2018), and the current study documents potential for age-related decline in maternal competence. These mixed results demonstrate the pressing need for further, detailed investigations into both the age dependence of live interbirth intervals and the possibility that individual quality contributes to variation in the age at onset or the rate of reproductive senescence (e.g., see Nussey et al. 2007; Bouwhuis et al. 2010).

Our results motivate future work to dissect the contributions of genetic and environmental differences among individuals to the phenotypic variation we have observed here. Such work would be feasible using the animal model (Lynch and Walsh 1998; Kruuk 2004; Wilson et al. 2010), which would also allow for the investigation of genetic contributions to variance in female quality and the estimation of the genetic correlation between our traits of interest and fitness (Rausher 1992; Morrissey et al. 2010). As investigation into the physiological, molecular, and genetic mechanisms underlying life-history traits increases, we highlight the importance of considering heterogeneity in individual quality—both in deciding where to look for the mechanisms of trade-offs (probably in individuals of low quality) and as a field of investigation in its own right.

Acknowledgments

E.M.M. was supported by National Science Foundation (NSF) grant IOS 1501971; in addition, we gratefully acknowledge the NSF and the National Institute on Aging (NIA) for support of the long-term research. In the past decade in particular, we acknowledge support from NSF grants DEB 0846286, DEB 0846532, DEB 0919200, IOS 0919200, IOS 1053461, and IOS 1456832 and NIA grants R01AG053330, R01AG053308, R01AG034513, P01AG031719, and R21AG049936. For shorter-term support at various times over the years, we thank the Princeton Center for the Demography of Aging (P30 AG024361), the Chicago Zoological Society, the Max Planck Institute for Demographic Research, the Leakey Foundation, and the National Geographic Society. We are particularly grateful to an anonymous donor who, since 2014, has provided critical financial support for the long-term field site in Amboseli. For cooperation and assistance in Kenya, we thank the Kenya Wildlife Services, Institute of Primate Research, National Museums of Kenya, National Council for Science and Technology, members of the Amboseli-Longido pastoralist communities, Tortilis Camp, Ker & Downey Safaris, Air Kenya, and Safarilink. A number of people contributed to the long-term data collection over the years, and we are grateful to all of them for their dedication and contributions. Particular thanks go to the Amboseli Baboon Project long-term field team (R. S. Mututua, S. Sayialel, and J. K. Warutere) and to V. Somen and T. Wango for their assistance in Nairobi. We are grateful to Karl Pinc for his contributions to the development of Babase, the Baboon Project database. We also thank numerous database managers over the years, particularly D. Onderdonk, C. Markham, T. Fenn, L. Maryott, P. Onyango, N. Learn, and J. Gordon. We thank Jean-Michel Gaillard, Anne Loison, Nigel G. Yoccoz, and two anonymous reviewers for exceptionally helpful comments on the manuscript during the editorial process. This research was approved by the Institutional Animal Care and Use Committee at Duke University, Princeton University, and University of Notre Dame and adhered to all the laws and guidelines of Kenya. For a complete set of acknowledgments of funding sources, logistical assistance, and data collection and management, please visit http://amboselibaboons.nd.edu/acknowledgements/.

Literature Cited

Alberts, S. C., and J. Altmann. 2001. Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. American Journal of Primatology 53:139–154.

———. 2003. Matrix models for primate life history analysis. Pages 66–102 *in* P. M. Kappeler and M. Pereira, eds. Primate life history and socioecology. University of Chicago Press, Chicago.

———. 2012. The Amboseli Baboon Research Project: themes of continuity and change. Pages 261–288 *in* P. M. Kappeler and D. Watts, eds. Long-term field studies of primates. Springer, Berlin.

Alberts, S. C., J. Altmann, D. K. Brockman, M. Cords, L. M. Fedigan, A. Pusey, T. S. Stoinski, Karen B. Strier, William F. Morris, and Anne M. Bronikowski. 2013. Reproductive aging patterns in primates reveal that humans are distinct. Proceedings of the National Academy of Sciences of the USA 110:13440–13445.

Altmann, J., and S. C. Alberts. 2003. Intraspecific variability in fertility and offspring survival in a nonhuman primate: behavioral control of ecological and social sources. Pages 140–169 *in* K. W. Watcher and R. A. Bulatao, eds. Offspring: the biodemography of fertility and family behavior. National Academy, Washington, DC.

Altmann, J., S. A. Altmann, and G. Hausfater. 1978. Primate infant's effects on mother's future reproduction. Science 201:1028–1029.

