OXFORD

Evolution Letters, 2026, **0**(XX), 1–8
https://doi.org/10.1093/evlett/qraf051
Letter

Longevity is heritable and negatively genetically correlated between the sexes in yellow-bellied marmots

Michela N. Dumas [1], Bennett Krasnay[1], Carol-Ann Chabot[1], Maxime Fraser Franco [2], Émilie Gagnon [1], Emil Isaksson [1], Lytana Lécuyer[2], Giulia Masoero [1,3], Paula Molina [2], Pierre-Olivier Montiglio [2], Sarah Saneeibajgiran[2], Sophia St. Lawrence [1], Daniel T. Blumstein [4,5], Julien G.A. Martin [1,5]

[1]University of Ottawa, Department of Biology, Ottawa, Canada
[2]Université du Québec à Montréal, Département des Sciences Biologiques, Montréal, Canada
[3]Swiss Ornithological Institute, Sempach, Switzerland
[4]Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, United States
[5]The Rocky Mountain Biological Laboratory, Crested Butte, United States

Corresponding author. Department of Biology, University of Ottawa, Ottawa, K1N 6N5, Canada. Email: julien.martin@uottawa.ca

Abstract

Longevity, a major fitness component, is heritable in multiple species, including both captive and wild populations, and often varies widely between the sexes. The sex-specific genetic architecture of longevity, however, has rarely been estimated in wild populations, despite its potentially large implication for the evolutionary dynamic of a species. Using a long-term study of wild yellow-bellied marmots, a hibernating rodent, we estimated sex-specific additive genetic variance V_A and the cross-sex genetic correlation r_{fm} of longevity. Given the challenges associated with accurately measuring longevity in the wild, we used a new analytical approach based on a Censored Poisson distribution allowing us to integrate measurement errors on longevity in the model. Our approach revealed moderate and comparable V_A in both sexes and a strongly negative r_{fm}, albeit with large credible intervals. This contrasts with the results from a classic model with a restricted dataset for which V_A in males was estimated as zero, rendering the r_{fm} inestimable and uninterpretable. Our results suggest that studying selection and evolution while focusing on only one sex can lead to erroneous predictions given that, in marmots, selection pressures increasing longevity in one sex would inherently select for the reverse effect in the other sex. Taken together, this suggests the possible presence of a self-reinforcing feedback loop for the development of different life-history strategies among sexes in marmots, with long-lived females producing short-lived males who must maximize early life reproductive success ("live-fast die-young" strategy) and vice versa. Our study provides rare evidence of heritable longevity in a wild population and highlights how genetic conflicts between the sexes may constrain evolution and help maintain sex-specific genetic variance in fitness.

Keywords: quantitative genetics, genetic architecture, sexual conflict, life history evolution

Introduction

Longevity, or an individual's lifespan, is defined as the time between birth and death and is a major fitness component. Indeed, longevity directly influences fitness in most iteroparous species with a slow pace-of-life (Clutton-Brock, 1988) and hence should be under strong positive selection. To understand the potential for evolution and the evolutionary trajectory of a species, we need to understand the genetic basis of fitness, since for evolution in response to selection to occur, variation in fitness must have a heritable basis (Falconer & Mackay, 1996; Lynch, 1998).

Heritability estimates for longevity vary tremendously across studies. For example, among laboratory studies, estimates range from 20% to 50% in the hermaphroditic nematode *Caenorhabditis elegans* (Johnson & Wood, 1982) and between 44% and 62% in laboratory mice (Klebanov et al., 2000). Heritability estimates of longevity in wild populations are less common (but see Kruuk et al., 2000) and may present even greater variability due to unpredictable variation occurring in natural conditions (i.e., heritability estimates tend to be higher in favorable than unfavorable conditions, Charmantier & Garant, 2005). As such, the conditions under which longevity may be heritable—particularly in wild populations—remain unclear.

Furthermore, many wild populations exhibit phenotypic differences in longevity between the sexes. For example, female spotted turtles *Clemmys guttatacan* live up to 45 years longer than males (Litzgus, 2006), while male black-tailed prairie dogs *Cynomys ludovicianus* live 25% longer than females (Clutton-Brock & Isvaran, 2007). These phenotypic differences in longevity can extend to differences in the genetic architecture for this trait, with heritability estimates for male and female longevity sometimes differing substantially. For example, in fruit flies *Drosophila melanogaster*, females live longer than males (Spencer et al., 2003), and the genetic architecture of longevity differs between the sexes (Lehtovaara et al., 2013). This may have strong implications for the evolution of the species, given that each sex may respond to selection differently. For instance, for a given fitness trait under directional selection, a cross-sex genetic correlation (r_{fm}; Lande, 1980) that differs from 0 could constrain the global

Received July 10, 2025; revisions received November 26, 2025; accepted December 8, 2025

evolution of the organism. Indeed, a weak r_{fm} approaching zero would suggest sex-specific genetic architectures and the possibility for the sexes to evolve toward sex-specific phenotypic optima (Bonduriansky & Chenoweth, 2009; Poissant et al., 2010). By contrast, a strong r_{fm} approaching (positive or negative) 1 would suggest evolutionary constraints with neither sex free to independently reach their specific selective optima (Bonduriansky & Chenoweth, 2009). For example, a strong r_{fm} approaching 1 for tarsus length in the collared flycatcher *Ficedula albicollis* has displaced the female optimum by 200% (Merilä et al., 1998). These principles have also been well documented in the laboratory (e.g., negative r_{fm} for adult fitness in *D. melanogaster*, Chippindale et al., 2001, and in the southern ground cricket *Allonemobius socius*, Fedorka & Mousseau, 2004).

