Influence of Early Reproductive Success on Longevity and Late Reproductive Success in an Alpine Ungulate

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ABSTRACT: The life-history theories of aging predict lifetime trade-offs between early reproductive allocation and late-life survival, reproduction, or both components of fitness. Recent studies in wild populations have found evidence for these early-late life trade-offs, but rarely have they been found across multiple traits while exploring the additional effects of variation in environmental conditions and individual quality. Benefiting from longitudinal data on adult female mountain goats (*Oreamnos americanus*), we investigated the influence of age at first reproduction (AFR) and early reproductive success (ERS) on longevity, late reproductive success, and senescence rates while accounting for the influence of natal environmental conditions and individual quality. Contrary to predictions, we did not find evidence for early-late life trade-offs. Instead, an earlier AFR and a greater ERS had positive but weak direct effects on late reproductive success. Natal population density, however, was the strongest determinant of all life-history traits, having a direct negative effect on female longevity, late reproductive success, AFR, and ERS. Although natal density reduced the probability of annual reproduction and annual survival during adulthood, higher allocation to reproduction in early life and poorer natal conditions did not lead to accelerated rates of senescence during adulthood. The results of this investigation provide an integrated picture of early-late life trade-offs, underscoring the importance of accounting for environmental conditions because of their potentially strong implications for population dynamics.

Keywords: life history, trade-offs, senescence, reproduction costs, environmental variability, ungulates.

Introduction

Compromise is a central organizing principle in life-history theory (Stearns 1992). Organisms must partition what is usually a limited supply of resources between three main competing life functions: reproduction, growth, and survival (Gadgil and Bossert 1970; Stearns 1992). Williams (1966) was the first to frame reproduction in terms of its costs and benefits. Empirical evidence supports the pervasive presence of fitness costs of reproduction, which range from reduced maternal survival in short-lived species, such as the bank vole (*Clethrionomys glareolus*; Koivula et al. 2003), to the reduced probability of subsequent reproduction, such as the reproductive pauses observed in long-lived species like ungulates (reindeer [*Rangifer tarandus*; Cameron 1994], red deer [*Cervus elaphus*; Moyes et al. 2006], and mountain goats and bighorn sheep [*Ovis canadensis*; Hamel et al. 2009a]). In addition, lifetime costs of reproduction may appear over the long term to be a result of the physiological and metabolic deterioration that accompanies advanced age in organisms (Kirkwood and Rose 1991).

The principal evolutionary explanations for the persistence of these age-related declines in survival and fecundity, formally known as senescence, consider this process an adverse consequence of natural selection promoting early reproductive investment over late-life reproduction and survival (Kirkwood 1977; Kirkwood and Rose 1991). The antagonistic pleiotropy hypothesis advanced by Williams (1957) posits that alleles selected for beneficial fitness effects early in life may have harmful effects later in life and that these harmful effects cannot be reined in by the countervailing forces of selection (Medawar 1952). The disposable soma hypothesis, which originated from physiological ecology, contends that resources devoted to reproduction come at the price of reduced somatic repair (Kirkwood and Rose 1991). Both of these "life-history theories of aging" therefore predict the presence of early-late life trade-offs between fitness components due to the costs of early reproduction (Reed et al. 2008; Lemaître et al. 2015).

Indirect selection for increased longevity in *Drosophila melanogaster* is associated with a reduction in early fecundity (Rose 1984). Subsequent experiments using a direct-selection design for longevity demonstrated a decline in general reproduction, including early-life fecundity (Zwaan et al. 1995), thereby providing experimental evidence for early-late

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life trade-offs in model organisms. Environmental conditions, however, are likely to affect resource availability and are thus expected to influence the form and extent (i.e., the rate of senescent declines) of the trade-offs in natural populations (Nussey et al. 2013). The prevailing environmental state may therefore influence how a female allocates resources to either reproduction or somatic maintenance, ultimately giving rise to variation in the rates of aging (Bouwhuis et al. 2010). Early environmental conditions, such as population density in the year of birth, are of particular interest, as they may have short-term reproductive consequences (e.g., on natal brood size) as well as long-term implications for fitness (Nussey et al. 2007, 2013; Bouwhuis et al. 2010). Early-life conditions experienced by an individual might also be used as a cue of their future somatic state, leading to the evolution of predictive adaptive responses (PARs; Gluckman et al. 2005; Nettle et al. 2013). The PAR hypothesis therefore predicts that the advantage of a developmental trajectory anticipating the future environment will occur at a later stage in life and that it will be advantageous only if the anticipated future environment matches the actual future environment (Gluckman et al. 2005; Monaghan 2008). Heterogeneity in individual quality may also obscure predicted life-history trade-offs at the population level due to the selective disappearance of lower-quality individuals in wild populations (Reid et al. 2003; Nussey et al. 2008). Indeed, the relative amount of variance in resource acquisition and allocation among individuals of a population affects whether the relationship between two life-history traits is negative or positive (van Noordwijk and de Jong 1986), emphasizing the need to account for heterogeneity in environmental and individual conditions when studying life-history trade-offs.

Rigorous longitudinal studies in natural populations have recently confirmed the existence of early-late life trade-offs (evidence in 21 of 26 studies reviewed by Lemaître et al. 2015), overcoming the methodological obstacles associated with variation in environmental conditions and individual quality. In North American red squirrels (*Tamiasciurus hudsonicus*), for example, age at first reproduction (AFR) was influenced by year of birth, with years of high resource availability linked to an early AFR (Descamps et al. 2006). This reproductive tactic carried survival costs over the short and long term but conferred greater lifetime reproductive success compared with that of late breeders (Descamps et al. 2006). The recent review by Lemaître et al. (2015), however, underscores the rather limited number of studies on this topic, in particular those concerning the influence of natal environmental conditions on late-life traits. The review also demonstrates that early-late life trade-offs can be heterogeneous among the traits studied, highlighting the importance of assessing lifetime trade-offs across multiple traits.

Our investigation aims to fill this current gap in knowledge by providing an integrated picture of early-late life trade-offs, benefiting from the high-quality longitudinal data set on mountain goats at Caw Ridge, Alberta (Festa-Bianchet and Côté 2008). Previous studies of the females of this population characterized the annual fitness costs of reproduction (Hamel et al. 2010*a*, 2011). Our research builds on this knowledge by focusing on the lifetime costs of two early-life traits, the onset of reproduction (AFR) and early reproductive success (ERS), while accounting for the effects of early environmental conditions and individual quality. We used confirmatory path analysis to examine the causal patterns of these variables through their direct and indirect effects on longevity and late reproductive success. Furthermore, we assessed whether AFR, ERS, and early environmental conditions affected the rate of reproductive and actuarial senescence. While most studies assessed early-late life trade-offs using one component of fitness (Hayward et al. 2014; Lemaître et al. 2015), our study profits from 27 years of data on both late-life reproduction and late-life survival, thereby capturing both fitness components (Dawkins 1976; Howard 1979).

On the basis of the life-history theories of aging, which attribute senescent declines to costs of reproduction during early adulthood, we expected that AFR and ERS would have a direct negative influence on longevity (an indirect measure of senescence corresponding to survival), late reproductive success, and senescence rates. Furthermore, the population density of mountain goats at Caw Ridge has fluctuated considerably over the course of the study, and we therefore predicted that a higher natal population density would negatively affect a female's longevity, late reproductive success, and senescence rates due to heightened resource competition. We expected the influence of natal population density to occur through both direct and indirect effects on individual quality, AFR, and ERS rather than independently of early-life allocation to reproduction. Finally, female mountain goats adopt a conservative reproductive tactic that favors their own survival over that of their offspring (Hamel et al. 2010*a*). As capital breeders, mountain goats finance their reproduction through stored capital in the form of body reserves accumulated prior to the winter gestation period (Stephens et al. 2009). The amount that is stored thereby affects the quantity of resources that are available for the mother to allocate to her young (Festa-Bianchet et al. 1998; Hamel et al. 2012). Female dominance also has a considerable positive influence on reproductive success (Côté and Festa-Bianchet 2001*b*). Consequently, we predicted that female quality, defined as a composite index of social rank and body mass, would have a positive effect on longevity and late reproductive success. We expected this effect to be both direct and indirect, through its influence on AFR and ERS, because individuals of higher quality should be in better condition and possess more efficient physiological mechanisms to support somatic maintenance and reproduction at all stages of life (Hamel et al. 2009*b*).

