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Authors
Kroeger, Svenja B
Blumstein, Daniel T
Armitage, Kenneth B
et al.

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Older mothers produce more successful daughters

Svenja B. Kroeger[a,b,1], Daniel T. Blumstein[c,d], Kenneth B. Armitage[d,e], Jane M. Reid[a,f], and Julien G. A. Martin[a,g]

[a]School of Biological Sciences, Zoology Building, University of Aberdeen, Aberdeen, AB24 2TZ, United Kingdom; [b]Department of Landscape and Biodiversity, The Norwegian Institute of Bioeconomy Research, 7031 Trondheim, Norway; [c]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1606; [d]The Rocky Mountain Biological Laboratory, Crested Butte, CO 81224; [e]Department of Ecology & Evolutionary Biology, The University of Kansas, Lawrence, KS 66045-7534; [f]Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Realfagbygget, Gløshaugen, N-7491 Trondheim, Norway; and [g]Department of Biology, University of Ottawa, Ottawa, ON K1N 6N5, Canada

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Annual reproductive success and senescence patterns vary substantially among individuals in the wild. However, it is still seldom considered that senescence may not only affect an individual but also affect age-specific reproductive success in its offspring, generating transgenerational reproductive senescence. We used long-term data from wild yellow-bellied marmots (*Marmota flaviventer*) living in two different elevational environments to quantify age-specific reproductive success of daughters born to mothers differing in age. Contrary to prediction, daughters born to older mothers had greater annual reproductive success on average than daughters born to younger mothers, and this translated into greater lifetime reproductive success. However, in the favorable lower elevation environment, daughters born to older mothers also had greater age-specific decreases in annual reproductive success. In the harsher higher elevation environment on the other hand, daughters born to older mothers tended to die before reaching ages at which such senescent decreases could be observed. Our study highlights the importance of incorporating environment-specific transgenerational parent age effects on adult offspring age-specific life-history traits to fully understand the substantial variation observed in senescence patterns in wild populations.

aging | life-history strategies | reproductive trade-offs | resource allocation

While there is compelling evidence that reproductive and actuarial senescence are commonplace in wild animal populations (reviewed by refs. 1 and 2), variation in senescence rates among individuals within the same population remains challenging to explain. Recent studies in natural populations have shown that developmental conditions can impact an individual's late-life reproductive performance and senescence rates (i.e., the decrease in individual reproduction and survival probability with increasing age; e.g., refs. 3–10). One potentially influential factor is the age of the individual's mother at the time of birth. Indeed, the rationale underlying classic evolutionary senescence theories can be extended to encompass fitness components of an individual's offspring, rather than solely the focal individual's own future fecundity and survival. Complex effects of parent age on offspring life histories could then arise, resulting in transgenerational senescence effects that could influence the offspring's senescence patterns and fitness and, more broadly, the evolution of lifespan and aging (11, 12).

Based on senescence theory, older mothers might be expected to have fewer resources to allocate to reproduction, and therefore produce offspring that reproduce less successfully and senesce faster themselves (13, 14). However, very few studies of natural populations have investigated effects of parental age on postindependence offspring performance (reviewed by ref. 15). In particular, few studies have quantified transgenerational senescence effects, defined as effects of parental age at birth on an offspring's age-specific decrease in a given trait (but see refs. 12, 16, and 17). As a consequence, it is unclear whether maternal age effects can in fact be sufficiently long-lasting to affect offspring age-specific reproduction and senescence expressed several years postbirth. It is also unclear how such effects might depend on other factors that affect offspring's adult phenotypes. Indeed, heterogeneity is a central component of dynamic natural systems, and a key hypothesis is that the form and magnitude of transgenerational effects on offspring phenotype could vary with environmental conditions (18). Specifically, lower allocation of older mothers may only negatively affect performance of offspring that live in harsher environments (e.g., harsher current or natal environments, as in refs. 3 and 19–25). Since studies on transgenerational senescence are rare overall, there is inevitably little knowledge on environment-dependent transgenerational senescence. One reason why such studies are rare is that detailed multigenerational data, including full life histories of individuals, their mother's age at birth, and developmental environmental conditions, are very difficult to obtain.

