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ORIGINAL ARTICLE

Sex-specific reproductive strategies in wild yellow-bellied marmots (*Marmota flaviventer*): senescence and genetic variance in annual reproductive success differ between the sexes

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Abstract

Owing to sex-specific reproductive strategies, the mean and variance in annual offspring production may differ between the sexes. In addition, there may be sex-specific changes in reproductive performance with age (e.g. senescence). We used 20 and 50 years of longitudinal data on male and female yellow-bellied marmots, respectively, to investigate sex-specific age effects and genetic variance in annual reproductive success. In both sexes, annual offspring production increased linearly with age until a peak was reached at 7 years. This was followed by a decline in annual offspring production in both sexes, indicative of reproductive senescence. However, the initial increase and the subsequent decline (senescence) in reproductive success were both faster in males compared to females. Genetic variance in annual offspring production was higher in males than in females, but heritability was low for both sexes. Additionally, we found no cross-sex genetic correlation in the number of offspring produced, possibly reflecting sex-specific selection related to the inter-sexual differences in reproductive strategies. There was an effect of year on annual offspring production in both sexes, with a high *yearly* correlation between the sexes emphasizing the importance of environmental variation in determining fitness. Overall, these results demonstrate the impact of sex-specific reproductive strategies on annual offspring production and suggest that male and female marmots may be evolving to separate phenotypic optima. This study further demonstrates the value and limitations of long-term studies investigating sex-based patterns of ageing in the wild.

Significance

This study on yellow-bellied marmots demonstrates the key constraints surrounding the research of age-related changes in reproduction in wild populations, which is especially challenging in males. Among these challenges are high immigration rates which prevent the estimation of exact age and maternal identity. Genetic analysis—the only reliable way to estimate paternity—has only been a recent development, limiting the number of father-son relationships available for analysis. The dataset used in this study is long term (20 years of data on males and 50 on females), partially overcoming these obstacles. Results show that reproductive success declines with age in both sexes, with a faster rate of decline in males compared to females, and is influenced by the environment. Genetically, male and female reproductive success is not correlated, revealing that both sexes may be following separate evolutionary trajectories.

Keywords Polygynous mating system · Life-history strategies · Cross-sex genetic correlation · Quantitative genetics · Long-term data

Introduction

Despite sharing much of the same genetic architecture and expressing similar phenotypic traits, males and females of most animal species differ from one another in a number of ways (Mazer and Damuth 2001; Poissant et al. 2010). This widespread sexual dimorphism in morphology, physiology,

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and/or behaviour typically results from differences in the strength and shape of selection acting on each sex (Shine 1989). Sexual size dimorphism (SSD) in particular has been extensively studied. In extreme cases, one sex may be an order of magnitude larger than the other. For example, in the cichlid fish *Lamprologus callipterus*, males are on average 12 times heavier than females (Schütz and Taborsky 2005). Sexual dimorphism may also be present in life history strategies, such as: (1) age at maturity (e.g. earlier in male than female Atlantic salmon (*Salmo solar*); Fleming 1996), (2) survival (e.g. male-biased mortality in multiple vertebrates; reviewed in Clutton-Brock and Isvaran 2007), (3) longevity (e.g. female-biased longevity in mammals; Lemaître et al. 2020), and (4) reproductive strategies (e.g. despite lifetime reproductive success of most male elephant seals (*Mirounga angustirostris*) being zero and most females reproducing each year, the theoretical maximum number of offspring a male can sire can be 17 times higher than females; Le Boeuf 1974).

With respect to sex-specific reproductive strategies, considerable differences between the sexes in the annual number of offspring produced may occur. For example, in polygynous species, the number of offspring a male sires annually primarily depends on the number of mating partners acquired during the breeding period, while females are limited by physiological and/or environmental factors (e.g. reproduction restricted by food abundance (Armitage, 2014)). Therefore, the maximum number of offspring a male can produce is higher than that of females. In addition, given that the adult sex ratio is mainly biased towards females in polygynous species, the mean number of offspring produced annually by males will be higher than that of females. Further, in polygynous mating systems, high male-male competition for access to females also drives variance in both male annual reproductive success (ARS) and lifetime reproductive success (LRS), with a few males producing the majority of the offspring (Andersson 1994). Collectively, these sex-specific differences lead to different resource allocation in reproduction between the sexes: Males incur high physical and energetic costs of intra-sexual competition (e.g. injuries, prolonged fasting, increased parasitization; Clutton-Brock and Isvaran 2007; Lloyd et al. 2020), while for females, the costs of reproduction stem from gestation, lactation, and parental care (Nussey et al. 2009; Lloyd et al. 2020).

