Interplay of abiotic, biotic, and individual factors in shaping individual growth and
demography in a high-elevation common toad population

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Abstract

1. Vital rates of individuals in natural populations, such as survival and breeding probabilities, can be affected by abiotic (i.e. environmental conditions), biotic (e.g. population density), and individual factors (i.e. individual traits). Many studies often consider the direct effects of one or two of these sources of vital-rate variations, but taking them all into account might reveal important relationships, including indirect trait-mediated effects.

2. We estimated survival and breeding probability in a high-elevation population of an ectotherm species while accounting for the effects of these three types of factors: abiotic (in the form of the length of the active season and temperature at emergence from hibernation), biotic (population size), and individual factors (body size). We expect this population living at the extreme range of the species’ distribution to be affected mainly by abiotic factors, given the harsh environmental conditions experienced.

3. Using 28 years of capture-mark-recapture data and individual body size measurements on an alpine population of the common toad (*Bufo bufo*), we estimated male survival probability with a Bayesian Cormack-Jolly-Seber model, female survival and female breeding probability with a Bayesian multistate model, and we estimated sex-specific growth curves.
4. Our findings reveal significant negative impacts of all three factor types on survival. Moreover, breeding probability exhibited a Markovian pattern, notably breeding biennially, with temperature at hibernation emergence, an abiotic factor, affecting the probability of skipping a breeding season, and population density, a biotic factor, influencing the resuming of breeding. We also found indication for the presence of indirect effects, with both abiotic and biotic factors potentially affecting asymptotic growth, and thus by extension, survival through changes in body size.

5. Our study reveals interesting and novel results for a population in a context seldom studied. It also highlights the complexity of factors affecting vital rates directly and indirectly, as well as the importance of long-term studies, especially in understudied habitats and taxa.
Introduction

Fluctuations in population size have historically been ascribed to the effects of abiotic (i.e. environmental) factors as well as biotic factors (e.g. population density) on vital rates (Lawton, 1994; Hanski et al., 1997). Abiotic and biotic factors can have similar, opposite, or interacting effects on vital rates (Gamelon et al., 2017; Conquet et al., 2023). More recently studies have shown that the effect 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 and biotic factors, aside from their direct effect on vital rates, can influence these individual traits as well, thus having also indirect (i.e. trait-mediated) effects on vital rates and by extension on population dynamics (e.g. Amarillo-Suárez et al., 2011).

Populations can thus be affected by abiotic, biotic, and individual factors. Nonetheless, studies in the past often have focused on one or two of these 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). To better understand the demography underlying population dynamics, it is thus important to investigate the relative importance of abiotic, biotic, and individual factors on vital rates. Investigating such effects on adult survival and breeding probability, two key vital rates that can contribute largely to population growth (e.g. Sæther & Bakke, 2000; Schmidt et al., 2005; Desprez et al., 2018), can give important insights into population responses to these factors. Whereas 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, this lack of
knowledge negatively affects conservation and hampers an in-depth understanding of vertebrate demography (Conde et al., 2019). Moreover, we decided to focus on a population living at the extreme range of its species’ distribution, more precisely its upper elevational limit. These high-elevation animal populations are rarely studied systematically and only few long-term studies exist. Such populations are exposed to harsh environmental conditions (e.g. cold temperatures), with known physiological effects (e.g. lower metabolic rate) which usually result in a slower life cycle (Laiolo & Obeso, 2017). We expect in these populations a stronger effect of abiotic factors on vital rates compared to biotic and individual factors, given how severely the environment acts as a selective force (e.g. Bassar et al., 2016; Paquette & Hargreaves, 2021).

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 abiotic, biotic, and individual factors in shaping dynamics of amphibian populations (Figure 1). The implemented analytical framework has two parts. The first part is a growth model, where we quantified the effect of abiotic and biotic factors on individual traits. The second part is a CMR model that we used to estimate survival and the breeding probabilities (the latter only for females), while assessing the direct effect of abiotic, biotic, and individual factors, as well as the indirect effect of abiotic and biotic factors.