Here, we analyze 48 y (1967 to 2014) of longitudinal data on individual life histories within a yellow-bellied marmot (*Marmota flaviventer*) population exhibiting substantial variation in litter size (0 to 10 pups) and inhabiting two different elevational sites with very different seasonal environmental conditions. Previous studies demonstrated typical patterns of within-generation senescence in female marmots (reproductive senescence, Alpine marmots, *Marmota marmota*; body mass senescence, yellow-bellied marmots, *M. flaviventer*; refs. 26 and 27), and revealed substantial differences in phenology and associated life history between the two elevational sites, reflecting major differences in local environmental harshness (28, 29). It is commonly expected that individuals will adopt a conservative reproductive strategy under harsh

Significance

There is substantial variation in aging patterns across individuals. Even more interesting is that these patterns may depend not only on an individual's own age but also on that of its parents. However, little is known about such transgenerational effects of parent age, especially regarding offspring reproduction and senescence during adulthood. Capitalizing on a long-term study of free-living yellow-bellied marmots in which individuals' fates were followed throughout their lives, we show that daughters born to older mothers had greater annual and lifetime reproductive success, but also senesced faster or tended to have shorter lifespans, depending on environmental harshness. Thus, parental age may have longer-lasting effects on offspring performance and should be considered in future studies of aging in wild populations.

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[1]To whom correspondence may be addressed. Email: svenja.kroeger@nibio.no.

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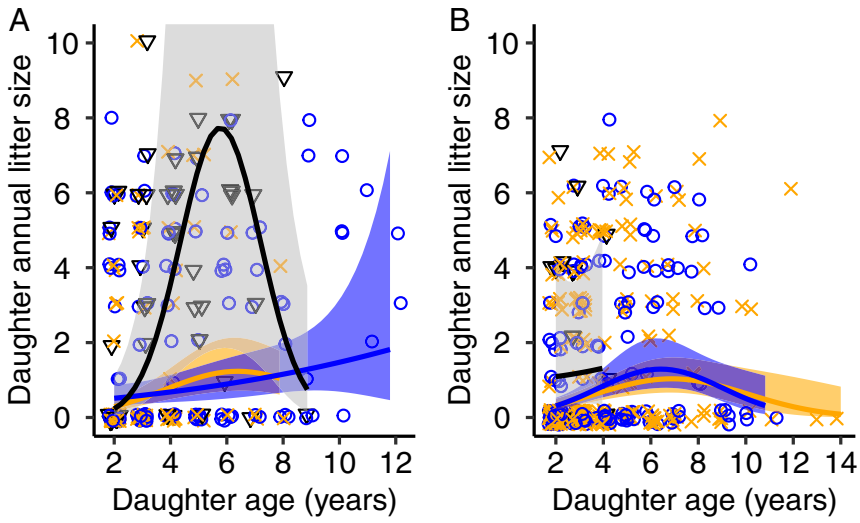

Fig. 1. Daughter annual reproductive success (i.e., annual litter size) as a function of daughter age (years), mother age at birth (years) and elevation. Daughters at (*A*) low and (*B*) high elevation were born to young (orange line, shading and crosses; 2 to 4 y), midaged (blue line, shading and empty circles; 5 to 8 y), or old (black line, shading and empty upside-down triangles; 8 y or more) mothers. Shaded areas show prediction approximated confidence intervals and points show the raw data. Mother age was fitted as a continuous variable and the three mother age categories depicted in this figure were used for illustration purposes.

conditions, which may involve transferring reproductive costs to offspring (30, 31). This system therefore provides a valuable opportunity to test two key hypotheses regarding long-term transgenerational effects of maternal age at birth (hereafter referred to as "mother age") on reproductive senescence of female offspring living under different environmental conditions (i.e., environment-dependent transgenerational senescence).

First, daughters born to older mothers have lower annual reproductive success (mother age effect on daughter annual litter size, quantified here as 0 to 10 weaned pups) and higher rates of reproductive senescence (mother age effect on daughter age-specific decreases in annual litter size) than daughters born to younger mothers. The latter hypothesis can be tested through a two-way interaction between mother age and daughter age on daughter annual reproductive success.

