

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

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20

21 **Abstract**

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

28

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

36

37 3. Using 28 years of capture-mark-recapture data and individual body size
38 measurements on an alpine population of the common toad (*Bufo bufo*), we
39 estimated male survival probability with a Bayesian Cormack-Jolly-Seber model,
40 female survival and female breeding probability with a Bayesian multistate model, and
41 we estimated sex-specific growth curves.

42

43 4. Our findings reveal significant negative impacts of all three factor types on survival.
44 Moreover, breeding probability exhibited a Markovian pattern, notably breeding
45 biennially, with temperature at hibernation emergence, an abiotic factor, affecting the
46 probability of skipping a breeding season, and population density, a biotic factor,
47 influencing the resuming of breeding. We also found indication for the presence of
48 indirect effects, with both abiotic and biotic factors potentially affecting asymptotic
49 growth, and thus by extension, survival through changes in body size.

50

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

55 **Introduction**

56 Fluctuations in population size have historically been ascribed to the effects of abiotic (i.e.
57 environmental) factors as well as biotic factors (e.g. population density) on vital rates
58 (Lawton, 1994; Hanski et al., 1997). Abiotic and biotic factors can have similar, opposite, or
59 interacting effects on vital rates (Gamelon et al., 2017; Conquet et al., 2023). More recently
60 studies have shown that the effect of individual traits such as body size on vital rates also
61 matter in driving population dynamics (Easterling et al., 2000; Rees et al., 2014). Abiotic and
62 biotic factors, aside from their direct effect on vital rates, can influence these individual traits
63 as well, thus having also indirect (i.e. trait-mediated) effects on vital rates and by extension
64 on population dynamics (e.g. Amarillo-Suárez et al., 2011).

65 Populations can thus be affected by abiotic, biotic, and individual factors. Nonetheless,
66 studies in the past often have focused on one or two of these factors at a time, but a more
67 complete understanding of vital rates and population dynamics and their drivers could be
68 obtained when incorporating all factors in demographic analyses (Benton et al., 2006; Ehlén
69 et al., 2016). To better understand the demography underlying population dynamics, it is thus
70 important to investigate the relative importance of abiotic, biotic, and individual factors on
71 vital rates. Investigating such effects on adult survival and breeding probability, two key vital
72 rates that can contribute largely to population growth (e.g. Sæther & Bakke, 2000; Schmidt
73 et al., 2005; Desprez et al., 2018), can give important insights into population responses to
74 these factors. Whereas there are many studies on these factors in birds and mammals, we
75 are lacking studies about amphibians, which are an often understudied taxon (Conde et al.,
76 2019), despite their important role in ecosystems (Whiles et al., 2006), and their worrying
77 status at the global scale (Houlahan et al., 2000; Luedtke et al., 2023). Thus, this lack of

78 knowledge negatively affects conservation and hampers an in-depth understanding of
79 vertebrate demography (Conde et al., 2019). Moreover, we decided to focus on a population
80 living at the extreme range of its species' distribution, more precisely its upper elevational
81 limit. These high-elevation animal populations are rarely studied systematically and only few
82 long-term studies exist. Such populations are exposed to harsh environmental conditions (e.g.
83 cold temperatures), with known physiological effects (e.g. lower metabolic rate) which usually
84 result in a slower life cycle (Laiolo & Obeso, 2017). We expect in these populations a stronger
85 effect of abiotic factors on vital rates compared to biotic and individual factors, given how
86 severely the environment acts as a selective force (e.g. Bassar et al., 2016; Paquette &
87 Hargreaves, 2021).

88 We used 28 years of capture-mark-recapture (CMR) data on a high-elevation
89 population of common toad (*Bufo bufo*) to quantify the relative importance of abiotic, biotic,
90 and individual factors in shaping dynamics of amphibian populations (Figure 1). The
91 implemented analytical framework has two parts. The first part is a growth model, where we
92 quantified the effect of abiotic and biotic factors on individual traits. The second part is a CMR
93 model that we used to estimate survival and the breeding probabilities (the latter only for
94 females), while assessing the direct effect of abiotic, biotic, and individual factors, as well as
95 the indirect effect of abiotic and biotic factors.

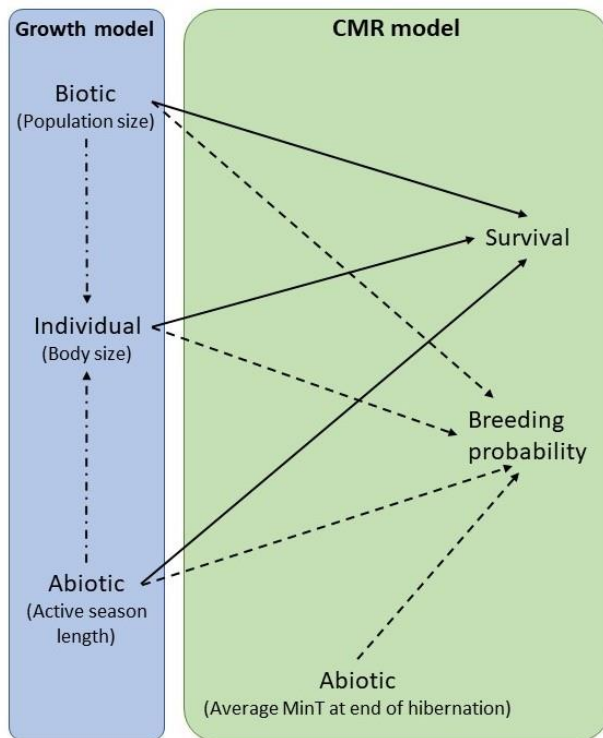
96 To obtain information on individual factors (i.e. body size), we implemented a von
97 Bertalanffy growth model in a Bayesian framework. We expect to obtain growth curves similar
98 to what Hemelaar (1988) estimated using three years of data for the same population through
99 skeletochronology. We investigated the effect of population density (a biotic factor) and the
100 length of the active season in the previous year (an abiotic factor) on the two von Bertalanffy
101 model coefficients, the growth rate k and the asymptotic size a . We hypothesise that a long

102 active season in the previous year has a positive effect on individual growth, as the individuals
103 can feed and grow for a longer period of time (Eastman et al., 2012). We expect on the other
104 hand high population sizes to have a negative effect on growth, as there will be less resources
105 per capita available (Berven, 2009).

106 In the second part of the analytical framework (i.e. the CMR model) we aimed at
107 estimating survival and breeding probabilities while assessing the direct effect of abiotic,
108 biotic, and individual factors, as well as indirect effects of abiotic and biotic factors. We
109 estimated breeding probabilities for females, as they are the only sex clearly showing
110 intermittent breeding in this population (Grossenbacher, 2002). Intermittent breeding can
111 arise where environmental conditions are unfavourable, such as at high elevations. In these
112 conditions, individuals can (and sometimes must) forfeit breeding in a year to breed the
113 following year. It can be either an adaptive response to environmental conditions which are
114 pessimal for successful breeding and therefore a way to avoid wasting energy in particularly
115 bad years (Bull & Shine, 1979), or it can arise in capital breeders due to the impossibility of
116 collecting enough resources to be able to breed every year (Jönsson, 1997; Houston et al.,
117 2007), either due to lower habitat production, or shorter feeding seasons. This is especially
118 the case for females, for whom reproduction is more demanding energetically (Jørgensen,
119 1992; Hayward & Gillooly, 2011). For female toads, we thus estimated survival and breeding
120 probabilities using a multistate model, defining breeder and non-breeder as the two states
121 (the latter as a non-observable state; Schaub et al., 2004). For males, we used a Cormack-
122 Jolly-Seber model instead. We investigated the effects of population size (biotic factor), active
123 season length (abiotic factor), and individual body size (individual factor) on survival and,
124 where applicable, breeding probabilities. For the latter, we also tested for the effect of
125 average minimum temperature around the timing of emergence. The latter covariate was

126 included following a previous study that hypothesised that the decision to skip breeding might
127 also be due to the environmental conditions experienced at emergence from hibernation
128 (Muths et al., 2013). More in detail, we expect the length of the active season in the previous
129 year to be positively associated with survival and the probability of resuming breeding, as well
130 as negatively associated with the probability of skipping breeding, as the individuals are able
131 to feed for longer and accumulate resources to prepare for the next breeding season (Bull &
132 Shine, 1979; Sainmont et al., 2014). On the other hand, longer active seasons might increase
133 mortality, as toads are more exposed to mortality compared to the hibernation period. Also,
134 individuals from high-elevation populations, where active seasons are shorter, tend to have
135 higher survival and live longer, probably due to the reduced speed of the life cycle (e.g.
136 Hemelaar, 1988). Additionally, we expect colder temperatures around the time of emergence
137 from hibernation to increase the probability of skipping breeding and decrease the probability
138 of resuming breeding, as toads might be able to perceive the unfavourable environmental
139 conditions, and forfeit breeding (Muths et al., 2013). Regarding the biotic factors, we
140 hypothesise that higher population sizes decrease the survival probability through density-
141 dependent regulation mechanisms (Kissel et al., 2020), as well as reduce the probability of
142 resuming breeding since fewer females will attain the necessary energetic requirements to
143 breed (Hamel et al., 2010). Concerning the individual factors, we expect bigger individuals to
144 survive better, as a bigger body size is generally linked to an increased fitness (Peters, 1986;
145 Hernández-Pacheco et al., 2020). Alternatively, intermediate sizes might be correlated with
146 higher survival (e.g. Weinbach et al., 2018), as increased mortality at bigger sizes might be
147 linked to actuarial senescence. Finally, we hypothesise that there might be a weak correlation
148 between body size and breeding probabilities. Bigger females might in fact be more successful
149 in accessing resources (Hin & de Roos, 2019). On the other hand, bigger individuals have

150 higher energetic requirements (Hin & de Roos, 2019), therefore a better access to resources
151 does not necessarily reflect a higher chance of resuming breeding or a lower chance of
152 skipping breeding. Assessing the effect of individual factors on vital rates, while accounting
153 for the effect of abiotic and biotic factors on the individual factor (in the growth model)
154 enables us to quantify the indirect effect that abiotic and biotic factors can have on vital rates.
155 We hypothesise to find synchrony in direct and indirect effects. For instance, the expected
156 negative direct effect of population size on survival should be matched by the negative effect
157 of population size on body size, which then could lead to a decrease in survival due to smaller
158 sizes. Similarly, a longer active season could both directly and indirectly increase survival, due
159 to its positive effect on body size, and the positive relationship between body size and
160 survival, but could also show asynchrony if it has a negative effect on survival. This
161 comprehensive analysis of key growth and vital rates, encompassing direct and indirect
162 influences of multiple factors, offers novel insights into amphibian population dynamics,
163 informing conservation efforts in high-elevation habitats.