Estimates of sex-specific heritability for longevity and its cross-sex genetic correlation are seldom (but increasingly) reported in wild populations (e.g., Kruuk et al., 2000; Teplitsky et al., 2009; Wheelwright et al., 2014). Indeed, obtaining longevity estimates from wild populations requires long-term monitoring of individuals of known age, which is challenging due to difficulties tracking individuals over their entire lifespan from birth to death. Further complicating the matter, estimating the heritability of longevity requires pedigree data; i.e., the relatedness of individuals must be known, and parental links must be determined reliably (Kruuk et al., 2000). Importantly, data collection on the longevity of wild populations may be subject to increased limitations for one sex compared to the other sex due to sex biases in immigration and mortality in early life (e.g., higher male than female immigration and mortality in early life in many species; Festa-Bianchet & Mann, 2022). In addition, the distribution of longevity can vary widely depending on the time scale, rounding used for measurement (i.e., days, months, or rounded years), and seasonality (e.g., high mortality associated with hibernation or harsh winter conditions). In field studies with annual seasonal fieldwork and high seasonal mortality, age and longevity are usually measured as rounded numbers of years since birth. Stemming from these data collection constraints, methodological considerations must be taken to address the problem of uncertainty around individual ages.

One such statistical approach is to use a Censored Poisson distribution to model longevity, that is, by providing a minimum and maximum potential longevity for individuals of unknown exact longevity. In doing so, we are able to integrate uncertainty around individual longevity directly into the model and hence address data gaps resulting from emigration and immigration, while utilizing all available longevities and minimizing biases in our estimates. This contrasts with other approaches, such as restricting the analysis to only individuals with known longevity or using the minimum longevity for individuals of unknown exact longevity as their exact longevity estimate, which come at the expense of power to detect effects for the former and potentially biased estimates and inflated type I error for the latter.

In this study, we leveraged a long-term dataset to examine the sex-specific genetic architecture of longevity in a wild population of yellow-bellied marmots *Marmota flaviventer*. Longevity is sexually dimorphic in this species, with males living on average 3 years and females living on average 4 years (St. Lawrence et al., 2022) and for a maximum of 14 and 16 years for males and females, respectively. Using a quantitative genetic approach, we assessed the sex-specific additive genetic variance and heritability of longevity as well as its cross-sex genetic correlation. Given that yellow-bellied marmots have contrasting life-history strategies and that the r_{fm} in the number of pups produced per year was estimated to be 0 (St. Lawrence et al., 2022), we expected to also find a r_{fm} close to 0 for longevity. Indeed, Poissant et al. (2010) have reported that the r_{fm} of fitness traits is more likely to be null or negative than other trait types, which by contrast are more likely to have strongly positive r_{fm}. To address sex-specific uncertainty in longevity, we used a novel approach allowing us to consider longevity measurement errors associated with emigration and immigration, by modeling longevity with a Censored Poisson distribution. This approach hence utilized observations from all individuals while considering the potential error for the estimated longevities of animals first trapped as adults and for dispersing yearlings by providing a minimum and maximum potential longevity.

Materials and methods

Study species and site

Yellow-bellied marmots are large (3–5 kg) hibernating rodents and may live up to 16 years in the wild (Armitage, 2014). They exhibit a harem-polygynous mating system in which males compete for access to groups of related females (Armitage, 2000; Blumstein, 2025a). Colonies are typically composed of one or more matrilines and one or more males that have immigrated to the site. Dispersal is male-biased and typically occurs at 1 year of age. Marmots reach sexual maturity at 2 years of age. On average (mean ± standard deviation), yellow-bellied marmot males sire 4.7 ± 6.7 pups per year, while females produce 2.2 ± 2.6 pups per year (St. Lawrence et al., 2022).

This population of yellow-bellied marmots is located at the Rocky Mountain Biological Laboratory (RMBL) in the upper East River Valley, Gothic, Colorado. At RMBL, colonies of marmots can be separated into two valleys (upper and lower) based on an elevation difference of approximately 200 m. This contrast in elevation is associated with a 2-week delay in snowmelt that also results in a 2-week delay in spring emergence at up-valley locations (Armitage, 2014). Since 1962, marmots have been trapped on a fortnightly basis throughout the active season from mid-April to mid-October using Tomahawk traps. When captured for the first time, individuals are sexed based on external genital anatomy and marked with numbered ear tags for permanent identification. Fur-dye is also applied to facilitate identification during social observations (Blumstein et al., 2013). At each subsequent capture, individuals are weighed to the nearest 10 g and assessed for reproductive status.

Importantly, most adult females (79.2%) are of precisely known age given that they were first trapped as juveniles, whereas adult males are most often immigrants to the study site, and hence their precise age is only known in 54.6% of cases. Immigrants and individuals not captured for the first time as juveniles or yearlings are assumed to enter the population at 2 years of age (Armitage, 2014), allowing us to approximate their age in subsequent captures.

An individual is presumed dead if the death is directly witnessed or if the individual is not observed the following spring. Given high re-capture rates (>0.9 for the primary sites; Ozgul et al., 2006, 2007), precise estimates of year of death can be obtained. Yearlings that disappeared within a 20-day window around the date of pup emergence in their colony (10 days before, 10 days after) were considered to have dispersed rather than died

(Blumstein et al., 2009; Montero et al., 2020). However, to estimate yearling dispersal daily observations of all colonies are needed, which was not the case before 2002. For individuals with approximated year of birth (i.e., first trapped as adults) and known year of death, we could estimate a minimum longevity as year of death—year of first observation + 2. For individuals dispersing as yearlings or yearlings with unknown dispersal status, the minimum longevity was estimated as 1. For individuals with a minimum longevity, we estimated an expected maximum longevity as the longevity of 90% of the individuals with the same sex that lived at least to that age.