Second, transgenerational effects of mother age depend on the environment, with daughters born to older mothers exhibiting faster senescence rates when living at higher elevation (i.e., harsher current environment) than when living at lower elevation (i.e., more favorable current environment), and when born into a larger litter. Since offspring born into larger litters or broods commonly have reduced survival, lower weights, and reduced subsequent probabilities of reproduction (e.g., refs. 21–25), larger natal litter size is expected to represent a harsher natal environment. These hypotheses can be tested through three-way interactions among mother age, daughter age, and elevation or litter size at birth, respectively.

In addition, while understanding effects of mother age on offspring reproductive senescence requires analyses of offspring age-specific reproduction rather than total lifetime reproduction (16), the form of selection on maternal life history can additionally depend on the total fitness of daughters produced at each age. Therefore, we additionally tested for effects of mother age on daughter lifespan and lifetime reproductive success, and hence explicitly evaluated whether mother age affects overall daughter fitness.

Results

Analyses of 656 observations of annual reproductive success for 218 individual known-aged daughters (2 to 14 y) with known-aged mothers showed that daughters born to older mothers had higher, not lower, annual reproductive success on average than daughters born to younger mothers (Fig. 1 *A* and *B* and Table 1). In line with prediction, we found a significant three-way interaction among a mother's age at daughter birth, daughter age, and elevation (Table 1). This showed that, as predicted, daughters born to older mothers had faster decreases in age-specific reproductive success than daughters born to younger mothers, and hence more rapid senescence (Fig. 1*A* and see *SI Appendix*, Fig. S1*A* for a three-dimensional [3D] plot). However, opposite to prediction, these effects were only observed in the less harsh lower-elevation environment, where model estimates imply that daughters born to midage mothers apparently did not senesce (Fig. 1*A*). In the harsher higher-elevation environment, daughters born to older mothers commonly died before reaching ages where senescent decreases may have been observed (Fig. 1*B* and see *SI Appendix*, Fig. S1*B* for a 3D plot). While explicit analyses of daughter lifespan showed no significant effect of mother age at daughter birth (*SI Appendix*, Table S2), the interaction between mother age and elevation suggested that daughters born to older mothers at higher elevation tended to have shorter lifespans ($\beta = -0.13$, ± 0.08; $z = -1.62$; $P = 0.11$; *SI Appendix*, Table S2). However, due to their higher mean annual reproductive success, daughters born to older mothers had higher lifetime reproductive success at both elevations ($\beta_{MAB} = 0.38$, ± 0.14; $z = 2.66$; $P < 0.001$; *SI Appendix*, Table S3).

Contrary to prediction, there was no significant three-way interactive effect of mother age, daughter age, and daughters' natal litter size on daughter annual reproductive success (*SI Appendix*, Table S1), and thus no evidence that resource restrictions arising in large litters affect daughter reproductive senescence. However, there was a significant two-way interactive effect of mother age and daughters' natal litter size on daughter annual reproductive success (Table 1), showing that effects of mother age depend on size of the litter into which the daughter was born. In daughters born to younger mothers, daughter annual reproductive success was higher on average when daughters were born into larger natal litters (Fig. 2). However, in daughters born to older mothers, daughter annual reproductive success was higher on average when daughters were born into smaller natal litters (Fig. 2).

Models fitted to data subsets comprising long-lived daughters, or daughters born to long-lived mothers, yielded qualitatively

Table 1. Generalized linear mixed-effects model quantifying effects of maternal age at birth (MAB), daughter age, natal litter size, elevation, and number of mature females in the colony (density) on daughter annual reproductive success (i.e., annual litter size)

	n = 656 daughter-year observations for 218 daughters (122 high elevation, 96 low elevation)			
	Estimate	SE	z	P-value
Intercept	**−0.44**	**0.20**	**−2.20**	**0.028**
Maternal age at birth	0.16	0.10	1.70	0.090
MAB^2	0.01	0.14	0.06	0.951
Age	**0.30**	**0.08**	**3.72**	**<0.001**
Age^2	**−0.34**	**0.13**	**−2.68**	**<0.01**
Natal litter size	**0.18**	**0.09**	**2.03**	**0.043**
Elevation[high]	−0.06	0.21	−0.28	0.782
Density	−0.17	0.10	−1.74	0.082
MAB^2 x Age^2	**−0.34**	**0.12**	**−2.79**	**<0.01**
MAB x Natal litter size	**−0.28**	**0.09**	**−3.05**	**<0.01**
Elevation[high] x MAB^2	0.08	0.19	0.44	0.663
Elevation[high] x Age^2	−0.04	0.16	−0.24	0.808
Elevation[high] x MAB^2 x Age^2	**0.45**	**0.18**	**2.56**	**0.010**