164

165 **Figure 1.** Framework of the study. To obtain estimates of body sizes for the years when the toads were
 166 not captured, we ran a von Bertalanffy (VB) growth model including a biotic (population size) and an
 167 abiotic factor (the length of the active season) as covariates on the two VB parameters: growth rate
 168 and asymptotic size. Subsequently, we ran two sex-specific capture-mark-recapture (CMR) models to
 169 estimate adult survival and breeding probabilities (i.e. the probability of skipping and resuming
 170 breeding), while including the effect of a biotic factor (population size), an individual factor (body size)
 171 and an abiotic factor (length of the active season). For the breeding probabilities we also included an
 172 additional abiotic factor (average minimum temperature in the two weeks around the emergence from
 173 hibernation). Following this framework, we are also able to assess the indirect effect of abiotic and
 174 biotic factors through their effect on body size.
 175

176 **Methods**

177 Toad mark-recapture and body size data

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

194

195 Climatic data

196 We used climatic data for the period 1993–2020 obtained from the DaymetCH dataset (Land
197 Change Science group, WSL, Switzerland). DaymetCH consists of interpolated estimates of
198 weather variables over a grid of a 100-metre resolution covering Switzerland. The estimates

199 are obtained using meteorological data from ground stations and the Daymet software
200 (Thornton et al., 1997). We extracted data for the cell containing the breeding site for daily
201 minimum temperatures and based on previous work (Muths et al., 2017), we calculated for
202 each year the approximate length of the active season (i.e. the period between the end of
203 hibernation in spring and the start of hibernation in autumn, which includes both the short
204 breeding season followed by the non-breeding feeding season). We define the start of the
205 active season as the end of the winter season, which corresponds to the day of the last killing
206 frost (minimum temperature < -4.4 °C), while the end of the active season is defined as the
207 start of the coming winter season, which corresponds to the first day with a killing frost in
208 autumn (minimum temperature < -4.4 °C) (Muths et a., 2017).

209

210 Growth model

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

$$218 \quad EL_{i,t} = a_i - (a_i - L_{i,t-1}) \exp \left[-\frac{k_{i,t}}{a_i} (\Delta t) \right] \quad (1)$$

219 Where $EL_{i,t}$ is the expected snout-to-vent (SVL) length of a toad i at time t , a_i is the asymptotic
220 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
221 between two captures, in days. We substituted k with k/a , to let individual variation in growth
222 rate k be independent from individual variation in asymptotic size a . The observed SVL $L_{i,t}$ is

223 obtained by sampling from a normal distribution with mean EL and standard deviation ε , to
224 account for imperfect measurement and individual variation (Equation 2).

$$225 \quad L_{i,t} \sim N(\text{mean} = EL_{i,t}, SD = \varepsilon) \quad (2)$$

226 To better understand the effect of abiotic and biotic factors, we modelled asymptotic size a
227 of a toad at year t as a function of population size (i.e. the number of individuals caught every
228 year at the breeding site) and the length of the active season of the year before ($t-1$). In other
229 words, we calculated each year the asymptotic size that a toad would reach if the length of
230 the active season and the population size would remain constant. We also modelled the log
231 of the growth rate as a function of population size and the length of the active season, with
232 an individual random effect, drawn from a normal distribution with a mean of zero and a
233 standard deviation estimated in the Bayesian framework. Moreover, we included temporal
234 (i.e., “year”) random effects on both asymptotic size and growth rate, drawing them from a
235 bivariate normal distribution, therefore estimating the among-year correlation between both
236 parameters. To account for differences in sex we modelled two sex-specific VB growth
237 models. Additionally, once the parameters a and k were estimated, we could build two sex-
238 specific growth curves, using as a starting size (size at metamorphosis) a value drawn from a
239 random normal distribution with a mean of 12 mm and standard deviation of 1, to encompass
240 the sizes of newly metamorphosed toads measured by Craioveanu et al. (2019).

241

242 CMR models

243 Since the data suggests that males show no (or only very limited) intermittent breeding, we
244 estimated breeding probabilities for females only. Therefore, we could model the capture-
245 recapture histories of males with a Cormack-Jolly-Seber (CJS), as we assumed that they will
246 always attempt breeding when alive, and thus we estimated only survival and detection

247 probability (Lebreton et al., 1992). On the other hand, given that females might skip breeding
248 in a given year (Schmidt et al., 2002; Loman & Madsen, 2010), we modelled the capture
249 histories of females with a multistate model, with the two states being *non-breeder* and
250 *breeder* (the phenomenon is often called “temporary emigration” in the mark-recapture
251 literature; Schaub et al., 2004). Since non-breeders do not show up at the pond, they are not
252 available for capture and the state *non-breeder* is unobservable (Schaub et al., 2004). In this
253 model we estimated survival, detection, and the probability of changing state (becoming a
254 non-breeder or becoming a breeder).

255

256 We were interested in the effect of abiotic (environment), biotic (population size), and
257 individual factors (body size) on the different vital rates (Figure 1). For both males and
258 females, for survival probability ($\phi_{i,t}$) in year t we added as covariates the length of the active
259 season at year t , the population size at year t , and the body mass of that individual at year t
260 obtained from the growth model (Table 1). In the estimation of the probability that a female
261 will skip breeding if it bred the year before ($\psi_{i,t}^{B-NB}$) and the probability that a female will
262 resume breeding if it did not breed the year before ($\psi_{i,t}^{NB-B}$) we included the effects of the
263 length of the active season of the year before, as well as the weather conditions (i.e. average
264 minimum temperature) in the two weeks before the first capture night (Table 1). The latter
265 was included based on the hypothesis that female toads might skip breeding once out of
266 hibernation based on the conditions they experience at awakening (Muths et al., 2013).
267 Muths et al. (2013) looked at conditions in the two months around breeding time (March and
268 April), while we focused on the two-week period prior to the first capture night. The first
269 capture night is done as soon as possible after the first signs of toads migrating to the breeding
270 pond are detected if the weather conditions allow it. The people responsible for the fieldwork

271 routinely check the snow cover at the study site either in person or using a webcam.
272 Therefore, this two-week period should cover well the precise moment of the end of the
273 hibernation, without covering too much of the hibernation period, where the external
274 environmental conditions should not influence the below-ground toads. Finally, we included
275 a random effect of year on the detection probability p_t (mean μ_p and standard deviation σ_p)
276 which was shared between the two sex-specific models to avoid identifiability issues. We
277 standardised all the covariates by subtracting the mean value and dividing by the standard
278 deviation. Correlation coefficients between population size, length of the active season, and
279 the two-week average minimum temperature were low ($-0.20 < r < 0.43$).

280 Given that for males we modelled a Cormack-Jolly-Seber model, we could test model
281 assumptions using goodness-of-fit tests (GoF; Pollock et al., 1985). We did this using the
282 *R2Ucare* package in RStudio (Gimenez et al., 2018). The tests showed that there might be a
283 transience effect and overdispersion. We are not aware of the existence of similar GoF tests
284 in the case of a multistate model with one unobservable state, therefore we assumed that
285 also for the female data we had to account for transience and overdispersion. If transience is
286 not accounted for correctly, survival or detection probabilities might be underestimated
287 (Pradel et al., 1997). The solution we applied here was to estimate a specific survival
288 probability for the first year after capture (Genovart & Pradel, 2019). Low values of this
289 survival probability do not necessarily indicate an increased mortality, but just a lower
290 probability for the animal of being available for recapture in the following years, either due
291 to true mortality or permanent emigration (i.e. apparent survival). Regarding overdispersion,
292 we know it leads to narrower standard errors around the estimated parameters, but the
293 estimate itself is not biased (Schmidt et al., 2002). To assess the magnitude of overdispersion
294 we calculated \hat{c} (the variance inflation factor), by dividing the chi-squared test statistic by the

295 number of degrees of freedom (Pradel et al., 1997). We obtained a value of 2.48 which indeed
 296 indicates overdispersion (Choquet et al., 2009). We addressed overdispersion by including an
 297 individual random effect in the detection probability (Abadi et al., 2013).
 298

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

	Vital rate / demographic parameter	Abiotic covariate	Biotic 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 $\psi_{i,t}^{B-NB}$	Length of active season, Mean minimum temperature in two weeks before first capture night	Population size	Body size
	Resume breeding $\psi_{i,t}^{NB-B}$	Length of active season, Mean minimum temperature in two weeks before first capture night	Population size	Body size

299 We implemented the growth model and the CMR model in a unified Bayesian
300 framework using Markov chain Monte Carlo (MCMC) sampling in Nimble (version 0.11.1, de
301 Valpine et al., 2017). We conducted all the analyses in R (R version 4.1.1; R Core Team, 2020)
302 with RStudio (version 2022.7.1.554; R Studio Team, 2022). We ran four chains for 770'000
303 sampling iterations each, including an initial burn-in of 70'000 iterations and a thinning value
304 of 7, resulting in 100'000 iterations per chain. We assessed model convergence by visually
305 inspecting MCMC trace plots and calculating the Brooks–Gelman–Rubin statistic \hat{R} (Brooks &
306 Gelman, 1998). To assess the goodness-of-fit of the growth model we performed posterior
307 predictive checks, where we compared two sums of squared residuals to obtain a Bayesian p-
308 value. The first sum compared observed and expected SVL values, the second sum compared
309 simulated and expected SVL values (Rose et al., 2022). To assess the goodness-of-fit of our
310 two CMR models (i.e. CJS for males and multistate model for females), we performed
311 posterior predictive checks (Conn et al., 2018), following Nater et al. (2020). We chose 500
312 evenly spaced samples from the posterior distributions of the estimated parameters and used
313 them to simulate 10 replicate capture-history datasets per sample. We then calculated the
314 number of recaptures in each set of capture history and obtained a distribution of 5000 values
315 for the number of recaptures. We then compared the observed number of recaptures to the
316 rest of the distribution both visually (Figure S2.1, Appendix S2) and by calculating a Bayesian
317 p-value.

318 **Results**

319 All parameters showed good convergence ($\hat{R} < 1.1$). The Bayesian p-values for the growth
320 model for females and males were 0.55 and 0.46 respectively, indicating overall a good fit.
321 The posterior predictive checks on the capture-mark-recapture models show a good fit as
322 well, with Bayesian p-values of 0.31 for males and 0.57 for females (Appendix S2).