To obtain information on individual factors (i.e. body size), we implemented a von Bertalanffy growth model in a Bayesian framework. We expect to obtain growth curves similar to what Hemelaar (1988) estimated using three years of data for the same population through skeletochronology. We investigated the effect of population density (a biotic factor) and the length of the active season in the previous year (an abiotic factor) on the two von Bertalanffy model coefficients, the growth rate k and the asymptotic size a. We hypothesise that a long
active season in the previous year has a positive effect on individual growth, as the individuals can feed and grow for a longer period of time (Eastman et al., 2012). We expect on the other hand high population sizes to have a negative effect on growth, as there will be less resources per capita available (Berven, 2009).

In the second part of the analytical framework (i.e. the CMR model) we aimed at estimating survival and breeding probabilities while assessing the direct effect of abiotic, biotic, and individual factors, as well as indirect effects of abiotic and biotic factors. We estimated breeding probabilities for females, as they are the only sex clearly showing intermittent breeding in this population (Grossenbacher, 2002). Intermittent breeding can arise where environmental conditions are unfavourable, such as at high elevations. In these conditions, individuals can (and sometimes must) forfeit breeding in a year to breed the following year. It can be either an adaptive response to environmental conditions which are pessimal for successful breeding and therefore a way to avoid wasting energy in particularly bad years (Bull & Shine, 1979), or it can arise in capital breeders due to the impossibility of collecting enough resources to be able to breed every year (Jönsson, 1997; Houston et al., 2007), either due to lower habitat production, or shorter feeding seasons. This is especially the case for females, for whom reproduction is more demanding energetically (Jørgensen, 1992; Hayward & Gillooly, 2011). For female toads, we thus estimated survival and breeding probabilities using a multistate model, defining breeder and non-breeder as the two states (the latter as a non-observable state; Schaub et al., 2004). For males, we used a Cormack-Jolly-Seber model instead. We investigated the effects of population size (biotic factor), active season length (abiotic factor), and individual body size (individual factor) on survival and, where applicable, 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 following a previous study that hypothesised that the decision to skip breeding might also be due to the environmental conditions experienced at emergence from hibernation (Muths et al., 2013). More in detail, 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 compared to 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 unfavourable environmental conditions, and forfeit breeding (Muths et al., 2013). Regarding the biotic factors, we hypothesise that higher population sizes decrease the survival probability through density-dependent regulation mechanisms (Kissel et al., 2020), as well as reduce the 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 an increased fitness (Peters, 1986; Hernández-Pacheco et al., 2020). Alternatively, intermediate sizes might be correlated with higher survival (e.g. Weinbach et al., 2018), as increased mortality at bigger sizes might be linked to actuarial senescence. Finally, we hypothesise 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. Assessing the effect of individual factors on vital rates, while accounting for the effect of abiotic and biotic factors on the individual factor (in the growth model) enables us to quantify the indirect effect that abiotic and biotic factors can have on vital rates. We hypothesise to find synchrony in direct and indirect effects. For instance, the expected negative direct effect of population size on survival should be matched by the negative effect of population size 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 key growth and vital rates, encompassing direct and indirect influences of multiple factors, offers novel insights into amphibian population dynamics, informing conservation efforts in high-elevation habitats.
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 biotic (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 a biotic factor (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 (average minimum temperature in the two weeks around the emergence from hibernation). Following this framework, we are also able to assess the indirect effect of abiotic and biotic factors through their effect on body size.
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 (Bufo 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 PIT tags. Every toad captured during a capture night is measured (SVL; snout-to-vent length in mm), 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 of population size the number of individuals caught every year at the pond. This proxy works well because detection probability in this population is high (mean = 0.89 and standard deviation = 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).

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-metre 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 followed by the non-breeding 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).