Daughters were born to 97 different mothers between 1965 and 2008. Eliminated interaction terms are shown in *SI Appendix*, Table S1. The reference for elevation is [low]. Fixed effects explained 12% of the variance in daughter litter size (marginal R^2; 79). Random effects variances are 0.23, 0.02, 0.12, and 0.05 for mother identity, daughter identity, year observed, and cohort, respectively. Estimated effects sizes are reported with SEs and z-test statistics (z). Significant terms are shown in bold.

similar results to the models fitted to the full dataset (*SI Appendix*, Tables S4 and S5). This implies that estimated effects of daughter and mother age are not due to selective disappearance (e.g., refs. 32 and 33) and can be interpreted at the individual level.

Discussion

Our analyses revealed three strong transgenerational effects of mother age. First, daughter age-specific variation in annual reproductive success exhibited different patterns depending on maternal age at birth, suggesting that mother age plays an important role in shaping offspring reproduction and senescence. Second, the form and magnitude of these effects depended on elevation and natal litter size, and hence on environmental harshness in both the current and natal environment. Third, and contrary to prediction, daughters born to older mothers had higher mean annual reproductive success, and hence lifetime reproductive success, than daughters born to younger mothers.

Following senescence theory, we predicted a negative rather than the observed positive association between a mother's age at daughter birth and daughter annual reproductive success. Positive effects of parental age on offspring fitness components are commonly attributed to increased experience of older individuals (e.g., refs. 34 and 35). The observed relationship could also be interpreted as terminal investment (36, 37), or terminal allocation (following ref. 38), which does not necessarily imply fitness costs resulting from increased allocation to reproduction at the end of individuals' lives (39, 40). Conversely, low annual reproductive success of daughters born to younger, less experienced mothers, may represent maternal constraint (lack of competence) and/or restraint, which implies lower investment in reproduction at younger ages when residual reproductive value is high (41, 42). All else being equal, one implication of older mothers producing daughters with higher annual reproductive success would be that older mothers produce daughters with higher lifetime reproductive success, and this is indeed what we found. This result contrasts with most of the few previous studies of mother age effects on offspring lifetime reproductive success, which either found a negative association (4, 12) or no association (refs. 12 and 16; but see ref. 17).

As predicted, patterns of variation in daughter annual reproductive success in relation to mother age differed between elevational environments. However, interestingly, the less harsh, lower-elevation environment showed both the fastest and slowest senescence rates, with daughters born to older mothers senescing rapidly and daughters born to midage mothers apparently senescing little. Meanwhile, daughters born to young mothers followed a classic pattern of increasing initial annual reproductive success followed by a decrease at older ages. This pattern was also observed in the harsher higher-elevation environment, but here daughters born to old mothers tended to die younger, and therefore more rarely reached ages at which senescence could be observed. These results support the idea that environmental harshness may influence senescence trajectories in terms of reproductive performance, and potentially longevity (43, 44). Our results show that such patterns can further depend on transgenerational effects of mother age at birth.

We also found that effects of mother age on daughter annual reproductive success depended on the daughter's natal litter size. Litter size at birth negatively impacted annual reproductive success of daughters born to older mothers, but had a positive effect on daughters born to younger mothers. This indicates a trade-off between number and quality of offspring in older females, as previously described in other systems (e.g., red squirrels, *Sciurus vulgaris*; lesser black-backed gulls, *Larus fuscus*; Columbian ground squirrels, *Urocitellus columbianus*; refs. 23, 45, and 46). Older mothers can produce fewer daughters with a higher annual reproductive success, or more daughters with lower annual

