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Erdkröten am Limit - Datenanalyse einer alpinen Population

Schlussbericht

Bestell.	110011554 / 8T20/20.0001.PJ/0002
Kredit-Nr.	A200.0001 Globalkredit/ Forschung
Vertrags-Nr.	20.0001.PJ / 46DBED0F1
Kostendach	CHF 336 000,00
Dauer	01.06.2020 - 30.11.2024

Bericht: Dr. Benedikt Schmidt
23. Dezember 2024

Forschungsvertrag betreffend «Erdkröten am Limit – Datenanalyse einer alpinen Population»

Mit dem Forschungsvertrag «Erdkröten am Limit – Datenanalyse einer alpinen Population»[1] hat das BAFU info fauna beauftragt,

- eine Datenanalyse in Form einer Dissertation an der Universität Zürich durchzuführen
- die Feldarbeit an weiterzuführen, so dass weiterhin Daten im Rahmen der Langzeit-Fang-Wiederfang-Studie, welche Grundlage für die Datenanalyse ist, gesammelt werden.

Dieser Schlussbericht hat zwei Teile

- Ein Bericht über die Konsequenzen des Klimawandels für die Amphibien.
- Die Dissertation, welche die Datenanalysen beschreibt. Die Dissertation wurde vom Doktoranden Omar Lenzi geschrieben. Eines der Kapitel ist die Masterarbeit von Daniel Breitenmoser, welche in die Dissertation integriert wurde.

Die Feldarbeit wurde wie im Forschungsvertrag beschrieben fortgesetzt.

Alle Aufgaben gemäss Ziffer 2 des Forschungsvertrags wurden erledigt.

Zwei wissenschaftliche Publikationen sind bereits veröffentlicht. Zwei weitere sind vorgesehen und werden im Lauf des Jahres 2025 zur Veröffentlichung an Fachzeitschriften eingereicht (wie im Zeitplan der Offerte beschrieben).

Über die Finanzen wird in einem separaten Bericht Rechenschaft abgelegt.

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[1] Details zum Vertrag wie Vertragsnummer finden sich auf der Titelseite dieses Berichts.

Abbildung. Ein Foto des Amphibienlaichgewässers nahe der Grossen Scheidegg bei Grindelwald auf 1850 m, wo seit Jahrzehnten eine Fang-Wiederfang-Studie an der Erdkröte durchgeführt wird. Foto: Benedikt Schmidt.

Teil 1

Bericht über die Konsequenzen des Klimawandels für die Amphibien

Konsequenzen des Klimawandels auf die Amphibien

Der Klimawandel verändert die Umwelt, in welcher die Amphibien leben. Arten, die an die aktuellen Bedingungen angepasst sind, werden sich auf die eine oder andere Art reagieren müssen. Es gibt grundsätzlich drei mögliche Reaktionen. Eine Art kann sich anpassen und am jetzigen Ort weiter leben, eine Art kann wandern und neue Lebensräume besiedeln oder die Art stirbt aus - die aus Sicht des Naturschutzes schlechteste Reaktion. Eine Auswertung der Reaktionen von Arten auf frühere Veränderungen im Klima zeigt, dass alle drei Reaktionen möglich sind (Nogués-Bravo et al. 2018).

Prognosen, wie sich der Klimawandel auf die einheimischen Amphibien auswirken wird, sind schwierig. Die einfache Tatsache, dass es im Durchschnitt wärmer wird, ist per se noch kein Grund zur Sorge. Im Mittelmeergebiet leben beispielsweise viele Amphibien. Die Frage ist bloss, ob unsere heimischen Arten den Wechsel in ein anderes Klima schaffen.

Es ist aber ein Fakt, dass die Wissenschaft den Klimawandel als grosses Problem für die Amphibien ansieht. Im zweiten „Global Amphibian Assessment“ der IUCN ist der Klimawandel einer der Bedrohungsfaktoren, welche enorm an Bedeutung gewonnen haben. Luedtke et al. (2023) schreiben: „Ongoing and projected climate change effects are now of increasing concern, driving 39% of status deteriorations since 2004, followed by habitat loss (37%).“[2] Urban (2024) hat 485 Studien und mehr als 5 Millionen Prognosen ausgewertet, um eine quantitative globale Bewertung des Artensterbens durch den Klimawandel zu erstellen. Er kommt zum Schluss, dass die Amphibien eine besonders vom Klimawandel betroffene Artengruppe sind, da besonders viele durch den Klimawandel aussterbende Arten zu erwarten sind. Begründet wird das wie folgt: «Amphibians might be vulnerable to climate change given their biphasic life histories, low dispersal abilities, endangerment from other threats, sensitivity to weather, and association with freshwater ecosystems characterized by high climate risks.”[3] Walls et al. (2013) beschreiben zahlreiche Beispiele, wie sich der Klimawandel und Wetterextreme auf Populationen von Amphibien ausgewirkt haben und sich noch auswirken könnten.

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[2] Deepl-Übersetzung: «Die anhaltenden und prognostizierten Auswirkungen des Klimawandels geben zunehmend Anlass zur Sorge und sind für 39 % der Verschlechterungen des Zustands seit 2004 verantwortlich, gefolgt vom Verlust von Lebensräumen (37 %).»

[3] Deepl-Übersetzung: „Amphibien könnten aufgrund ihres zweiphasigen Lebenszyklus, ihrer geringen Ausbreitungsfähigkeit, ihrer Gefährdung durch andere Bedrohungen, ihrer Wetterempfindlichkeit und ihrer Verbindung mit Süßwasserökosystemen, die durch hohe Klimarisiken gekennzeichnet sind, anfällig für den Klimawandel sein. »

Welche Auswirkungen kann der Klimawandel auf Amphibien haben?

Nahezu jeder Aspekt des Lebens der Amphibien ist von der Temperatur abhängig. Wenn sich durch den Klimawandel Temperaturen, aber auch die Verfügbarkeit von Wasser, ändern, dann kann das eine Vielzahl von Wirkungen auf Amphibien haben. Der Klimawandel kann Individuen beeinflussen, deren Verhalten und Phänologie, aber auch die Demographie und Dynamik von Populationen und letztlich die Verbreitung von Arten. Der Klimawandel kann aber auch Interaktionen mit anderen Arten, vor allem Pathogenen beeinflussen. Der Klimawandel kann aber auch die Lebensräume beeinflussen. Diese Aspekte sollen hier beispielhaft beschrieben werden. Weitere Informationen zum Thema finden sich in diversen Übersichtsartikeln und -zusammenstellungen (z.B., Blaustein et al. 2010, Li et al. 2013, Walls et al. 2013, Steigerwald 2021). Die Komplexität der Beziehung zwischen Klima, Wetter, Demographie und Populationsdynamik beschreibt Schmidt (2016) am Beispiel der Gelbbauchunke.

Temperatur, und daher auch der Klimawandel beeinflussen Amphibien. Reading konnte beispielsweise zeigen, dass der Konditionsindex von Weibchen der Erdkröte (*Bufo bufo*) zwischen 1983 und 2005 stark gesunken ist. Der Konditionsindex hängt von der Temperatur ab und diese ist im Untersuchungsgebiet von Reading (2007) angestiegen. Der Konditionsindex korrelierte mit der jährlichen Überlebenswahrscheinlichkeit der Weibchen: Je höher die Temperatur war, desto tiefer der Konditionsindex und desto tiefer die Überlebenswahrscheinlichkeit. Bei den Wasserfröschen der Gattung *Pelophylax* ist es genau umgekehrt: Bei diesen Fröschen ist die Überlebenswahrscheinlichkeit in kalten Wintern tief und in milden Wintern hoch (Anholt et al. 2003).

Die Temperatur beeinflusst aber nicht nur die adulten Amphibien, sondern auch die Kaulquappen. Je kälter die Wassertemperatur, desto langsamer die Entwicklung. Das kann den Zeitpunkt der Metamorphose beeinflussen und somit auch, wieviel Zeit die Jungtiere noch haben, um vor der ersten Überwinterung noch zu wachsen und Reserven anzulegen (Reading 2010, Reading & Jofré 2023).

Der Klimawandel beeinflusst die Phänologie von Amphibien, denn der Zeitpunkt der Wanderung zum Laichgewässer ist unter anderem von der Temperatur gesteuert. Bei vielen Arten konnte gezeigt werden, dass sie heute früher laichen (z.B., Beebee 1995). Die Kaulquappen entwickeln sich langsamer, wenn früh gelaicht wird, aber dennoch erreichen sie die Metamorphose früher als bei einem späten Laichzeitpunkt (Reading 2003). Das frühe Laichen birgt aber auch Risiken, denn beim Grasfrosch (*Rana temporaria*) ist der Laich dann vermehrt Frost ausgesetzt, was zu Mortalität bei den Embryonen führt (Bison et al. 2023). Mit den Daten zum Grasfrosch in England haben Phillimore et al. (2010) interessante Analysen zur Phänologie gemacht. Sie zeigen, dass der Zeitpunkt des Laichgeschäfts beim Grasfrosch von der Frühlingstemperatur abhängt, aber auch, dass es lokale genetische Anpassung an den Zeitpunkt des Laichgeschäfts gibt. Phillimore et al. (2010) prognostizieren dann, dass sich der

Laichzeitpunkt um 21-39 Tage nach früher verschieben müsste, wenn der Klimawandel ungebremst weiter geht. Weil der Laichzeitpunkt aber auch genetisch gesteuert ist, können die Frösche den Laichzeitpunkt aber nur um 5-9 Tage vorverschieben. Damit eine grössere Vorverschiebung möglich ist, würde es eine mikroevolutionäre Änderung bei der genetischen Bestimmung des Laichzeitpunkts brauchen.

Wie oben beschrieben konnte Reading (2007) zeigen, dass die jährlichen Überlebenswahrscheinlichkeit der Weibchen der Erdkröte vom Konditionsindex und somit indirekt von der Temperatur abhängt. Da die Temperatur gestiegen ist, ist die Überlebenswahrscheinlichkeit in der von Reading (2007) untersuchten Population gesunken.

Temperatur aber auch die Verfügbarkeit von Wasser (Niederschlag), aber auch grossräumige Wetterphänomene wie die «North Atlantic Oscillation» (NAO) beeinflussen die Demographie (einerseits die Überlebenswahrscheinlichkeit der Adulttiere, aber auch die Rekrutierung von neuen jungen Adulttieren) von Amphibienpopulationen in mannigfaltiger Art und Weise. Oft, und das ist wichtig, gibt es grosse Unterschiede innerhalb einer Art zwischen Populationen. Cayuela et al. (2017) untersuchten die Wirkung des NAO auf den Kammmolch (*Triturus cristatus*). Bei drei von vier Populationen war der NAO negativ mit der jährlichen Überlebenswahrscheinlichkeit korreliert (ein hoher NAO-Wert bedeutet warmes und trockenes Wetter, während ein tiefer NAO-Wert kaltes und feuchtes Wetter bedeutet). Bei der vierten Population war die Korrelation jedoch positiv. Die Rekrutierung war in drei Populationen positiv vom NAO beeinflusst während der NAO in der vierten Population keine Rolle für die Rekrutierung spielte. Grosse Unterschiede zwischen Arten und Populationen einer Art im Zusammenhang zwischen Klima und Demographie (wiederum Überlebenswahrscheinlichkeit und Rekrutierung) konnten auch Muths et al. (2018) nachweisen.

Es ist oft nicht klar, wieso Populationen der gleichen Art unterschiedlich auf die gleichen Wetterbedingungen reagieren. Es scheint aber so zu sein, die lokalen klimatischen Bedingungen mitbestimmen, wie eine Population auf eine Veränderung reagiert (Amburgey et al. 2018). Beispielsweise ist es so, dass für Populationen des nordamerikanischen Frosches *Rana sylvatica* ein Populationswachstum prognostiert wird, wenn es feuchter wird – dies aber nur in eher kühlen Regionen des Verbreitungsgebiets der Art. In wärmeren Gefilden ist eine negative Reaktion der Population zu erwarten. Ebenso reagierten die Populationen auf Hitzewellen negativ in warmen Gegenden während in kühleren Gegenden die Populationen positiv reagierten. Miller et al. (2018) haben ähnliche Zusammenhänge gezeigt, allerdings mit Daten zur Verbreitung von Arten und nicht wie Amburgey et al. (2018) mit Daten zur Populationsgrösse.

Der Klimawandel wird auch die Verbreitung von Arten beeinflussen. Wenn es wärmer wird, kann es sein, dass eher warme Bereiche des Verbreitungsgebiets einer Art zu warm und somit als Lebensraum ungeeignet werden; die kann zu einer Fragmentierung des Verbreitungsgebiets führen (Teixeira & Arntzen 2002). Ob der Klimawandel zu einer Verkleinerung des Verbreitungsgebiets führt, hängt davon ab, wie der Zusammenhang zwischen dem Vorkommen einer Art und der Klimavariable aussieht. Gibt es ein Optimum (es darf nicht zu warm und nicht zu kalt sein), dann verlieren Arten, sonst gewinnen sie (Kafash et al. 2018). Bei Arten, die Gebirge bewohnen, geht man davon aus, dass sie mit dem Klimawandel höhere Lagen besiedeln; diese Entwicklung kann auch beobachtet werden (Vitasse et al. 2021). Dies gilt in der Schweiz auch beim Alpensalamander. Diese Art hat aber auch eine zweite Möglichkeit: Sie wandert nicht höher, sondern auf die nordexponierte Seite der Berge (Feldmeier et al. 2020). Durch den Klimawandel ausgelöste Bestandesverluste wurden aus Italien beschrieben. Diet Studie aus Italien zeigte, dass zahlreiche Amphibienpopulationen erloschen sind und dass die Verluste neben der Landschaftsveränderung auch durch den Klimawandel erklärt werden können. Die Bestandesverluste waren dort besonders stark, wo sich die Jahresmitteltemperatur und/oder die Anzahl trockener Tage erhöht und die Regenmenge verringert hatte (D'Amen & Bombi 2009).

Der Klimawandel hat auch die Zusammensetzung von Artengemeinschaften verändern. Beispielsweise hängt die Zusammensetzung von Mischpopulationen von Wasserfröschen (Pelophylax sp.) von der Wassertemperatur ab. Bei höheren Temperaturen ist der Anteil des Hybrid *Pelophylax esculentus* kleiner (Negovetic et al. 2021). Somit könnten durch den Klimawandel erhöhte Wassertemperaturen dazu führen, dass der Anteil der *Pelophylax esculentus* noch kleiner wird.

Die wichtigste Interaktion zwischen Arten, welche der Klimawandel verändern kann, sich Interaktionen mit Parasiten und Pathogenen. Das Zusammenleben mit Krankheitserregern hängt immer auch von der Umwelt ab und da oft von der Temperatur. Denkbar ist also, dass Krankheitserreger sich ausbreiten können und virulenter werden (Walker et al. 2010, Clare et al. 2016).

Manche Resultate zur Wirkung des Klimawandels auf Amphibien (Individuen und Populationen) können als widersprüchlich gesehen werden. Individuen scheinen stärker auf die Bedingungen im Winter zu reagieren während Population erlöschen, wenn die Sommer zu trocken sind Es muss kein Widerspruch sein, sondern zeigt wohl eher die relative Bedeutung von Fortpflanzung und Überleben der Adulttiere für den Fortbestand der Populationen. Wenn die Fortpflanzung ausfällt, scheint das schneller zum Erlöschen von Populationen zu führen als wenn die Mortalität der Adulttiere erhöht ist.

Der Aspekt der durch den Klimawandel ausgelösten Trockenheit muss betont werden. Es gibt Studien, welche belegen, dass wegen des Klimawandels Laichgewässer austrocknen und sich Amphibienpopulationen nicht mehr fortpflanzen können (z.B. im Yellowstone Nationalpark in den USA; McMenamin et al. 2008).

Es dürften unberechenbare Ereignisse sein, welche potenziell die stärksten negativen Auswirkungen haben dürften. Ein Monat ohne Regen oder eine Hitzewelle sind dann besonders gefährlich, wenn die frisch metamorphosierten Amphibien das Gewässer verlassen. Die kleinen Amphibien von der Austrocknung besonders gefährdet. Es ist aber schwierig vorherzusagen, wie sich Extremereignisse verändern werden. Das ist mit ein Grund, warum Prognosen über das Schicksal der Amphibien im Klimawandel schwierig mit Unsicherheiten behaftet sind (Schmidt 2019).

Welche Massnahmen gegen die negativen Auswirkungen des Klimawandels sind denkbar?

Da der Klimawandel negative Auswirkungen auf Amphibien haben kann, braucht es Massnahmen zum Schutz der Amphibien vor dieser Bedrohung, die bisher im Amphibienschutz kaum beachtet wurde. Dementsprechend ist die Liste der Massnahmen kurz und basieren auf die Ausführungen in Schmidt (2019).

Direkte Massnahmen gegen den Klimawandel gibt es keine. Die hier vorgeschlagenen Massnahmen dienen dazu, die Widerstandsfähigkeit der Amphibienpopulationen generell zu erhöhen. Widerstandsfähigkeit braucht es in erster Linie gegen extremes Wetter wie Hitzewellen und lange Trockenheit. Beides wird in der Schweiz zunehmen. Interessanterweise werden auch Starkregenereignisse häufiger, so dass das Problem der Überschwemmungen hinzu kommt (Scherrer et al. 2016).

Wie soll man damit umgehen, dass die Wirkungen des Klimawandels mit Unsicherheiten behaftet sind und dass auch nicht mit Sicherheit bekannt ist, wie welche Massnahme wirkt? Wie geht man mit solchen Unwägbarkeiten und Risiken um? In der Finanzwelt wird bei Unsicherheiten das Portfolio diversifiziert. Das ist auch im Amphibienschutz, und generell im Naturschutz, notwendig. Die ganze Bandbreite der jetzigen Vielfalt muss erhalten werden, konkret also Populationen an klimatisch unterschiedlichen Standorten. Die Erhaltung der innerartlichen Diversität dürfte ein Schlüssel zum Fortbestand der Arten sein (Schmidt 2019). Diversität sollte aber auch bei den Lebensraumtypen erhalten werden. Auch die Heterogenität der Lebensräume kann als Puffer gegen den Klimawandel dienen. Dies insbesondere im Alpenraum, wo die mikroklimatische Heterogenität sehr gross ist (Scherrer & Körner 2011). Es ist also auch wichtig, eine Vielfalt an unterschiedlichen Lebensräumen zu erhalten.

Amphibien gehören zu den Bewohnern der Feuchtgebiete und sind auf Wasser angewiesen. Wenn man bedenkt, dass ein Fünftel der landwirtschaftlichen Nutzfläche und auch viele Wälder drainiert sind, so wäre es sinnvoll, eine Wiedervernässung zuzulassen. Das dient den Amphibien, aber es wäre generell sinnvoll, wenn die Fähigkeit unserer Böden, Wasser zu speichern, wieder gestärkt würde (z.B. als „Schwamm“, der als Schutz vor Starkregen dient). Das Schwammlandkonzept bietet zahlreiche Hinweise, wie man eine Landschaft gestalten kann, in der das Wasser zurückbehalten wird (Werdenberg et al. 2023). Das Schwammlandkonzept bringt viele Vorteile, auch für Amphibien und deren aquatische und terrestrische Lebensräume. So würde beispielsweise die Wiedervernässung von Wäldern Schwammlandfunktionen übernehmen, aber auch die Qualität des Landlebensraums für die terrestrischen Lebensstadien der Amphibien verbessern. Bei den aquatischen Lebensräumen ist der Biber eine Art, welche für die Amphibien sehr wichtig ist, denn Biberlebensräume sind sehr gute Lebensräume für Amphibien.

Die Laichgewässer sind im Amphibienschutz zentral. Wie können Weiher aussehen, die auch in einem anderen Klima funktionieren? Trockenheit kann dazu führen, dass Gewässer und Feuchtgebiete austrocknen. Bei Weihern mit einer künstlichen Abdichtung, heutzutage meist eine Kautschukfolie, können eine Lösung sein. Weiher mit Abdichtung sind unabhängig vom Grundwasser und dessen Schwankungen. Abgedichtete Weiher können so tief angelegt werden, dass sie auch bei längeren Trockenphasen nicht austrocknen bzw. nicht zu früh im Jahr austrocknen. Da aber das Austrocknen eines Weihers für Amphibien gut ist (Schmidt et al. 2015), können Weiher mit einem Ablass ausgerüstet werden. So kann die Wasserführung gesteuert werden, wie im Mittelalter bei den Karpfenteichen. Shoo et al. (2011) schlagen ebenfalls vor, eine Vielfalt von Gewässertypen zu erhalten und wo nötig zu schaffen, darunter auch solche, deren Wasserstand gesteuert werden kann.

Neuere Konzepte beim Weiherbau wie die „étangs agroécologiques“, die im Park Jura Vaudois angelegt wurden (Pellet et al. 2023), sind für die Zukunft vielversprechend. Diese Weiher dienen einerseits als Lebensraum für die aquatische Biodiversität, aber auch zur Bewässerung in der Landwirtschaft. Durch diese Doppelfunktion entsteht eine win-win-Situation für Biodiversität und Landwirtschaft; letztere wird in Zukunft ebenfalls mehr auf Wasser angewiesen sein.

Unabhängig von der Art der angelegten Gewässer ist ein dichtes Netz unterschiedlicher Gewässertypen wichtig, um die Widerstandsfähigkeit der Amphibienpopulationen auf Landschaftsebene zu erhöhen. Dazu braucht es aber viel mehr Amphibienlaichgewässer als heute, und diese sollten aus mehreren Gewässern bestehen, die zusammen eine grosse Wasserfläche haben (Siffert et al. 2022, Moor et al. 2024). In einem funktionierenden Netzwerk von Populationen in einer Landschaft kann eine Population klimabedingt erlöschen, aber der Standort kann durch Individuen aus benachbarten Populationen wieder besiedelt werden.

Im Zusammenhang mit dem Klimawandel mag es überraschen, dass der Schwerpunkt bei den Massnahmen auf den Lebensräumen liegt. Es liegt jedoch auf der Hand, dass qualitativ hochwertige aquatische und terrestrische Lebensräume für den Amphibienschutz in einem wärmeren und extremeren Klima von entscheidender Bedeutung sind. Zahlreiche Studien und die Erfahrung zeigt uns, dass der Bau von Amphibienlaichgebieten eine wirksame Massnahme zum Erhalt und zur Förderung von Amphibienpopulationen sind; dies auch in einer Landschaft, in der zahlreiche Stressfaktoren negativ auf die Amphibien einwirken (z.B. Moor et al. 2022). Selbstverständlich sind auch andere Schutzmassnahmen, wie in der Schweiz von info fauna karch beschrieben und dokumentiert, sinnvoll um Verluste von Individuen zu reduzieren (z.B. Amphibienschutz an Verkehrswegen).

Andere Ansätze als Lebensraumschutz sind denkbar, aber weder konzeptionell noch praktisch entwickelt. In der Forstwirtschaft wird der Wald unter anderem dadurch klimatauglich gemacht, indem klimaresistente Sorten angepflanzt werden. Bei Amphibien ist bekannt, dass sie ans lokale Klima angepasst sein können. Es gibt also eine Vielzahl von Genotypen, die potenziell an neue Orte gebracht werden könnten. Sinnvoller erscheint aber, durch Lebensraumvielfalt die innerartliche genetische Vielfalt zu erhalten, so dass natürliche Prozesse der Anpassung an den Klimawandel stattfinden können.

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Teil 2

Dissertation

Toads at the Elevational Limit - Analysis of a Long-Term Demographic Study of a High-Elevation Amphibian Population

Dissertation

zur
Erlangung der naturwissenschaftlichen Doktorwürde (Dr. sc. nat.)

vorgelegt der Mathematisch-naturwissenschaftlichen Fakultät der
Universität Zürich

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Zürich, 2025

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Summary

The ultimate goal of population ecology is to understand, explain, and predict the dynamics of populations. These dynamics are the outcome of the current population size and processes such as survival, reproduction, and migration in and out of the population. It is thus crucial to understand how these processes act and how they are influenced by extrinsic factors, such as environmental conditions, and intrinsic ones (i.e., of the population) such as density, to accurately determine the state of a population. Studying population dynamics is particularly important in understudied taxa or habitats to provide an important contribution to the scientific literature and help filling knowledge gaps. It can also be critical for elaborating conservation and management measures. Hence, this thesis focuses primarily on the effects of the environment and density on various aspects of the demography of an alpine population of an amphibian species (common toad; *Bufo bufo*), an understudied taxon in an understudied habitat, where in particular environmental conditions are expected to have a significant impact.

In **Chapter 1**, to understand how the environment influences one key aspect of this population, I analysed the changes in the breeding phenology, and assessed the main determinants of these changes. Using piecewise regression models and principal component analysis I found that warm temperatures and reduced snow cover in winter and spring, as well as low spring precipitation were all associated with earlier breeding, while the lunar cycle had no effect. The resulting breeding phenology pattern shows an advancement towards earlier breeding dates at the start of the study period (1980s) followed by stabilisation, although with increased year-to-year variation. Overall, breeding occurs on average a month earlier than at the start of the study period. Moreover, we found low repeatability of the arrival date over an individual’s lifetime, indicating that the act of moving to the breeding site is mainly due to external (i.e., environmental) factors rather than genetics.

In **Chapter 2**, I was interested in gaining insight into vital rates and assess how they can be affected directly or indirectly (i.e., mediated by individual traits) by extrinsic factors (environmental conditions) or intrinsic ones (density). To investigate this question, I estimated survival and breeding probability while accounting for the direct and indirect (body-size-mediated) effects of environment and population density on these vital rates. To do this, I used individual capture-mark-recapture data as well as

individual body-size measurements, and coupled a capture-mark-recapture model with a von Bertalanffy growth model in a Bayesian framework. The main findings show that density dependence is acting on adult survival, which has rarely, if ever, been showed in natural amphibian populations. Moreover, I confirmed the presence of a quite regular biennial breeding cycle (i.e., intermittent breeding) in females, which probably arises due to the interplay between high costs of breeding in females and harsh conditions reducing the energy intake. On the other hand, intermittent breeding essentially does not occur in males. I also found possible indirect (trait-mediated) effects. For instance, the negative association between population density and body size could buffer the negative effect of body size on survival at high densities. Overall, this chapter shows the complexity of the relationships at play and underlines the importance of comprehensive approaches in producing accurate estimates of vital rates, with potentially significant consequences on conservation and management decisions.

Chapter 3, conducted by a master student that I supervised, focused on the mating system and in particular on the drivers of successful mating in males. Due to intermittent breeding and older age at sexual maturity in females, the study population shows in fact a highly male-skewed operational sex ratio at the breeding site, meaning that not all males can successfully breed. Access to breeding is obviously key to achieve high fitness, and therefore it is a very important aspect in ecological studies. Moreover, such studies are usually conducted in an experimental setting rather than on natural populations, thus limiting our full understanding of this topic. We analysed the patterns of breeding behaviour, assessing in particular the roles of body size and age in the probability of a toad attempting breeding. We show that, as expected from experimental studies, body size is an important factor in determining successful breeding attempts (i.e., entering amplexus) and resisting displacement from other males, while there are only weak indications of size-assortative mating. Moreover, we show that older males might be less performant than younger ones, possibly due to a senescence effect. Finally, by running a survival analysis using individual capture-mark-recapture data we show that there are no costs for males attempting breeding (i.e., found in amplexus), as their survival in a year is not markedly different from individuals not found in amplexus. Overall, this chapter contextualised hypotheses that are known for other contexts, but were seldomly, if ever, investigated in high-elevation natural populations, both finding support for some hypotheses, or not, for others.

Finally, in **Chapter 4**, I focused on the peculiar dynamics of the focal population. This population, contrary to many other populations that are showing declines, shows in fact a very interesting trend. This trend is characterised by a sharp and massive increase around 2013 of the number of breeding adults captured every year, followed by a stabilisation in the following years. The aim of the chapter was therefore to understand the causes of the observed population trend. Building up from Chapter 2 and including recruitment into the breeding population by applying a capture-mark-recapture Jolly-Seber model, I show that the increase in the number of individuals is due to new individuals entering in the breeding population, rather than an increase in survival. I investigate if this increase is due to environmental conditions being more favourable, especially during the sensitive first year of life of the toads, and I discuss the possibility of one cohort born in the mid-2000s being primarily responsible for this increase. I use as supporting arguments the similarity of the male and female trends both in entry in the adult population and in the changes in body size in first-time breeders. Females show a 4–5-year lag compared to males in these two metrics, which corresponds to the previously observed difference in age at sexual maturity, indicating that they might belong to the same cohort. These findings further support the hypothesis of populations persisting, or even thriving, while experiencing mainly harsh years, thanks to sporadic instances of good years.

To conclude, in this thesis I analyse various aspects of a high-elevation amphibian population, in particular highlighting the importance of the environment and density, and their interplay, in driving breeding (i.e., phenology and mating system) and demography. Furthermore, the frameworks I used are flexible and can be easily applied to other studies. Finally, this thesis also highlights the importance of long-term studies, which allow the uncovering of patterns that would remain invisible in shorter-term studies. Failing to properly characterise population dynamics over a sufficiently long time period can potentially have significant consequences for conservation and management actions, in particular for populations of endangered taxa living in threatened habitats.

General Introduction

Population ecology is the discipline that studies the processes determining how a population is structured, and how and why its abundance is changing in space and time. These processes are mortality, reproduction, immigration, and emigration. Temporal and spatial patterns in these processes determine whether a population is growing or declining. Thus, demographic analyses focusing on these processes help in better understanding population fluctuations and pinpoint the causes of these fluctuations. Different populations of the same species might show different population trends, depending on these underlying processes, with the overall species status determined by the state of all populations of a species. Globally, numerous species are threatened or are going extinct due to the so called 'sixth mass extinction', mainly attributed to anthropogenic influence, with potential catastrophic consequences for biodiversity and human survival (Ceballos et al., 2015). A recent study shows that 48% of 71000 animal populations are declining, and only 3% are increasing (Finn et al., 2023). There is high species-specific variability in the amount of knowledge on the status of species, and in many cases data deficiency is an important issue, as shown by Conde et al. (2019). Although this study did not include all available data for specific taxa, such as amphibians (e.g., Muths et al., 2017; Earl, 2019), it highlights that species data deficiency is a significant issue, particularly in the case of specific taxa and habitats (e.g., 75% of insect species have an unknown population trend; Finn et al. 2023). Reasons for data deficiency include—among many causes—the lack of fundings and workforce, and inaccessibility of the study areas.

Another reason leading to data deficiency is 'taxonomic chauvinism' (Bonnet et al., 2002). That is, some 'charismatic' taxa are more studied than others possibly due to their perceived higher interest or relevance. This is the case for taxa such as birds and mammals, whereas amphibians are less studied, despite the key role they play in communities, often acting as a link between aquatic and terrestrial habitats (Whiles et al., 2006). Amphibians face multiple threats, and are among the most at-risk taxonomic groups (Beebee & Griffiths, 2005; Wake & Vredenburg, 2008; Foden et al., 2013; Grant et al., 2016). Therefore, increased knowledge both at species and population level is needed to develop efficient conservation and monitoring programs and guarantee long-term persistence of amphibian populations. Moreover, focusing only on a reduced subset of species can be problematic as it might limit our full understanding of certain general key features of life (e.g., senescence and longevity; Reinke et al., 2022).

Since there is a lot of among-population variation in terms of local abundance due to the unique context of each population, it is important to look at different contexts to obtain a more comprehensive picture of the global situation of the species. An example of populations that can differ substantially from each other are marginal and core populations (Brown, 1984; Amburgey et al., 2018). Marginal populations occupy the edges of the species distribution, in opposition to core populations that occupy its centre. Typical marginal population habitats are high latitudes or elevations. Marginal and core populations can differ in many aspects, such as local adaptation of individuals and local abundance, with trade-offs playing an important role in determining physiology and life history (Willi & Van Buskirk, 2022). For instance, under the abundant-centre theory (Brown, 1984; Sagarin & Gaines, 2002), core populations are generally exposed to better conditions, thus have higher densities. On the other hand, individuals from marginal populations might show stronger plasticity and local adaptations given the highly selective environment they reside in. Overall, marginal populations, such as high-elevation populations, are considered less stable than core populations, due to the harsher environment and increased stochasticity they experience (Kawecki, 2008; Kolzenburg, 2022) and could be more strongly affected by climate change, which has particularly strong effects on habitats such as mountains (Diaz et al., 2003). On the other hand, these populations might be more capable of adapting. They might also fare better against disease or human activities, given their relative isolation compared to core populations (Brown, 1984). Consequently, studies on marginal populations are vital to understand population dynamics that are representative of the entire species distribution. Long-term studies in particular are crucial to capture a relevant portion of the changing environmental conditions that these populations can experience, thus obtaining a more precise description of population dynamics (Reinke et al., 2019).

Thesis goal

The main goal of this thesis is to fill the above-mentioned gap in our knowledge of marginal populations by analysing different aspects (e.g., phenology, vital rates, demography, and individual traits such as body size and growth) of a high-elevation population of an amphibian species, with a particular focus on how the environment and density affect these aspects. More in detail, I focused on the breeding phenology, the mating system, individual traits such as body size and growth, and vital rates such as survival, breeding probability, and recruitment. Movement between populations (dispersal, emigration, immigration…) are not relevant for the study population, therefore I did not focus on them. In fact, toads show high fidelity to the natal pond (Reading et al., 1991), and the other ponds surrounding the study population have been occasionally controlled and only very limited amount of toads has ever been found over 40 years. The uniqueness of the dataset and of the context of the study population enabled the creation of important and novel insights beyond the narrow focus on amphibian marginal populations. Moreover, the methodology developed and applied can easily be extended to populations in other contexts.

Study species

This thesis focuses on the common toad (*Bufo bufo,* Figure 1), a nocturnal amphibian belonging to the Anura order, and widespread in most of Europe and parts of Northwest Asia and Northwest Africa. Globally and in Switzerland it is classified as of 'Least Concern' under IUCN criteria, but like many other amphibian species it faces multiple threats affecting its local abundance. There is widespread evidence of common-toad populations declining across Europe (e.g., in Italy, Switzerland, and United Kingdom; Bonardi et al., 2011; Petrovan & Schmidt, 2016). Habitat loss and fragmentation (both of the terrestrial and aquatic habitat), climate change, diseases, and anthropogenic activity (e.g., roadkill and pollution) are among the main factors responsible for these declines (Beebee & Griffiths, 2005; Wake & Vredenburg, 2008; Grant et al., 2016).

Toads show a highly seasonal life cycle. In spring they emerge from hibernation belowground and immediately migrate to the breeding site to reproduce. The breeding season is usually quite short at high elevations (i.e., a couple of weeks) (Morrison & Hero, 2003; Lenzi pers. obs.) and sees adult females and males gather to spawn and fertilize egg strings. The eggs will then hatch into tadpoles and undergo metamorphosis. Newly metamorphosed juveniles and adults will spend the feeding season in summer and autumn preparing for winter hibernation. It is common for females to skip breeding in a given year if they reproduced the previous year (i.e., 'intermittent breeding') (Bull & Shine, 1979; Muths et al., 2013), thus creating a highly male-skewed operational sex ratio at the breeding site, with the consequence being that not all males will successfully breed. The lengths of the hibernation period and the active feeding season are highly variable across populations, mainly due to the external environmental conditions, with high elevation and latitude populations having a shorter active season and a longer hibernation period (e.g., Hemelaar, 1988). Aside from the environment, some studies believe that genetics plays an important role, with the existence of an ‘internal’ genetically-determined component linked to the length of the active season (e.g., Heusser & Ott, 1968; Sinsch, 1988).

Figure 1. Photograph of a male and female common toad in amplexus, on their way to their breeding site in Ticino, Switzerland. The male, smaller, clasps the female (bigger, below) around the waist and will try to resist displacement from other males to be able to fertilize the eggs as soon as the female lays them. Photo credit: Ivan Lenzi.

Study area

The breeding site of the study population is a pond located above Grindelwald (Canton Bern, Switzerland) just below the Grosse Scheidegg Mountain pass at 1850 masl (46°39’ N and 08°05’ E). The pond measures approximately 10m x 30m, with a maximum depth of about 1m. (Figure 2). The study area is covered in snow usually from late autumn to late spring, and fieldwork is conducted as soon as snow melts in spring and the toads gather to breed.

Figure 2. Photograph of the breeding site of the study population, situated at 1850 masl next to the road leading to the Grosse Scheidegg mountain pass, above Grindelwald (Canton Bern, Switzerland). Photo credit: Benedikt Schmidt.

Data and general methods

Data collection started in 1982 (Hemelaar, 1988) and follows a robust design (Pollock, 1982) consisting in visiting the pond at night repeatedly during the breeding season in mid-late spring, for about five nights on average (mean: 5.22, range: 3-17), usually alternated with three-day breaks. Within a capture night, three capture rounds are performed and all individuals captured are sexed, measured (snout-to-vent length, in mm), weighed (in grams), uniquely marked and, if found in amplexus, their partner ID is noted. Unique marking initially consisted in individual toe-clipping patterns (for the period 1982-1984), then from 1985 to 1992 toads were marked by cohort, with all new individuals captured in a year having the same toe clipped. Starting in 1993, passive integrated transponders (PIT tags) have been used to uniquely mark individuals. In total, more than 2400 unique males and 1400 unique females have been captured over 42 years of fieldwork, making this study one of the longest and largest long-term studies on amphibians. The temporal trend of the number of captured individuals is quite unusual, with a sharp and strong increase around 2013 from around 100 individuals to 500-600. This increase happened initially in males, with females showing a similar, but smaller, increase 4-5 years later (Figure 3). This trend will be the focus of one of the four chapters.

The main methods that I will use in the thesis are capture-mark-recapture models in a Bayesian framework (Chapters 2, 3, and 4), as well as classical statistical models (e.g., piecewise and linear regressions in Chapters 1 and 3).

