OPTIMAL REPRODUCTIVE STRATEGY IN YELLOW-BELLIED MARMOTS: UNVEILING THE CONSEQUENCES OF AGE AT FIRST REPRODUCTION ON SURVIVAL AND LIFETIME REPRODUCTIVE SUCCESS

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Abstract

When to reproduce for the first time is a key question in evolutionary ecology. Indeed, age at first reproduction has clear impacts on population dynamics and fitness. Breeding early in life may impair survival due to a resource allocation trade-off between survival, growth, and reproduction. Postponing reproduction, however, reduces reproductive opportunities and increases the chances of dying before reproducing. Here, I investigate the consequences of age at first reproduction on both survival and lifetime reproductive success by using long-term monitoring data of a population of yellow-bellied marmots (*Marmota flaviventer*) at the Rocky Mountain Biological Laboratory (Colorado, USA). Mixed models were employed to analyze the relationships between age at first reproduction in females and their lifetime reproductive success, as well as three survival components: longevity, the number of years after first reproduction, and annual survival probability. The results showed that postponing reproduction until 2 years of age increased longevity, but delaying it beyond 2 years did not yield additional survival benefits. Females reproducing for the first time after 3 years exhibited high rates of actuarial senescence. Furthermore, delaying first reproduction beyond 3 years old did not lead to a compensatory increase in lifetime reproductive success that would offset the reduction in survival associated with postponing first reproduction. These results suggest that the optimal age at first reproduction, in terms of survival and reproductive success, is 2 years. The reproductive strategy might be governed by body condition or environmental factors. These findings shed light on the trade-offs between early reproduction and survival, as well as reproductive success, illustrating the complexity of reproductive strategies in relation to individual fitness.

Résumé

Quand débuter la reproduction est une question clef en écologie évolutive. En effet, l'âge à la première reproduction a des répercussions évidentes sur la dynamique des populations et l'aptitude phénotypique d'un individu. Une première reproduction à un jeune âge peut nuire à la survie en raison d'un compromis d'allocation des ressources entre la survie, la croissance et la reproduction. Cependant, le report de la reproduction réduit les opportunités de reproduction et augmente les chances de mourir sans avoir produit de rejetons. J'étudie ici les conséquences de l'âge à la première reproduction sur la survie et le succès reproducteur à vie à partir d'un suivi à long-terme d'une population de marmottes à ventre jaune (*Marmota flaviventer*) au Rocky Mountain Biological Laboratory situé au Colorado (États-Unis). Des modèles mixtes ont été utilisés pour analyser les relations entre l'âge à la première reproduction et le succès reproducteur à vie ainsi que trois aspects de la survie des femelles: la longévité, le nombre d'années après la première reproduction et la probabilité de survie annuelle. Les résultats ont montré que reporter la reproduction à l'âge de 2 ans augmentait la longévité, mais que la décaler au-delà de 2 ans n'apportait pas de bénéfices supplémentaires en termes de survie. Les femelles se reproduisant pour la première fois après 3 ans présentaient des taux élevés de sénescence actuarielle. De plus, retarder la première reproduction au-delà de 3 ans n'entraînait pas d'augmentation compensatoire du succès reproducteur à vie qui aurait compensé la réduction de la survie associée au report de la première reproduction. Cela suggère un âge optimal à la première reproduction de 2 ans pour la survie et le succès reproducteur. La stratégie reproductive pourrait être régie par l'état corporel ou des facteurs environnementaux. Cette étude expose les compromis entre la reproduction précoce et la survie ainsi que le succès reproductif et illustre la complexité des stratégies de reproduction.

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These acknowledgements would not be complete without mentioning the open software I used: R and RStudio. I also would like to thank the development team of the powerful — and quite worrying — Open AI ChatGPT for the help it provided me for coding, sometimes. I sincerely hope people will use it wisely and I look forward to seeing the evolution of this platform.

I would finally like to express my thanks to my dedicated coffee machine for keeping me sharp when needed and providing me with the truly required energy potion to get through this degree.

Introduction

In a place without much light, a shark can live as long as an estimated 392 years (Nielsen et al., 2016). The Greenland shark (*Somniosus microcephalus*) matures at an estimated 150 years and can give birth to 200 to 700 pups (Augustine et al., 2017; Nielsen et al., 2016). In comparison, fruit flies (*Drosophila melanogaster*) mature in about two weeks, have a lifespan of 40-50 days, and lay a hundred eggs a day. These tremendously contrasting life history strategies — age- and state-specific patterns of resource allocation — highlight an extreme, yet interesting, diversity of life.

Life history theory seeks to understand how resource allocation varies among diverse traits throughout the lifetime of individuals to shape life history strategies. The theory assumes that time and resources are limited, and thus should be allocated strategically among growth, survival (self-maintenance), and reproduction in a way that maximizes fitness (Bell, 1980; Stearns, 1992; Williams, 1966). Trade-offs then occur when an investment of limited resources into one component comes at the expense of others (Stearns, 1992), due to the principle of energy allocation (Levins, 1968; Williams, 1966). The distribution of resources in animals revolves around maximizing benefits and mitigating fitness costs at each age.

Reproduction plays a pivotal role in the evolution of life history strategies; it directly affects individual fitness and the evolutionary success of a species. In addition, divergent reproductive strategies involve different costs and benefits (Bell, 1980; Stearns, 1992; Williams, 1966). Costs of reproduction are divided into two major categories: cost in survival and cost in future reproduction (Bell, 1980; Stearns, 1992). If reproduction is not costly, natural selection should favor individuals that start reproducing at the earliest opportunity and invest in reproduction as much as possible (Bell, 1980; McGraw &

Caswell, 1996; Sibly & Calow, 1986). However, the first reproduction in an individual's life has been shown to be costly in many species, both in terms of survival (Blomquist, 2009; Descamps et al., 2006; Festa-Bianchet et al., 1995; Reiter & Le Boeuf, 1991) and reproductive success (Clutton-Brock et al., 1983; Green & Rothstein, 1991), because of trade-offs between self-maintenance, growth and reproductive activities over a shared pool of limited resources. One way to reduce reproductive costs is by delaying first reproduction (Bell, 1980; Stearns, 1992), a strategy employed by a variety of taxa and commonly found in hibernators (Findlay-Robinson et al., 2023).

For iteroparous species, age at first reproduction (AFR) is linked to multiple trade-offs. Indeed, individuals must balance investment of resources in breeding early in life to maximize current reproductive success, or postponing reproduction to optimize future reproductive potential (Bell, 1980; Stearns, 1992). Maturing early eliminates the risk of dying without reproducing and increases the number of reproductive events. Conversely, delaying reproduction provides additional time for achieving sexual maturity, acquiring sufficient resources, and obtaining more experience, thereby increasing the chances of successfully reproducing. For species that can start to reproduce prior to reaching adult body size, maturing later allows the completion of somatic growth, thereby eliminating the trade-off between growth and reproduction (Bell, 1980; Stearns, 1992). For species with only a single breeding event per year, delaying reproduction can further erode individual fitness, especially in low annual survival conditions. Hence, there is a delicate balance in AFR to optimize fitness while reducing the costs of the initial breeding event.

In those trade-offs involved in AFR, the intra-individual trade-offs between early reproduction and survival, and between current and future reproduction are of great importance. Each strategy is associated with its own set of benefits and costs, showing the significance of studying the life history consequences of AFR. It is also a crucial trait as it impacts individual fitness and population dynamics (Proaktor et al., 2008; Sæther et al., 2013). Indeed, the growth rate and age structure of a population are sensitive to the recruitment rate (Ozgul et al., 2007), which, in turn, is influenced by AFR.

The existence and magnitude of the trade-offs in AFR vary among and within species. On the one hand, there are examples of systems that failed to find an effect of early reproduction on females' survival; this is the case for Columbian ground squirrels (*Urocitellus columbianus*; Neuhaus et al., 2004), southern elephant seals (*Mirounga leonina*; Oosthuizen et al., 2019), reindeers (*Rangifer tarandus*; Weladji et al., 2008) and bighorn sheep (*Ovis canadensis*; Martin & Festa-Bianchet, 2012) for example. On the other hand, effects of early maturity were found in Asian elephants (*Elephas maximus*; Hayward et al., 2014), Northern elephant seals (*Mirounga angustirostris*; Reiter & Le Boeuf, 1991), and Wandering Albatross (*Diomedea exulans*; Fay et al., 2016). Hamel and collaborators (2010) extended these results by linking reproductive costs with the "life speed" of mammalian species. They suggested that long-lived species adopt a conservative strategy, prioritizing survival over reproduction, while fast-lived species invest heavily in reproduction at the expense of survival. The general conclusion is often that maturing early confers a fitness advantage and should be selected for (Bell, 1980). These conflicting viewpoints regarding the impacts of AFR illustrate the importance of better understanding the consequences of AFR in more species.