Altmann, J., L. Gesquiere, J. Galbany, P. O. Onyango, and S. C. Alberts. 2010. Life history context of reproductive aging in a wild primate model. Annals of the New York Academy of Sciences 1204:127–138.

Altmann, J., G. Hausfater, and S. A. Altmann. 1988. Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). Pages 403–418 *in* T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.

Altmann, S. A. 1973. The pregnancy sign in savannah baboons. Journal of Zoo Animal Medicine 4:8–12.

———. 1991. Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. Proceedings of the National Academy of Sciences of the USA 88:420–423.

———. 1998. Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago.

Archie, E. A., J. Tung, M. Clark, J. Altmann, and S. C. Alberts. 2014. Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. Proceedings of the Royal Society B 281. https://doi.org/10.1098/rspb.2014.1261.

Arnold, S. 1983. Sexual selection: the interface of theory and empiricism. Pages 67–107 *in* P. Bateson, ed. Mate choice. Cambridge University Press, Cambridge.

Bates, D., M. Machler, B. M. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beauplet, G., C. Barbraud, W. Dabin, C. Kussener, and C. Guinet. 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. Oikos 112:430–441.

Beehner, J. C., N. Nguyen, E. O. Wango, S. C. Alberts, and J. Altmann. 2006. The endocrinology of pregnancy and fetal loss in wild baboons. Hormones and Behavior 49:688–699.

Berman, M., J. M. Gaillard, and H. Weimerskich. 2009. Contrasted patterns of age-specific reproduction in long-lived seabirds. Proceedings of the Royal Society B 276:375–382.

Blomberg, E. J., J. S. Sedinger, D. V. Nonne, and M. T. Atamian. 2013. Seasonal reproductive costs contribute to reduced survival of female greater sage-grouse. Journal of Avian Biology 44:149–158.

Bonnet, T., P. Wandeler, G. Camenishch, and E. Postma. 2017. Bigger is fitter? quantitative genetic decomposition of selection reveals an adaptive evolutionary decline of body mass in a wild rodent population. PLoS Biology 15:e1002592.

Bouwhuis, S., A. Charmantier, S. Verhulst, and B. C. Sheldon. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. Journal of Animal Ecology 79:1251–1261.

Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. Proceedings of the Royal Society B 276:2769–2777.

Brommer, J. E., L. Gustafsson, H. Pietiäinen, and J. Merilä. 2004. Single-generation estimates of individual fitness as proxies for long-term genetic contribution. American Naturalist 163:505–517.

Brommer, J. E., J. Merilä, and H. Kokko. 2002. Reproductive timing and individual fitness. Ecology Letters 5:802–810.

Brown, D. 1988. Components of lifetime reproductive success. Pages 439–453 *in* T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.

Cam, E., J. E. Hines, J. Y. Monnat, J. D. Nichols, and E. Danchin. 1998. Are adult nonbreeders prudent parents? the Kittiwake model. Ecology 79:2917–2930.

Cam, E., and J. Y. Monnat. 2000. Apparent inferiority of first-time breeders in the Kittiwake: the role of heterogeneity among age classes. Journal of Animal Ecology 69:380–394.

Cartwright, S. J., M. A. C. Nicoll, C. G. Jones, V. Tatayah, and K. Norris. 2014. Anthropogenic natal environmental effects on life histories in a wild bird population. Current Biology 24:536–540.

Cheverud, J. 1984. Evolution by kin selection: a quantitative genetic model illustrated by maternal performance in mice. Evolution 38:766–777.

Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago.

Coale, A. 1972. The growth and structure of human populations. Princeton University Press, Princeton, NJ.

Cubaynes, S., P. F. Doherty Jr., E. A. Schreiber, and O. Gimenez. 2011. To breed or not to breed: a seabird's response to extreme climatic events. Biology Letters 7:303–306.

Descamps, S., S. Boutin, D. Berteaux, and J. Gaillard. 2008. Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. Oikos 117:1406–1416.

Descamps, S., S. Boutin, A. G. McAdam, D. Berteaux, and J.-M. Gaillard. 2009. Survival costs of reproduction vary with age in North American red squirrels. Proceedings of the Royal Society B 276:1129–1135.

Descamps, S., J. Gaillard, S. Hamel, and N. G. Yoccoz. 2016. When relative allocation depends on total resource acquisition: implication for the analysis of trade-offs. Journal of Evolutionary Biology 29:1860–1866.

Gaillard, J., M. Festa-Bianchet, D. Delorme, and J. Jorgenson. 2000. Body mass and individual fitness in female ungulates: bigger is not always better. Proceedings of the Royal Society B 267:471–477.