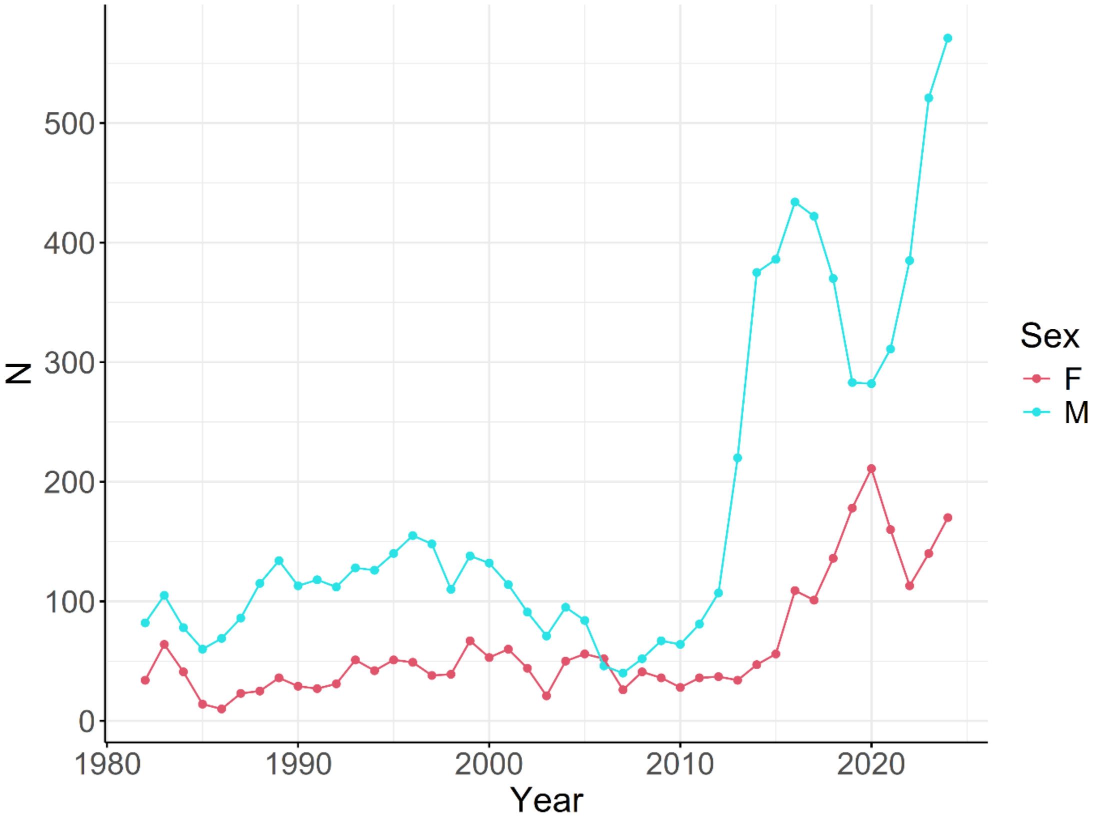

Figure 3. Number of individuals captured yearly between 1982 and 2024, split by sex (males in light-blue, females in red).

Thesis outline

The thesis is composed of six chapters: a general introduction, four data chapters, and a general discussion. Each data chapter is an analysis of one or multiple aspects of a high-elevation amphibian population (phenology, demography and growth, mating system, and population dynamics), with a particular focus on the roles of the environment and population density on these aspects. The following chapters are presented as self-standing scientific articles.

In **Chapter 1**, I aimed to understand how the breeding phenology of this population has been changing over the last 40 years, and what are the most probable causes of these changes. To do this, I applied piecewise regressions on the breeding dates and conducted a principal component analysis (PCA) on a series of environmental variables hypothesised *a priori.* I used the outcome of the PCA as explanatory variables in a linear regression with the dates of breeding as response variables. I found that an initial advancement towards earlier breeding dates was followed by a stabilisation, although with an increased year-to-year variation. On average, toads breed 30 days earlier now than in the early 1980s. I could link the phenology shifts to changes in winter and spring snow cover and temperatures, as well as spring precipitation. Changes in these environmental variables are not linear over the study period (i.e., temperatures do not get steadily warmer over time), as perhaps expected under climate change, highlighting the complexity of the underlying processes and factors at play. For instance, although alpine habitats are expected to be responding most strongly to climate change, the existence of a 'mosaic of micro-climates' (Scherrer & Körner, 2011) due to aspects such as topography, can reduce the exposure of alpine populations to climate change. These findings about breeding phenology are of great interest in this era of changing climate and can help understand how this population is reacting to it. They also raise a series of relevant questions about the risks and benefit of breeding earlier. This chapter was published in *Peer Community Journal* in 2023 (https://doi.org/10.24072/pcjournal.240).

Subsequently, in **Chapter 2**, I was interested in assessing the relative importance of the environment and population density on vital rates, either through direct effects, or indirect ones (trait-mediated). The focal trait acting as mediator was body size, a common key life-history trait across species (Peters, 1986). I applied a unified framework consisting of a capture-mark-recapture model and a von Bertalanffy growth model and estimated male and female survival, as well as female breeding probability. I could show that females follow a somewhat consistent two-year breeding cycle. Moreover, I found various significant direct effects, such as that of density on survival, which has rarely, if ever, been found in the adult stage of a wild amphibian population. I also found support for indirect effects; for instance, the negative association between population density and body size potentially buffers the negative effect of body size on survival at high densities. I show that only by incorporating multiple drivers we can obtain more accurate estimates of the vital rates and unravel the underlying relationship between environment, density, individual traits, and vital rates. This chapter was published in *Ecosphere* in 2024 (https://doi.org/10.1002/ecs2.70048).

In **Chapter 3**, conducted by a master student (Daniel Breitenmoser) whom I supervised, we focused on the mating system and male-mating success. Females show intermittent breeding, typical of high elevation or latitude habitats, likely due to the high energetic costs of breeding that they experience (Bull & Shine, 1979; Hayward & Gillooly, 2011) combined with the lower productivity of the habitats they reside in. Females skipping breeding, along with the older age at sexual maturity compared to males, create a male-skewed operational sex ratio at the breeding site, implying that not all males can breed. Given the fitness-related consequences of breeding, it is crucial to investigate how the mating system is structured and what determines successful breeding, especially in natural populations, as many amphibian studies on this subject so far were conducted in an experimental setting. We therefore examined the factors leading to a successful male breeding attempt, with a particular focus on body size, age, sex ratio, and the length of the breeding season. The main results show that there is a positive effect of body size on entering amplexus and resisting displacement from other males, and that if the breeding season is long enough size-assortative mating might arise. We could also show that older males have a lower probability of being found in amplexus, hinting at a senescence effect impacting their reproductive capabilities. Moreover, using a Bayesian capture-mark-recapture model, we showed that there are no survival costs for males that attempted breeding (i.e., found in amplexus) compared to males that did not. The findings of this chapter helped us scale up hypotheses evaluated mostly in an experimental setting to a natural population, helping to bridge the gap between the two contexts.

Finally, in **Chapter 4**, I built on the modelling framework of Chapter 2 to focus on the peculiar fluctuations shown by the study population. I aimed to understand the proximate cause of the increase in the number of captured individuals, applying a Jolly-Seber capture-mark-recapture model. This model let me understand if the increase is due to an increase in survival, or in recruitment. The results indicate a rather stable survival, but a massive increase in the number of new breeders. I hypothesised that environmental conditions during the sensitive initial stages of the life cycle (i.e., egg, tadpole, and juvenile phases) could be the ultimate cause of this observed high recruitment into the population, finding partial support for this hypothesis, with in particular a positive association between temperature during the egg phase and the number of females entering the adult population in the following years. I further speculated that the increase could be mainly due to a single cohort from the mid-2000s which profited from particularly good conditions, based on the sex-specific trends of the body size and of the timing of entry in the breeding population. Overall, this chapter contributes to our understanding of the mechanisms driving population dynamics in amphibian populations and suggests that rare events can drive population dynamics way past the perceived equilibrium states.

Chapter 1 – Breeding Phenology

Four decades of phenology in an alpine amphibian: trends, stasis and climatic drivers

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The layout and formatting of this chapter are slightly modified from the original publication in the scope of the thesis.

Abstract

1. Strong phenological shifts in response to changes in climatic conditions have been reported for many species, including amphibians, which are expected to breed earlier. Phenological shifts in breeding are observed in a wide number of amphibian populations, but less is known about populations living at high elevations, which are predicted to be more sensitive to climate change than lowland populations.
2. The goal of this study is to assess the main factors determining the timing of breeding in an alpine population of the common toad (*Bufo bufo*) and to describe the observed shifts in its breeding phenology.
3. We modelled the effect of environmental variables on the start and peak dates of the breeding season using 39 years of individual-based data. In addition, we investigated the effect of the lunar cycle, as well as the individual variation in breeding phenology. Finally, to assess the individual heterogeneity in the timing of breeding, we calculated the repeatability of the timing of arrival at the breeding site.
4. Breeding advanced to earlier dates in the first years of the study but the trend continued only until the mid-1990s and stabilised afterwards. Overall, toads are now breeding on average around 30 days earlier than at the start of the study period. High temperatures and low snow cover in winter and spring, as well as reduced spring precipitation were all associated with earlier breeding. Additionally, we found evidence of males arriving on average before females at the breeding site but no clear and strong effect of the lunar cycle. We only found weak evidence of among-individual variation in shifts in the breeding phenology, as well as a low repeatability of arrival timing.
5. Our findings show that the observed changes in breeding phenology are strongly associated with the environmental conditions. These results contribute to filling a knowledge gap on the effects of climate change on alpine amphibian populations. Moreover, we show that changes in phenology, especially in the mountains, can be hard to predict as local microclimatic conditions do not necessarily reflect the observed global climatic trends.

Keywords: Phenology, climate change, *Bufo bufo*, mountains, principal component analysis, repeatability

Introduction

Phenology refers to the timing of periodical events (e.g., seasonal migration, spring flowering) in relation to biotic and abiotic factors and is a key element of the life cycle in a multitude of organisms. Phenology is normally determined by a combination of a genetic and an environmental component (Quinn & Wetherington, 2002; Tang et al., 2016). Thus, climate change can shift the phenology of many species, potentially leading to mismatches between demand and availability of resources (Parmesan & Yohe, 2003; Visser & Gienapp, 2019; Iler et al., 2021). These shifts can have large effects on the demography of populations, as individuals cannot benefit from the optimal conditions at the right time, with consequences on their fitness (Visser & Gienapp, 2019; Iler et al., 2021). Therefore, it is important to describe and quantify phenological shifts and their causes.

Phenology has a key role in amphibians as well, especially in species living in temperate regions, where various aspects of the annual cycle are determined by seasonality (Duellman & Trueb, 1986; Gotthard, 2001; Hartel et al., 2007). The environmental component is more important than the genetic component in explosive breeders (*sensu* Wells, 1977). In fact, explosive breeders reproduce once a year around springtime and the timing is linked to specific environmental signals such as increasing day length, temperature, and rainfall, which can trigger the migration of amphibians from the hibernation sites to the breeding ponds (Semlitsch, 1985; Oseen & Wassersug, 2002; While & Uller, 2014; Ficetola & Maiorano, 2016). Other important environmental factors affecting the timing of breeding in explosive breeders can be the lunar cycle (Grant et al., 2009; Green et al., 2016; Arnfield et al., 2012; Jarvis et al., 2021) or the hydrological cycle of breeding ponds (Semlitsch et al., 1993). Previous studies have also identified a possible genetic component in triggering the migration to the breeding site and thus the start of the breeding season (Heusser & Ott, 1968; Semlitsch et al., 1993; Phillimore et al., 2010). Breeding phenology also shows individual variation, as the animals will arrive at different times at the breeding site. The causes of individual-level variation are multifold and can include genetics (Heusser & Ott, 1968; Semlitsch et al., 1993), sex and size (Loman & Madsen, 1986), body condition (Kokko, 1999) as well as features of the hibernation site, such as distance from the breeding site, which in *Bufo bufo* can be up to more than 1000 m (Sztatecsny & Schabetsberger, 2005; Kovar et al., 2009).

While most studies on amphibians across species and locations have found earlier spring breeding in response to climate change (Beebee, 1995; Blaustein et al., 2001;

Parmesan, 2007; While & Uller, 2014), phenological delays have also been observed (e.g., Arnfield et al., 2012; Arietta et al., 2020). In other cases, non-linear responses to environmental drivers such as the North Atlantic Oscillation were observed (Prodon et al. 2020). The direction and magnitude of phenological shifts are therefore variable among and within species, as they can depend on the specific environmental conditions that the populations are experiencing at the local scale, or on the genetic structure of said populations (Phillimore et al., 2010; Bison et al., 2021).

Shifts in phenology can have adverse effects on amphibians, as phenological mismatches can affect predator-prey dynamics and food availability (Todd et al., 2011; Reinhardt et al., 2015; Jara et al., 2019; Visser & Gienapp, 2019). In temperate regions, early breeding can expose eggs and hatched tadpoles more frequently to late frost events, thus increasing mortality (Muir et al., 2014; Bison et al., 2021). On the other hand, in the absence of frost or drying events, earlier breeding might be beneficial as it allows post-metamorphic toadlets more time to fully develop in summer before hibernation (Reading & Clarke, 1999; Reading, 2010). Delayed breeding can also have a negative outcome on the population, as it can result in increased mortality in juveniles that could not fully grow before their first hibernation (Morin et al., 1990; Garner et al., 2011; Sinsch & Schäfer, 2016). Even though this phenomenon can be compensated in some cases with an accelerated growth rate, this can come at the cost of reduced defences against predation (Orizaola et al., 2016). Thus, phenological shifts and their causes should be identified and better understood, as they can help design and prioritise conservation and management actions.

The consequences of phenological shifts could be exacerbated in ecosystems less resilient to climate change. Mountains are among the most threatened ecosystems (Thompson, 2000; Diaz et al., 2003, but see Körner & Hiltbrunner, 2021) and are predicted to warm more rapidly in the northern hemisphere (Nogués-Bravo et al., 2007; Keiler et al., 2010; Vitasse et al., 2021). The phenology of plant and animal populations at high elevations is shifting on average towards earlier dates (Vitasse et al., 2021). Long-term studies on amphibian populations living at high elevations are scarce, and not much is known about how their breeding phenology is changing. These populations experience different environmental conditions (e.g., increased amount of snow and colder temperatures) compared to their lowland counterparts. Thus, different environmental variables potentially play a bigger role in determining breeding phenology compared to what is observed at lower elevations (Nufio et al., 2010; Bison et al., 2020).

Using 39 years of data on an explosive-breeding amphibian population living at a high elevation (*B. bufo*), we study the relationship between breeding phenology and the environment. More specifically, our goal is to (i) identify the environmental variables (e.g., temperature, snow cover, moon cycle) that could be driving the observed breeding phenology of this population (both the start and the peak of the breeding season), (ii) analyse if there is significant variation in the phenological shifts among individuals, (iii) obtain a measure of individual heterogeneity, by calculating individual-level repeatability (i.e., upper limit of heritability; Falconer, 1981; Lessells & Boag, 1987; Semlitsch et al., 1993) of the timing of arrival at the breeding site for both males and females.

Material and Methods

Life-history data

The study site is a pond located above Grindelwald, below the Grosse Scheidegg Mountain pass (canton of Bern, Switzerland, 46.65240 N, 8.09683 E), at an elevation of 1841 m a.s.l. The pond measures approximately 10 m x 30 m, with a maximum depth of about 1 m. Since 1982, we have captured annually all the toads that come to breed at the study pond. We then marked (first by toe-clipping, then starting in 1993 by implanting PIT tags), measured, and released them in the same place (Hemelaar, 1988; Grossenbacher, 2002). To make sure we captured both early and late arrivers, we repeated this procedure for on average 5–6 nights, with breaks in-between of about 2-4 days (i.e., the data conform to Pollock's (1982) robust design). The length of the fieldwork period usually covers the breeding season duration, which typically lasts about two weeks at our study pond. This design also had the advantage of not overly stressing the toads. In total, for the period 1982–2020, 3053 uniquely recognizable individuals have been caught, of which 1852 were males and 1201 females. For each individual we have a record of presence for each capture night over the study period. Given the reduced size of the pond and the repeated capture rounds within a capture night, we assumed high capture probabilities (capture probability $p \approx 0.85$ per year based on a preliminary analysis of the mark-recapture data). At the population level we determined for each year a start, a peak, and an end date of breeding (i.e., first capture night, the capture night when most toads were captured, and last capture night, respectively). These calendar dates were all transformed into days of the year (where January 1st = 1), to facilitate modelling of long-term trends. These dates come with a degree of uncertainty, given the sampling done every 2–4 days and not daily. The date of start of the breeding comes with additional uncertainty as the first capture night is not always reflective of the same toad activity at the pond over the study period. We accounted for these sources of uncertainty in all following analyses, using simulated data on start and peak breeding dates.

Climatic data

We obtained climatic data for the period 1980–2020 from the DaymetCH dataset (data obtained from *Bioclimatic maps of Switzerland © WSL*, based on station data from the Federal Office of Meteorology and Climatology MeteoSwiss, and elaborated by the Land

Change Science group, WSL). This dataset consists of a 100-metre resolution grid of interpolated estimates of weather variables, using meteorological data from ground stations and the Daymet software (Thornton et al., 1997). We obtained data for the cell containing the breeding pond for the following variables: daily minimum, maximum, and mean temperature, daily total precipitation, and daily snow water equivalent (SWE; the equivalent amount of water stored in the snowpack). We then calculated average seasonal minimum, maximum, and mean daily temperatures, and cumulative seasonal precipitation and SWE.

Data analysis

Population trend

A visual inspection of the data suggests that the trends in the breeding phenology across the study period are non-linear, both for start and peak breeding (Figure 1). Therefore, to better describe the observed trends, we conducted a piecewise regression on both start and peak breeding using the R package *segmented* (Muggeo, 2008). This analysis enables the identification of possible breakpoints in a trend, in our case a year (or several years) when a significant change occurs in the temporal trends of the breeding phenology. We set the year 1982 as year 0 in the model, to obtain a more intuitive interpretation of the intercept. Moreover, we decided to assess the robustness of our analysis to possible imperfect assignment of start and peak dates, as the toad sampling is not done daily. To do this, we simulated 1000 datasets of breeding start dates over the study period, allowing the date of the start of the breeding to be as early as seven days before the originally assigned first capture night. The process was described by a uniform distribution, where each date between 0 and 7 days earlier than the assigned date had the same probability of being chosen. We also simulated 1000 datasets for peak breeding dates, allowing the dates to deviate from the originally assigned date by letting it vary between the previous and the following capture night, again with the dates being picked from a uniform distribution. Using these simulated datasets, we ran 1000 piecewise regressions for both start and peak breeding dates and calculated the 2.5th and the 97.5th percentiles of the values of each model parameter, including p-values testing for the significance of the breakpoint.

Moreover, to check how the standard deviation (SD) of the start or the peak breeding dates changes over time, we calculated for both start and peak breeding the SD of the residuals of each of the 1000 piecewise regressions, using a rolling window approach (with a 10-year window) with the function *rollapply* of the package *zoo* (Zeileis & Grothendieck, 2005).

Determinants of variation in the breeding phenology in the population

To understand the climatic causes of the observed shifts in the breeding phenology of this population, we investigated the effects of several climatic variables on the timing of breeding at the population level. We identified *a priori* the climatic covariates that most reasonably could influence the breeding phenology in spring based on previous literature and expert knowledge (Oseen & Wassersug, 2002; Reading, 2003; While & Uller, 2014; Ficetola & Maiorano, 2016; Green, 2017). These climatic covariates are: average minimum daily temperature in spring (T_{Sp}) and winter (T_W), total precipitation in spring ($Prec_{Sp}$, which includes both rainfall and snowfall), total snow water equivalent in spring (SWE_{Sp}), and winter (SWE_W). We then performed a piecewise regression on the time series of these five climatic covariates (Figure 2, Table S4). We used minimum temperatures because toads are nocturnal animals and are therefore more exposed to colder temperatures and less to average or warmer temperatures. Moreover, minimum temperatures will determine if the ground stays above freezing conditions. Changing the temperature variable (mean vs minimum vs maximum) in the subsequent analyses did not change the results as they were highly correlated ($r > 0.93$).

With warmer winters and springs, toads should emerge sooner from their hibernation burrows as the snow will melt and the ground unfreeze earlier (Corn, 2003). The higher the snow water equivalent, the later the toads will emerge, as the snow cover will keep them blocked underground (Corn, 2003). Finally, precipitation can either favour or delay the breeding season. Snowfall should delay breeding as the snow cover will increase (Corn, 2003), but rainfall could potentially lead to an earlier start of the breeding season, as toads need high humidity levels to be active (Todd et al., 2011; Green, 2017). After standardising these climatic variables by subtracting the mean value and dividing by the standard deviation, we performed a principal component analysis (PCA, function *prcomp*, R package *stats* (R Core Team, 2020)), to reduce dimensionality and obtain uncorrelated variables (Figure S1).

In addition to these five climatic variables, the lunar cycle has also been identified to be an important factor for the timing of breeding in amphibians, with in general peak migration to the breeding site under waxing or full moon phases (Grant et al., 2009; Arnfield et al., 2012; Green et al., 2016; Jarvis et al., 2021). To assess the effect of the lunar cycle on the breeding phenology in our population, we first obtained the moon phase for each date of breeding start and peak breeding over the study period using the package *lunar* (Lazaridis, 2014). Following Arnfield et al. (2012) and Jarvis et al. (2021), we transformed the lunar phases in lunar angles (in radians, where 0 = new moon and π = full moon).

To quantify both the effects of climate and of the moon cycle on the breeding phenology, we modelled two separate linear regressions on the day of the breeding start and the day of peak breeding over the period 1982–2020. As explanatory variables we used the scores of the first two principal components (PC), as they explained an important amount of the variance in the data (>70%). As an additional explanatory variable, to better understand the role of the moon cycle, we included the cosine of the lunar angles of the start and peak breeding dates respectively. We first modelled the originally assigned dates, and then, as we did for the piecewise regression, we ran 1000 models with simulated datasets with varying dates of start and peak breeding, drawn from a uniform distribution. Each date could vary to be any date between the previous and following capture night.

To further study the association between the moon cycle and breeding phenology we tested if start and peak breeding tended to happen more frequently under certain moon phases. To do this, we used the *rayleigh.test* function of the *circular* R package (Agostinelli & Lund, 2017) to perform the Rayleigh test, a circular goodness-of-fit test that is particularly suited for checking if the values of a circular variable show a unimodal departure from a uniform distribution (Landler et al., 2018). To check for significant multimodal departures, we performed the Hermans-Rasson test instead, using the *HR_test* from the *CircMLE* package (Fitak & Johnsen, 2017; Landler et al., 2018). Both tests were performed on the values in radians of the lunar angles. Also in this case we first ran the tests on the originally assigned dates and then we ran them on 1000 simulated datasets of start and peak breeding dates and obtained the 2.5th and 97.5th percentile of the p-values.

Determinants of individual variation in breeding phenology

In addition to considering phenology at the population level, we also wanted to understand whether individuals can show different patterns of changes in their reproductive phenology over time through different responses to climatic variables, possibly indicating a genetic component that mediates the effect of the changing environment. We therefore modelled the effect of the previously used principal components PC1 and PC2, as well as of the cosine of the lunar angle on each individual first capture occasion in any given year (6735 occurrences for 3053 uniquely marked individuals, as many individuals were breeding in multiple years (mean = 2.21 years, SE = 0.02)), using a linear mixed model (package *lmerTest*; Kuznetsova et al., 2017). Also in this case, we first ran the model on the originally assigned arrival dates, and then, to account for uncertainty in the assignment of the dates of arrival to the pond we simulated 1000 new datasets where every individual arrival date is newly sampled from an uniform distribution and can be as early as the capture night preceding the original arrival date, or if it was the first capture night of the season, up to seven days before. Using these 1000 new datasets we ran 1000 models and obtained the 2.5th and the 97.5th percentile values for each parameter.

As a random effect, applied on both the intercept and the slope of both PC1 and PC2, we included individual identity (ID). This was done not only to observe if individuals react differently to changing environmental conditions, but also to account for the non-independence of the data. Moreover, we also included *year* as a random effect on the intercept, to account for unexplained year-specific variation in the data. Finally, we included the effect of sex to account for differences between males and female. To properly be able to compare the effects of continuous variables (i.e., the two PCs and the cosine of the lunar angles) with the effect of a categorical variable (i.e., sex), we standardised the three continuous variables by subtracting the mean and dividing by two times the standard deviation (Gelman, 2008). Finally, as a measure of model fit, we calculated the conditional R^2 value using the *r.squaredGLMM* function from the package *MuMIn* (Barton, 2019).

Repeatability of arrival date

Finally, we also estimated repeatability (i.e., the upper limit of heritability) of arrival dates at the breeding site. High values of repeatability (*r*) mean that individuals are consistent in their relative arrival timing (e.g., always among the first ones), and vice versa. To calculate *r*, we used for each individual the date of first capture for each year that it was captured. This date is a relatively good proxy for the date of arrival at the breeding site, as the data collection usually starts every year approximately when the first toads arrive at the pond. The date was converted to the day of the year (where January 1st = 1), and then standardised by subtracting the year-specific mean and dividing by the year-specific standard deviation. We then used the function *rpt* from the package *rptR* to calculate *r* using individual ID as the group variable (Stoffel et al., 2017), and bootstrapping 1000 times to obtain the 95% CI.

As for all the other analyses, to account for the uncertainty in the assignment of the dates, we repeated the calculation of *r* 1000 times, sampling different arrival dates every time from a uniform distribution, where the arrival date of each individual can be up to the previous capture night, or up to seven days earlier if they were caught during the first capture night of the season. We then calculated the 2.5th and the 97.5th percentiles of *r* to show the spread it can have. Given the different reproductive strategies that males and females toads have, with females on average coming to the breeding site later than males and for a shorter period of time (Reading & Clarke, 1983; Loman & Madsen, 1986), we performed sex-specific calculations of *r*.

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).

Results

Population trend

Both the breeding start dates and the dates of peak breeding show very similar trends (Pearson's correlation coefficient = 0.91), with both also showing marked between-year variation over the study period. Nonetheless, a shift towards earlier breeding dates is observable, with breeding happening now on average around 30 days earlier compared to the start of the study period (Figure 1). The piecewise regression on breeding start dates identified a single breakpoint in the temporal trend in the year 1993 with a pre-1993 steep advancement of breeding dates followed by a post-1993 almost flat trend (Figure 1A; Table 1). The analysis of the robustness of the piecewise regression, done by simulating data and running 1000 piecewise regressions, performed very similarly, with 910 cases out of 1000 where the year 1993 was identified as breakpoint and the model coefficients were very close to the piecewise regression conducted on the originally assigned breeding dates (Table S1). The piecewise regression on peak breeding dates also identified 1993 as a breakpoint year (Figure 1B; Table 1). In this case, the analysis of the robustness showed slightly more variation, with the breakpoint years mostly obtained being 1993 and 1996 (274 and 283 out of 1000 respectively) (Table S1). Moreover, we found the standard deviation (SD) of the residuals of the piecewise regressions on both start and peak breeding dates to vary considerably, with higher SDs at the start and the end of the study period (Figure S2). To further check the pattern in the residuals we split them in four different decades and checked their distribution (Figure S3).

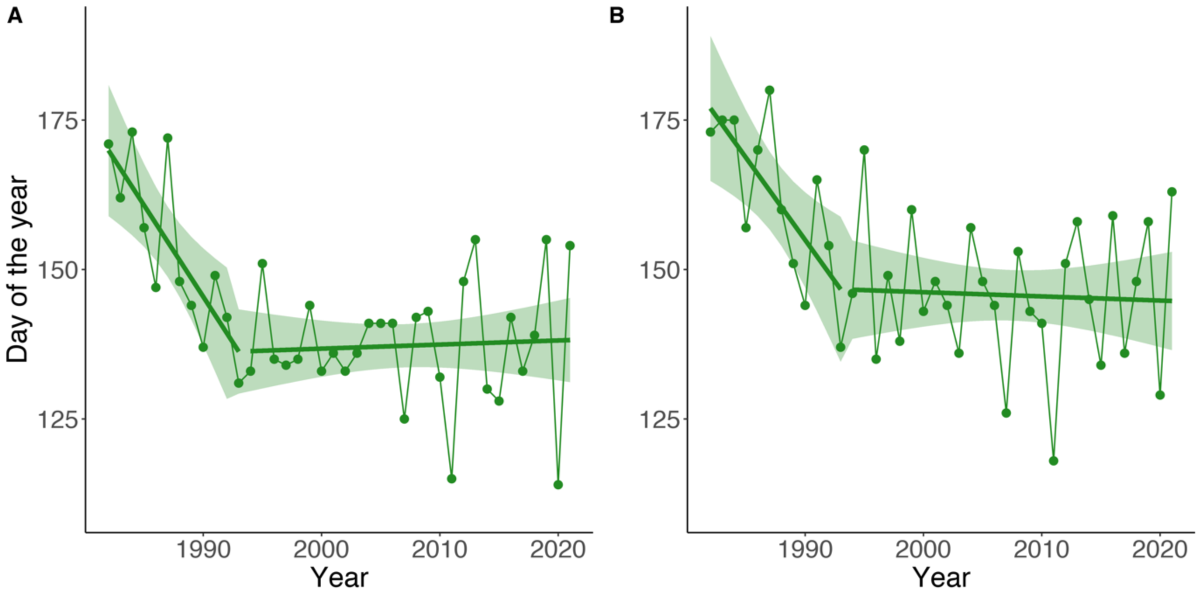

Figure 1. Trends of breeding phenology over the study period (1982–2021). **(A)** First day of the breeding season (day of the year, where January 1st = 1). The segmented green line is the result of a piecewise regression, where the year 1993 (± 5; 95% CI) was identified as a breakpoint, thus creating two distinct trends. **(B)** Date of peak breeding (i.e., date where most toads were captured in a given breeding season. The segmented green line is the result of a piecewise regression, where the year 1993 (± 6, 95% CI) was identified as a breakpoint. The green band in both plots represents the 95% CI for the piecewise regression.

Table 1. Summary of the piecewise regressions on the start and peak of the breeding season. For both intercept and slopes we show the estimate, its standard error, and the t-value and p-value associated with it. Slope1 refers to the segment before the breakpoint and Slope2 refers to the segment after the breakpoint. Asterisks next to the p-values show significance at the 0.05 level. The p-value for Slope2 is NA since standard asymptotics do not apply (Muggeo, 2008). No p-values are provided for the intercept because this test is not of biological interest.

	Estimates	Std. Error	t-value	p-value
Intercept	169.92	5.60	30.32	-
Slope1	-3.06	0.95	-3.23	0.0027*

Start	Slope2	0.069	0.22	0.31	NA
	Breakpoint	1993	2.36	-	< 0.001*
Peak	Intercept	176.96	6.19	28.57	-
	Slope1	-2.75	0.95	-2.89	0.0066*
	Slope2	-0.07	0.27	-0.26	NA
	Breakpoint	1993	2.84	-	0.0023*

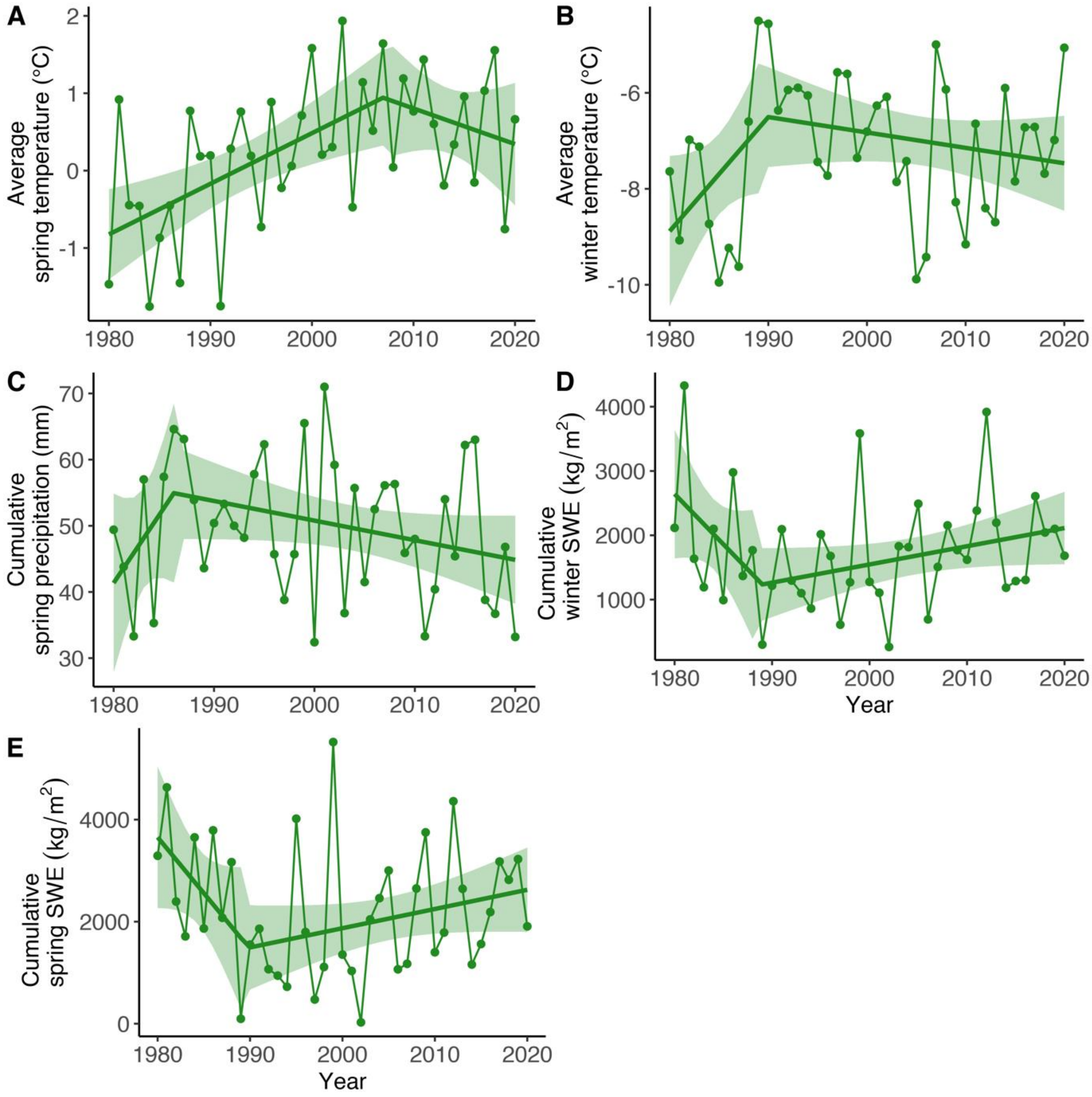

Figure 2. Trends over the study period of the five focal environmental variables. **(A)** Average minimum daily temperature in spring. The piecewise regression identified the year 2007 (± 9, 95% CI) as a breakpoint. **(B)** Average minimum daily temperature in winter. The year 1990 (± 7, 95% CI) was a breakpoint. **(C)** Cumulative precipitation in spring. The year 1986 (± 8, 95% CI) was a breakpoint. **(D)** Cumulative snow water equivalent (SWE) in winter. The year 1989 (± 7, 95% CI) was a breakpoint. **(E)** Cumulative SWE in Spring. The year 1990 (± 7, 95% CI) was a breakpoint. In all plots green ribbons represent the 95% CI for the linear regressions. Table S4 in the Appendix shows the summary of these five piecewise regressions.

Determinants of variation in the breeding phenology in the population

The first two principal components (PC) of the principal component analysis (PCA) described together more than 70% of the variation in the data, and both had a standard deviation (i.e., the squared root of their eigenvalue) above one (Figure S1; Table S5). Therefore, applying the Kaiser rule, we kept the scores of these two PCs (PC1 and PC2) as explanatory variables in the following linear regressions on the start of the breeding season and on peak breeding (also including the scaled cosine of lunar angle). PC1 was mostly determined by winter temperature (+0.45 loading) and winter and spring SWE (-0.61 and -0.64, respectively). PC2 was mostly determined by spring weather conditions. Spring temperature had a negative loading (-0.68), while precipitation had a positive loading (+0.68) (Figure S1; Table S6).

Regarding the start of the breeding season, the model (adjusted R^2 = 0.41) indicated a significant negative relationship with PC1 and a significant positive relationship with PC2 (Table 2). The cosine of the lunar angle had a non-significant effect. Similarly, for the regression on the dates of peak breeding, we found a significant negative relationship with PC1 and a significant positive relationship with PC2, while the cosine of the lunar angle had a small and non-significant effect (Table 2). The adjusted R^2 was 0.54. In both cases the outcome is that warmer temperatures in winter and spring, less snow cover, and weaker precipitations are all associated with an earlier start and peak of the breeding season. Both the 1000 linear regressions on the simulated dates of the start of the breeding season and the 1000 on the simulated dates of peak breeding performed similarly to the two regressions on the originally assigned dates (Table S2), indicating that our analysis is robust to possible imperfect assignment of dates of start and peak breeding.

Table 2. Summary of the linear regression on the start and peak of the breeding season. For each variable we show the estimate, its standard error, and the t-value and p-value associated with it. Asterisks next to the p-value show significance at the 0.05 level. No p-values are provided for the intercept because this test is not of biological interest.

		Estimates	Std. Error	t-value	p-value
Start	Intercept	141.72	1.65	85.92	-
	PC1	-5.48	1.67	-3.28	0.0024*
	PC2	7.00	1.68	4.17	0.00019
	cos(moon)	1.32	1.68	0.79	0.44
Peak	Intercept	150.21	1.56	96.59	-
	PC1	-5.47	1.58	-3.47	0.0014*
	PC2	9.37	1.60	5.86	< 0.0001*
	cos(moon)	0.24	1.60	0.15	0.88

Effect of the moon cycle on breeding phenology

To further understand if the lunar cycle is associated with the breeding phenology, we performed two statistical tests. To check for unimodal deviation, we ran a Rayleigh's test on the moon phases on breeding season start and on peak dates. In both cases we obtained a non-significant p-value (0.27 and 0.08 respectively), indicating that we could not confidently reject the null-hypothesis of the data being uniformly distributed in the circular space. In addition, the outcome of the Hermans-Rasson test for multivariate deviations indicated that the null hypothesis could not be rejected for both start and peak breeding (p-value = 0.38 and 0.21 respectively). To further assess the robustness of our analysis to imperfect assignment of dates we ran both the Rayleigh's and Hermans-Rasson test on 1000 simulated datasets of dates of start and peak breeding. The outcome is similar to the tests performed on the originally assigned dates. The p-values of the Rayleigh's test were 0.36 [2.5th and 97.5th percentiles: 0.07 ; 0.80] and 0.16 [0.008 ; 0.60] respectively. The p-values for the Hermans-Rasson test on start and peak breeding were 0.43 [0.05 ; 0.90] and 0.25 [0.011 ; 0.78] respectively. This means that there was no clear pattern between lunar phases and the start of the breeding season or the peak breeding (Figure 3).