In most studies on large mammals, the first reproduction is defined as the time when the first juveniles are born, therefore measuring the first parturition. In small mammals, particularly rodents, age at first weaning is often used instead, which occurs later in the reproductive process. However, the ability to detect costs is thought to be affected by the timing of measurements (Weladji et al., 2008), as some costs may be masked due to the physical condition of individuals when measured at later stages in the reproductive cycle (Hamel et al., 2010). Previous authors have acknowledged the possibility of failed litters in rodents (Armitage, 2014; Kroeger et al., 2018b; Oli & Armitage, 2008; Rödel et al., 2009), but few studies evaluated the reproductive costs using a measure of AFR that accounts for this bias. There is a need for studies that employ a comprehensive measure of AFR, especially for systems where the occurrence of failed litter is unknown. Given the possible pitfalls associated with using weaning events as an indicator of AFR, it would be important to detect reproductive attempts earlier in the reproductive cycle, potentially during the gestation period. Additionally, individual heterogeneity (among-individual variation) is another factor that can conceal trade-offs (Hamel et al., 2010; Weladji et al., 2008). It should therefore be incorporated into research on reproductive costs as well.

The purpose of this study was to investigate the consequences of AFR on survival and lifetime reproductive success (LRS) in female yellow-bellied marmots (*Marmota flaviventer*). We have capitalized on the existence of the long-term study of yellow-bellied marmots at the Rocky Mountain Biological Laboratory (Colorado, USA) to conduct our research. Females are iteroparous, polytocous, and exhibit large variation in AFR and social structure (Armitage, 2014; Oli and Armitage, 2003). While previous studies have shown that yellow-bellied marmots, hereafter referred to as marmots, exhibit some attributes of reproductive cooperation (Armitage, 2014; Blumstein et al., 2004; Blumstein & Armitage, 1999), they also display signs of reproductive competition (Armitage, 2003;

Huang et al., 2011; Oli & Armitage, 2003, 2008), which can create a delay in the first reproduction. Marmots have a short active season to breed and accumulate enough fat to hibernate (Armitage, 2014). Their capacity to reproduce before completing somatic growth (Martin et al., 2013), combined with diverse social structures and annual environmental fluctuations, makes them an excellent study system for evaluating the consequences of AFR on survival and reproduction.

If early maturity is costly, we would anticipate a lower survival rate among females that first reproduce at a younger age due to the trade-off between reproduction and growth, as well as survival. Older females (age 4 or older) have completed their growth (Martin et al., 2013); hence, they should have more resources available for reproduction and can better tolerate the costs of reproducing without compromising survival. In essence, we expect lower longevity, number of years survived after first reproduction, and probability of survival for early breeders compared to females that delay their first reproduction until older ages. Furthermore, to assess the extent of the possible trade-off between reproduction and survival, we also analyzed lifetime reproductive success (LRS), with the prediction that early breeders have a lower LRS.

Methods

Study species

Yellow-bellied marmot is a facultatively social ground-dwelling rodent found in western America in a wide range of elevations (Armitage, 2014). Marmots have a harem-polygynous mating system and females form matrilines from 1 to 5 individuals (Armitage, 2014). The short active season, lasting for 4-5 months from May to September, is when they mate and accumulate energy reserves to survive the following obligated hibernation. There is a single breeding event per year. An individual that postpones first reproduction is exposed to predation and the risk of dying overwinter — the main causes of mortality in marmots (Armitage, 2014) — over an entire year before having another reproductive opportunity. Marmots could live up to 15 years (average 1.2 ± 1.8 years; 4.7 ± 2.6 years for reproductive females) and grow until 4 years of age (Martin et al., 2013). On average, females give birth to 5±1.79 pups (Monclús & Blumstein, 2012) and reproduce 2.5 times in their lifetime (Oli & Armitage, 2003). The majority of female marmots (79.7%) however never reproduce as most of them die during the first year (59.7%).

Typically, female yellow-bellied marmots are sexually mature at 2 (Armitage, 2014; Monclús & Blumstein, 2012; Oli and Armitage, 2003; 2008). A few females were documented to reproduce at 1, but most start at two or older (Armitage, 2014). On average, females start reproducing at 2.5 ± 0.9 years of age, but the age at first reproduction ranges from 1 to 6 years. Females copulate in April-May, gestate for 30 days, and give birth underground. Lactation lasts 25 days and pups emerge from the burrows in early July (Armitage, 2014).

Study area and field methods

This study was conducted using data from the long-term monitoring of yellow-bellied marmots at the Rocky Mountain Biological Laboratory, Colorado, USA. Marmots have been studied at this location since 1962. Colonies are distinguished between two elevations (down and up-valley) with approximately 2 weeks delay in spring emergence between the two sites (Blumstein et al., 2004).

Individuals are trapped bi-weekly using Tomahawk traps and observed using binoculars or scopes during their peak of activity (0700-1000 h and 1600-1900 h from May to September). While trapping, animals are sexed, weighted, identified, or marked and tagged. Morphological measurements and reproductive status are also recorded. The latter is determined by the condition of the nipples via palpation and visual inspection, which is categorized into one of four categories: visible (normal) if the nipple is just visible and flat, prominent if it is raised off the surface but not swollen, swollen if both the nipple and its base are enlarged, or lactating if there is hair loss around the nipple or the presence of milk leakage. Except for the "visible" state, all other nipple conditions are considered an indication of a reproductive state. The nipple index returns to its normal state after the reproductive season. The first time a female is scored as reproductive is considered the AFR — age at first gestation. Successful as well as failed reproductions can be assessed with the reproductive status using the nipple development and provide an accurate estimator of AFR (Armitage & Wynne-Edwards, 2002). The reproductive status was also employed in previous studies in other rodents (Descamps et al., 2006; Neuhaus et al., 2004).

An animal is considered dead if we did not observe the individual the following spring or if we directly witnessed the death. The recapture rate of adult females has been estimated to exceed 98% for most colonies (Ozgul et al., 2006; Ozgul et al., 2007), providing an accurate estimation of female longevity.

Since 2000, the parentage assignment is determined genetically. Pups were assigned exclusively with behavioral observations before the year 2000. Lifetime reproductive success was obtained with the total number of pups captured and attributed to a female in the course of her life. Immigrants arriving in the study population are presumed to be 2 years old, or yearling if they seem younger. Our dataset had 76% of reproductive females of known exact age. Doing the analysis on a restricted dataset with only females of known age gave similar conclusions. Mass was estimated for each individual using best linear unbiased predictors (BLUPs) for June 1st as done previously (Kroeger et al., 2018a; Ozgul et al., 2010; Maldonado-Chaparro & al., 2015), using linear mixed-effect models with mass collected while trapping.

Data analysis

All statistical analyses were performed using R v4.2.1 (R Core Team, 2023) with the following packages: lme4 v1.1-33 (Bates et al., 2015), lmerTest v3.1-3 (Kuznetsova et al., 2017), tidyverse v2.0.0 (Wickham et al., 2019), marmotdata v20.2.5 (Martin & Blumstein, 2022), multcomp v1.4-23 (Horton et al., 2008), effects v4.2-2 (Fox 2003; Fox & Weisberg, 2018; Fox & Weibserg, 2019), ggeffects v1.2.1 (Lüdecke, 2018), performance v0.10.3 (Lüdecke et al., 2021), car v3.1-2 (Fox & Weisberg, 2019), mgcv 1.8-40 (Wood, 2017), DHARMa v0.4.6 (Hartig, 2022), patchwork v1.1.2 (Pederson, 2022) and kableExtra (Zhu, 2021).

To estimate the effect of AFR on survival and reproduction, we fitted models on four fitness-related traits: longevity, the number of years survived after first reproduction (reproductive longevity), annual probability of survival, and LRS. Longevity represents the total number of years an animal lived, thus is the cumulative effect of annual survival over the entire lifespan. The number of years after the first reproduction characterizes the reproductive longevity and quantifies the reproductive opportunities remaining following the first event as marmots reproduce only once a year. The annual survival probability was used to gauge the impact of AFR on the short- and long-term at the population level. LRS quantifies the number of offspring weaned during each female's lifetime.

