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ARTICLE

Animal Ecology

Interplay of abiotic conditions, density, and body size in shaping demography in a high-elevation toad population

Omar Lenzi[1] | **Kurt Grossenbacher**[2] | **Silvia Zumbach**[3] | **Beatrice Lüscher**[4] | **Sarah Althaus**[4] | **Marco Thoma**[2] | **Daniela Schmocker**[5] | **Helmut Recher**[6] | **Arpat Ozgul**[1] | **Benedikt R. Schmidt**[1,3]

[1]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[2]Independent Researcher, Bern, Switzerland

[3]Info Fauna Karch, Neuchâtel, Switzerland

[4]Info Fauna Karch - Regionalvertretung Bern, Münsingen, Switzerland

[5]Impuls AG, Thun, Switzerland

[6]Abteilung Biodiversität und Landschaft, Bundesamt für Umwelt, Ittigen, Switzerland

Correspondence
Omar Lenzi
Email: omar.lenzi@ieu.uzh.ch

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Abstract

In natural populations, vital rates such as survival and reproduction are influenced by a complex interplay of abiotic conditions (e.g., environment), density dependence, and individual factors (e.g., phenotypic traits). Studies at the extremes of species distributions, particularly high elevations, offer unique insights due to the intensified effects of abiotic stressors, which can amplify both direct and indirect effects on vital rates. In this study, we focus on a high-elevation population of the common toad (*Bufo bufo*) located near the upper limit of its elevational range in the Swiss Alps. This setting provides a critical context for examining how extreme abiotic conditions interact with density dependence and individual factors to influence life history traits. Utilizing 28 years of capture–mark–recapture data and individual body size measurements from nearly 2500 toads, we applied in a Bayesian statistical framework a Cormack–Jolly–Seber model for estimating male survival probabilities, and a multistate model for assessing female survival and breeding probabilities, alongside sex-specific growth curves. Our analysis indicates that survival probabilities are significantly impacted by interactions between abiotic conditions such as the active season length and temperature at emergence from hibernation, density dependence, and individual phenotypic traits such as body size. The breeding patterns of females showed a biennial cycle, with temperature at hibernation emergence influencing the likelihood of skipping breeding events and density affecting the resumption of breeding. These results highlight the role of abiotic conditions and density in shaping physiological and reproductive strategies in a high-stress ecological niche. Moreover, we uncovered indications of indirect effects, where both abiotic conditions and density potentially affect asymptotic growth and thus survival, mediated through changes in body size. Our findings illustrate the complex dynamics at play in high-elevation populations and the importance of long-term, individual-based data in studying these processes. This study underscores the value of integrating multiple sources of variation to understand population dynamics comprehensively, particularly in understudied, extreme environments where traditional ecological models may not fully capture the nuanced interdependencies of natural systems.

KEYWORDS
alpine environment, amphibian, capture–mark–recapture, demography, growth, vital rate

INTRODUCTION

Fluctuations in population size have historically been ascribed to the effects of abiotic (i.e., environmental) conditions as well as density dependence on vital rates (Hanski et al., 1997; Lawton, 1994). Abiotic conditions and density can have similar, opposite, or interacting effects on vital rates (Conquet et al., 2023; Gamelon et al., 2017). In addition, the effects of individual traits such as body size on vital rates also matter in driving population dynamics (Easterling et al., 2000; Rees et al., 2014). Abiotic conditions and density, aside from their direct effect on vital rates, can influence these individual traits as well, leading to indirect (i.e., trait-mediated) effects on vital rates and on population dynamics (e.g., Amarillo-Suárez et al., 2011).

Studies in the past often have focused on one or multiple factors at a time, but a more complete understanding of vital rates and population dynamics and their drivers could be obtained when incorporating all factors in demographic analyses (Benton et al., 2006; Ehrlén et al., 2016). Investigating these factors and their effects on adult survival and breeding probability, two key vital rates that can contribute to population growth (e.g., Desprez et al., 2018; Sæther & Bakke, 2000; Schmidt et al., 2005), can give important insights into the causes of population fluctuations. Populations at high elevations are exposed to harsh environmental conditions (e.g., cold temperatures), with known physiological effects (e.g., lower metabolic rates) that usually result in a slower life cycle (Laiolo & Obeso, 2017). We expect in these populations a stronger effect of abiotic conditions on vital rates compared to density and individual factors, given how severely the environment acts as a selective force (e.g., Bassar et al., 2016; Paquette & Hargreaves, 2021).

Although there are many studies on these factors in birds and mammals, we are lacking studies about amphibians, which are an often understudied taxon (Conde et al., 2019), despite their important role in ecosystems (Whiles et al., 2006) and their worrying status at the global scale (Houlahan et al., 2000; Luedtke et al., 2023). Thus, a lack of knowledge hampers an in-depth understanding of vertebrate demography and negatively affects conservation (Conde et al., 2019).

We used 28 years of capture–mark–recapture (CMR) data on a high-elevation population of common toad (*Bufo bufo*) to quantify the relative importance of density, abiotic conditions, and individual factors in shaping the dynamics of amphibian populations (Figure 1). The implemented analytical framework has two parts. The first part is a model where we quantified the effect of abiotic conditions and density on individual body size. The second part is a CMR model that we used to describe the direct and indirect effects of abiotic conditions and density and the direct effects of size, that is, an individual factor, on survival and breeding probabilities (the latter only for females).

We used a von Bertalanffy (VB) growth model to obtain information on body size, an individual factor to be used in the CMR analysis. Hemelaar (1988) estimated growth curves using 3 years of data for the same population through skeletochronology; we expected to obtain similar growth curves. We investigated the effect of density and the length of the active season in the previous year (an abiotic factor) on the VB model coefficients, the growth rate *k* and the asymptotic size *a*.