**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 von Bertalanffy (VB; von Bertalanffy, 1938) growth model on common toad size data following Rose et al. (2022) and Armstrong and Brooks (2013). Previous work on the study population suggests that a VB model is appropriate to model toad size data (Hemelaar, 1988). The VB growth model is defined by the following equation (Equation 1):

\[
EL_{i,t} = a_i - (a_i - L_{i,t-1}) \exp \left[-\frac{k_{i,t}}{a_i} (\Delta t) \right]
\]  

Where \(EL_{i,t}\) is the expected snout-to-vent (SVL) length 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 \(\Delta t\) 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 from individual variation in asymptotic size \(a\). The observed SVL \(L_{i,t}\) is
obtained by sampling from a normal distribution with mean $EL_i$ and standard deviation $\varepsilon$, to account for imperfect measurement and individual variation (Equation 2).

$$L_{i,t} \sim N(\text{mean} = EL_{i,t}, SD = \varepsilon)$$

(2)

To better understand the effect of abiotic and biotic factors, we modelled asymptotic size $a$ of a toad at year $t$ as a function of population size (i.e. the number of individuals caught every year at the breeding site) and the length of the active season of the year before ($t$-1). In other words, we calculated each year the asymptotic size that a toad would reach if the length of the active season and the population size would remain constant. We also modelled 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 a standard deviation 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 modelled 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 standard deviation of 1, to encompass the sizes of newly metamorphosed toads measured by Craioveanu et al. (2019).

**CMR models**

Since the data suggests 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 Cormack-Jolly-Seber (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 (Schmidt et al., 2002; Loman & Madsen, 2010), we modelled the capture histories of females with a multistate model, with the two states being non-breeder and breeder (the phenomenon is often called “temporary emigration” in the mark-recapture literature; Schaub et al., 2004). Since non-breeders do not show up at the pond, they are not available for capture and the state non-breeder is unobservable (Schaub et al., 2004). In this model we estimated survival, detection, and the probability of changing state (becoming a non-breeder or becoming a breeder).

We were interested in the effect of abiotic (environment), biotic (population size), 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 ($\Psi_{i,t}^{B,\text{NB}}$) and the probability that a female will resume breeding if it did not breed the year before ($\Psi_{i,t}^{\text{NB,B}}$) we included the effects of the length of the active season of the year before, as well as the weather conditions (i.e. average minimum temperature) in the two 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 two months around breeding time (March and April), while we focused on the two-week period prior to the first capture night. The first capture night is done as soon as possible after the 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 two-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 below-ground toads. Finally, we included a random effect of year on the detection probability $p_t$ (mean $\mu_p$ and standard deviation $\sigma_p$) which was shared between the two sex-specific models to avoid identifiability issues. We standardised all the covariates by subtracting the mean value and dividing by the standard deviation. Correlation coefficients between population size, length of the active season, and the two-week average minimum temperature were low ($-0.20 < r < 0.43$).

Given that for males we modelled a Cormack-Jolly-Seber model, we could test model assumptions using goodness-of-fit tests (GoF; Pollock et al., 1985). We did this using the R2Ucare package in RStudio (Gimenez et al., 2018). The tests showed that there might be a transience effect and overdispersion. We are not aware of the existence of similar GoF tests in the case of a multistate model with one unobservable state, therefore we assumed that also for the female data we had to account for transience and overdispersion. If transience is not accounted for correctly, survival or detection probabilities might 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). Low values of this survival probability do not necessarily indicate an increased mortality, but just a lower probability for the animal of being available for recapture in the following years, either due to true mortality or permanent emigration (i.e. apparent survival). Regarding overdispersion, we know it leads to narrower standard errors around the estimated parameters, but the estimate itself is not biassed (Schmidt et al., 2002). To assess the magnitude of overdispersion we calculated $\hat{c}$ (the variance inflation factor), by dividing the chi-squared test statistic by the
number of degrees of freedom (Pradel et al., 1997). We obtained a value of 2.48 which indeed indicates overdispersion (Choquet et al., 2009). We addressed overdispersion by including an individual random effect in the detection probability (Abadi et al., 2013).