Pedigree

Because pups are trapped for the first time when they emerge from their maternal burrow, behavioral observations are sufficient to determine maternal linkages. Given the marmot mating system, paternities can only be assigned with confidence using a genetic approach. Prior to 2002, maternity was assigned based on behavioral observations and paternity was unknown (Armitage, 2014). Since 2002, genetic parentage assignments have been used for both maternities and paternities. Detailed methods are described in Blumstein et al. (2010). DNA was extracted using a QiaGen QIAamp DNA minikit and analyzed using GeneMapper 4.1 software (Applied Biosystems) for 12 microsatellite alleles before assigning a maximum-likelihood parentage with CERVUS (Kalinowski et al., 2007) at 95% confidence for the trio.

The pruned pedigree used in this study was 10 generations deep and included data on 2,734 individuals, with 1,174 maternities and 1,201 paternities (Table S1). The pedigree statistics were determined using the R package *pedtricks* (Martin et al., 2024).

Statistical analyses

All statistical analyses were conducted in R version 4.3.1 (R Core Team, 2024) using the R package *MCMCglmm* (Hadfield, 2010). We fitted the model with a Censored Poisson distribution, as this allowed us to explicitly consider measurement errors on longevity associated with emigration and immigration by providing a minimum and maximum potential longevity for individuals of unknown exact longevity.

To estimate quantitative genetic parameters of longevity, we used a generalized linear mixed effects model including pedigree data (an "animal model" Kruuk et al., 2000). We fit longevity as a function of sex, valley (up, down), and the sex by valley interaction to estimate sex differences in longevity and control for micro-environmental effects on longevity associated with the position in the valley (low vs. high elevation sites). To estimate the heritability of longevity in both sexes, as well as estimate the cross-sex genetic correlation of this trait (and hence the presence of genetic constraints), we included individual identity linked to the pedigree as a random effect. We also included the cohort and colony as random effects to capture variation due to the year of birth and due to the local environment, respectively. The cohort effect was fitted as sex-specific effect to evaluate if year of birth effect differed between sexes. The colony effect, however, was estimated as a combined sex effect due to the limited number of males per colony. Including a sex-specific colony effect in the model led to extremely poor mixing of the chain for the parameter, which was essentially bounded to 0.

For random effects for which a cross-sex correlation was to be estimated, we used parameter expanded priors (V = diag(2) * 0.02, nu = 3, alpha.mu = rep(0,2), and an alpha.V = diag(2) * c(1000)) to get a weakly informative prior on the correlation scale. For the colony effect, which was not sex-dependent, we used weak priors (V = 1, nu = 0.002). The prior for residual variances was non-informative (V = diag(2), nu = 2). We sampled every 2,000 iterations with a burn-in of 50,000 iterations for a total of 1,500 samples. We visually checked trace plots, and all models had an autocorrelation under 0.10. We also used the Heidelberg and Welch convergence diagnostic (*heidel.diag()* function) to verify model convergence (Hadfield, 2010). Following Pick et al. 2023, we interpreted model parameters using the median of the posterior distribution with the 95% highest posterior density intervals (HPDI) but we also reported the mean and mode for each parameter in the appendix (Table S2). Variance ratio estimates were calculated as the proportion of total phenotypic variation explained by the given variance parameter, i.e., heritability on the latent scale conditioned on the fixed effects was estimated as the sex-specific additive genetic variance divided by the (conditional) total phenotypic variance. We also estimated back-transformed variance components and ratios using the R package *QGglmm* (de Villemereuil et al., 2016) for a multivariate Poisson distribution.

We additionally fitted two models of longevity using a more traditional modeling approach that does not consider emigration or immigration and either restricts the dataset to only individuals of exact known longevity or assumes no error in longevity estimations. Results from these additional models are reported only in the appendix (Table S2; Table S3; Table S4).

Ethical note

All marmots were trapped in accordance with the Animal Use and Care Committees of the University of California and the RMBL (UCLA Protocol No. 2001-191-01 renewed annually) and permits from the Colorado Division of Wildlife (TR917 issued annually). Traps were set in the morning and afternoon near burrow entrances and checked after 2–3 hrs. Traps were provided shade on warm days, and we did not trap 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 conical cloth bag to reduce stress. We swabbed the ears with alcohol before affixing 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 (unpub. data).

Results

Overall, the model was fitted with 2681 longevity observations but assumed that 745 individuals had a range of potential longevities (Table 1; Table S4). The model mixed well, all parameters converged, and the autocorrelations were below 0.1. Of these 2681 individuals, 195 individuals (73 females and 122 males) were first captured as adults, and 550 individuals (206 females and 344 males) disappeared at age 1 having either died or dispersed. The mean longevity (mean ± standard error) was 1.29 ± 0.06 years for females and 0.72 ± 0.03 years for males (raw data). The average longevity of individuals that reached a minimum age of 2 years was 4.44 ± 0.17 years for females and 2.97 ± 0.15 years for males (raw data). Females lived longer in the down valley sites as compared to the up valley sites,

Table 1. Parameter estimates (median and 95% highest posterior density intervals) of longevity in male and female yellow-bellied marmots using a Censored Poisson distribution and all estimates of longevity (known and approximated; $n = 2681$).