Our dataset consisted of 396 females observed over a 59-year period (1962-2020). We used generalized mixed-effects models (GLMM) with a Poisson distribution to analyze the effects of AFR on both longevity and the number of years after first reproduction. We used the optimizer BOBYQA (Powell, 2009) to improve model convergence. Valley location and scaled mass in June in the year of first reproduction were treated as fixed effects to account for environmental and body condition variability, while year of first reproduction, year of birth, and colony were fitted as random effects. We tested the significance of the random effects via a likelihood ratio test. We performed type III ANOVA and multiple comparisons with Tukey’s all-pairs comparisons to compare longevity and the number of years survived after first reproduction among different AFR. We applied a Benjamini-Hochberg adjustment to account for an increase in type I error when conducting multiple comparisons (Lee & Lee, 2018).

We analyzed the annual probability of survival for each AFR with a generalized additive mixed-effect model (GAMM) using a binomial distribution including age, AFR, the interaction between age and AFR, and valley location as fixed effects. Year, year of birth, colony, and animal identity were added as random effects. These effects account for repeated observations on the same individuals, avoiding pseudoreplication and other possible autocorrelation within years and locations (Crawley, 2007; Harrison et al., 2018). Improvement of fit with age, using spline instead of a linear effect, was based on the values of effective degrees of freedom, which exceeded 2 for most of AFR. These values indicate a highly non-linear relationship (Wood, 2006; Zuur et al., 2009). We omitted the effect of body mass from this model for two reasons. First, to mitigate potential confounding indirect effects of body mass (Harvey & Zammuto, 1985). Second, our main interest was to assess a trade-off between survival and AFR, rather than the mechanism underlying the trade-off.

Finally, we fitted a GLMM with a Poisson distribution to analyze lifetime reproductive success (LRS). The model included fixed effects of AFR, longevity, scaled mass in June in the year of first reproduction, valley location, and a two-way interaction between longevity and AFR. Random effects for the year of birth, colony, and year were also included. We tested the significance of the random effects via a likelihood ratio test. To address the nonlinear relationship between the number of offspring produced and age (St. Lawrence et al., 2022), we included scaled longevity as a linear and second-order orthogonal polynomial effect, which also controlled for the impact of actuarial senescence on other predictors. To help with model convergence, the longevity variable was scaled. As there may not be sufficient variation in longevity among certain AFR categories to justify the inclusion of the interaction between AFR and the polynomial effect of longevity in the model, we excluded it. When tested, the interaction effect was also not significant and was thus removed from the model since non-significant interactions can bias estimates of main terms (Engqvist, 2005). We further excluded the yearlings from this analysis because of data limitation.

Results

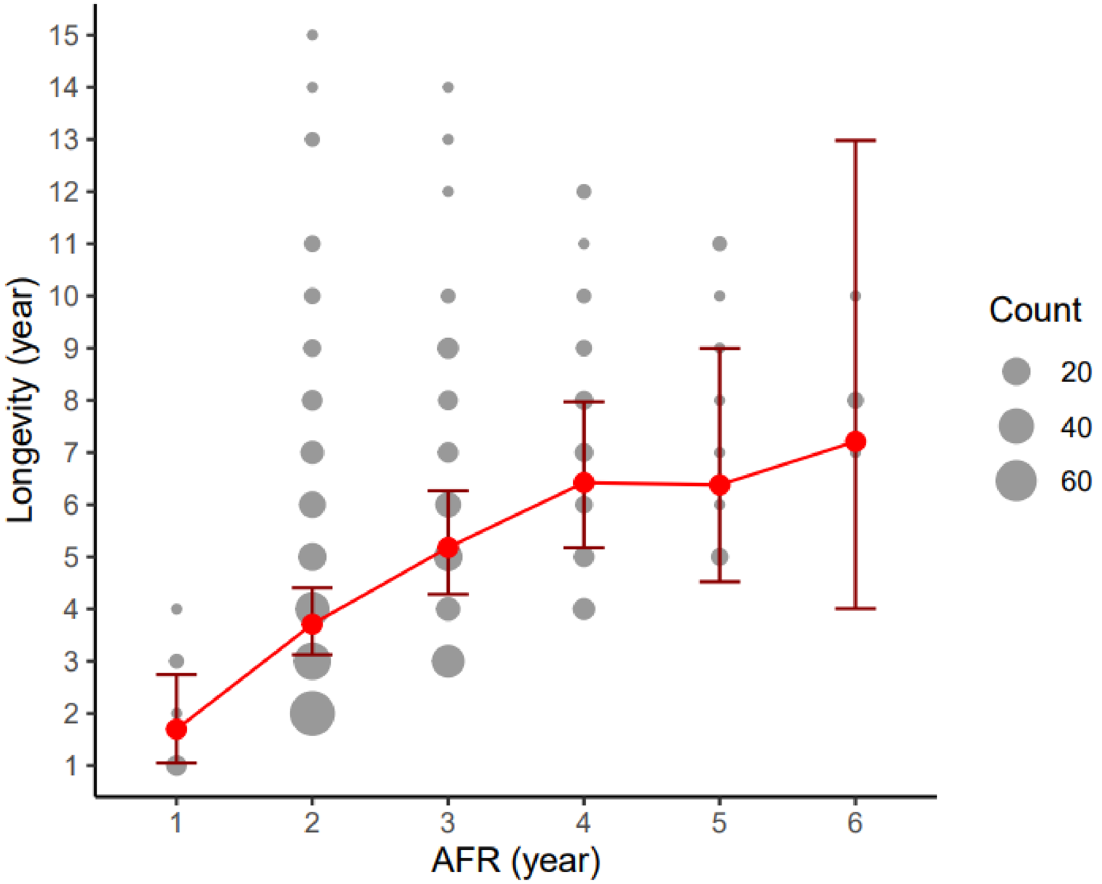
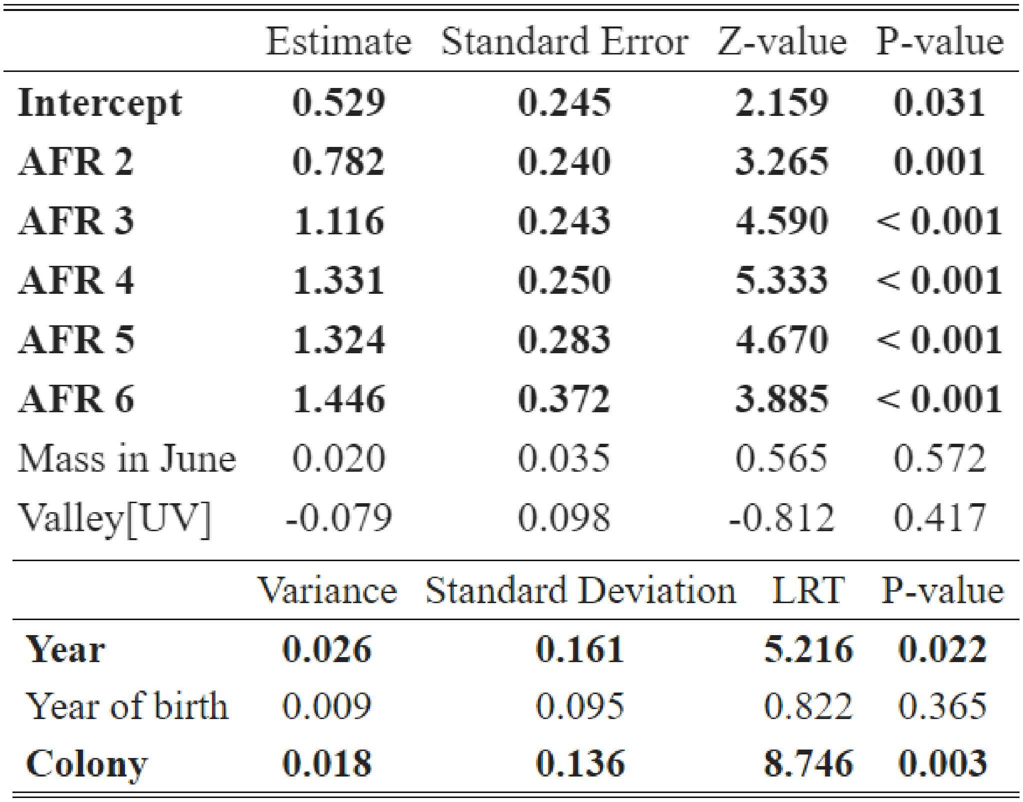


Figure 1: The relationship between longevity and age at first reproduction (AFR) in female yellow-bellied marmots (*n* = 332) in grey with estimates from the GLMM (Table 1) and the associated 95% confidence intervals in red. The count represents the number of occurrences.