In the second part of the analytical framework (i.e., the CMR model), we quantified the direct and direct effects of abiotic conditions, density, and individual size on survival and breeding probabilities. The latter were estimated only for females because they breed intermittently in this population (Grossenbacher, 2002). Intermittent breeding can arise where environmental conditions are unfavorable. In these conditions, individuals can or must forfeit breeding in a year. Skipping breeding can be either an adaptive response when environmental conditions are pessimal for successful breeding and therefore a way to avoid wasting energy in bad years (Bull & Shine, 1979). In capital breeders, individuals can skip breeding due to the impossibility of collecting enough resources to build a clutch (Houston et al., 2007; Jönsson, 1997). This can happen when the active season is short due to poor environmental conditions, and therefore, opportunities for foraging are limited. Skipping breeding happens commonly in females, for whom reproduction is more demanding energetically (Hayward & Gillooly, 2011; Jørgensen, 1992). For female toads, we thus estimated

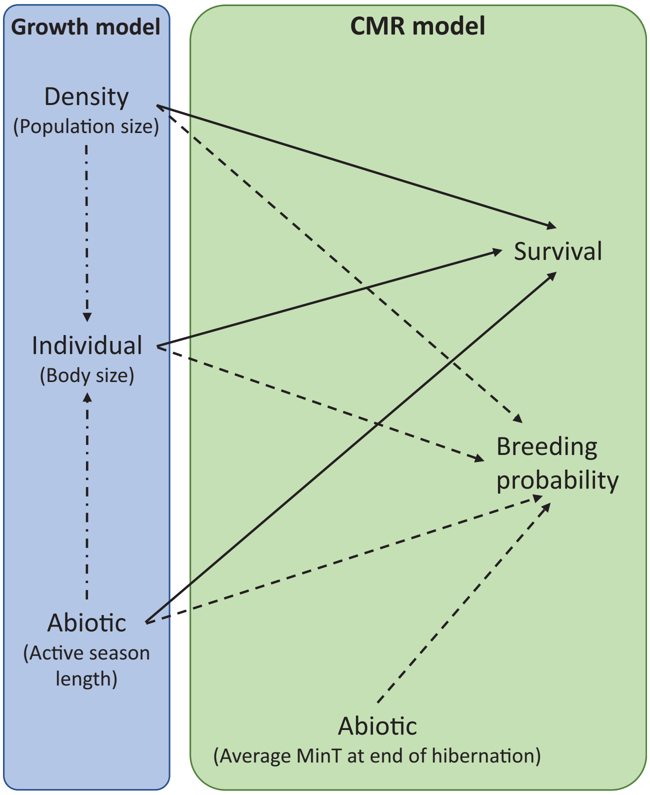

FIGURE 1 Framework of the study. To obtain estimates of body sizes for the years when the toads were not captured, we ran a von Bertalanffy (VB) growth model including a density proxy (population size) and an abiotic factor (the length of the active season) as covariates on the two VB parameters: growth rate and asymptotic size. Subsequently, we ran two sex-specific capture–mark–recapture (CMR) models to estimate adult survival and breeding probabilities (i.e., the probability of skipping and resuming breeding) while including the effect of density (population size), an individual factor (body size), and an abiotic factor (length of the active season). For the breeding probabilities, we also included an additional abiotic factor (MinT, the average minimum temperature in the 2 weeks around the emergence from hibernation). Following this framework, we are also able to assess the indirect effect of density and abiotic conditions through their effect on body size.

survival and breeding probabilities using a multistate model, defining breeder and nonbreeder as the two states (Schaub et al., 2004). For males, we used a Cormack–Jolly–Seber (CJS) model. We investigated the effects of density, active season length (abiotic factor), and individual body size (individual factor) on survival and, in females, breeding probabilities. For the latter, we also tested for the effect of average minimum temperature around the timing of emergence. The latter covariate was included because the decision to skip breeding might also be due to the environmental conditions experienced at emergence from hibernation (Muths et al., 2013).

Assessing the effect of individual factors on vital rates while accounting for the effect of abiotic conditions and density on the individual factor (in the growth model) enables us to quantify the indirect effect that they can have on vital rates. We expect that factors have similar direct and indirect effects. For instance, the expected negative direct effect of density on survival should be matched by the negative effect of density on body size, which then could lead to a decrease in survival due to smaller sizes. Similarly, a longer active season could both directly and indirectly increase survival, due to its positive effect on body size and the positive relationship between body size and survival, but could also show asynchrony if it has a negative effect on survival. This comprehensive analysis of growth and key vital rates, encompassing direct and indirect influences of multiple factors, offers novel insights into amphibian population dynamics, informing conservation efforts in high-elevation habitats.

METHODS

Toad mark–recapture and body size data

To estimate survival rates for male and female toads, as well as breeding probabilities for females, we used data on 1615 male and 933 female common toads (*B. bufo*) collected from 1993 to 2020. Within each breeding season, we performed multiple capture nights at the breeding site, at a pond in the proximity of the Grosse Scheidegg pass (Canton Bern, Switzerland, 1850-m elevation, 46°39′ N and 08°05′ E). Data have been collected for this population since 1982, but unique marking of individuals has been consistently applied starting in 1993, by implanting subcutaneous passive integrated transponders tags. Every toad captured during a capture night is measured (snout-to-vent length [SVL], in millimeters), weighed, sexed, and uniquely marked. At the end of the capture night, all toads are released back at the pond. For a more precise description of the study site and methods, see Hemelaar (1988) and Grossenbacher (2002). We use as a proxy for density the breeding population size (hereafter population size), which consists of the number of individuals caught every year at the pond. This proxy works well because the detection probability in this population is high (mean = 0.89, SD = 0.06; Wood et al., 1998). Since the measuring of the toads over the study period has been done by different people, we tested for the presence of a possible measurement difference by running a Tukey test for pairwise mean comparisons, finding a biologically insignificant difference among fieldworkers (Appendix S1: Section S1).

Climatic data

We used climatic data for the period 1993–2020 obtained from the DaymetCH dataset (Land Change Science Group, WSL, Switzerland). DaymetCH consists of interpolated estimates of weather variables over a grid of a 100-m resolution covering Switzerland. The estimates are obtained using meteorological data from ground stations and the Daymet software (Thornton et al., 1997). We extracted data for the cell containing the breeding site for daily minimum temperatures, and based on previous work (Muths et al., 2017), we calculated for each year the approximate length of the active season (i.e., the period between the end of hibernation in spring and the start of hibernation in autumn, which includes both the short breeding season and the following nonbreeding feeding season). We define the start of the active season as the end of the winter season, which corresponds to the day of the last killing frost (minimum temperature $< -4.4°C$), while the end of the active season is defined as the start of the coming winter season, which corresponds to the first day with a killing frost in autumn (minimum temperature $< -4.4°C$) (Muths et al., 2017).

Hypotheses

Concerning growth, we hypothesize that a long active season in the previous year has a positive effect on individual growth due to individuals feeding and growing for a longer period of time (Eastman et al., 2012). Moreover, we expect high density to have a negative effect on growth, as there will be less resources per capita available (Berven, 2009).