These sex-specific energetic investments in reproduction will lead to sex-specific trade-offs with other life-history traits such as growth, survival, and future reproduction (Stearns 1992). For example, trade-offs between current and future reproductive success and survival can occur if individuals invest energy and resources into reproduction early in their lives, thereby leaving fewer resources available for the future. Early-life investments may include an earlier age at first reproduction or higher early-life fecundity, which has been associated with decreased survival or reproductive success in later life (Nussey et al. 2006). For example, Lemaître et al. (2014) reported that male red deer (*Cervus elaphus*) that invested early in reproduction experienced greater declines in reproductive success than those that did not. This "live fast, die young" strategy can occur in both sexes, but is generally predicted to occur in males as a consequence of their reproductive strategy (Travers et al. 2015), which results in an earlier onset of senescence (Lemaître et al. 2020). Senescence is defined as "a within-individual process caused by deterioration in molecular and physiological function" resulting in a decrease in survival probability and reproductive output with age (Nussey et al. 2008). While the onset of senescence is generally predicted to be earlier in males than in females, sex differences in the rate of senescence can vary between species and populations (Lemaître et al. 2020). These differences are driven by variations in the immediate environment and/or different selection pressures between populations resulting in faster senescence in males compared to females, faster senescence in females compared to males, or the same rate of senescence between the sexes (Lemaître et al. 2020). Specifically, in wild populations that live in severe environments, the rate of senescence is expected to be faster in males (Lemaître et al. 2020). For example, Nussey et al. (2009) reported that in a wild population of red deer living in a harsh environment (Clutton-Brock et al. 1982), males experienced a faster rate of senescence than females. Indeed, reproductive success is expected to decline rapidly with age from repeated male-male competitions incurring accumulated costs, which will hamper a males' ability to acquire and defend females over time (Clutton-Brock and Isvaran 2007; Nussey et al. 2009). The reproductive success of females will also decline with age, caused by declining oocyte numbers, as well as cost and damage accumulation (Nussey et al. 2009). Males are therefore expected to experience higher fitness if they invest more heavily in current reproduction at the expense of future reproduction and survival, while females will produce more offspring by living longer. Thus, owing to differences in reproductive costs and benefits between males and females (Trivers 1972), the rate and onset of senescence may be sex-specific (Bonduriansky et al. 2008).

From an evolutionary standpoint, fitness traits shared between the sexes (such as offspring production) may be subject to positive, negative, or null genetic correlations, and similar or opposing selective pressures (Kruuk et al. 2008). In cases where the fitness optima of a shared trait differ between the sexes (Parker 1979), intra-locus sexual conflict is predicted. The evolution of sexual dimorphism may partially or fully resolve this conflict, the presence of which can be assessed via cross-sex genetic correlations (r_{MF}; Lande 1980). An r_{MF} approaching one indicates shared genetic architecture between the sexes, suggesting the presence of sexual conflict and constraints on sex-specific evolution

(Poissant et al. 2010). An r_{MF} less than one would mean that each sex may evolve to their own sex-specific selection optimum, a potential resolution to the conflict (Poissant et al. 2010). Few studies have estimated the genetic variance of traits associated with reproductive success and their genetic correlations in both sexes in the wild (Bonduriansky and Chenoweth 2009). Wolak et al. (2018) found a potential positive cross-sex genetic correlation in fitness in a wild population of song sparrows (*Melospiza melodia*) suggesting that positive selection on fitness in one sex may lead to an associated increase in the other. In addition, some laboratory studies have showed intra-locus sexual conflict. Chippindale et al. (2001) found the presence of intra-locus sexual conflict in a population of *Drosophila melanogaster.* They reported a negative correlation for fitness between the sexes in adults, indicating that selection for higher fitness in one sex would lead to decreased fitness in the other (Chippindale et al. 2001).