Methods

Study Area and Population

We studied mountain goats at Caw Ridge (54°N, 119°W), located in the foothills of the Canadian Rocky Mountains in west-central Alberta. Goats use an area of approximately 28 km² of alpine tundra and subalpine open forest ranging from 1750 to 2170 m in elevation. The climate is subarctic-arctic with snowfall that can occur during any month (Festa-Bianchet and Côté 2008). Major predators include grizzly bears (*Ursos arctos*), wolves (*Canis lupus*), and cougars (*Puma concolor*). In addition, black bears (*Ursus americanus*), coyotes (*Canis latrans*), wolverines (*Gulo gulo*), and golden eagles (*Aquila chrysaetos*) represent potential predators (Festa-Bianchet and Côté 2008).

Beginning in 1988, we captured goats using remote-controlled box traps baited with salt and marked the goats with color-coded ear tags and visual collars (Festa-Bianchet and Côté 2008). We aged goats captured as adults by counting their horn annuli, a method that is reliable up to 7 years of age (Festa-Bianchet and Côté 2008). We recorded goat masses (±0.5 kg) during captures with a spring scale as well as with use of three remote electronic platform scales baited with salt (Festa-Bianchet and Côté 2008). Since 1993, 98% of the population has been marked, excluding kids to avoid maternal abandonment (Côté et al. 1998). The initial total population size of approximately 80 goats in 1988 peaked in June 2008 at just over 160 and has since declined to 52 individuals as of June 2015.

Field Observations

From mid-May through mid-September between 1988 and 2015, we collected observational data using spotting scopes (15–45×) almost daily. In the spring (mid-May to mid-June), females isolate themselves to give birth to singletons. Births are highly synchronized, with about 80% of births occurring within a 2-week period (Côté and Festa-Bianchet 2001*a*). During this period, we intensively surveyed the ridge to determine the parturition success (birth or no birth) of all females through observations of the presence/absence of a kid as well as nursing behavior. These observations were continued throughout the field season to determine the survival of offspring and, hence, the weaning success (kid survival to September 15) of all females each year. We determined the annual survival of females by their presence in the study area the following summer as of June 1. Annual survival was accurate because there has been no known instance of emigration/immigration by adult females or kids in this population, and adult females or kids missing for 1 year have never been resighted (Festa-Bianchet and Côté 2008).

To determine a female's social rank, we observed agonistic interactions ad lib. between adult females (≥3 years old;

Altmann 1974). For each interaction, we recorded the identity of the initiator, the winner, and the loser. For each adult female dyad, we designated a female as dominant if she won more than 50% of the interactions (Côté 2000). Each year, we established a dominance matrix of adult females using the de Vries linear ordering procedure (de Vries 1998). Because the matrix size varied each year depending on the number of adult females present (N_i), the social ranks were transformed to vary from 0 (subordinate) to 1 (dominant) using the formula $1 - (\text{rank}/N_i)$ (Côté 2000). Since age is highly correlated with social rank in mountain goats ($r > 0.90$; Côté 2000), we used the residuals from the polynomial regression of social rank on age to calculate female age-specific social rank each year, hereafter referred to as social rank (Hamel et al. 2009*b*).

Measures of Reproductive Success and Longevity

We monitored female mountain goats from birth to death and therefore obtained the longevity, AFR, annual parturition success, and annual weaning success for almost all females. For females that reached adulthood, longevity averaged 9 years, ranging from 3 to 18 years ($n = 142$). AFR occurred between 3 and 8 years of age, with most cases (79%) occurring at age 4 or 5 years. Because AFR is one of the major determinants of fitness (Pärt 1995), we used it as a measure of the timing of ERS, with lower values representing females that began their reproductive allocation earlier than other females. Moreover, females reproducing between the ages of 3 and 6 years, prior to attaining asymptotic mass at approximately 7 years of age, face especially high energetic demands because they must allocate resources to both reproduction and growth (Côté and Festa-Bianchet 2001*b*). We therefore defined ERS as the total parturition success during the period of resource allocation to both reproduction and growth–that is, between age 3 and 6 years—and late reproductive success as the total number of births from age 7 years until death (for details on other measures of early and late reproductive success considered, see the appendix). Since lifetime reproductive success and longevity are highly correlated in long-lived species such as mountain goats (Gaillard and Yoccoz 2003), late reproductive success was highly correlated with longevity ($r = 0.91$). We therefore regressed late reproductive success on longevity to obtain a metric of late reproductive success that was independent of longevity. Higher values represented females that produced more offspring later in life compared with females that survived to the same age.

Environmental Conditions

To account for the influence of environmental conditions on the reproductive success and longevity of each female,

we considered two measures of population density based on the total number of goats on June 1. First, we calculated the median population density during the ERS period from ages 3 through 6 years, which reflects the conditions during the time females allocate resources to both reproduction and growth. Second, we calculated the population density in the year of a female's birth, which represents the conditions during a female's early growth and development. Because the two measures were highly correlated ($r = 0.63$) and hence could not be included in the same model, we retained density in the year of birth, hereafter called density at birth, to take cohort effects into consideration (Gaillard et al. 2003). Using median density during the ERS period produced similar results.

Female Quality

Earlier studies of this mountain goat population demonstrated a quality effect on the reproductive success of females, with heavier and dominant females performing consistently better than lighter and subordinate females (Côté and Festa-Bianchet 2001b; Hamel et al. 2009b). To account for this effect, we used an index of female quality during ERS derived from an orthogonal regression between social rank and body mass (as developed by Hamel et al. 2009b). Because female social rank varied slightly from year to year, we computed the median social rank for each female during the ERS period, that is, between ages 3 and 6 years. To obtain the median body mass for each female during the ERS period, we first adjusted all masses to July 15 because goat masses were measured at different times during the summer. We used age-specific seasonal growth curves based on linear mixed models (LMMs) with female identity and year as random intercepts and Julian day as a covariate (see Hamel et al. 2010a). Because not all females were measured every year between ages 3 and 6 years, we then used an interannual growth model (a LMM including female identity and year as random intercepts and female age and reproductive status as covariates) to predict the mass of each female at age 5 years based on all of her masses collected between ages 3 and 6 years. We thus obtained between one and four predicted masses at age 5 years for each female and used the median prediction as the median body mass during ERS. All analyses were performed in R (ver. 3.2.2; R Development Core Team 2015). We used the lme4 function in the lme4 package for all LMMs (Bates et al. 2015).

Subsequently, we performed an orthogonal regression using the median social rank and median body mass of each female during the ERS period. While ordinary least squares regression minimizes the sum of the squared differences between the observed and predicted values along the Y-axis, orthogonal or total least squares regression does this for both the X- and the Y-axis (de Groen 1996). A fitted orthogonal

regression line thereby corresponds to the first axis of a principal component analysis (PCA) using two variables. We thus performed a PCA on median social rank and median body mass using the function imputePCA from the missMDA package (Husson and Josse 2015), which predicted the PCA scores for the missing values (Nakagawa and Freckleton 2011). The first axis of the PCA explained 75% of the variance between social rank and body mass. We used the scores of this axis as an index of female quality during the ERS period, with higher values representing females that were heavier and more dominant than females with lower values.