	Females	Males	r_{fm}
Fixed Effects			
Intercept	−0.103 [−0.407; 0.250]	−0.016 [−0.276; 0.303]	
Valley [Up]	−0.131 [−0.491; 0.195]	0.314 [−0.040; 0.686]	
Random Effects			
V_A latent	0.318 [0.053; 0.623]	0.399 [0.065; 0.721]	−0.521 [−0.901; 0.026]
V_{Cohort} latent	0.610 [0.329; 0.972]	0.458 [0.250; 0.764]	0.946 [0.840; 1.000]
V_{Colony} latent	0.006 [0.000; 0.056]		
$V_{Residual}$ latent	1.044 [0.724; 1.331]	0.623 [0.371; 0.922]	
h^2 latent	0.160 [0.028; 0.300]	0.264 [0.074; 0.469]	
$Cohort^2$ latent	0.306 [0.202; 0.423]	0.305 [0.184; 0.422]	
V_P observed	36.405 [13.055; 89.649]	21.062 [7.936; 49.599]	
h^2 observed	0.045 [0.010; 0.090]	0.099 [0.026; 0.179]	−0.521 [−0.901; 0.026]
CV_A observed	56.366 [29.880; 82.381]	63.190 [33.138; 88.781]	
I_A observed	0.318 [0.053; 0.623]	0.399 [0.065; 0.721]	
$Cohort^2$ observed	0.088 [0.061; 0.117]	0.115 [0.074; 0.151]	0.946 [0.840; 1.000]

Variance component estimates: additive genetic variance, cohort, colony, residual. Variance ratios: heritability, cohort, and colony (permanent environment) effects on both the latent and observed scales. The coefficient of additive genetic variation (CV_A) and evolvability (I_A) are reported. The colony effect, as well as the cross-sex covariances and correlations, are estimated as between the sexes and hence displayed in the table only once.

while males lived longer up valley as compared to down valley (Table 1).

We report comparable additive genetic variance of longevity in both sexes, of 0.318 [0.053; 0.623] (median [95% HPDI]) in females and 0.399 [0.065; 0.721] in males (Table 1). Heritability of longevity was 45% greater for males (0.099 [0.026; 0.179]) than females (0.045 [0.01; 0.09]) likely reflecting the lower residual variance for males as compared to females. We found a negative genetic correlation across the sexes of −0.521 [−0.901; 0.026] (Table 1; Figure 1). The 95% HPDI for the correlation is wide and includes zero but 96% of the posterior distribution is negative.

We likewise report a comparably positive effect of cohort on longevity in both sexes, 75% higher for females (0.61 [0.329; 0.972]) than males (0.458 [0.25; 0.764]), with a cross-sex correlation close to 1 (0.946 [0.84; 1]) (Table 1; Figure 1). The colony effect was not different from zero, showing a negligible effect on longevity for both sexes (Table 1). The coefficient of variation (CV_A) and evolvability (I_A) were moderate for both sexes (Table 1).

Discussion

In this study, we investigated the sex-specific genetic architecture of longevity, a key fitness trait, in a wild population of yellow-bellied marmots. We leveraged a Censored Poisson distribution, allowing us to model a range of potential longevities in cases where exact longevity was unknown, to mitigate data uncertainty constraints. We show that on average, males have a shorter longevity than females and that this trait is negatively genetically correlated between the sexes.

We report strong evidence of moderate additive genetic variance and heritability as well as evolvability of longevity in both sexes. As such, longevity—and hence fitness—has the potential to evolve in response to selection in both male and female yellow-bellied marmots, should genetic variance in other fitness components allow it. Males had greater additive genetic variance than females, suggesting potential for a faster evolutionary response. Overall, this is in line with results by Bonnet et al. (2022), who demonstrated that fitness in many wild populations has sufficient additive genetic variance for rapid evolution.

However, we also report evidence of a negative cross-sex genetic correlation for longevity in this population of yellow-bellied marmots, suggesting a genetic constraint on any potential evolutionary responses. That is, long-lived mothers produce long-lived daughters and short-lived sons, while short-lived fathers produce short-lived sons and long-lived daughters. Assuming that longevity is under positive selection in both sexes, such a negative correlation would suggest that alleles coding for higher longevity in one sex would be maladaptive when expressed in the other sex. Sexual antagonism at the genetic level has been identified for various traits across multiple taxa (mammals: e.g., fitness in red deer *Cervus elaphus*, Foerster et al. (2007); body mass in mountain goats *Oreamnos americanus*, Mainguy et al. (2009); birds: e.g., lifetime reproductive success in collared flycatchers *F. albicollis*, Brommer et al. (2007); reptiles: e.g., immune function in side-blotched lizards *Uta stansburiana*, Svensson et al. (2009)). A cross-sex genetic correlation with an absolute value different than 1 (positive or negative) suggests that longevity—and hence fitness—should evolve at least partly independently between the sexes (Bonduriansky & Rowe, 2005), though the persisting genetic constraints would limit the evolution of sexual dimorphism and may instead contribute toward maintaining variance in fitness between the sexes. Hence, this negative cross-sex genetic correlation may act as a genetic constraint on the evolution of longevity in this population and on the evolutionary dynamic of any traits related to survival and longevity.

Assuming that longevity is a good fitness proxy, then a negative cross-sex genetic correlation has implications far beyond the longevity trait alone. Indeed, a trait for which female and male genetic architecture is the same ($V_{Af} = V_{Am}$ and $r_{fm} = 1$) and which, for example, is positively selected for in females (e.g., a positive correlation with longevity), would in fact lead to a correlated negative response in males. Hence, the only traits that would lead to a positive selection with longevity for both sexes would be traits that have a negative genetic correlation across the sexes.