Despite predictions on sex-specific differences in reproductive success, empirical analysis of reproductive success on both sexes are lacking in wild populations. Long-term studies collecting data on the same individuals over multiple reproductive attempts in the wild are still relatively rare. Furthermore, constraints to collecting life history data in males (e.g. high immigration, relatively recent implementation of molecular paternity assessment) have prevented detailed analysis in both sexes (Murgatroyd et al. 2018). Here, we analyse 50 years of data on reproductive success in females and 20 years of data on reproductive success in males originating from a longitudinal study on yellow-bellied marmots (*Marmota flaviventer*; hereafter marmots).

Marmots are sexually dimorphic, reach sexual maturity at 2 years old, and live up to 15 years in the wild. They have a harem-polygynous mating strategy: Males will compete with one another over access to matrilines consisting of groups of related females (Armitage 2000, 2014). Colonies are thus composed of matrilines and one or more reproducing males. Importantly, only 15.6% of male marmots survive to reproductive maturity (Armitage 2014) and are typically immigrants to the site (Armitage and Downhower 1974). As such, the reproductive success of males is mainly determined by their ability to survive until reproductive maturity and subsequently acquire and defend a territory with females (Armitage 2014). In contrast, the reproductive success of females is influenced by the presence (or absence) of male and environmental factors such as extended periods of snow cover following emergence (Armitage 2014). Sex differences in reproductive resource allocation are therefore expected in marmots, which may result in different onsets and rates of senescence between the sexes.

In this study, we compared the annual number of offspring produced by male and female marmots and analysed the sex-specific impacts of age. Using a quantitative genetic approach, we also estimated the sex-specific genetic variance in annual reproductive success and the associated cross-sex genetic correlation. We predicted that male marmots would have an earlier onset and faster rate of senescence compared to females due to the increased cost of reproduction for males in this harem-polygynous mating system. Further, we predicted a null cross-sex genetic correlation because of the differences in sex-specific reproductive strategies of this species.

Methods

Study site and subjects

Yellow-bellied marmots have been studied in and around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, in the Upper East River Valley since 1962. The Upper East River Valley is divided in two parts, an up-valley and down-valley, that differ in elevation, phenology, and human disturbance. Colonies were found between 2,700 and 3,100 m.a.s.l. (Armitage 2014). Marmots are large (3–5 kg), semi-fossorial, sciurid rodents which live in colonies that consist of one or more matrilineal groups. Marmots are active from mid-April to mid-October and hibernate through the winter (Blumstein et al. 2006). We live-trapped marmots on a regular basis (approximately fortnightly) throughout the active season using Tomahawk traps. During the first capture, individuals were marked with numbered ear tags for permanent identification, and fur dye (Nyanzol D) was applied to facilitate identification from afar for social observations (Blumstein et al. 2013). Beginning in 2001, we also took a hair sample for genetic parentage assignments at first trapping. At each trapping, individuals were weighed to the nearest gram, sexed, and assessed for their reproductive status. Most adult females (83%) were trapped for the first time as juveniles and are of known age, whereas adult males are often immigrants (37%). Immigrants and individuals not captured as juveniles are assumed to enter the population at 2 years old or older (Armitage 2014). Given that all individuals must be identified to estimate their survival and reproduction, we are unable to use blinded methods.

Pedigree

Because juveniles were trapped the first time they emerged out of their maternal burrow, we were able to behaviourally match juveniles to mothers. Given the marmot reproductive system, however, paternities can only be inferred using a genetic approach. Before 2000, maternity was assigned behaviourally and paternity was unknown (Armitage 2014). Since 2000, genetic parentage assignments were used for both maternities and paternities. Detailed methods are described in Blumstein et al. (2010); Lea et al. (2010), and Olson et al. (2012). We extracted DNA using Quigen QIAamp DNA Mini kits and genotyped individuals at 12 hypervariable microsatellites. We used GENEMAPPER to visualize and score alleles, and we used CERVUS 3.0 (Kalinowski et al. 2007) to confirm maternity and used a maximum likelihood method at 95% trio confidence to match paternity. A list of candidate dams was chosen based on nipple size measurement taken during trapping and handling, while candidate sires were based on larger geographic location (up vs. down valley). Because we regularly trapped and observed marmot colonies, we assumed a sampling proportion of 99% for candidate mothers and 96% for candidate fathers. Since 2000, genetic assignment confirmed the behavioural observations in over 96% of cases indicating that the method used for maternal assignment was not impacting the estimation of reproductive success for females. Given that before 2000 maternities were assigned behaviourally, analyses were restricted to the main colonies where recapture rate is over 95% and pups were easily assigned to a mother based on behavioural observations.