**Table 1. List of vital rates and demographic parameters estimated in the capture-mark-recapture models with the covariates of interest.**

<table>
<thead>
<tr>
<th>Vital rate / demographic parameter</th>
<th>Abiotic covariate</th>
<th>Biotic covariate</th>
<th>Individual covariate</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survival $\phi_{i,t}$</td>
<td>Length of active season</td>
<td>Population size</td>
<td>Body size</td>
</tr>
<tr>
<td>Survival first year $\phi'_{i,t}$</td>
<td>Length of active season</td>
<td>Population size</td>
<td>Body size</td>
</tr>
<tr>
<td>Detection $p_{i,t}$</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survival $\phi_{i,t}$</td>
<td>Length of active season</td>
<td>Population size</td>
<td>Body size</td>
</tr>
<tr>
<td>Survival first year $\phi'_{i,t}$</td>
<td>Length of active season</td>
<td>Population size</td>
<td>Body size</td>
</tr>
<tr>
<td>Detection $p_{i,t}$</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Skip breeding $\Psi^{B, NB}_{i,t}$</td>
<td>Length of active season, Mean minimum temperature in two weeks before first capture night</td>
<td>Population size</td>
<td>Body size</td>
</tr>
<tr>
<td>Resume breeding $\Psi^{NB,B}_{i,t}$</td>
<td>Length of active season, Mean minimum temperature in two weeks before first capture night</td>
<td>Population size</td>
<td>Body size</td>
</tr>
</tbody>
</table>
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 $\hat{R}$ (Brooks & Gelman, 1998). To assess the goodness-of-fit of the growth model we performed posterior predictive checks, where 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). To assess the goodness-of-fit of our two CMR models (i.e. CJS for males and multistate model for females), we performed posterior predictive checks (Conn et al., 2018), 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 to the rest of the distribution both visually (Figure S2.1, Appendix S2) and by calculating a Bayesian p-value.
Results

All parameters showed good convergence ($\hat{R} < 1.1$). 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 capture-mark-recapture models show a good fit as well, with Bayesian p-values of 0.31 for males and 0.57 for females (Appendix S2).

Direct effects on growth and body size

We were able to estimate sex-specific growth parameters and estimate sizes when individuals were not measured. By providing 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 a biotic factor (population size) and an abiotic one (length of the active season) on both the coefficient of growth $k$ and the asymptotic size $a$. We did not find strictly significant effects of neither population size nor length of active season on either growth model parameters, but there seems to be clear trends with population size positively and negatively associated with growth rate $k$ and asymptotic size $a$ respectively (Table 2).
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 $a$. We show the mean coefficient value, its standard deviation (SD), and the 95% credible intervals (CRI). 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. $\hat{R}$ values show convergence of the MCMC chains.

<table>
<thead>
<tr>
<th>Name</th>
<th>Mean</th>
<th>SD</th>
<th>2.5% limit of CRI</th>
<th>97.5% limit of CRI</th>
<th>Proportion</th>
<th>$\hat{R}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>PopSize on $k$</td>
<td>0.066</td>
<td>0.053</td>
<td>-0.034</td>
<td>0.175</td>
<td>0.907</td>
<td>1.00</td>
</tr>
<tr>
<td>ActiveSeason on $k$</td>
<td>-0.038</td>
<td>0.058</td>
<td>-0.159</td>
<td>0.072</td>
<td>0.246</td>
<td>1.00</td>
</tr>
<tr>
<td>PopSize on $a$</td>
<td>-0.583</td>
<td>0.408</td>
<td>-1.404</td>
<td>0.208</td>
<td>0.07</td>
<td>1.00</td>
</tr>
<tr>
<td>ActiveSeason on $a$</td>
<td>0.469</td>
<td>0.421</td>
<td>-0.369</td>
<td>1.294</td>
<td>0.875</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Figure 2. Growth curves for males (left) and females (right), for low population size (red) and high population size (blue). We looked at realistic population size values, using a value of -1 on the standardised scale for the low population size scenario (corresponding to 73 individuals) and a value of 2 for the high population size (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 where 50% of males and females are sexually mature according to Hemelaar (1988).
Direct effects on vital rates