Statistical Analyses

Influence of Early Reproductive Allocation on Longevity and Late Reproductive Success

Twenty-nine of 142 females never reproduced during their lifetime. The longevity of these females averaged 4 years (ranging from 3 to 11 years), compared with 11 years for females that did reproduce (ranging from 4 to 18 years). These females could not be analyzed in the complete analysis looking at the influence of early reproductive allocation on both longevity and late reproductive success (see path analysis below) because the information on their AFR was missing and their late reproductive success was 0 by default (i.e., 0 for these females does not have the same meaning as 0 for females that survived to late age but did not reproduce). We therefore first analyzed whether longevity was influenced by early reproductive allocation using reproduction as a binary predictor, that is, comparing females that never reproduced to those that reproduced at least once. We used a generalized linear model (GLM; glm function in the stats package) with a Poisson distribution and a log link to account for the increasing variance with an increase in mean longevity. We included female quality and density at birth (fitted as a quadratic function based on the nonlinear pattern observed in the residual plot; see fig. S1 in the supplemental material; supplemental material is available online) as covariates and assessed the influence of reproduction (reproduced vs. never reproduced) and its interaction with female quality and density at birth on longevity. We then evaluated whether the probability of dying before reproduction was influenced by female quality and density at birth using a GLM with a binomial distribution and a logit link. For both analyses, we evaluated the support for these effects by performing model selection based on Akaike's information criterion corrected for small samples (AICc; see model selection details below).

Second, we performed confirmatory path analysis (Shipley 2009) to assess whether the amount of early reproductive allocation (i.e., used as a continuous variable) affected

longevity and late reproductive success. We therefore only included females that reproduced at least once before death ($n = 113$). Path analysis tests hypothesized causal models that specify the structural relationships between the predictors in terms of their direct and indirect effects (Shipley 2009). On the basis of our knowledge of the ecology of the mountain goats, we created 22 causal models a priori to characterize the hypothesized links among ERS, AFR, female quality, density at birth (fitted as a quadratic function based on the nonlinear pattern observed in the residual plot with longevity), longevity, and late reproductive success (see "Path analysis models evaluated" in the supplemental material). We followed Shipley's AIC model selection technique developed for d-separation tests (Shipley 2013) to evaluate the support for the different causal models. All relationships were fitted with linear models except for longevity, which was fitted with a GLM with a Poisson distribution and a log link. The path analysis included 14 females that were still alive at the end of the study in 2015, thereby underestimating their longevity, but including these females did not influence the results (see "Cohorts included in longevity analyses" in the supplemental material).

Influence of Early Reproductive Allocation on Rates of Reproductive and Actuarial Senescence

To determine the influence of early reproductive allocation on the rate of reproductive and actuarial senescence, we examined the effect of ERS, AFR, and density at birth on the late-life (i.e., from age 7 years until death) probability of both annual reproduction (offspring produced vs. no offspring) and annual survival. For the probability of annual reproduction late in life, we used a generalized LMM (glmer function in the lme4 package with a binomial distribution and a logit link) that included female identity as a random intercept. Because the annual reproductive success of females has been previously studied in detail in this population (Hamel et al. 2010*a*), we included as covariates the variables that were shown to influence annual reproduction: female age, female reproductive status the previous year (lactating vs. nonlactating), annual population density, female quality, and the interactions between age and reproductive status and between annual density and reproductive status. These covariates formed what we called the "base model" for the model selection. This base model was tested against models including the additional influence of ERS, AFR, and density at birth, along with their interactions with age, to assess whether the rate of senescence changed with ERS, AFR, and density at birth. We also included the interaction between density at birth and annual density to test the expectation from the PAR hypothesis that late-life fitness is improved when the early environment matches conditions experienced in adulthood. ERS and AFR were never included in

the same model because of their strong negative correlation ($r = -0.69$).

For the probability of annual survival late in life, we used Cox proportional hazard (CPH; Cox 1972) regression models to assess changes in mortality risk with age using the coxph function in the survival package (Therneau 2016). As for the probability of annual reproduction, we used a base model including covariates known to affect annual survival in this population (Hamel et al. 2010*a*). In this case, the base model included age and annual density, and we tested this base model against the same models as those defined above for the probability of annual reproduction. Because annual density changed at every age, we fitted CPH models with time-varying covariates, following Thomas and Reyes (2014). Because this method splits time into smaller intervals for each individual, we used female identity as a cluster variable to account for repetition and thus obtain estimates based on robust variance.

Multiple Imputation and Model Selection Process

Our data set included missing data in the explanatory variables. We therefore used multiple imputation to avoid obtaining biased parameter estimates that may result from simply deleting the missing data (Nakagawa and Freckleton 2008, 2011; Penone et al. 2014; Ellington et al. 2015). We used the function amelia in the package Amelia (Honaker et al. 2011), a bootstrapping-based algorithm, to fill in the missing values by generating nine imputed data sets, as recommended by Rubin (1987), in order to obtain estimates of the standard errors that accurately reflect the uncertainty of the imputed data. Each data set contains distinct imputed values for the missing data that are consistent with the variability in the original observed data (Honaker et al. 2011).

We thus carried out all analyses on the nine imputed data sets. For model selection, we calculated AICc, ΔAICc, and AICc weights for the different models according to each of the nine imputed data sets. To evaluate support for the best model, we computed (i) the mean AICc weights of each model over the nine imputed data sets and (ii) the number of times each model had the highest AICc weight out of the nine imputed data sets. We directly compared the best-supported model with the next closest competing models that received statistical support by computing their evidence ratio (Burnham et al. 2011) using the ratio of their mean AICc weights. Once we selected the best-supported model for each analysis on the basis of these criteria, we calculated the estimates for this model. We also computed the estimates of variables that were included in the next closest competing models but were excluded from the best-supported model.

Because we had nine imputed data sets, we obtained nine estimates for each parameter or path estimate, one from each imputed data set. We used the function mi.inference

in the norm package (based on Rubin 1987; Novo and Scha-fer 2013) to combine them into one inference (the mean estimate) with an associated standard error (the sum of the within- and between-imputation variance) and a 95% confidence interval (CI). We also totaled the number of times the 95% CIs for each estimate excluded zero out of the nine imputed data sets. In addition, for the path analysis we calculated the global effects of a predictor—that is, the sum of its direct and indirect effects on a response variable—by regressing the response variable on the predictor (Shipley 2000), combining estimates from the nine imputed data sets.

Results

Influence of Early Reproductive Allocation on Longevity and Late Reproductive Success

The best-supported model (model 5; table 1, pt. A) for assessing the effect of reproductive allocation (reproduced vs. never reproduced) on longevity contained an interaction between reproductive allocation and density at birth as well as an additive effect of quality, but this latter effect was weak (table S1, pt. A, in the supplementary material). The longevity of females that reproduced at least once started to decline once density passed a threshold of just over 100 individuals and was reduced by close to half if a female was born at the highest density compared with the threshold (fig. 1A).

Females that never reproduced had a much lower longevity than females that reproduced, nearly always below 5 years and with almost no variation with density at birth (fig. 1A). On the basis of its evidence ratio, this model received 2.8 times more support than the next closest model in the candidate set (model 6), which also included an interaction between reproductive allocation and female quality (table 1, pt. A), but this effect was weak (0.03 [95% CI: −2.28 to 2.35]). The remaining models in the candidate set received no support (table 1, pt. A). Regarding the influence of density at birth and female quality on reproductive allocation, the best-supported model (model 2; table 1, pt. B) included only density at birth. The probability of reproducing before death declined from about 0.9 for females born at low density to 0.6 for those born at high density (fig. 1B; table S1, pt. B, in the supplemental material). The best-supported model received 2.6 and 5.5 times more support than the two closest models (models 4 and 5; table 1, pt. B). These models included the additive effect of female quality and an interaction between density at birth and female quality, but these effects were weak and inconclusive (quality: 0.04 [95% CI: −0.30 to 0.38]; density × quality: 1.51 [95% CI: −1.96 to 4.98]).