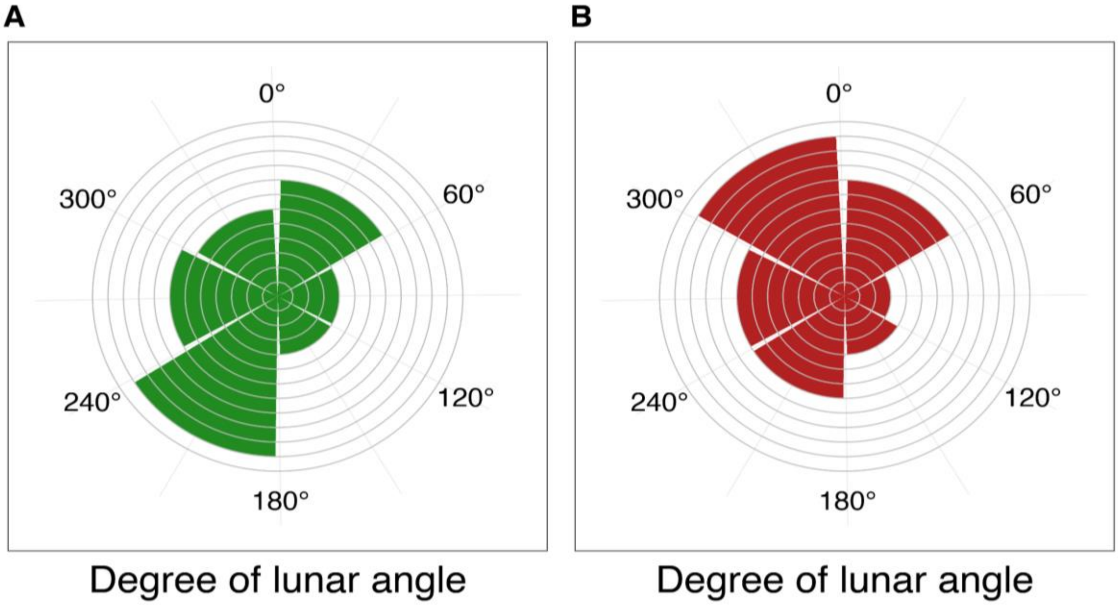

Figure 3. Circular histogram showing counts of **(A)** the originally assigned breeding start dates and **(B)** the originally assigned peak breeding dates under different lunar phases for the period 1982–2021 (e.g., the breeding season started eight times under a moon phase with a lunar angle between 0° and 60°). Lunar angles, initially in radians, were back-transformed to degrees, so that the new moon is at 0° and full moon is at 180°.

Determinants of individual variation in breeding phenology

To better understand if there are among-individual differences in the phenological response to changing climatic variables, we used a linear mixed model to test for the effect of climatic variables on the individual breeding start dates (i.e., the date on which an individual was first captured). We found only a small difference in the response of breeding phenology to climatic variables among individuals (i.e., low values for the random effect ID, both on intercept and slopes, Table 3). We found a strong significant positive effect of PC2 on the breeding dates (17.51 ± 3.27 SE), meaning that stronger precipitation and lower minimum spring temperatures are associated with a delay in the breeding. We also found a significant and strong negative effect of PC1 (-10.14 ± 2.85 SE), indicating that colder winter temperatures and higher SWE are associated with a delay in the breeding. We also found a significant but weak effect of the cosine of the lunar angle (1.57 ± 0.14 SE), suggesting a possible small role of the lunar cycle. Finally, we observed an effect of sex indicating that males arrived on average earlier than females (-1.45 ± 0.14 SE) (Table 3). The 1000 models on the 1000 simulated datasets, ran to assess the robustness of the analysis to imperfect assignment of arrival dates, showed a similar outcome to the main model (Table S3).

Table 3. Detailed description of the model used to check for the effect of environmental variables on the phenology at the individual level. Sex is included to observe differences between males and females. The response variable ArrivalDate is a vector of dates of arrival at the breeding site for each individual over the study period. PC1 and PC2 are the first two components of the PCA performed on the climatic data. Cos(moon) is the cosine of the lunar angle for the arrival date. ID refers to the identity of each individual, and it is used as a random effect on both intercept and the slopes of PC1 and PC2. Finally, Year is included as a random effect to account for additional unexplained variation that might be caused by sampling variation. The second and third part of the table provide details on the estimates for the fixed and random effects respectively. No p-values are provided for the intercept because this test is not of biological interest.

Model name	Variables			Conditional R^2
Full_model	ArrivalDate ~ PC1 + PC2 + Sex + cos(moon) + (1|Year) + (1|ID) + (0 + PC1|ID) + (0 + PC2|ID)			0.92
	Effect size	**Std. Error**	**t-value**	**P-value**
Intercept	147.87	1.66	89.24	-
Sex (male)	-1.45	0.14	-10.44	< 0.0001*
PC1	-10.14	2.85	-3.56	0.0011*
PC2	17.51	3.27	5.36	< 0.0001*
cos(moon)	1.57	0.14	11.08	< 0.0001*
	Variance			
ID (intercept)	2.47			
ID on PC1	2.89			
ID on PC2	0.58			
Year (intercept)	101.78			

Residuals	17.73

Repeatability of arrival date

In total, 453 females and 1092 males visited the pond over multiple years. The repeatability value calculated with the originally assigned arrival dates was 0.15 [2.5th and 97.5th percentiles 0.08 ; 0.21] for females and 0.12 [2.5th and 97.5th percentiles CI 0.09 ; 0.15] for males. To again assess the robustness of our analysis we simulated 1000 new datasets with varying arrival dates and calculated 1000 repeatability values for females and 1000 for males. We found a mean repeatability value *r* of 0.14 [2.5th and 97.5th percentiles 0.12 ; 0.17] for females and 0.10 [2.5th and 97.5th percentiles 0.09 ; 0.11] for males.

Discussion

Our results show that variation in the breeding phenology is strongly associated with climatic conditions, which vary substantially among years but also show trends across times. We also found low repeatability values and low variability in individual responses, suggesting that the genetic component contributing to the observed variation of individuals in the breeding phenology is weak. Finally, we found indications of a possibly significant, but weak, effect of the lunar cycle. A signal might indeed exist, but the climatic variables probably have a stronger effect.

Our results support the hypothesis of a strong link between the breeding phenology of high-elevation amphibian populations and climatic conditions. Increasing temperatures are a key driver of snow melt and ground defrosting, which in turn act as important environmental cues for toads to initiate migration to their breeding grounds (Corn & Muths, 2002; Green, 2017). During particularly warm springs, the snow melts and the ground defrosts earlier, leading to a shift of the onset of breeding to earlier dates. Our findings on the importance of temperature are in line with previous studies on *B. bufo* (Reading & Clarke, 1983; Reading, 2003; Tryjanowski et al., 2003; Arnfield et al., 2012). On the other hand, where past studies have identified rainfall to be an important trigger for migration in lowland populations (Reading & Clarke, 1983; Sinsch, 1988; Jarvis et al., 2021), we did not clearly observe this in our data, as our measure of precipitation included both snow- and rainfall. We found that a higher amount of precipitation in spring (combined with a decrease of spring temperature) was associated with a later breeding date. In fact, at low temperatures, precipitation in the form of snowfall or freezing rain can delay the melting of the snow cover, therefore leading to a delay in the breeding. The observed negative association between snow water equivalent (SWE) and breeding timing is in line with the rest of the findings. In fact, SWE depends considerably on temperatures and precipitation, as well as other aspects such as exposition, and it is a key factor that influences phenology (Corn, 2003). The very similar trend observed for peak activity in breeding indicates that both start and peak breeding are influenced mostly in the same way by the same climatic variables.

When looking at the individual timing of arrival we still found an important effect on the breeding phenology of PC1 (T_W and $SWE_{Sp/W}$) and PC2 (T_{Sp} and $Prec_{Sp}$) (Table 3). However, we found only non-significant and small among-individual variation in phenological response to changing climatic conditions (Table 3). As reproduction happens only once a year in explosive breeders living in temperate zones, synchronisation in breeding could be key to maximise reproductive output (Ims, 1990). Such an accurate synchronisation can be achieved more easily when all individuals hibernating close to each other express similar responses to external cues triggering their migration to the breeding pond, instead of responding individually in different ways, highlighting once more that the breeding phenology is mainly driven by climatic conditions.

Moreover, the low values of *r* (i.e., the upper limit of heritability) that we found for the timing of arrival show that there is some individual heterogeneity in this trait, and it could further indicate that there is only a small contribution of the genetic component to variation in the breeding phenology. This conclusion is in line with what most studies on amphibian phenology found (Semlitsch et al., 1993; Blaustein et al., 2001; Parmesan, 2007; While & Uller, 2014; but see Heusser & Ott, 1968; Phillimore et al., 2010). In other species, for instance birds, higher values of repeatability have been found for migration phenology, a trait linked to breeding. Franklin et al. (2022) found in their meta-analysis an average value of repeatability of 0.414, while Kürten et al. (2022) found repeatability values above 0.60 for various traits (but see Clermont et al., 2018; Vaillant et al., 2021 for examples of low repeatability in birds), but in amphibians that follow an explosive breeding strategy, the genetic component does not appear to be the main determinant of variation in breeding phenology. This might be due to either populations being truly able to respond plastically to changing climatic conditions, and therefore there is no strong selection on genetic variation in the trait, or there might be little genetic variation in the population to begin with. Low values of repeatability might also indicate a non-consistent choice of the hibernation site (and therefore distance to the pond). Not much is known about hibernation site fidelity in anurans, and future studies should address this question.

Finally, we found that on average males tend to arrive earlier than females (Table 3), similarly to what has been found in lowland populations of *B. bufo* (Loman & Madsen, 1986; Höglund & Robertson, 1987, 1988; but see Gittins et al., 1980). In these studies, males, especially bigger ones, were observed to arrive on average earlier at the breeding pond. Smaller males, on the other hand, were observed intercepting females on their way to the pond, betting on the fact that the females would lay the eggs as soon as they arrived at the pond, avoiding competition from the other bigger males. A more detailed future analysis of body size and its effects on the timing of migration to the breeding site could confirm this theory also for our study population.

Climate change is leading to on-average increasing temperatures both globally but also at smaller scales such as in the European Alps (Vitasse et al., 2021) and in Switzerland (Rebetez & Reinhard, 2008). The start of data collection for this study (early 1980s) coincides with an important increase of temperatures in Switzerland (Bundesamt für Umwelt (BAFU), 2020). In fact, each year since the mid-80s, the deviation from the mean yearly temperature (average calculated over the period 1864–2019) has always been positive (Begert & Frei, 2018). In the Swiss Alps, mean temperature increased by about 1.7 °C from 1975 to 2004, nearly twice the global average (Rebetez & Reinhard, 2008). Despite these general trends, we observe at our study site stable or even decreasing trends in temperatures during the study period, especially in the second half (Figure 2). Initially, the shift towards earlier breeding (pre-1993/1996) can be explained by warming temperatures and decreasing SWE (Figure 2). On the other hand, the absence of a trend in the breeding dates observed after the mid-1990s (Figure 1) could be explained by a change in trajectories of winter temperature, which started decreasing around 1990 (Figure 2), as well as of winter and spring SWE, which started increasing around the same time. These combined changes are acting against the increasing spring temperature (which has increased until around 2007; Figure 2), therefore slowing down and ultimately halting the shift towards earlier breeding dates of the toads.

While we could expect climate change to act linearly on the shift towards earlier breeding dates, it is possible that other site-specific conditions prevail at different temporal and geographical scales, creating an heterogenous mosaic of climate conditions. An example of this is the influence of the North Atlantic Oscillation (NAO) on the breeding phenology of amphibians and reptiles in southern France, where shifts in the breeding phenology in the last forty years were related to variation in the NAO index (Prodon et al., 2020). High elevation habitats can also show different climates at very small geographical scales (Scherrer & Körner, 2011; Feldmeier et al., 2020). The phenology of populations experiencing these different microclimates will therefore not necessarily be affected in the same way (Miller et al., 2018; Arietta et al., 2020; Turner & Maclean, 2022). In our case, the data on climatic variables was limited to the 100 metres x 100 metres cell which includes the pond, and since we do not exactly know where the toads hibernate in the surrounding landscape, we cannot exclude that they are experiencing different microclimates compared to the pond and its surrounding area. Hibernating toads have been found more than 1000 metres away from the breeding site horizontally, and up to almost 400 metres away vertically (Sztatecsny & Schabetsberger, 2005). Since the breeding pond and surrounding area are often still partially covered by snow during peak night, the hibernation sites are probably warmer than the breeding site itself. Differences in microclimates between hibernation sites and the breeding site could further explain individual variation in breeding timing (e.g., arrival at the pond). Further studies on how the hibernation sites of the toads in this population can affect the breeding phenology should be conducted.

Despite the observed stabilisation of the trend of the breeding dates (Figure 1), the study population appears to experience increased variation in the dates of the start of the breeding season (Figure S2 and Figure S3). This increased variation could be explained by extreme weather events whose occurrence is expected to increase under climate change (Rahmstorf & Coumou, 2011; National Academies of Sciences, Engineering, and Medicine, 2016). Such unpredictability and extremeness of environmental conditions could threaten populations if they lead to either excessively early or late breeding, especially in temperate regions. In fact, extreme early breeding is associated with reduced hibernation periods which can decrease the body condition in spring (Reading, 2007). Additionally, early breeding can expose eggs and tadpoles to late frost events (Muir et al., 2014; Bison et al., 2021; Turner & Maclean, 2022). Delayed breeding can potentially pose a problem as well if the pond dries out during warm periods in late spring or if juveniles cannot accomplish full growth before hibernation. Indeed, smaller and younger juveniles are more at risk of death before and during the first hibernation period (Morin et al., 1990; Sinsch & Schäfer, 2016). This seems to be compensated in some cases by an accelerated growth at the larval stage in case of late breeding, but with a cost of reduced defences against predation (Orizaola et al., 2016). Such riskful situations can have strong negative effects on individual survival and reproductive output, ultimately leading to population declines (Reading, 2007; Iler et al., 2021). On the other hand, at least initially, climate change could lead to longer growing seasons during which individuals would have the opportunity to gather more energy before the onset of hibernation (Zani, 2008; Iler et al., 2021), with potentially positive effects at the population level. Climate change can as well lead to species expanding upward (Vitasse et al., 2021), with *Bufo bufo* populations observed locally extending their upper range limit to higher elevations (Lüscher et al., 2016). If moving upwards is not possible, high-elevation populations adapted to their environments could face local extirpation (Urban, 2018).

Conclusion

In this study we showed the important association between climatic variables such as temperature, snow cover, and precipitation with the breeding phenology of a *Bufo bufo* population living at high elevations. Breeding happens on average around 30 days earlier now compared to four decades ago, and interestingly the shift towards earlier breeding dates has not been constant but is better described by two different trends. After an initial steep advancement until the mid-90s, the trend stabilised. This is reflected in the trends of the time series of the focal climatic variables, which explain the observed temporal variation in breeding phenology. The stabilisation in the trend suggests that there might be spatial heterogeneity in climate change and its effects, therefore different populations might show different trends in their breeding phenology. This stabilisation is accompanied by an increased variation in the dates of the start of the breeding season, with potential consequences for the population that should be further investigated in the future. To conclude, this 40-year study is one of the first and most detailed studies on the breeding phenology of alpine populations of *B. bufo*, and it highlights the influence of changing environmental conditions on the timing of reproduction.

Acknowledgements

We warmly thank all the people involved in data collection and management since 1982 and everybody who facilitated fieldwork during the past 40 years. Capture, handling and marking of toads were done under an animal welfare permit issued by the Veterinäramt des Kantons Bern. We also thank the Land Change Science of the Swiss Federal Research Institute WSL for kindly providing us with the climatic data. Finally, we thank Sergio Estay, Nigel Yoccoz and an anonymous reviewer for comments on a previous version of the manuscript.

Authors contribution

O.L. and B.R.S. conceived the study. K.G., S.Z., S.A., B.L., D.S., M.T., 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 and script accessibility

Data and scripts for this publication are available on the Zenodo Repository: https://doi.org/10.5281/zenodo.7333319.

Supplementary material

Extra tables and figures are available in the Appendix.

Conflict of interest and disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article.

Funding

This project was funded by the Federal Office for the Environment (contract numbers: 20.0001.PJ/46DBED0F1 and 06.0126-PZ Artenförderung / N494-1379) and the Stiftung Temperatio.

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Appendix

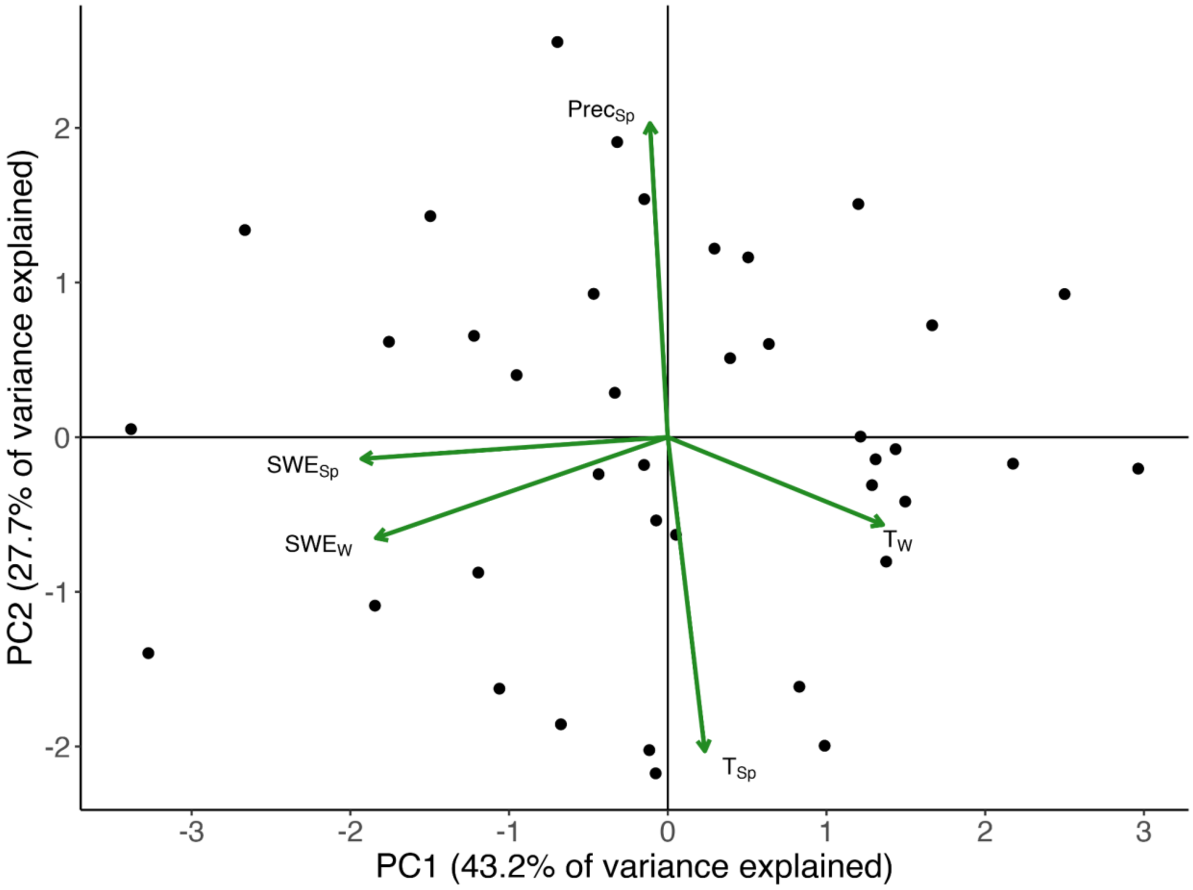

Figure S1. Graphical visualisation of the first two principal components of our principal component analysis. The points represent the scores over the two axes, while the arrows represent the loadings of the five environmental variables. The first principal component explained 43.2% of the variance in the data, while the second principal component explained 27.7%. T_{Sp} is the average minimum daily spring temperature, T_{W} is the average minimum daily winter temperature, $Prec_{Sp}$ is the total precipitation in spring, SWE_{Sp} is the total spring snow water equivalent and SWE_{W} is the total winter snow water equivalent

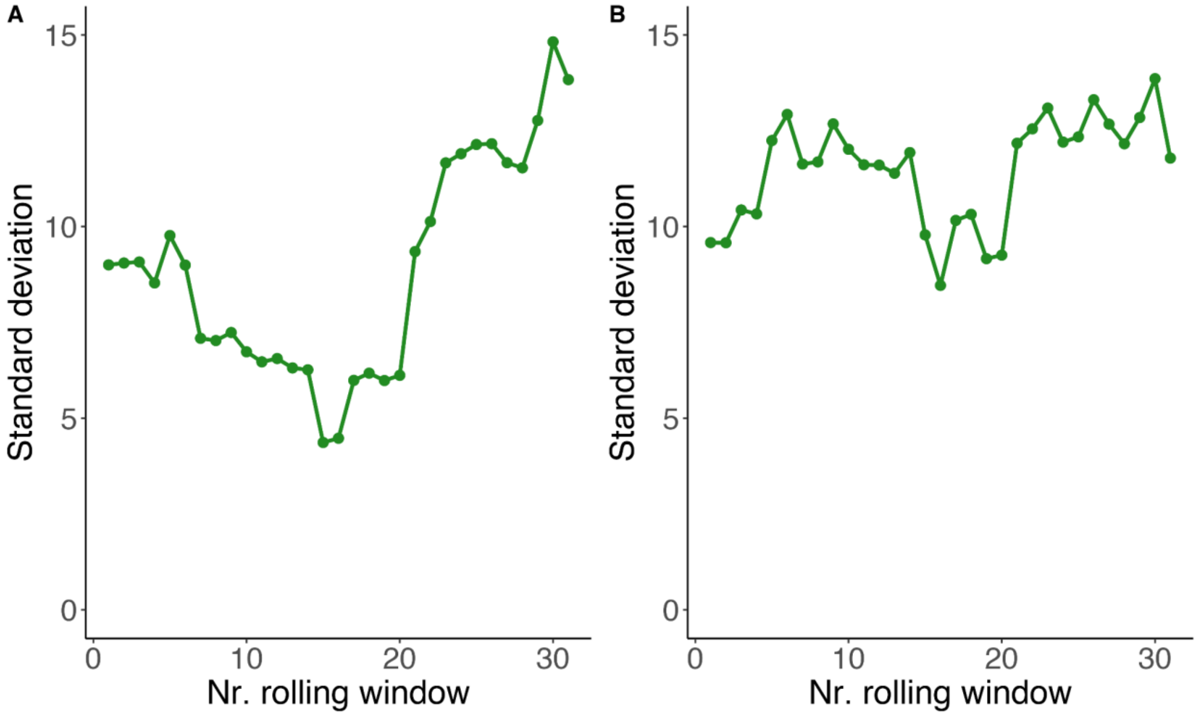

Figure S2. Mean standard deviation of the residuals of the 1000 piecewise regressions on start of the breeding season **(A)** and 1000 piecewise regression on peak of the breeding season **(B)**, calculated with a rolling window approach. Window size was 25% of the length of the timeseries (i.e., 10 years out of 40 years, therefore we had 31 windows).

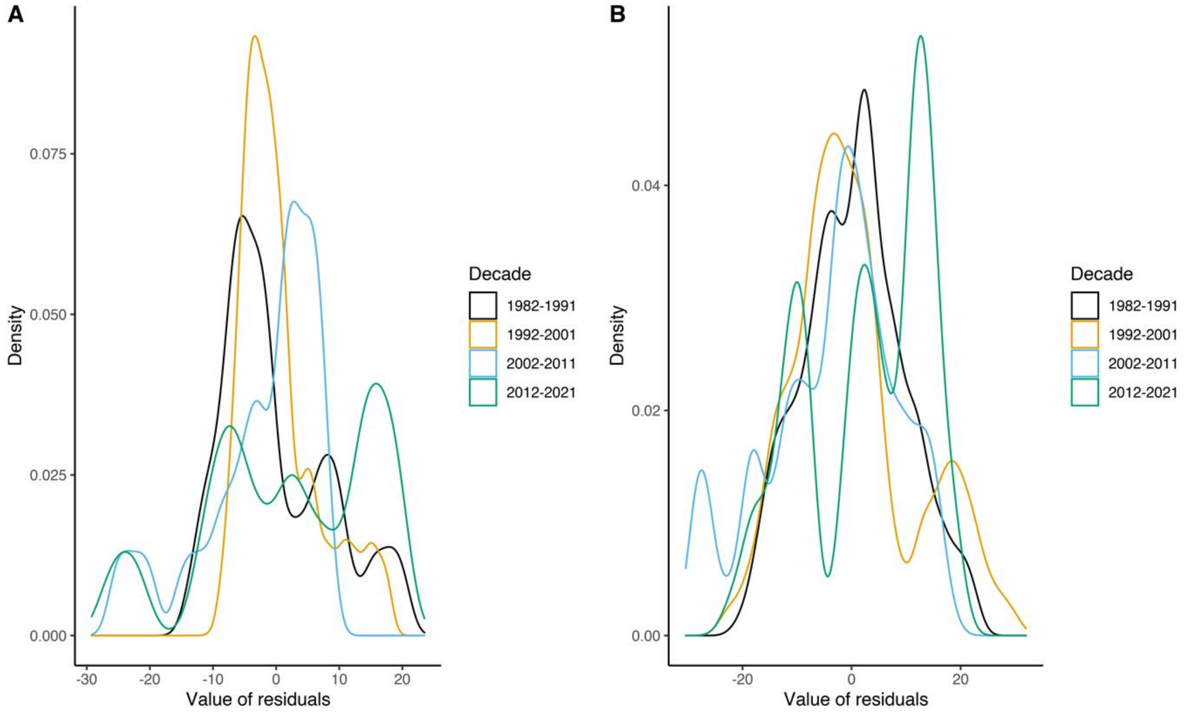

Figure S3. Distribution of the residuals of the 1000 piecewise regression on start of the breeding season **(A)** and peak breeding **(B)**. We divided the residuals in four different decades: decade 1 (1982-1991), decade 2 (1992-2001), decade 3 (2002-2011) and decade 4 (2012-2021).

Table S1. Summary of the simulated piecewise regressions on the start and peak of the breeding season. For both intercept and slopes we show the estimate, its standard error, and the t-value and p-value associated with it. Moreover, for each parameter we show in square brackets the 2.5th and the 97.5th percentiles of the values obtained by running 1000 models. Slope1 refers to the segment before the breakpoint and Slope2 refers to the segment after the breakpoint. Asterisks next to the p-values show significance at the 0.05 level. The p-value for Slope2 is NA since standard asymptotics do not apply (Muggeo, 2008). No p-values are provided for the intercept because this test is not of biological interest.

		Estimates	Std. Error	t-value	p-value
Start	Intercept	166.59 [164.24 ; 169.07]	5.70 [5.22 ; 6.17]	29.29 [27.03 ; 31.87]	-
	Slope1	-3.11 [-3.60 ; -2.78]	0.95 [0.81 ; 1.11]	-3.30 [-3.85 ; -2.86]	0.0027* [0.0005 ; 0.0069]
	Slope2	0.062 [-0.043 ; 0.16]	0.23 [0.21 ; 0.25]	0.271 [-0.201 ; 0.679]	NA
	Breakpoint	1993	2.30 [1.93 ; 2.69]	-	<0.001* [0.00013 ; 0.0020]
Peak	Intercept	174.47 [167.99 ; 179.56]	5.52 [4.11 ; 6.88]	32.34 [25.78 ; 41.35]	-
	Slope1	-2.10 [-3.10 ; -1.12]	0.67 [0.26 ; 1.16]	-3.43 [-4.69 ; -2.38]	0.0046* [< 0.001 ; 0.022]
	Slope2	0.41 [-0.11 ; 1.62]	0.47 [0.25 ; 1.11]	0.54 [-0.40 ; 1.64]	NA
	Breakpoint	1993 / 1996	3.17 [2.52 ; 3.83]	-	0.0023* [0.0005 ; 0.0064]

Table S2. Summary of the simulated linear regressions on the start and peak of the breeding season. For each variable we show the estimate, its standard error, and the t-value and p-value associated with it. In square brackets we show the 2.5th and the 97.5th percentile values, obtained by simulating 1000 times the dates and running 1000 models. Asterisks next to the p-value show significance at the 0.05 level. No p-values are provided for the intercept because this test is not of biological interest.

		Estimates	Std. Error	t-value	p-value
Start	Intercept	138.22 [137.54 ; 139.00]	1.69 [1.58 ; 1.80]	81.93 [76.79 ; 87.63]	-
	PC1	-5.52 [-6.34 ; -4.59]	1.73 [1.60 ; 1.86]	-3.20 [-3.73 ; -2.60]	0.0038* [0.00068 ; 0.013]
	PC2	6.99 [5.98 ; 7.84]	1.75 [1.62 ; 1.90]	4.01 [3.35 ; 4.69]	0.00048* [< 0.0001 ; 0.0019]
	cos(moon)	0.93 [-1.34 ; 2.86]	1.77 [1.63 ; 1.93]	0.53 [-0.72 ; 1.60]	0.55 [0.11 ; 0.97]
Peak	Intercept	150.35 [149.41 ; 151.28]	1.58 [1.45 ; 1.70]	95.43 [88.14 ; 104.06]	-
	PC1	-5.37 [-6.42 ; -4.32]	1.61 [1.48 ; 1.75]	-3.34 [-4.07 ; -2.63]	0.0032* [0.00025 ; 0.012]
	PC2	9.48 [8.38 ;10.55]	1.62 [1.48 ; 1.76]	5.88 [4.99 ; 6.81]	< 0.0001* [< 0.0001 ; < 0.0001]
	cos(moon)	-2.11 [-4.11 ; -0.22]	1.63 [1.49 ; 1.79]	-1.31 [-2.61 ; -0.14]	0.27 [0.013 ; 0.83]

Table S3. Detailed description of the model used to check for the effect of environmental variables on the phenology at the individual level. Sex is included to observe differences between males and females. The response variable ArrivalDate is a vector of dates of arrival at the breeding site for each individual over the study period. PC1 and PC2 are the first two components of the PCA performed on the climatic data. Cos(moon) is the cosine of the lunar angle for the arrival date. ID refers to the identity of each individual, and it is used as a random effect on both intercept and the slopes of PC1 and PC2. Finally, Year is included as a random effect to account for additional unexplained variation that might be caused by sampling variation. The second and third part of the table provide details on the estimates for the fixed and random effects respectively. The values shown are the mean value out of the 1000 models ran on simulated datasets and in square brackets we show the 2.5th and the 97.5th percentiles of each parameter. No p-values are provided for the intercept because this test is not of biological interest.

Model name	Variables			Conditional R^2
Full_model	ArrivalDate ~ PC1 + PC2 + Sex + cos(moon) + (1|Year) + (1|ID) + (0 + PC1|ID) + (0 + PC2|ID)			0.883 [0.880 ; 0.885]
	Effect size	Std. Error	t-value	P-value
Intercept	145.86 [145.77 ; 145.95]	1.68 [1.67 ; 1.69]	86.84 [86.25 ; 87.36]	-
Sex (male)	-1.76 [-1.760 ; -1.754]	0.164 [0.162 ; 0.166]	-10.72 [-11.29 ; -10.17]	< 0.0001*
PC1	-10.04 [-10.17 ; -9.91]	2.89 [2.87 ; 2.91]	-3.47 [-3.53 ; -3.42]	0.0014* [0.0012 ; 0.0016]
PC2	16.74 [16.56 ; 16.92]	3.32 [3.29 ; 3.34]	5.05 [4.99 ; 5.10]	< 0.0001*
cos(moon)	1.06 [0.84 ; 1.29]	0.147 [0.145 ; 0.148]	7.26 [5.70 ; 8.76]	< 0.0001*
	Variance			

ID (intercept)	3.06 [2.77 ; 3.36]
ID on PC1	1.96 [1.23 ; 2.72]
ID on PC2	0.32 [0.00 ; 1.19]
Year (intercept)	104.37 [103.04 ; 105.82]
Residuals	26.08 [25.53 ; 26.60]

Table S4. Summary of the piecewise regressions on the five focal environmental variables. MinT_Spring is the average minimum daily spring temperature, MinT_Winter is the average minimum daily winter temperature, Prec_Spring is the total precipitation in spring, SWE_Spring is the total spring snow water equivalent and SWE_Winter is the total winter snow water equivalent. We rescaled year to obtain more intuitive intercept estimates (year 1980 = 0). Slope1 refers to the segment before the breakpoint and Slope2 refers to the segment after the breakpoint. We also show the statistics associated with the identified breakpoint. Asterisks next to the p-values show significance at the 0.05 level. The p-value for Slope2 is NA since standard asymptotics do not apply (Muggeo, 2008). No p-values are provided for the intercept because this test is not of biological interest.

		Estimates	Std. Error	t-value	p-value
MinT_Spring	Intercept	-0.82	0.30	-2.76	-
	Slope1	0.07	0.02	3.33	0.002*
	Slope2	-0.05	0.05	-0.87	NA
	Breakpoint	2007	4.60	-1.92	0.06
MinT_Winter	Intercept	-8.88	0.80	-11.10	-
	Slope1	0.24	0.14	1.76	0.09
	Slope2	-0.03	0.03	-1.07	NA
	Breakpoint	1990	3.56	-1.05	0.30

Prec_Spring	Intercept	41.35	6.90	6.00	-
	Slope1	2.26	1.91	1.18	0.24
	Slope2	-0.30	0.18	-1.68	NA
	Breakpoint	1986	3.91	-1.51	0.14
SWE_Spring	Intercept	3654.0	707.3	5.17	-
	Slope1	-219.20	132.49	-1.65	0.11
	Slope2	37.68	24.17	1.56	NA
	Breakpoint	1990	3.55	2.23	0.03*
SWE_Winter	Intercept	2643.3	511.4	5.17	-
	Slope1	-156.42	107.41	-1.46	0.15
	Slope2	28.31	15.93	1.78	NA
	Breakpoint	1989	3.62	1.88	0.07

Table S5. Details of the five principal components. For each principal component we report its standard deviation, the proportion of variance explained and the cumulative proportion of this variance. In our linear regression we kept the first two principal components as their standard deviation is >1 (i.e., their eigenvalue >1) and combined they explain >70 % of the variance.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.47	1.18	0.83	0.82	0.33
Proportion of variance	0.43	0.28	0.14	0.13	0.02
Cumulative proportion	0.43	0.71	0.85	0.98	1.00

Table S6. Loadings of the five original environmental variables from which the five principal components are constructed. MinT_Spring is the average minimum daily spring temperature, MinT_Winter is the average minimum daily winter temperature, Prec_Spring is the total precipitation in spring, SWE_Spring is the total spring snow water equivalent and SWE_Winter is the total winter snow water equivalent. PC1 is mainly driven by MinT_Winter, SWE_Spring and SWE_Winter, while PC2 mostly by MinT_Spring and Prec_Spring.

	PC1	PC2	PC3	PC4	PC5
MinT_Spring	0.08	-0.68	0.33	-0.65	0.09
MinT_Winter	0.45	-0.19	0.64	0.58	0.07
Prec_Spring	-0.04	0.68	0.60	-0.41	-0.06
SWE_Spring	-0.64	-0.05	0.20	0.17	0.72
SWE_Winter	-0.61	-0.22	0.27	0.19	-0.69

Chapter 2 – Growth and Vital Rates

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

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Lenzi O., Grossenbacher K., Zumbach S., Lüscher B., Althaus S., Thoma M., Schmocker D., Recher H., Ozgul A., Schmidt B.R. 2024. Interplay of abiotic conditions, density, and body size in shaping demography in a high-elevation toad population. *Ecosphere 15(11)*: e70048. https://doi.org/10.1002/ecs2.70048.

The layout and formatting of this chapter are slightly modified from the original publication in the scope of the thesis.

Abstract

1. In natural populations, vital rates such as survival and reproduction are influenced by a complex interplay of abiotic conditions (e.g., environment), density dependence, and individual factors (e.g., phenotypic traits). Studies at the extremes of species distributions, particularly high elevations, offer unique insights due to the intensified effects of abiotic stressors, which can amplify both direct and indirect effects on vital rates.
2. In this study, we focus on a high-elevation population of the common toad (*Bufo bufo*) located near the upper limit of its elevational range in the Swiss Alps. This setting provides a critical context for examining how extreme abiotic conditions interact with density dependence and individual factors to influence life-history traits. Utilizing 28 years of capture-mark-recapture data and individual body size measurements from nearly 2500 toads, we applied in a Bayesian statistical framework a Cormack-Jolly-Seber model for estimating male survival probabilities, and a multistate model for assessing female survival and breeding probabilities, alongside sex-specific growth curves.
3. Our analysis indicates that survival probabilities are significantly impacted by interactions between abiotic conditions such as the active season length and temperature at emergence from hibernation, density dependence, and individual phenotypic traits such as body size. The breeding patterns of females showed a biennial cycle, with temperature at hibernation emergence influencing the likelihood of skipping breeding events, and density affecting the resumption of breeding. These results highlight the role of abiotic conditions and density in shaping physiological and reproductive strategies in a high-stress ecological niche.
4. Moreover, we uncovered indications of indirect effects, where both abiotic conditions and density potentially affect asymptotic growth and thus survival, mediated through changes in body size. Our findings illustrate the complex dynamics at play in high-elevation populations and the importance of long-term, individual-based data in studying these processes.
5. This study underscores the value of integrating multiple sources of variation to understand population dynamics comprehensively, particularly in under-studied,

extreme environments where traditional ecological models may not fully capture the nuanced interdependencies of natural systems.

Introduction

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

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

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

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

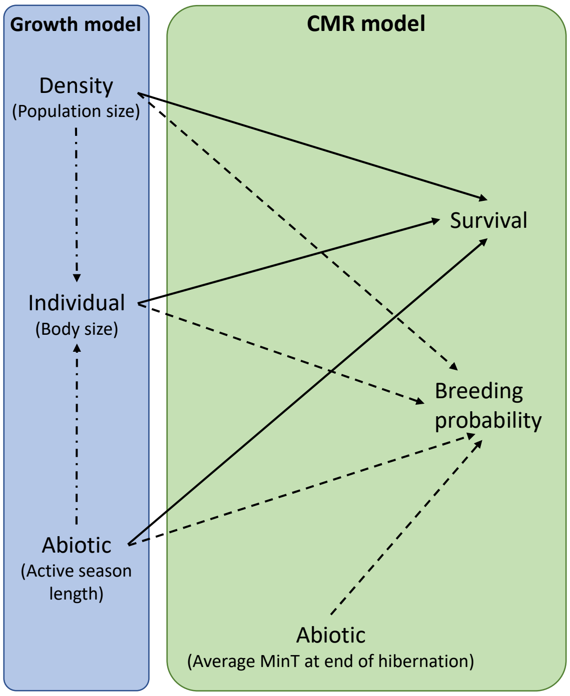

Figure 1. Framework of the study. To obtain estimates of body sizes for the years when the toads were not captured, we ran a von Bertalanffy (VB) growth model including a density proxy (population size) and an abiotic factor (the length of the active season) as covariates on the two VB parameters: growth rate and asymptotic size. Subsequently, we ran two sex-specific capture-mark-recapture (CMR) models to estimate adult survival and breeding probabilities (i.e., the probability of skipping and resuming breeding), while including the effect of density (population size), an individual factor (body size), and an abiotic factor (length of the active season). For the breeding probabilities we also included an additional abiotic factor (MinT; 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 density and abiotic conditions through their effect on body size.

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

In the second part of the analytical framework (i.e., the CMR model) we quantified the direct and indirect effect of abiotic conditions, density and individual size on survival and breeding probabilities. The latter were estimated only for females because they breed intermittently in this population (Grossenbacher, 2002). Intermittent breeding can arise where environmental conditions are unfavourable. In these conditions, individuals can or must forfeit breeding in a year. Skipping breeding can be an adaptive response when environmental conditions are pessimal for successful breeding and therefore a way to avoid wasting energy in bad years (Bull & Shine, 1979). In capital breeders, individuals can skip breeding due to the impossibility of collecting enough resources to build a clutch (Jönsson, 1997; Houston et al., 2007). This can happen when the active season is short due to poor environmental conditions, and therefore, opportunities for foraging are limited. Skipping breeding happens commonly in females, for whom reproduction is more demanding energetically (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 (Schaub et al., 2004). For males, we used a Cormack-Jolly-Seber (CJS) model. We investigated the effects of density, active season length (abiotic factor), and individual body size (individual factor) on survival and, in females, breeding probabilities. For the latter, we also tested for the effect of average minimum temperature around the timing of emergence. The latter covariate was included because the decision to skip breeding might also be due to the environmental conditions experienced at emergence from hibernation (Muths et al., 2013).