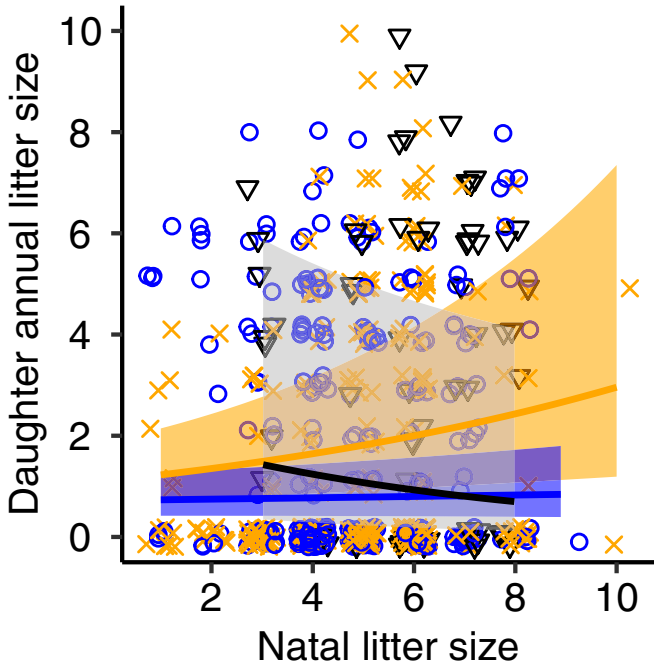

Fig. 2. Daughter annual reproductive success (i.e., annual litter size) as a function of mother age at birth (years) and daughter natal litter size. Daughters were born to young (orange line, shading and crosses; 2 to 4 y), midaged (blue line, shading and empty circles; 5 to 8 y), or old (black line, shading and empty upside-down triangles; 8 y or more) mothers. Shaded areas show prediction approximated confidence intervals, and points show the raw data. Mother age was fitted as a continuous variable and the three mother age categories depicted in this figure were used for illustration purposes.

reproductive success (Fig. 2). There was no evidence of such a trade-off in young mothers.

Taken together, our results show that age-specific variation in daughter annual reproductive success depends on combinations of mother age at birth and current and natal environmental conditions. Studies that assess relationships between mother age and offspring early-life performance may therefore fail to capture the full extent of transgenerational senescence effects, because some effects are only expressed some considerable time post-weaning (i.e., in old offspring) or under specific environmental conditions. Our findings obviously raise the question of what underlies the varying effects of mother age. One mechanism could be that mothers of different ages differentially allocate resources to their own somatic maintenance versus that of their daughters, resulting in offspring that differ in biological age at birth or weaning (18, 47, 48). These possibilities are supported by mechanistic studies of telomeres and oxidative stress (49–52), and are consistent with previous long-term studies of maternal effects on offspring senescence and lifespan (e.g., refs. 16, 53, and 54). For example, offspring born to older mothers had earlier onset and increased rate of reproductive senescence in great tits (16), male common terns (*Sterna hirundo*) that were sired by older fathers had reduced lifespans (54), and female Asian elephants (*Elephas maximus*) born to older mothers had reduced overall survival and lifetime reproductive success (17). Our results then imply that mothers may adjust allocation depending on environmental conditions.

In the case of lower maternal resource allocation, daughters may compensate, for example, through catch-up growth (55), and such compensatory strategies are known to translate into increased costs later in life, including earlier onset and/or increased senescence rates (55, 56). Alternatively, daughters may use reduced maternal allocation as a cue for their future environment and/or somatic state, potentially leading to predictive adaptive responses (refs. 57 and 58). If so, daughters at higher elevation may adopt a life history strategy that matches their anticipated environment and/or future state (e.g., ref. 7). A previous study suggests that female marmots prepare offspring for current environmental conditions through prenatal glucocorticoid levels and by adopting different age-dependent reproductive strategies (59). Such hypotheses require explicit empirical tests, and future studies could do so by experimentally altering environmental conditions and resource availability for mothers and daughters at different times in life (60). The increasing availability of long-term multigenerational datasets from wild populations will also allow comparative analyses across multiple species and environments, to further improve our understanding of transgenerational senescence.

One firm current conclusion is that daughter age-specific reproductive trajectories are associated with mother age at daughter birth, and that these associations vary with environmental harshness. Thus, our study adds insights to the small but growing body of research in natural populations showing that mother age effects can be dynamic and sufficiently long-lasting to affect offspring senescence several years postbirth, as well as offspring fitness, supporting the idea that such transgenerational effects may play an important role in shaping overall senescence (16).