Analyses

To look at the differences between the sexes in annual reproductive success (ARS), we fitted a model of the number of offpsring as a function of sex using a generalized linear mixed model with a Poisson error distribution. We included a linear and quadratic effect of age, along with the interaction of both with sex to estimate sex differences in ageing. To account for environmental variation due to elevation, we included a fixed effect of valley position (up-valley or down-valley). For females only, we also included mass in June as a fixed effect because females are capital breeders. Capital breeders use stored energy towards reproduction, and this creates a trade-off between current and future reproduction (Stearns 1992). June mass reflects the energy available for reproduction and is estimated from best linear unbiased predictors from a linear mixed effects model for each individual each year based on 2 to 8 masses per individual (Kroeger et al. 2018a). Body mass is therefore a key factor in determining whether or not females reproduce and may further determine the quantity of resources available for young. Given that male trappability is much lower than that of females, and mass estimations are not available for all males each year, we did not include June mass for males. Age and mass were mean-centered and scaled to a variance of 1 in all models. In addition to these fixed effects, we estimated the sex-specific additive genetic (V_A, identity linked to pedigree), permanent environment (V_{PE}, identity), and year (V_{Y}) variances as well as the genetic and year cross-sex correlations. Variance parameters were estimated as the posterior mean and reported with their 95% highest posterior density intervals (HPDI). We did not include age at first reproduction or age at death (van de Pol and Verhulst 2006) because previous studies on females showed that these factors have no or weak effects on senescence estimates in this population (Kroeger et al. 2018b). These terms were also not included in our model on males because exact age is unknown for 51 out of 163 adult males (31%). Variance ratio estimates were calculated as the proportion of the total phenotypic variance explained by the corresponding variance component. For example, heritability was conditional to the variance explained by the fixed effects and estimated as the additive genetic variance divided by the total phenotypic variance. Evolvability was estimated as the additive genetic variance divided by the squared population mean. Since fitness components are not on a continuous scale (count data with Poisson distributions), variance components, heritability, and evolvability were first estimated on the latent scale. All analyses were done in R v.4.1.2 (R Core Team 2021) with the main analysis done in the MCMCglmm package v.2.33 (Hadfield 2010). We estimated the heritability and evolvability on the observed scale using the QGglmm package v.0.7.4 (de Villemereuil et al 2016). All variance ratios were estimated for the entire posterior distribution and reported as posterior mean with 95% HPDI.

For residuals and permanent environment effects, the cross-sex correlation cannot be estimated, thus fixed to 0, and we used standard priors with $V = \mathrm{diag}(2)$, nu = 1.002, that are weakly informative for the variance parameters. For random effects for which a cross-sex correlation can be estimated, it is possible to use parameter expanded priors (e.g. V = diag(2)*0.002, nu = 3, alpha.mu = rep(0,2), and an alpha.V = diag(2) * c(1000)) to get a weakly informative (flat) prior on the correlation scale. However, those priors tend to be quite informative for small variance values (high frequency of values below 0.01) which might be problematic when variance parameters are small (e.g. for genetic effects). Thus, we used standard priors for the genetic effect and parameter expanded priors for the year effect. It should be noted that using parameter expanded priors for genetic variance provided similar results (Appendix Table S1). All models sampled every 2000 iterations with a burn-in of 50,000 iterations for a total of 1500 samples. We visually checked trace plots and all models had an autocorrelation under 0.10. We also used the Heidelberger and Welch's convergence diagnostic (heidel.diag() function) to verify model convergence (Hadfield 2010).

Ethical note

Traps were set in the morning and afternoon near burrow entrances and checked after 2–3 h. Traps were provided shade on warm days and closed during inclement weather. After trapping, individuals were released immediately at the trap location. Marmots were handled quickly, typically 5–15 min depending upon data collected. All individuals were handled in a cone, cloth bag to reduce stress. We swabbed all ears with alcohol before administering ear tags. All handlers were trained by DTB, JGAM, or senior personnel. Although not formally tested, we see no obvious long-term effect of trapping and handling on marmot survival or reproduction (JGAM personal comm.).