Regarding vital rates, we expect the length of the active season in the previous year to be positively associated with survival and the probability of resuming breeding, as well as negatively associated with the probability of skipping breeding, as the individuals are able to feed for longer and accumulate resources to prepare for the next breeding season (Bull & Shine, 1979; Sainmont et al., 2014). On the other hand, longer active seasons might increase mortality, as toads are more exposed to mortality risks than in the hibernation period. Also, individuals from high-elevation populations, where active seasons are shorter, tend to have higher survival and live longer, probably due to the reduced "speed" of the life cycle (e.g., Hemelaar, 1988). Additionally, we expect colder temperatures around the time of emergence from hibernation to increase the probability of skipping breeding and decrease the probability of resuming breeding, as toads might be able to perceive the unfavorable environmental conditions and forfeit breeding (Muths et al., 2013). Regarding density, we hypothesize a lower survival at higher population sizes due to density-dependent regulation mechanisms (Kissel et al., 2020), as well as a lower probability of resuming breeding since fewer females will attain the necessary energetic requirements to breed (Hamel et al., 2010). Concerning the individual factors, we expect bigger individuals to survive better, as a bigger body size is generally linked to increased fitness (Hernández-Pacheco et al., 2020; Peters, 1986). Alternatively, intermediate sizes might be correlated with higher survival (e.g., Weinbach et al., 2018), because bigger individuals might be older and suffer from senescence. Finally, we hypothesize that there might be a weak correlation between body size and breeding probabilities. Bigger females might in fact be more successful in accessing resources (Hin & de Roos, 2019). On the other hand, bigger individuals have higher energetic requirements (Hin & de Roos, 2019); therefore, a better access to resources does not necessarily reflect a higher chance of resuming breeding or a lower chance of skipping breeding.

Growth model

To include individual body size as a covariate for survival in the CMR model, we needed to impute missing size data when toads were not captured (e.g., because they skipped breeding in a year). To do this, we fit a VB (von Bertalanffy, 1938) growth model on common toad size data following Armstrong and Brooks (2013) and Rose et al. (2022). Previous work on the study population suggests that a VB model is appropriate for modeling toad size data (Hemelaar, 1988). The VB growth model is defined by Equation (1):

$$\mathrm{EL}_{i,t} = a_i - (a_i - L_{i,t-1}) \exp\left[-\frac{k_{i,t}}{a_i}(\Delta t)\right] \tag{1}$$

where $\mathrm{EL}_{i,t}$ is the expected SVL of a toad i at time t, a_i is the asymptotic size of a toad i, $k_{i,t}$ is the growth rate parameter of toad i at time t, and Δt is the time interval between two captures, in days. We substituted k with k/a, to let individual variation in growth rate k be independent of individual variation in asymptotic size a. The observed SVL $L_{i,t}$ is obtained by sampling from a normal distribution with a mean EL and an SD ε, to account for imperfect measurement and individual variation (Equation 2).

$$L_{i,t} \sim N(\mathrm{mean} = \mathrm{EL}_{i,t}, \mathrm{SD} = \varepsilon) \tag{2}$$

To better understand the effect of abiotic conditions and density, we modeled asymptotic size a of a toad at year t as a function of population size and the length of the active season of the year before $(t - 1)$. In other words, we calculated for each year the asymptotic size that a toad would reach if the length of the active season and the population size of that year would remain constant over the toad's lifetime. We note that toads are exposed to different abiotic conditions and densities each year. Therefore, growth depends on these yearly values and sets the growth trajectory to a new asymptotic size. We also modeled the log of the growth rate as a function of population size and the length of the active season, with an individual random effect, drawn from a normal distribution with a mean of zero and an SD estimated in the Bayesian framework. Moreover, we included temporal (i.e., "year") random effects on both asymptotic size and growth rate, drawing them from a bivariate normal distribution, therefore estimating the among-year correlation between both parameters. To account for differences in sex, we modeled two sex-specific VB growth models. Additionally, once the parameters a and k were estimated, we could build two sex-specific growth curves, using as a starting size (size at metamorphosis) a value drawn from a random normal distribution with a mean of 12 mm and an SD of 1, to encompass the sizes of newly metamorphosed toads measured by Craioveanu et al. (2019).

CMR models

Since the data suggest that males show no (or only very limited) intermittent breeding, we estimated breeding probabilities for females only. Therefore, we could model the capture–recapture histories of males with a CJS, as we assumed that they will always attempt breeding when alive, and thus, we estimated only survival and detection probability (Lebreton et al., 1992). On the other hand, given that females might skip breeding in a given year (Loman & Madsen, 2010; Schmidt et al., 2002), we modeled the capture histories of females with a multistate model, with the two states being *nonbreeder* and *breeder* (the phenomenon is often called "temporary emigration" in the mark–recapture literature; Schaub et al., 2004). Since nonbreeders do not show up at the pond, they are not available for capture and the state *nonbreeder* is unobservable (Schaub et al., 2004). In this model, we estimated survival, detection and the probability of changing state (becoming a nonbreeder or becoming a breeder).

We were interested in the effect of density (population size), abiotic conditions (environment), and individual factors (body size) on the different vital rates (Figure 1). For both males and females, for survival probability ($\phi_{i,t}$) in year t, we added as covariates the length of the active season at year t, the population size at year t, and the body mass of that individual at year t obtained from the growth model (Table 1). In the estimation of the probability that a female will skip breeding if it bred the year before ($\Psi_{i,t}{}^{\mathrm{B\_NB}}$) and the probability that a female will resume breeding if it did not breed the year before ($\Psi_{i,t}{}^{\mathrm{NB\_B}}$), we included the effects of the length of the active season and the population size of the year before, as well as the weather conditions (i.e., average minimum temperature) in the 2 weeks before the first capture night (Table 1). The latter was included based on the hypothesis that female toads might skip breeding once out of hibernation based on the conditions they experience at awakening (Muths et al., 2013). Muths et al. (2013) looked at conditions in the 2 months around breeding time (March and April), while we focused on the 2-week period prior to the first capture night. The first capture night is done as soon as possible after the

TABLE 1 List of vital rates and demographic parameters estimated in the capture–mark–recapture models with the covariates of interest.

Sex	Vital rate/demographic parameter	Abiotic covariate	Density covariate	Individual covariate
Males	Survival $\phi_{i,t}$	Length of active season	Population size	Body size
	Survival first year $\phi'_{i,t}$	Length of active season	Population size	Body size
	Detection $p_{i,t}$	...		
Females	Survival $\phi_{i,t}$	Length of active season	Population size	Body size
	Survival first year $\phi'_{i,t}$	Length of active season	Population size	Body size
	Detection $p_{i,t}$	...		
	Skip breeding $\Psi_{i,t}{}^{\mathrm{B\_NB}}$	Length of active season; mean minimum temperature in 2 weeks before first capture night	Population size	Body size
	Resume breeding $\Psi_{i,t}{}^{\mathrm{NB\_B}}$	Length of active season; mean minimum temperature in 2 weeks before first capture night	Population size	Body size

first signs of toads migrating to the breeding pond are detected if the weather conditions allow it. The people responsible for the fieldwork routinely check the snow cover at the study site either in person or using a webcam. Therefore, this 2-week period should cover well the precise moment of the end of the hibernation, without covering too much of the hibernation period, where the external environmental conditions should not influence the belowground toads. Finally, we included a random effect of year on the detection probability p_t (mean μ_p and SD σ_p), which was shared between the two sex-specific models to avoid identifiability issues. We standardized all the covariates by subtracting the mean value and dividing by the SD. Correlation coefficients between population size, length of the active season, and the 2-week average minimum temperature were low ($-0.20 < r < 0.43$).