We found that longevity increased with AFR (Figure 1; Table 1), but the increase was not constant with AFR. Reproducing for the first time at 1 or 2 significantly curtailed longevity compared to delaying to older ages (Table S1). Delaying the first reproduction to 2 years increased longevity significantly (*z-value* = 3.27, *p-value* < 0.01) by approximately 2 years. After the age of 2, longevity elevated only slightly and not differently from other AFR. There was substantial variation in longevity, especially for intermediate values of AFR (2-3 years), with females dying in the year following first reproduction (30.7%) or living up to 15 years. Reproducing female yearlings lived a maximum of 4 years. The effects of the year of reproduction and colony were significantly different from zero showing differences in environmental conditions over time and locations. The effect of mass in June at the first reproduction was not significant.

Table 1: Generalized linear mixed-effects model (GLMM) with a Poisson distribution to evaluate the effect of age at first reproduction (AFR) on longevity in female yellow-bellied marmots ($n = 332$; $n_{year} = 52$, $n_{year\ of\ birth} = 51$, $n_{colony} = 25$). The effect of mass in June in the year of the first reproduction was scaled. The reference level for AFR is set at 1 year, while for the valley, the reference level is defined as down-valley.



	Estimate	Standard Error	Z-value	P-value
Intercept	**0.529**	**0.245**	**2.159**	**0.031**
AFR 2	**0.782**	**0.240**	**3.265**	**0.001**
AFR 3	**1.116**	**0.243**	**4.590**	**< 0.001**
AFR 4	**1.331**	**0.250**	**5.333**	**< 0.001**
AFR 5	**1.324**	**0.283**	**4.670**	**< 0.001**
AFR 6	**1.446**	**0.372**	**3.885**	**< 0.001**
Mass in June	0.020	0.035	0.565	0.572
Valley[UV]	-0.079	0.098	-0.812	0.417
	Variance	**Standard Deviation**	**LRT**	**P-value**
Year	**0.026**	**0.161**	**5.216**	**0.022**
Year of birth	0.009	0.095	0.822	0.365
Colony	**0.018**	**0.136**	**8.746**	**0.003**

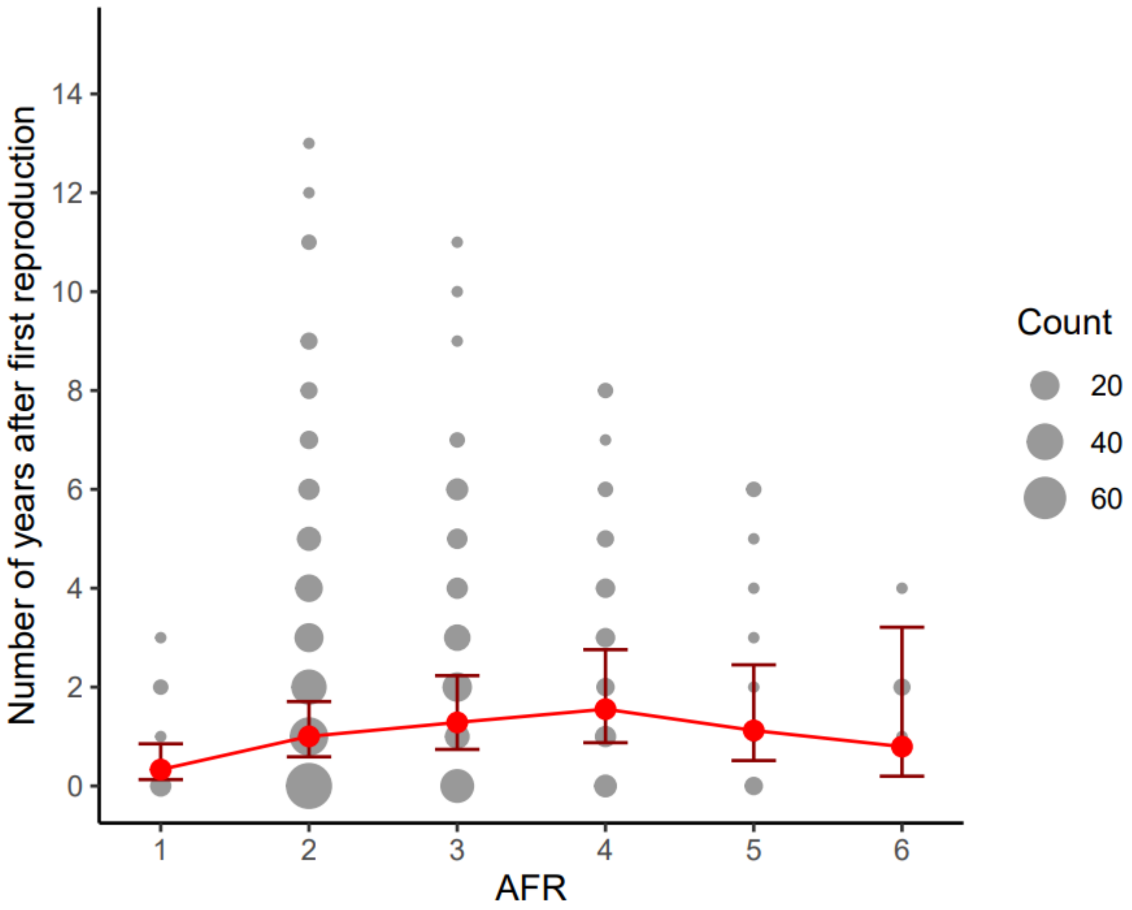
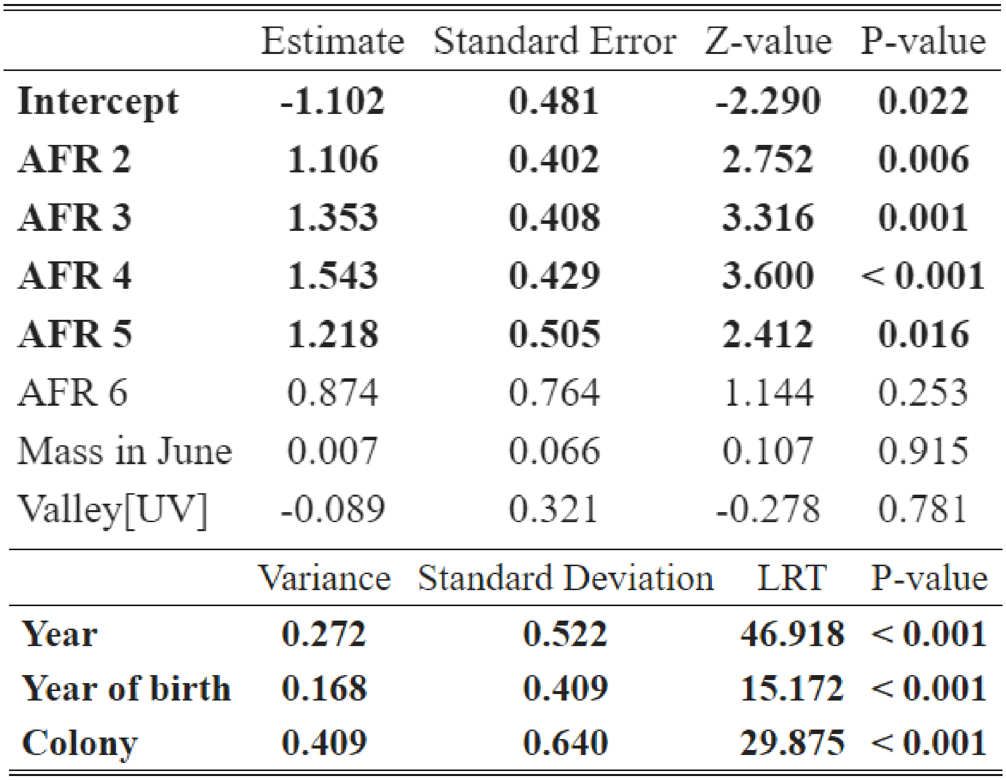


Figure 2: The relationship between the number of years survived after the first reproductive event and age at first reproduction (AFR) in female yellow-bellied marmots (*n* = 332) with estimates from the GLMM (Table 2), and the 95% confidence interval in red. The count represents the number of occurrences.

Females reproducing at 1 have a lower number of years after first reproduction compared to females reproducing at 3 and 4. While females first reproducing at 2 years tended to live on average a greater number of years after first reproduction than yearlings, this did not reach statistical significance after adjustment for multiple comparisons (Table S2). All other AFR did not differ in the number of years after the first reproduction (Figure 2); there was no gain in reproductive longevity of delaying reproduction by a year beyond 2 years of age. There was substantial variation in reproductive longevity, but females lived on average 1.5 years after first reproduction (Table 2). The effects of year of birth, year of first reproduction, and colony were significantly different from 0. The effect of mass in June was not significant.