Gesquiere, L., J. Altmann, E. Archie, and S. Alberts. 2018. Interbirth intervals in wild baboons: environmental predictors and hormonal correlates. American Journal of Physical Anthropology 166:107–126.

Gesquiere, L. R., E. O. Wango, S. C. Alberts, and J. Altmann. 2007. Mechanisms of sexual selection: sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. Hormones and Behavior 51:114–125.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. Pages 454–471 *in* T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.

Hamel, S., S. D. Côté, and M. Festa-Bianchet. 2010*a*. Maternal characteristics and environment affect the costs of reproduction in female mountain goats. Ecology 91:2034–2043.

Hamel, S., S. D. Côté, J.-M. Gaillard, and M. Festa-Bianchet. 2009*a*. Individual variation in reproductive costs of reproduction: high-quality females always do better. Journal of Animal Ecology 78: 143–151.

Hamel, S., J. Gaillard, M. Festa-Bianchet, and S. Cote. 2009*b*. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90:1981–1995.

Hamel, S., J. M. Gaillard, N. G. Yoccoz, A. Loison, C. Bonenfant, and S. Descamps. 2010*b*. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. Ecology Letters 13:915–935.

Hamel, S., N. G. Yoccoz, and J. Gaillard. 2014. A standardized approach to estimate life history tradeoffs in evolutionary ecology. Oikos 123:151–160.

———. 2017. Assessing variation in life-history tactics within a population using mixture regression models: a practical guide for evolutionary ecologists. Biological Reviews 92:754–775.

Hastings, K. K., and J. W. Testa. 1998. Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. Journal of Animal Ecology 67:722–740.

Hayward, A. D., K. U. Mar, M. Lahdenperä, and V. Lummaa. 2014. Early reproductive investment, senescence and lifetime reproductive success in female Asian elephants. Journal of Evolutionary Biology 27:772–783.

Hayward, A. D., I. Nenko, and V. Lummaa. 2015. Early-life reproduction is associated with increased mortality risk but enhanced lifetime fitness in pre-industrial humans. Proceedings of the Royal Society B 282:20143053.

Hayward, A. D., A. J. Wilson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2013. Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. Functional Ecology 27:184–195.

Hereford, J., T. F. Hansen, and D. Houle. 2004. Comparing strengths of directional selection: how strong is strong? Evolution 58:2133–2143.

Herfindal, I., M. Van De Pol, J. T. Nielsen, B. Sæther, and A. P. Møller. 2015. Climatic conditions cause complex patterns of covariation between demographic traits in a long-lived raptor. Journal of Animal Ecology 84:702–711.

Kern, S., M. Ackermann, S. C. Stearns, and T. J. Kawecki. 2001. Decline in offspring viability as a manifestation of aging in *Drosophila melanogaster*. Evolution 55:1822–1831.

King, E. G., D. A. Roff, and D. J. Fairbairn. 2011. Trade-off acquisition and allocation in *Gryllus firmus*: a test of the Y model. Journal of Evolutionary Biology 24:256–264.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. American Naturalist 157:245–261.

Kooyers, N. J., B. James, and B. K. Blackman. 2017. Competition drives trait evolution and character displacement between *Mimulus* species along an environmental gradient. Evolution 71:1425–1427.

Krakauer, A. H. 2005. Kin selection and cooperative courtship in wild turkeys. Nature 434:69–72.

Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the "animal model." Philosophical Transactions of the Royal Society B 359:873–890.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Langeloh, L., J. Behrmann-Godel, and O. Seppälä. 2017. Natural selection on immune defense: a field experiment. Evolution 71:227–237.

Lea, A. J., J. Altmann, S. C. Alberts, and J. Tung. 2015. Developmental constraints in a wild primate. American Naturalist 185:809–821.

Lea, A. J., N. H. Learn, M. J. Theus, J. Altmann, and S. C. Alberts. 2014. Complex sources of variance in female dominance rank in a nepotistic society. Animal Behaviour 94:87–99.

Lemaitre, J. F., and J. Gaillard. 2017. Reproductive senescence: new perspectives in the wild. Biological Reviews 92:2182–2199.

Lenski, R. E., and P. M. Service. 1982. The statistical analysis of population growth rates calculated from schedules of survivorship and fecundity. Ecology 63:655–662.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, MA.

McCleery, R., C. Perrins, B. Sheldon, and A. Charmantier. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. Proceedings of the Royal Society B 275:963–970.

McGraw, J. B., and H. Caswell. 1996. Estimation of individual fitness from life-history data. American Naturalist 147:47–64.