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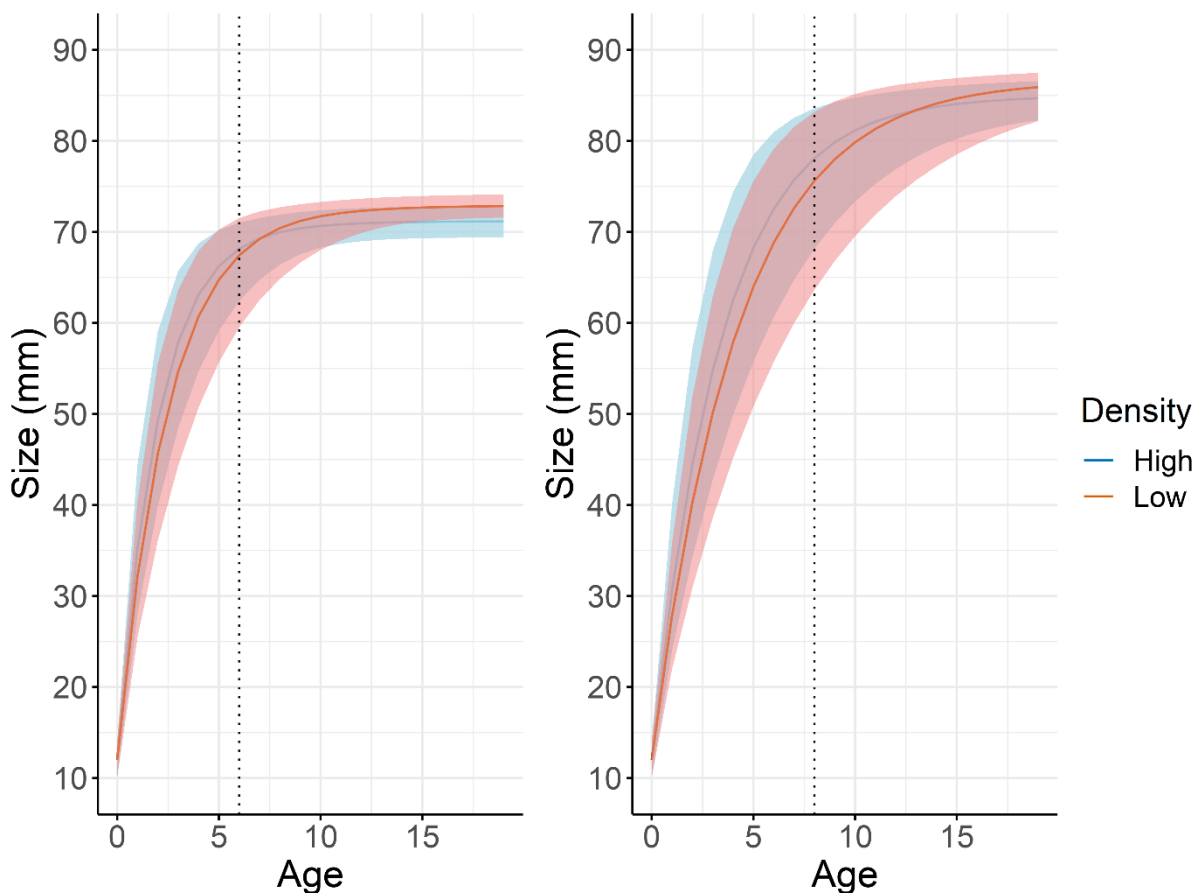
324 Direct effects on growth and body size

325 We were able to estimate sex-specific growth parameters and estimate sizes when individuals
326 were not measured. By providing initial size at metamorphosis, and using the parameters
327 estimated from the model, we built sex-specific growth curves (Figure 2). We tested for the
328 effects of a biotic factor (population size) and an abiotic one (length of the active season) on
329 both the coefficient of growth k and the asymptotic size a . We did not find strictly significant
330 effects of neither population size nor length of active season on either growth model
331 parameters, but there seems to be clear trends with population size positively and negatively
332 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.

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

333
334



335
336 **Figure 2.** Growth curves for males (left) and females (right), for low population size (red) and high
337 population size (blue). We looked at realistic population size values, using a value of -1 on the
338 standardised scale for the low population size scenario (corresponding to 73 individuals) and a value
339 of 2 for the high population size (521 individuals). We show the median growth trajectory, while the
340 shaded ribbons represent the 95% credible intervals. These curves represent a situation with an
341 average year effect, and an average length of the active season. The vertical dotted lines indicate the
342 age where 50% of males and females are sexually mature according to Hemelaar (1988).

343 Direct effects on vital rates

344 We modelled CMR data of 1615 male toads and 933 female toads to estimate survival of
345 males with a Cormack-Jolly-Seber model, and female survival and breeding probabilities with
346 a multistate model. Average detection probability was 0.89 and varied little among years (SD
347 = 0.06). Survival ϕ of males and females did not vary much across the study period, with male
348 survival fluctuating more (mean values across the study period were 0.74 and 0.73
349 respectively). Both showed a decrease in the last years (Appendix S3, Figure S3.1). Survival in
350 the year after the first capture ϕ' showed a similar pattern, but with lower values (Appendix
351 S3, Figure S3.2). Finally, the probability of skipping breeding if an individual bred the year
352 before ψ^{B_NB} was high, with an average of 0.66 over the study period, but the probability of
353 resuming breeding if an individual skipped breeding the year before ψ^{NB_B} was higher, with an
354 average of 0.80 (Appendix S3, Figure S3.3). This indicates that there is a strong Markovian
355 pattern in breeding, with the breeding status in the previous year strongly determining if an
356 individual will attempt breeding.

357

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

367 (i.e. body size) we found evidence of a negative effect of body size on male survival, and a
 368 very clear negative trend on female survival (Figure 5).

369

370 Indirect effects on vital rates

371 Although strictly not significant, we could find indications for an effect of both abiotic and
 372 biotic factors on body size. This means, along with the negative association of body size with
 373 survival, that there might be also indirect (i.e. trait-mediated) effects of abiotic and biotic
 374 factors on vital rates.

375

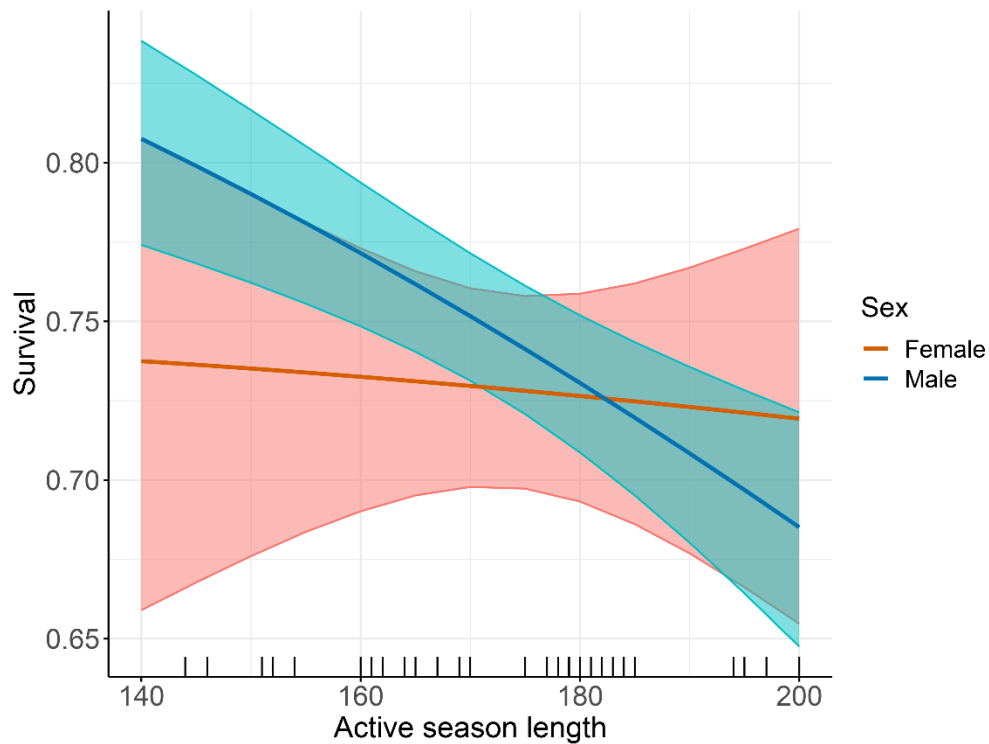
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Table 3. Summary of the intercepts for the focal vital rates (logit scale) and of the effects of abiotic (length of the active season and the average minimum temperature around emergence; *ActiveSeason* and *EmergenceMinT* in the table), biotic (population 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.

	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
Biotic	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

377



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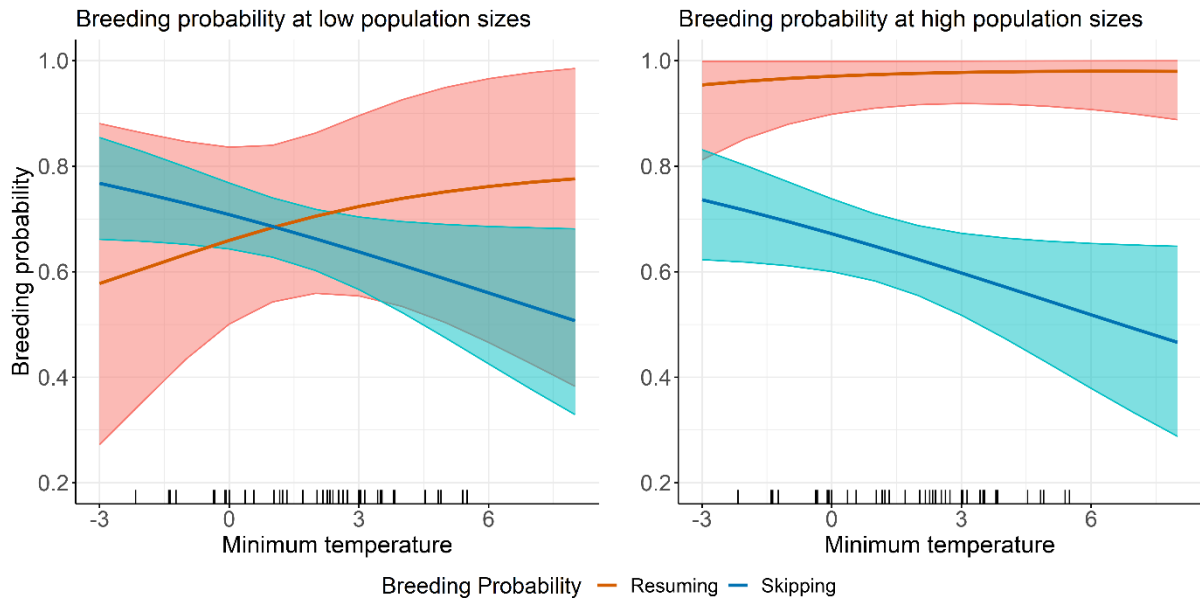
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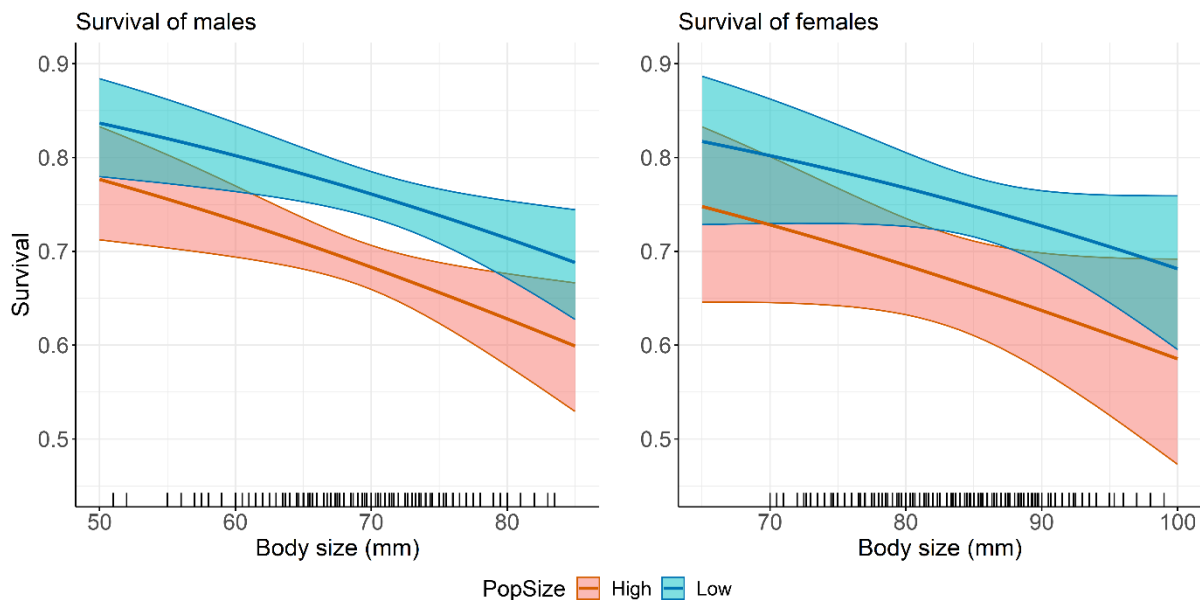
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Figure 3. Relationship between the length of the active season (in days) and the survival of males (blue) and females (red), based on the predictions of the model. The lines represent the mean value, while the shaded ribbons the 95% credible intervals. The relationships shown assumed average body size and population size. The rug on the x-axis shows the observed values.