Table 2*:* Generalized linear mixed-effects model (GLMM) with a Poisson distribution to evaluate the effect of age at first reproduction (AFR) on the number of years survived after first reproduction in female yellow-bellied marmots (*n* = 332; n_{year} = 52, $n_{year\ of\ birth}$ = 51, n_{colony} = 25). The effect of mass in June in the year of first reproduction was scaled. The reference level for AFR is set at 1 year, while for the valley, the reference level is defined as down-valley.



	Estimate	Standard Error	Z-value	P-value
Intercept	**-1.102**	**0.481**	**-2.290**	**0.022**
AFR 2	**1.106**	**0.402**	**2.752**	**0.006**
AFR 3	**1.353**	**0.408**	**3.316**	**0.001**
AFR 4	**1.543**	**0.429**	**3.600**	**< 0.001**
AFR 5	**1.218**	**0.505**	**2.412**	**0.016**
AFR 6	0.874	0.764	1.144	0.253
Mass in June	0.007	0.066	0.107	0.915
Valley[UV]	-0.089	0.321	-0.278	0.781
	Variance	Standard Deviation	LRT	P-value
Year	**0.272**	**0.522**	**46.918**	**< 0.001**
Year of birth	**0.168**	**0.409**	**15.172**	**< 0.001**
Colony	**0.409**	**0.640**	**29.875**	**< 0.001**

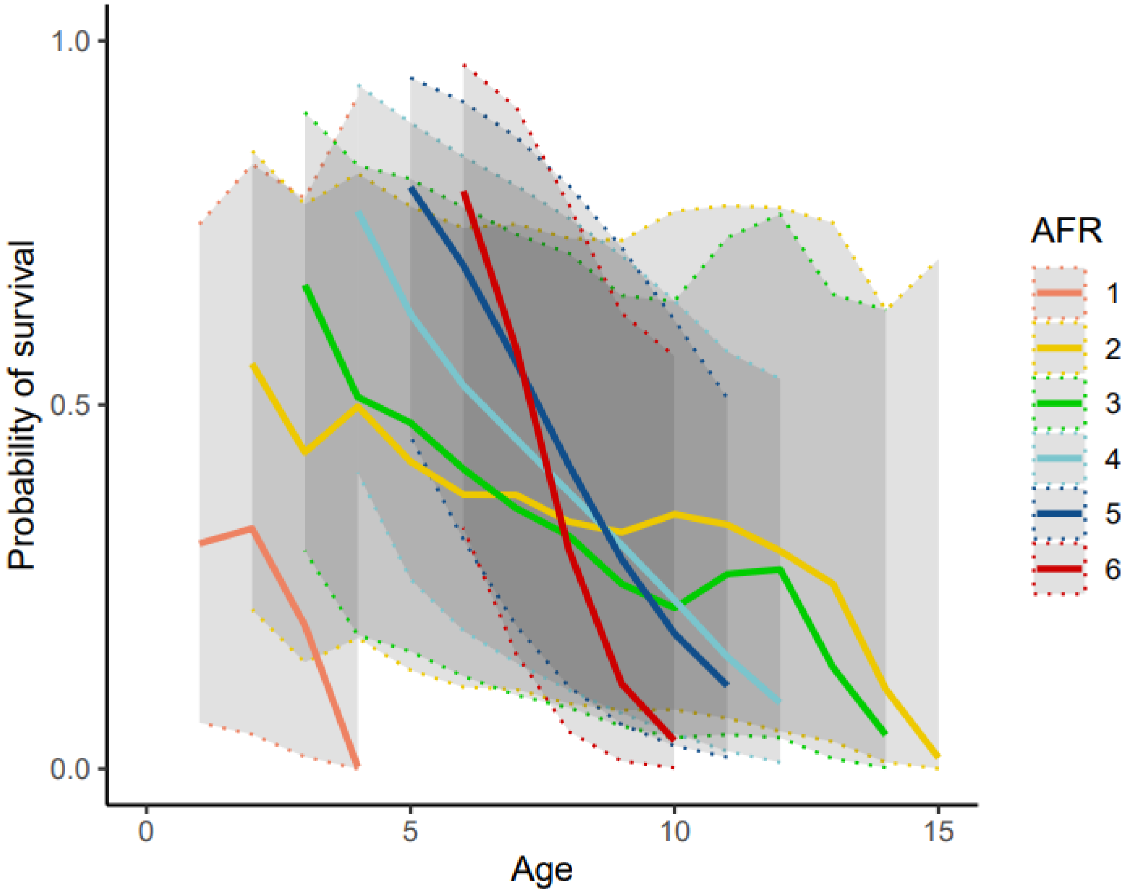
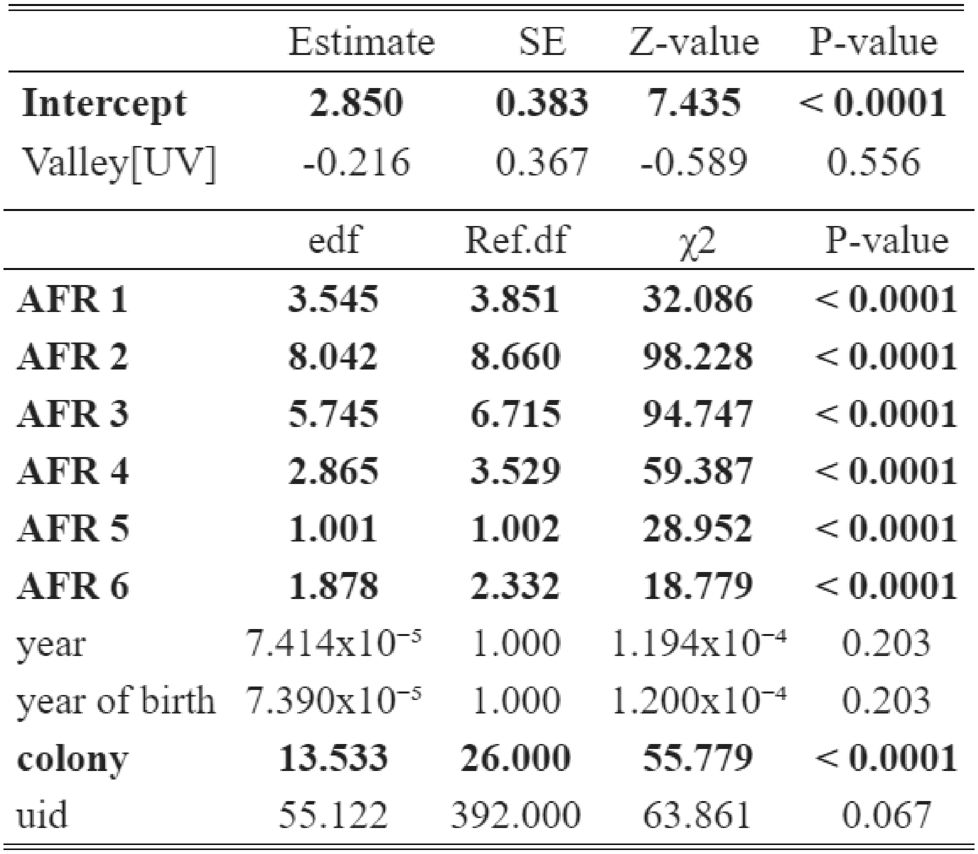


Figure 3: Probability of survival with age for each age at first reproduction (AFR) with 95% confidence interval obtained with the GAMM (Table 3) in female yellow-bellied marmots (*n* for each AFR: $n_1 = 11$, $n_2 = 226$, $n_3 = 105$, $n_4 = 38$, $n_5 = 11$ and $n_6 = 5$; total $n = 396$). Predictions were kept within the limits of observed data.

The probability of survival varies with age and across AFR (Figure 3; Table 3). Notably, females reproducing at 1 year of age exhibit consistently lower survival than their counterparts in other AFR categories. Conversely, females reproducing at age 2 or 3 maintain a relatively high probability of survival across all ages. Survival rates decline rapidly once a female commences reproduction, with ages 4, 5 and 6 showing low annual survival rates. Colony location had a significant effect on survival probabilities, and individual identity showed a trend, but the effect was not statistically significant (Table 3).