Materials and Methods

Study System. Yellow-bellied marmots are typically polygynous, and most individuals live in colony groups consisting of one or several matrilines (related females), juveniles, yearlings, and a resident adult male that defends its harem. Females are sexually mature from age 2 y, mate after emerging from hibernation in late April or early May, and successfully reproducing females give birth underground to a single litter of 1 to 10 pups, between mid-May and mid-June (61, 62). Pups are nursed for 25 to 35 d and are fully weaned and independent when they emerge from late June to mid-July (63).

The study area comprises a 5-km segment of the Colorado East River Valley (38°57′N, 106°59′W; 2,900 m elevation) and spans two major sites that differ in elevation by about 165 m (hereafter high elevation and low elevation). All females in the current dataset remained in the same elevation site throughout their lives. At high elevation, snowmelt is later, thus delaying and shortening the vegetation growing season (refs. 28 and 63, pp. 119 to 129), and marmots emerge 2 wk later than at low elevation (62, 64).

Data Collection and Organization. Since 1962, every year between mid-May and mid-September, marmots were repeatedly captured on a fortnightly schedule with baited Tomahawk traps at known burrow locations at both elevations. Since newly born litters cannot be accessed underground, pups are first captured at emergence in June or July. During the pup emergence season, colonies were monitored daily to identify and capture new pups within a week of emerging from their maternal burrows. Marmots were studied under University of California, Los Angeles (UCLA) research protocol ARC 2001-191-01 (approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually). Permits were issued by the Colorado Division of Wildlife.

All individuals included in current analyses were first captured as pups at emergence. They were hence of known age, identifiable by uniquely numbered ear tags. Captured individuals were also sexed and dorsally marked with fur dye to allow identification from afar. Offspring were assigned to mothers from behavioral observations, and since 2002, genetic analyses were used to confirm assigned maternities based on a likelihood approach of 8 to 12 microsatellite loci at 95% trio confidence level, which returned 98% congruence with field observations (see methods in ref. 65). As a measure of daughter annual reproductive success, we focused on the number of offspring weaned in a given year (i.e., annual litter size). This is a relevant measure to quantify reproduction, because in female mammals, lactation is the most energetically expensive component of reproduction (66, 67). Thus, even if some unobserved pups died underground prior to emergence, the majority of reproductive costs per litter are likely captured by this measure. Natal litter size of a daughter was defined as the total number of weaned pups in the daughter's birth litter.

Our dataset comprised all observations of sexually mature daughters (i.e., age ≥2 y) for which age of the mother at the time of the daughter's birth was known. Since colonies are monitored intensively and annual recapture probability of adults was estimated to exceed 98% by multistate mark-recapture analyses (68, 69), it is highly likely that unobserved females have died. Based on this, maternal and daughter lifespan were estimated as the age at which a mother or daughter was last observed.

All mother-daughter pairs lived either at high elevation or low elevation throughout their entire lives, and hence experienced the same elevational environment. We only included daughters from cohorts in which almost all individuals were already dead to minimize selective disappearance biases in the data structure. We retained four cohorts that only had one or two surviving individuals (contributing 52 daughters in total).

Data Summary. The data comprised a total of 656 daughter-year observations between 1967 and 2014, for 218 daughters (122 at high elevation; 96 at low elevation), born to 97 different mothers between 1965 and 2008 (*SI Appendix*, Fig. S2*A*). Mother cohorts ranged between 1962 and 2005 (*SI Appendix*, Fig. S2*B*; also see *SI Appendix*, Figs. S3 and S4). The total number of daughters produced per mother ranged between 1 and 46 (median = 4; *SI Appendix*, Fig. S5). Of the 218 daughters, 128 weaned at least one litter during their lifetime (distributions of daughter litter sizes and how they vary with daughter age are shown in *SI Appendix*, Figs. S6 and S7). Each daughter's natal litter size, including the daughter, ranged between 1 and 10 pups (median = 5), and colony density ranged between 1 and 23 sexually mature females (median = 6). Mother and daughter ages ranged from 2 to 13 and 2 to 14 y respectively (median mother and daughter age across all observations = 4.0 and 3.0 y, respectively; *SI Appendix*, Fig. S8).