When assessing the influence of the amount of early reproductive allocation on longevity and late reproductive success using path analysis based only on females that reproduced during their lifetime, the best-supported causal model was 20 (fig. 2; "Path analysis models evaluated" and

Table 1: Model selection results for the influence of reproductive allocation (reproduced vs. never reproduced during lifetime) on longevity (pt. A) and the influence of density at birth and female quality on reproductive allocation (pt. B), based on 142 adult female mountain goats at Caw Ridge, Alberta, Canada (1988–2015)

Model	Structure	K	AICc weight Mean	AICc weight Range	AICc weight Highest
A:					
1	I	1	.00	.00–.00	0
2	I + DensityBirth + Quality	4	.00	.00–.00	0
3	I + DensityBirth + Quality + Repro	5	.00	.00–.00	0
4	I + DensityBirth + Quality + Repro + Repro × Quality	6	.00	.00–.00	0
5	**I + DensityBirth + Quality + Repro + Repro × DensityBirth**	**7**	**.73**	**.73–.74**	**9**
6	I + DensityBirth + Quality + Repro + Repro × DensityBirth + Repro × Quality	8	.26	.26–.26	0
B:					
1	I	1	.04	.04–.04	0
2	**I + DensityBirth**	**2**	**.61**	**.61–.62**	**9**
3	I + Quality	2	.01	.01–.01	0
4	I + DensityBirth + Quality	3	.23	.22–.23	0
5	I + DensityBirth + Quality + DensityBirth × Quality	4	.11	.11–.11	0

Note: The best-supported model is presented in boldface type. For each model, K refers to the total number of parameters that must be estimated. The Akaike's information criterion corrected for small samples (AICc) weight range excludes the maximum and minimum AICc weight among the nine imputed data sets, and the highest AICc weight is the number of times each model had the highest weight out of the nine imputed data sets. DensityBirth = density in the year of a female's birth (included as a quadratic effect in pt. A; see "Statistical Analyses"); I = intercept; Repro = reproductive allocation (reproduced vs. never reproduced); Quality = female quality index.
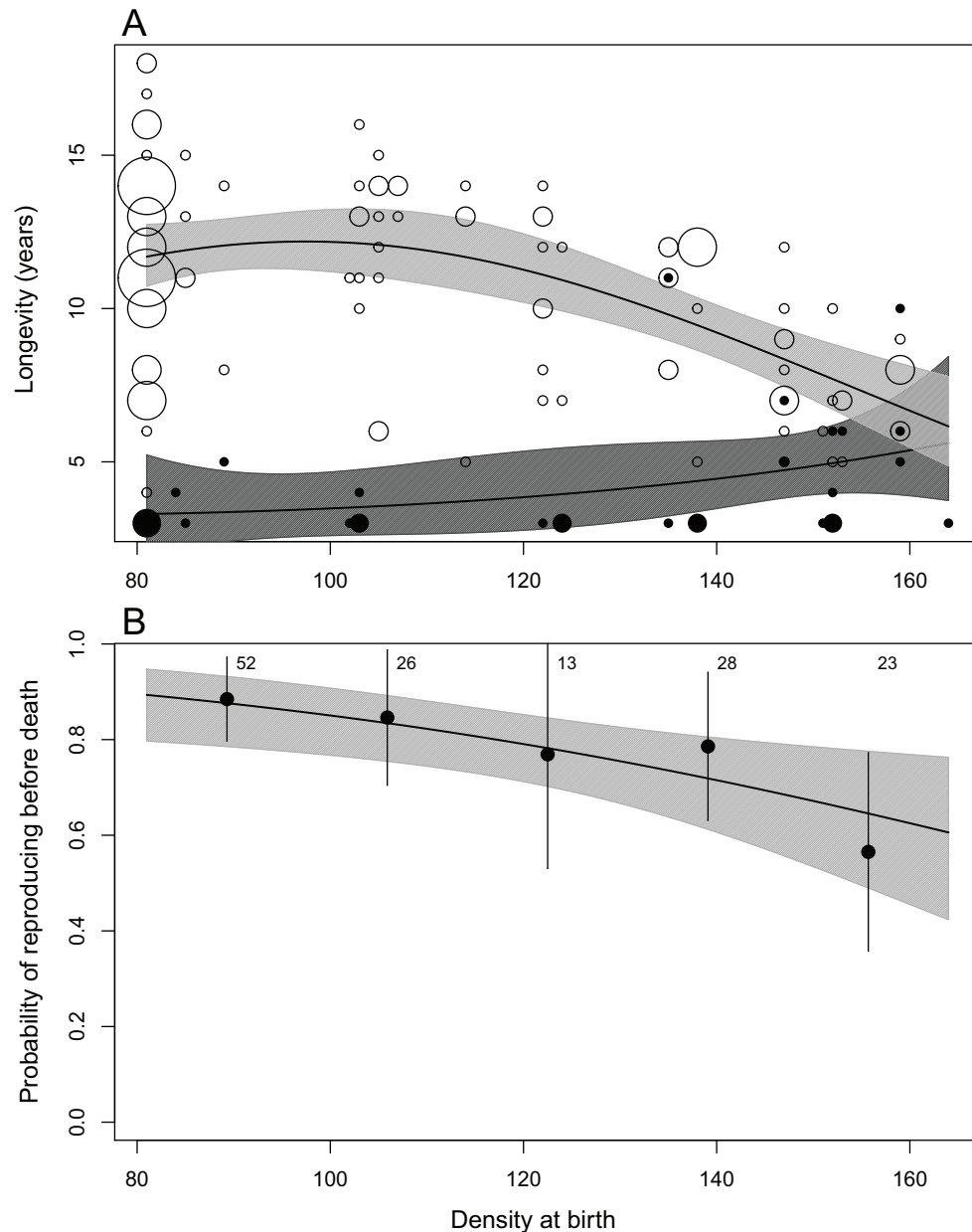
Figure 1: Influence of density in the year of a female's birth on female longevity (*A*), for females that reproduced (light gray shaded zone, open circles) and females that never reproduced (dark gray shaded zone, closed circles), and on the probability of reproducing before death (*B*) in adult female mountain goats at Caw Ridge, Alberta, Canada (1988–2015). Solid lines represent the predicted values from the model, and shaded zones are the 95% confidence intervals (CIs). Points are the raw data. In *A*, point size is proportional to the number of individuals. In *B*, binary raw data were binned in five density intervals. The points represent the mean and the bars are their 95% CIs, with the numbers indicating the number of females per density interval.

table S2 in the supplemental material). The only determinant of female longevity was the direct, negative, nonlinear effect of density at birth (fig. 2; note that this effect was already captured by the interaction between density at birth and reproductive allocation in the first analysis that included