Table 3*:* Generalized additive mixed-effects model (GAMM) with a binomial distribution to evaluate the effect of age at first reproduction (AFR) on the probability of survival in female yellow-bellied marmots (*n* for each AFR: $n_1 = 11$, $n_2 = 226$, $n_3 = 105$, $n_4 = 38$, $n_5 = 11$ and $n_6 = 5$; total $n = 396$; $n_{year} = 58$, $n_{year\ of\ birth} = 57$, $n_{colony} = 29$). The variable *uid* represents the identity of the individuals. The reference level for the valley effect is defined as down-valley.



	Estimate	SE	Z-value	P-value
Intercept	**2.850**	**0.383**	**7.435**	**< 0.0001**
Valley[UV]	-0.216	0.367	-0.589	0.556
	edf	Ref.df	χ2	P-value
AFR 1	**3.545**	**3.851**	**32.086**	**< 0.0001**
AFR 2	**8.042**	**8.660**	**98.228**	**< 0.0001**
AFR 3	**5.745**	**6.715**	**94.747**	**< 0.0001**
AFR 4	**2.865**	**3.529**	**59.387**	**< 0.0001**
AFR 5	**1.001**	**1.002**	**28.952**	**< 0.0001**
AFR 6	**1.878**	**2.332**	**18.779**	**< 0.0001**
year	7.414×10^{-5}	1.000	1.194×10^{-4}	0.203
year of birth	7.390×10^{-5}	1.000	1.200×10^{-4}	0.203
colony	**13.533**	**26.000**	**55.779**	**< 0.0001**
uid	55.122	392.000	63.861	0.067

Note: The edf represents the number of effective degrees of freedom. It gives an indication of the complexity of the curve, where a value of 1 suggests a linear relationship, 2 implies a quadratic relationship and >2 designates a highly non-linear relationship. Ref.df stands for the reference degrees of freedom and is used for the statistical test.

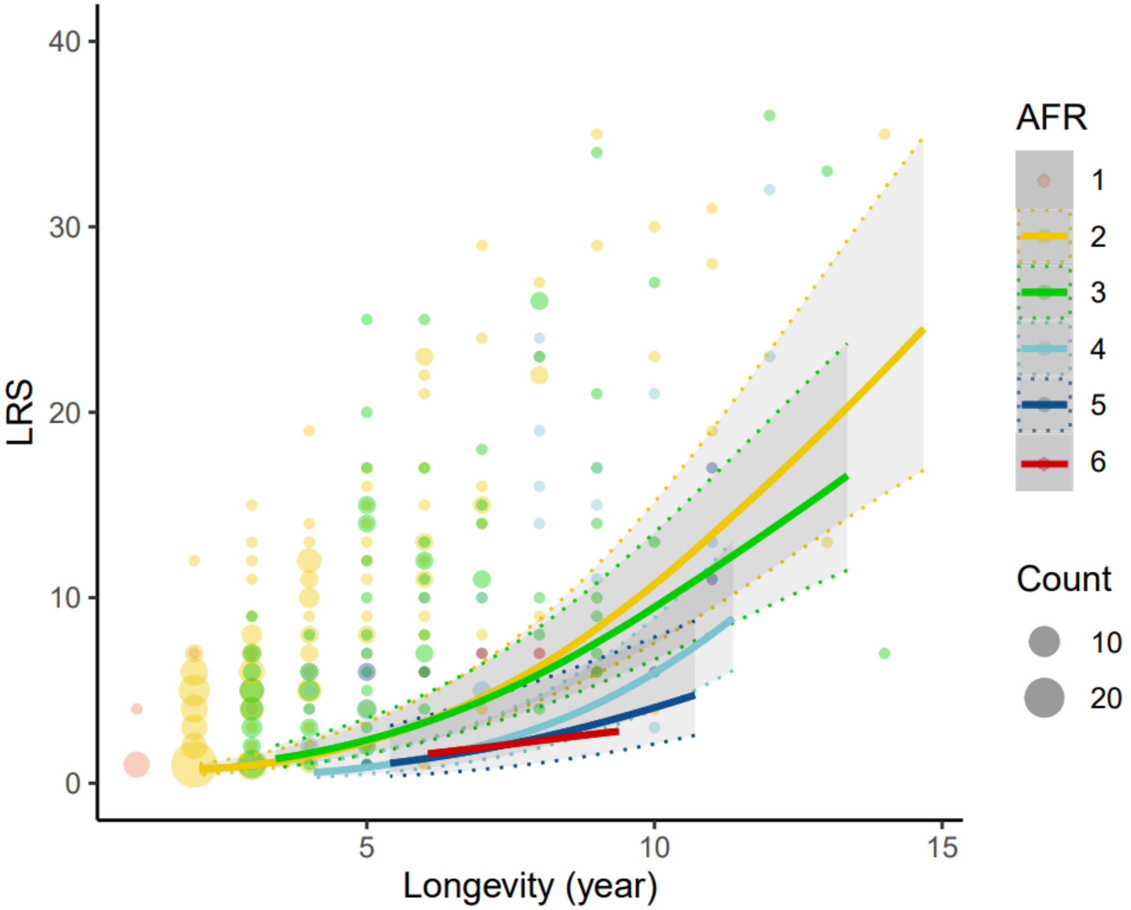
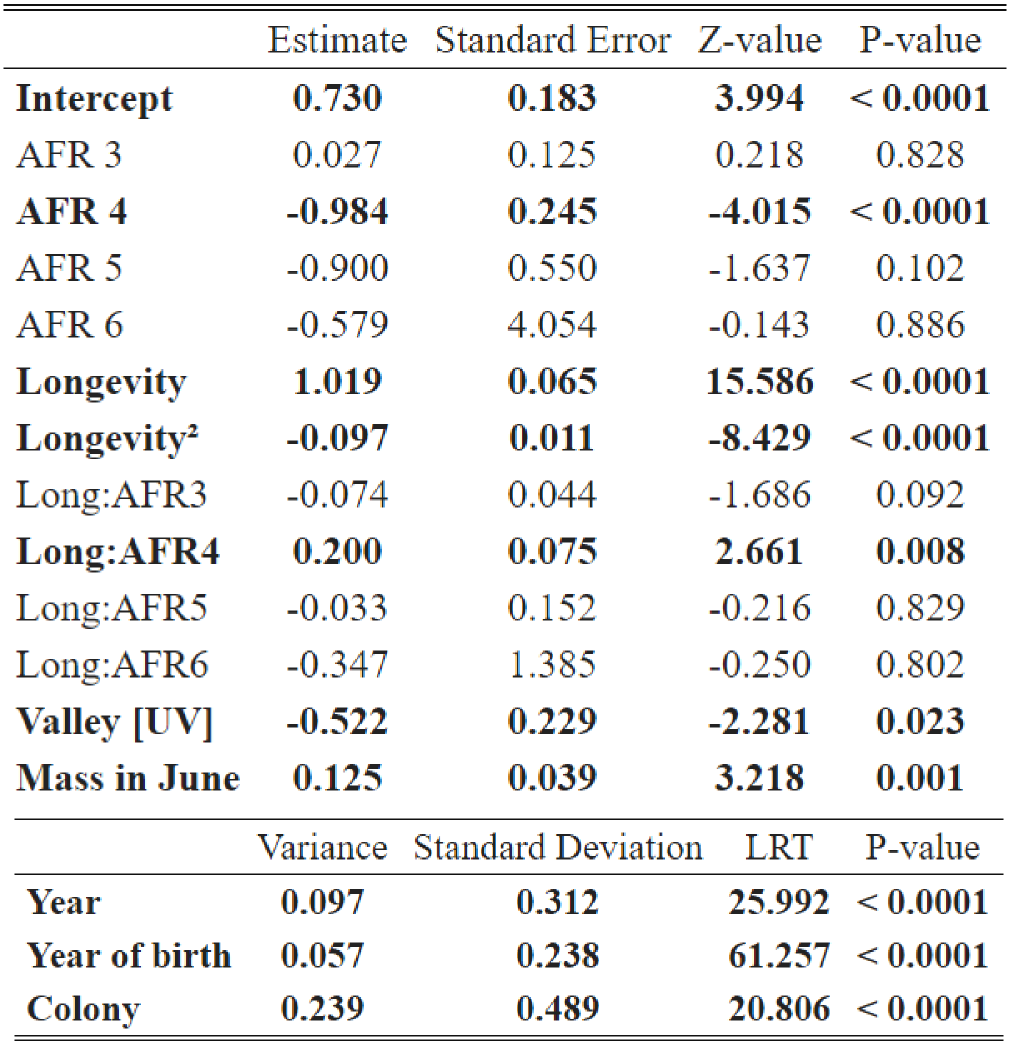


Figure 4: The back-transformed relationship between lifetime reproductive success (LRS) and longevity for each age at first reproduction (AFR) in female yellow-bellied marmots (*n* for each AFR: $n_1 = 11$, $n_2 = 191$, $n_3 = 92$, $n_4 = 29$, $n_5 = 7$ and $n_6 = 2$; total $n = 332$). The count represents the number of occurrences. The regression lines with the 95% confidence intervals were obtained from the GLMM (Table 4). Predictions were kept within the limits of observed data.