384
 385 **Figure 4.** Relationship between the mean minimum temperature (in degrees Celsius) in the two weeks
 386 around emergence from hibernation and the probabilities of skipping (blue) and resuming (red)
 387 breeding of females, based on the predictions of the model, at low (left panel) and high (right panel)
 388 population sizes. We defined low population size as 100 individuals and high population size as 500
 389 individuals. The lines represent the mean value, while the shaded ribbons the 95% credible intervals.
 390 The relationships shown assumed average body size and active season length. The rug on the x-axis
 391 shows the observed values.
 392
 393
 394



395
 396 **Figure 5.** Relationship between body size and survival for two different measures of population size for
 397 males (left panel) and females (right panel). We defined low population size as 100 individuals and
 398 high population size as 500 individuals. The solid lines represent the mean value, while the shaded
 399 ribbons the 95% credible intervals. The relationships shown assumed average active season length.
 400 The rug on the x-axis shows the observed values for body size.
 401

402 **Discussion**

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

409

410 The von Bertalanffy model enabled us to obtain growth curves similar to Hemelaar's (1988)
411 curves for the same population. Males grow faster than females and to smaller asymptotic
412 sizes, which based on the model's prediction are reached at about 10 years of age, on average
413 a year later than estimated by Hemelaar (1988). Females seem to reach their asymptotic size
414 at around 17 years of age (Figure 2; Hemelaar (1988) reported the same age). These findings
415 indicate that growth patterns are not varying massively over time in this population. We also
416 observe both males and females becoming sexually mature many years before reaching their
417 asymptotic size, at least four and nine years if the age at sexual maturity has not changed
418 considerably since the start of the study period (Hemelaar, 1988), more if it has shifted to
419 earlier ages, which could happen if it is a plastic trait responding to environmental conditions.
420 In any case, given the annual survival rates (~ 0.75), few will reach asymptotic size and will
421 therefore grow during their entire lifespan. This suggests that there is probably a trade-off
422 between growth and reproduction, which could partly explain why females show intermittent
423 breeding.

424 Direct effects on growth and body size

425 As hypothesised, we found indication of an effect (although not strictly significant) of an
426 abiotic factor (length of the active season) on growth, with longer seasons associated with
427 bigger asymptotic sizes. Longer active seasons allow for a longer growth period, and possibly
428 to higher availability of resources. We also found indications for a negative effect of a biotic
429 factor (population size) on the asymptotic size, but a positive on the growth rate k indicating
430 that at higher densities individuals might grow faster but to smaller sizes (Green & Middleton,
431 2013). This is what is generally expected, given the predicted lower per capita resource
432 availability at higher densities and the need to grow faster to outcompete other individuals.
433 Moreover, smaller females might have lower fecundity due to smaller and fewer eggs
434 (Reading, 1986; Hernández-Pacheco et al., 2020), which could be a way density dependence
435 acts on the population. There are many studies showing spatial variation in body size, but only
436 a few studies showed that the determinants of asymptotic size could be pinpointed to
437 context-specific situations such as population size and active season length (e.g. Paterson &
438 Blouin-Demers, 2018). Concerning the other growth parameter, k , the absence of strong
439 evidence for an effect on it could also mean that k is an important fitness trait and is buffered
440 against factors like the environment or density (environmental canalisation, Gaillard &
441 Yoccoz, 2003). Indeed, growing faster might be more important than growing to larger sizes.
442 Despite the large body of literature on the effect of density and the environment on
443 amphibian larval growth (Reading & Clarke, 1999; Ruthsatz et al., 2018), we found no studies
444 on their effects on the parameters of the VB growth model that covers the growth period
445 post-metamorphosis in amphibians, highlighting the importance of our study.

446

447 Direct effects on vital rates

448 The relatively high male and female survival rates that we found over the study period (0.74
449 and 0.73 respectively, at average body size) are typical of populations living at higher
450 elevations, where generally the pace of life is slow, mostly due to energy constraints. Our
451 values are in line with previous studies on *Bufo bufo* populations (Table 4 of Muths et al.,
452 2013), where populations living in similar conditions had a higher survival rate than lowland
453 populations. The estimates of our breeding probabilities (mean $\psi_{i,t}^{B-NB} = 0.66$ and mean
454 $\psi_{i,t}^{NB-B} = 0.80$) revealed a Markovian breeding pattern in females, meaning that most adult
455 females breeding in a given year will skip breeding the following year, and most females that
456 did not breed will attempt breeding, creating a relatively regular biennial cycle of breeding as
457 previously observed in this population (Grossenbacher, 2002). This is expected as they are
458 capital breeders living in harsh conditions (Bull & Shine, 1979). This outcome has been found
459 in previous studies on amphibians (e.g. Muths et al., 2013; Cayuela et al., 2014), and further
460 supports the hypothesis that individuals attempt breeding only upon reaching a certain
461 energy threshold, which females often can reach only every two years as their life cycle is
462 slower and habitat production is lower at higher elevations (Houston et al., 2007; McNamara
463 & Houston, 2007). In more recent years, we observe in our population more females
464 reproducing in consecutive years, indicating that there might be other factors influencing the
465 probability of skipping breeding that we have not properly identified.

466 Concerning abiotic factors, we found that the length of the active season was
467 negatively associated with adult survival of males. This could be explained by the intrinsic
468 higher mortality of being more active (Werner & Anholt, 1993; Houston et al., 1997), which
469 exposes the animals to more risks, such as diseases, predation, road kill and higher sensibility
470 to extreme weather events (e.g. drought). On the other hand, we did not find a meaningful

471 correlation between the active season length and female survival, nor with the probabilities
472 of either skipping or resuming breeding. For the first case, females might be more cautious
473 than males (e.g. in rats, Jolles et al., 2015). For the second case, it is possible that even the
474 longest active season lengths observed in our system are not long enough to enable most
475 females to build up the energy necessary to breed in consecutive years, and therefore we do
476 not detect a significant correlation.

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

490 Regarding biotic factors (population size), we found evidence that population size has
491 a negative effect on both male and more weakly, female survival. This hints at the presence
492 of density-dependence effects in the terrestrial stage of amphibians. We expect density
493 regulation due to a decrease in the per capita resource availability or an increased
494 competition for shelters, especially in a context where habitats might be less productive, and

495 shelters scarcer than at lower elevations. There are only a few studies investigating this aspect
496 in adult amphibians, in contrast to the large number of studies on density dependence in the
497 larval aquatic stage (e.g. Reading & Clarke, 1999). Density dependence in the adult terrestrial
498 stage could play a significant role in regulating the population (Hellriegel, 2000). Previous
499 studies tested density dependence in adults in an experimental setting (Altwegg, 2003;
500 Harper & Semlitsch, 2007), showing that density-dependence processes can indeed operate,
501 while our study is one of the few that investigated this aspect in a wild population, indicating
502 that density dependence acts also in the wild, within the limits of observational field studies
503 (see also Berven, 2009; Kissel et al., 2020). Counter to our hypothesis, we found a strong
504 positive association between population size and the probability of resuming breeding,
505 indicating that the bigger the population, the higher the probability of resuming breeding. A
506 possible mechanism explaining this relationship is the decision by females to breed rather
507 than delaying due to increased mortality at higher densities (McNamara et al., 2004).
508 Alternatively, this finding might indicate just a correlation and not causation, hinting at a
509 common cause that is affecting both population size and the probability of resuming
510 breeding. If in general the conditions experienced by this population are getting better, we
511 could expect both an increase in population size, and a higher probability of resuming
512 breeding in females.

513 Finally, regarding individual factors, we found a negative association between body
514 size and male survival, and an almost significant negative association also with female
515 survival. This result can be explained by actuarial senescence, so a higher mortality at older
516 ages (Hamilton, 1966), and therefore bigger sizes, as growth slows down but does not stop
517 over the lifetime of individuals (Duellman & Trueb, 1994). It could also be explained by the
518 higher costs in maintaining bigger body sizes. Previous studies also looked at the role that

519 body condition can have on survival and breeding, finding support for the idea that for
520 breeding to happen, body condition must reach a threshold value (Baron et al., 2013; Reading
521 & Jofré, 2021). In our case, we did not find any correlation between increased body condition
522 and a lower chance of skipping breeding, or a higher chance of resuming breeding (Appendix
523 S1).

524

525 Indirect effects on vital rates

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

537

538 Conclusion

539 We could not only demonstrate the presence of intermittent breeding for females in this
540 population living at high elevation, but also estimate key vital rates and assess the importance

541 that abiotic, biotic, and individual factors can have on these rates. The fact that females show
542 strong intermittent breeding seems to further indicate that the major onus energetically
543 speaking is on them, and this seems to apply to most anurans (Jørgensen, 1992; Hayward &
544 Gillooly, 2011). Even though we could not find a clear effect of the active season length on
545 the breeding probabilities, we can hypothesise that under current climate scenarios future
546 active seasons will be long enough to lead to a more frequent annual breeding. However,
547 current effects of climate change on this population are not as strong and predictable as
548 expected. For instance, winter and spring temperatures are not constantly increasing, nor is
549 snow cover constantly decreasing (Lenzi et al., 2023), perhaps due to topologically driven
550 micro-climatic conditions (Scherrer & Körner, 2011). If indeed females slowly move more
551 consistently towards an annual breeding, there might be consequences for the population, as
552 many more individuals will be produced. On the other hand, we expect stronger regulatory
553 effects due to density dependence both at the larval and the adult stage, with a decrease in
554 survival, compensating the increase in reproduction.

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

564 important insights on the dynamics and persistence of amphibian populations under changing
565 environmental conditions.

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578 data used in their study, with significant benefits for this study.

579 **Authors contribution**

580 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.
581 O.L. prepared and analysed the data. B.R.S and A.O. provided feedback on the analyses. O.L.
582 wrote the paper with input from all authors.