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

Methods

Toad mark-recapture and body size data

To estimate survival rates for male and female toads, as well as breeding probabilities for females, we used data on 1615 male and 933 female common toads (*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 passive integrated transponders (PIT tags). Every toad captured during a capture night is measured (snout-to-vent length [SVL]; in millimetres), 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 density the breeding population size (hereafter population size) which consists in 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: Section S1).

Climatic data

We used climatic data for the period 1993–2020 obtained from the DaymetCH dataset (Land Change Science group, WSL, Switzerland). DaymetCH consists of interpolated estimates of weather variables over a grid of a 100-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 a., 2017).

Hypotheses

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

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

Growth model

To include individual body size as a covariate for survival in the CMR model we needed to impute missing size data when toads were not captured (e.g., because they skipped breeding in a year). To do this, we fit a VB (von Bertalanffy, 1938) growth model on common toad size data following 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):

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

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

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

To better understand the effect of abiotic conditions and density, we modelled asymptotic size a of a toad at year t as a function of population size and the length of the active season of the year before (t-1). In other words, we calculated for each year the asymptotic size that a toad would reach if the length of the active season and the population size of that year would remain constant over the toad's lifetime. We note that toads are exposed to different abiotic conditions and densities each year. Therefore, growth depends on these yearly values and sets the growth trajectory to a new asymptotic size. We also 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 based on measurements 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 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 *nonbreeder* and *breeder* (the phenomenon is often called “temporary emigration” in the mark-recapture literature; Schaub et al., 2004). Since nonbreeders do not show up at the pond, they are not available for capture and the state *nonbreeder* is unobservable (Schaub et al., 2004). In this model we estimated survival, detection, and the probability of changing state (becoming a nonbreeder or becoming a breeder).

We were interested in the effect of density (population size), abiotic conditions (environment) and individual factors (body size) on the different vital rates (Figure 1). For both males and females, for survival probability ($\phi_{i,t}$) in year *t* we added as covariates the length of the active season at year *t,* the population size at year *t*, and the body mass of that individual at year *t* obtained from the growth model (Table 1). In the estimation of the probability that a female will skip breeding if it bred the year before ($\Psi_{i,t}^{B\_NB}$) and the probability that a female will resume breeding if it did not breed the year before ($\Psi_{i,t}^{NB\_B}$) we included the effects of the length of the active season and the population size of the year before, as well as the weather conditions (i.e., average minimum temperature) in the 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 that 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 μ_p and standard deviation σ_p) which was shared between the two sex-specific models to avoid identifiability issues. We standardized all the covariates by subtracting the mean value and dividing by the 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 fitted a CJS model to the data, we could test model assumptions using goodness-of-fit (GoF) tests (Pollock et al., 1985). We used the *R2Ucare* package in RStudio (Gimenez et al., 2018). The tests indicated the presence of a transience effect and overdispersion. We are not aware of the existence of similar GoF tests for multistate models with one unobservable state, therefore we assumed that we had to account for transience and overdispersion for the female data as well. If transience is not accounted for, survival or detection probabilities can be underestimated (Pradel et al., 1997). The solution we applied here was to estimate a specific survival probability for the first year after capture (Genovart & Pradel, 2019). Overdispersion leads to narrower standard errors around the estimated parameters, but the estimate itself is not biased (Schmidt et al., 2002). To assess the magnitude of overdispersion we calculated $\hat{c}$ (the variance inflation factor), by dividing the chi-squared test statistic by the number of degrees of freedom (Pradel et al., 1997). We obtained a value of 2.48 which indicates overdispersion (Choquet et al., 2009). We addressed overdispersion by including an individual random effect in the detection probability (Abadi et al., 2013).

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

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

Sex	Vital rate / demographic parameter	Abiotic covariate	Density covariate	Individual covariate
Males	Survival $\phi_{i,t}$	Length of active season	Population size	Body size
	Survival first year $\phi'_{i,t}$	Length of active season	Population size	Body size
	Detection $p_{i,t}$	-		
Females	Survival $\phi_{i,t}$	Length of active season	Population size	Body size
	Survival first year $\phi'_{i,t}$	Length of active season	Population size	Body size
	Detection $p_{i,t}$	-		
	Skip breeding $\Psi_{i,t}^{B\_NB}$	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,	Population size	Body size

	Mean minimum temperature in two weeks before first capture night

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 showed a good fit as well, with Bayesian p-values of 0.31 for males and 0.57 for females. Also the prior-posterior overlaps were satisfactory (Appendix S2).

Direct effects on growth and body size

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

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. $\hat{\mathrm{R}}$ 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 *k*	0.066	0.053	-0.034	0.175	0.907	1.00
ActiveSeason on *k*	-0.038	0.058	-0.159	0.072	0.246	1.00
PopSize on *a*	-0.583	0.408	-1.404	0.208	0.070	1.00
ActiveSeason on *a*	0.469	0.421	-0.369	1.294	0.875	1.00

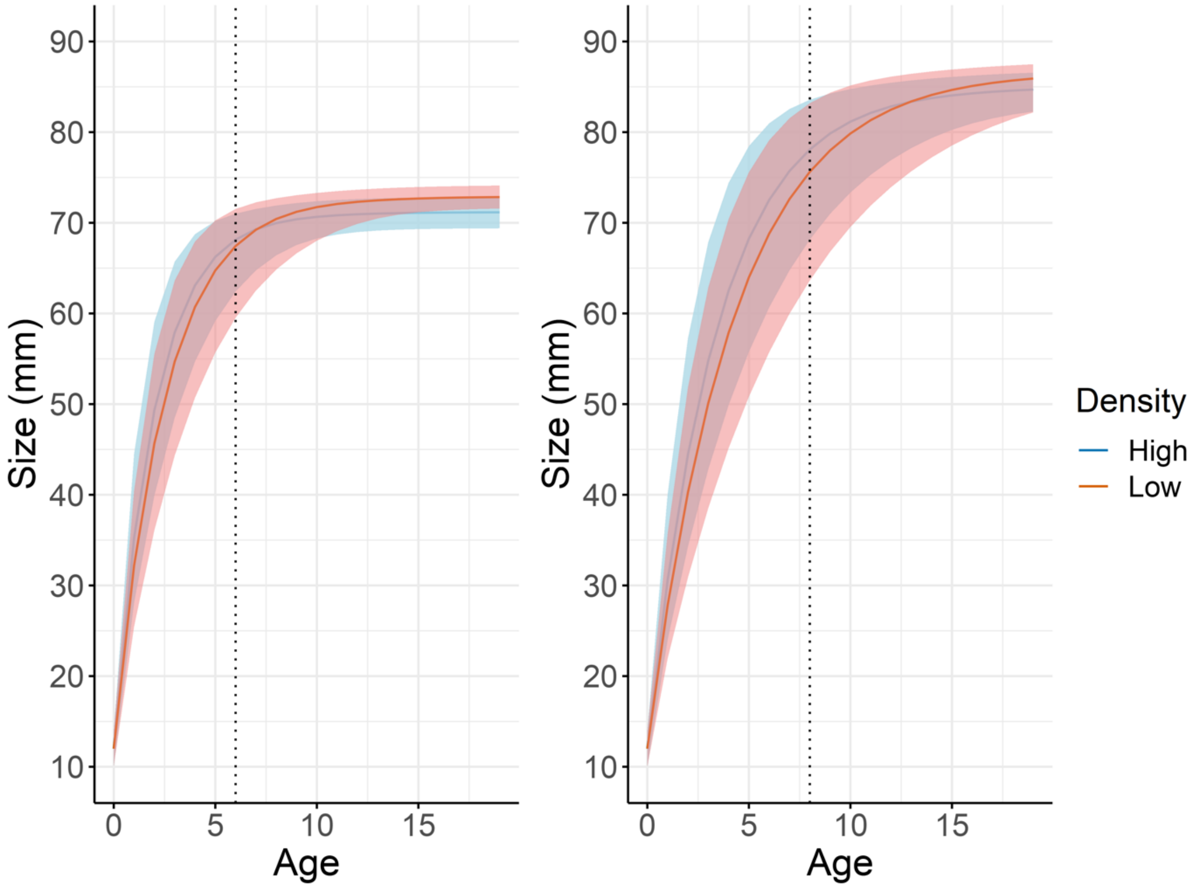

Figure 2. Growth curves for males (left) and females (right), for low population size (red) and high population size (blue). We looked at realistic population size values, using a value of -1 on the standardized scale for the low population size scenario (corresponding to 73 individuals) and a value 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 male survival with a Cormack-Jolly-Seber model, and female survival and breeding probabilities with a multistate model. The mean detection probability was 0.89 and varied little among years (SD = 0.06). Survival ϕ of males and females did not vary much across the study period, with male survival fluctuating more (mean values were 0.74 and 0.73 respectively). Both showed a decrease in the last years (Appendix S3: Figure S1). Survival in the year after the first capture ϕ' showed a similar pattern, but with lower values

(Appendix S3: Figure S2). Finally, the probability of skipping breeding if a female bred the year before Ψ^{B_NB} was high, with an average of 0.66 over the study period, but the probability of resuming breeding if a female skipped breeding the year before Ψ^{NB_B} was higher, with an average of 0.80 (Appendix S3: Figure S3). This indicates that there is a strong Markovian pattern in breeding, with the breeding status in the previous year strongly determining whether a female will attempt breeding.

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

Table 3. Summary of the intercepts for the focal vital rates (logit scale) and of the effects of abiotic conditions (length of the active season and the average minimum temperature around emergence; ActiveSeason and EmergenceMinT in the table), density (population size; PopSize), and individual factors (body size; BodySize) on survival, the probability of resuming breeding, and the probability of skipping breeding. 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 $\widehat{\mathrm{R}}$ values were equal to 1 and thus indicated convergence of the MCMC chains. For density, abiotic conditions, and individual factors we highlighted in bold the variables whose 95% CRI did not overlap zero, therefore showing strong evidence for an effect in a certain direction.

	Name	Mean	SD	2.5% limit of CRI	97.5% limit of CRI	Proportion
Intercept	Male survival	1.065	0.05	0.961	1.171	1

			4			
	Male survival in the first year	0.5	0.065	0.374	0.627	1
	Female survival	0.99	0.078	0.836	1.143	1
	Female survival in the first year	0.342	0.116	0.123	0.577	0.9991
	Skipping breeding	0.694	0.094	0.509	0.879	1
	Resuming breeding	1.855	0.446	1.15	2.879	1
Abiotic	**ActiveSeason on male survival**	**-0.161**	**0.039**	**-0.239**	**-0.085**	**0.000013**
	ActiveSeason on female survival	-0.023	0.078	-0.177	0.130	0.383
	ActiveSeason on resuming breeding	-0.278	0.268	-0.839	0.222	0.137
	ActiveSeason on skipping breeding	0.101	0.094	-0.083	0.287	0.859
	EmergenceMinT on resuming breeding	0.188	0.279	-0.341	0.766	0.761
	EmergenceMinT on skipping breeding	**-0.186**	**0.094**	**-0.372**	**-0.003**	**0.023**
Density	**PopSize on male survival**	**-0.146**	**0.031**	**-0.207**	**-0.085**	**0**
	PopSize on female survival	**-0.156**	**0.047**	**-0.249**	**-0.063**	**0.00054**
	PopSize on resuming breeding	**1.24**	**0.473**	**0.488**	**2.339**	**0.99989**
	PopSize on skipping breeding	-0.101	0.086	-0.271	0.068	0.121
Individual	BodySize on female survival	-0.101	0.058	-0.215	0.013	0.041
	BodySize on male survival	**-0.103**	**0.037**	**-0.176**	**-0.031**	**0.0026**
	BodySize on resuming breeding	0.516	0.452	-0.263	1.509	0.891
	BodySize on skipping breeding	-0.101	0.086	-0.271	0.068	0.121

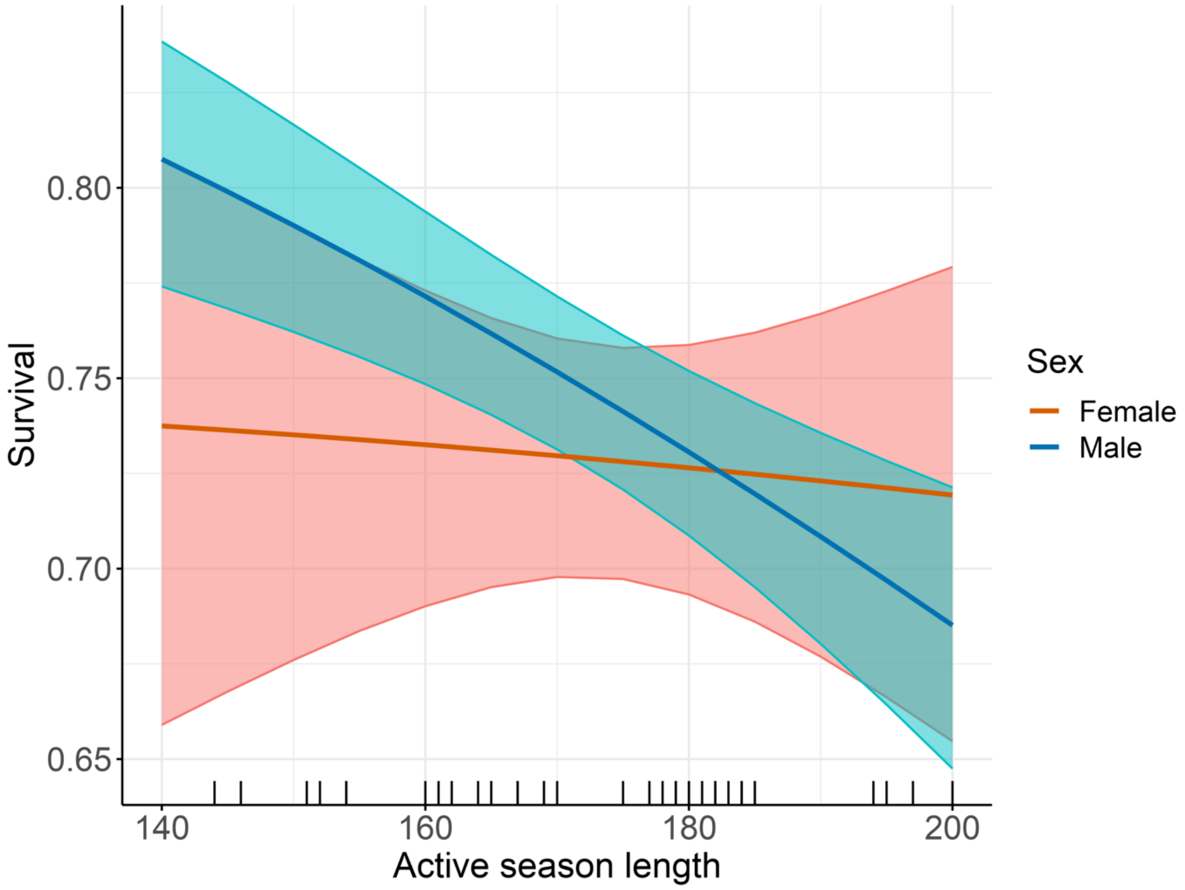

Figure 3. Relationship between the length of the active season (in days) and the survival of males (blue) and females (red), based on the predictions of the model. The lines represent the mean value, while the shaded ribbons the 95% credible intervals. The relationships shown assumed average body size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

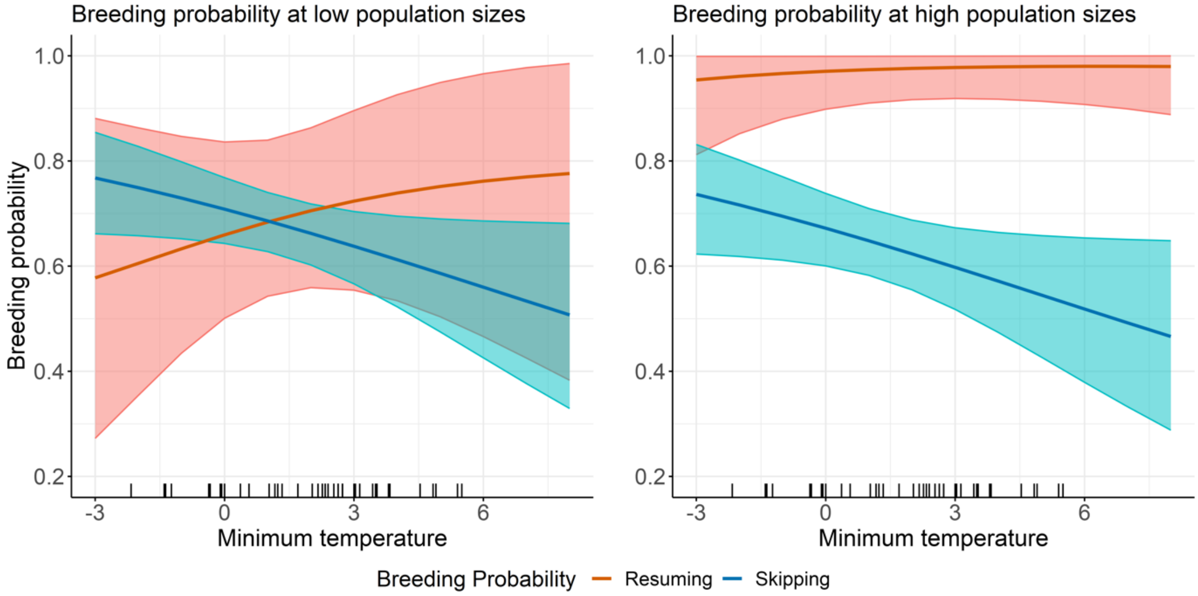

Figure 4. Relationship between the mean minimum temperature (in degrees Celsius) in the two weeks around emergence from hibernation and the probabilities of skipping (blue) and resuming (red) breeding of females, based on the predictions of the model, at low (left panel) and high (right panel) population 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 tick marks on the x-axis show the observed values.

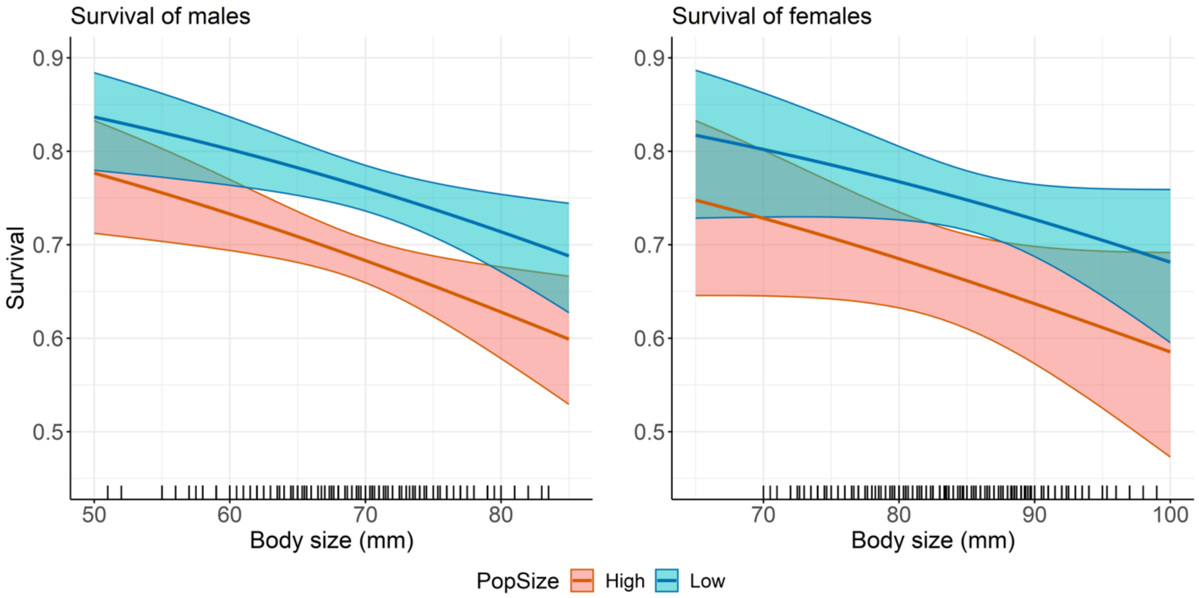

Figure 5. Relationship between body size (in mm) and survival for two different measures of population size for males (left panel) and females (right panel). We defined low population size as 100 individuals and high population size as 500 individuals. The solid lines represent the mean value, while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

Indirect effects on vital rates

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

Discussion

We found evidence that density, abiotic conditions, and individual factors had direct effects on vital rates. We also found indications for indirect effects of density and abiotic conditions on vital rates mediated by individual traits. These findings highlight the complexity of amphibian demography and the importance of a comprehensive analysis of the network of factors affecting vital rates.

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

Direct effects on growth and body size

As hypothesized, we found indication of an effect (although not strictly significant) of an abiotic factor (length of the active season) on growth, with longer seasons associated with bigger asymptotic sizes. Longer active seasons allow for a longer growth period, and possibly higher availability of resources. We also found indications for a negative density effect on the asymptotic size, but a positive one on the growth rate *k* indicating that at higher densities individuals might grow faster but to smaller sizes (Green & Middleton, 2013). This is what is generally expected, given the predicted lower per capita resource availability at higher densities and the need to grow faster to outcompete other individuals. Moreover, smaller females might have lower fecundity due to smaller and fewer eggs (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 density and active season length (e.g., Paterson & Blouin-Demers, 2018). Concerning the other growth parameter, *k*, the absence of strong effects on it could also mean that *k* is an important fitness trait and is buffered against factors like environment or density (environmental canalization, Gaillard & Yoccoz, 2003). Indeed, growing faster might be more important than growing to larger sizes. Despite the large body of literature on the effect of density and the environment on amphibian larval growth (Reading & Clarke, 1999; Ruthsatz et al., 2018), we found no studies on their 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 *B. 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 with a relatively regular biennial cycle of breeding as previously observed in this population (Grossenbacher, 2002). This is expected as they are capital breeders living in harsh conditions (Bull & Shine, 1979). This outcome has been found in previous studies on amphibians (e.g., 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, especially at higher elevations (Houston et al., 2007; McNamara & Houston, 2007). In more recent years, more females are reproducing in consecutive years, indicating that there might be other factors influencing the probability of skipping breeding that were not properly identified.

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

We also found evidence of the minimum temperature around emergence from hibernation negatively affecting the probability of skipping breeding. This supports the hypothesis that under harsh weather conditions females might forfeit breeding to not risk unsuccessful breeding or dying (Muths et al., 2013), especially in alpine 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 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.

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

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

Indirect effects on vital rates

Our findings suggest the presence of direct and indirect (body-size mediated) effects of population density and active season length on survival and breeding probabilities. The magnitudes of these effects do not seem to be so different to warrant a claim about their relative importance when estimating vital rates. Interestingly, we could observe the synchrony of the direct and indirect effects of the active season length on male survival. Longer active seasons are associated with decreased survival (direct effect) and an increased body size, which in turn is negatively associated with male survival (indirect effect). On the other hand, the negative associations between population size and body size, and between body size and survival (globally a positive indirect effect) 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 conditions, density, and individual factors can have on these rates. The fact that females show strong intermittent breeding seems to further indicate that the major onus energetically speaking is on them, and this seems to apply to most anurans (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 hypothesize that under current climate scenarios future active seasons will be long enough to lead to a more frequent annual breeding. However, current effects of climate change on this population are not as strong and predictable as expected. For instance, winter and spring temperatures are not constantly increasing, nor is snow cover constantly decreasing (Lenzi et al., 2023), perhaps due to topologically driven microclimatic conditions (Scherrer & Körner, 2011). If indeed females slowly move more consistently 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 at both 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 adult stage, which in amphibians has been rarely detected. Moreover, the relationships we found between environment and vital rates, combined with the ongoing and predicted scenarios of climate change, show the importance of integrating the outcome of such analyses into population models to obtain important insights on the dynamics and persistence of amphibian populations under changing environmental conditions.

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 supported by 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. We also thank Rose et al. (2022) for their open data policy, which enabled us to access code and data used in their study, with significant benefits for this study. Finally, we thank an anonymous reviewer and Brian Halstead for the constructive comments on a previous version of this manuscript.

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 analyzed the data. B.R.S. and A.O. provided feedback on the analyses. O.L. wrote the paper with input from all authors.

Conflict of interest

We declare no conflicts of interest.

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Appendix S1 – Other analyses

Section S1: 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 standardized 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 and S2). 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.

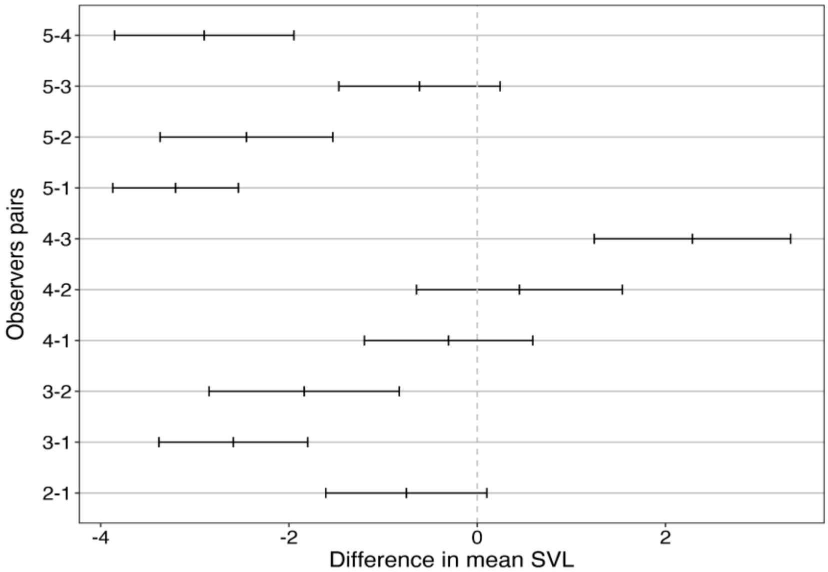

Figure S1. Piecewise comparison of the mean differences in measured snout-to-vent length (SVL, in mm), obtained with a Tukey's test. Measurers (i.e., observers) are identified with a number from 1 to 5. If the difference, accounting for 95% confidence intervals, overlaps zero is not considered significant.

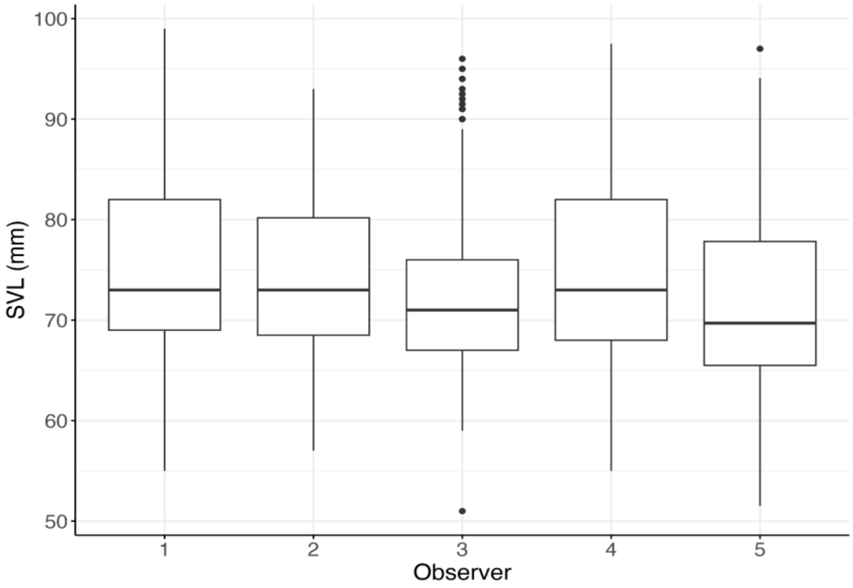

Figure S2. Boxplots showing the range of measured snout-to-vent (SVL, in mm) for each measurer (i.e., observer), identified with numbers going from one to five.

Section S2: Body condition

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 standardized 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 S3). We analysed the relationship between body condition and environmental conditions and population size. We hypothesized higher body condition in the breeding season if the previous active season was long. We also hypothesized 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 S4 and S5). 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 S6), further suggesting the presence of a threshold in body condition necessary to attempt breeding.

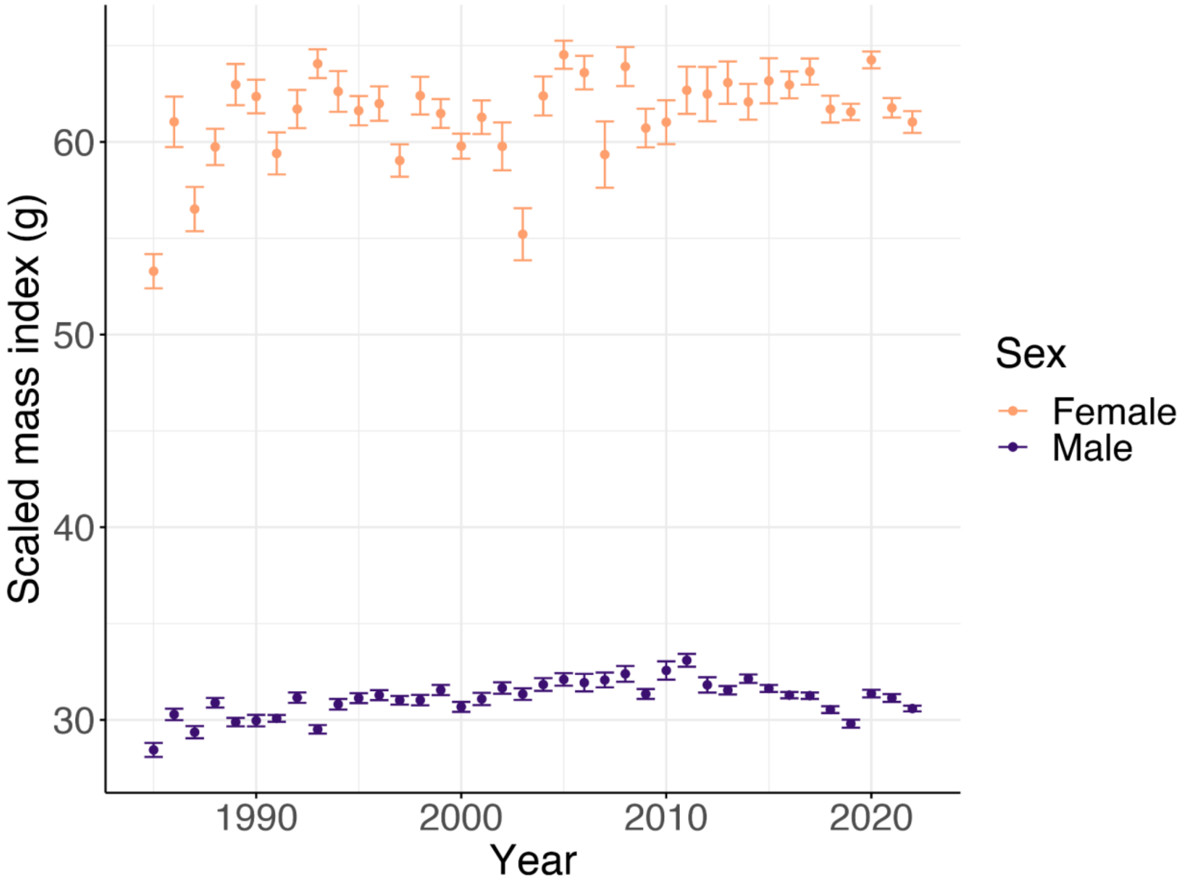

Figure S3. Average scaled mass index (calculated following Peig & Green, 2009) for females (red) and males (blue) over the period 1985-2022.

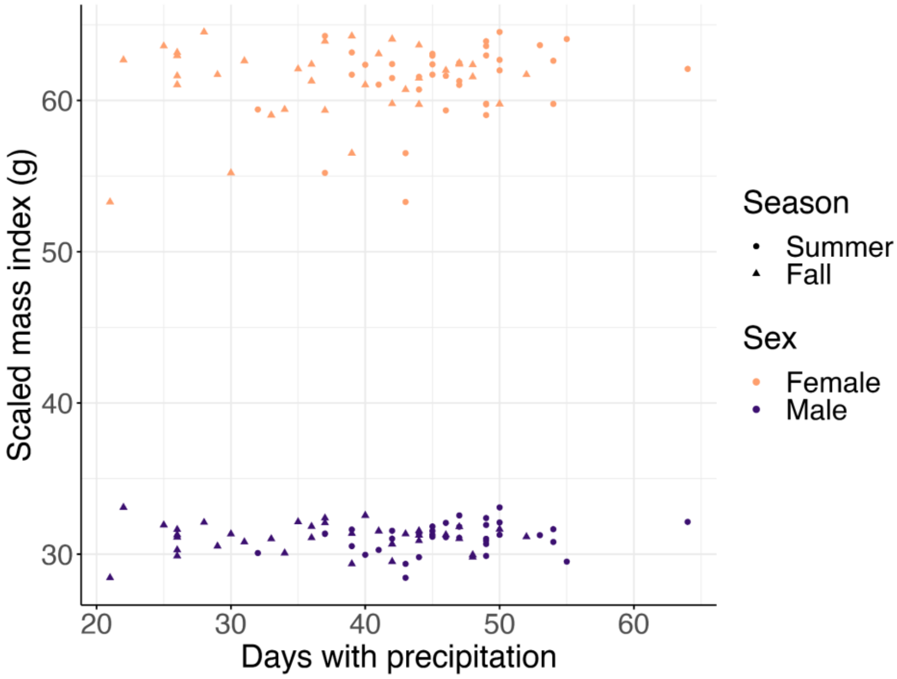

Figure S4. Relationship between mean scaled index and number of days with precipitation in summer (green) and autumn (red), for females (circles) and males (triangles).

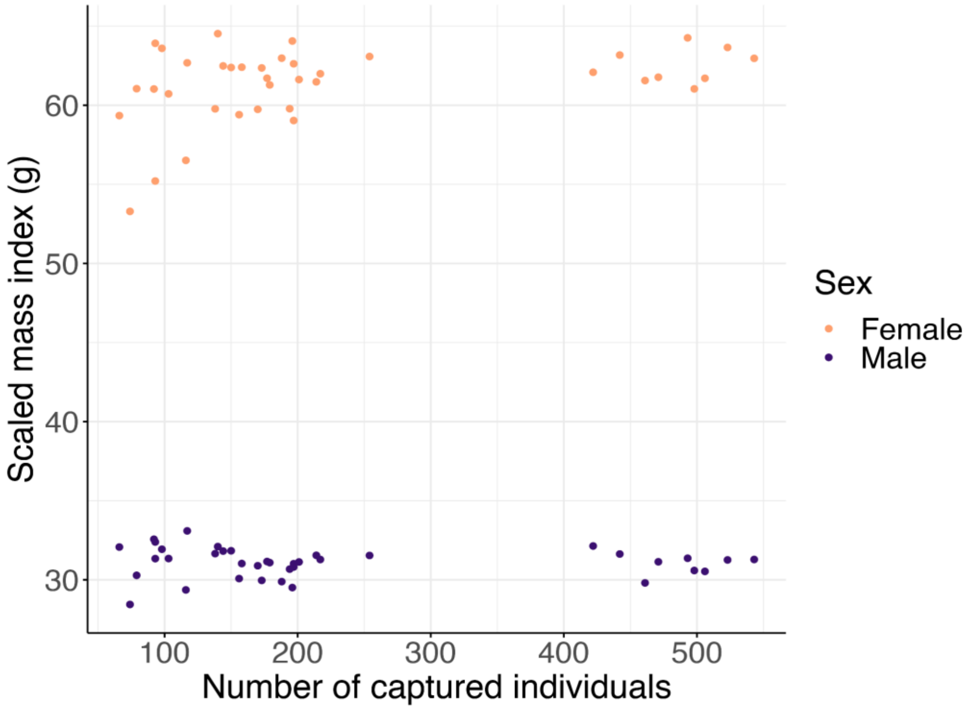

Figure S5. Relationship between the average yearly scaled mass index and the number of captured individuals during a breeding season (proxy of population size) for males (blue) and females (red).

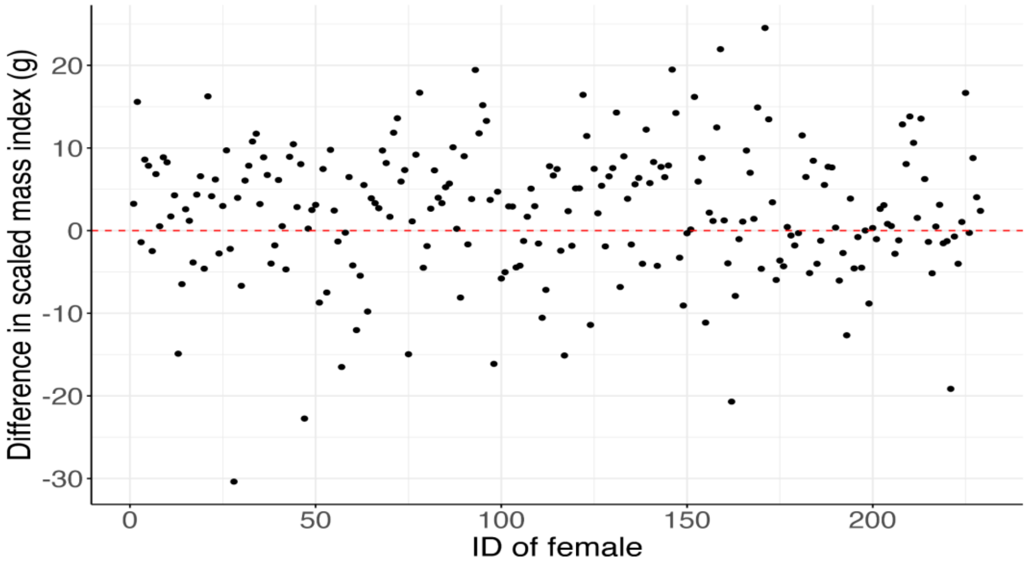

Figure S6. For each female we show the difference in scaled mass index between a year which followed a breeding year and a year which followed a non-breeding year. The horizontal dotted line at zero represents the case where a female experienced no difference in scaled mass index when reproducing after 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.

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Appendix 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 S1). In case of good fit, the true value should lay somewhere in the distribution, and the closer to the mean the better.