all females [fig. 1*A*]). In addition to longevity, density at birth was also the strongest direct determinant of late reproductive success (fig. 2). For females surviving to the same age, females born at high density produced about one fewer offspring later in life compared with females born at low density
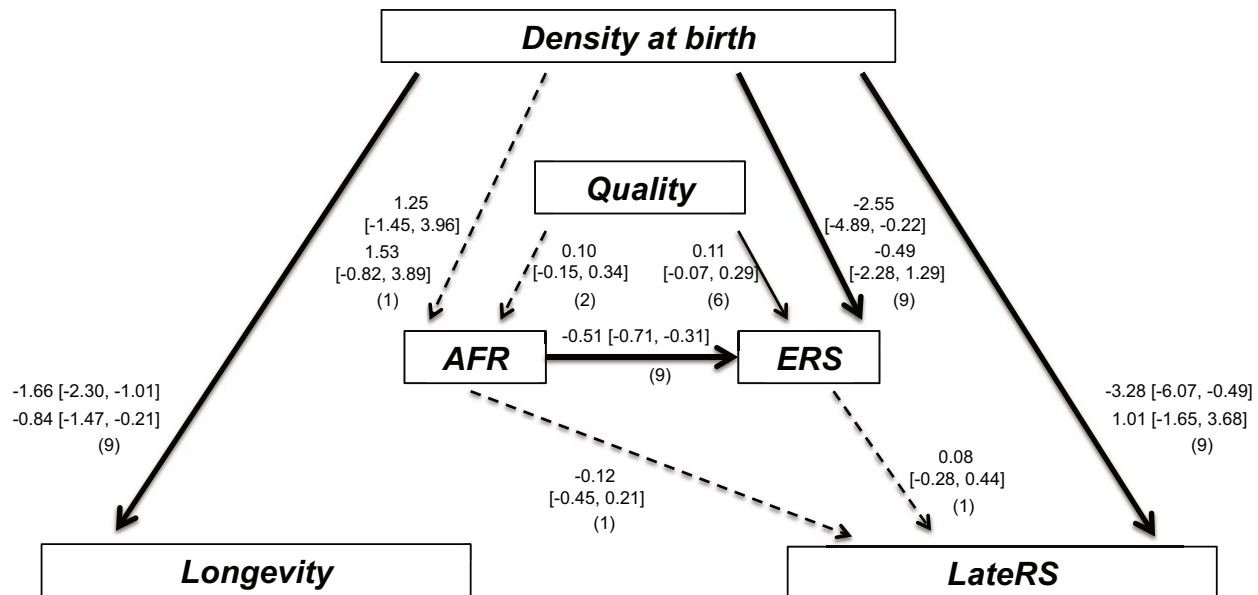
Figure 2: Best-supported path analysis model describing the direct and indirect effects of density in the year of a female's birth (quadratic effect), female quality, age at first reproduction (AFR), and early reproductive success (ERS) on late reproductive success (LateRS) and longevity of adult female mountain goats at Caw Ridge, Alberta, Canada (1988–2015). Path coefficients and their corresponding 95% confidence intervals (CIs; in brackets) were computed on the basis of nine imputed data sets and are presented adjacent to each path. For the quadratic effects of density at birth, the linear coefficients are presented above the quadratic coefficients (note that longevity was the only variable to support a quadratic effect of density at birth). Below each path coefficient (in parentheses) is indicated the number of times the 95% CIs for each estimate excluded zero out of the nine imputed data sets. Arrows indicate the direction of the causal relationship. Thick black solid lines indicate strong evidence of an effect (95% CIs do not overlap with zero), thin black solid lines indicate the tendency toward an effect (95% CIs marginally overlapped with zero), and dashed lines indicate suggestive but inconclusive relationships (95% CIs widely overlapped with zero).

(fig. 3*A*). The global effect of density at birth was slightly strengthened through its indirect effects on AFR and ERS (global linear coefficient: −3.67 [95% CI: −6.33 to −1.01]; global quadratic coefficient: −0.73 [95% CI: −1.96 to 3.42]). While an earlier AFR and a greater ERS tended to slightly augment a female's late reproductive success, the evidence was weak, as eight of the nine CIs from the imputed data sets overlapped with zero (fig. 2). With respect to predictors of ERS, density at birth had a strong negative influence on a female's ERS (fig. 2), diminishing the number of kids born in early life by about one when a female was born at high compared with low density (fig. 3*B*). Female quality had the opposite effect (fig. 2), with high-quality females (i.e., heavier and more dominant between ages 3 and 6 years) giving birth to approximately one more offspring compared with lighter subordinate females (fig. 3*C*). Not surprisingly, females that gave birth to their first offspring at an earlier age experienced greater ERS than those that delayed AFR (fig. 2).

The best-supported model received 1.6 times more support than the next closest model in the candidate set (model 22; "Path analysis models evaluated" and table S2 in the supplemental material). This second-best model was nested inside

the top-ranked model, that is, excluding the direct effects of AFR and ERS on late reproductive success. Models 17 and 19 also received some support from the imputed data sets (table S2 in the supplemental material). Compared with the top-ranked model, they included the direct effect of female quality on longevity and late reproductive success ("Path analysis models evaluated" in the supplemental material), but these effects were weak and inconclusive (quality on longevity: 0.01 [95% CI: −0.05 to 0.06]; quality on late reproductive success: 0.07 [05% CI: −0.21 to 0.35]). The remaining models in the candidate set received little to no support (table S2 in the supplemental material).

Influence of Early Reproductive Allocation on Rates of Reproductive and Actuarial Senescence

In addition to the previously reported effects on the probability of annual reproduction (i.e., the effects included in the base model), the model selection supported an effect of density at birth and its interaction with annual density (model 4; table 2, pt. A; table S3, pt. A, in the supplemen-
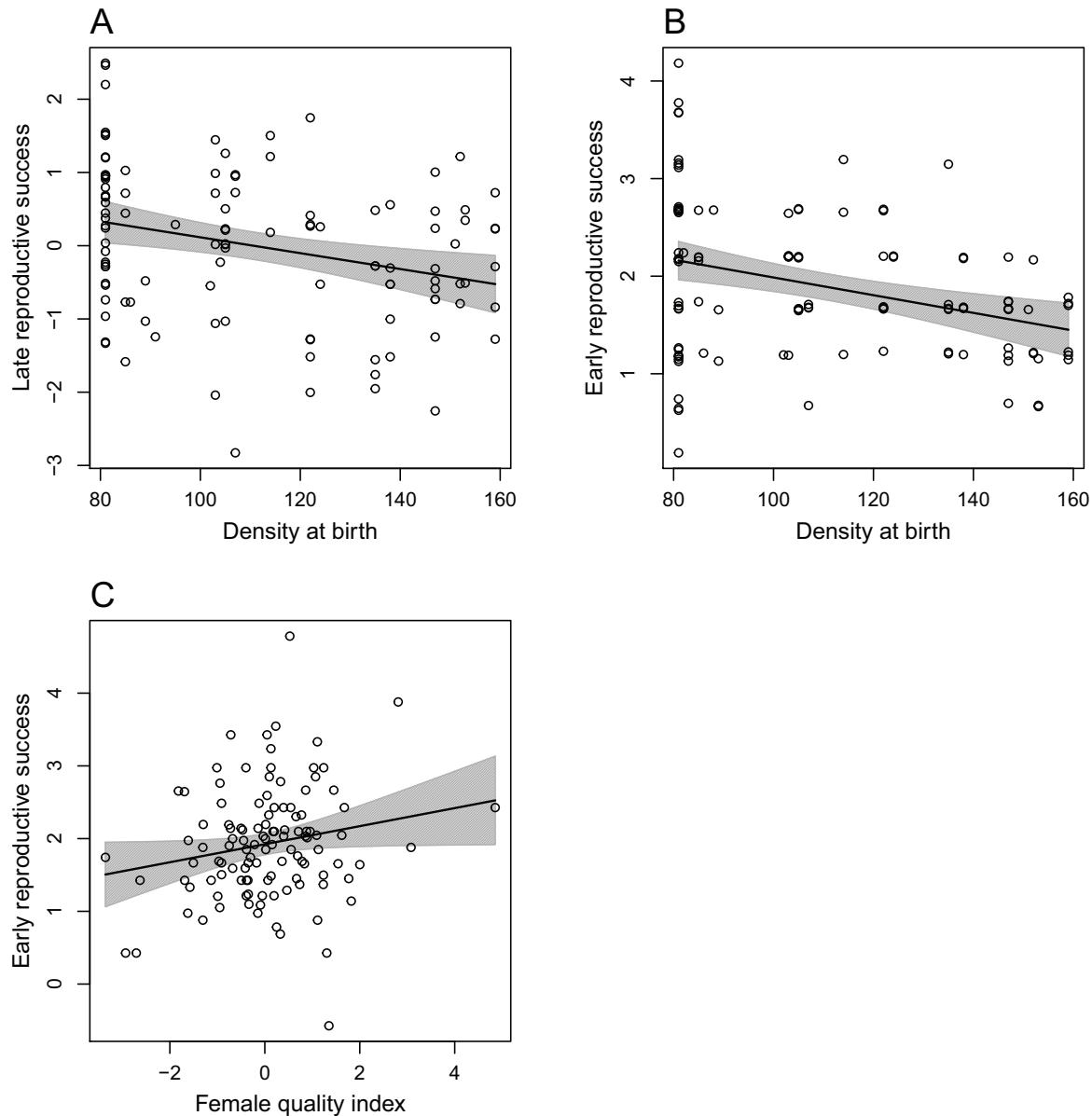
Figure 3: Influence of density in the year of a female's birth on late reproductive success (*A*) and early reproductive success (*B*) as well as influence of female quality on early reproductive success (*C*). Data are from adult female mountain goats at Caw Ridge, Alberta, Canada (1988–2015). Solid lines represent the predicted values from the models, shaded zones are the 95% confidence intervals, and points are the partial residuals, accounting for the influence of other effects included in the model.