583 **Data accessibility**

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

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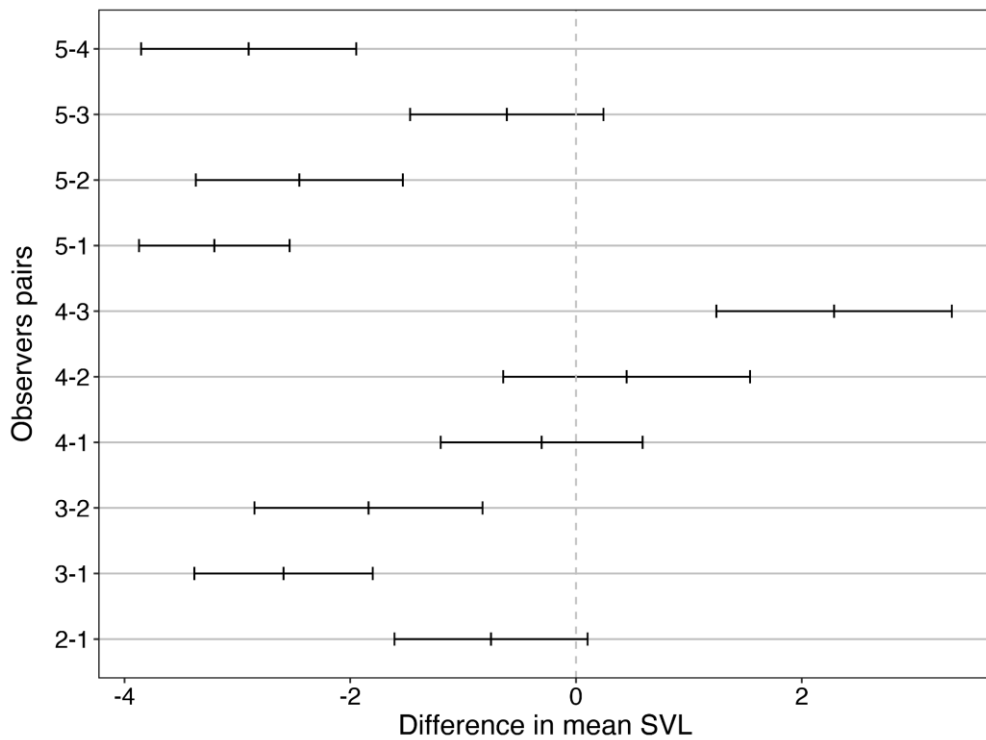
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849 **Appendix**

850 S1. Other analyses

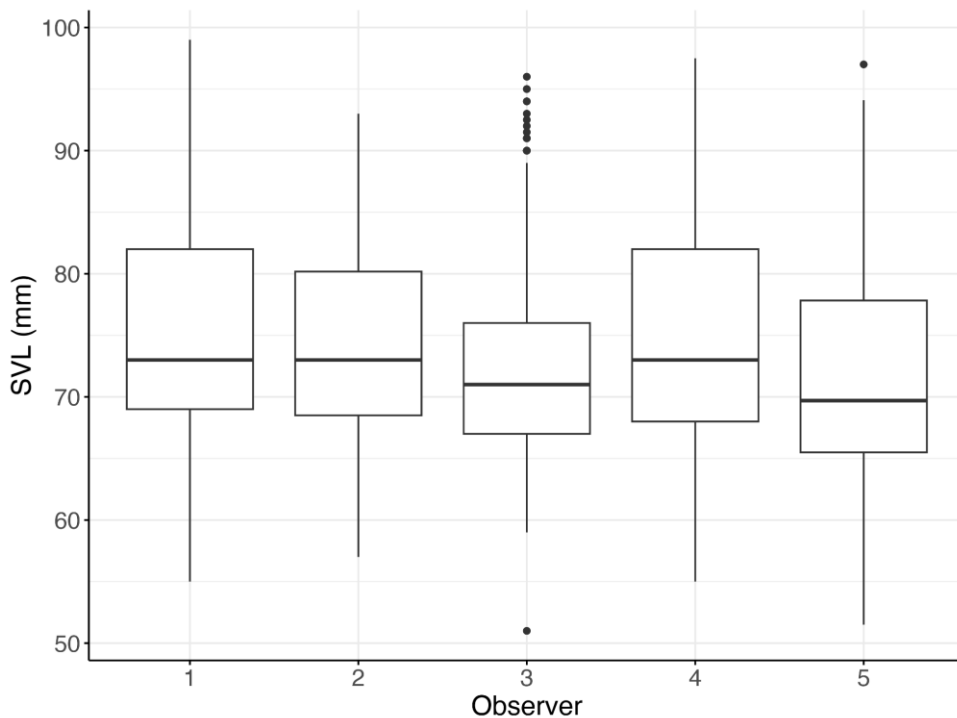
851 Measurer bias

852 This analysis relies on data collected over a study period of almost 30 years (1993-2020), and
853 data have been collected in a standardised way, but by different people. This can cause a
854 measurer bias when it comes to size measurements. To better understand if there is a
855 potentially confounding bias in the size data, we assessed if there were significant differences
856 in the people tasked with data collection over the study period. To do this we ran a Tukey test
857 where we compare the mean value of body size measured by each person with the others
858 (piecewise comparison). The results showed a significant difference in certain cases, but
859 overall the differences were low in terms of absolute values. Indeed, the maximum difference
860 in mean values between two measurers was 3.2 mm, which is approximately 4.5% of the
861 mean body size (Figure S1.1 and S1.2). Differences could also arise for other reasons than
862 measurement bias, such as the population structure. For instance, if more young individuals,
863 or more males than females are showing up at the breeding site in a given year, the mean
864 measured size will be lower than in years with more females and older (and bigger)
865 individuals. For these reasons, we did not include the measurer effect further in the analyses.



866
 867 **Figure S1.1.** Piecewise comparison of the mean differences in measured snout-to-vent length (SVL),
 868 obtained with a Tukey's test. Measurers (i.e. observers) are identified with a number from 1 to 5. If the
 869 difference, accounting for 95% confidence intervals, overlaps zero is not considered significant.

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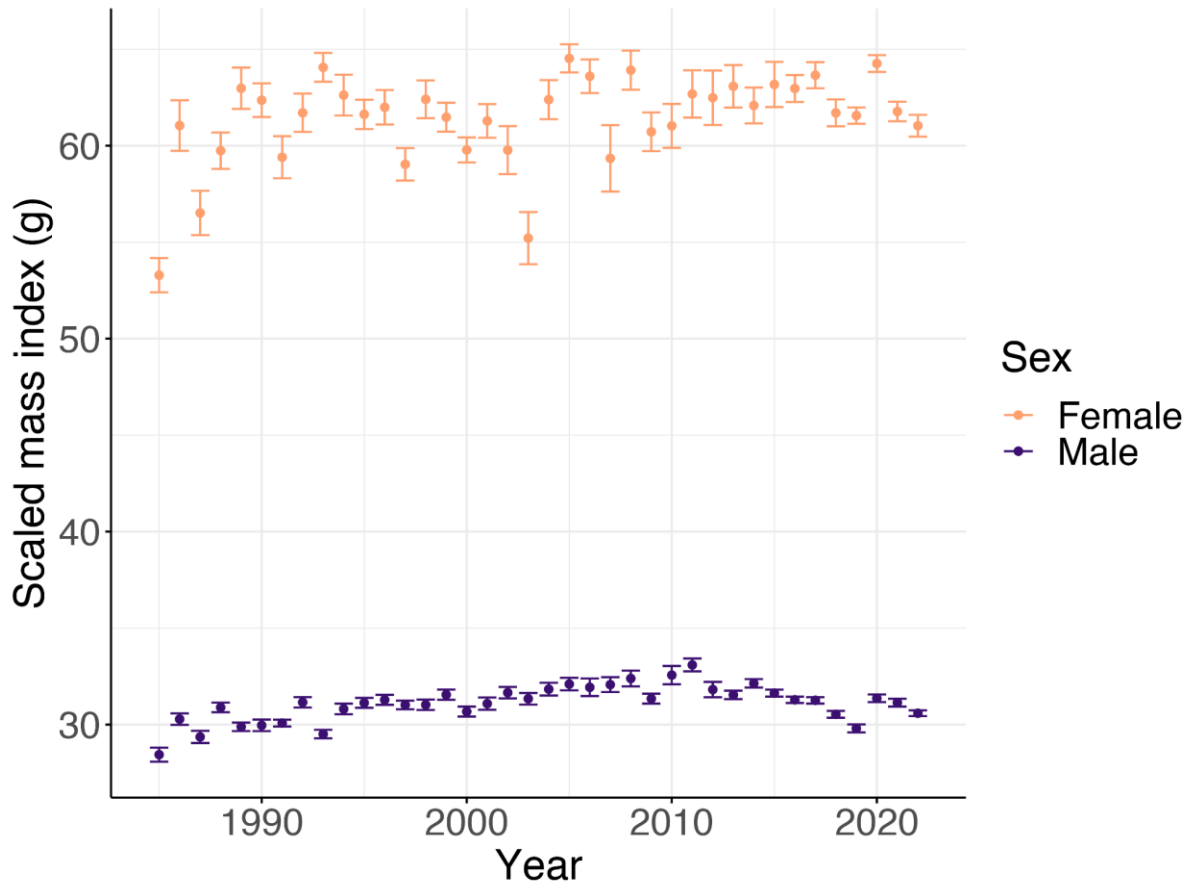
873
 874 **Figure S1.2.** Boxplots showing the range of measured SVL for each measurer (i.e. observer), identified
 875 with numbers going from one to five.

876 Body condition

877 Another interesting concept linked to physiology is the body condition. Body condition is a
878 measure that usually considers both body size and body mass. It is useful to distinguish
879 individuals with similar sizes but that might be in quite different states, for instance due to
880 different levels of fat reserves. Following Moldowan et al. (2022), we calculated for each
881 individual at each capture occasion its body condition, in the form of the scaled mass index
882 (SMI; Peig & Green, 2009). This method consists in calculating a standardised mass relative to
883 the body size in the population (divided by sex), while considering the allometric relationship
884 between size and mass. This measure of body condition was determined to consider
885 accurately the fat reserves in some amphibians (MacCracken & Stebbings, 2012).