Male and female marmots have different reproductive strategies, where females seem to favor a conservative strategy with

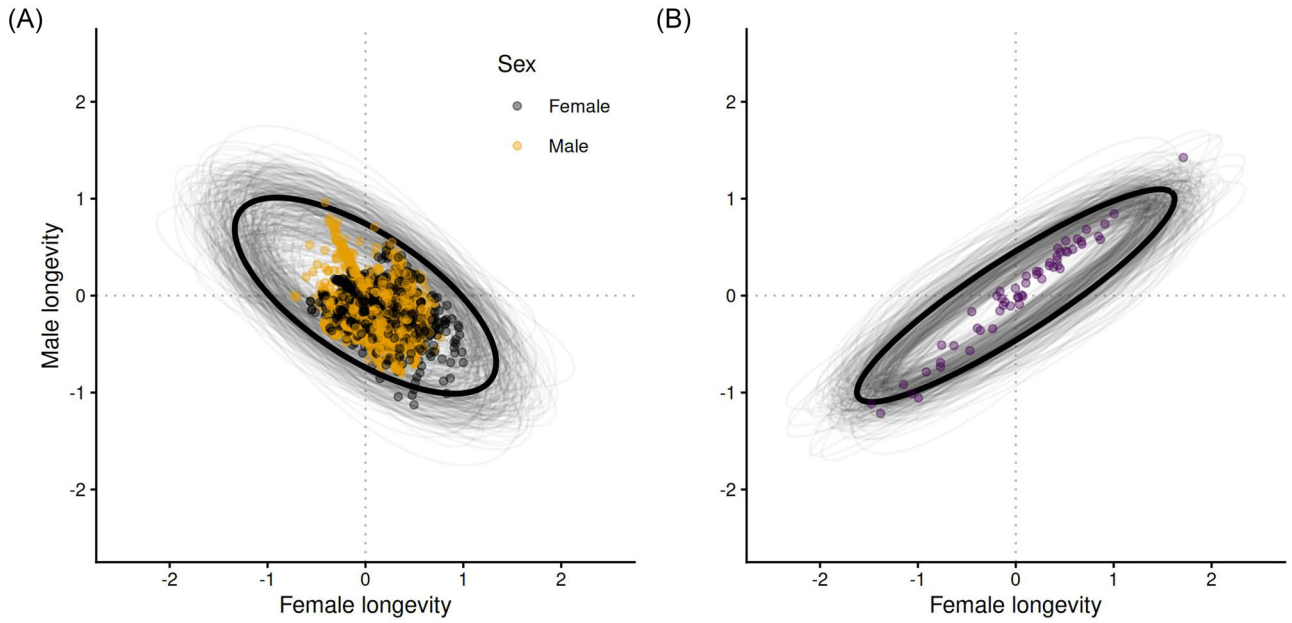

Figure 1. The cross-sex (A) additive genetic and (B) cohort correlations of longevity in yellow-bellied marmots. Black and yellow points (A) represent predicted breeding values (PBVs) for females and males, respectively, and purple points (B) are BLUPs for cohorts. The bold ellipses represent the posterior mode of the variance matrices. Uncertainty of the estimates is indicated with the gray ellipses, which represent 300 randomly selected estimates from the posterior distribution.

higher survival and lower annual reproduction (Armitage, 2014), whereas males tend to have a lower yearly survival, die at a younger age, and produce more offspring per year (Armitage, 2014). Given the sex-specific life-history strategies of yellow-bellied marmots, and hence potentially different fitness consequences of longevity between the sexes, it may appear unsurprising for this negative cross-sex genetic correlation for fitness to have occurred. Indeed, a longer lifespan may contribute more to fitness in females than in males. Females have physiological constraints that limit the number of pups they can produce each year, and as such must reproduce for as many years as possible to achieve higher lifetime reproductive success. By contrast, males disperse as yearlings with only a small percentage (<16%) reaching adulthood (Armitage, 2014), and they must successfully monopolize access to a harem of females to reproduce. The duration of male residence is short—typically less than 3 years—during which they maximize their reproductive success by increasing the number of reproductive females in their harems and can sire over 40 pups in a given year (St. Lawrence et al., 2022). As such, while a longer tenure will yield higher reproductive success for males as well, they can by far exceed the reproductive success of a single female in a much shorter window of time, following a "live-fast die-young" strategy. Hence, sexual dimorphism in longevity could be an adaptive strategy to resolve intra-locus sexual conflict over optimal life-history strategies in this species. Moreover, the negative genetic correlation might in fact act as a self-reinforcing feedback loop for the evolution of sexual dimorphism in reproductive strategies, given that females that live longer and reproduce more would produce sons that live shorter lives, and males that live long would produce daughters with shorter lives with lower opportunity for reproduction. Thus, a logical next step will be to estimate the genetic variances of (and correlation between) longevity and lifetime reproductive success, and hence whether the identified intra-locus sexual conflict presents a persistent source of constraint on adaptation (Ruzicka et al., 2020). Unfortunately, we do not yet have sufficient data on male annual and lifetime reproductive success to perform such an analysis (Blumstein, 2025b).