Statistical Analyses. To quantify elevation-dependent relationships between daughter annual reproductive success and mother age, we fitted a generalized linear mixed-effects model assuming a Poisson distribution with log link. Fixed effects included second-order orthogonal polynomials for mother age and daughter age, elevation as a two-level factor (high vs. low), and natal litter size. The linear and quadratic effects for daughter and mother age were included to test for direct senescence and transgenerational senescence effects. Elevation accounted for the major between-site difference in environmental conditions encountered throughout a daughter's entire lifetime. We included key interactions between these effects to test specific hypotheses. To test if daughters born to older mothers have higher rates of reproductive senescence than daughters born to younger mothers, we fitted two-way interactions between mother and daughter age for both linear and quadratic effects. To test if effects of mother age on daughter

age-specific reproductive success and senescence differ between elevational environments, we fitted three-way interactions of elevation with linear and quadratic mother age and daughter age. To test if effects of mother age on daughter age-specific reproductive success and senescence are affected by natal resource availability, as inferred from natal litter size, we fitted three-way interactions of natal litter size with linear and quadratic mother age and daughter age. If three-way interactions were not significant, we also tested two-way interactions of the environmental variable with linear and quadratic mother age. To account for potential density dependence or reproductive suppression effects on daughter annual reproductive success (as previously reported in yellow-bellied marmots, *M. flaviventer* and Alpine marmots, *M. marmota*; refs. 70 and 71), we additionally fitted the number of sexually mature females within a daughter's colony (i.e., density) in each year of reproduction as a covariate.

Finally, we fitted two further generalized linear mixed-effects models (again assuming Poisson distributions) to test whether mother age at daughter birth affects daughter lifespan and/or lifetime reproductive success (LRS). Daughter LRS was primarily measured as the total number of offspring weaned during a daughter's lifespan (i.e., a time-independent measure). We additionally calculated a time-dependent measure, individual λ, which down-weights offspring born later in life (see ref. 72), but this measure was highly correlated with time-independent LRS (Spearman's *rho* = 0.99, n = 218 daughters). Models for daughter LRS and lifespan included fixed effects of mother age (second-order orthogonal polynomials), elevation, natal litter size, and interactions between elevation and mother age.

To account for nonindependence of repeated observations of individuals, years, and cohorts, models of daughter annual reproductive success included daughter identity nested within mother identity, year, and daughter year of birth as random effects, and models of daughter LRS and lifespan included mother identity and year of birth as random effects. Since estimates of the dispersion parameter (ratio of residual deviance to residual degrees of freedom) indicated overdispersion of daughter annual reproductive success and LRS (ratios of 1.8 and 4.2, respectively), we additionally fitted observation-level random effects in those models (73).

Results are presented for full models, including nonsignificant fixed effects (74). However, to avoid biasing other estimates (75), nonsignificant interactions ($P > 0.05$) were backward eliminated on the basis of ANOVA (type III) tests. When a three-way interaction was significant, all associated significant and nonsignificant two-way interactions were retained. Mother and daughter ages were fitted as orthogonal polynomials up to the second order, which removed the correlation between linear and quadratic age, making them independently interpretable and allowing them to be independently fitted in interactions (76). To facilitate interpretation of coefficients and model convergence, all continuous predictors were scaled and centered with a mean of 0 and a variance of 1. Models were fitted with the glmer function from the package lme4 (77) in R version 3.6.1 (78). Model R^2 values were calculated according to Nakagawa and Schielzeth's method (79), which allows calculation of two types of R^2: marginal R^2 and conditional R^2. The marginal R^2 describes the proportion of variance that is explained by fixed effects only, and the conditional R^2 describes the proportion of variance explained by both fixed and random effects (79).

Finally, because biases can arise in cross-sectional analyses of age effects due to individual heterogeneity and selective disappearance (32, 33), we fitted a series of additional models to different data subsets to confirm effects of polynomial terms and interactions estimated across the full dataset (detailed explanations in *SI Appendix*, "Supplementary analyses: Robustness of observed effects"; *SI Appendix*, Figs. S9–S11 and Tables S4–S11).

Data Availability. The data and code for this study are available through the Open Science Framework at https://doi.org/10.17605/OSF.IO/GU4SP.

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