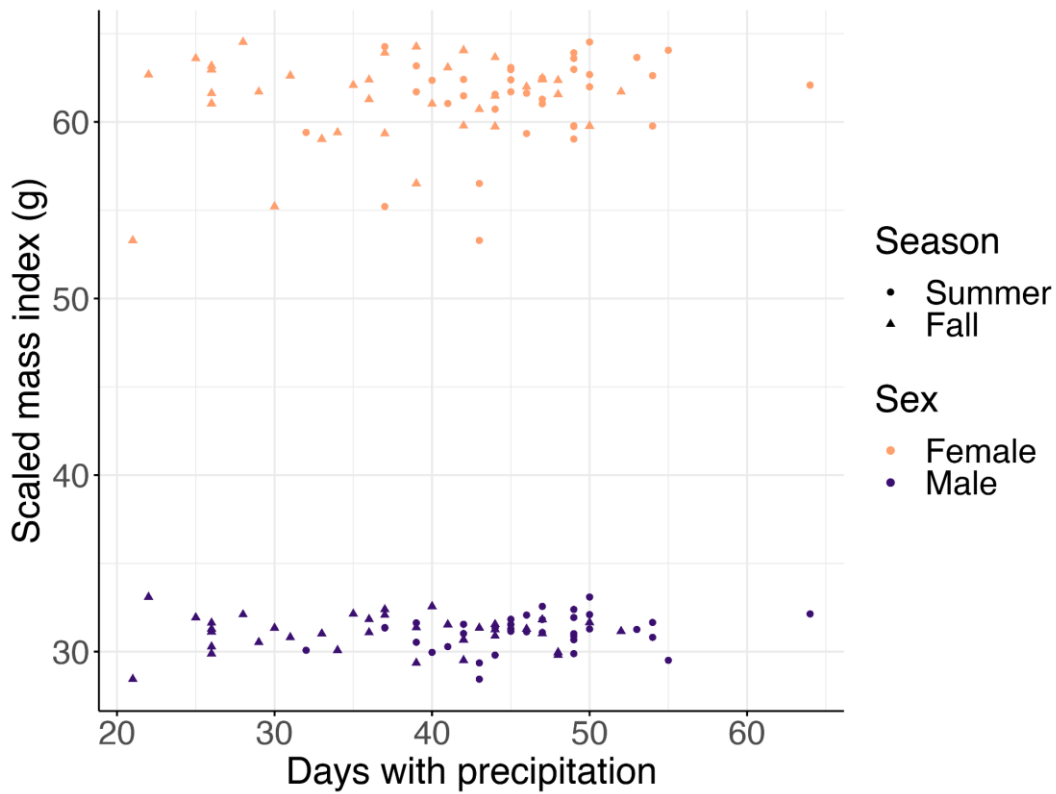
886 Body condition seems to vary little over the study period (1985-2022), especially in males
887 (Figure S1.3). We analysed the relationship between body condition and environmental
888 conditions and population size. We hypothesised higher body condition in the breeding
889 season if the previous active season was long. We also hypothesised a lower body condition
890 the higher the population size. We both inspected visually these relationships and ran linear
891 models. The results suggest that body condition is not correlated with environmental
892 conditions nor population size, at least in breeding adults (Figures S1.4 and S1.5). This might
893 be a further indication that there is a threshold in energetical requirements that must be
894 reached for the toads to go to the breeding site, which is typical of “capital” breeders (Bull &
895 Shine, 1977). If body condition is lower, an individual might skip breeding, if it is higher the
896 individual will migrate to the pond to breed. This might explain the small observed variation
897 in SMI. To corroborate this hypothesis, we focused on females that both bred in consecutive
898 years and bred after skipping breeding the year before. For these females, we compared their
899 SMI in a year where they bred the year before with the SMI in a year where they skipped

900 breeding the previous year. We expected a lower SMI in years following a breeding attempt,
901 as reproduction is energy demanding, especially in such harsh environments (Muths et al.,
902 2013). We observed that there are no meaningful differences (Figure S1.6), further suggesting
903 the presence of a threshold in body condition necessary to attempt breeding.



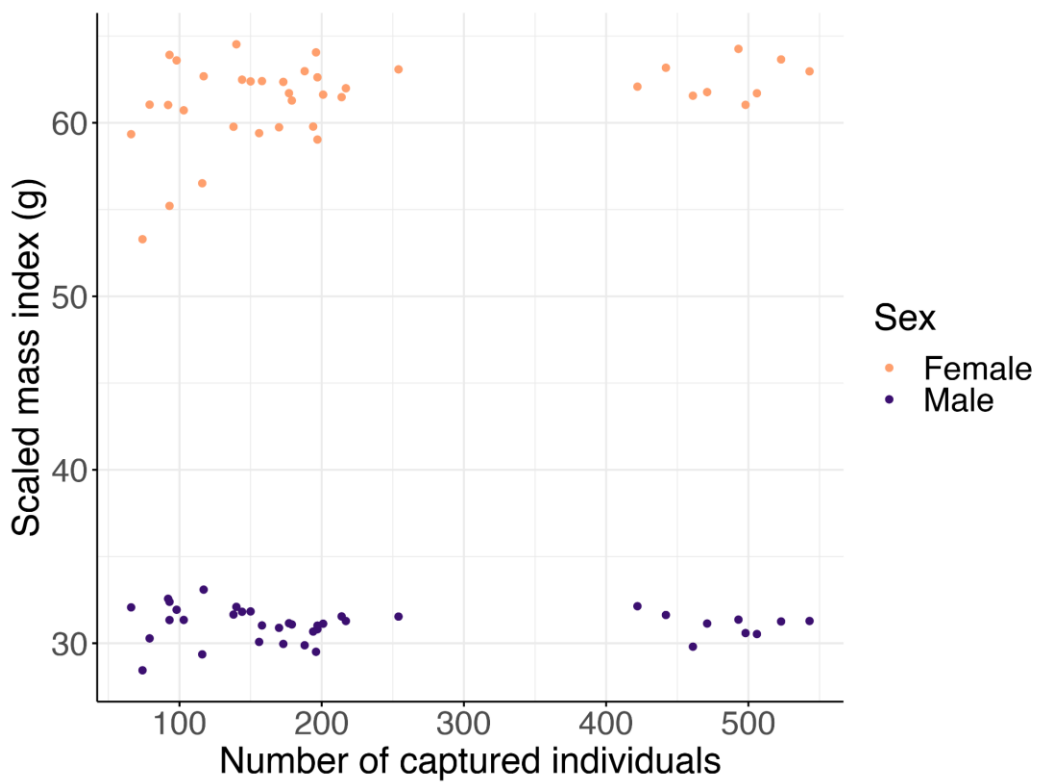
904 **Figure S1.3.** Average scaled mass index (calculated following Peig & Green, 2009) for females (red) and
905 males (blue) over the period 1985-2022.
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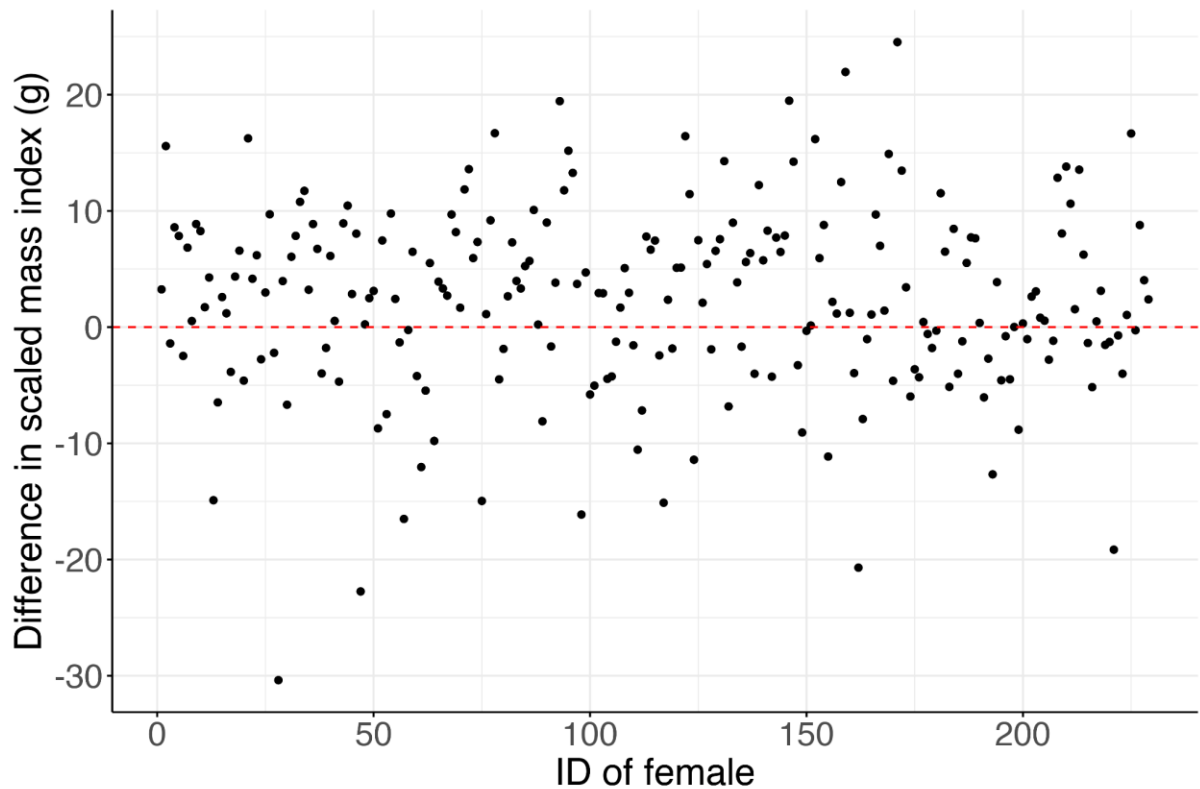
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911 **Figure S1.4.** Relationship between mean scaled index and number of days with precipitation in summer
 912 (green) and autumn (red), for females (circles) and males (triangles).
 913



914

915 **Figure S1.5.** Relationship between the average yearly scaled mass index and the number of captured
 916 individuals during a breeding season (proxy of population size) for males (blue) and females (red).

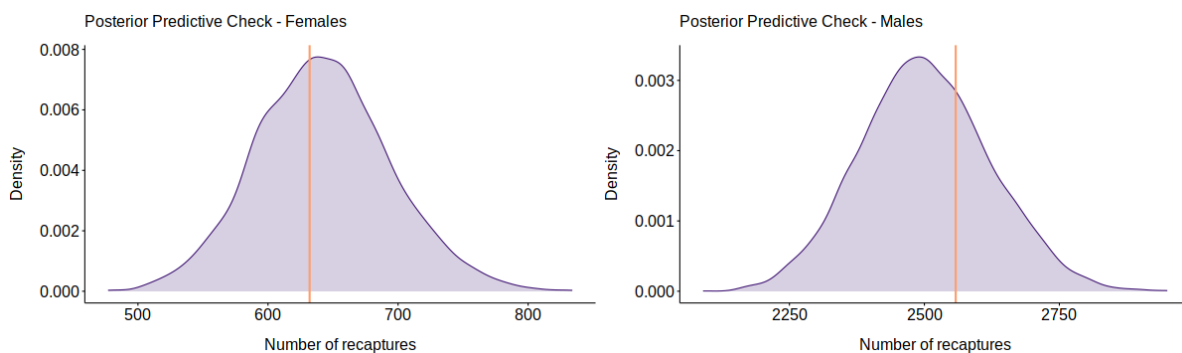


917

918 **Figure S1.6.** For each female we show the difference in scaled mass index between a year which
 919 followed a breeding year and a year which followed a non-breeding year. The horizontal dotted line at
 920 zero represents the case where a female experienced no difference in scaled mass index when
 921 reproducing after either skipping or not skipping reproduction the year before. We expected the
 922 distribution of points to be consistently above the red dotted line, indicating that the scaled mass index
 923 is higher after a year without reproducing, but it is not what we observe. No clear trend is observable,
 924 indicating perhaps that the scaled mass condition (i.e. the body condition) is mainly influenced by other
 925 factors. Moreover, the scaled mass indices we show for females might be in some cases biased by the
 926 individual mass measured during fieldwork, as sometimes the females are caught and measured
 927 before or after laying eggs. Females weighed before they laid eggs will be heavier than when weighed
 928 after they laid eggs.