Given that for males we fitted a CJS model to the data, we could test model assumptions using goodness-of-fit (GoF) tests (Pollock et al., 1985). We used the R2Ucare package in RStudio (Gimenez et al., 2018). The tests indicated the presence of a transience effect and overdispersion. We are not aware of the existence of similar GoF tests for multistate models with one unobservable state; therefore, we assumed that we had to account for transience and overdispersion for the female data as well. If transience is not accounted for, survival or detection probabilities can be underestimated (Pradel et al., 1997). The solution we applied here was to estimate a specific survival probability for the first year after capture (Genovart & Pradel, 2019). Overdispersion leads to narrower SEs around the estimated parameters, but the estimate itself is not biased (Schmidt et al., 2002). To assess the magnitude of overdispersion, we calculated $\hat{c}$ (the variance inflation factor), by dividing the χ^2 test statistic by df (Pradel et al., 1997). We obtained a value of 2.48, which indicates overdispersion (Choquet et al., 2009). We addressed overdispersion by including an individual random effect in the detection probability (Abadi et al., 2013).

We implemented the growth model and the CMR model in a unified Bayesian framework using Markov chain Monte Carlo (MCMC) sampling in Nimble (version 0.11.1; de Valpine et al., 2017). We conducted all the analyses in R (R version 4.1.1; R Core Team, 2020) with RStudio (version 2022.7.1.554; R Studio Team, 2022). We ran four chains for 770,000 sampling iterations each, including an initial burn-in of 70,000 iterations and a thinning value of 7, resulting in 100,000 iterations per chain. We assessed model convergence by visually inspecting MCMC trace plots and calculating the Brooks–Gelman–Rubin statistic $\widehat{R}$ (Brooks & Gelman, 1998) and by looking at prior–posterior overlaps. To further assess the GoF of our model, we conducted posterior predictive checks (Conn et al., 2018) on both sections of the model. For the growth model, we compared two sums of squared residuals to obtain a Bayesian p-value. The first sum compared observed and expected SVL values; the second sum compared simulated and expected SVL values (Rose et al., 2022). For the CMR models (i.e., CJS for males and multistate model for females), we performed posterior predictive checks following Nater et al. (2020). We chose 500 evenly spaced samples from the posterior distributions of the estimated parameters and used them to simulate 10 replicate capture-history datasets per sample. We then calculated the number of recaptures in each set of capture history and obtained a distribution of 5000 values for the number of recaptures. We then compared the observed number of recaptures with the rest of the distribution both visually (Appendix S2: Figure S1) and by calculating a Bayesian p-value.

RESULTS

All parameters showed good convergence ($\widehat{R} < 1.1$). The Bayesian p-values for the growth model for females and males were 0.55 and 0.46, respectively, indicating overall a good fit. The posterior predictive checks on the CMR models showed a good fit as well, with Bayesian p-values of 0.31 for males and 0.57 for females. Also, the prior–posterior overlaps were satisfactory (Appendix S2).

Direct effects on growth and body size

We estimated sex-specific growth parameters and estimated size when individuals were not measured. By providing the initial size at metamorphosis and using the parameters estimated from the model, we built sex-specific growth curves (Figure 2). We tested for the effects of population size and the length of the active season on both the coefficient of growth k and the asymptotic size a. We did not find significant effects of either factor on either growth model parameter, but the parameter estimates suggest positive and negative effects on k and a, respectively (Table 2).

Direct effects on vital rates

We modeled the CMR data of 1615 male toads and 933 female toads to estimate male survival with a CJS model and female survival and breeding probabilities with a multistate model. The mean detection probability was 0.89 and varied little among years (SD = 0.06). The survival ϕ of males and females did not vary much across