Results

Our dataset included 163 males and 358 females. Males and females showed both a positive linear and negative quadratic effect of age in the number of offspring produced. There were inter-sexual differences in both the linear and quadratic effect of age (significant interactions with sex; Table 1; Fig. 1). According to the model, both sexes had peak reproductive output at age 7 with a faster increase and decrease for males (Fig. 1). For females, there was no effect of mass in June. Based on raw data, the average number of offspring for males across all ages was 4.679 (± 6.687 SD). It peaked at age 10 (mean ± SD: 14.25 ± 9.67) and was lowest at age 2 (mean ± SD: 1.506 ± 3.389). No males aged 12 or 13 successfully reproduced. Average adult male longevity was 3.03 (± 1.74 SD), and 25% of 2-year-old males died at or after 4 years old. Based on raw data, across all ages, females averaged 2.124 (± 2.564 SD) offspring per year and had a peak number of offspring at age 8 (mean ± SD: 3.466 ± 3.123) and were lowest at age 2 (mean ± SD: 1.213 ± 2.121). No females older than 14 successfully reproduced. Adult females had an average longevity of 4.023 (± 2.41 SD) years and 25% of those who made it to 2 years old died at 6 years old or older.

Table 1 Estimates and 95% credible intervals for the relationship between fixed effects and the annual number of offspring for both males and females in yellow-bellied marmots at Rocky Mountain Biological Laboratory

Fixed effect	Posterior mean estimate	95% lower CI	95% upper CI
Sex (F)	− 0.251	− 0.584	0.051
Sex (M)	0.393	− 0.214	1.003
Valley (Up)	− 0.178	− 0.578	0.226
Age	**0.265**	**0.134**	**0.411**
Age^2	**− 0.271**	**− 0.384**	**− 0.146**
Sex (M) * valley (Up)	− 0.611	− 1.429	0.186
Sex (M) * age	**0.423**	**0.104**	**0.689**
Sex (M) * age^2	**− 0.492**	**− 0.761**	**− 0.205**
Female mass in June	0.172	− 0.059	0.369

Estimates that exclude 0 were deemed significant and are in bold. Female is the reference level. Valley is a factor with 2 levels down and up valley, down valley being used as the reference

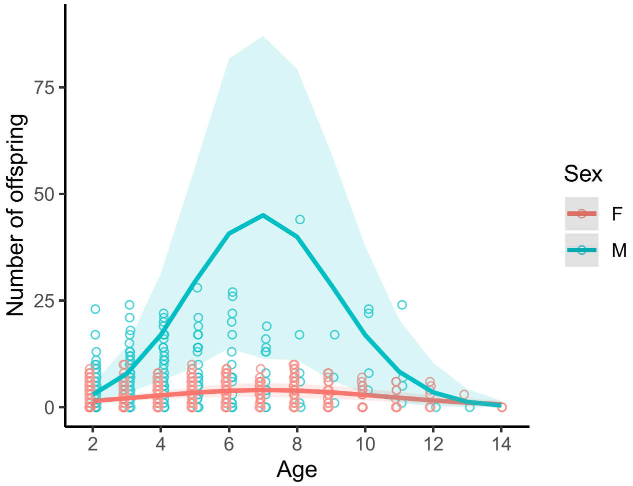

Fig. 1 Relationship between age and number of offspring produced for both males and females. Points are raw data. Lines and 95% credible intervals are based off of predicted values from males and females located down valley. Females were considered of average mass (scaled mass = 0). Males are in turquoise and females in red

We found large year effects in both sexes with a strong positive correlation between the sexes suggesting that yearly environmental conditions play a large role in the number of offspring produced for both sexes (Table 2; Fig. 2b). We found low, but non-zero additive genetic variance for both sexes (Table 2; Fig. 2a). The cross-sex genetic correlation was estimated close to zero with a wide credible interval that included zero (Table 2; Fig. 2a). All variance parameters for males (additive genetic, permanent environment, year, and residuals) were larger than estimates for females (Table 2), indicating that the annual reproductive success of males is more variable than that of females. The heritability estimated on the latent scale was similar for both sexes at around 0.17 (Table 2). However, compared to the latent scale, heritability on the observed scale was much smaller in both sexes, but larger for females than for males (Table 2). When looking at the evolvability, males had a lower estimate on the latent scale than females but a much larger estimate on the observed scale.