929 S2. Model diagnostics

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

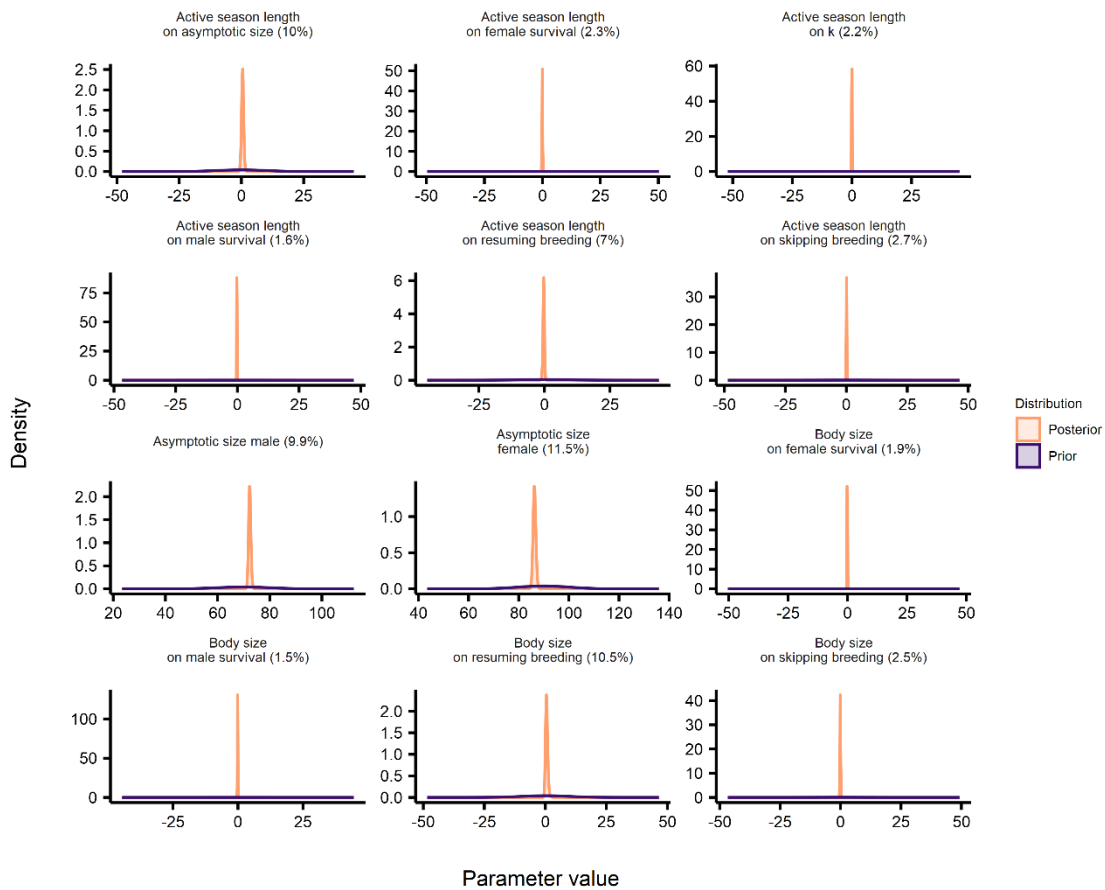


938 **Figure S2.1.** Posterior predictive checks to assess the goodness-of-fit of the capture-mark-recapture
939 models. Following Nater et al. (2020), we chose 500 evenly spaced samples from the posterior
940 distributions of the estimated parameters and used them to simulate 10 replicate capture-history
941 datasets per sample. We then calculated the number of recaptures in each set of capture histories and
942 obtained a distribution of 5000 number of recaptures. On the left we show the distribution of the
943 number of recaptures for females and on the right for males. We then compared the real observed
944 number of recaptures (shown with the orange vertical line) to the rest of the distribution. To have a
945 good fit, the observed number of recaptures should fall in the distribution, and the closer to the median
946 the better. The Bayesian p-value (i.e. the ratio between the number of simulated datasets with a higher
947 number of recaptures than the observed versus the total amount of simulated datasets) was 0.57 for
948 females and 0.31 for males.
949

950 Both models on males and females show a very good fit, validating the assumptions about
951 the same temporal pattern in detection probability and about males always attempting
952 breeding. To evaluate parameter identifiability, we also checked the prior-posterior overlap
953 for all non-derived parameters (Garrett & Zeger, 2000; Gimenez et al., 2009). An overlap of

954 35% or more between prior and posterior distributions results in a weakly-identifiable
 955 parameter. In our case, all overlaps but one were below 35% indicating overall good
 956 identifiability (Figure S2.2). Only Rho , which is the correlation of the year random effects on
 957 asymptotic size a and growth rate k , had a high overlap of 76.3%, hinting that there is no
 958 actual correlation between them.

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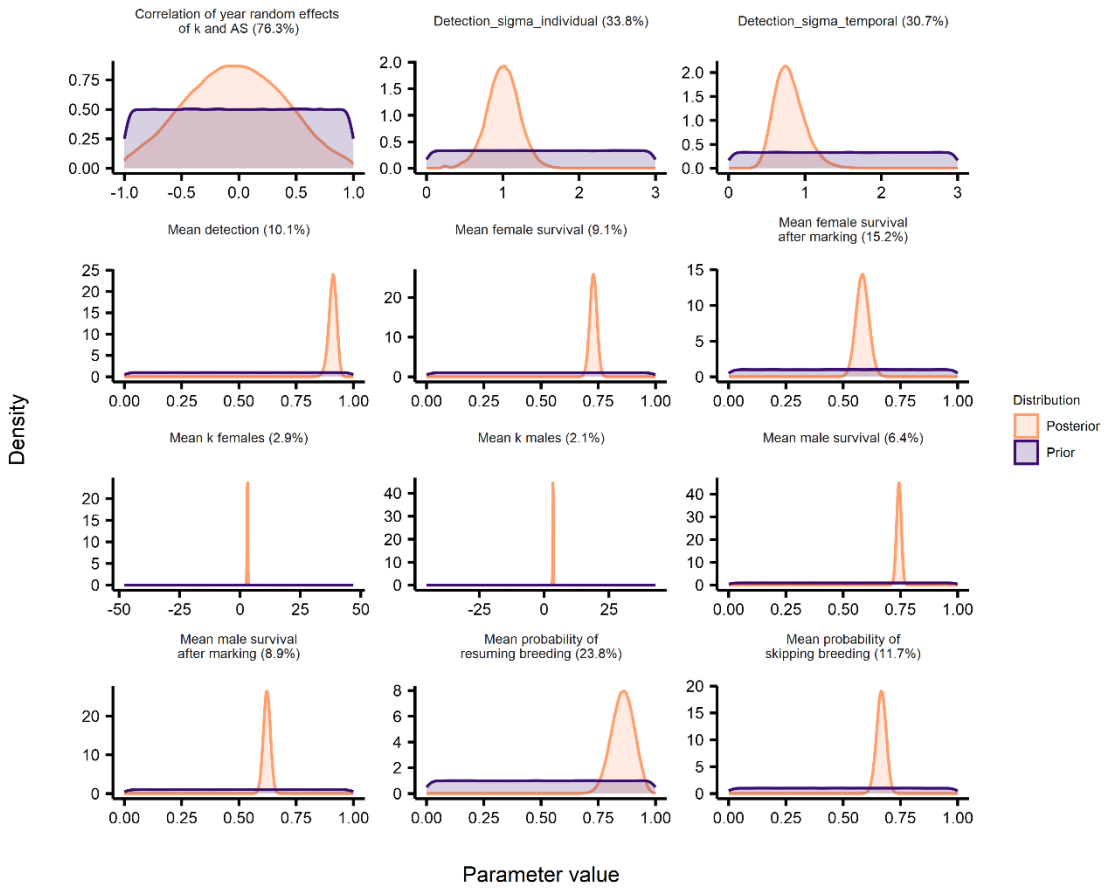
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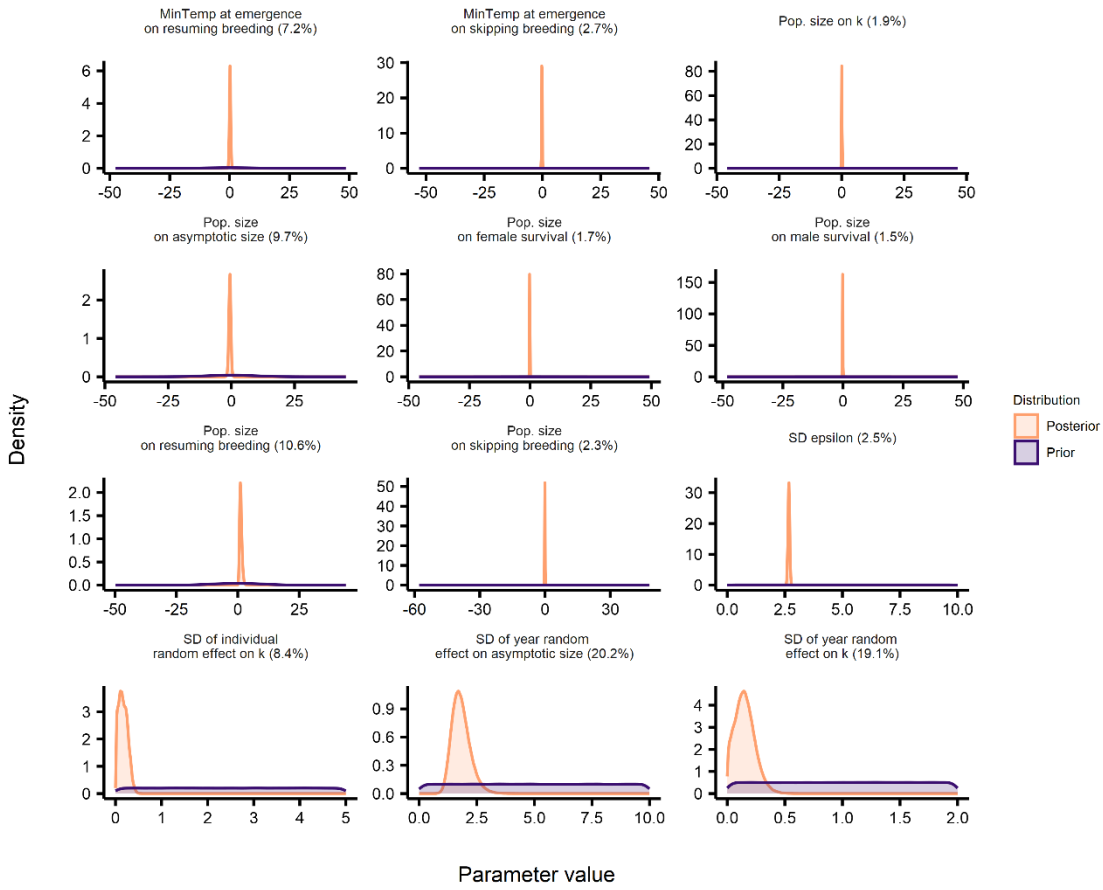
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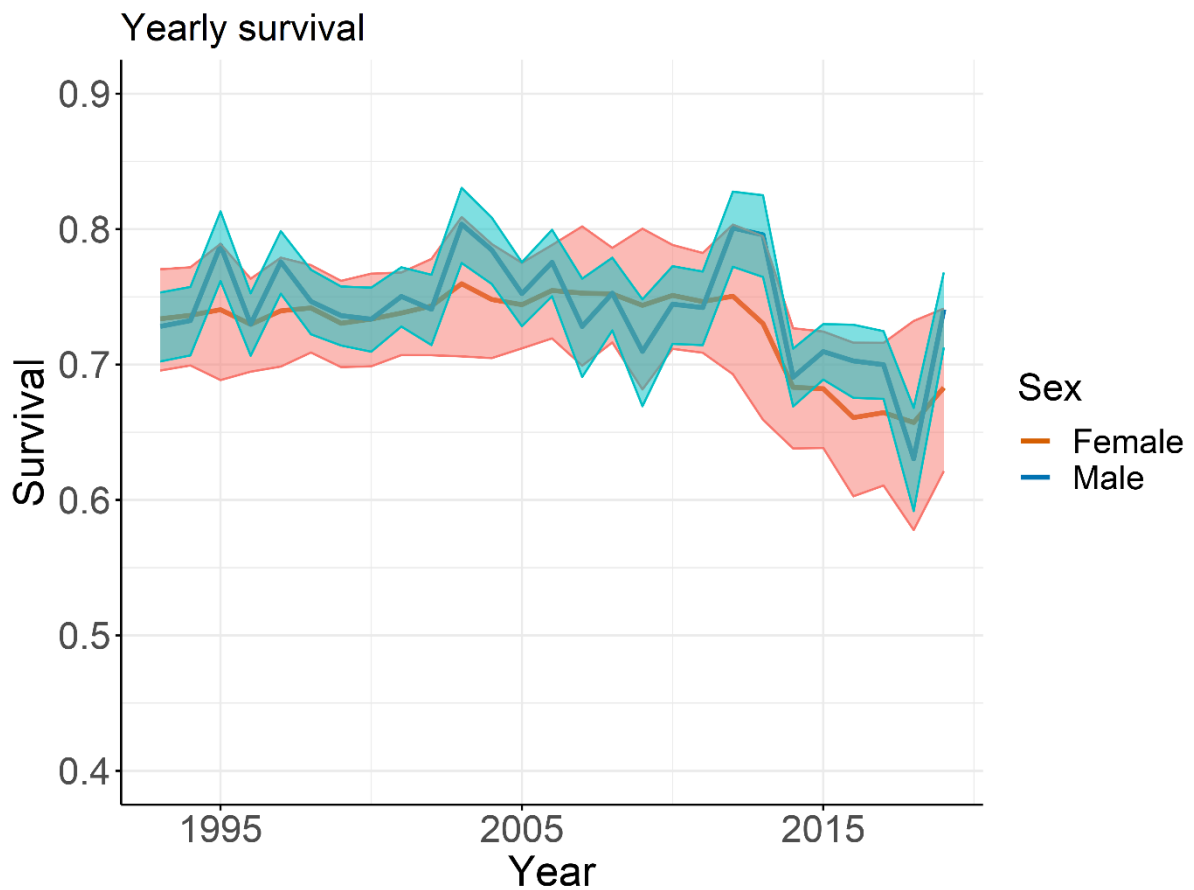