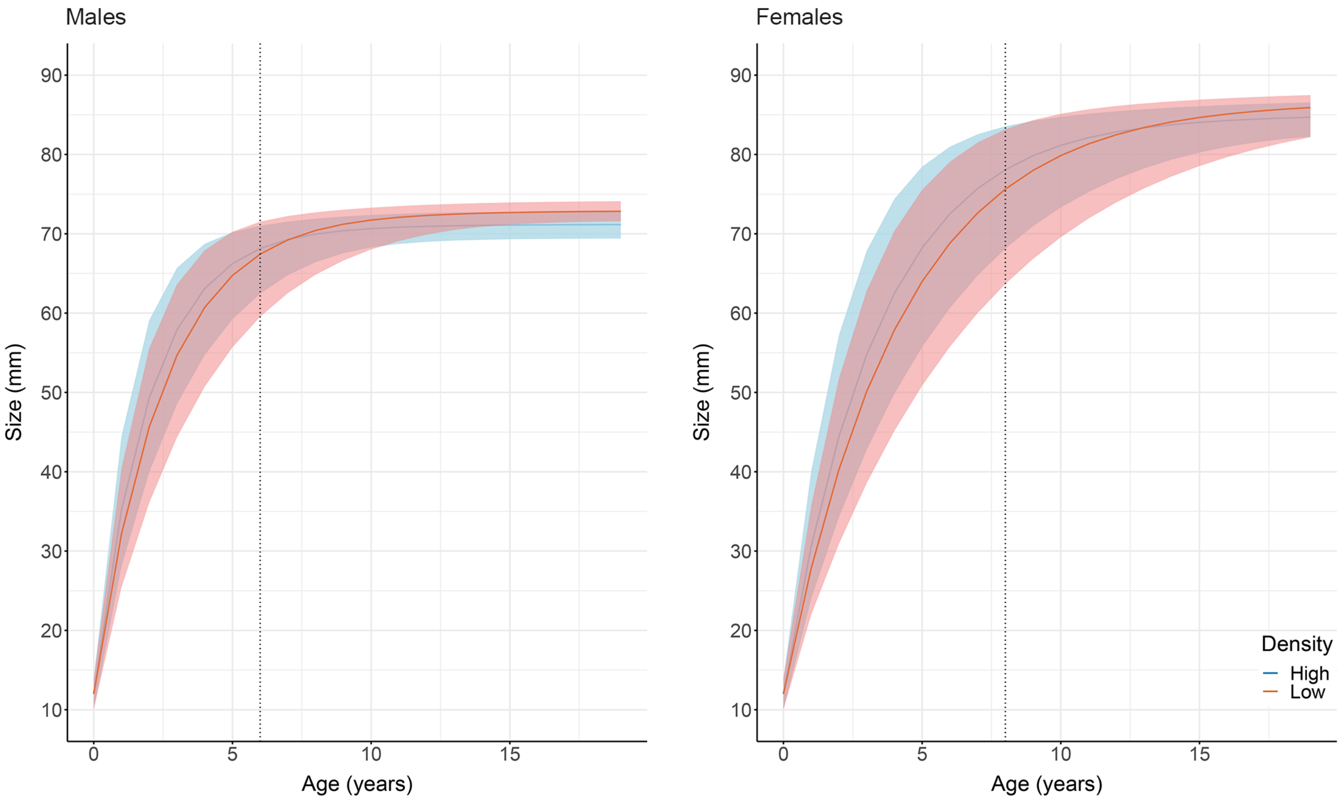

FIGURE 2 Growth curves for males and females, for a low population size and a high population size. We looked at realistic population size values, using a value of −1 on the standardized scale for the low-population-size scenario (corresponding to 73 individuals) and a value of 2 for the high-population-size one (521 individuals). We show the median growth trajectory, while the shaded ribbons represent the 95% credible intervals. These curves represent a situation with an average year effect and an average length of the active season. The vertical dotted lines indicate the age at which 50% of males and females are sexually mature according to Hemelaar (1988).

TABLE 2 Summary of the effects of population size (PopSize) and active season length (ActiveSeason) on the coefficient of growth k and the asymptotic size a.

Name	Mean	SD	2.5% limit of CRI	97.5% limit of CRI	Proportion	$\widehat{R}$
PopSize on k	0.066	0.053	−0.034	0.175	0.907	1.00
ActiveSeason on k	−0.038	0.058	−0.159	0.072	0.246	1.00
PopSize on a	−0.583	0.408	−1.404	0.208	0.070	1.00
ActiveSeason on a	0.469	0.421	−0.369	1.294	0.875	1.00

Note: We show the mean coefficient value, its SD, and the 95% credible intervals (CRIs). The Proportion column shows the proportion of samples from the posterior distribution with a value above zero. Values close to 0 or 1 suggest the presence of a negative or positive effect, respectively. $\widehat{R}$ values show convergence of the Markov chain Monte Carlo chains.

the study period, with male survival fluctuating more (mean values were 0.74 and 0.73, respectively). Both showed a decrease in the last years (Appendix S3: Figure S1). Survival in the year after the first capture ϕ' showed a similar pattern, but with lower values (Appendix S3: Figure S2). Finally, the probability of skipping breeding if a female bred the year before Ψ^{B_NB} was high, with an average of 0.66 over the study period, but the probability of resuming breeding if a female skipped breeding the year before Ψ^{NB_B} was higher, with an average of 0.80 (Appendix S3: Figure S3). This indicates that there is a strong Markovian pattern in breeding, with the breeding status in the previous year strongly determining whether a female will attempt breeding.

We analyzed the effect of individual body size, population size, and length of the active season on survival and breeding probabilities, including weather at emergence from hibernation for the latter (Table 3). For abiotic conditions, we found evidence of a negative effect of the active season length on male survival (Figure 3). Moreover, we found a negative effect of the minimum temperature at emergence on the probability of skipping breeding (i.e., the colder it is, the higher the probability of skipping breeding if a female bred the year before; Figure 4). We also found evidence of a positive effect on the probability of resuming breeding, as well as a negative effect of population size on both male and female survivals (Figures 4 and 5, respectively). Finally, for individual effects (i.e., body size), we found evidence of a negative effect of body size on male survival and a clear negative trend on female survival (Figure 5).

Indirect effects on vital rates

Although strictly not significant, we could find indications of an effect of both active season length and population size on body size. This means, along with the negative association of body size with survival, that there might be also indirect (i.e., trait-mediated) effects of abiotic conditions and density on vital rates.

DISCUSSION

We found evidence that density, abiotic conditions, and individual factors had direct effects on vital rates. We also found indications of indirect effects of density and abiotic

TABLE 3 Summary of the intercepts for the focal vital rates (logit scale) and of the effects of abiotic conditions (length of the active season and the average minimum temperature around emergence; ActiveSeason and EmergenceMinT in the table), density (population size; PopSize), and individual factors (body size; BodySize) on survival, the probability of resuming breeding, and the probability of skipping breeding.

Name	Mean	SD	2.5% limit of CRI	97.5% limit of CRI	Proportion
Intercept					
Male survival	1.065	0.054	0.961	1.171	1
Male survival in the first year	0.5	0.065	0.374	0.627	1
Female survival	0.99	0.078	0.836	1.143	1
Female survival in the first year	0.342	0.116	0.123	0.577	0.9991
Skipping breeding	0.694	0.094	0.509	0.879	1
Resuming breeding	1.855	0.446	1.15	2.879	1
Abiotic					
ActiveSeason on male survival	**−0.161**	**0.039**	**−0.239**	**−0.085**	**0.000013**
ActiveSeason on female survival	−0.023	0.078	−0.177	0.130	0.383
ActiveSeason on resuming breeding	−0.278	0.268	−0.839	0.222	0.137
ActiveSeason on skipping breeding	0.101	0.094	−0.083	0.287	0.859
EmergenceMinT on resuming breeding	0.188	0.279	−0.341	0.766	0.761
EmergenceMinT on skipping breeding	**−0.186**	**0.094**	**−0.372**	**−0.003**	**0.023**
Density					
PopSize on male survival	**−0.146**	**0.031**	**−0.207**	**−0.085**	**0**
PopSize on female survival	**−0.156**	**0.047**	**−0.249**	**−0.063**	**0.00054**
PopSize on resuming breeding	**1.24**	**0.473**	**0.488**	**2.339**	**0.99989**
PopSize on skipping breeding	−0.101	0.086	−0.271	0.068	0.121
Individual					
BodySize on female survival	−0.101	0.058	−0.215	0.013	0.041
BodySize on male survival	**−0.103**	**0.037**	**−0.176**	**−0.031**	**0.0026**
BodySize on resuming breeding	0.516	0.452	−0.263	1.509	0.891
BodySize on skipping breeding	−0.101	0.086	−0.271	0.068	0.121

Note: We show the mean coefficient value, its SD and the 95% credible intervals (CRIs). The Proportion column shows the proportion of samples from the posterior distribution with a value above zero. Values close to 0 or 1 suggest the presence of a negative or positive effect respectively. All $\widehat{R}$ values were equal to 1 and thus indicated convergence of the Markov chain Monte Carlo chains. For density, abiotic conditions, and individual factors, we highlighted in bold the variables whose 95% CRI did not overlap zero, therefore showing strong evidence for an effect in a certain direction.