McLean, E., E. A. Archie, and S. Alberts. 2019. Data from: Lifetime fitness in wild female baboons: trade-offs and individual heterogeneity in quality. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.fv3t300.

Morrissey, M. B., L. E. B. Kruuk, and A. J. Wilson. 2010. The danger of applying the breeder's equation in observational studies of natural populations. Journal of Evolutionary Biology 23:2277–2288.

Morrissey, M. B., D. J. Parker, P. Korsten, J. M. Pemberton, L. E. B. Kruuk, and A. J. Wilson. 2012. The prediction of adaptive evolution: empirical application of the secondary theorem of selection and comparison to the breeder's equation. Evolution 66:2399–2410.

Muller, M. N., M. E. Thompson, and R. W. Wrangham. 2006. Male chimpanzees prefer mating with old females. Current Biology 16:2234–2238.

Newton, I. 1989. Lifetime reproduction in birds. Academic Press, Toronto.

Nussey, D. H., H. Froy, J. F. Lemaitre, J. Gaillard, and S. N. Austad. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. Ageing Research Reviews 12:214–225.

Nussey, D. H., L. E. B. Kruuk, A. Morris, and T. H. Clutton-Brock. 2007. Environmental conditions in early life influence ageing rates in a wild population of red deer. Current Biology 17:1000–1001.

Oli, M. K., G. R. Hepp, and R. A. Kennamer. 2002. Fitness consequences of delayed maturity in female wood ducks. Evolutionary Ecology Research 4:563–576.

Olijnyk, A. M., and W. A. Nelson. 2013. Positive phenotypic correlations among life-history traits remain in the absence of differential resource ingestion. Functional Ecology 27:165–172.

Pigeon, G., M. Festa-Bianchet, and F. Pelletier. 2017. Long-term fitness consequences of early environment in a long-lived ungulate. Proceedings of the Royal Society B 284:20170222.

Pilastro, A., G. Tavecchia, and G. Marin. 2003. Long living and reproduction skipping in the fat dormouse. Ecology 84:1784–1792.

Pusey, A. 2012. Magnitude and sources of variation in female reproductive performance. Pages 343–366 *in* J. C. Mitani, J. Call, P. M. Kappeler, R. Palombit, and J. B. Silk, eds. Evolution of primate societies. University of Chicago Press, Chicago.

Rausher, M. 1992. The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. Evolution 46:616–626.

Reid, J. M., P. Arcese, G. Bocedi, A. B. Duthie, M. E. Wolak, and L. F. Keller. 2015. Resolving the conundrum of inbreeding depression but no inbreeding avoidance: estimating sex-specific selection on inbreeding by song sparrows (*Melospiza melodia*). Evolution 69:2846–2861.

Reid, J. M., E. Bignal, S. Bignal, D. McCracken, and P. Monaghan. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. Journal of Affective Disorders 72:765–776.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267.

Robbins, A. M., T. Stoinski, K. Fawcett, and M. M. Robbins. 2011. Lifetime reproductive success of female mountain gorillas. American Journal of Physical Anthropology 146:582–593.

Roff, D. A. 2002. Life history evolution. Sinauer, Sunderland, MA.

Sanz-Aguilar, A., G. Tavecchia, R. Pradel, E. Minguez, and D. Oro. 2008. The cost of reproduction and experience-dependent vital rates in a small petrel. Ecology 89:3195–3203.

Siepielski, A. M., J. D. Dibattista, and S. M. Carlson. 2009. It's about time: the temporal dynamics of phenotypic selection in the wild. Ecology Letters 12:1261–1276.

Silk, J. B., S. C. Alberts, and J. Altmann. 2003. Social bonds of female baboons enhance infant survival. Science 302:1231–1234.

Stearns, S. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.

Tanner, J., J. Ward, R. Shaw, and M. Bee. 2017. Multivariate phenotypic selection on a complex sexual signal. Evolution 71:1742–1754.

Théoret-Gosselin, R., S. Hamel, and S. D. Côté. 2015. The role of maternal behavior and offspring development in the survival of mountain goat kids. Oecologia 178:175–186.

Tinbergen, J. M., and J. J. Sanz. 2004. Strong evidence for selection for larger brood size in a great tit population. Behavioral Ecology 15:525–533.

Torres, R., H. Drummond, and A. Velando. 2011. Parental age and lifespan influence offspring recruitment: a long-term study in a seabird. PLoS ONE 6:e27245.

Tung, J., E. A. Archie, J. Altmann, and S. C. Alberts. 2016. Cumulative early life adversity predicts longevity in wild baboons. Nature Communications 7:11181.