We modelled CMR data of 1615 male toads and 933 female toads to estimate survival of males with a Cormack-Jolly-Seber model, and female survival and breeding probabilities with a multistate model. Average detection probability was 0.89 and varied little among years (SD = 0.06). Survival $\phi$ of males and females did not vary much across the study period, with male survival fluctuating more (mean values across the study period were 0.74 and 0.73 respectively). Both showed a decrease in the last years (Appendix S3, Figure S3.1). Survival in the year after the first capture $\phi'$ showed a similar pattern, but with lower values (Appendix S3, Figure S3.2). Finally, the probability of skipping breeding if an individual bred the year before $\psi_{NB}$ was high, with an average of 0.66 over the study period, but the probability of resuming breeding if an individual skipped breeding the year before $\psi^{NB,*}$ was higher, with an average of 0.80 (Appendix S3, Figure S3.3). This indicates that there is a strong Markovian pattern in breeding, with the breeding status in the previous year strongly determining if an individual will attempt breeding.

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

Indirect effects on vital rates

Although strictly not significant, we could find indications for an effect of both abiotic and
biotic factors 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 and biotic
factors on vital rates.

Table 3. Summary of the intercepts for the focal vital rates (logit scale) and of the effects of
abiotic (length of the active season and the average minimum temperature around emergence;
ActiveSeason and EmergenceMinT in the table), biotic (population size; PopSize), and individual
factors (body size; BodySize) on survival, the probability of resuming breeding, and the
probability of skipping breeding. We show the mean coefficient value, its standard deviation (SD)
and the 95% credible intervals (CRI). 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 \( \hat{R} \) values were equal to 1 and thus
indicated convergence of the MCMC chains. For the abiotic, biotic, 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.

<table>
<thead>
<tr>
<th>Name</th>
<th>Mean</th>
<th>SD</th>
<th>2.5% limit of CRI</th>
<th>97.5% limit of CRI</th>
<th>Proportion</th>
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<tr>
<td>Intercept</td>
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<td>0.054</td>
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<td>Male survival</td>
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<td>Male survival in the first year</td>
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<td>0.836</td>
<td>1.143</td>
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<tr>
<td>Female survival</td>
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<td>0.116</td>
<td>0.123</td>
<td>0.577</td>
<td>0.9991</td>
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<td>Female survival in the first year</td>
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<td>0.094</td>
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<td>0.879</td>
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<td>Skipping breeding</td>
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<td>1.15</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Abiotic</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------</td>
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<td>------------</td>
<td>------------</td>
<td>------------</td>
<td>------------</td>
</tr>
<tr>
<td></td>
<td><strong>ActiveSeason on male survival</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
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<tr>
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<td>Individual</td>
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<td></td>
<td></td>
<td></td>
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<tr>
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<td></td>
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</tr>
<tr>
<td></td>
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<td>-0.101</td>
<td>0.086</td>
<td>-0.271</td>
<td>0.068</td>
</tr>
</tbody>
</table>

Figure 3. Relationship between the length of the active season (in days) and the survival of males (blue) and females (red), based on the predictions of the model. The lines represent the mean value, while the shaded ribbons the 95% credible intervals. The relationships shown assumed average body size and population size. The rug on the x-axis shows the observed values.
Figure 4. Relationship between the mean minimum temperature (in degrees Celsius) in the two weeks around emergence from hibernation and the probabilities of skipping (blue) and resuming (red) breeding of females, based on the predictions of the model, at low (left panel) and high (right panel) 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 the 95% credible intervals. The relationships shown assumed average body size and active season length. The rug on the x-axis shows the observed values.

Figure 5. Relationship between body size and survival for two different measures of population size for males (left panel) and females (right panel). We defined low population size as 100 individuals and high population size as 500 individuals. The solid lines represent the mean value, while the shaded ribbons the 95% credible intervals. The relationships shown assumed average active season length. The rug on the x-axis shows the observed values for body size.
Discussion

We found evidence that abiotic, biotic, and individual factors had direct effects on vital rates. We also found indications for indirect effects of abiotic and biotic factors on vital rates mediated by individual traits. These findings show that all three factors are acting approximately with the same magnitude on vital rates, highlighting the complexity of amphibian demography and the importance of a comprehensive analysis of the network of factors affecting vital rates.