Discussion

Using 20 and 50 years of longitudinal data on male and female marmots respectively, this study examined the sex-specific patterns of age-related change in annual reproductive success. As predicted, the ageing patterns of offspring production differed between males and females, reflecting their sexually dimorphic reproductive strategies. Contrary

Table 2 Estimates and 95% credible intervals for variance components and variance ratios of annual reproductive success for both males and females in yellow-bellied marmots at Rocky Mountain Biological Laboratory

Effects	Male Mean estimate	Male Lower 95%CI	Male Upper 95%CI	Female Mean estimate	Female Lower 95%CI	Female Upper 95%CI
V_A	0.578	0.100	1.311	0.381	0.136	0.645
V_{PE}	0.781	0.159	1.548	0.230	0.074	0.413
V_Y	0.540	0.052	1.197	0.269	0.086	0.493
Residual	1.658	1.067	2.284	1.241	0.954	1.531
Cor genetic	−0.175	−0.663	0.578			
Cor year	0.677	0.139	0.986			
h^2	0.162	0.031	0.335	0.179	0.068	0.287
h^2_{obs}	0.018	0.001	0.041	0.049	0.019	0.079
pe^2	0.219	0.048	0.399	0.108	0.039	0.194
y^2	0.147	0.0263	0.304	0.126	0.041	0.216
I_A	0.026	0.005	0.060	0.085	0.030	0.143
I_{Aobs}	0.578	0.100	1.311	0.381	0.136	0.645

The upper half includes the estimated variance components, including additive genetic (V_A), permanent environment (V_{PE}), year (V_Y), and residual variance, and the cross-sex genetic and year correlations. The bottom half includes the estimated effect ratios adjusted heritability (h^2), heritability on the observed scale (h^2_{obs}), permanent environment (pe^2), and year effects (y^2). We also provide the evolvability on both the latent (I_A) and observed (I_{Aobs}) scales

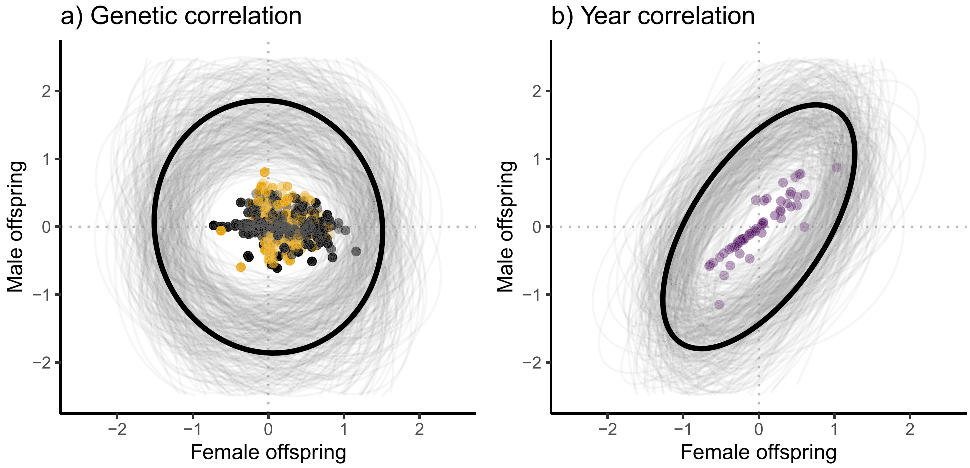

Fig. 2 The (**a**) additive genetic and (**b**) year cross-sex variance matrices of annual reproductive success. Points in each graph are the posterior mode of the best linear unbiased predictors (BLUPs) from the bivariate models. Points in yellow are males, in black are females and purple are years. Bold ellipses represent the posterior mode of the variance matrices, while grey ellipses are from 300 randomly selected estimates from the posterior distribution. Grey ellipses offer a sense of uncertainty around the estimate