Tung, J., M. J. E. Charpentier, D. A. Garfield, J. Altmann, and S. C. Alberts. 2008. Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population. Molecular Ecology 17:1998–2011.

Van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. American Naturalist 167:766–773.

Vedder, O., and S. Bouwhuis. 2018. Heterogeneity in individual quality in birds: overall patterns and insights from a study on common terns. Oikos 127:719–727.

Viallefont, A., F. Cooke, and J. D. Lebreton. 1995. Age-specific costs of first-time breeding. Auk 112:67–76.

Visser, M. E., and C. M. Lessells. 2001. The costs of egg production and incubation in great tits (*Parus major*). Proceedings of the Royal Society B 268:1271–1277.

Weladji, R. B., J. Gaillard, N. G. Yoccoz, Ø. Holand, A. Mysterud, A. Loison, M. Nieminen, and N. C. Stenseth. 2006. Good reindeer mothers live longer and become better in raising offspring. Proceedings of the Royal Society B 273:1239–1244.

Weladji, R. B., A. Loison, J. M. Gaillard, Ø. Holand, A. Mysterud, N. G. Yoccoz, M. Nieminen, and N. C. Stenseth. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia 156:237–247.

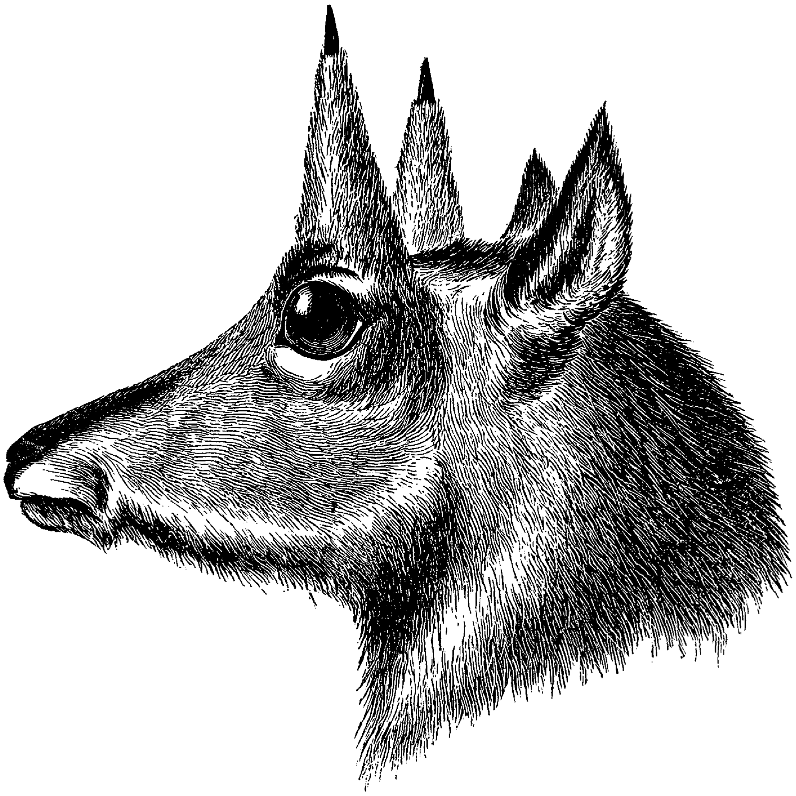
Wilson, A. J., and D. H. Nussey. 2010. What is individual quality? an evolutionary perspective. Trends in Ecology and Evolution 25:207–214.

Wilson, A. J., J. G. Pilkington, J. M. Pemberton, D. W. Coltman, A. D. J. Overall, K. A. Byrne, and L. E. B. Kruuk. 2005. Selection on mothers and offspring: whose phenotype is it and does it matter? 59:451–463.

Wilson, A. J., D. Reale, M. N. Clements, M. M. Morrissey, E. Postma, C. A. Walling, L. E. B. Kruuk, and D. H. Nussey. 2010. An ecologist's guide to the animal model. Journal of Animal Ecology 79:13–26.

Wolf, J. B., and M. J. Wade. 2001. On the assignment of fitness to parents and offspring: whose fitness is it and when does it matter? Journal of Evolutionary Biology 14:347–356.

Associate Editor: Jean-Michel Gaillard
Editor: Alice A. Winn



"The animal, from which I have made the drawings, is now developing his fourth pair of horns. The second pair of horns were about three inches longer than the first, and the same difference existed between the second and third pair." From "The Prong-Horn Antelope" by W. J. Hays (*The American Naturalist*, 1868, 2:131–133).