tal material). The probability of giving birth was higher for females born at low density than for females born at high density, but this effect was mostly observed in years of high density (fig. 4*A*; "Parameter estimates for the late-life probability of annual reproduction and annual mortality," table S3, pt. A, in the supplemental material). The best-supported model received 1.7 times more support than the two closest models: one (model 2) that was nested inside the top model

but excluded the interaction and one (model 7) that contained the additional effect of ERS and the interaction between age and both ERS and density at birth (table 2, pt. A). Nonetheless, there was little evidence to support these effects (ERS: 0.22 [95% CI: −0.09 to 0.52]; ERS × age: −1.87 [95% CI: −7.87 to 4.12]; density at birth × age: 1.65 [95% CI: −4.15 to 7.46]), suggesting little support for accelerated reproductive senescence with higher ERS or density at birth.

Table 2: Model selection results for annual probability of reproduction late in life (pt. A) and annual mortality risk late in life (pt. B), based on adult female mountain goats at Caw Ridge, Alberta, Canada (1988–2015)

Model	Structure	K	AICc weight Mean	AICc weight Range	AICc weight Highest
A:					
1	˙B	8	.00	.00–.00	0
2	˙B + DensityBirth	9	.22	.14–.31	1
3	˙B + DensityBirth + DensityBirth × Age	10	.12	.07–.17	0
4	**˙B + DensityBirth + DensityBirth × Annual Density**	**10**	**.37**	**.22–.55**	**5**
5	˙B + ERS	9	.00	.00–.00	0
6	˙B + ERS + ERS × Age	10	.00	.00–.00	0
7	˙B + ERS + DensityBirth + ERS × Age + DensityBirth × Age	12	.22	.07–.46	2
8	˙B + AFR	9	.00	.00–.00	0
9	˙B + AFR + AFR × Age	10	.00	.00–.00	0
10	˙B + AFR + DensityBirth + AFR × Age + DensityBirth × Age	12	.07	.02–.06	1
B:					
1	˙B	2	.00	.00–.00	0
2	**˙B + DensityBirth**	**3**	**.39**	**.28–.49**	**7**
3	˙B + DensityBirth + DensityBirth × Age	4	.17	.12–.22	0
4	˙B + DensityBirth + DensityBirth × Annual Density	4	.15	.11–.19	0
5	˙B + ERS	3	.00	.00–.00	0
6	˙B + ERS + ERS × Age	4	.00	.00–.00	0
7	˙B + ERS + DensityBirth + ERS × Age + DensityBirth × Age	6	.16	.04–.25	1
8	˙B + AFR	3	.00	.00–.00	0
9	˙B + AFR + AFR × Age	4	.00	.00–.00	0
10	˙B + AFR + DensityBirth + AFR × Age + DensityBirth × Age	6	.13	.04–.23	1

Note: ˙B represents the base model that included effects already shown in a previous study to influence annual reproduction and annual mortality (see "Statistical Analyses"). The additional effects to the base model are the same for parts A and B, but the base model differs: ˙B for annual reproduction = I + Age + Status + Annual Density + Quality + Age × Status + Annual Density × Status, and ˙B for annual mortality risk = Age + Annual Density. The best-supported model for each analysis is presented in boldface type. K refers to the total number of parameters estimated. The Akaike's information criterion corrected for small samples (AICc) weight range excludes the maximum and minimum AICc weight among the nine imputed data sets, and the highest AICc weight is the number of times each model had the highest weight out of the nine imputed data sets. AFR = age at first reproduction; Age = female age from 7 years until death; Annual Density = annual population density; DensityBirth = density in the year of a female's birth; ERS = early reproductive success; I = intercept; Quality = female quality index; Status = female reproductive status the previous year (lactating vs. nonlactating).

The best-supported model for annual mortality risk late in life (model 2) included only the additional effect of density at birth (table 2, pt. B; table S3, pt. B, in the supplemental material). Females born at high density had a lower probability of survival than females born at low density (fig. 4B). Although there seemed to be a tendency for the decline in survival with age to be stronger for females born at higher densities (density at birth × age: −1.35 [95% CI: −4.88 to 2.18]; fig. 4B; table 2, pt. B), the best-supported model, which excluded this interaction, received more than twice the support of the model including it (model 3; table 2, pt. B). The best-supported model also received between two and three times as much support as three other competing models (models 4, 7, and 10; table 2, pt. B). The additional effects included in these competing models were weak and inconclusive (density at birth × annual density: −0.03 [95% CI: −0.20 to 0.13]; ERS: 0.00 [05% CI: −0.36 to 0.35]; ERS × age: 0.91 [95% CI: −6.62 to 8.43]; AFR: −0.11 [95% CI: −0.41

to 0.19]; AFR × age: 0.81 [95% CI: −6.13 to 7.76]). Data underlying all tables and figures are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.48kf0 (Panagakis et al. 2017).