Year of birth explained a comparable percentage of the variance in longevity in males and females (8.8% and 11.5%, respectively). Coupled with this result, we found a strong positive correlation (above 0.95) between the sexes, indicating similar cohort effects on female and male longevity. However, although the additive genetic variance was slightly higher among males than females, the phenotypic variance in longevity of females was 1.73 times higher than that of males, suggesting that females may be more susceptible to environmental fluctuations than males. This is often observed in systems where males do not provide care for their offspring (Festa-Bianchet et al., 2019; Thiemann et al., 2011). In marmots, annual survival, and ultimately longevity, are strongly affected by mass gain over the summer (Armitage, 2014). Males start to gain weight earlier during the spring immediately after mating, whereas females start to gain weight later in the summer after weaning their pups (Armitage, 2014). Therefore, females may experience stronger effects of yearly environmental fluctuations than males because they have a shorter time window to prepare for the winter. Likewise, longevity was higher in down valley colonies as compared to the upper valley colonies, likely arising from the different elevations (Woods et al., 2009) and associated 2-week delay in spring onset (Blumstein et al., 2004).

Our statistical approach, using a Censored Poisson distribution, offered two advantages when dealing with data from wild populations such as yellow-bellied marmots. Specifically, this method addresses gaps in the available information on individual age, which, in marmots, differs considerably between the sexes (see supplementary for model outputs for all three approaches; Table S2; Table S3; Table S4). First, the model accounted for the uncertainty introduced by dispersing males arriving at the focal colonies, whose exact age could not be known, and by emigrating males whose exact longevity cannot be known. Including a range of possible longevities for these males (e.g., for

immigrating males min: number of years observed before death plus two, assuming arrival of immigrants at two years of age; max: maximum longevity of a marmot, 14 years) allowed for a more conservative estimate than that of a model where estimated longevities would be treated as exact. Second, this approach drastically increased the available sample size, and hence statistical power of the analysis, as compared to a classic approach that considers only individuals whose exact age of birth and death were known.

To conclude, we identified a negative cross-sex genetic correlation for longevity, a key fitness trait, in a wild population of yellow-bellied marmots. Indeed, responses to selection for any phenotypic trait, even in cases where that selection is the same in both sexes, may be constrained by this identified negative cross-sex genetic correlation for fitness. To understand the evolutionary trajectories of an organism, it is critical to quantify sex-specific heritability and the cross-sex genetic correlation not only for phenotypic traits of interest, but also measures of overall fitness. This remains challenging to do in the wild given data limitations and constraints, but can be mitigated, at least in part, through the use of statistical methods such as a Censored Poisson distribution.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

The data and code for this study are available on OSF https://doi.org/10.17605/OSF.IO/PDTCK (Martin et al. 2025).

Author contributions

Conceptualization: B.K., M.D., J.G.A.M. Data curation: J.G.A.M. Formal analysis: B.K., J.G.A.M. Funding acquisition: J.G.A.M., D.T.B., P.O.M. Supervision: M.D., J.G.A.M. Visualization: J.G.A.M. Writing—original draft: B.K., M.D. Writing—review & editing: M.D., C.A.B., M.F.F., E.G., E.I., L.L., G.M., P.M., P.O.M., S.S., S.S.L., D.T.B., J.G.A.M.

Funding

J.G.A. Martin was supported by the University of Ottawa and a NSERC Discovery grant (DGECR-2019-00289, RGPIN-2019-05000). D.T.B. was supported by the National Geographic Society, the University of California, Los Angeles (Faculty Senate and Division of Life Sciences), an RMBL research fellowship, and the U.S. National Science Foundation (NSF IDBR-0754247 and DEB-1119660 and 1557130 to D.T.B., as well as DBI 0242960, 07211346, 1226713, and 1755522 to RMBL).

Conflict of interest

The authors have no conflict of interests to declare.

Acknowledgments

We thank all the marmoteers who have collected these data over the years and the Rocky Mountain Biological Laboratory for staff and logistical support.

References

Armitage, K. B. (2000). The evolution, ecology, and systematics of Marmots. *Oecologia Montana*, *9*, 1–18. https://om.vuvb.uniza.sk/index.php/OM/article/view/116.

Armitage, K. B. (2014). *Marmot biology: Sociality, individual fitness, and population dynamics*. Cambridge University Press. https://doi.org/10.1017/CBO9781107284272

Blumstein, D. T. (2025a). Society formation and maintenance in yellow-bellied marmots. *Animal Behaviour*, *226*, 123250. https://doi.org/10.1016/j.anbehav.2025.123250

Blumstein, D. T. (2025b). The end of long-term ecological data? *PLoS Biology*, *23*, e3003102. https://doi.org/10.1371/journal.pbio.3003102.

Blumstein, D. T., Im, S., Nicodemus, A., & Zugmeyer, C. (2004). Yellow-bellied Marmots (*Marmota flaviventris*) hibernate socially. *Journal of Mammalogy*, *85*, 25–29. https://doi.org/10.1644/1545-1542(2004)085<0025:YMMFHS>2.0.CO;2

Blumstein, D. T., Lea, A. J., Olson, L. E., & Martin., J. G. A. (2010). Heritability of anti-predatory traits: Vigilance and locomotor performance in marmots. *Journal of Evolutionary Biology*, *23*, 879–887. https://doi.org/10.1111/j.1420-9101.2010.01967.x

Blumstein, D. T., Petelle, M. B., & Wey, T. W. (2013). Defensive and social aggression: Repeatable but independent. *Behavioral Ecology*, *24*, 457–461. https://doi.org/10.1093/beheco/ars183

Blumstein, D. T., Wey, T. W., & Tang., K. (2009). A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3007–3012. https://doi.org/10.1098/rspb.2009.0703