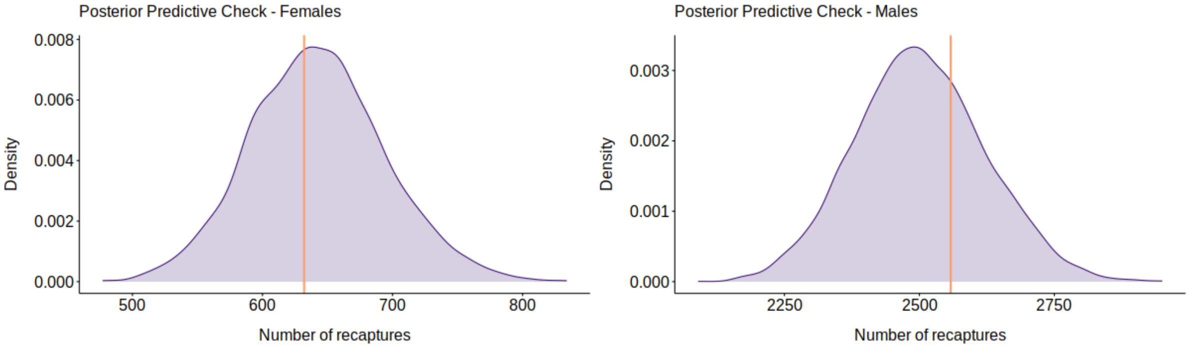
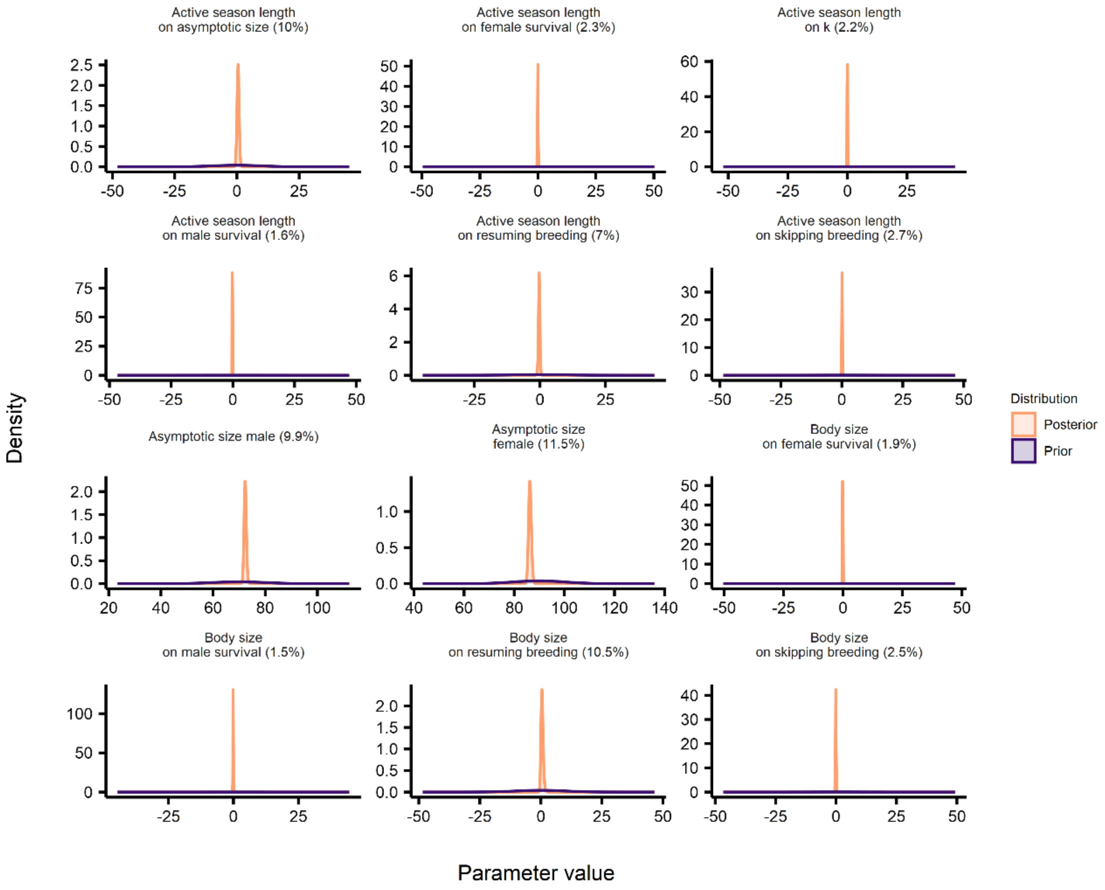
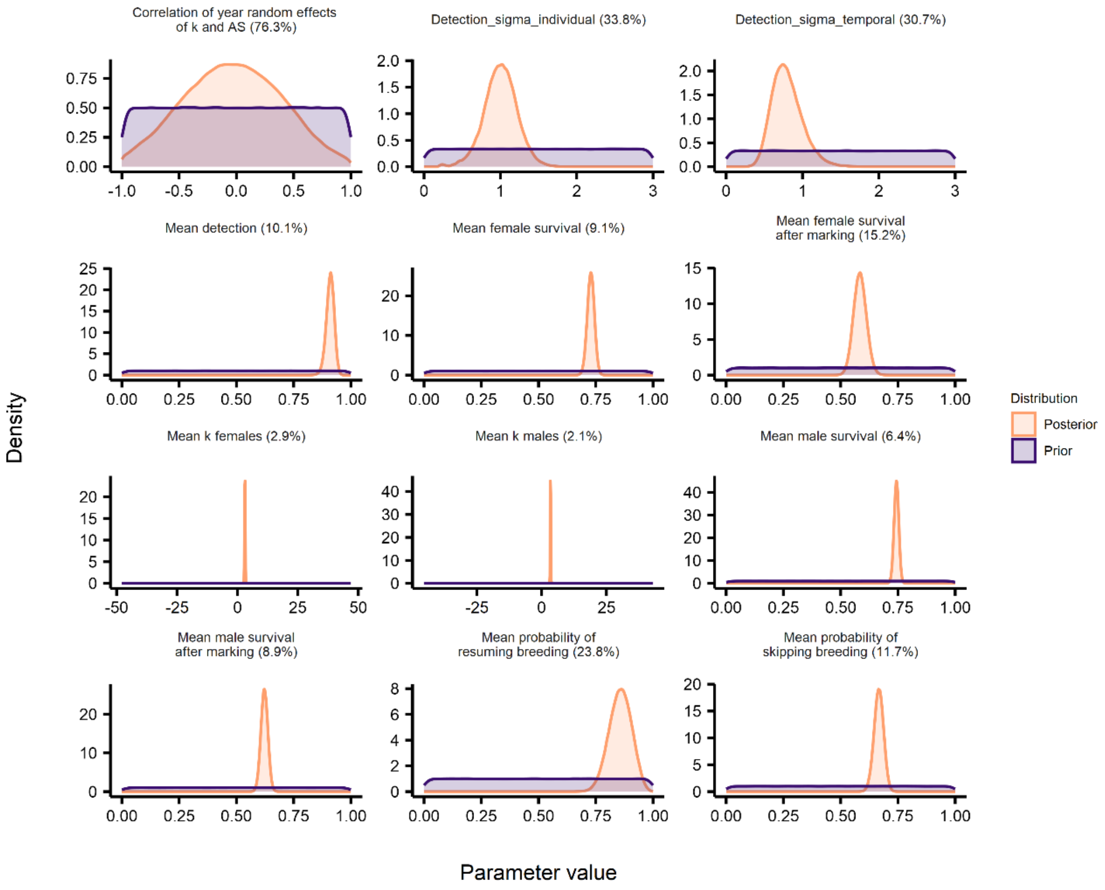


Figure S1. Posterior predictive checks to assess the goodness-of-fit of the capture-mark-recapture models. Following Nater et al. (2020), we chose 500 evenly spaced samples from the posterior distributions of the estimated parameters and used them to simulate 10 replicate capture-history datasets per 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). 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.




Correlation of year random effects of k and AS (76.3%)
Detection_sigma_individual (33.8%)
Detection_sigma_temporal (30.7%)
Mean detection (10.1%)
Mean female survival (9.1%)
Mean female survival after marking (15.2%)
Mean k females (2.9%)
Mean k males (2.1%)
Mean male survival (6.4%)
Mean male survival after marking (8.9%)
Mean probability of resuming breeding (23.8%)
Mean probability of skipping breeding (11.7%)
Density
Parameter value
Distribution
Posterior
Prior
0.00
0.25
0.50
0.75
1.00
-1.0
-0.5
0.0
0.5
1.0
0
1
2
3
1.5
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4
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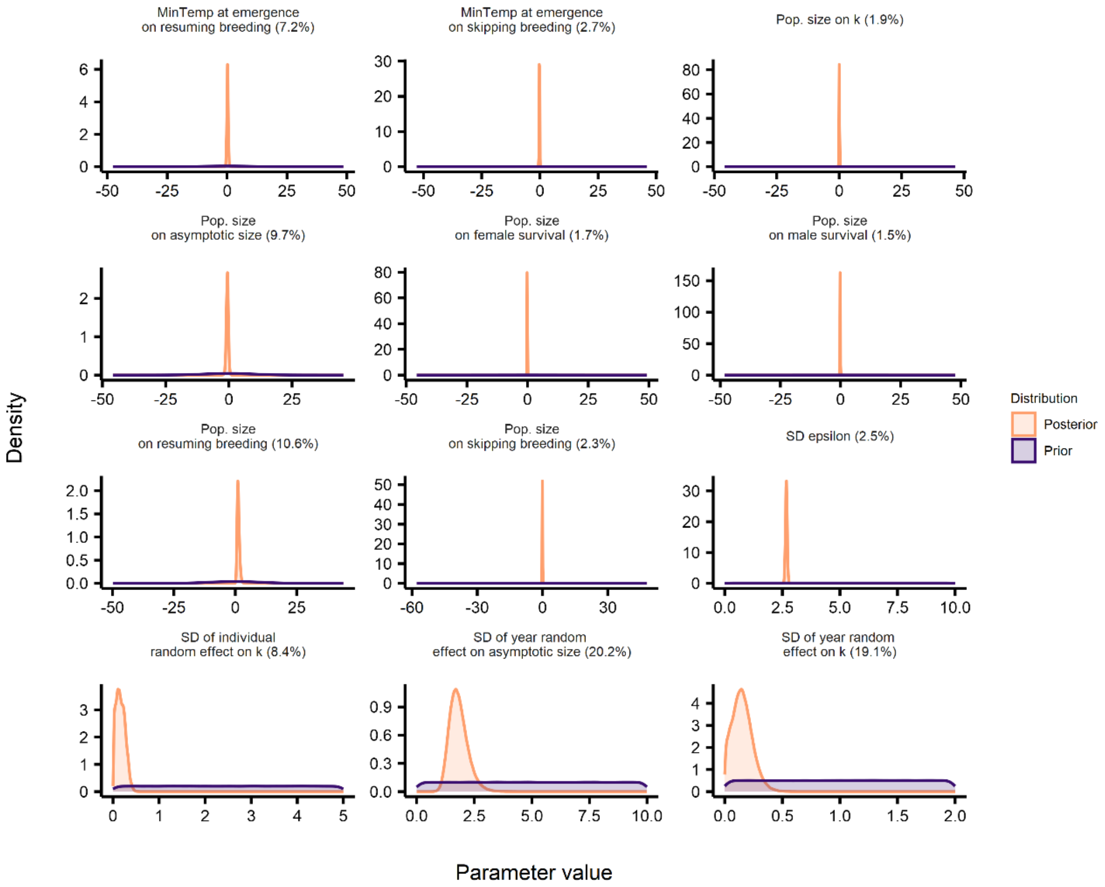

Figure S2. Prior-posterior overlap plots. For each of the estimated parameters we plotted prior (purple) and posterior (orange) distributions. In brackets we put the percentage of overlap of the two distributions.

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Nater, C. R., Vindenes, Y., Aass, P., Cole, D., Langangen, Ø., Moe, S. J., Rustadbakken, A., Turek, D., Vøllestad, L. A., & Ergon, T. (2020). Size- and stage-dependence in cause-specific mortality of migratory brown trout. *Journal of Animal Ecology*, *89*(9), 2122–2133. https://doi.org/10.1111/1365-2656.13269

Appendix S3 - Other plots from results

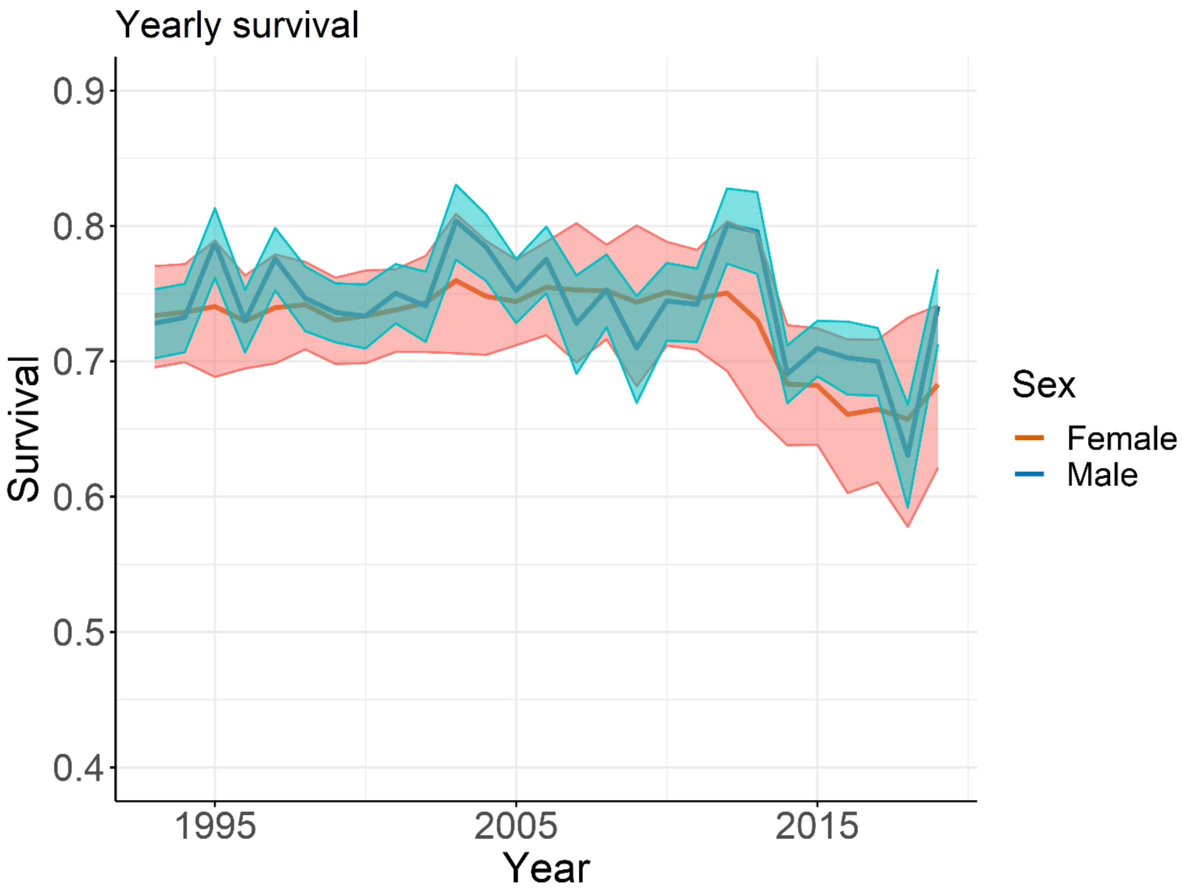

Figure S1. Year-specific survival rates for males (blue) and females (red). The solid line represents the average, while the shaded ribbons are the 95% credible intervals, obtained from the posterior distribution. The values are calculated assuming an average body size.

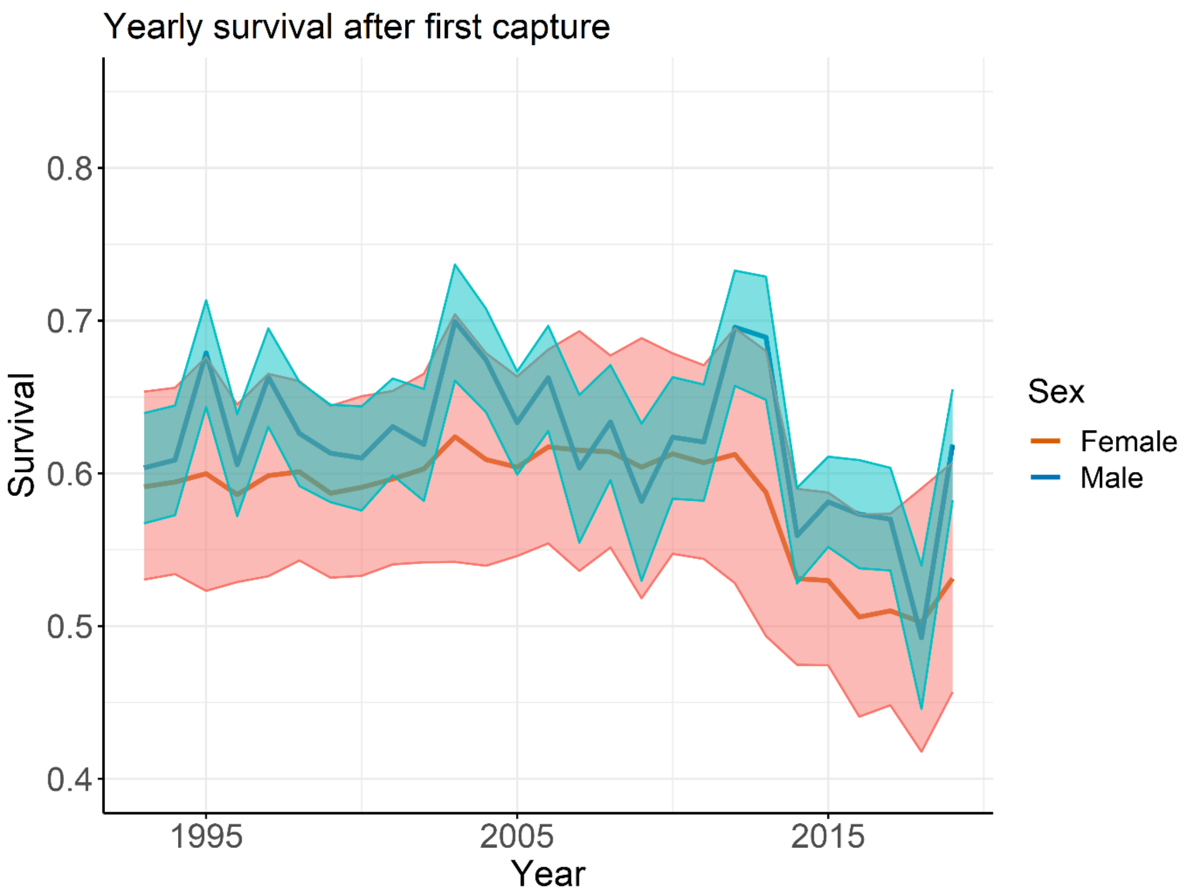

Figure S2. Year-specific survival rates in the year after first capture, for males (blue) and females (red). The solid line represents the average, while the shaded ribbons are the 95% credible intervals. The values are calculated assuming an average body size.

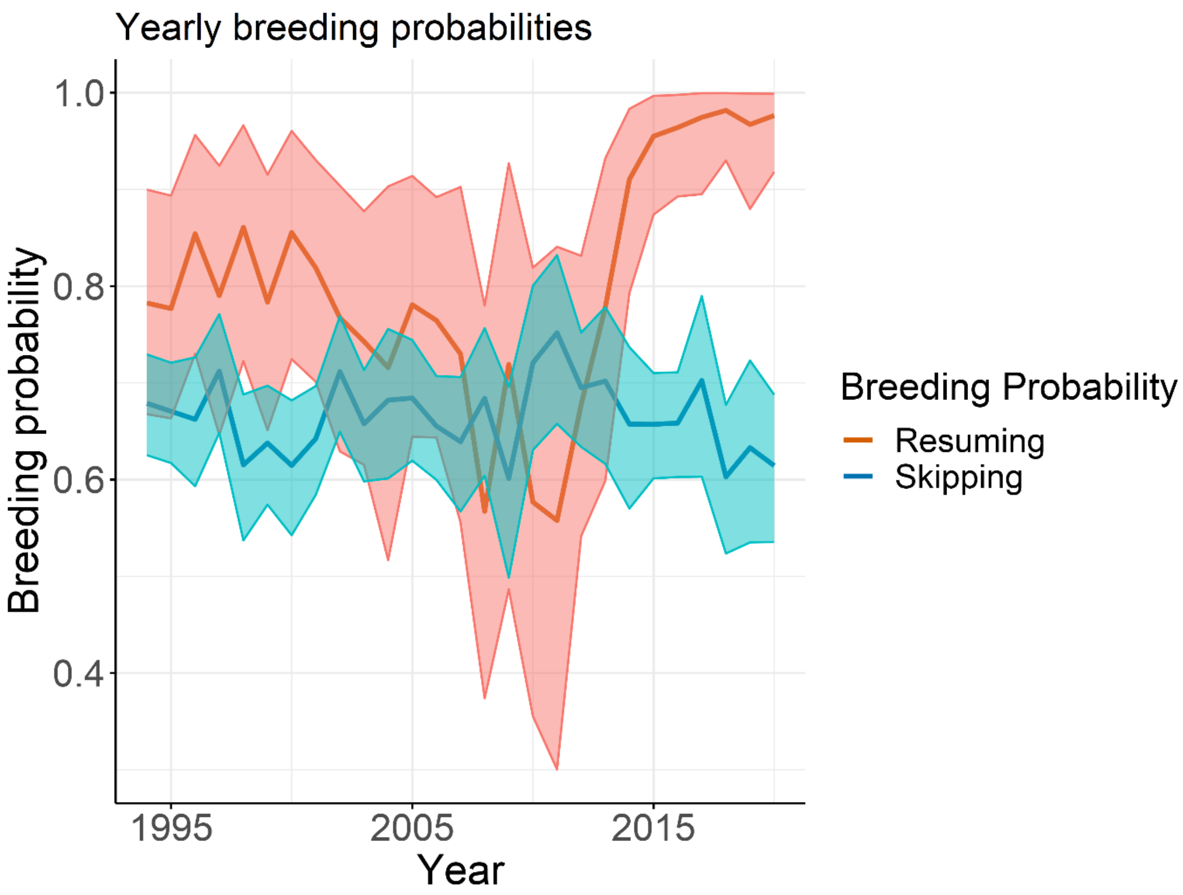

Figure S3. Year-specific probability of resuming (red) and skipping breeding (blue). The solid line is the average, while the shaded ribbons are the 95% credible intervals.

Chapter 3 – Mating System

Effects of body size and senescence on the mating patterns of an alpine population of the common toad

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Breitenmoser D., Lenzi O., Grossenbacher K., Zumbach S., Lüscher B., Althaus S., Thoma M., Schmocker D., Recher H., Ozgul A., Schmidt B.R. 2024. Effects of body size and senescence on the mating patterns of an alpine population of the common toad. *Master thesis*.

The layout and formatting of this chapter are slightly modified from the Master thesis in the scope of this thesis.

Abstract

1. Reproductive success is a key determinant of individual fitness. It is often shaped by a combination of intrinsic traits, such as body size or age, behaviour, and extrinsic factors, like environmental conditions and resource availability. The importance of these traits and behaviours in gaining a competitive advantage is amplified in situations of intense intrasexual competition, which can for instance arise in amphibian populations due to the often high male-skewed operational sex ratio during the breeding season. Consequently, there has been a strong focus on identifying important factors influencing mating success, such as male body size and the duration of the breeding season.
2. Many studies on this subject in amphibians have been conducted in experimental settings. Therefore, the analysis of long-term studies on natural populations can offer additional insights into the reproductive patterns of amphibians compared to experimental studies, contributing to the identification of the most important factors driving mating success.
3. Using an individual-based capture mark-recapture dataset spanning from 1982 to 2022, we analysed the reproductive patterns of an alpine population of the common toad (*Bufo bufo*). We tested for the effect of body size and age on the probability of a male to be in amplexus and on the probability of a male in amplexus to be displaced by another male while accounting for the density of individuals and the sex ratio. Furthermore, using a multistate modelling framework, we investigated whether males show intermittent breeding and whether males in amplexus have different survival rates compared to those not in amplexus.
4. The main findings concerned the size and age of the males and showed that body size was positively correlated with the probability of being in amplexus and negatively correlated with the probability of being displaced by another male, suggesting that larger males are more successful in securing mates. Age had a negative effect on the mating probability, suggesting a potential senescence effect. Additionally, there was weak evidence of size-assortative mating, as the correlation between male and female body size slightly increased the longer the females remained at the breeding pond. Finally, we found no evidence of intermittent breeding and no significantly different survival rates between males in amplexus and not in amplexus.
5. This study represents an in-depth investigation of the reproductive patterns of a natural amphibian population. Moreover, the combined benefits of long-term data and studying it in a natural setting offer a unique possibility to confirm experimental results using a long-term field study and to highlight the crucial role of body size and age as life-history traits.

Introduction

Which factors predict whether a male is in amplexus?

The reproductive strategies of animals are shaped by the need to maximize fitness under varying environmental conditions. Some of these strategies involve intense competition during brief breeding events. Many amphibian species exemplify this with explosive breeding (Wells, 1977), where their annual breeding effort is concentrated into a short period lasting only a few days to a few weeks. Explosive breeding is characterised by a massive gathering of breeders at the breeding site after hibernation. The consequence of such gatherings is the high-intensity competition to secure successful breeding in a short period of time. This competition is compounded by skewed operational sex ratios, which can arise when one sex is less abundant than the other at the breeding site. Sex ratios are typically skewed towards males for two main reasons. Females reach sexual maturity at an older age than males (Hemelaar, 1988; Schmidt et al., 2012) and frequently breed intermittently (Loman & Madsen, 2010; Lenzi et al., 2024). Intermittent breeding can arise due to the energy costs of reproduction, especially in females (Bull & Shine, 1979; Hayward & Gillooly, 2011; Davies et al., 2012). In certain contexts, such as in populations living in harsh environments, females might need more than one year to accumulate the resources necessary to breed. On the other hand, male reproduction, which is less energetically demanding, is limited by the availability of female partners. Thus, especially in explosive breeders, in a situation of skewed operational sex ratio, strong intrasexual competition is expected, and not all individuals can successfully reproduce.

The traits associated with successful reproduction in amphibians have been studied before Davies & Halliday, 1977; Gittins et al., 1980; Halliday, 1983; Loman & Madsen, 1986; Höglund, 1989; Höglund & Säterberg, 1989; Arntzen, 1999), but rarely in natural populations. Thus, the main focus of this thesis is to describe the mating system of a natural high-elevation population displaying a strong male-skewed operational sex ratio during their short breeding season and understand what factors drive successful breeding in males. We used individual-based data spanning 36 years (1987-2022) from a common toad (*Bufo bufo*) population located at the Grosse Scheidegg pass in the Swiss Alps. This population shows a highly variable operational sex ratio during the breeding season, ranging from 0.8 to 8 males per female, thus making it an ideal case study to explore patterns in the mating systems and identify the drivers of successful breeding under various levels of skewed sex ratio. Previous studies highlighted the importance of both individual-level traits, such as body size (Davies & Halliday, 1979), and population-level characteristics, such as the sex ratio and the total number of individuals at the breeding site (Gittins et al., 1980; Höglund, 1989). We expect body size to be positively associated with the probability of a male being found in amplexus (i.e., paired) with a female. In fact, larger males are stronger and can displace other males more easily (Davies & Halliday, 1977; Gittins et al., 1980) and can better hold on to females once they enter amplexus (Davies & Halliday, 1979). We use amplexus as a proxy for mating success since we do not observe fertilization of the eggs in most cases. Furthermore, we expect the sex ratio to be a significant predictor for amplecting success since the higher the sex ratio, the lower the number of females available per male. Moreover, we expect a positive correlation between the total number of individuals at the breeding site and the probability of being in amplexus. The higher the number of toads, the higher the number of encounters, thus the higher the chance of finding a mate. A previous study even suggested that females in amplexus might actively search locations with a high density of males to increase male-male competition (Davies & Halliday, 1977). Finally, age could negatively influence pairing success in males (Reading & Jofré, 2021), possibly due to a senescence effect (but see Kara, 1994). Alternatively, age could be positively correlated with pairing success due to its correlation with body size. In fact, older toads are on average bigger, as growth does not stop throughout a toad's lifetime; it only slows down (Duellman & Trueb, 1994). Taken together, the aim of this study is to confirm or reject previous studies, largely done in an experimental setting, and thereby to better integrate theory, experiments, and field studies (Werner, 1998).

Besides understanding what factors promote entering amplexus in males, it is crucial to identify what factors enable a male currently in amplexus to resist being displaced by another male. Displacements of males by other males are quite common, often resulting in new pairs at each sampling occasion, and only the male currently in amplexus during spawning will successfully reproduce. Displacements of males by other males are generally assumed to be the outcome of male-male competition (Halliday, 1983; Höglund & Robertson, 1987; Höglund, 1989). However, few studies argue that female choice might play a role, with females delaying spawning until a suitable male is in amplexus (Gittins et al., 1980) or actively moving towards more suitable males (Davies & Halliday, 1977). In this analysis, we investigate the drivers of displacement in males. Body size is probably an important factor again, with smaller males having a higher chance of being displaced (Davies & Halliday, 1979). Age could also play an important role if physical condition decreases as age increases. Finally, we expect higher density at the breeding site, and thus an increased number of encounters, to be positively associated with the probability of being displaced.

Size-assortative mating

Intrasexual competition in male common toads can result in three different outcomes. The first case is the absence of size-dependent or size-assortative mating (i.e., mating is random) (Höglund & Robertson, 1987). The second case is characterised by a higher probability of being found in amplexus for larger males than smaller ones (Davies & Halliday, 1979; Gittins, 1983; Reading & Clarke, 1983). Finally, the third case is when size-assortative mating occurs. Size-assortative mating refers to a situation where larger males are in amplexus with larger females and smaller males with smaller females (Davies & Halliday, 1977; Höglund, 1989; Arntzen, 1999). In other words, there is a positive correlation between the body size of females and males. Since female choice is thought to not exist in common toads, size-assortative mating likely occurs because a male of the same relative size as the female is harder to displace than males of different sizes (Höglund & Robertson 1987; Höglund, 1989). The factor that primarily determines which of the three mating patterns is observed is the duration of the competition period between males (i.e., the amount of time females spend at the breeding site). When there is very little time for competition (< 3 days) or when there is no male bias in the sex ratio, random mating is observed. When male competition lasts longer (>10 days), size-assortative mating should arise. With intermediate time for competition, larger males are expected to be overrepresented among amplecting males (Höglund, 1989). In this analysis, we aim to determine if size-assortative mating occurs in this population and whether it depends on how much time females spend at the pond. We expect the correlation between the body sizes of paired individuals to increase the longer the females are present at the pond.

Reproductive strategies of small and large males

Another interesting aspect we investigated in this thesis is the size-dependent differential arrival time at the breeding site. Large males have been observed to arrive at the breeding pond earlier than small males (Loman & Madsen, 1986), where they wait in the pond for the females to arrive and compete with other males to obtain mating opportunities. This is a reasonable strategy because large males have an advantage when competing for females in the pond (Davies & Halliday, 1977, 1979). However, amplexus can already initiate on land, and it appears to be more random than at the pond, with respect to body size. As postulated by Loman & Madsen (1986), the best strategy for small males is to wait on land and enter amplexus with incoming females. Because females arrive later at the breeding pond than males (Davies & Halliday, 1979), small males should also arrive later if this hypothesis is true. The later a female arrives, the less time she spends in the pond before spawning, and thus, less time is available for the male in amplexus to be displaced. In this study, we assessed whether small males employ this alternative breeding strategy. To do this, we compared the body size of males with their arrival time at the pond to see if large males arrived earlier than small males. In this population, males are not usually observed waiting outside the pond for females (K. Grossenbacher, *personal communication*). For this reason, we do not expect to find any difference in arrival time at the pond between small and large males.

Survival differences in males

Finally, the last aspects we analysed are the cost of reproduction and potential intrinsic differences in the quality of males. Given that resources are finite, individuals face trade-offs between reproduction, movement, somatic growth, and maintenance (Williams, 1966). Investing resources into reproduction leaves fewer resources available for the other processes. This common trade-off was found in a study on male common toads, where individuals who successfully bred showed a decreased body condition and survival rate (Reading & Jofré, 2021). Our study population lives in a harsh environment, with long winters and short summers. Therefore, potential costs of reproduction could be exacerbated by the difficult conditions that toads experience, such as low temperatures and lower food availability, especially during the breeding season. Thus, we expect to find decreased survival in paired males (i.e., males found in amplexus) compared to unpaired males (i.e., males at the breeding pond but not in amplexus) because amplexing males can spend multiple days without access to food (Davies & Halliday, 1979). Alternatively, if no differences in survival rates are observed, it could be because certain males are of better intrinsic quality, thus being able to enter amplexus without paying a survival cost.

Using 41 years of individual-based capture-mark-recapture data, we estimated survival rates of paired and unpaired males with a multistate model. Multistate models (Arnason, 1973; Schwarz, 2005) are an extension of the single-state Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), where individuals can survive or die but also transition between states. States can be geographical locations, disease states, developmental states, social states, etc. In our model, the states are reproductive status, namely paired and unpaired. This modelling framework also allows us to assess the presence of temporary emigration and quantify its magnitude (Burnham, 1993). Temporary emigration is the non-permanent absence of individuals from the study area, causing them to be unavailable for sampling in a given occasion. This is, for instance, the case when individuals skip breeding in a year with the prospect of returning in a better condition the following year. Failure to account for temporary emigration can cause bias in survival estimates (Kendall et al., 1997; Schaub et al., 2004) if the probability of being absent depends on the individual's presence in the previous year ("Markovian temporary emigration"). Temporary emigration has been observed in female common toads in the form of intermittent breeding (e.g., Lenzi et al., 2024), but its presence in male common toads is less certain (Muths et al., 2013; but see Frétey et al., 2004; Loman & Madsen, 2010). We thus investigate the presence of temporary emigration in male common toads and aim to see if survival differs between paired and unpaired males.

Methods

Study system

The common toad (*Bufo bufo*) is a widespread amphibian species of the Anura order. It occurs throughout most of Europe and reaches over the Ural Mountains into parts of Russia, China, and northern Kazakhstan. It is found between sea level and 3000 masl, though the high-elevation populations are only found in the southern part of the distribution. Its current protection status is Least Concern (IUCN SSC Amphibian Specialist Group, 2023). The common toad hibernates during winter in terrestrial hides and migrates to a breeding pond in spring, where they breed for 2-3 weeks before leaving the pond. The eggs hatch into tadpoles, which develop in the water for 10 to 12 weeks before undergoing metamorphosis, transforming them into lung-breathing, terrestrial animals. The juveniles stay on land during the breeding season until they reach sexual maturity, the age of which varies depending on sex and environmental conditions.

Figure 1. A common toad on the snow-covered shore of the breeding pond. Photo credit: Marco Thoma

The study site consists of a single pond of approximately 10x30 metres with a depth of roughly one metre. It is located below the Grosse Scheidegg pass in Switzerland

(46.6524 N and 8.0968 E, 1850 masl). The pond is in an open area with mostly grassy vegetation and is easily accessible by car.

Figure 2. The breeding pond of the study population is located in the Swiss Alps below the Grosse Scheidegg mountain pass, at 1850 masl. Photo credit: Daniel Breitenmoser

Data collection

Data collection began in 1982 with Agnes Hemelaar (Hemelaar, 1988), who used toe-clipping to mark toads until 1984. In 1985, the study system was taken over by Kurt Grossenbacher, who stopped using toe-clipping for individual marking because of the number of toes (4) that needed to be removed. Instead, batch-marking was done, with the removal of the same single toe from every new individual captured each year. This allowed the categorization of toads into cohorts for individuals first appearing between 1985 and 1992 (Grossenbacher, 2002). Passive Integrated Transponder (PIT) tags have been used since 1993 to mark and identify toads uniquely. The PIT tags are subcutaneously injected into the toad's back and can be read by a portable scanning device. Fieldwork is conducted at night about five times a year (mean: 5.22, range: 3-17) during a 1-3 week period in the common toad's mating season in spring. The weather and availability of fieldwork personnel largely determine the number of capture nights. The first capture night is conducted as soon as the first migrating toads are detected. Field workers check the study site regularly in person or using a webcam to assess the extent of snow cover, which helps determine when the toads initiate migration to the breeding site. Data collection begins after sunset with the help of head torches. Toads are caught with fishing nets and kept in plastic boxes, pairs separated from single individuals, until they are processed. All toads are sexed, weighed (in grams), measured (snout-vent length, in mm), and uniquely tagged if they do not already have a tag. It is noted whether toads are caught alone or in amplexus and who they are in amplexus with. After all the toads are processed, they are released back into the pond. Over the study period, more than 2100 males and 1300 females were uniquely marked.

Data analysis

All analyses were performed in R (version 4.4.0; R Core Team, 2024) with RStudio (version 2024.4.2.764; R Studio Team, 2024).

Which factors predict whether a male is in amplexus?

We used the binary variable *amplexus* and tested which covariates can be used to best predict the probability of a male to be in amplexus at any capture occasion. This was done using a generalised linear mixed-effects model of the binomial family. The covariates of interest were the size of the male (*size*, in mm), the sex ratio and count of all captured individuals in a given year (*sex ratio* and *count,* respectively), and the number of years since the first capture of a given male (*ysfc*, in years) (Table 1). We did not calculate daily sex ratio values because multiple observations of the same individual could have multiple associated daily sex-ratio values. This caused perfect separation of the response variable and did not let the models converge. The same was the case for the count covariate. The covariate *ysfc* acts as a proxy for age because the age of the toads upon breeding for the first time is unknown.

Table 1. Description of the covariates and their hypothesised effect on the probability of a male to be in amplexus.

Covariate	Hypothesis
size	The probability of amplexus increases as male size increases because large males are stronger.

sex ratio	The probability of amplexus decreases as the sex ratio increases because fewer females are available per male.
count	The probability of amplexus increases as the count increases because higher density leads to more encounters and fewer females that find no males.
ysfc	The probability of amplexus decreases with increasing age because of a senescence effect.

The model was defined as follows:

$$\text{logit}(\pi_{ij}) = \beta_0 + \beta_1 * size_{ij} + \beta_2 * sex\ ratio_j + \beta_3 * count_j + \beta_4 * ysfc_{ij} + \beta_5 * (size_{ij} \text{ X } sex\ ratio_j) + \beta_6 * (size_{ij} \text{ X } count_j) + \beta_7 * (size_{ij} \text{ X } ysfc_{ij}) + u_i + v_j ,$$

where π_{ij} is the probability of an individual i being in amplexus in year j, β_0 is the intercept, β_1- β_7 are the regression coefficients, u_i is the random intercept for the individual, and v_j is the random intercept for the year.