Discussion

Our study provides a rare integrated view of early-late life trade-offs in a natural population of a large mammal. Ecology often concerns cause-effect hypotheses for which controlled randomized experiments are not feasible or cannot differentiate between the underlying causal mechanisms (Shipley 2000). Path analyses allowed us to consider both direct and indirect causal effects of ERS, early environmental conditions, and individual quality on late-life performance. Contrary to the predictions made by the life-history theories of aging, we did not find evidence for the negative influ-
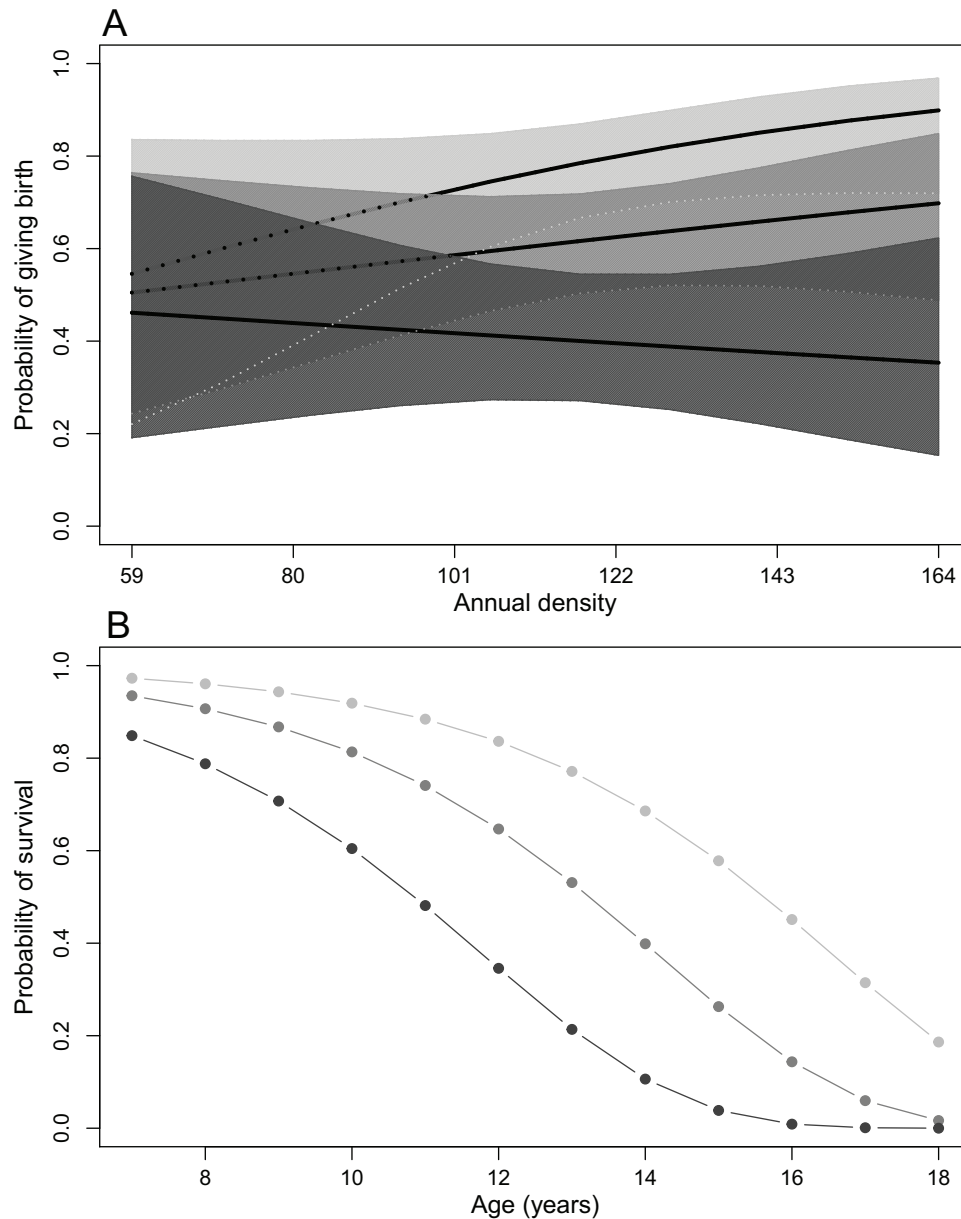
Figure 4: Probability of giving birth in late life according to annual population density and population density in the year of a female's birth (*A*; low density at birth in light gray, medium density at birth in medium gray, and high density at birth in dark gray) and survival in late life according to female age and population density in the year of a female's birth (*B*; low density at birth in light gray, medium density at birth in medium gray, and high density at birth in dark gray) in adult female mountain goats at Caw Ridge, Alberta, Canada (1988–2015). Lines represent the predicted values from the model, and shaded zones are the 95% confidence intervals.

ence of ERS on longevity or late reproductive success even after accounting for heterogeneity in the natal environment and female quality. Furthermore, early reproductive allocation did not affect the rates of reproductive and actuarial senescence late in life. Our hypothesis concerning population density in the year of a female's birth, however, was supported, with density at birth emerging as a strong negative

determinant of longevity, late reproductive success, and ERS. Natal population density also reduced the annual probability of both reproduction and survival during adulthood, but it did not lead to accelerated rates of senescence. Our study also confirms the positive effect of quality on ERS, but we did not find evidence to support the positive influence of quality on longevity or late reproductive success. The only

link between quality and late-life fitness was an indirect but inconclusive effect on late reproductive success through ERS.

Early environmental conditions may have major implications for the population dynamics of iteroparous species such as the mountain goat. Climatic conditions or population density are expected to influence resource availability, which may generate delayed effects in the population growth rate (Sæther 1997). In addition, abundant resources may mask reproductive costs (Nussey et al. 2013), while conversely limited resources may exacerbate such costs (Reed et al. 2008). Environmental conditions in the year of a female's birth are especially critical, as they coincide with a female's early growth and development (Albon et al. 1987). Our results demonstrate the strong, far-reaching consequences that such cohort effects may have for individual fitness throughout life. Indeed, density in the year of a female's birth was the only predictor to emerge with substantial evidence for direct effects on both longevity and late reproductive success. In addition to late reproductive success, we found that density at birth also strongly reduced ERS. Combining early and late reproductive success, females born at high population density gave birth to approximately two fewer offspring over the course of a lifetime compared with females born at low density. This amounts to just under half of the average lifetime reproductive success for a female in this population, underscoring the substantial influence of natal environmental conditions on lifetime reproductive success.

Population density at birth was also found to be a major factor in late-life performance at the annual level. In keeping with other studies of long-lived species (Hayward and Lummaa 2013; Douhard et al. 2014), our results support the existence of silver spoon effects rather than PARs. Contrary to what the PAR hypothesis predicts (Gluckman et al. 2005; Monaghan 2008; Nettle et al. 2013), females born at high density had a later rather than an earlier AFR, and they had the lowest probability of annual reproduction and annual survival, irrespective of the environmental conditions experienced during adulthood. The latter finding suggests that low population density at birth allows individuals benefiting from a good start in life to outperform those experiencing a bad start in life over the course of their entire lifetime, thereby supporting the occurrence of silver spoon effects (Grafen 1988; Madsen and Shine 2000; van de Pol et al. 2006).

Furthermore, although we expected density at birth to affect late-life fitness both directly and indirectly through female quality, we found it to be independent of female quality in the best-supported path analysis model, which is consistent with previous results for this population (Hamel et al. 2009b). This suggests that the mechanism underlying the strong negative influence of natal density on longevity and reproduction may be related to more subtle developmental effects other than body mass and dominance, which were included in our female quality index. High population density during development may be related to other key factors, such as metabolic rate (Verhulst et al. 2006), resistance to oxidative stress (Alonso-Alvarez et al. 2006), and telomere length dynamics (Fairlie et al. 2016). These physiological factors can have long-term implications for somatic maintenance and thus for longevity and/or late-life reproductive performance (Nussey et al. 2007; Bouwhuis et al. 2010).

The large disparity in longevity between females that never reproduced during their lifetime and females that did supports the fundamental fitness costs that are expected with delays in reproduction (Cole 1954; Bell 1980). For females that survived to reproduce, their longevity and actuarial senescence rate were not influenced by an earlier AFR or a greater ERS. These findings are in keeping with previous analyses of this population (Hamel et al. 2014), which did not find evidence to support a trade-off between early AFR and longevity. Consistent with our findings, researchers tend to discern reproductive costs of reproduction over survival costs of reproduction in species on the slow end of the life-history continuum, such as long-lived birds and ungulates (Nussey et al. 2006), while the converse is true for short-lived species like the North American red squirrel (Descamps et al. 2006; Hamel et al. 2010b). Female mountain goats, like other long-lived species, adopt a conservative reproductive tactic (Festa-Bianchet and Côté 2008) that prioritizes their survival over that of their offspring. This strategy evolved because it provides them with greater opportunities for future reproduction and thus greater lifetime reproductive success (Gaillard and Yoccoz 2003). While these results are not incompatible with the hypothesis of an early-late life trade-off, our results thus further support the occurrence of environmental canalization of adult survival (Hamel et al. 2010b).

In addition, while we expected ERS to entail costs for late-life reproduction under a conservative reproductive tactic, we did not find evidence to support this. Both an earlier AFR and a greater ERS had little direct effect on late reproductive success, as the effects were inconclusive and tended toward a positive rather than a negative covariation between early and late reproduction. Furthermore, the analyses investigating the influence of AFR and ERS on annual reproduction late in life found only weak evidence for an association between early reproductive allocation and the rate of reproductive senescence. Moreover, earlier work on this population also found that females investing in heavier offspring had a reduced probability of subsequent reproduction (Hamel et al. 2011), as did primiparous and prime-aged females (Hamel et al. 2010a). Overall, our results suggest that these fitness costs of reproduction do not accumulate over the long term to carry lifetime consequences.