Bonduriansky, R., & Chenoweth, S. F. (2009). Intralocus sexual Conflict. *Trends in Ecology and Evolution*, *24*, 280–288. https://doi.org/10.1016/j.tree.2008.12.005

Bonduriansky, R., & Rowe., L. (2005). Intra-locus sexual conflict and the genetic architecture of sexually dimorphic traits in *Prochyl iza xanthostoma* (Diptera: Piophilidae). *Evolution; International Journal of Organic Evolution*, *59*, 1965–1975. https://doi.org/10.1111/j.0014-3820.2005.tb01066.x

Bonnet, T., Morrissey, M. B., de Villemereuil, P., Alberts, S. C., Arcese, P., Bailey, L. D., Boutin, S., Brekke, P., Brent, L. J. N., Camenisch, G., Charmantier, A., Clutton-Brock, T. H., Cockburn, A., Coltman, D. W., Courtiol, A., Davidian, E., Evans, S. R., Ewen, J. G., Festa-Bianchet, M., … Kruuk, L. E. B., (2022). Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. *Science*, *376*, 1012–1016. https://doi.org/10.1126/science.abk0853.

Brommer, J. E., Kirkpatrick, M., Qvarnström, A., & Gustafsson, L. (2007). The intersexual genetic correlation for lifetime fitness in the wild and its implications for sexual selection. *PLoS ONE*, *2*, e744. https://doi.org/10.1371/journal.pone.0000744.

Charmantier, A., & Garant, D. (2005). Environmental quality and evolutionary potential: Lessons from wild populations. *Proceedings of the Royal Society B*, *272*, 1415–1425. https://doi.org/10.1098/rspb.2005.3117

Chippindale, A. K., Gibson, J. R., & Rice, W. R. (2001). Negative genetic correlation for adult fitness between sexes reveals ontogenetic conflict in Drosophila. *Proceedings of the National Academy of Sciences of the United States of America*, *13*, 1671–1675. https://doi.org/10.1073/pnas.98.4.1671

Clutton-Brock, T. H. , ed. (1988). *Reproductive success: Studies of individual variation in contrasting breeding systems*. University of Chicago Press.

Clutton-Brock, T. H., & Isvaran., K. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society B*, *274*, 3097–3104. https://doi.org/10.1098/rspb.2007.1138

de Villemereuil, P., Schielzeth, H., Nakagawa, S., & Morrissey, M. (2016). General methods for evolutionary quantitative genetic inference from generalised mixed models. *Genetics, 204*, 1281–1294. https://doi.org/10.1534/genetics.115.186536

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics* 4th Edition. Pearson Education

Fedorka, K. M., & Mousseau, T. A. (2004). Female mating bias results in conflicting sex-specific offspring fitness. *Nature*, *429*, 65–67. https://doi.org/10.1038/nature02492.

Festa-Bianchet, M., & Mann., J. (2022). Introduction to topical Collection 'measuring Individual reproductive Success in the wild'. *Behavioral Ecology and Sociobiology*, *76*, 114. https://doi.org/10.1007/s00265-022-03225-2

Festa-Bianchet, M., Côté, S. D., Hamel, S., & Pelletier., F. (2019). Long-term studies of bighorn sheep and mountain goats reveal fitness costs of reproduction. *Journal of Animal Ecology*, *88*, 1118–1133. https://doi.org/10.1111/1365-2656.13002

Foerster, K., Coulson, T., Sheldon, B. C., Pemberton, J. M., Clutton-Brock, T. H., & Kruuk, L. E. (2007). Sexually antagonistic genetic variation for fitness in red deer. *Nature*, *8*, 1107–1110. https://doi.org/10.1038/nature05912.

Hadfield, J. (2010). MCMC methods for multi-response generalized linear mixed models: The *MCMCglmm* R package. *Journal of Statistical Software*, *33*, 1–22. https://doi.org/10.18637/jss.v033.i02.

Johnson, T. E., & Wood., W. B. (1982). Genetic analysis of life-span in *Caenorhabditis elegans*. *Proceedings of the National Academy of Sciences of the United States of America*, *79*, 6603–6607. https://doi.org/10.1073/pnas.79.21.6603

Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, *16*, 1099–1106. https://doi.org/10.1111/j.1365-294X.2007.03089.x

Klebanov, S., Flurkey, K., Roderick, T. H., Archer, J. R., Astle, M., Chen, J., & Harrison, D. E. (2000). Heritability of life span in mice and its implication for direct and indirect selection for longevity. *Genetica*, *110*, 209–218. https://doi.org/10.1023/A:1012790600571

Kruuk, L. E. B., Clutton-Brock, T. H., Slate, J., Pemberton, J. M., Brotherstone, S., & Guinness, F. E. (2000). Heritability of fitness in a wild mammal population. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 698–703. https://doi.org/10.1073/pnas.97.2.698

Lande, R. (1980). Sexual dimorphism, Sexual selection, and adaptation in polygenic characters. *Evolution; International Journal of Organic Evolution*, *34*, 292–305. https://doi.org/10.1111/j.1558-5646.1980.tb04817.x

Lehtovaara, A., Schielzeth, H., Flis, I., & Friberg., U. (2013). Heritability of life span is largely sex limited in Drosophila. *The American Naturalist*, *182*, 653–665. https://doi.org/10.1086/673296

Litzgus, J. D. (2006). Sex differences in longevity in the spotted turtle (*Clemmys Guttata*). *Copeia*, *2006*, 281–288. https://doi.org/10.1643/0045-8511(2006)6[281:SDILIT]2.0.CO;2

Lynch, M. (1998). *Genetics and analysis of quantitative traits*. Sinauer.