We found a positive linear and a negative quadratic effect of longevity (Figure 4; Table 4) on LRS. We also observed a positive effect of AFR in interaction with longevity. Individuals starting to reproduce at age 2 or 3 had a higher LRS at any given longevity and the difference increased at longer lifespans. Animals with higher body mass in June in the year of first reproduction and those situated down-valley demonstrated higher LRS when compared to lighter individuals and individuals found up-valley. The effects of year of birth, year of first reproduction, and colony were significantly different from 0.

Table 4: Generalized linear mixed-effects model (GLMM) with a Poisson distribution to evaluate the effect of age at first reproduction (AFR) on lifetime reproductive success (LRS) in female yellow-bellied marmots with scaled longevity as linear and quadratic effect (n for each AFR: $n_2 = 191$, $n_3 = 92$, $n_4 = 29$, $n_5 = 7$ and $n_6 = 2$; total $n = 321$; $n_{year} = 52$, $n_{year\ of\ birth} = 51$, $n_{colony} = 25$). The effect of mass in June in the year of first reproduction was scaled. The reference level for AFR is set at 2 years, while for the valley, the reference level is defined as down-valley.



	Estimate	Standard Error	Z-value	P-value
Intercept	**0.730**	**0.183**	**3.994**	**< 0.0001**
AFR 3	0.027	0.125	0.218	0.828
AFR 4	**-0.984**	**0.245**	**-4.015**	**< 0.0001**
AFR 5	-0.900	0.550	-1.637	0.102
AFR 6	-0.579	4.054	-0.143	0.886
Longevity	**1.019**	**0.065**	**15.586**	**< 0.0001**
Longevity²	**-0.097**	**0.011**	**-8.429**	**< 0.0001**
Long:AFR3	-0.074	0.044	-1.686	0.092
Long:AFR4	**0.200**	**0.075**	**2.661**	**0.008**
Long:AFR5	-0.033	0.152	-0.216	0.829
Long:AFR6	-0.347	1.385	-0.250	0.802
Valley [UV]	**-0.522**	**0.229**	**-2.281**	**0.023**
Mass in June	**0.125**	**0.039**	**3.218**	**0.001**
	Variance	Standard Deviation	LRT	P-value
Year	**0.097**	**0.312**	**25.992**	**< 0.0001**
Year of birth	**0.057**	**0.238**	**61.257**	**< 0.0001**
Colony	**0.239**	**0.489**	**20.806**	**< 0.0001**

Discussion

We found three key results in relation to the consequences of age at first reproduction (AFR) in yellow-bellied marmots. First, as anticipated, delaying AFR is associated with a longer life, but if delaying from age 1 to 2 tended to increase the number of reproductive opportunities, delaying after age 2 did not increase the reproductive longevity. Second, starting to reproduce at age 2 or 3 was associated with the longest longevity and the highest annual survival probability. Delaying reproduction thereafter was associated with a sharp reduction in annual survival probability. Third, lifetime reproductive success was higher for individuals starting to reproduce at age 2 or 3 for any longevity. Overall, these findings suggest the existence of an optimal reproductive strategy, which consists of an AFR of 2 years old.

We report that reproducing as yearlings was associated with a negative effect on survival and reproductive success compared to those who reproduced at 2 years or older. This outlines a trade-off between early reproduction and survival, as well as between current reproduction and future reproductive success (Bell, 1980; Stearns, 1992). This is potentially because yearlings, not yet fully grown, need to transfer a larger amount of energy relative to their body mass. They also had only one active season to accumulate enough energy reserves before reproducing and marmots are capital breeders. As a result, they face greater challenges as survival, growth, and reproductive activities are competing for limited resources. Similar survival costs of early maturity were also found in northern elephant seals (Reiter & Le Boeuf, 1991) and rhesus macaques (*Macaca mulatta*; Blomquist, 2009). Early first breeders can also be doing “the best of a bad job” (Dawkins, 1980), ensuring a minimum of reproductive success. Previous research on North American red squirrel *Tamiasciurus hudsonicus* documented two reproductive strategies: early breeding and shorter lifespan or late maturity associated with a longer lifespan. They suggested that early breeding is adopted by low-quality individuals (Descamps et al., 2006). Similarly, marmots in suboptimal environments or of lower body condition can opt to first reproduce early. Only an extremely small fraction of females start to reproduce at age 1 in the study population. This provides evidence for strong negative selection against early reproduction, likely because the costs are much higher than the benefits when opting for this strategy.

In addition to finding that reproducing as yearlings was associated with strong detrimental effects on individual fitness, we also report survival and reproductive costs for females who reproduced for the first time after 3 years of age. These females showed faster rates of actuarial senescence and lower LRS compared to females with an AFR of 2 or 3 years old. As individuals age, they may be in lower body condition (Kroeger et al., 2018a) or have impaired immune functions, which increases mortality risks. Late first reproduction can intensify these costs as the self-maintenance costs can increase with age (Kirkwood, 2017), and resources directed to reproduction are no longer serving self-maintenance processes. Individuals who postpone their first reproduction after 3 years of age might opt for this reproductive strategy, even though we report no benefits of doing so, because of other constraints such as genetics (Blomquist, 2009; Martin & Festa-Bianchet, 2012), body mass (Gaillard et al., 2000; Green & Rothstein, 1991), population density (Gaillard et al., 2000; Martin & Festa-Bianchet, 2012), and social suppression (Oli & Armitage, 2003; Armitage, 2007). Heritability of life history traits, such as AFR, is expected to be low (Blomquist, 2009; Houle, 1992; Martin & Festa-Bianchet, 2012). Consequently, environmental factors potentially contribute significantly to the variation in AFR. The combination of environmental conditions could affect the individuals in a way that allows them to gauge when the conditions are favorable to start reproducing.

The majority of females reproduce for the first time at the age of 2. This appears to be the optimal strategy for survival and lifetime reproductive success as we found no apparent reproductive costs. This could be due to an individual response to the previously mentioned cues or a preselection of females in optimal body condition who are capable of bearing the reproductive costs at this age (Weladji et al., 2008). Rodents are considered to have a fast "life-speed" and low reproductive variability (Hamel et al., 2010). However, the yellow-bellied marmot is a special case of long-lived rodent (Kroeger et al., 2018b), and individuals exhibit diverse biological aging rates (Pinho et al., 2022). The variation in longevity is also wider for the AFR of 2 and 3 — extending up to 15 years — than for both younger and older AFR. Hence, yellow-bellied marmots adopt, at least to some extent, a conservative strategy similar to long-lived species (slow life-speed; Hamel et al., 2010), where they prioritize their own survival over reproductive success. Additionally, female marmots that weaned large litters during previous reproduction also weaned large litters in the next reproductive events (Kroeger et al., 2018b). Similarly, in the Columbian ground squirrel, early breeders were in better condition and more successful throughout their lifetime (Neuhaus et al., 2004). The large among-individual variation in survival and reproductive success we hereby report points toward the evidence of persistent inter-individual differences in performance as females maturing early also perform better and other individuals opt for alternatives such as reproducing as a yearling or delaying first reproduction to older age, which aligns with previous research (Kroeger et al., 2018b).

Reproduction reduces fat gain rates (Armitage, 1991, 2014; Woods et al., 2009) and for species that can reproduce before reaching adult size, reproduction can jeopardize growth (Martin & Festa-Bianchet, 2012; Roff, 2002). Time spent weaning the pups reduces time available to forage and gain weight for winter, a crucial factor for surviving hibernation (Armitage, 2014). There is possibly a resource acquisition and allocation strategy by accumulating or allocating energy reserves in a way that buffers the costs of reproduction with AFR. For instance, rodents are known to adjust their litter size and the size of offspring to align with their reproductive capacity (e.g., Alpine marmots *Marmota marmota,* Berger et al., 2015; Columbian ground squirrels, Neuhaus, 2000), or they may abort the litter if the conditions are unfavorable (optimal investment hypothesis; Morris, 1992), which further entails reproductive costs. Alternatively, a large variance in resource acquisition or a narrow variation in resource allocation is expressed at the population level. This can affect the magnitude of trade-offs (Van Noordwijk & De Jong, 1986) and offers another explanation for the absence of trade-offs between early reproduction and survival or reproductive success beyond 1 year of age.