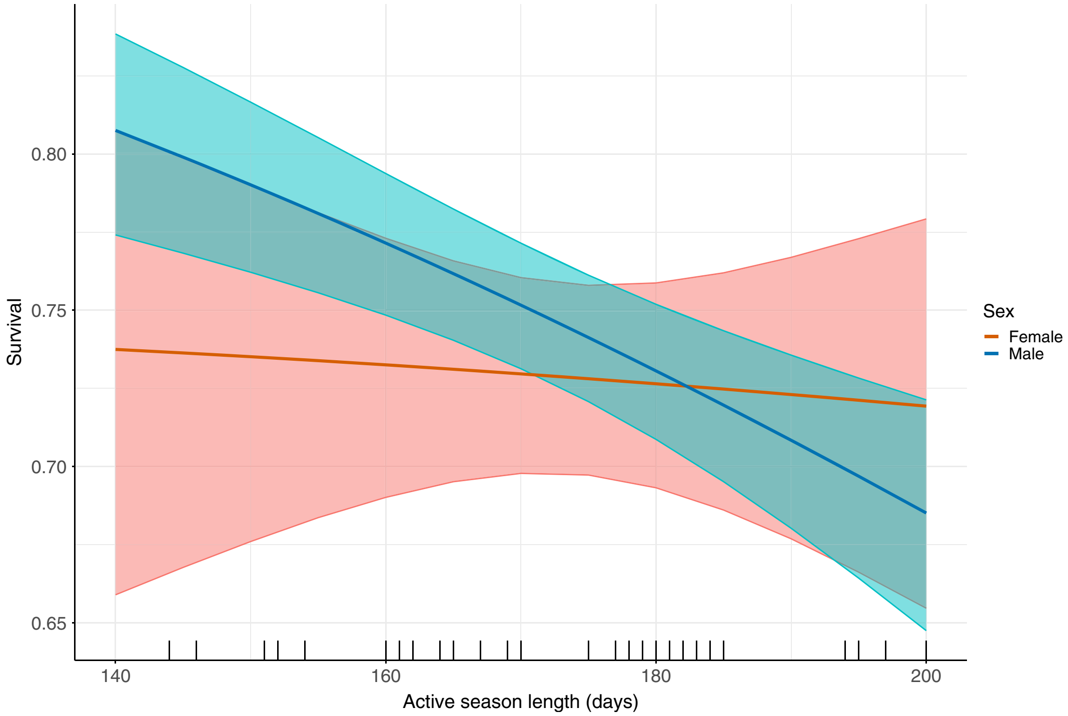

FIGURE 3 Relationship between the length of the active season and the survival of males and females, based on the predictions of the model. The lines represent the mean value, while the shaded ribbons represent the 95% credible intervals. The relationships shown assumed average body size and population size. The tick marks along the *x*-axis show the observed values.

conditions on vital rates mediated by individual traits. These findings highlight the complexity of amphibian demography and the importance of a comprehensive analysis of the network of factors affecting vital rates.

The VB model enabled us to obtain growth curves similar to Hemelaar's (1988) curves for the same population. Males grow faster than females and to smaller asymptotic sizes, which based on the model's prediction are reached at about 10 years of age, on average a year later than estimated by Hemelaar (1988). Females seem to reach their asymptotic size at around 17 years of age (Figure 2; Hemelaar (1988) reported the same age). These findings indicate that growth patterns are not varying much over time in this population. Given the annual survival rates (~0.75), few will reach asymptotic size and will therefore grow during their entire lifespan, suggesting that there might be a trade-off between growth and reproduction, which could partly explain why females show intermittent breeding.

Direct effects on growth and body size

As hypothesized, we found indication of an effect (although not strictly significant) of an abiotic factor (length of the active season) on growth, with longer seasons associated with bigger asymptotic sizes. Longer active seasons allow for a longer growth period and possibly higher availability of resources. We also found indications of a negative density effect on the asymptotic size but a positive one on the growth rate *k*, indicating that at higher densities, individuals might grow faster but to smaller sizes (Green & Middleton, 2013). This is what is generally expected, given the predicted lower per capita resource availability at higher densities and the need to grow faster to outcompete other individuals. Moreover, smaller females might have lower fecundity due to smaller and fewer eggs (Hernández-Pacheco et al., 2020; Reading, 1986), which could be a way that density dependence acts on the population. There are many studies showing spatial variation in body size, but only a few studies showed that the determinants of asymptotic size could be pinpointed to context-specific situations such as density and active season length (e.g., Paterson & Blouin-Demers, 2018). Concerning the other growth parameter, *k*, the absence of strong effects on it could also mean that *k* is an important fitness trait and is buffered against factors like environment or density (environmental canalization; Gaillard & Yoccoz, 2003). Indeed, growing faster might be more important than growing to larger sizes. Despite the large body of literature on the effect of density and the environment on amphibian larval growth (Reading & Clarke, 1999; Ruthsatz et al., 2018), we found no studies on their