Mainguy, J., Côté, S. D., Festa-Bianchet, M., & Coltman, D. W. (2009). Father-offspring phenotypic correlations suggest intralocus sexual conflict for a fitness-linked trait in a wild sexually dimorphic mammal. *Proceedings of the Royal Society B*, *276*, 4067–4075. https://doi.org/10.1098/rspb.2009.1231

Martin, J. G. A., Dumas, M. N., & Blumstein, D. T. (2025). Data for: Fitness is heritable and negatively genetically correlated between the sexes in yellow-bellied marmots. Archived on OSF: https://doi.org/10.17605/OSF.IO/PDTCK.

Martin, J., Wolak, M. E., Johnston, S., & Morrissey, M. M. (2024). Pedtricks: Visualize, summarize and simulate data from pedigrees. R Package Version 0.4.3. https://juliengamartin.github.io/pedtricks/.

Merilä, J., Sheldon, B. C., & Ellegren, H. (1998). Quantitative genetics of sexual size dimorphism in the collared flycatcher, *Ficedula albicollis*. *Evolution; International Journal of Organic Evolution*, *52*, 870–876. https://doi.org/10.1111/j.1558-5646.1998.tb03711.x

Montero, A. P, Williams, D. M., Martin, J. G. A., & Blumstein, D. T. (2020). More social female yellow-bellied marmots, *Marmota flaviventer*, have enhanced summer survival. *Animal Behaviour*, *160*, 113–119. https://doi.org/10.1016/j.anbehav.2019.12.013

Ozgul, A., Armitage, K. B., Blumstein, D. T., & Oli, M. K. (2006). Spatiotemporal variation in survival rates: Implications for population dynamics of yellow-bellied marmots. *Ecology*, *87*, 1027–1037. https://doi.org/10.1890/0012-9658(2006)87[1027:SVISRI]2.0.CO;2

Ozgul, A., Oli, M. K., Olson, L. E., Blumstein, D. T., & Armitage, K. B. (2007). Spatiotemporal variation in reproductive parameters of yellow-bellied marmots. *Oecologia*, *154*, 95–106. https://doi.org/10.1007/s00442-007-0817-9

Pick, J. L., Kasper, C., Allegue, H., Dingemanse, N. J., Dochtermann, N. A., Laskowski, K. L., Lima, M. R., Schielzeth, H., Westneat, D. F., & Wright, J., & (). . , , . https://doi.org/10.1111/2041-210X.14200

Poissant, J., Wilson, A. J., & Coltman, D. W. (2010). Sex-specific genetic variance and the evolution of sexual dimorphism: A systematic review of cross-Sex genetic correlations. *Evolution; International Journal of Organic Evolution*, *64*, 97–107. https://doi.org/10.1111/j.1558-5646.2009.00793.x

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Ruzicka, F., Dutoit, L., Czuppon, P., Jordan, C. Y., Li, X.-Y., Olito, C., Runemark, A., Svensson, E. I., Yazdi, H. P., & Connallon, T. (2020). The search for sexually antagonistic genes: Practical insights from studies of local adaptation and statistical genomics. *Evolution Letters*, *4–5*, 398–415. https://doi.org/10.1002/evl3.192.

Spencer, C. C., Howell, C. E., Wright, A. R., & Promislow, D. E. L. (2003). Testing an 'aging gene' in long-lived drosophila strains: Increased longevity depends on sex and genetic background. *Aging Cell*, *2*, 123–130. https://doi.org/10.1046/j.1474-9728.2003.00044.x

St. Lawrence, S., Dumas, M. N., Petelle, M., Blumstein, D. T., & Martin, J. G. A. (2022). Sex-specific reproductive strategies in wild yellow-bellied marmots (*Marmota Flaviventer*): Senescence and genetic variance in annual reproductive success differ between the sexes. *Behavioral Ecology and Sociobiology*, *76*, 84. https://doi.org/10.1007/s00265-022-03191-9

Svensson, E. L., McAdam, A. G., & Sinervo, B. (2009). Intralocus sexual conflict over immune defense, gender load, and sex-specific signaling in a natural lizard population. *Evolution; International Journal of Organic Evolution*, *63*, 3124–3135. https://doi.org/10.1111/j.1558-5646.2009.00782.x

Teplitsky, C., Mills, J., Yarrall, J. W., & Merillä, J. (2009). Heritability of fitness components in a wild bird population. *Evolution; International Journal of Organic Evolution*, *63-3*, 716–726. https://doi.org/10.1111/j.1558-5646.2008.00581.x.

Thiemann, G. W., Iverson, S. J., Stirling, I., & Obbard, M. E. (2011). Individual patterns of prey selection and dietary specialization in an arctic marine carnivore. *Oikos*, *120*, 1469–1478. https://doi.org/10.1111/j.1600-0706.2011.19277.x

Wheelwright, N. T., Keller, L. F., & Postma, E. (2014). The effect of trait type and strength of selection on heritability and evolvability in an island bird population. *Evolution; International Journal of Organic Evolution*, *68*, 3325–3336. https://doi.org/10.1111/evo.12499.

Woods, B. C., Brown, C., & Cobb, M. A. (2009). Elevation variation in life-history characteristics of populations of yellow-bellied marmots (*Marmota Flaviventris*). *Ethology Ecology and Evolution*, *21*, 381–392. https://doi.org/10.1080/08927014.2009.9522493.

Received July 10, 2025; revisions received November 26, 2025; accepted December 8, 2025