978

979 **Figure S2.2.** Prior-posterior overlap plots. For each of the estimated parameters we plotted prior
 980 (purple) and posterior (orange) distributions. In brackets we put the percentage of overlap of the two
 981 distributions.
 982

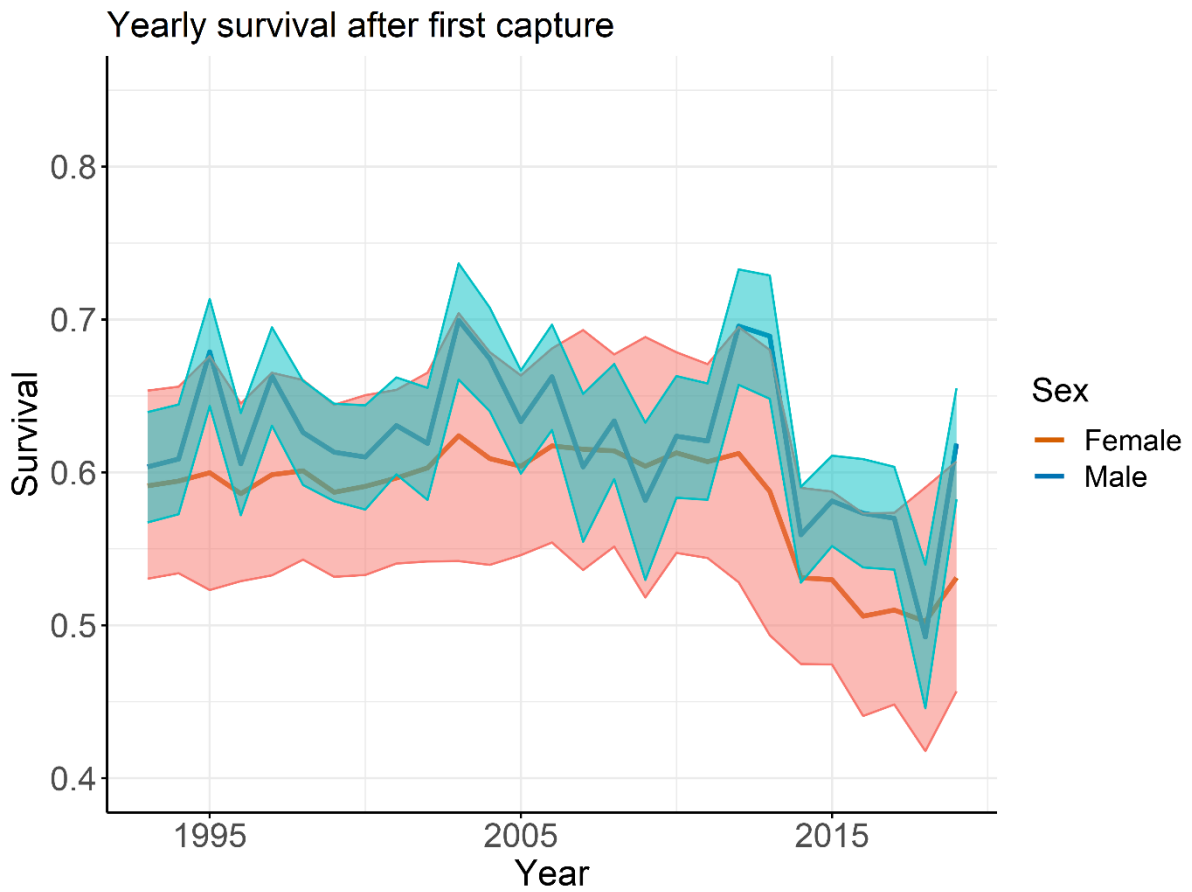
983 S3. Other plots from results

984

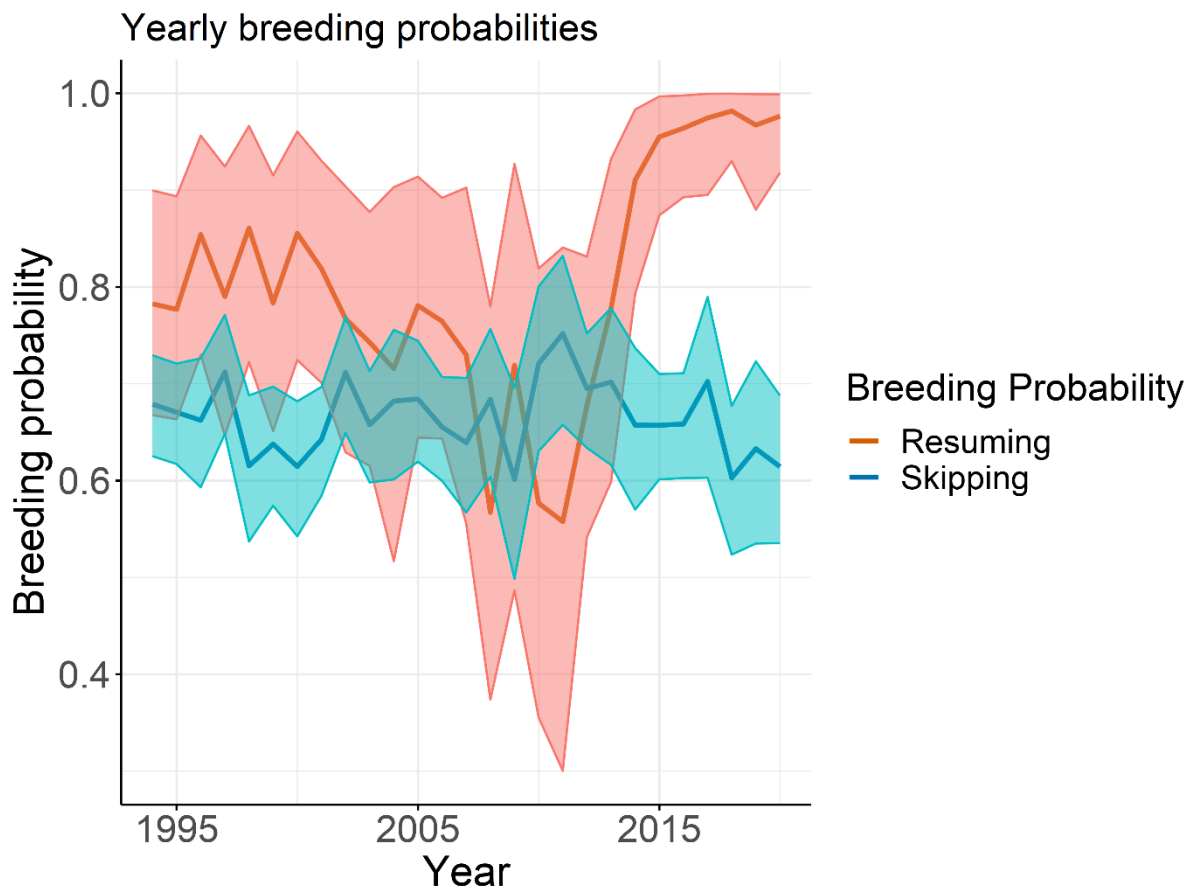


985

986 **Figure S3.1.** Year-specific survival rates for males (blue) and females (red). The solid line represents
987 the average, while the shaded ribbons are the 95% credible intervals, obtained from the posterior
988 distribution. The values are calculated assuming an average body size.



989 **Figure S3.2.** Year-specific survival rates in the year after first capture, for males (blue) and females
 990 (red). The solid line represents the average, while the shaded ribbons are the 95% credible intervals.
 991 The values are calculated assuming an average body size.
 992



993
 994 **Figure S3.3.** Year-specific probability of resuming (red) and skipping breeding (blue). The solid line is
 995 the average, while the shaded ribbons are the 95% credible intervals.

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