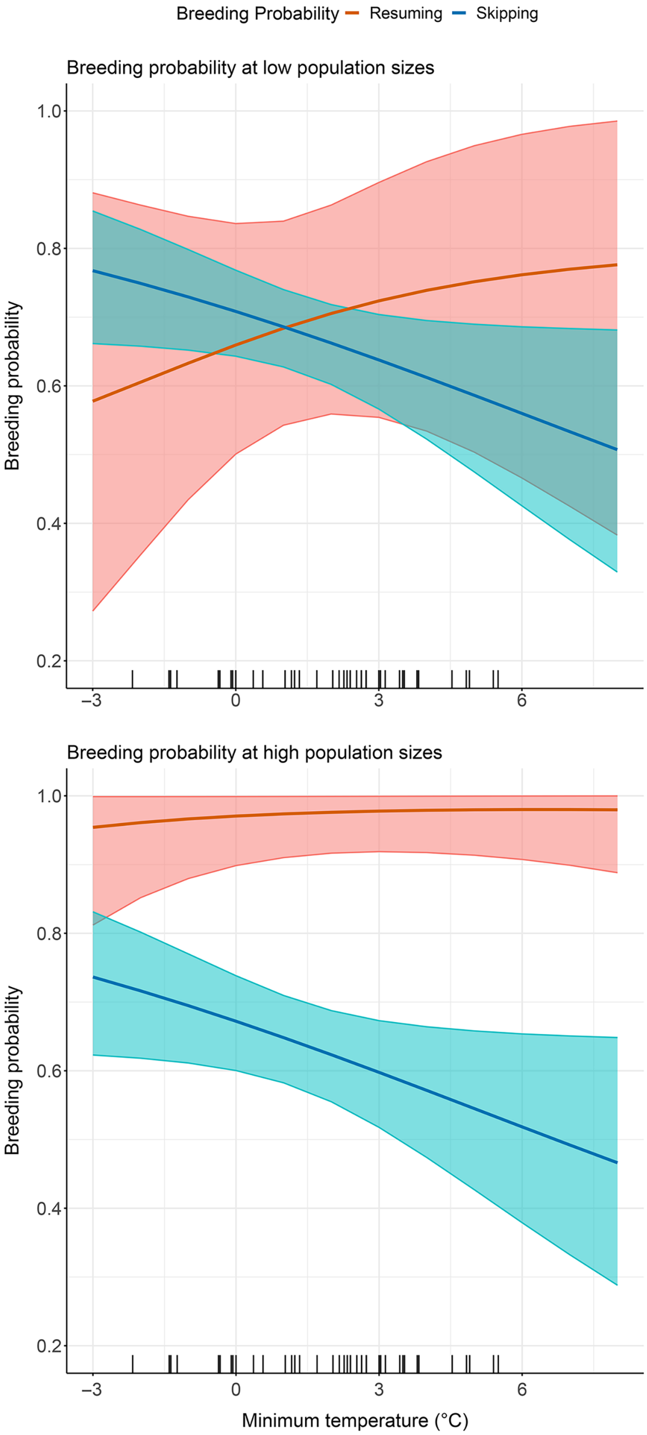

FIGURE 4 Relationship between the mean minimum temperature in the 2 weeks around emergence from hibernation and the probabilities of skipping and resuming breeding of females, based on the predictions of the model, at low and high population sizes. We defined low population size as 100 individuals and high population size as 500 individuals. The lines represent the mean value, while the shaded ribbons represent the 95% credible intervals. The relationships shown assumed average body size and active season length. The tick marks along the *x*-axis show the observed values.

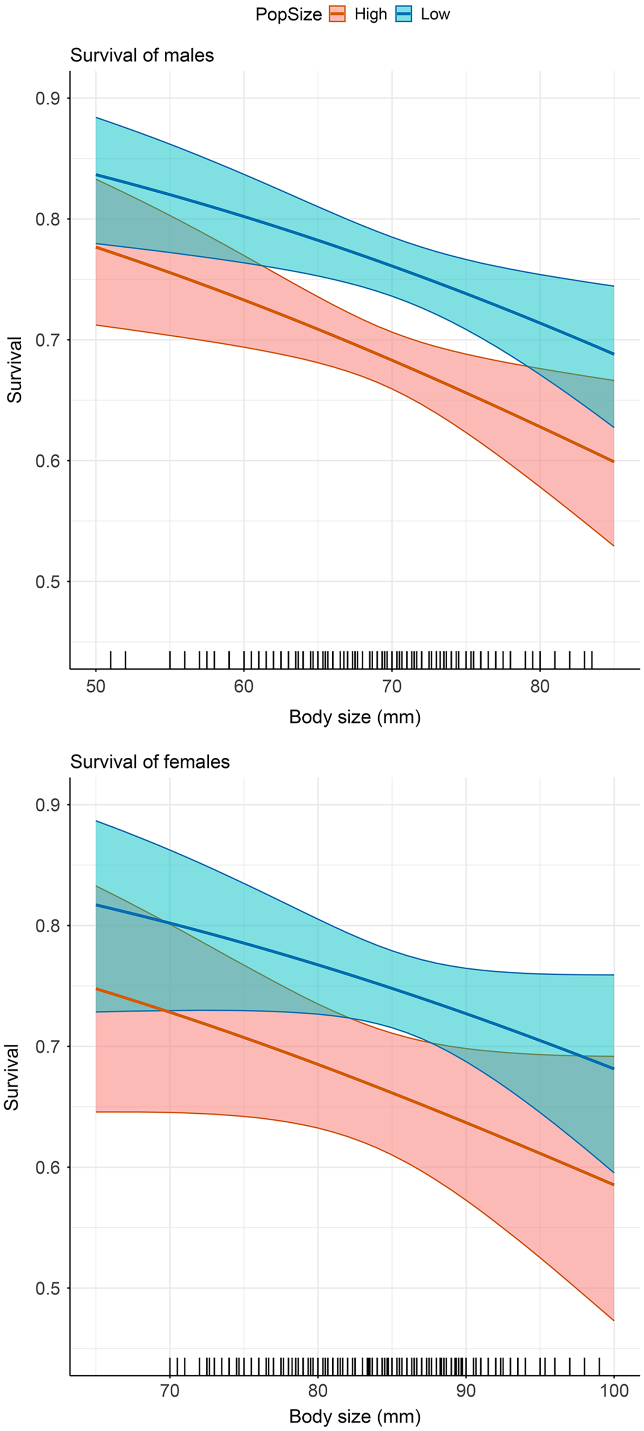

FIGURE 5 Relationship between body size and survival for two different measures of population size for males and females. We defined low population size as 100 individuals and high population size as 500 individuals. The solid lines represent the mean value, and the shaded ribbons represent the 95% credible intervals. The relationships shown assumed average active season length. The tick marks along the *x*-axis show the observed values for body size.

effects on the parameters of the VB growth model that covers the growth period postmetamorphosis in amphibians, highlighting the importance of our study.

Direct effects on vital rates

The relatively high male and female survival rates that we found over the study period (0.74 and 0.73, respectively, at average body size) are typical of populations living at higher elevations, where generally the pace of life is slow, mostly due to energy constraints. Our values are in line with previous studies on *B. bufo* populations (Muths et al., 2013, tab. 4), where populations living in similar conditions had a higher survival rate than lowland populations. The estimates of our breeding probabilities (mean $\Psi_{i,t}{}^{B\_NB} = 0.66$ and mean $\Psi_{i,t}{}^{NB\_B} = 0.80$) revealed a Markovian breeding pattern in females with a relatively regular biennial cycle of breeding as previously observed in this population (Grossenbacher, 2002). This is expected as they are capital breeders living in harsh conditions (Bull & Shine, 1979). This outcome has been found in previous studies on amphibians (e.g., Cayuela et al., 2014; Muths et al., 2013) and further supports the hypothesis that individuals attempt breeding only upon reaching a certain energy threshold, which females often can reach only every 2 years, especially at higher elevations (Houston et al., 2007; McNamara & Houston, 2007). In more recent years, more females are reproducing in consecutive years, indicating that there might be other factors influencing the probability of skipping breeding that were not properly identified.