Females who start to breed later could invest more heavily into reproduction compared to those who start reproducing earlier, as they have completed their growth and may be trying to compensate for the missed opportunities resulting from the delayed first reproduction. This would result in a trade-off between reproduction and somatic maintenance that explains the decrease in survival for older AFR. However, LRS or the litter size did not increase with AFR (Oli & Armitage, 2003; but see Ozgul et al., 2007). Alternatively, the body size of the offspring can differ between young mothers and those who postponed (Festa-Bianchet et al., 1995). Interestingly, older yellow-bellied marmots produce daughters with higher annual reproductive success, showing that investment in reproduction can vary with age (Kroeger et al., 2020). We further report a positive effect of mass on LRS, which suggests an effect of mass on reproductive investment. Females first reproducing at later ages are possibly investing more than younger females as their residual reproductive value is lower and they had more active seasons to accumulate resources and skills. Whether or not the reproductive investment varies with AFR remains to be tested.

One can argue that reproductive costs vary among individuals when using age at first gestation instead of age at first weaning for the first reproduction. Age at first gestation considers both successful and unsuccessful reproductions, but the reproductive outcome can have divergent consequences on survival and individual fitness (Clutton-Brock et al., 1983). We argue that age at first gestation is more appropriate than age at first weaning for this particular system for three reasons. First, age at first weaning might not be the best measure of AFR since females give birth underground. The reproduction process, from copulation to weaning, takes two months. Throughout this period, numerous events could affect weaning success: embryo resorption, litter abortion, predation, diseases or infanticide (Armitage, 2014; Rödel et al., 2009). While most females successfully wean during their first reproduction, many females' AFR is positively biased using age at first weaning — up to 5 years. Females that attempt reproduction can also endure some costs (Clutton-Brock et al., 1983), depending on the timing of the litter loss. However, these costs are completely overlooked using age at first weaning. Second, the intrinsic reproductive potential of females who manage to wean is potentially greater than females who fail. Therefore, measuring reproductive costs at weaning can reduce the ability to detect such costs as individuals vary less extensively than at an early stage of the reproductive cycle (Hamel et al., 2010). It is also generally admitted that mammals bear more costs of lactating than gestating (Clutton-Brock et al., 1983; Oftedal, 1985; Randolph et al., 1977). Nonetheless, the magnitude of these costs is thought to vary according to resource availability. This could contribute to increase the allocation of energy to gestation more importantly than to lactation (Hamel et al., 2010), hence the need to use age at first gestation. Third, age at first gestation is more representative of the milestone between the immature state and the sexual maturity, because it does not depend on the survival of the offspring. Thus, it captures the age at which an animal can start to produce offspring, which is more consistent across species and populations. Furthermore, our research yield similar conclusions to previous study that used age at first weaning (Oli & Armitage, 2003). However, it must be noted that the determination of reproductive status is subject to experimenter bias and the development of nipples lasts only for a short window of time. Since we included all kinds of reproductive effort in the analysis, our results can also be interpreted on a broader perspective.

While the reproductive status can be used to determine AFR, accurately measuring LRS requires counting and correctly assigning offspring to the appropriate female. As previously mentioned, our study is subject to limitations as it is possible that we may not have captured all the pups a female weaned, thus underestimating LRS. We strongly believe the error margin remains low since we closely monitored the burrows almost daily. Implementing camera traps or echography methods could further reduce potential errors in future studies. However, portable ultrasound technology is still limited for studies in natural environments with constraints that are too detrimental for wild animals (e.g., fur shaving).

Our analysis of females in the AFR 1-year category was constrained owing to a paucity of statistical power. To strengthen the conclusions regarding survival and reproductive success, it would be advantageous to obtain a larger sample size of yearling reproductive females. Similarly, AFR affects mass, and mass has a direct effect on survival (Jebb et al., 2021). Therefore, having mass in the model of the annual probability of survival was problematic. To account for the direct and indirect relationships between AFR, mass, and annual probability of survival, a structural causal model could be fit in follow-up studies.

Most studies on reproductive costs are conducted on females while males remain understudied (Hamel et al., 2010). To gain a comprehensive understanding of reproductive costs associated with early breeding, it is crucial to investigate its effects on males. Additionally, considering the potential impacts of AFR on the offspring (Festa-Bianchet et al., 1995), it becomes imperative to explore the transgenerational effects AFR may have. Therefore, future studies should aim to address these aspects to provide a more holistic perspective on the reproductive costs involved.

Our study constitutes the first to document the reproductive costs using a comprehensive measure of AFR tailored to the study system. This research represents one of the few studies to report reproductive costs for yearlings, uncovering a higher senescence rate and lower LRS with early breeding. Interestingly, our results divert from previous findings reported by Oli and Armitage (2003), suggesting that AFR is likely under stabilizing rather than directional selection in this population of yellow-bellied marmots.

The plasticity observed in this trait has strong importance, particularly in a rapidly changing environment. Ultimately, by unraveling the complexities of AFR and its consequences, this research contributes to our broader understanding of life history evolution and fitness outcomes of different reproductive strategies.

Conclusions

Through this research, we evidenced different reproductive strategies in the socially complex yellow-bellied marmots. Our results suggest that first reproducing at 2 years old is optimal for survival and lifetime reproductive success. Yearlings experienced significant survival challenges and postponing reproduction past 3 years old negatively impacted individual fitness. Female yearlings face a trade-off between early reproduction and survival, as well as between early reproduction and total reproductive success. Therefore, the trait is probably under a stabilizing selection regime with an optimum age of first reproduction at 2. The rates of actuarial senescence vary in relation to AFR, emphasizing the importance of considering the long-term effects of reproductive strategies on survival. Age at first gestation also emerges as a suitable indicator of AFR for this system. AFR of female marmots is likely influenced by the body condition, as some individuals are highly successful while others perform poorly. Considering the strong implications of AFR on individual fitness, future research should focus on investigating the potential causes of the plasticity in AFR within populations and understanding the adaptive nature of this flexibility.

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Appendix

Table S1: Multiple comparisons with Tukey's all-pairs comparisons to compare longevity with each age at first reproduction (AFR) using the estimates of the generalized linear mixed-effects model in female yellow-bellied marmots (*n* = 332).

	Estimate	Standard Error	Z-value	P-value
2-1	**0.782**	**0.240**	**3.265**	**0.0106**
3-1	**1.116**	**0.243**	**4.590**	**< 0.001**
4-1	**1.331**	**0.250**	**5.333**	**< 0.001**
5-1	**1.324**	**0.283**	**4.670**	**< 0.001**
6-1	**1.446**	**0.372**	**3.885**	**0.001**
3-2	**0.334**	**0.066**	**5.061**	**< 0.001**
4-2	**0.549**	**0.087**	**6.327**	**< 0.001**
5-2	**0.542**	**0.157**	**3.442**	**0.006**
6-2	0.664	0.290	2.288	0.165
4-3	0.215	0.091	2.366	0.138
5-3	0.208	0.160	1.298	0.749
6-3	0.331	0.294	1.123	0.846
5-4	-0.007	0.169	-0.040	1.000
6-4	0.116	0.300	0.386	0.999
6-5	0.123	0.327	0.375	0.999

Table S2*:* Multiple comparisons with Tukey's all-pairs comparisons to compare the number of years after first reproduction for each age at first reproduction (AFR) using the estimates of the generalized linear mixed-effects model in female yellow-bellied marmots (*n* = 332).

AFR	Estimate	Standard Error	Z-value	P-value
2-1	**1.106**	**0.402**	**2.752**	**0.050**[1]
3-1	**1.353**	**0.408**	**3.316**	**0.009**
4-1	**1.543**	**0.429**	**3.600**	**0.003**
5-1	1.218	0.505	2.412	0.121
6-1	0.874	0.764	1.144	0.832
3-2	0.248	0.117	2.118	0.232
4-2	**0.437**	**0.155**	**2.829**	**0.040**[1]
5-2	0.113	0.301	0.374	0.999
6-2	-0.231	0.655	-0.353	0.999
4-3	0.190	0.160	1.188	0.801
5-3	-0.135	0.305	-0.443	0.997
6-3	-0.479	0.662	-0.719	0.974
5-4	-0.325	0.321	-1.011	0.893
6-4	-0.669	0.673	-0.994	0.900
6-5	-0.344	0.725	-0.474	0.996

[1] Does not reach statistical significance after Benjamini-Hochberg adjustment.