The von Bertalanffy 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 massively over time in this population. We also observe both males and females becoming sexually mature many years before reaching their asymptotic size, at least four and nine years if the age at sexual maturity has not changed considerably since the start of the study period (Hemelaar, 1988), more if it has shifted to earlier ages, which could happen if it is a plastic trait responding to environmental conditions.

In any case, given the annual survival rates (~0.75), few will reach asymptotic size and will therefore grow during their entire lifespan. This suggests that there is probably a trade-off between growth and reproduction, which could partly explain why females show intermittent breeding.
Direct effects on growth and body size

As hypothesised, 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 to higher availability of resources. We also found indications for a negative effect of a biotic factor (population size) on the asymptotic size, but a positive 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 (Reading, 1986; Hernández-Pacheco et al., 2020), which could be a way 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 population size and active season length (e.g. Paterson & Blouin-Demers, 2018). Concerning the other growth parameter, \( k \), the absence of strong evidence for an effect on it could also mean that \( k \) is an important fitness trait and is buffered against factors like the environment or density (environmental canalisation, 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 effects on the parameters of the VB growth model that covers the growth period post-metamorphosis 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 *Bufo bufo* populations (Table 4 of Muths et al., 2013), 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, meaning that most adult females breeding in a given year will skip breeding the following year, and most females that did not breed will attempt breeding, creating 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. Muths et al., 2013; Cayuela et al., 2014), and further supports the hypothesis that individuals attempt breeding only upon reaching a certain energy threshold, which females often can reach only every two years as their life cycle is slower and habitat production is lower at higher elevations (Houston et al., 2007; McNamara & Houston, 2007). In more recent years, we observe in our population more females reproducing in consecutive years, indicating that there might be other factors influencing the probability of skipping breeding that we have not properly identified.

Concerning abiotic factors, 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 (Werner & Anholt, 1993; Houston et al., 1997), which exposes the animals to more risks, such as diseases, predation, road kill and higher sensibility to extreme weather events (e.g. drought). On the other hand, we did not find a meaningful
correlation between the active season length and female survival, nor with the probabilities of either skipping or resuming breeding. For the first case, females might be more cautious than males (e.g. in rats, Jolles et al., 2015). For the second case, 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, and therefore we do not detect a significant correlation.

We also found evidence of the minimum temperature around emergence from hibernation negatively affecting the probability of skipping breeding. This supports the hypothesis that when the weather would allow for breeding to happen, but it is still harsh, females might forfeit breeding that year to not risk unsuccessful breeding or dying (Muths et al., 2013), especially in alpine habitat 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 lifetime fitness of both the female, as she avoids an increased risk of mortality, and tadpoles, as they would be exposed to bad conditions upon hatching. We therefore expect this trait to be under selection (Erikstad et al., 1998; Cubaynes et al., 2010). 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 (six years). It is possible that given our longer study period we were able to successfully find this association.

Regarding biotic factors (population size), we found evidence that population size has a negative effect on both male and more weakly, female survival. This hints at the presence of density-dependence effects in the terrestrial 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 terrestrial 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-dependence 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). 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, so a higher mortality at older ages (Hamilton, 1966), and therefore bigger sizes, 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 in maintaining bigger body sizes. Previous studies also looked at the role that
body condition can have on survival and breeding, finding support for the idea 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).

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) seems 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, biotic, 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 (Jørgensen, 1992; Hayward &
Gillooly, 2011). Even though we could not find a clear effect of the active season length on
the breeding probabilities, we can hypothesise 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
micro-climatic conditions (Scherrer & Körner, 2011). If indeed females slowly move more
consistently towards 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 both at the larval and the adult stage, with a decrease in
survival, compensating the increase in reproduction.