to our prediction, age at onset of senescence was similar in both sexes, but, as predicted, there were sex differences in the rate of senescence. Males dramatically increased offspring production from age 2 until age 7, at which point production drastically declined (Fig. 1). Females experienced a more subtle increase in offspring production from age 2 until age 7, followed by a gradual decline (Fig. 1). These results suggest that both females and males experience reproductive senescence, but males senesce at a faster rate compared to females. Additionally, the sexes differed in their genetic variance for annual reproductive success, with higher genetic variance in males compared to females. Finally, and in line with our prediction, there was no cross-sex genetic correlation, but a strong yearly cross-sex correlation in offspring production. Respectively, these results demonstrate that the sexes may evolve differently and that environmental conditions greatly impact offspring production in this population.

There was a linear increase in the annual number of offspring produced until 7 years of age in both females and males (Fig. 1). This increase was substantially larger in males than in females because of the difference in mean number of offspring produced at peak age (Fig. 1), suggesting that while both sexes improve their breeding success with age until a peak of performance is reached, the effect is stronger in males (Fig. 1; Table 1). This increase in both sexes at younger ages may be explained by the constraint hypothesis, which proposes that new breeders may be limited by a lack of experience or skills necessary for reproduction (Curio 1983). The constraint hypothesis further predicts that individuals will develop strategies to increase their reproductive success as they gain experience (Dugdale et al. 2011). In females, this experience gain may be related to improvements in individual foraging capacities, increases in the ability to provide maternal care in multiparous versus primiparous mothers (e.g. reindeer (*Rangifer tarandus*); Weladji et al. 2006), or a greater ability to suppress reproduction among younger females. In males, the gain in reproductive success might reflect better fighting abilities, continuous mass gain, experience, and the ability to better defend their harem (e.g. elephant seals (*Mirounga leonina*); Lloyd et al. 2020). The apparent increase with age in reproduction for males might also be a population effect only and could be driven by the disappearance of males who do not reproduce. Of males that reach 2 years old, 75% die before the age of 4, and most do not reproduce.

Following this increase in reproductive success, both males and females experienced a decline in reproductive output, albeit with larger confidence intervals in males than females. This suggests that both sexes experience reproductive senescence, with a marked decline in offspring production in the last years of life. The rate of this reproductive senescence was faster in males compared to females (Table 1; Fig. 1). However, 92% of those males who survived to 2 years old, died at or before they were 6 years old, whereas in females, 20% of those who survived to 2 years old, died at 7 years or later. These results suggest that relatively few males reached senescence age, but quite a few females did. These findings were in line with our prediction and can be expected due to the mating system of this species and the resulting differences in reproductive strategies between the sexes. In females, reproductive senescence may be expected due to physiological costs accumulation or declining oocyte numbers with age, while in males, faster senescence may be attributed to the higher costs of reproduction (Clutton-Brock and Isvaran 2007; Nussey et al. 2009). Despite both sexes incurring comparable reproductive costs (Armitage 2014), male marmots may pay these costs for longer than females do, as they need to defend territories throughout the active season (Armitage 2004). Hence, males may have a higher overall cost of reproduction than females. Alternatively, the ageing pattern in males may be explained by the "live fast/die young" hypothesis (Travers et al. 2015), where those males that monopolize access to reproduction at a young age reproduce for a few years and die shortly after. This may partly explain the observation that 92% of adult males die by age 6. In addition, we report that male marmots have both a higher average and variance in the number of offspring produced compared to females. This pattern can be explained by a few males successfully monopolizing females and thus producing the majority of the offspring, while those that do not will produce few to none. However, these results should be interpreted with caution (see detailed discussion of the limitations of data collection in males below) given the relatively small number of males reaching senescence age and the large confidence intervals.