Concerning abiotic conditions, we found that the length of the active season was negatively associated with adult survival of males. This could be explained by the intrinsic higher mortality of being more active (Houston et al., 1997; Werner & Anholt, 1993), which exposes the animals to more risks, such as diseases, predation, roadkill, and higher susceptibility to extreme weather events (e.g., drought). On the other hand, we did not find a meaningful correlation between active season length and female survival or breeding probability. Females might be more cautious than males (e.g., in rats; Jolles et al., 2015), and it is possible that even the longest active season lengths observed in our system are not long enough to enable most females to build up the energy necessary to breed in consecutive years.

We also found evidence of the minimum temperature around emergence from hibernation negatively affecting the probability of skipping breeding. This supports the hypothesis that under harsh weather conditions, females might forfeit breeding to not risk unsuccessful breeding or dying (Muths et al., 2013), especially in alpine habitats where environmental conditions are highly variable. In fact, the ability to voluntarily forfeit breeding when conditions at the start of the breeding season are not optimal can increase the lifetime fitness of both the female and tadpoles, as they would be exposed to bad conditions upon hatching. We therefore expect this trait to be under selection (Cubaynes et al., 2010; Erikstad et al., 1998). Muths et al. (2013) could not find strong support for their hypothesis in their study. One of the reasons they pointed out was the relatively short study period (6 years). It is possible that given our longer study period, we were able to successfully find this association.

Moreover, we found evidence of population size negatively affecting both male and, more weakly, female survivals. This suggests the presence of density dependence effects in the adult stage of amphibians. We expect density regulation due to a decrease in the per capita resource availability or an increased competition for shelters, especially in a context where habitats might be less productive and shelters scarcer than at lower elevations. There are only a few studies investigating this aspect in adult amphibians, in contrast to the large number of studies on density dependence in the larval aquatic stage (e.g., Reading & Clarke, 1999). Density dependence in the adult stage could play a significant role in regulating the population (Hellriegel, 2000). Previous studies tested density dependence in adults in an experimental setting (Altwegg, 2003; Harper & Semlitsch, 2007), showing that density-dependent processes can indeed operate, while our study is one of the few that investigated this aspect in a wild population, indicating that density dependence acts also in the wild, within the limits of observational field studies (see also Berven, 2009; Kissel et al., 2020). Counter to our hypothesis, we found a strong positive association between population size and the probability of resuming breeding, indicating that the bigger the population, the higher the probability of resuming breeding. A possible mechanism explaining this relationship is the decision by females to breed rather than delaying due to increased mortality at higher densities (McNamara et al., 2004). Another possible explanation is that nonbreeding females operate under a positive feedback loop scenario, whereby higher densities experienced during the feeding season in the previous year imply increased mating opportunity in the following year and thus stimulate their return to breeding. Alternatively, this finding might indicate just a correlation and not causation, hinting at a common cause that is affecting both population size and the probability of resuming breeding. If in general the conditions experienced by this population are getting better, we could expect both an increase in population size and a higher probability of resuming breeding in females.

Finally, regarding individual factors, we found a negative association between body size and male survival and an almost significant negative association also with female survival. This result can be explained by actuarial senescence (Hamilton, 1966), with older (and thus bigger) individuals more likely to die, as growth slows down but does not stop over the lifetime of individuals (Duellman & Trueb, 1994). It could also be explained by the higher costs of maintaining bigger body sizes. Previous studies also looked at the role that body condition can have on survival and breeding, hypothesizing that for breeding to happen, body condition must reach a threshold value (Baron et al., 2013; Reading & Jofré, 2021). In our case, we did not find any correlation between increased body condition and a lower chance of skipping breeding or a higher chance of resuming breeding (Appendix S1: Section S2).

Indirect effects on vital rates

Our findings suggest the presence of direct and indirect (body-size-mediated) effects of population density and active season length on survival and breeding probabilities. The magnitudes of these effects do not seem to be so different to warrant a claim about their relative importance when estimating vital rates. Interestingly, we could observe the synchrony of the direct and indirect effects of the active season length on male survival. Longer active seasons are associated with decreased survival (direct effect) and an increased body size, which in turn is negatively associated with male survival (indirect effect). On the other hand, the negative associations between population size and body size, and between body size and survival (globally a positive indirect effect), seem to indicate that density might buffer the negative effect of body size on survival while still maintaining itself a direct negative effect.

CONCLUSION

We could not only demonstrate the presence of intermittent breeding for females in this population living at high elevation but also estimate key vital rates and assess the importance that abiotic conditions, density, and individual factors can have on these rates. The fact that females show strong intermittent breeding seems to further indicate that the major onus energetically speaking is on them, and this seems to apply to most anurans (Hayward & Gillooly, 2011; Jørgensen, 1992). Even though we could not find a clear effect of the active season length on breeding probabilities, we can hypothesize that under current climate scenarios, future active seasons will be long enough to lead to a more frequent annual breeding. However, current effects of climate change on this population are not as strong and predictable as expected. For instance, winter and spring temperatures are not constantly increasing, nor is snow cover constantly decreasing (Lenzi et al., 2023), perhaps due to topologically driven microclimatic conditions (Scherrer & Körner, 2011). If indeed females slowly move more consistently toward an annual breeding, there might be consequences for the population, as many more individuals will be produced. On the other hand, we expect stronger regulatory effects due to density dependence at both the larval and the adult stage, with a decrease in survival, compensating for the increase in reproduction.

This study is an important addition to the literature on the demography of amphibians, especially on populations living at the elevational edge of the species distribution, in a highly threatened habitat (Diaz et al., 2003). Our main findings indicate that multiple factors act on adult survival and breeding probability, and proper estimates of these vital rates can be obtained only with a comprehensive approach. In particular, we found a possible strong effect of population density on the survival of the adult stage, which in amphibians has been rarely detected. Moreover, the relationships we found between environment and vital rates, combined with the ongoing and predicted scenarios of climate change, show the importance of integrating the outcome of such analyses into population models to obtain important insights on the dynamics and persistence of amphibian populations under changing environmental conditions.

AUTHOR CONTRIBUTIONS

Omar Lenzi and Benedikt R. Schmidt conceived the study. Kurt Grossenbacher, Silvia Zumbach, Beatrice Lüscher, Sarah Althaus, Marco Thoma, Daniela Schmocker, and Helmut Recher collected the data. Omar Lenzi prepared and analyzed the data. Benedikt R. Schmidt and Arpat Ozgul provided feedback on the analyses. Omar Lenzi wrote the paper with input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and scripts (Lenzi et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.10908913.

ORCID

Omar Lenzi https://orcid.org/0000-0003-1938-6786
Benedikt R. Schmidt https://orcid.org/0000-0002-4023-1001

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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