To check for collinearity between covariates, we calculated the Pearson correlation coefficient (Table S1; Appendix). The highest correlation was between *ysfc* and *size* (0.385), indicating no collinearity issues overall. All the covariates were standardised to avoid numerical issues when fitting the models. We compared models with different random effect structures, and an analysis of deviance determined that the best random effect structure included temporal (*year*) and individual-level random intercepts (Table S2; Appendix). Then, the intercept-only model and multiple biologically relevant models with different fixed effects were compared using AIC (Anderson & Burnham, 2002), and the model with all four covariates (*size*, *sex ratio*, *count*, *ysfc*) but no interactions was identified as the best (Table S3; Appendix). Nonetheless, we included the interactions of *size* with the three other covariates because of their biological relevance. Since the outcome of the model is binary (amplexus: Yes/No), no dispersion parameter needs to be investigated. Moreover, all observations are considered independent because individuals grow from one year to the next and are, therefore, not identical in subsequent years. A few data points may be regarded as outliers according to the binned plot (Figure 3), but there is no reason to believe that any of the values are impossible, and they were kept in the model.

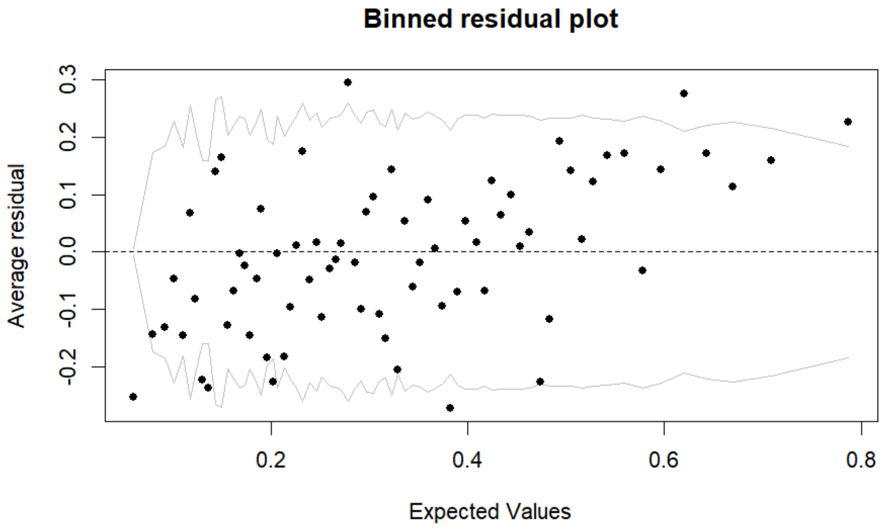

Figure 3. Binned residual plot to assess outliers. Data are divided into categories (bins) based on their fitted values and plotted against the average residual. The grey lines depict the +/- 2 standard error bounds. If the model was true, 95% of the dots would be within the grey lines. In this plot, 63/71 (88.7%) black dots fall within the grey bounds.

The variance inflation factor of the model without interaction terms was below 1.17 for all covariates, indicating no collinearity issues. The assumption of the linearity of the covariates with the log odds of the outcome was violated for the covariate *sex ratio*. This issue was fixed by log-transforming it. To assess the fit of the model, the theoretical pseudo-R-squared values (Nakagawa & Schielzeth, 2013) were calculated using the r.squaredGLMM function from the *MuMIn* package (version 1.48.4; Bartoń, 2024). The *marginal* R^2_{GLMM} (0.188) represents the variance explained by the fixed effects, and the *conditional* R^2_{GLMM} (0.232) represents the variance explained by the entire model.

We also tested what covariates can predict whether a male in amplexus will be displaced by another male. When a specific combination of male and female was caught more than once within the same year, only the last observation was considered to avoid violating the assumption of independent observations. The potential explanatory variables were the size of the male (*size*), the sex ratio (*sex ratio*), the count (*count*), and the years since the first capture of the male (*ysfc*: a proxy for age or experience). All potential explanatory variables were standardised to avoid numerical problems with the models. No high correlations were detected between the covariates (all below 0.291) (Table S4; Appendix).

We fit different combinations of biologically meaningful covariates and compared them to the null model. AIC (Anderson & Burnham, 2002) favoured a generalised linear model of the binomial family, including *size*, *count*, *ysfc*, and all the two-way interactions (Table 2; Table S5, Table S6; Appendix).

Table 2. Description of the covariates in the selected model, and their hypothesised effect.

Covariate	Hypothesis
size	The probability of being displaced decreases as male size increases because large males are stronger.
sex ratio	The probability of being displaced increases as the sex ratio increases because fewer females are available per male, meaning that male competition is stronger.
count	The probability of being displaced increases as the count increases because more encounters lead to more displacement possibilities.
ysfc	The probability of being displaced increases with increasing age because of a senescence effect.

The model was defined as follows:

$$\mathrm{logit}(\pi_{ij}) = \beta_0 + \beta_1 * size_{ij} + \beta_2 * count_j + \beta_3 * ysfc_{ij} + \beta_4 * (size_{ij} \times count_j) + \beta_5 * (size_{ij} \times ysfc_{ij}) + \beta_6 * (count_j \times ysfc_{ij}) \, ,$$

where π_{ij} is the probability of an individual i being displaced in year j, β_0 is the intercept, and β_1- β_6 are the regression coefficients.

The binned plot for this model indicates no issues (Figure 4). The assumption of linearity of the covariates with the log-odds of success is mostly met. There is one datapoint that looks like a potential outlier. This datapoint represents a male individual who has been observed at the pond for 17 years. Even though it is somewhat of an outlier, there is no reason to suspect that the datapoint is faulty. We ran the model both with and without that datapoint and there was almost no difference except obtaining a slightly better plot when assessing the linearity of predictors with the log-odds of success. We used the "nagelkerke" method from the R package *piecewiseSEM* (version 2.3.0; Lefcheck, 2016) to calculate the R^2 value.

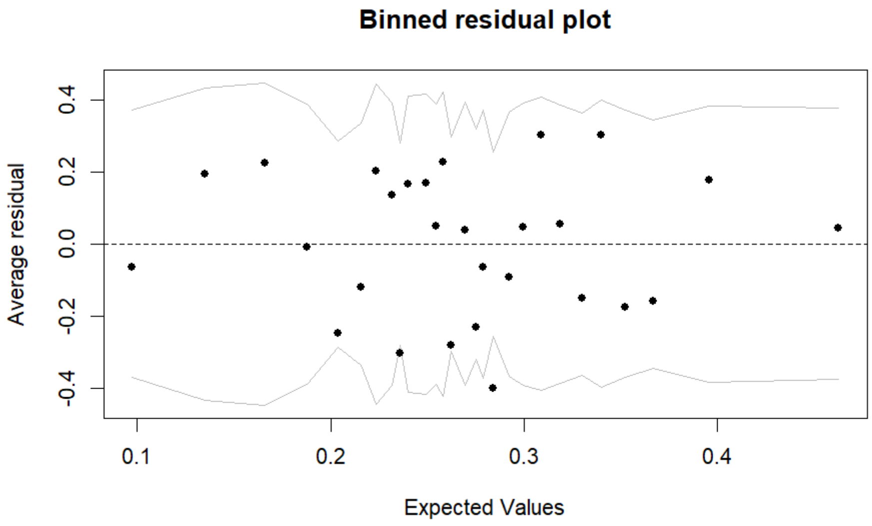

Figure 4. The binned plot of the residuals shows a good fit of the model to the data.

Size-assortative mating

We tested for size-assortative mating by calculating the Pearson correlation coefficient of the body sizes of pairs in amplexus, as previously done (Davies & Halliday, 1977; Böll & Linsenmair, 1998; Gramapurohit & Radder, 2012). We calculated the Pearson correlation once for all observations, then split them into two groups depending on how long the female was present at the breeding pond (< 5 days or ≥ 5 days) and calculated the Pearson correlation again. The assumptions of the Pearson correlation were mostly met (Schober et al., 2018). The only issue was the assumption of normality of the body sizes, which was violated for both males and females due to the large dataset and the artificial binning of the measurements caused by a lack of precision. However, the histograms of the variables show underlying normal distributions (Figure 5).

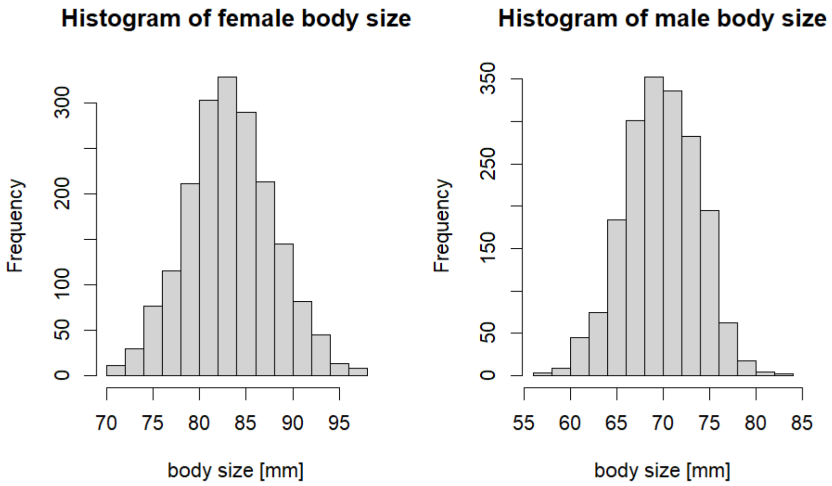

Figure 5. The histograms of the female and male body size variables show a normal distribution.

Reproductive strategies of small and large males

Previous research has postulated the theory of an alternative reproductive strategy employed by small males, where they wait for females along common migrating routes. This strategy is supposed to reduce intrasexual competition because the small males do not need to displace another male before getting a chance to enter amplexus. If this strategy is employed, small males should arrive at the breeding pond together with the females and later than the other males. For every male, we calculated the difference in time between its arrival and the arrival of the first male in that year. Because of the synchronous nature of the breeding migration, many male toads arrive at the pond on the same day. Additionally, the fact that sampling does not occur daily causes many of the arrival times of the toads to be clumped together on certain days rather than evenly distributed (Figure 6).

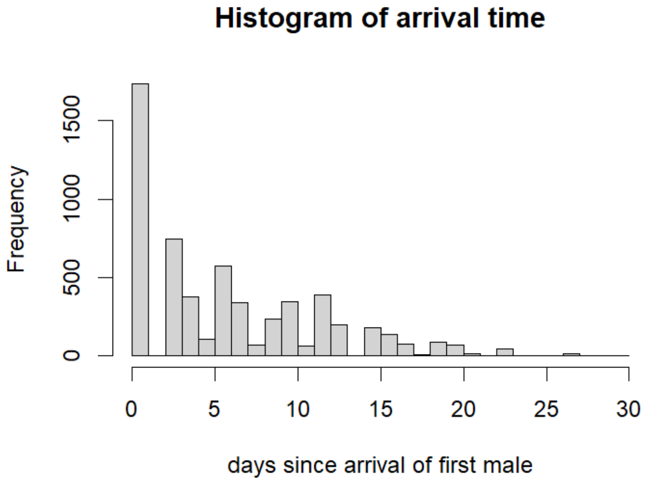

Figure 6. The histogram shows the unevenly distributed arrival time of males. Day 0 is when the first male was observed at the pond each year.

Almost 30% of all observations occur on day zero, requiring zero inflation to be accounted for. A likelihood ratio test showed that a zero-inflated negative binomial (ZINB) model was the best, with *arrival time* as the dependent variable and the male size as the explanatory variable. The best model had the count submodel defined by male size and year, and the zero-inflation submodel was defined by *year* only (Table S7; Appendix).

Count model (negative binomial): $\log(\lambda_{ij}) = \beta_0 + \beta_1 * size_{ij} + \beta_2 * year_j$,

where λ_{ij} is the expected count of the dependent variable *arrival time*, β_0 is the intercept, and β_1 and β_2 are the coefficients for the predictors *size* and *year*, respectively.

Zero-inflation model (logistic): $\text{logit}(\pi_j) = \gamma_0 + \gamma_1 * year_j$,

where π_j is the probability of an observation being an excess zero, γ_0 is the intercept, and γ_1 is the coefficient for the predictor *year*.

Survival differences in males

Given that reproduction is costly, especially in harsh environments (Laiolo & Obeso, 2017), we wanted to assess if attempted breeding leads to reduced survival. Therefore, we ran a capture-mark-recapture multistate model (Lebreton et al., 2009) to compare survival estimates for males found in amplexus (paired) with males at the breeding site but not found in amplexus (unpaired). Moreover, we wanted to verify if males show intermittent breeding, as previously shown in male boreal toads (*Bufo boreas*) (Muths et al., 2006) and female common toads (e.g., Lenzi et al., 2024). Intermittent breeding consists of skipping breeding in a year with the prospect of resuming breeding in a better condition in the following year. We tested for this behaviour, also known as temporary emigration in the capture-mark-recapture literature (Schmidt et al., 2002), with the goodness-of-fit test 2ct, which is available in the R2ucare package (Gimenez et al., 2018). No evidence of temporary emigration was found. Other tests (test3sr, test2cl, test3sm) from this package showed possible transience effects and overdispersion in the capture histories. We accounted for overdispersion by including an individual-level random effect for the detection probability (Abadi et al., 2013). We accounted for the transience effect by separating the states of the survival model into two stage classes (Genovart & Pradel, 2019). The first stage class is composed of first-time captures and the second stage class of all the others. This allowed us to separately estimate the survival probabilities of first-time captured adults from the older adults. We fit multiple models with temporally varying detection probability and survival probabilities and did model selection using WAIC (Watanabe, 2013), as is commonly done in the used package NIMBLE. A year random effect on the detection probability improved the model further and was thus included.

There are five different states in the model: unpaired first-time males (UP'), paired first-time males (P'), unpaired older males (UP), paired older males (P), and dead. Captured animals are assigned the state UP', P', UP, or P depending on whether they were in amplexus with a female or not during capture and depending on the capture occasion. Animals survive in their state from one year to the next with probabilities $\Phi_{UP'}$, $\Phi_{P'}$,Φ_{UP}, and Φ_{P}, respectively. They die with probabilities $1-\Phi_{UP'}$, $1-\Phi_{P'}$, $1-\Phi_{UP}$, and $1-\Phi_{P}$. Animals can transition from one state to another, except dead animals. Ψ_{UPP} describes the probability of transitioning from UP to P while $(1-\Psi_{UPP})$ describes the probability of staying in state UP. Conversely, Ψ_{PUP} is the probability of transitioning from P to UP while $(1-\Psi_{PUP})$ is the probability of staying in state P (Figure 7).

$$\begin{array}{c|ccccc} & \text{UP'} & \text{P'} & \text{UP} & \text{P} & \text{dead} \\ \hline \text{UP'} & 0 & 0 & \Phi_{UP'} * (1 - \Psi_{UPP}) & \Phi_{UP'} * \Psi_{UPP} & 1 - \Phi_{UP'} \\ \text{P'} & 0 & 0 & \Phi_{P'} * \Psi_{PUP} & \Phi_{P'} * (1 - \Psi_{PUP}) & 1 - \Phi_{P'} \\ \text{UP} & 0 & 0 & \Phi_{UP} * (1 - \Psi_{UPP}) & \Phi_{UP} * \Psi_{UPP} & 1 - \Phi_{UP} \\ \text{P} & 0 & 0 & \Phi_{P} * \Psi_{PUP} & \Phi_{P} * (1 - \Psi_{PUP}) & 1 - \Phi_{P} \\ \text{dead} & 0 & 0 & 0 & 0 & 1 \end{array}$$

Figure 7. The state-transition matrix describes how the states at time t (rows) transition into the states at time t+1 (columns). The parameter Φ represents a survival rate and the parameter Ψ represents a transition rate. UP' refers to the first-time unpaired males, UP to the older unpaired males, P' to the first-time paired males, and P to the older paired males.

Toads are observed in their state with detection probability *p*. They cannot be observed in the wrong state, meaning there is no state assignment error. Living toads are not observed with probability 1-*p*, and dead toads are not observed with probability 1 (Figure 8).

$$\begin{array}{c|ccccc} & \text{seen UP'} & \text{seen P'} & \text{seen UP} & \text{seen P} & \text{not seen} \\ \hline \text{UP'} & p & 0 & 0 & 0 & 1 - p \\ \text{P'} & 0 & p & 0 & 0 & 1 - p \\ \text{UP} & 0 & 0 & p & 0 & 1 - p \\ \text{P} & 0 & 0 & 0 & p & 1 - p \\ \text{dead} & 0 & 0 & 0 & 0 & 1 \end{array}$$

Figure 8. The observation matrix links the true states to the observed states. The parameter p describes the detection probability.

We estimated the survival probabilities, detection probability, and transition rates in a Bayesian framework, using a multistate Hidden Markov Model. The model was developed using Markov chain Monte Carlo (MCMC) sampling with R-package NIMBLE (version 1.2.0, de Valpine et al., 2017). We ran the final model with four chains for 30'000 iterations each, preceded by 10'000 iterations of burn-in samples. To assess model convergence, we compared the posterior distributions to the prior distributions and computed the Brooks-Gelman-Rubin statistic R-hat (Brooks & Gelman, 1998). We evaluated the goodness-of-fit of the multistate model using posterior predictive checks, after Nater et al. (2020). For this, we selected 500 evenly spaced samples from the posterior distributions of the estimated parameters and generated ten replicate datasets per sample, resulting in 5000 simulated datasets. We then calculated the number of recaptures per simulated dataset. Additionally, we calculated the number of recaptures by state to assess the validity of the transition rates. Finally, we visually compared the observed number of recaptures to the simulated values and computed a Bayesian p-value.

Results

Which factors predict whether a male is in amplexus?

To assess the factors influencing whether a male was in amplexus or not, we fit generalised linear mixed models to the data. The best model, according to AIC, included *male size*, *sex ratio*, count of other males present (*count*), years since first capture (*ysfc*), and all the interactions with *male size*, as fixed effects. The results (Table 3) indicated that larger male size was positively associated with amplexing success (estimate = 0.508, SE = 0.086, z = 5.906, $p < 0.001$), with an estimated odds ratio of 1.66 (95% CI: 1.40–1.97). On the original scale of measurement, this equates to an absolute increase in the probability of being in amplexus by 0.18 for a 70 mm male compared to a 60 mm male when all other covariates are held constant at their mean (Figure 9).

Table 3. Summary of the model investigating the predictors for males in amplexus. The significant predictors are in bold.

	estimate	odds-ratio	std. error	p-value
intercept	**0.695**	**2.00**	**0.160**	**<0.001**
male size	**0.508**	**1.66**	**0.086**	**<0.001**
log(sex ratio)	**-1.375**	**0.25**	**0.139**	**<0.001**
count	0.103	1.11	0.065	0.114
ysfc	**-0.207**	**0.81**	**0.044**	**<0.001**
male size:log(sex ratio)	-0.055	0.95	0.073	0.452
male size:count	0.055	1.06	0.037	0.132
male size:ysfc	-0.057	0.94	0.041	0.159

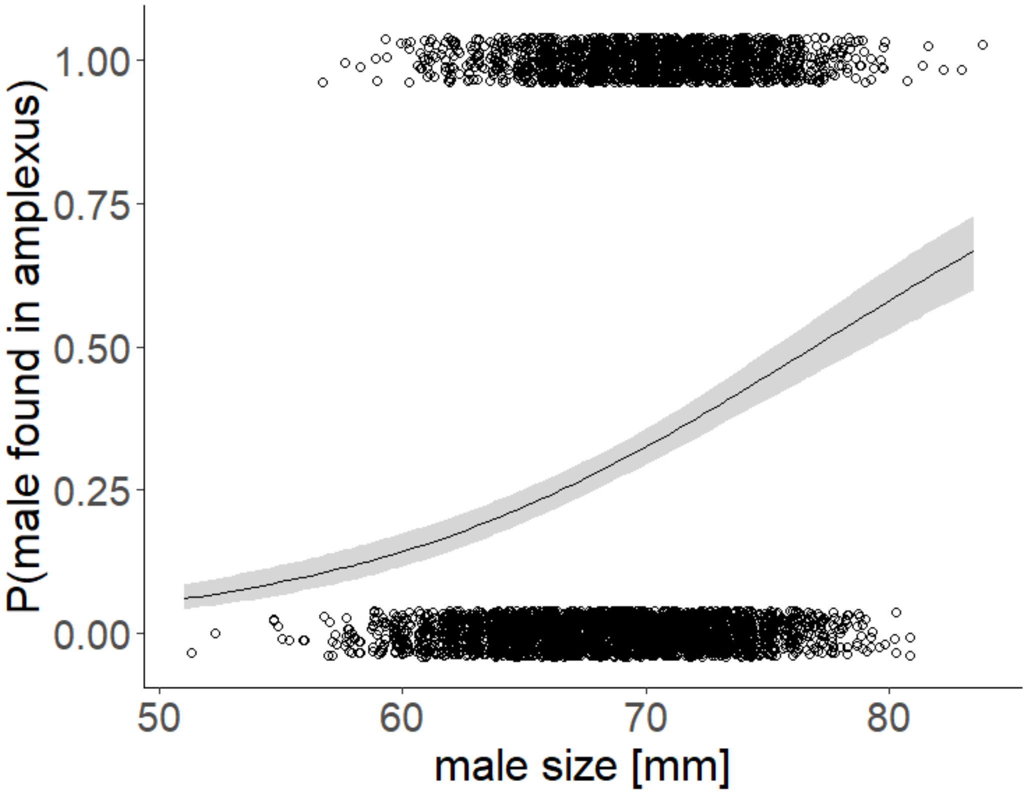

Figure 9. Prediction plot for the probability of a male being found in amplexus with respect to the variable "male size", back-transformed to the original measurement scale. All other covariates were held constant at their mean. The grey ribbon represent the 95% CI.

In contrast, the sex ratio had a significant negative effect on the probability that a male was found in amplexus (estimate = -1.375, SE = 0.139, z = -9.872, $p < 0.001$), corresponding to an odds ratio of 0.25 (95% CI: 0.19–0.33). This means that an increase from 1:1 to 8:1 in the sex ratio results in a decrease of 0.564 in the probability of being in amplexus when all other covariates are held constant at their mean (Figure 10).

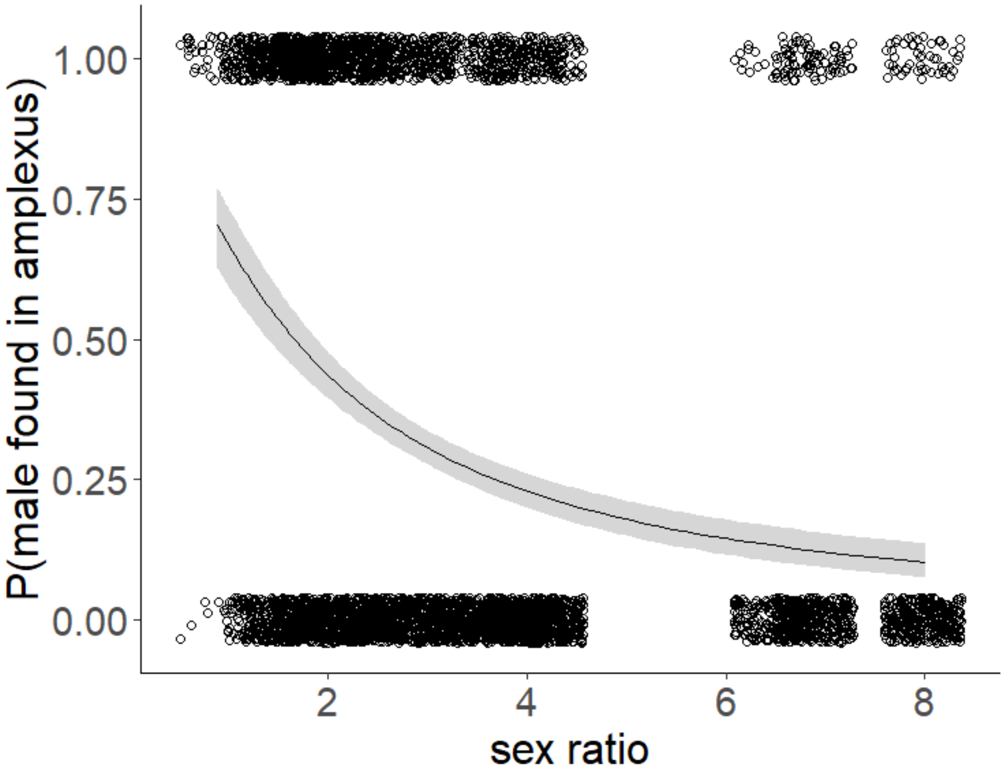

Figure 10. Prediction plot for the probability of a male being found in amplexus with respect to the variable "sex ratio", back-transformed to the original measurement scale. All other covariates are held constant at their mean. The grey ribbon represent the 95% CI.

Finally, the effect of years since the first capture (*ysfc*) was also significant, with a negative association with amplexing success (estimate = -0.2067, SE = 0.044, z = -4.747, p < 0.001), resulting in an odds ratio of 0.81 (95% CI: 0.75–0.89). This indicates that an individual who has been visiting the pond for ten years has a 0.154 lower probability of being in amplexus than a first-time visitor if all other covariates are held constant at their mean (Figure 11).

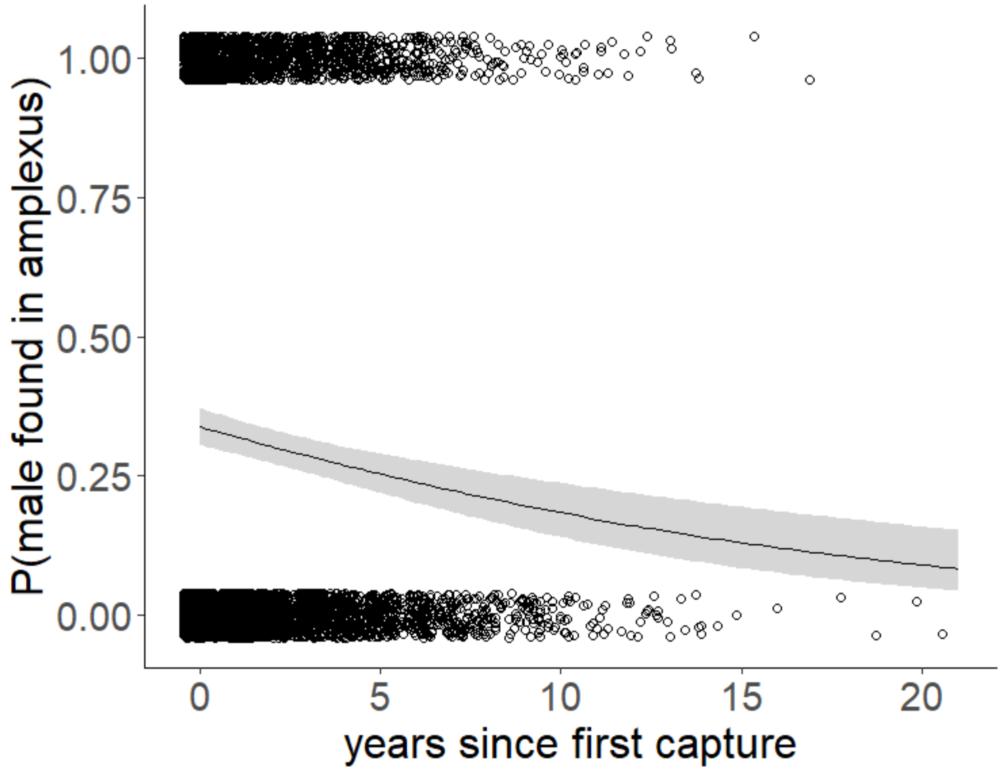

Figure 11. Prediction plot for the probability of a male being found in amplexus with respect to the variable "years since first capture" (*ysfc*), a proxy for age, back-transformed to the original measurement scale. All other covariates are held constant at their mean. The grey ribbon represent the 95% CI.

The interaction terms were not significant. The standard deviations of the random effects for individual (ID) and year were estimated at 0.342 and 0.269, respectively. The *marginal* R^2_{GLMM} was 0.188 and the *conditional* R^2_{GLMM} was 0.232.

To assess the factors influencing whether a male was displaced over the course of a breeding season, we fit a generalised linear model. The results (Table 4) show a significant decrease in the probability of being displaced as male size increases (estimate = -0.261, SE = 0.088, z = -2.958, p = 0.003) with an accompanying odds ratio of 0.77 (95% CI: 0.65–0.91). On the original measurement scale, this equates to a 0.14 lower probability of being displaced for a 70 mm male compared to a 60 mm male, with all other variables held constant at their mean (Figure 12).

Table 4. Summary of the model investigating the predictors for displacement of males. The significant predictors are in bold.

	estimate	odds-ratio	std. error	p-value
intercept	**-1.059**	**0.347**	**0.087**	**<0.001**
male size	**-0.261**	**0.77**	**0.088**	**0.003**
count	-0.079	0.92	0.083	0.341
ysfc	-0.055	0.95	0.099	0.579
male size:count	-0.142	0.87	0.085	0.092
male size:ysfc	-0.087	0.92	0.088	0.325
count:ysfc	**-0.231**	**0.79**	**0.086**	**0.007**

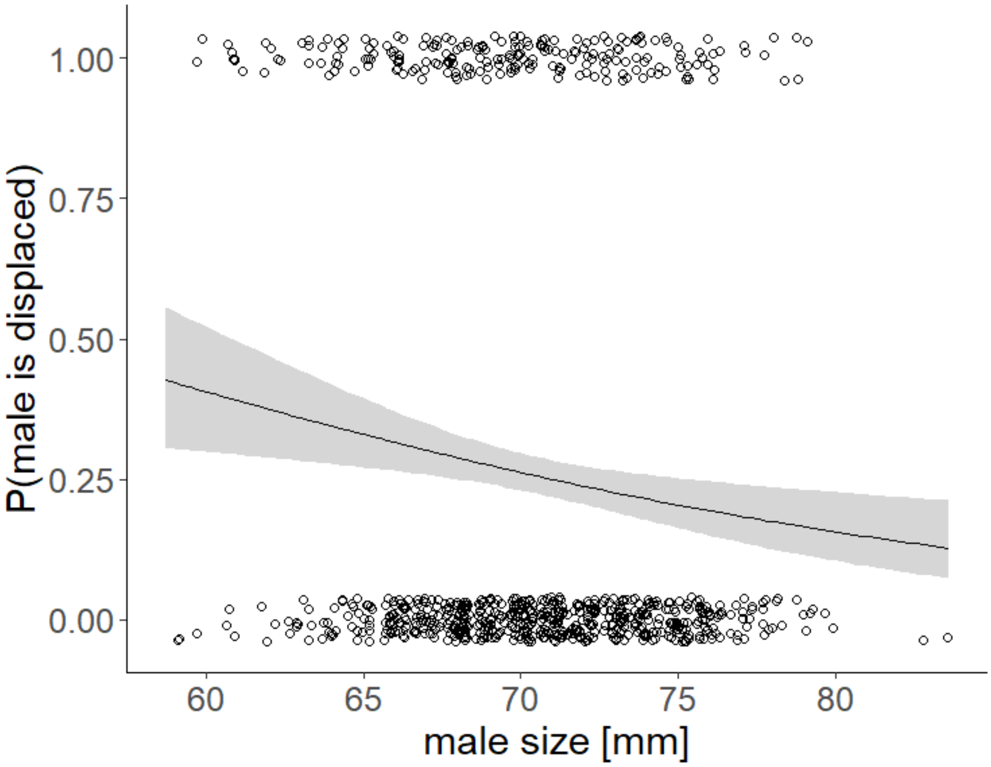

Figure 12. Prediction plot for the probability of a male being displaced with respect to the variable "male size", back-transformed to the original measurement scale. All other covariates are held constant at their mean. The grey ribbon represent the 95% CI.

The only other significant predictor was the interaction between *count* and *ysfc* (estimate = -0.231, SE = 0.086, z = -2.695, p = 0.007), which had an odds ratio of 0.79 (95% CI: 0.67–0.94). This indicates that the more individuals are present at the breeding pond, the bigger the negative effect of age is on the probability of being displaced. In other words, age increases the probability of being displaced, but only when there are few individuals (Figure 13). The R^2 value of the model was 0.045.

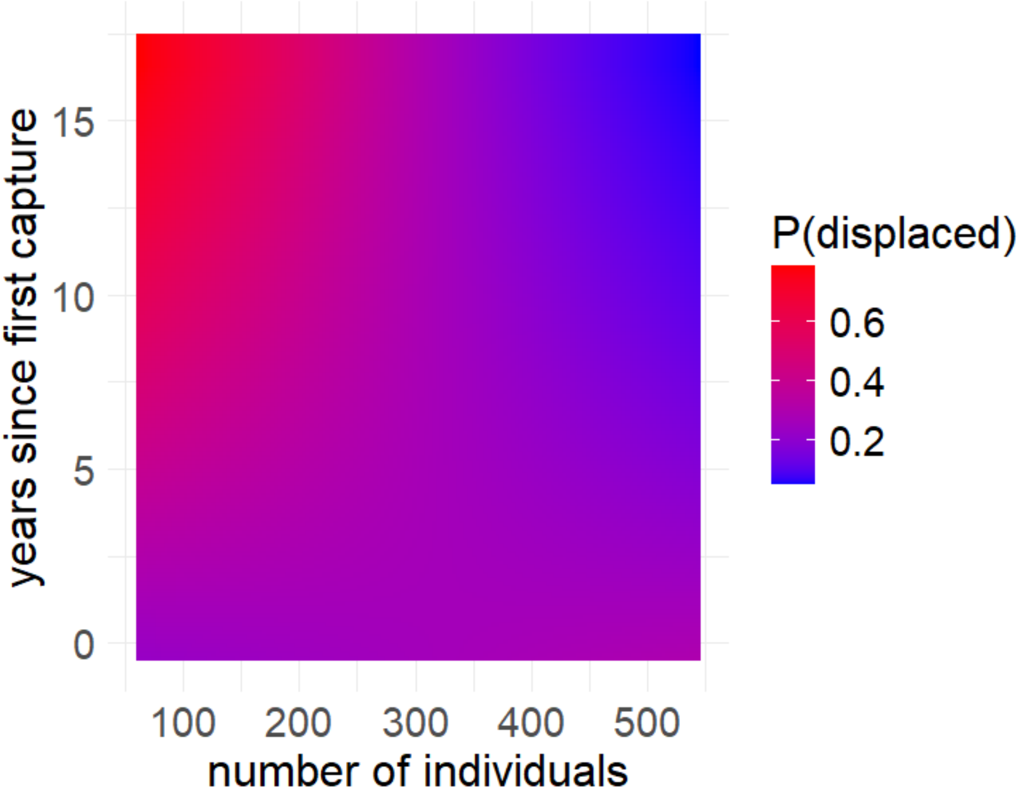

Figure 13. A heatmap of the interaction between "years since first capture" and "count" (number of individuals). The colour gradient displays a change in the probability of a male being displaced from amplexus.

Size-assortative mating

To assess if size-assortative mating occurs in this population, we calculated the Pearson correlation coefficient between female and male body size (Table 5). We found a positive coefficient (*r* = 0.071, df = 1870, p = 0.002), but although statistically significant, the effect is very small (Figure 14). We separated pairs where the female had been present for less than five days from pairs where the female had been present for five days or longer at the time of data collection to see how that affected the magnitude of the correlation. The Pearson correlation increased when the female spent five or more days at the pond (*r* = 0.088, df = 798, p = 0.01) and decreased when the female spent less than five days at the pond (*r* = 0.057, df = 1070, p = 0.06) but the effect was minimal (Figure 15).

Table 5. Summary of the analysis of size-assortative mating.

group	Pearson correlation coefficient	df	p-value
all	0.071	1870	0.002
female present ≥ 5 days	0.088	798	0.01
female present < 5 days	0.057	1070	0.06

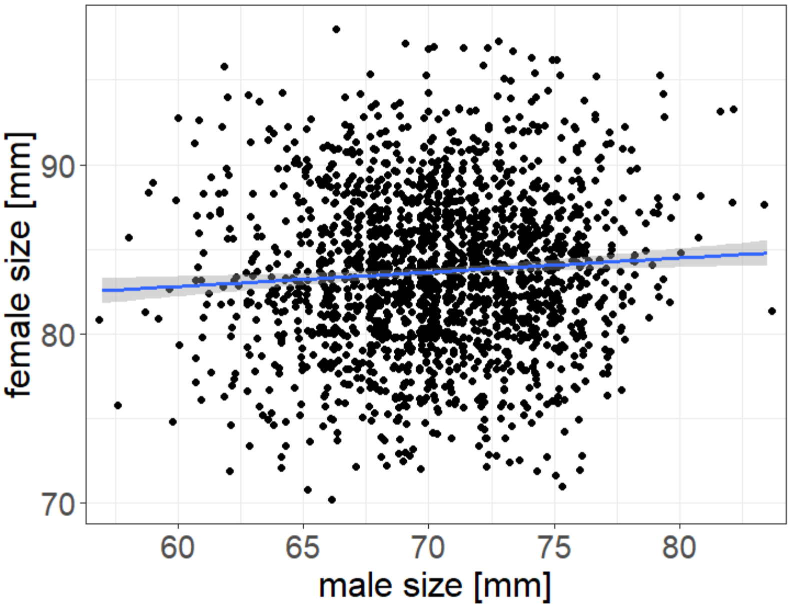

Figure 14. Correlation of the body size of the males and females found in amplexus. A slight positive correlation can be observed. The grey ribbon represent the 95% CI.

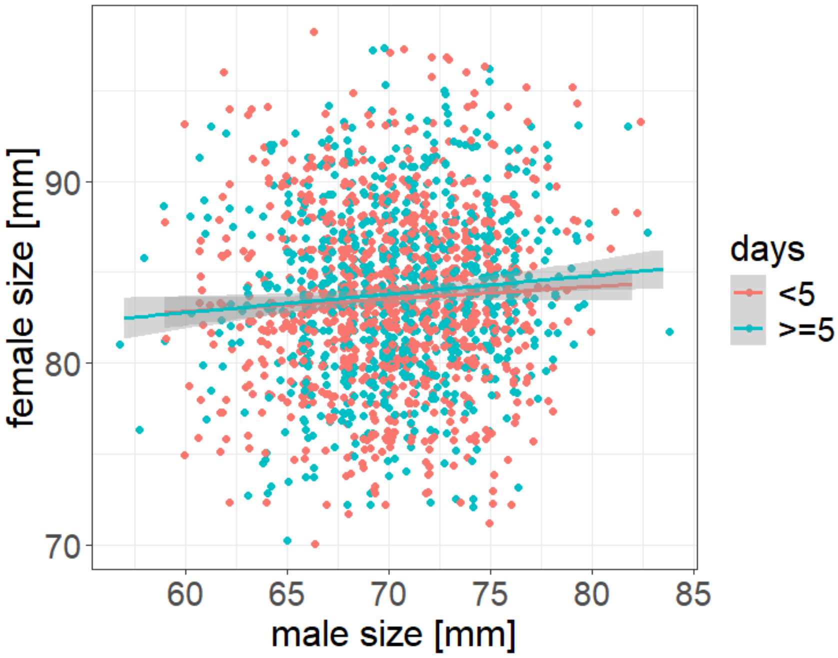

Figure 15. Correlation between size of males and females found in pairs, based on the number of days the female spent at the pond at the time of data collection. The correlation increases when the female spends more time at the pond. The grey ribbon represent the 95% CI.