These sex-specific reproductive strategies were also reflected by differences in the additive genetic variance, an absence of a cross-sex genetic correlation, and differences in the permanent environment effect. Males had a higher estimate of additive genetic variance compared to females, but with a wider credible interval. Heritability estimates were low for both sexes, which is not surprising because fitness traits often have relatively low heritabilities (Merilä and Sheldon 2000). The evolvability of the trait on the observed scale was non-negligible and larger in males than in females. Taken together, these results indicate a potential for selection and evolution of traits related to reproductive success in both sexes in marmots. Additionally, the absence of a cross-sex genetic correlation shows that reproductive success could evolve independently across the sexes and should facilitate the evolution of different fitness optima. This absence of cross-sex genetic correlation also strongly suggests that the suite of traits determining annual reproductive success also differ across the sexes, with these traits being dimorphic or a different suite of traits entirely. One might thus expect that behavioural phenotypes differ across sexes to maximize annual reproductive success with behaviours associated with risk taking, aggressivity, exploration, and boldness favoured in males compared to females. There was also a significant permanent environment effect in both sexes (larger in males than in females) indicating developmental plasticity and an impact of early-life environment on reproductive success later in life. It is possible that the lower depth in the pedigree in regard to father-son relations, smaller sample size, and potential errors in genetic parentage assignment might have inflated the permanent environment variance for males. Longer data collection with more individuals would thus be required.

Further, the year of measurement explained 14% and 12% of the variance in annual reproductive success in males and females, respectively (Table 2). This is unsurprising since the reproductive success of female marmots is influenced by environmental factors such as extended periods of snow cover following emergence (Armitage 2014). Consequently, fat reserves are depleted, limiting and even preventing reproduction due to a lack of expendable resources (Armitage 2014). Coupled with this result is a strong and significant year correlation between males and females. Such a correlation suggests that in years where females have high annual reproductive success, the few successful males in the population will also experience heightened reproductive success. These results point towards the importance of environmental effects in driving inter-individual variation in the number of offspring produced.

Despite annual data collection since 1962, this dataset is subject to many of the common limitations affecting long-term studies, resulting in 50 years of data on females but only 20 on males. This reduction in sample size for males is due to genetic paternity assignment only beginning in 2000, which is the only reliable way of determining paternity in polygynous species. A further reduction of the sample size in males occurred as a result of the harem-polygynous mating system: only a few males reproduce each year. Consequently, not only is the absolute sample size smaller in males than in females (163 versus 358 individuals, respectively), but there are also substantially fewer males reproducing within each age class, and especially so in the older age classes (Fig. 1). This may impact the power of the study and may potentially explain the large confidence intervals that are reported in Tables 1 and 2. In addition, most reproducing males are immigrants to the study sites (Armitage 2014), and thus, their pedigrees and life histories (including age) can be less precise. The effect of mass could only be estimated in females as males often die early in the season, after reproducing but before they are weighed. It is only because our system has such a long-term pedigree that we are able to quantify sex- and age-specific effects and estimate heritability in this population (Clutton-Brock and Sheldon 2010). As more data become available, estimates may become more precise. For instance, by excluding the last 5 years of available data from analysis, the effect of senescence and additive genetic variance in males was masked, suggesting that even a few additional years of data will allow for much greater power and precision.

Overall, these results demonstrate that the ageing patterns of annual offspring production in marmots are sex-specific, with both sexes experiencing reproductive senescence at different rates despite similar ages of onset. These results emphasize how different reproductive strategies and environmental conditions affect annual offspring production in both sexes. We encourage future work on decomposing the effect of environmental variation on offspring production in both sexes and age classes within. Other measures of reproductive success such as the number of offspring that survive to reproductive maturity should also be examined, as these may better represent fitness. Given the null cross-sex genetic correlation reported here, future work on fitness and fitness-related traits in yellow-bellied marmots should examine males and females separately given that they may be evolving to their own sex-specific phenotypic optima. Finally, these results should be reexamined when additional data on males become available, as precision may increase, and additional effects may be modelled.

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Author contribution SSL, MND, MP, and JGAM developed the idea of the study. SSL, MNP, and JGAM ran the analysis. SSL and MND wrote a first draft of the manuscript, and all authors contributed to develop and write the manuscript. SSL and MND had similar contributions to the manuscript.

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Data availability The data and code for this study are available on OSF https://doi.org/10.17605/OSF.IO/VSBMA.

Declarations

Ethics approval All applicable national and institutional guidelines for the use of animals were followed. Marmots were studied under ARC protocol 2001–191-01 by the University of California Los Angeles Animal Care Committee on 13 May 2002, and renewed annually, as well as annual permits issued by the Colorado Division of Wildlife (TR917) and the Rocky Mountain Biological Laboratory's Animal Care Committee.

Conflict of interest The authors declare no competing interests.

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