This study is an important addition to the literature on 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 terrestrial stage (i.e. adult), 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.
Acknowledgements

We thank all the people responsible for data collection and management, and who made fieldwork possible since 1982. This study is funded by the Federal Office for the Environment (contract numbers: 20.0001.PJ/46DBED0F1 and 06.0126-PZ Artenförderung / N494-1379), Stiftung Temperatio and the Department of Evolutionary Biology and Environmental Studies of the University of Zurich. All procedures in the field such as capture, handling and marking of toads were done under animal welfare permits issued by the Veterinäramt des Kantons Bern. Moreover, we thank Dirk Schmaltz and the Land Change Science group of the Swiss Federal Research Institute WSL for providing us with the climate dataset DaymetCH, which is comprised of data obtained from Bioclimatic maps of Switzerland © WSL, based on station data from the Federal Office of Meteorology and Climatology MeteoSwiss. Finally, we thank Rose and colleagues (2022) for their open data policy, which enabled us to access code and data used in their study, with significant benefits for this study.

Authors contribution

O.L. and B.R.S. conceived the study. K.G., S.Z., B.L., S.A., M.T., D.S., and H.R. collected data. O.L. prepared and analysed the data. B.R.S and A.O. provided feedback on the analyses. O.L. wrote the paper with input from all authors.

Data accessibility

Extra figures and tables are available in the Supporting Information. Data and scripts for this publication are available online on Zenodo: doi.org/10.5281/zenodo.10908913.


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RStudio, PBC., Boston, MA.


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Appendix

S1. Other analyses

Measurer bias

This analysis relies on data collected over a study period of almost 30 years (1993-2020), and data have been collected in a standardised way, but by different people. This can cause a measurer bias when it comes to size measurements. To better understand if there is a potentially confounding bias in the size data, we assessed if there were significant differences in the people tasked with data collection over the study period. To do this we ran a Tukey test where we compare the mean value of body size measured by each person with the others (piecewise comparison). The results showed a significant difference in certain cases, but overall the differences were low in terms of absolute values. Indeed, the maximum difference in mean values between two measurers was 3.2 mm, which is approximately 4.5% of the mean body size (Figure S1.1 and S1.2). Differences could also arise for other reasons than measurement bias, such as the population structure. For instance, if more young individuals, or more males than females are showing up at the breeding site in a given year, the mean measured size will be lower than in years with more females and older (and bigger) individuals. For these reasons, we did not include the measurer effect further in the analyses.
Figure S1.1. Piecewise comparison of the mean differences in measured snout-to-vent length (SVL), obtained with a Tukey’s test. Measurers (i.e. observers) are identified with a number from 1 to 5. If the difference, accounting for 95% confidence intervals, overlaps zero is not considered significant.

Figure S1.2. Boxplots showing the range of measured SVL for each measurer (i.e. observer), identified with numbers going from one to five.
Another interesting concept linked to physiology is the body condition. Body condition is a measure that usually considers both body size and body mass. It is useful to distinguish individuals with similar sizes but that might be in quite different states, for instance due to different levels of fat reserves. Following Moldowan et al. (2022), we calculated for each individual at each capture occasion its body condition, in the form of the scaled mass index (SMI; Peig & Green, 2009). This method consists in calculating a standardised mass relative to the body size in the population (divided by sex), while considering the allometric relationship between size and mass. This measure of body condition was determined to consider accurately the fat reserves in some amphibians (MacCracken & Stebbings, 2012).

Body condition seems to vary little over the study period (1985-2022), especially in males (Figure S1.3). We analysed the relationship between body condition and environmental conditions and population size. We hypothesised higher body condition in the breeding season if the previous active season was long. We also hypothesised a lower body condition the higher the population size. We both inspected visually these relationships and ran linear models. The results suggest that body condition is not correlated with environmental conditions nor population size, at least in breeding adults (Figures S1.4 and S1.5). This might be a further indication that there is a threshold in energetical requirements that must be reached for the toads to go to the breeding site, which is typical of “capital” breeders (Bull & Shine, 1977). If body condition is lower, an individual might skip breeding, if it is higher the individual will migrate to the pond to breed. This might explain the small observed variation in SMI. To corroborate this hypothesis, we focused on females that both bred in consecutive years and bred after skipping breeding the year before. For these females, we compared their SMI in a year where they bred the year before with the SMI in a year where they skipped
breeding the previous year. We expected a lower SMI in years following a breeding attempt, as reproduction is energy demanding, especially in such harsh environments (Muths et al., 2013). We observed that there are no meaningful differences (Figure S1.6), further suggesting the presence of a threshold in body condition necessary to attempt breeding.