Reproductive strategies of small and large males

To assess the effect of the body size on the arrival day of the males, we fit a zero-inflated negative binomial model. Body size could not explain the differences in the arrival times (estimate = -0.0009, SE = 0.0017, z = -0.536, p = 0.592) (Figure 16). Instead, most of the variation in the data was accounted for by year effects. The R^2 value of the model was 0.5.

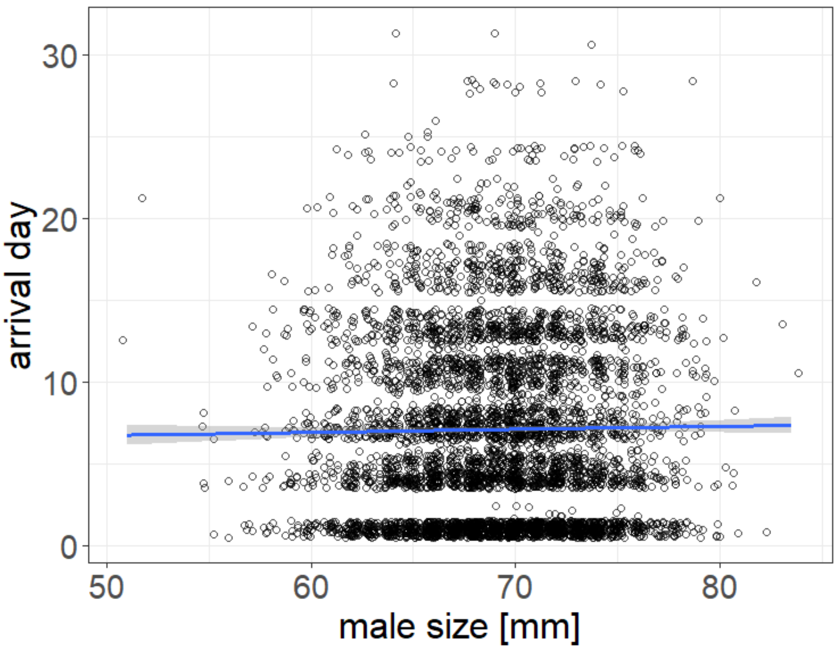

Figure 16. Relationship between male size and relative day of arrival at the breeding site (where 0 is the first capture night in a given year). Male size cannot explain the observed differences in arrival time of the males. The grey ribbon represent the 95% CI.

Survival differences in males

To assess the cost of reproduction on the survival of paired males (P, P’) compared to unpaired males (UP, UP’), we ran a multistate capture-mark-recapture model (Table 6). The posterior predictive check indicated satisfactory goodness-of-fit (Bayesian p-value = 0.75, Figure S1, Figure S2, Figure S3; Appendix). For both age classes (“first capture” and “older”), the survival of individuals that were found in amplexus did not differ from the survival of individuals that were not found in amplexus. First-time breeding individuals had a lower survival rate ($\Phi_{P'}$ = 0.61, 95% CRI = 0.569–0.611 and $\Phi_{UP'}$= 0.61, 95% CRI = 0.584–0.612) than older individuals (Φ_{P} = 0.74, 95% CRI = 0.718–0.745 and Φ_{UP} = 0.73, 95% CRI = 0.706–0.744). The transition rate from paired to unpaired was Ψ_{PUP} = 0.58 (95% CRI = 0.546–0.605) and, therefore, the probability of staying paired was 1-Ψ_{PUP} = 0.42 (95% CRI = 0.395–0.454). The transition rate from unpaired to paired was Ψ_{UPP}= 0.32 (95% CRI = 0.300–0.340) and the accompanying rate of remaining unpaired was 1-Ψ_{UPP}= 0.68 (95% CRI = 0.660–0.700). The mean detection probability (p) was 0.96 (95% CRI = 0.958–0.968) and had little variance (SD = 0.002). Adding more age classes and body size at first capture provided no additional insights (Table S8; Appendix).

Table 6. Parameter estimates of the multistate capture-mark-recapture model

parameter	mean	95% CRI
$\Phi_{P'}$	0.61	0.569–0.611
$\Phi_{UP'}$	0.61	0.584–0.612
Φ_{P}	0.74	0.718–0.745
Φ_{UP}	0.73	0.706–0.744
Ψ_{PUP}	0.58	0.546–0.605
$1-\Psi_{PUP}$	0.42	0.395–0.454
Ψ_{UPP}	0.32	0.300–0.340
$1-\Psi_{UPP}$	0.68	0.660–0.700
p	0.96	0.958–0.968

Discussion

This study investigates the mating system of a natural amphibian population. We could investigate hypotheses developed mostly in an experimental setting and assess their validity in the context of a wild population, thus contributing to a better understanding of the drivers of mating success.

We investigated the predictors of successful pairing for males in a natural population of the common toad. The effects of the body size of the male and the sex ratio have frequently been analysed, but rarely in natural settings. Moreover, potential density-dependent effects and the impact of age are still unclear. We found that a larger size increases the probability of successful mating, whereas an increase in sex ratio decreases it. We further found a negative correlation between age and mating success. Finally, no density-dependent effects were found on the pairing success. The findings regarding body size are not surprising, as the same effect has been observed in many different studies (Davies & Halliday, 1977, 1979; Gittins et al., 1980) and can be explained by the fact that larger males can more easily remove smaller males in amplexus (Davies & Halliday, 1979). The negative correlation between sex ratio and pairing success was also expected. When the proportion of males is higher, fewer females are available per capita to males at the pond, providing fewer mating opportunities. The lack of density dependence indicates that more encounters do not lead to a higher mating chance. This is likely the case because the density is already large enough that it does not act as a limiting factor on the probability of encountering other individuals. Finally, our findings reveal reduced pairing success in older individuals, consistent with the findings of senescence in amphibians (Cayuela et al., 2021; Reading & Jofré, 2021; but see Kara, 1994), thus hinting at a reduced competitivity at older ages. This might seem contradictory at first because common toads grow throughout their lives, and larger males are known to be more successful in accessing mating opportunities. However, as Halliday and Verrell (1988) suggest, for most amphibians and reptiles, the growth rate before the age of first breeding is a much larger source of body-size variation than age. This means that large animals are not more successful at mating because of age but because they experienced more rapid juvenile growth.

Another aspect that we investigated is the displacement of amplecting male toads and its causes. Previous research found that larger individuals are stronger and more likely to displace other males (Davies & Halliday, 1979). However, it is mainly unknown how age and density affect displacement probabilities. We found, as hypothesised, a significantly decreasing risk of being displaced with increasing body size of males. This finding complies nicely with the existing body of research. Furthermore, we found a significant interaction between density and age, meaning that as the number of individuals at the breeding pond increases, the less likely an old male is to be displaced. This outcome is not quite as easy to explain as the body-size effect. We found a negative effect of age on the probability of being in amplexus in our first research question, hinting at potential senescence. However, it seems that old individuals are only easy to displace when density is low. A plausible explanation is that the significant interaction is due to single (or few) old individuals in high or low-density years. The low-density years cover the period between 1982 and 2013, where the total number of individuals was stable at around 100-200. The high-density years occurred from 2013 onwards, where the total count was stable at around 500 individuals (Figure S4; Appendix). Given that only 29 individuals came to the pond for more than seven years, they could be driving the interaction with their increased statistical weight. However, the interaction remains even when removing any old individuals (ysfc>7) (Table S9, Figure S5; Appendix).

Additionally, we investigated the occurrence of size-assortative mating patterns, and we found a biologically irrelevant but statistically significant positive correlation between male and female body size. The correlation increased when the females spent more time at the pond, but it remained very small and was probably only significant because of the large sample size. Size-assortative mating is thought to occur when the female stays at the pond long enough for male-male competition to resolve mating pairs (Höglund, 1989). The only other prerequisite is a male-biased sex ratio, which is the case in this population. Generally, throughout the breeding season, mating is random at first; then large males are favoured through scramble competition, and lastly, size assortative mating is established. This pattern emerges because the probability of remaining paired depends eventually on both female and male body size, with an ideal ratio between the body size of the two individuals enabling the male to grasp better and hold on to the female (Höglund, 1989). Therefore, small males may be able to displace large males paired with (relatively speaking) smaller females given enough time, thus establishing a size-assortative pattern. In this study population, sampling occurred on average five times a year over a period of 1-3 weeks. This can result in inaccuracies in the arrival of the individuals. If a female arrived one day after a sampling occasion and the time between the sampling occasions was five days, then the female was present a lot longer than we observed. This could result in pairs being assigned to the “less than five days present” category even though the time available for competition was longer. It is unclear how more precise information about the timing of arrival would affect the results, but we are not expecting major differences.

An additional aspect that we analysed is the presence of alternative mating strategies of small males. Previous studies showed that small males wait for females along migrating routes and enter amplexus before the females reach the pond, thus avoiding competition with the larger males (Loman & Madsen, 1986). Conversely, Gittins et al. (1980) found the exact opposite to be true. They found that small males arrived earlier at the pond and postulated that by arriving earlier, small males prolong the length of their breeding season, therefore increasing the chances of mating. On the other hand, large males can wait until female density at the pond is higher because they have better chances of securing a mate. If either of these strategies are indeed employed, body size should accurately predict the time of arrival of males at the pond, but we found no evidence of it. Therefore, we believe no alternative mating strategies are present in this population.

Finally, we investigated the survival cost of reproduction in male common toads by looking at survival differences and the presence of intermittent breeding. We were interested in these questions because costs of survival and a decreased body condition after breeding were observed in a previous study on male common toads (Reading & Jofré, 2021), highlighting a classic life-history trade-off between survival and reproduction. Given the harsh environmental conditions the study population experiences, we also expected to find either a survival cost in males which reproduce or intermittent breeding, as individuals might need two years to be ready to reproduce again. While intermittent breeding in this population was found in females, its presence in males has not been tested in detail. We found no difference in the survival rates of paired and unpaired males and no evidence of intermittent breeding. The hypothesised proximate reason for survival costs in males during breeding is that searching for females, entering amplexus, and then fighting off attacking males requires a lot of energy. This has been found to deteriorate the body condition of paired males (Reading & Jofré, 2021). The lack of a difference in survival rates of paired and unpaired individuals suggests that there is no survival cost when reproducing in this population. One possible explanation could be that even though unpaired males can move freely, the energy cost of attempting to displace other males is not outweighed by the benefit of having access to food during breeding. Alternatively, it is possible that males found in amplexus are of higher intrinsic. quality than unpaired males, thus able to enter amplexus and retain a survival similar to unpaired, lower quality, males.

Concerning intermittent breeding, it is not entirely surprising that we found no evidence of its presence in males, even though it is quite common in females. In fact, males have to invest less energy into breeding than females (Hayward & Gillooly, 2011). Thus, they might not need two years to accumulate enough resources before attempting breeding again. Muths et al. (2013) further speculate that males, contrary to females, do not need to take environmental conditions experienced right before breeding into account because a failed breeding attempt due to bad conditions does not hamper reproductive success over multiple years.

Interestingly, an additional finding of our analysis shows that first-time breeders have a reduced survival probability regardless of sex. This could be due to multiple reasons. (1) The subcutaneous tagging of the animals, which happens in their first breeding year upon their first capture, might have a negative effect, for example, by causing an infection (2) Physiological costs of breeding for the first time are higher due to being inexperienced, causing higher mortality. Similarly, the first breeding event might be a strong selection process, separating low-quality toads from high-quality ones. (3) An age effect causes the reduced survival rate and is unrelated to breeding, whereby younger individuals have lower survival because, for example, they lack energy reserves or are the preferred prey of a predator. While the stress of initial PIT-tagging is unknown (Tornabene et al., 2023), subsequent infections are uncommon (Pyke, 2005). No short-term effects on survival or growth have been observed from using PIT tags (Ott & Scott, 1999; Perret & Joly, 2002; Rowley et al., 2024). Therefore, a marking effect (1) seems unlikely to cause reduced survival. If an age effect reduced survival at younger ages (3), we would expect a gradual increase in the survival rate in the first few years after the first breeding. This was not observed (Table S8; Appendix). Rather, the survival rate jumped from ~0.60 in the first breeding year to ~0.73 in subsequent years and stayed mostly constant. Thus, it seems that the most likely reason for reduced survival in first-time breeders is the physiological cost of being an inexperienced or lower-quality breeder (2).

In conclusion, this study provides new insights into male common toads' reproductive patterns and survival across multiple decades. We found that larger body size consistently enhances the probability of being in amplexus and, therefore, presumably, mating success in males. At the same time, age negatively impacts pairing success and increases the probability of being displaced, the latter only under low-density conditions. Contrary to previous findings, no evidence was found for alternative breeding strategies adopted by small males. Additionally, while size-assortative mating was observed, it was minimal. Finally, survival analysis revealed no reproductive costs for paired males but highlighted reduced survival in first-time breeders, likely due to the physiological challenges of the first reproductive event. Future research may explore why there are two apparently stable density states at the breeding pond (pre and post-2013). This might also be useful to shed light on the observed interaction effect of density and age on the probability of displacement. Furthermore, more research could be done to investigate the lower survival rate of first-time breeders. Overall, the findings of this thesis underscore the interplay between environmental, demographic, and individual-level factors in shaping reproductive success and survival and frame them in the context of a natural amphibian population.

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 supported by 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.

Authors contribution

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

Supplementary material

Extra analyses, tables, and figures are available in the Appendix.

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Appendix

Which factors predict whether a male is in amplexus?

Table S1. Correlations of the fixed effects of the analysis investigating which males are found in amplexus. None of the correlations are large enough to be problematic.

	male size	*log(sex ratio)*	*count*	*ysfc*
male size	1	-0.274	-0.172	0.385
log(sex ratio)	-0.274	1	0.277	-0.238
count	-0.172	0.277	1	-0.167
ysfc	0.385	-0.242	-0.167	1

Table S2. Different models that we fit to assess the best random-effect structure. The model including the individual random effect (ID) and the year random effect (Year) is favored by the AIC.

model formula	AIC values	delta AIC	Akaike weights
amplecting ~ s.size * log_Ratio * s.count * s.ysfc + (1|ID)	5914.621	3.948	0.098
amplecting ~ s.size * log_Ratio * s.count * s.ysfc + (1|Year)	5913.213	2.541	0.198
amplecting ~ s.size * log_Ratio * s.count * s.ysfc + (1|ID) + (1|Year)	5910.672	0.000	0.704

model formula	AIC values	delta AIC	Akaike weights
amplecting ~ 1 + (1|ID) + (1|Year)	6106.833	199.465	<0.001
amplecting ~ s.size * log_Ratio * s.count * s.ysfc + (1|ID) + (1|Year)	5910.672	3.305	0.088
amplecting ~ s.size * (log_Ratio + s.count + s.ysfc) + (1|ID) + (1|Year)	5908.794	1.427	0.225
amplecting ~ s.size * (log_Ratio + s.count)+ s.ysfc + (1|ID) + (1|Year)	5908.751	1.383	0.229

amplecting ~ s.size + log_Ratio + s.count + s.ysfc + (1|ID) + (1|Year)	5907.367	0.000	0.458

Table S3. Different models that we fit to assess the best fixed effects structure. The best model included all four covariates with no interactions. However, we selected the third-best model because we were interested in potential interactions with the covariate *size*.

Table S4. Correlations of the fixed effects of the analysis investigating displacement probabilities. None of the correlations are large enough to be problematic.

	male size	*count*	*ysfc*
male size	1	-0.113	0.291
count	-0.113	1	-0.104
ysfc	0.291	-0.104	1

Table S5. Different models that we fit to assess the best random-effect structure. Including random effects led to a singular fit, indicating that the model is overfitted and no variance can be explained by the random effects. Therefore, we selected the model without any random effect.

	AIC values	delta AIC	Akaike weights
displaced ~ s.size_m * s.Ratio * s.count * s.m_ysfc + (1|Year)	930.451	2	0.175
displaced ~ s.size_m * s.Ratio * s.count * s.m_ysfc + (1|ID_male)	930.451	2	0.175
displaced ~ s.size_m * s.Ratio * s.count * s.m_ysfc + (1|ID_female)	930.451	2	0.175
displaced ~ s.size_m * s.Ratio * s.count * s.m_ysfc	928.451	0	0.475

Table S6. Different models that we fit to assess the best fixed-effect structure. The best model included *size*, *count*, and *ysfc* with all of their two-way interactions.

model formula	AIC values	delta AIC	Akaike weights
displaced ~ s.size_m * s.count * s.m_ysfc * s.Ratio	928.451	9.804	0.004
displaced ~ s.size_m	924.199	5.551	0.032
displaced ~ s.size_m * s.count	921.396	2.749	0.129
displaced ~ s.size_m * s.count * s.m_ysfc	919.527	0.880	0.327
displaced ~ s.size_m * s.count * s.m_ysfc - s.size_m:s.count:s.m_ysfc	918.647	0.000	0.508

Reproductive strategies of small and large males

Table S7. Different models that we fit to assess the best fit for the analysis investigating arrival times of males and their potentially different reproductive strategies. Covariates on the left of the vertical bar inform the count submodel, and covariates on the right inform the zero-inflation submodel. Neither the addition of the *Year* covariate for the zero-inflation submodel (third model from the bottom) nor the addition of the age covariate (*ysfc*) for the count submodel (last model) improved the performance significantly; therefore, the simplest model of the three (second model from the bottom) was selected.

model formula	AIC values	delta AIC	Akaike weights
time ~ 1	31112.14	3855.417	<0.001
time ~ size	31104.21	3847.488	<0.001
time ~ size | size + Year	29995.53	2738.801	<0.001
time ~ size * ysfc | Year	29995.05	2738.329	<0.001
time ~ size | Year	29994.32	2737.599	<0.001
time ~ size + ysfc | Year	29993.70	2736.971	<0.001
time ~ size * Year | Year	27276.10	19.374	<0.001
time ~ size + Year | size + Year	27259.55	2.822	0.139
time ~ size + Year | Year	27258.06	1.335	0.292
time ~ size + Year + ysfc | Year	27256.72	0	0.569

Multistate survival model

We performed a posterior predictive check for the multistate model following Nater et al. (2020). We selected 500 evenly spaced samples from the posterior distributions of the estimated parameters and generated ten replicate datasets per sample, resulting in 5000 simulated datasets. We then calculated the number of recaptures per simulated dataset (Figure S1). Additionally, we calculated the number of recaptures by state (paired or unpaired) to assess the validity of the transition rates (Figure S2 & Figure S3). Finally, we visually compared the observed number of recaptures to the simulated values and computed a Bayesian p-value. All the Bayesian p-values are satisfactory and indicate a good model fit.

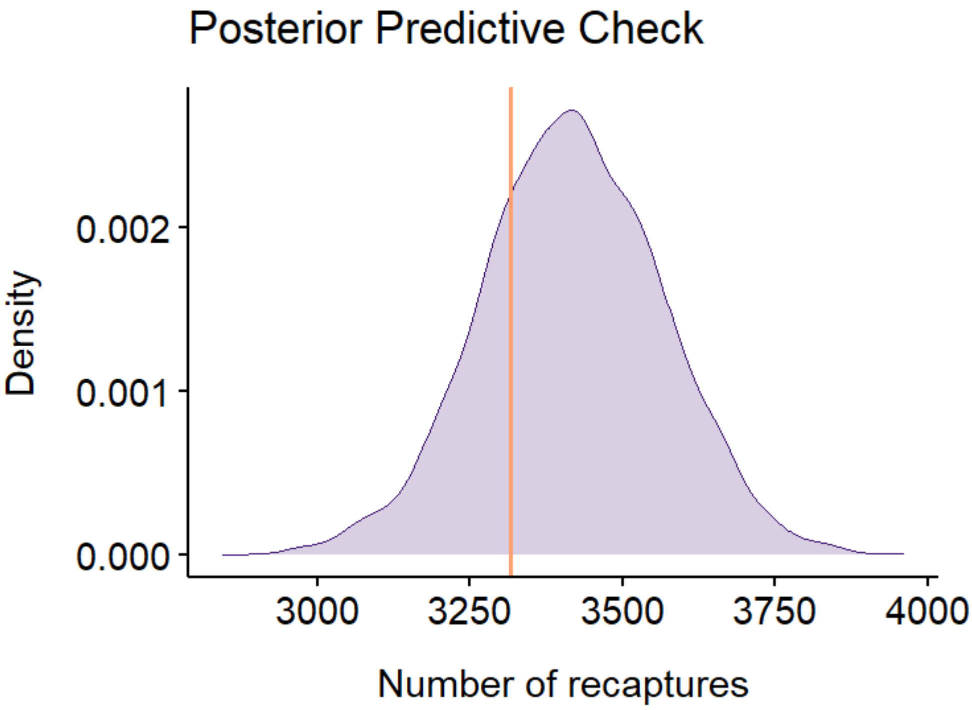

Figure S1. Density plot of the simulated number of recaptures based on the posterior distribution of the multistate survival model. The true number of recaptures from the original data was 3316 (orange line). The Bayesian p-value was 0.75, meaning that 75% of the simulated number of recaptures are above the true number of recaptures and 25% are below.

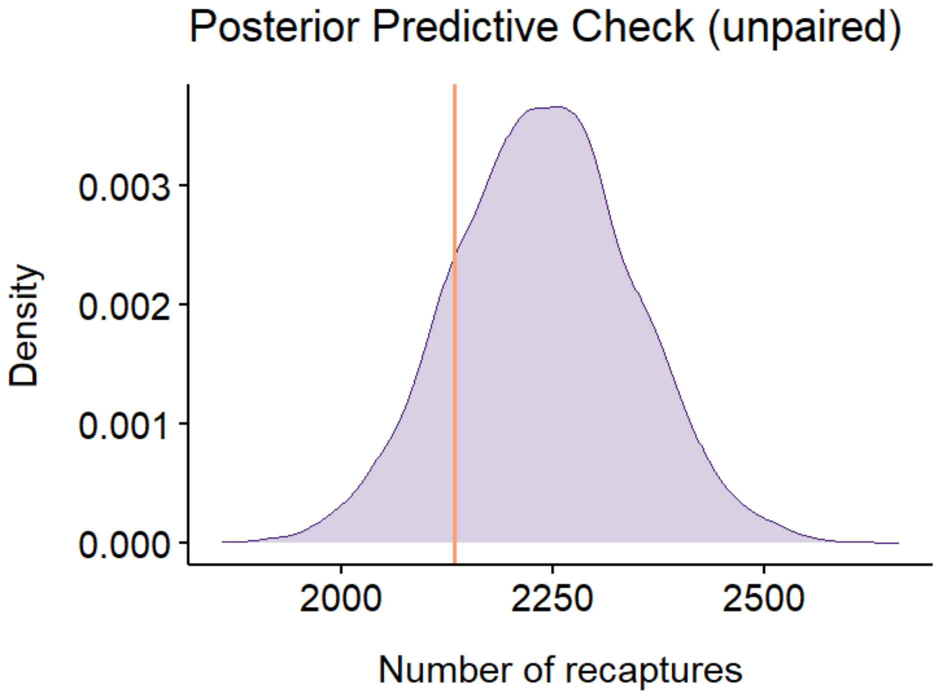

Figure S2. Density plot of the simulated number of recaptures in the unpaired state. The true number of recaptures in the unpaired state was 2134. This equates to a Bayesian p-value of 0.832

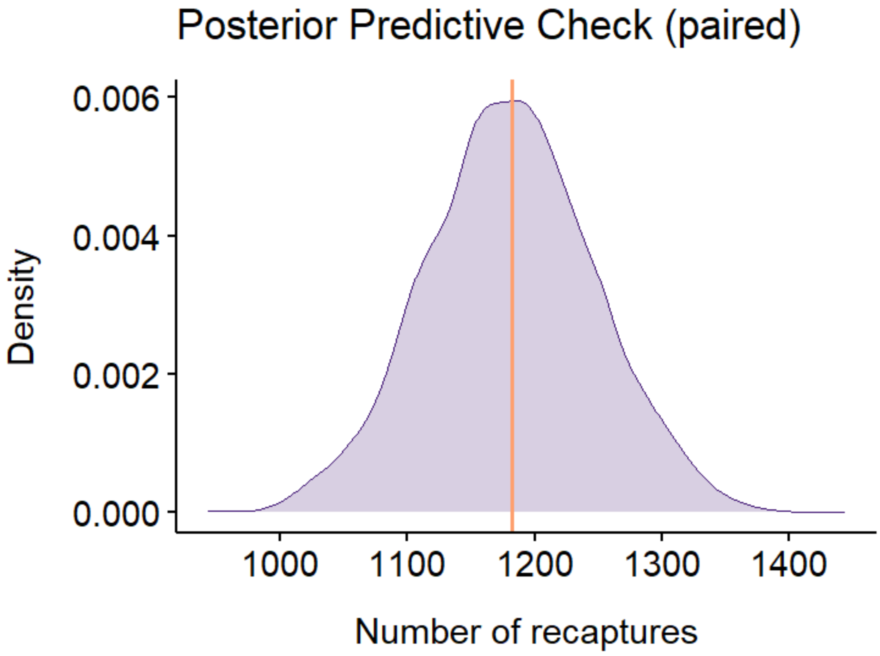

Figure S3. Density plot of the simulated number of recaptures in the paired state. The true number of recaptures in the paired state was 1182. This equates to a Bayesian p-value of 0.487.

Table S8. Parameter estimates of the extended multistate capture-mark-recapture model. It includes a male body size covariate at first capture to see if it can predict the survival of first-year individuals. It also has four different stage classes based on ages: *first year*, *second year*, *third year*, and *older*, denoted by their respective number of apostrophes next to the survival rate.

parameter	mean	95% CRI
male size	-0.06	-0.158–0.050
$\Phi_{P'}$	0.61	0.569–0.611
$\Phi_{UP'}$	0.62	0.584–0.612
$\Phi_{P''}$	0.68	0.627–0.731
$\Phi_{UP''}$	0.74	0.705–0.777
$\Phi_{P'''}$	0.79	0.734–0.839
$\Phi_{UP'''}$	0.70	0.651–0.742
$\Phi_{P''''}$	0.75	0.707–0.780
$\Phi_{UP''''}$	0.73	0.697–0.753
Ψ_{PUP}	0.58	0.546–0.607
$1-\Psi_{PUP}$	0.42	0.393–0.454
Ψ_{UPP}	0.32	0.298–0.337
$1-\Psi_{UPP}$	0.68	0.663–0.702
p	0.91	0.895–0.916

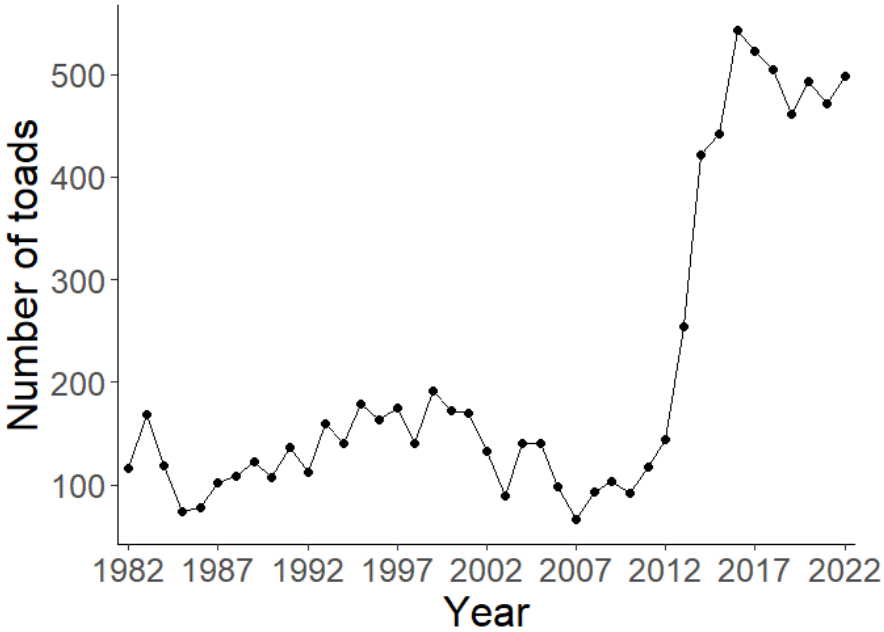

Figure S4. Temporal trend of the number of captured toads at the breeding site over the study period. The number of toads was stable at around 100-200 individuals between 1982 and 2013. After 2013, the number sharply increased to around 500 and seems to remain stable.

Alternative fit of the displacement model without old toads (ysfc>7)

Table S9. Summary of the model investigating the predictors for displacement of males. Only males which have visited the pond for fewer than 8 years are included. The significant interaction remains. The significant predictors are in bold.

	estimate	odds-ratio	std. error	p-value
intercept	**-1.064**	**0.34**	**0.091**	**<0.001**
male size	**-0.249**	**0.78**	**0.095**	**0.008**
count	-0.144	0.87	0.086	0.341
ysfc	0.004	1.00	0.118	0.579
male size:count	-0.127	0.88	0.087	0.092
male size:ysfc	-0.035	0.97	0.119	0.325
count:ysfc	**-0.467**	**0.63**	**0.116**	**<0.001**

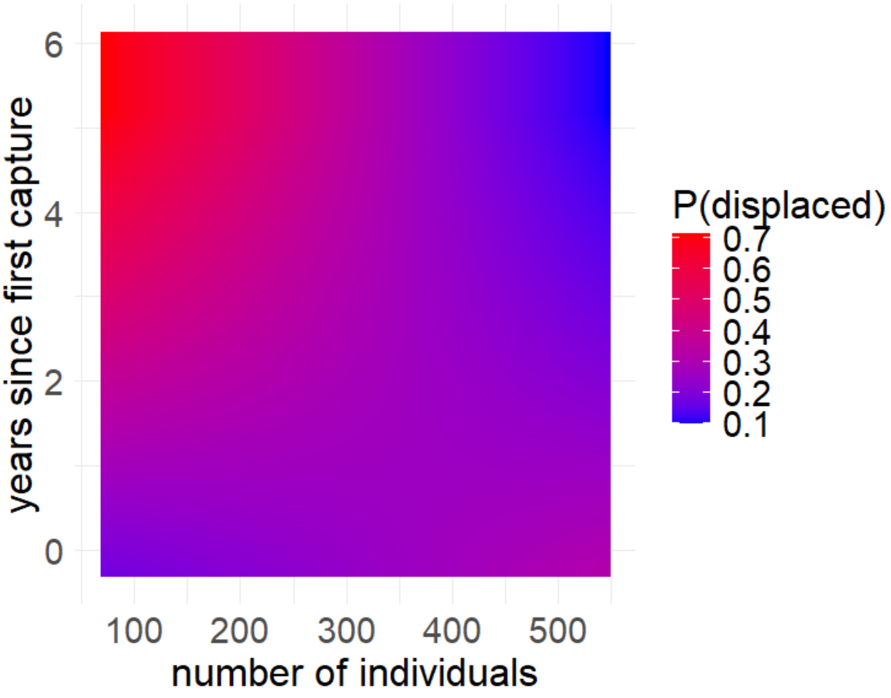

Figure S5. Heatmap of the interaction between the number of individuals (*count*) and the years since the first capture (*ysfc*). The interaction is clearly visible, even for toads which visited the pond fewer than 8 times (i.e., "young" toads).

Preferential mating

Common toads show high site fidelity to their breeding pond, frequently returning to the pond they were born in (Reading et al., 1991). In the study population, there are multiple individuals which return to the pond for more than 10 years. Therefore, it is not unlikely that a certain pair of individuals will be found in amplexus more than once over their lifetime. This sparks the question of whether preferential mating with the same individual occurs more often than expected under the assumption of random mating. Preferential mating would imply that individuals must be able to recognise each other. This does not seem to be the case for male common toads, as they were found to not discriminate between males and females, and even green frogs when searching for a mate (Marco & Lizana, 2002). We intended to investigate if certain pairs of individuals breed more often with each other than expected under the assumption of random mating. However, there were no instances where two toads were caught in amplexus more than once. Therefore, there is no evidence of preferential mating in this population.

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Chapter 4 – Population Dynamics

A single cohort drives the rapid and massive increase in the size of an alpine amphibian population

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Lenzi O., Grossenbacher K., Zumbach S., Lüscher B., Althaus S., Thoma M., Schmocker D., Recher H., Ozgul A., Schmidt B.R. A single cohort drives the rapid and massive increase in the size of an alpine amphibian population. *In preparation*.

The layout and formatting of this chapter are slightly modified from the version in preparation in the scope of the thesis.

Abstract

1. To understand the ecology of populations, it is crucial to study their dynamics, which can vary significantly across different taxa, ranging from stable abundance patterns to highly fluctuating population trajectories. Amphibian populations, for instance, can often show erratic fluctuations in abundance, which are particularly challenging to study due to their complex life cycles. These fluctuations can become even more extreme in harsh and variable environments, such as those found at high elevations.
2. Here, we aimed to understand the causes of the unusual population dynamics of a high-elevation common toad *Bufo bufo* population over four decades. This population is characterised by a stable breeding population in the first three decades of monitoring (1982-2012), followed by a rapid four-fold increase in abundance in the fourth decade.
3. Using a Jolly-Seber mark-recapture model, we estimated survival, breeding probability, and recruitment. We then tested which environmental drivers acting at various stages of the complex life cycle, could be responsible for the sudden increase in population size.
4. We found that the massive increase in the number of breeders from 2013 onwards was mainly determined by the entry of a large number of male recruits into the breeding population first, followed by an influx of female recruits 4-5 years later, matching the known sex difference in age at maturity in this species, therefore hinting at a single cohort driving the increase. We further show that ecological conditions during early-life stages can affect recruitment to the adult population, with in particular a positive correlation of temperature during the egg phase with the number of females entering 7-12 years later. Our results also hint at a potential shift towards earlier sexual maturity, which partly contributes to the increase in the breeding population size.
5. While most amphibians face declining population trends, this study reveals that our focal population is in a positive state. We also show that this population seems to have moved to a new state at higher abundance, escaping the previous equilibrium state, possibly due to one exceptional cohort. Moreover, we showcase the importance of early life-stages for amphibian populations. Finally, we highlight the importance of long-term studies, as a shorter study period could have missed

the sudden and strong increase in population size.

Introduction

Population dynamics describe the variation in abundance of individuals in a population over time. Abundance is determined by survival and recruitment processes, as well as emigration and immigration. Information about these processes and the resulting population dynamics are key to assess if a population is stable, increasing, or decreasing, thus potentially informing conservation or management actions. A recent study showed that globally, 48% of 71000 assessed animal populations are declining, and only 3% are increasing (Finn et al., 2023), with marked differences across taxa. For instance, amphibians have the highest proportion of declining populations (63% [43%-75%]) (Finn et al., 2023). In addition, up to 31% of the amphibian populations assessed in the study falls under the unknown category, highlighting a taxonomic bias (Bonnet et al., 2002). Moreover, amphibians have a complex life cycle which can facilitate the appearance of highly fluctuating population dynamics, thus complicating our understanding of population trends.

Aside from inherent population fluctuations, amphibians experience a multitude of threats, ranging from habitat degradation to pollution, diseases, and climate change (Beebee & Griffiths, 2005) with severe consequences for the populations. The magnitude of these threats and their interplay depends on many factors, including the location of the focal population with respect to the species distributional range. For instance, the abundant-centre theory (Brown, 1984; Sagarin & Gaines, 2002) states that core populations experience more favourable environmental conditions and thus have higher population density. This implies that, at least initially, climate change might have limited effects on core populations, whereas diseases might spread more easily due to increased interactions between individuals. On the contrary, certain edge habitats such as high-elevation areas are highly sensitive to climate change (Diaz et al., 2003). Marginal populations could thus suffer greatly from changing environmental conditions, but on the other hand, might be less exposed to diseases, as population density and connectivity are lower (Brown, 1984). In general, core populations tend to be more stable than marginal populations of the same species (Kawecki, 2008; Kolzenburg, 2022). Although marginal populations seem to be generally more studied, probably due to their perceived higher interest (Guo, 2014), knowledge on how they respond to threats is still limited, due to the specific context of each focal population, which hinders generalisations.

To fill these taxon- and range-specific gaps, we analysed individual capture-history data of adults of a common toad *Bufo bufo* population living close to its elevational upper range in the Swiss Alps. This population has been monitored since 1982 as part of capture-mark-recapture study (Hemelaar, 1988) and shows a rather unusual trend in the annual number of captured adults (Figure 1). In the first 30 years of the study, the abundance varied between 100 and 200 individuals, hinting at a density dependence effect keeping the abundance fluctuating around a return point (i.e., carrying capacity). In 2013 the number of captured individuals massively increased, stabilising now at around 500-600 individuals per year, suggesting that the population escaped the tendency to fluctuate around the previous return point. This observed trend is in opposition with the majority of amphibian populations in Switzerland, which are declining (Schmidt et al., 2023), and is of high interest due to the magnitude and rapidity of the shift. The main objective of this study is therefore to understand if the population was regulated by density dependence prior to the sudden increase in abundance, and what processes are responsible for the observed population dynamics.

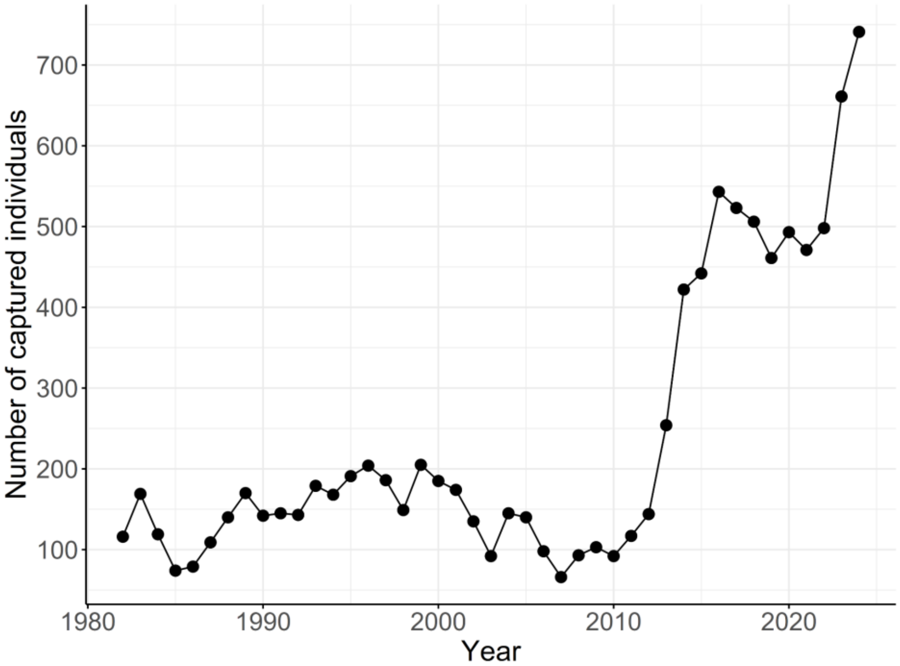

Figure 1. Number of adults captured during each breeding season over the study period 1982-2024

There are generally three main, potentially co-occurring, processes that can lead to an increase in the number of breeders in a population: (1) An increased immigration (or decreased emigration) into (or out of) the population, (2) an increased survival of adults, juveniles, or both, or (3) an increased reproductive success (e.g., higher number of eggs produced). Previous knowledge of the species and study population allows us to isolate the process that is most likely leading to the observed population increase. First, we expect immigration and emigration in and out of this population to be negligible, as common toads generally show high fidelity to the breeding site where they were born (Reading et al., 1991). Immigration into our study population could occur if neighbouring breeding sites disappeared, but our knowledge of the nearby ponds indicates that it is not the case. In fact, the study population is the only relevant population in the surrounding area (Grossenbacher, *pers. obs.*) indicating that neither immigration or emigration are major processes for the studied population. Secondly, a previous capture-mark-recapture analysis of this population shows that adult survival is not increasing, and even slightly decreased in recent years (Lenzi et al., 2024); it is therefore unlikely to be the cause of the increased population size. Finally, juvenile survival and reproductive success cannot be disentangled in the monitored population, and can be combined into a metric of recruitment into the breeding population. We hypothesise that increased recruitment is the main proximate reason that is driving population dynamics. The ultimate reason for such an increased recruitment is hard to pinpoint, but can include environmental conditions favouring a higher number of eggs produced or hatched, or an increased survival of tadpoles or newly metamorphosed (i.e., first-year) juveniles. Additionally, a decreased age at sexual maturity can contribute to the observed pattern as well, with a higher number of younger individuals entering the breeding population. If that is the case, we should observe smaller first-time breeders in recent years, as they had less time to grow.