The tendency toward positive rather than negative covariations among early- and late-life traits suggests that het-

erogeneity among females may mask potential lifetime trade-offs. Indeed, although life-history theory predicts that costs of reproduction should result in negative covariations between early and late life-history traits (Stearns 1992), empirical support has been mixed (Lemaître et al. 2015). In red-billed choughs (*Pyrrhocorax pyrrhocorax*), Reid et al. (2003) found that females that were more productive when young ultimately experienced shorter life spans, supporting lifetime costs of reproduction. In contrast, Bérubé et al. (1999) found that female bighorn sheep that were reproductively successful early in life experienced greater longevity than unsuccessful breeders. Similar to the results found with lifetime trade-offs, positive covariance has also been observed with fitness costs of reproduction that were assessed annually (Hamel et al. 2010*b*). The van Noordwijk and de Jong (1986) model has been pivotal in explaining these positive covariances (Metcalf 2016), demonstrating that they arise when the relative variation in resource acquisition exceeds the relative variation in resource allocation among individuals. Conversely, trade-offs between two life-history traits should be apparent only when the relative among-individual variation in resource allocation exceeds that of resource acquisition. The variation in individual quality that accompanies variation in resource acquisition may therefore mask the predicted costs of reproduction at the population level (McNamara and Houston 1996), which necessitates that this potentially confounding effect be taken into account when studying life-history trade-offs.

Earlier studies of this mountain goat population demonstrated a quality effect on the reproductive success of females, with heavier and dominant females experiencing greater reproductive success than lighter and subordinate females (Côté and Festa-Bianchet 2001*b*; Hamel et al. 2009*b*). We therefore accounted for this influence by including in our analyses a composite index of female quality based on social rank and body mass. Female quality, however, did not affect late reproductive success or longevity; it only showed a tendency toward a positive effect on ERS. Accounting for this effect still resulted in a positive but weak and inconclusive effect on late reproductive success. It is likely that other characteristics remain important for female performance, including physiological traits such as metabolic efficiencies (van Noordwijk and de Jong 1986) and immune system states (McNamara and Houston 1996), which could explain why we did not find evidence to support early-late life trade-offs in this population. Furthermore, our study did not assess potential male quality effects, which could attenuate some of the costs that females may experience as a result of reproductive allocation early in life. Mountain goats have a polygynous mating system in which males do not provide parental care (Festa-Bianchet and Côté 2008). Older females tend to mate with older, higher-quality males, that is to say, heavier and more dominant males (Mainguy et al. 2008). Although

the mass of adult males has been shown to have a positive influence on the offspring mass of their sons, it has a negative effect on the mass of their daughters (Mainguy et al. 2009), meaning that mate choice is likely to be balanced. Hence, while it is possible that females that have allocated to reproduction early in life may benefit from reproducing with higher-quality males later in life, an analysis with sufficient data would be required to evaluate the possibility of such a benefit.

To conclude, the recent review concerning studies that explicitly tested for trade-offs between early reproductive allocation and late-life performance (Lemaître et al. 2015) highlighted that all eight studies that accounted for individual heterogeneity in quality found support for such trade-offs. Our study, based on high-quality longitudinal data, found no evidence for such early-late life trade-offs even when carefully accounting for variation in female quality and natal environmental conditions. Still, our study demonstrates the strong fundamental repercussions that population density in the year of a female's birth have on early- and late-life traits related to fitness, demonstrating how natal environmental conditions may potentially affect the population dynamics of a long-lived species. Our investigation advances our understanding of the evolution of life-history strategies and encourages additional study of the relationship between the natal environment and lifetime trade-offs.

APPENDIX

Measures of Early and Late Reproductive Success

We defined four measures of early reproductive success (ERS; table A1). Two measures (ERS 3–6 years birth, ERS 1–3 birth) were based on the annual parturition success of females

(0.43 ± 0.18 SD), and two others (ERS 3–6 years weaning, ERS 1–3 weaning) were based on the annual weaning success of females (0.32 ± 0.18 SD). ERS 1–3 birth and ERS 1–3 weaning controlled for age at first reproduction (AFR) by calculating the number of births and the number of kids weaned during the three consecutive years commencing with the year of first reproduction (table A1). If a female started to reproduce at age 6 years, for example, this measure used the total number of births or kids weaned at ages 6, 7, and 8 years.

The four measures considered could not be used in the same models because they were strongly correlated (e.g., ERS 3–6 years birth and ERS 1–3 birth: $r = 0.65$; ERS 3–6 years weaning and ERS 1–3 weaning: $r = 0.79$). Therefore, to avoid having to consider too many similar models during the model selection process, we first performed a model selection to determine which of the four measures had the greatest influence on longevity and late reproductive success. We used generalized linear models (glm function in R software) with a Poisson distribution and a log link for longevity and linear models (lm function) for late reproductive success. We included each of the four measures of ERS in different models, with density at birth (fitted as a quadratic function based on the nonlinear pattern observed in the residual plot) and female quality as fixed effects in each model, along with their interactions with ERS. We assessed model selection on the basis of Akaike's information criterion corrected for small samples (AICc).

The influence of the four measures of ERS on longevity and late reproductive success produced equivalent results, with all ΔAICc values <2 (Burnham and Anderson 2002). We therefore decided to retain ERS 3–6 years birth (ERS based on the number of births between the ages of 3 and 6 years; table A1) for the analyses, for two reasons. First, ERS 3–6 years birth could be used in the analysis for both late reproductive success and longevity, unlike ERS 1–3 birth and ERS 1–3 weaning, which are based on the three consecutive years commencing with AFR and therefore contain overlapping data with late reproductive success for those females with a late AFR. Second, as the ERS measures based on the number of births and those based on the number of kids weaned are highly correlated ($r = 0.73$ for ERS 3–6 years birth, $r = 0.63$ for ERS 1–3 years weaning), we simply retained the measure based on parturition success.

Furthermore, we considered two measures of late reproductive success: one based on parturition and one based on weaning success. Because results were similar for the two metrics of late reproductive success, we retained late reproductive success based on the number of births to be consistent with the definition of ERS we selected. In the article, ERS refers to ERS 3–6 years birth, and late reproductive success refers to late reproductive success based on the number of births (mean ± SD: 3.31 ± 2.48). Overall, mean lifetime reproductive success (the total number of births over the course of a female's lifetime) in this population was 4.81 ± 2.8.

Table A1: Measures of early reproductive success (ERS) considered in the analyses of longevity and late reproductive success of adult female mountain goats at Caw Ridge, Alberta, Canada (1988–2015)

ERS measure	Mean	SD	Biological criteria	Reference
ERS 3–6 years birth	1.73	.81	Total parturition success during period of resource allocation to both reproduction and growth (between ages 3 and 6 years), that is, before reaching asymptotic body mass at age 7 years	Hamel et al. 2010*a*
ERS 3–6 years weaning	1.28	.88	Total weaning success during period of resource allocation to both reproduction and growth (between ages 3 and 6 years), that is, before reaching asymptotic body mass at age 7 years	Hamel et al. 2010*a*
ERS 1–3 birth	2.22	.62	Total parturition success during the three consecutive years commencing with AFR, thereby controlling for differences in AFR among females	Forslund and Pärt 1995
ERS 1–3 weaning	1.68	.84	Total weaning success during the three consecutive years commencing with AFR, thereby controlling for differences in AFR among females	Forslund and Pärt 1995

Note: AFR = age at first reproduction.

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Alpine icons: mountain goats (*Oreamnos americanus*) at Caw Ridge, Alberta, Canada. Photo credit: Edouard Bélanger (2014).