**Figure S1.3.** Average scaled mass index (calculated following Peig & Green, 2009) for females (red) and males (blue) over the period 1985-2022.
Figure S1.4. Relationship between mean scaled index and number of days with precipitation in summer (green) and autumn (red), for females (circles) and males (triangles).

Figure S1.5. Relationship between the average yearly scaled mass index and the number of captured individuals during a breeding season (proxy of population size) for males (blue) and females (red).
Figure S1.6. For each female we show the difference in scaled mass index between a year which followed a breeding year and a year which followed a non-breeding year. The horizontal dotted line at zero represents the case where a female experienced no difference in scaled mass index when reproducing after either skipping or not skipping reproduction the year before. We expected the distribution of points to be consistently above the red dotted line, indicating that the scaled mass index is higher after a year without reproducing, but it is not what we observe. No clear trend is observable, indicating perhaps that the scaled mass condition (i.e. the body condition) is mainly influenced by other factors. Moreover, the scaled mass indices we show for females might be in some cases biased by the individual mass measured during fieldwork, as sometimes the females are caught and measured before or after laying eggs. Females weighed before they laid eggs will be heavier than when weighed after they laid eggs.
S2. Model diagnostics

To assess the goodness-of-fit of the capture-mark-recapture models we performed posterior predictive checks by following Nater et al. (2020). We simulated 10 replicate capture-history datasets by using 500 evenly spaced samples from the posterior distribution of the estimated parameters. For each of the total 5000 sets of capture histories we calculated the total number of recaptures and obtained a distribution, which we then compared with the true number of recaptures from the original capture histories dataset (Figure S2.1). In case of good fit the true value should lay somewhere in the distribution, and the closer to the mean the better.

Figure S2.1. Posterior predictive checks to assess the goodness-of-fit of the capture-mark-recapture models. 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 histories and obtained a distribution of 5000 number of recaptures. On the left we show the distribution of the number of recaptures for females and on the right for males. We then compared the real observed number of recaptures (shown with the orange vertical line) to the rest of the distribution. To have a good fit, the observed number of recaptures should fall in the distribution, and the closer to the median the better. The Bayesian p-value (i.e. the ratio between the number of simulated datasets with a higher number of recaptures than the observed versus the total amount of simulated datasets) was 0.57 for females and 0.31 for males.

Both models on males and females show a very good fit, validating the assumptions about the same temporal pattern in detection probability and about males always attempting breeding. To evaluate parameter identifiability, we also checked the prior-posterior overlap for all non-derived parameters (Garrett & Zeger, 2000; Gimenez et al., 2009). An overlap of
35% or more between prior and posterior distributions results in a weakly-identifiable parameter. In our case, all overlaps but one were below 35% indicating overall good identifiability (Figure S2.2). Only Rho, which is the correlation of the year random effects on asymptotic size $a$ and growth rate $k$, had a high overlap of 76.3%, hinting that there is no actual correlation between them.
Figure S2.2. Prior-posterior overlap plots. For each of the estimated parameters we plotted prior (purple) and posterior (orange) distributions. In brackets we put the percentage of overlap of the two distributions.
**Figure S3.1.** Year-specific survival rates for males (blue) and females (red). The solid line represents the average, while the shaded ribbons are the 95% credible intervals, obtained from the posterior distribution. The values are calculated assuming an average body size.
Figure S3.2. Year-specific survival rates in the year after first capture, for males (blue) and females (red). The solid line represents the average, while the shaded ribbons are the 95% credible intervals. The values are calculated assuming an average body size.
Figure S3.3. Year-specific probability of resuming (red) and skipping breeding (blue). The solid line is the average, while the shaded ribbons are the 95% credible intervals.
Appendix References