To determine if the increase in the number of adults is caused by an increased recruitment of juveniles into the breeding population, we used capture histories of 2152 males and 1194 females and a Jolly-Seber (JS) capture-mark-recapture model implemented in a Bayesian framework (Schwarz, 2001; Kéry & Schaub, 2012), over a 20 year period (1994-2023). A JS model uses the entirety of the individual capture histories (i.e., not conditional on the first capture) to provide information about survival and the entry into the adult population (i.e., recruitment), allowing us to disentangle the processes leading to the observed trend. Since females in this population show intermittent breeding (Grossenbacher, 2002; Lenzi et al., 2024), we can also estimate their breeding probability.

To assess the effect of environmental covariates on the survival and the breeding probability, we modelled these vital rates as a function of the length of the active season and the average minimum temperature in the two-week period before the first capture night (i.e., during emergence from hibernation). We hypothesise that the better the environmental conditions (i.e., the longer the active season and the warmer around the emergence from hibernation) the higher the survival and the probability of breeding in females. Given the presence of density dependence effects on this population (Lenzi et al., 2024), we also accounted for the population size, approximated by the total number of captured individuals per year.

Moreover, we investigated the effect of relevant environmental covariates on the recruitment into the breeding population. Given the sensibility and the importance of the first life-cycle stages in the first year of life (e.g., Blaustein et al., 1994; Mann et al., 2009; Petrovan & Schmidt, 2019), we focused on temperatures during the egg, tadpole, and first-year juvenile phases, as well as the date of winter onset in the first year of life. Age at sexual maturity is not fixed and varies between 5 to 10 years in males and 7 to 12 in females (Hemelaar, 1988). Thus, since we do not have age data, we expect new breeders entering the breeding population at year *t* to be influenced by the aforementioned environmental variables in a year between *t*-5 to *t*-10 for males, and *t*-7 to *t*-12 for females. We hypothesise that warmer temperatures during these phases lead to earlier metamorphosis (Alves-Ferreira et al., 2024). Earlier metamorphosis, along with a later winter onset, could result in a higher survival in this first critical year of life due to the increased time available to first-year juveniles to grow and survive overwintering, or could reduce survival, if it exposes them more to risks. Consequently, if more juveniles survive, it is probable that more individuals will enter the breeding population once they reach sexual maturity.

Finally, to assess if a shift towards an earlier age of breeding might be happening, thus contributing to an increased number of breeders, we also investigated changes in the body size of first-time breeders over the study period. We expect younger individuals to be smaller, as they had less time to grow.

Overall, this study takes advantage of an impressive dataset to investigate the population dynamics of a peculiar marginal population, with a particular focus on understanding the drivers of recruitment of individuals to adulthood. Moreover, this study highlights the importance of long-term studies, as a short-term study could have missed one of the two abundance states observed, which could lead to erroneous assumptions about the dynamics of the population.

Methods

Toad mark-recapture and body size data

To study and explain the observed population dynamics, we used individual-based data on 2152 male and 1194 female common toads (*Bufo bufo*) collected between 1994 and 2023. The study of this population started in 1982, but toads were cohort-marked before 1994. Data is collected during each breeding season in spring, when multiple capture nights (~5) are conducted at the breeding site of this population, a pond below the Grosse Scheidegg mountain pass (Canton Bern, Switzerland, 1850 m elevation, 46°39’ N and 08°05’ E). Every toad captured during a capture night is measured (snout-to-vent length in mm; SVL), weighed, sexed and uniquely marked with a PIT tag before being released back at the pond at the end of the night. For a more precise description of the study site and methods, see Hemelaar (1988), Grossenbacher (2002) and Lenzi et al. (2024).

Test for density dependence

To assess the presence of density-dependence regulatory effect on the population, we ran a partial rate correlation analysis on the yearly number of captured individuals on the period 1982-2012 (i.e., prior to the massive increase observed in 2013), testing for a significant correlation with the number of captured individuals in the previous years (“lag”, ranging from one to eight years).

Environmental data

We obtained environmental data for the period 1994–2023 from the DaymetCH dataset (Land Change Science group, WSL, Switzerland). This dataset provides interpolated estimates of various environmental variables over a 100-metre grid covering Switzerland, obtained combining ground stations data and the Daymet software (Thornton et al., 1997). We extracted for the gridcell containing the breeding site the daily minimum, mean, and maximum temperatures.

For the environmental covariates associated with survival and breeding probability, following previous works (Muths et al., 2017), we calculated for each year the length of the active season (i.e., the period between the end of hibernation in spring and the start of hibernation in autumn). We defined 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), and the end of the active season as the start of the incoming winter season, which corresponds to the first day in autumn with a killing frost (minimum temperature < -4.4 °C) (Muths et al., 2017). Moreover, we derived the average minimum temperature in the two weeks (*MinT_two_weeks*) around emergence from hibernation and included it as covariate for the probability of skipping and resuming breeding in females (Muths et al., 2013; Lenzi et al., 2024). Both variables are varying considerably over the study period, but only *MinT_two_weeks* might be showing a trend (Figure S1 and S2, Appendix S1), although the decline might be mainly driven by the late summer breeding which occurred in the first years of the study period.

The environmental covariates associated with recruitment into the population were (i) mean temperature during the egg phase (i.e., from the day with highest breeding activity until 20 days later); (ii) mean temperature during tadpole phase (i.e., from 20 to 100 days after the day with highest breeding activity); (iii) mean air temperature during the first-year juvenile phase (July-October); and (iv) date of winter onset, calculated following Muths et al. (2017). It corresponds to the period with three consecutive days with a minimum air temperature below -4.4 °C (Figures S3 to S6, Appendix S1, show the temporal trends of the four covariates). These variables were selected a priori based on knowledge of the system (Grossenbacher, *pers. comm.*) and of toad biology (Kuhn, 1997). For the first two variables, we used maximum daily air temperature as a proxy for water temperature, as according to the occasional temperature measurements conducted at the study site over the study period, they matched the most.

Capture-mark-recapture model

We modelled the individual capture histories with two sex-specific Jolly-Seber models, formulated as multistate models (Chapter 10; Kéry & Schaub, 2012). The states were the following: *not yet entered*, *alive,* and *dead* for males, and *not yet entered*, *breeder, non-breeder*, and *dead* for females (Figure 2). In fact, the data indicates that only females show intermittent breeding (i.e., temporary emigration; Schaub et al., 2004). Following Kéry and Schaub (2012), we opted for data augmentation and thus included pseudo-individuals to account for the individuals that were never captured during the study period (i.e., the capture histories are strings of 0s). Given the high detection probability in the study system (Lenzi et al., 2024), we included a relatively small number of pseudo-individuals. In total we modelled 2252 capture histories of males (2152 real individuals and 100 pseudo-individuals) and 1294 of females (1194 real individuals and 100 pseudo-individuals).

We were interested in the effects of the environment and population size on survival. Therefore, for both sexes, for survival probability in year t (ϕ_t) we included as covariates the length of the active season and the population size at year t (Table 1). As a proxy for population size we used the number of individuals captured every year, which is appropriate given the high and little-varying detection probability in this population (Wood et al., 1998; Bart et al., 2004). Following the previous finding of transience in the capture histories (Lenzi et al., 2024), we estimated a different survival probability for the year following the first capture.

For the breeding probabilities (i.e., the probability that a female skips breeding if it bred the year before ($\Psi_t^{B–NB}$) and the probability that a female resumes breeding if it did not breed the year before ($\Psi_t^{NB–B}$)), we included the effects of the length of the active season of the year before *(t-1)*, as well as the weather conditions (i.e., average minimum temperature) in the two weeks prior to the first capture night (Table 1). According to previous studies, the latter covariate might be important in determining if a female breeds or not, based on the conditions experienced at the end of hibernation (Muths et al., 2013; Lenzi et al., 2024). 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 small and no reason for concern ($-0.2 < r < 0.4$).

For the probability of removal entry probability (γ_t) (i.e., the probability for an available individual to enter the population a time *t*), we included a random effect of the year. Following Kéry and Schaub (2012) we used γ_t to obtain the derived parameter b_t (entry probability in a given year, scaled to sum up to 1 across years).

Furthermore, for detection probability p, which was shared between the two sexes to avoid identifiability issues, we included a random year effect, and a random individual effect to account for the overdispersion detected in the capture histories (Abadi et al., 2013; Lenzi et al., 2024).

Within the modelling framework, we calculated a series of derived parameters, including the total number of individuals in the population per year N_t (i.e., the sum of the number of males, the number of breeding females, and the number of non-breeding females), the number of individuals in each stage per year, as well as the yearly number of new entries in the population B_t (Kéry & Schaub, 2012). To assess the effect of the environmental conditions on recruitment, we then ran two sex-specific linear regressions with the per capita recruitment B_t/N_t as a function of four relevant environmental covariates: the maximum air temperature during the egg phase, the maximum air temperature during the tadpole phase, the mean air temperature during the first-year juvenile phase (July-October), and the date of winter onset (Table 1). For all of them, given that we lack individual age data, we averaged the yearly values over the possible period where a new entry could have been born, based on the information about age at sexual maturity (Hemelaar, 1988) namely 5 to 10 years prior to entry for males, and 7 to 12 years for females. The highest correlation coefficients between the four covariates were between the temperatures during the egg phase and the tadpole phase and they were low enough to not be problematic (-0.56 and -0.53 for females and males respectively).

We implemented the Jolly-Seber models in a Bayesian framework using Markov chain Monte Carlo (MCMC) sampling in Nimble (version 0.13.0; de Valpine et al., 2017). We conducted all the analyses in R (R version 4.2.2; R Core Team, 2020). We ran four chains for 250’000 sampling iterations each, including an initial burn-in of 150’000 iterations and a thinning value of 1, resulting in 100’000 iterations per chain. We treat as significant the correlations of the environmental and density covariates with survival and breeding probability whose 95% credible interval (CRI) of the posterior distribution does not overlap with 0.

We assessed model convergence by visually inspecting MCMC trace plots and calculating the Brooks–Gelman–Rubin statistic $\hat{R}$ (Brooks & Gelman, 1998). We evaluated the goodness-of-fit of the two sex-specific JS models by performing posterior predictive checks (Conn et al., 2018), following Nater et al. (2020). We selected 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 obtained the total number of recaptures in each set of capture histories and thus obtained a distribution of 5000 values for the total number of recaptures. We then compared the observed number of recaptures to these 5000 values both visually (Figure S1, Appendix S2) and by calculating a Bayesian p-value. Values close to 0 or 1 indicate poor fit, while values close to 0.5 indicate good fit.

Finally, to assess the possible shift towards an earlier sexual maturity (i.e., at smaller sizes) we both assessed graphically and statistically the changes over time of mean SVL (i.e., body size) for both males and females in individuals breeding for the first time (i.e., “first-time breeders”). More precisely, to assess the role of the environment and population density, we ran sex-specific linear regressions including body size of first-time breeders as a response variable. As explanatory variables we included the average population density over the period *t*-9 to *t*-1 for males and *t*-11 to *t*-1 for females, to encompass the possible growth period from the first year after birth (in the first year of life we do not expect an effect of adult population size on growth) to the year preceding their first capture (see age at sexual maturity in Hemelaar, 1988). We also included the length of the active season, averaged over the period from *t*-10 to *t*-1 for males and *t*-12 to *t*-1 for females, as we hypothesise that the active season in the first year of life could already contribute to growth of newly metamorphosed individuals. We selected these two explanatory variables because we hypothesise a negative effect of density (i.e., the more individuals, the smaller the resource intake per capita with consequences on body size), and a positive one of the active season, with longer seasons associated with an increased time for growing, resulting in different body sizes upon the first capture.

Table 1. List of vital rates and demographic parameters estimated with the Jolly-Seber model with the covariates of interest.

Sex	Vital rate / demographic parameter	Environmental covariate	Density
Males	Survival φ_t	Length of active season	Population size
	Survival first year φ'_t	Length of active season	Population size
	Per capita recruitment B_t/N_t	Mean temperature during the egg phase Mean temperature during the tadpole phase Mean temperature during the first-year juvenile phase (July-October) Date of winter onset	-
Females	Survival φ_t	Length of active season	Population size
	Survival first year φ'_t	Length of active season	Population size
	Skip breeding $\Psi_t^{B\_NB}$	Length of active season Mean minimum temperature in two weeks before first capture night	Population size

	Length of active season	
Resume breeding $\Psi_t^{NB\_B}$	Mean minimum temperature in two weeks before first capture night	Population size
Per capita recruitment B_t/N_t	Mean temperature during the egg phase Mean temperature during the tadpole phase Mean temperature during the first-year juvenile phase (July-October) Date of winter onset	-

$$\begin{array}{c|ccc} & \text{not yet entered} & \text{alive} & \text{dead} \\ \hline \text{not yet entered} & 1-\gamma & \gamma & 0 \\ \text{alive} & 0 & \varphi & 1-\varphi \\ \text{dead} & 0 & 0 & 1 \end{array}$$

$$\begin{array}{c|cccc} & \text{not yet entered} & \text{breeder} & \text{non-breeder} & \text{dead} \\ \hline \text{not yet entered} & 1-\gamma & \gamma & 0 & 0 \\ \text{breeder} & 0 & \varphi * (1-\psi_{BNB}) & \varphi * \psi_{BNB} & 1-\varphi \\ \text{non-breeder} & 0 & \varphi * \psi_{NBB} & \varphi * (1-\psi_{NBB}) & 1-\varphi \\ \text{dead} & 0 & 0 & 0 & 1 \end{array}$$

$$\begin{array}{c|cc} & \text{seen} & \text{not seen} \\ \hline \text{not yet entered} & 0 & 1 \\ \text{alive} & p & 1-p \\ \text{dead} & 0 & 1 \end{array}$$

$$\begin{array}{c|cc} & \text{seen} & \text{not seen} \\ \hline \text{not yet entered} & 0 & 1 \\ \text{breeder} & p & 1-p \\ \text{non-breeder} & 0 & 1 \\ \text{dead} & 0 & 1 \end{array}$$

Figure 2. State transition matrices (left) and observation matrices (right) for males (above) and females (below). γ is the removal entry probability, φ is the survival probability, Ψ^{NB_B} is the probability of resuming breeding, Ψ^{B_NB} is the probability of skipping breeding, and p is the detection probability

Results

The two sex-specific JS models converged well and all $\hat{R}$ values were below 1.1, indicating good convergence of the four chains. Moreover, the posterior predictive checks indicate a good fit as well, with a value of 0.63 for females, and of 0.86 for males (Figure S1, Appendix S2).

The partial rate correlation analysis showed a significant negative correlation of the number of captured individuals in a year with the number of captured individuals in the previous year (lag = 1; Figure 3).

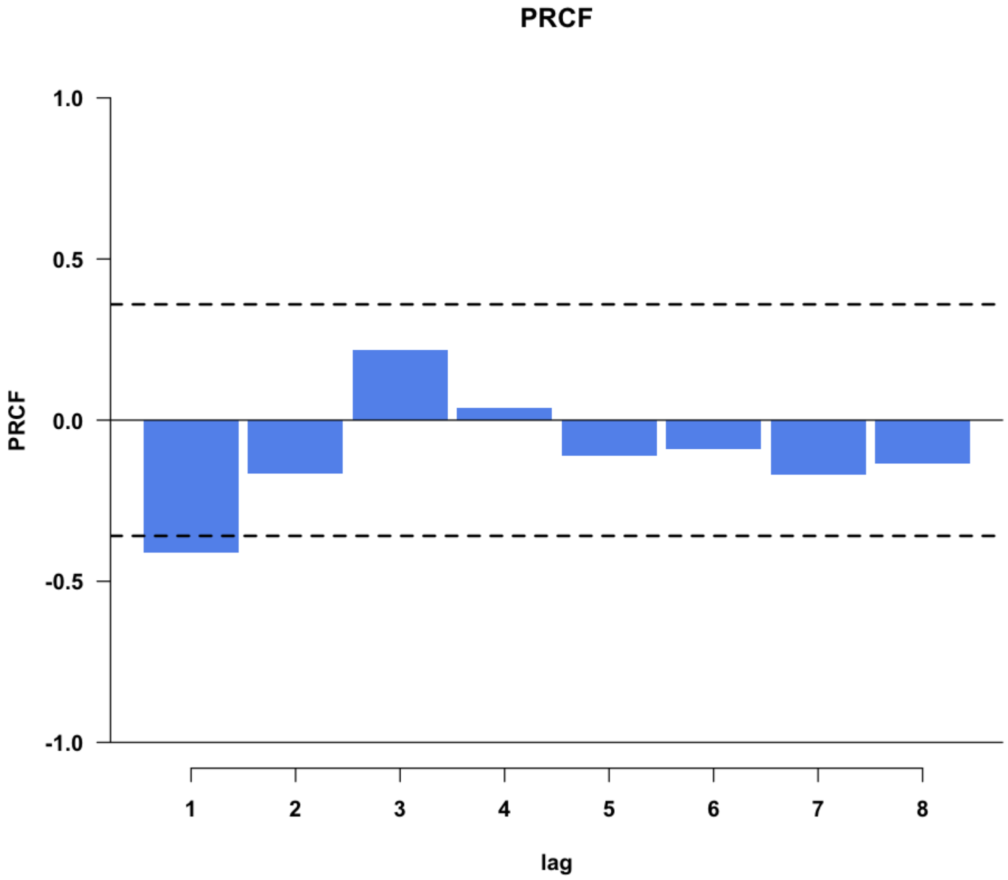

Figure 3. Result of the partial rate correlation of the number of captured individuals for the period 1982-2012 (pre-increase), with respect to the number of captured individuals in the previous years (lag). The significant correlation at *t*-1 suggests that density dependence is acting on keeping the population fluctuating around a return point.

Average male survival φ was 0.74 (95% credible interval CRI; [0.72 ; 0.76]) and it varied little over the study period (Figure 4). Average female survival was 0.73 [0.71 ; 0.76] for females and it showed a slight decrease in the last ten years (Figure 5). We found an average survival in the year following the first capture φ' of 0.63 [0.61 ; 0.66] for males (Figure 4) and 0.57 [0.53 ; 0.62] for females (Figure 5). The average probability of skipping breeding Ψ^{B_NB} was 0.65 [0.61 ; 0.69] and showed moderate variation over the study period (Figure 6), while the average probability of resuming breeding Ψ^{NB_B} was 0.84 [0.76 ; 0.91] and showed stronger variation, with an increase followed by a stabilisation in the last 10 years (Figure 7). We found an average detection probability p of 0.92 [0.89 ; 0.95]. The highest number of new male breeders entering is 233 [212 ; 256] in 2014, while for females it is 132 [120 ; 146] in 2019 (Figure 8).

There are negative correlations of population size with survival (females: -0.12 [-0.20 ; -0.04], males: -0.07 [-0.13; -0.01]; Table 2) and of the length of the active season on male survival (-0.07 [-0.14 ; -0.002]; Table 2). We also found a positive correlation of population size with the probability of resuming breeding in females (0.85 [0.38 ; 1.52]; Table 2).

We found a positive effect of temperature during the egg phase on the per capita recruitment B_t/N_t of females (regression coefficient = 0.10 [0.02 ; 0.18]; Table 2). All other covariates had no significant effects on recruitment of males or females, but some trends were nonetheless observable, such as the positive association between the temperature during the first-year juvenile phase (July-October) and the recruitment of both males and females.

To assess if there was a change in the sexual maturity age we visually assessed the trend of the average snout-to-vent length for first-time breeders over the study period (Figure 9). For males the smallest first-time breeders occurred in 2011 and they were around 5 mm shorter than in the previous years. In females the smallest first-time breeders occurred in 2016, but the difference from the previous years is less pronounced. The linear regression including body size of first-time breeders as a response of population density and length of active season indicated a significant negative effect of density and active season length in males (Table 3; r-squared = 0.02), and only of population density in females (Table 3; r-squared = 0.09).

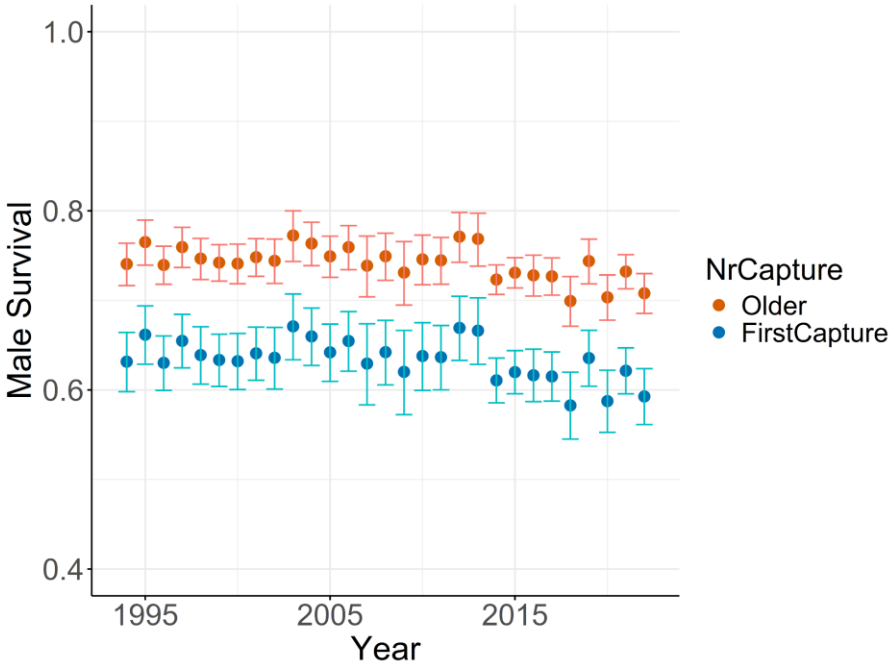

Figure 4. Yearly male survival probability. The blue dots refer to the average survival after the first capture, while the red dots refer to the average survival of individuals from their second capture on. The vertical bars represent the 95% credible intervals.

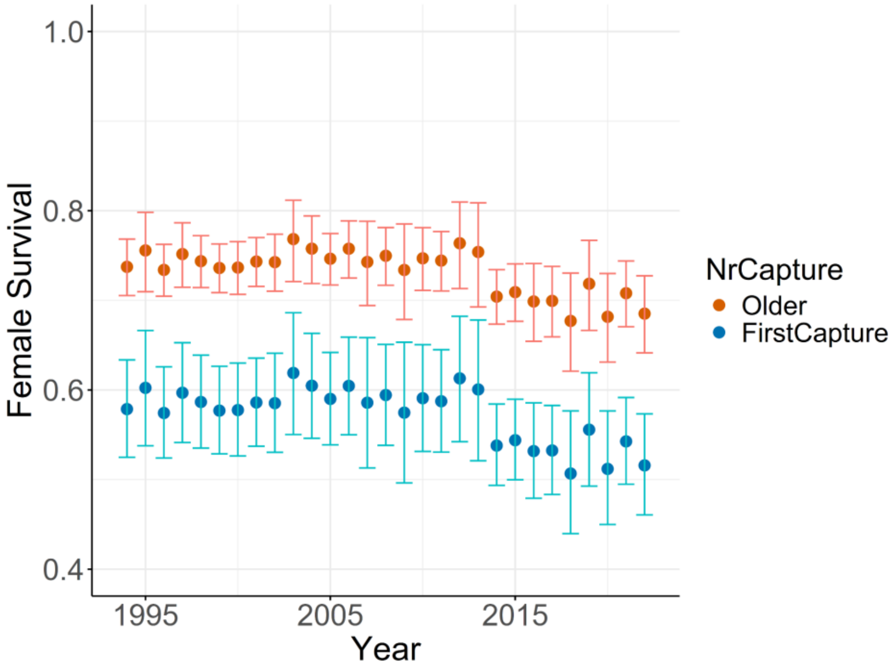

Figure 5. Yearly female survival probability over the study period. The blue dots refer to the average survival after the first capture, while the red dots refer to the average survival of individuals from their second capture on. The vertical bars represent the 95% credible intervals.

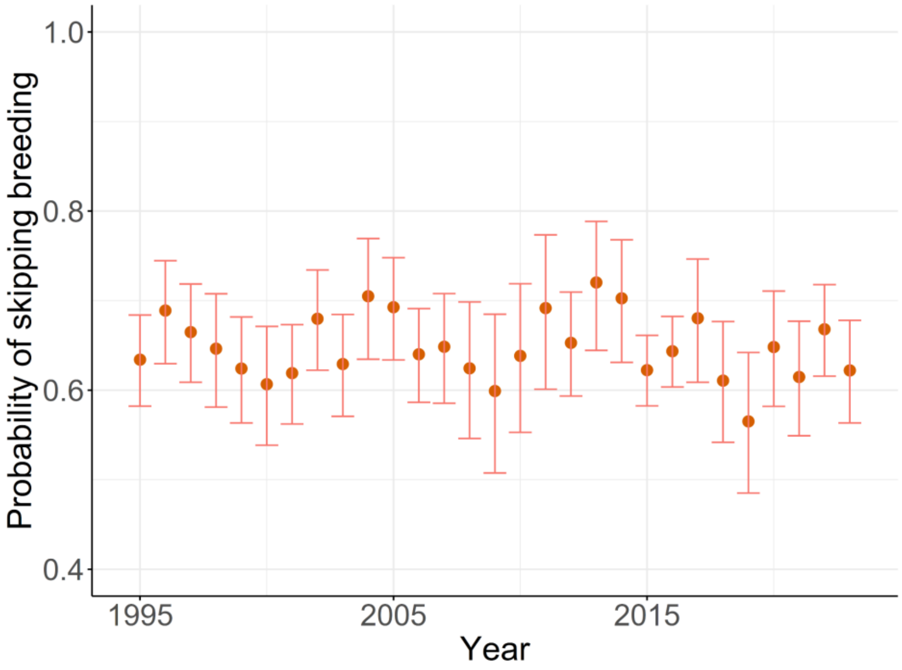

Figure 6. Yearly probability of a female skipping breeding after having bred in the previous year over the study period. The red dots represent the mean value, while the vertical bars the 95% credible intervals.

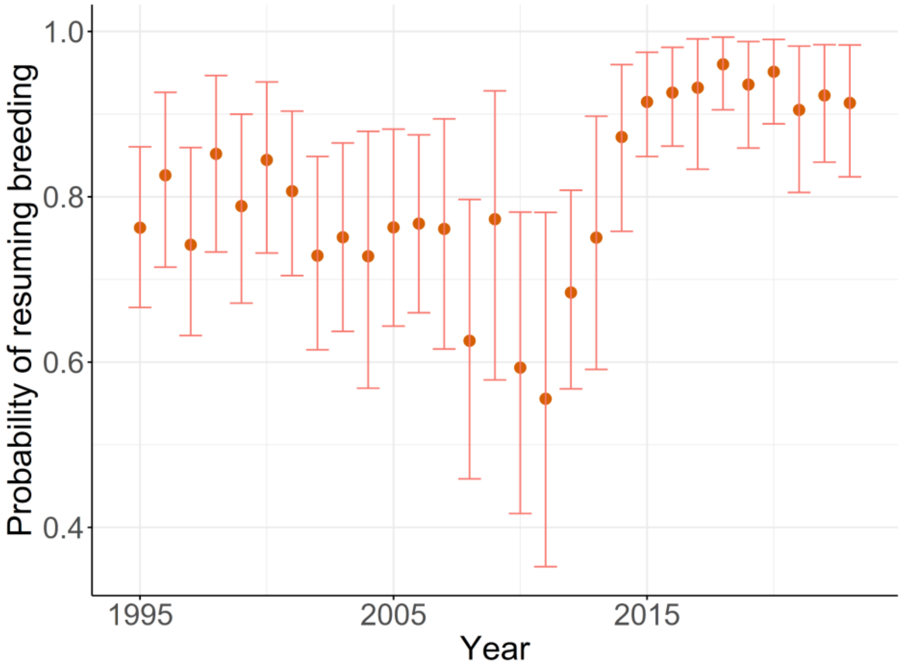

Figure 7. Yearly probability of a female resuming breeding after skipping breeding in the previous year over the study period. The red dots represent the mean value, while the vertical bars the 95% credible intervals.

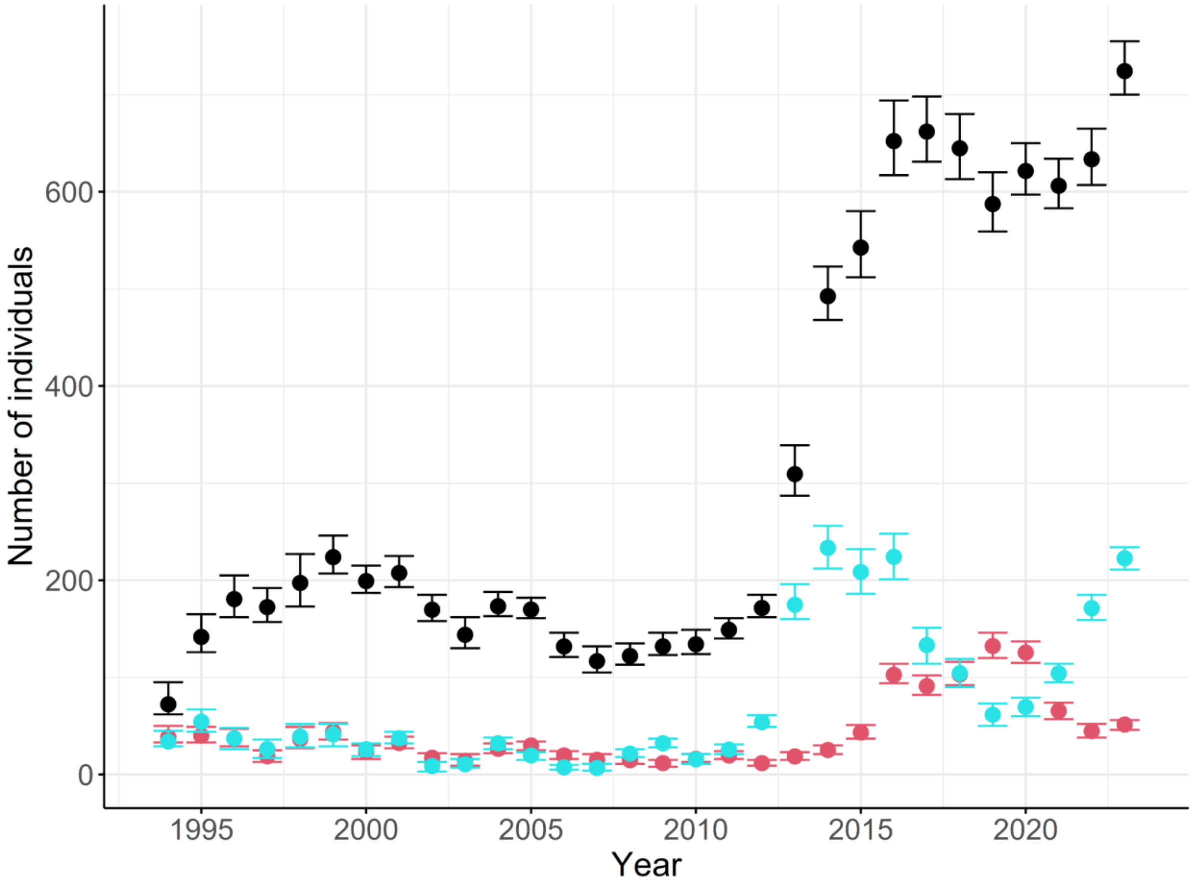

Figure 8. Trends over the period 1994-2023 for the total number of adults (sum of the number of males, breeding females, and non-breeding females; black dots), the number of new male breeders (blue) and new female breeders (red). The vertical bars show the 95% credible intervals.

Table 2. List of the covariates investigated and their correlation with the different focal vital rates. For each covariate we indicate the estimated mean correlation coefficient and its 95% credible interval (CRI), as well as the proportion of positive values (>0) from the posterior distribution. Proportion values close to 1 hint at significant positive correlations, while values close to 0 suggest a significant negative correlation. In bold we highlight the significant correlations (i.e., the 95% CRI did not overlap 0).

Vital rate	Covariate	Coefficient [95% CRI]	Proportion
Survival males	**Population size**	**-0.07 [-0.13 ; -0.01]**	**0.01**
Survival males	**Length of the active season**	**-0.07 [-0.14 ; -0.01]**	**0.02**
Survival females	**Population size**	**-0.12 [-0.20 ; -0.04]**	**0.002**
Survival females	Length of the active season	-0.06 [-0.19 ; 0.08]	0.20
Resuming breeding	**Population size**	**0.85 [0.38 ; 1.52]**	**0.99**
Resuming breeding	Length of the active season	-0.28 [-0.69 : 0.10]	0.07
Resuming breeding	Temperature during the two-week period before breeding	0.27 [-0.15 ; 0.73]	0.90
Skipping breeding	Population size	-0.08 [-0.22 ; 0.06]	0.14
Skipping breeding	Length of the active season	-0.07 [-0.22 ; 0.07]	0.17
Skipping breeding	Temperature during the two-week period before breeding	-0.12 [-0.28 ; 0.04]	0.07
Recruitment males	Temperature egg phase	0.06 [-0.03 ; 0.15]	0.92
Recruitment males	Temperature tadpole phase	-0.01 [-0.11 ; 0.09]	0.42
Recruitment males	Temperature first-year juvenile phase	0.08 [-0.01 ; 0.16]	0.97
Recruitment males	Winter onset date	-0.07 [-0.15 ; 0.02]	0.05
Recruitment females	**Temperature egg phase**	**0.10 [0.02 ; 0.18]**	**0.99**
Recruitment females	Temperature tadpole phase	-0.02 [-0.10 ; 0.07]	0.35

Recruitment females	Temperature first-year juvenile phase	0.06 [-0.01 ; 0.12]	0.94
Recruitment females	Winter onset date	-0.06 [-0.13 ; 0.02]	0.06

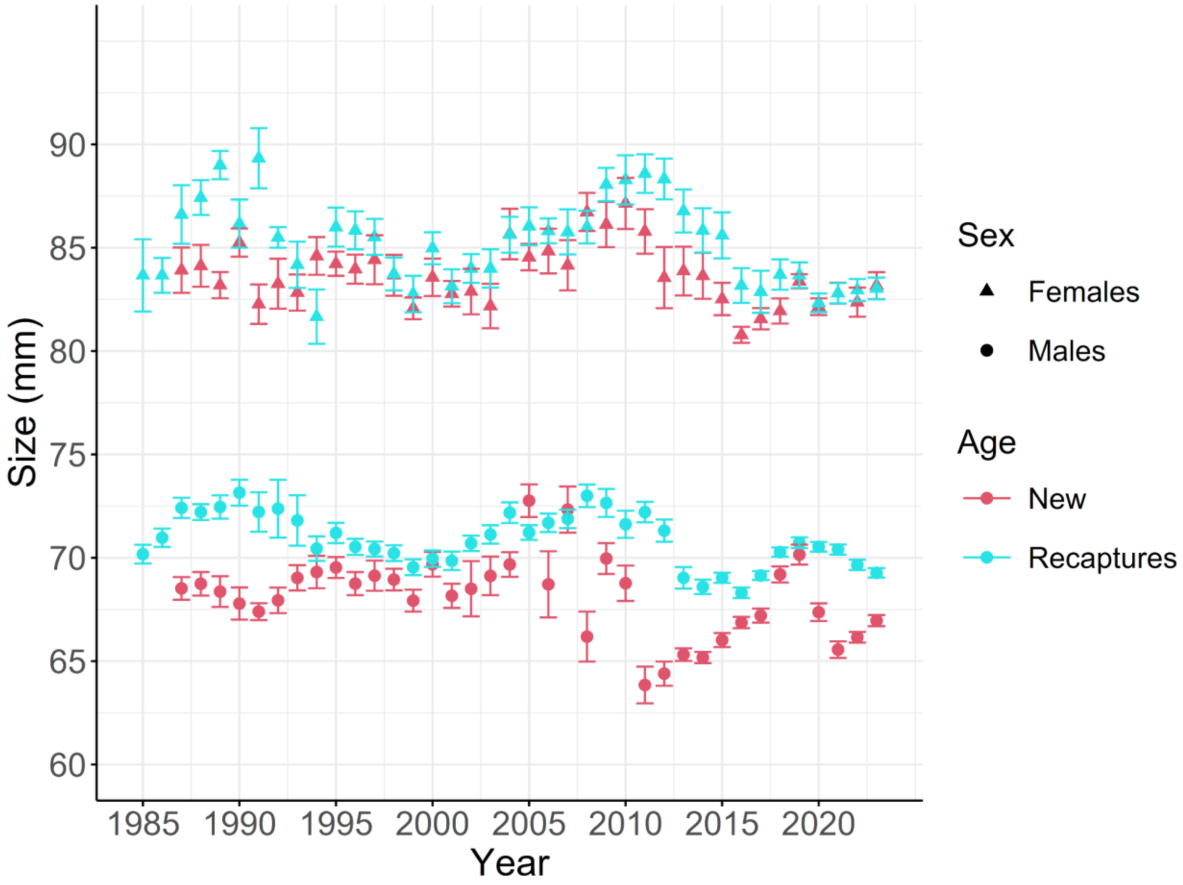

Figure 9. Average snout-to-vent length (in mm) of first-time breeders (red) and recaptured breeders (blue) from 1985 to 2023 for males (circles) and females (triangles). The vertical bars represent the standard error.

Table 3. Summary of the models investigating the correlation between active season length and population size with the body size of first-time breeders. We highlight in bold the significant correlations.

Sex	Intercept/Covariate	Estimate	Std. error	p-value
Females	Intercept	0.042	0.032	0.185
	Active season length	0.009	0.034	0.799
	Population size	**-0.09**	**0.027**	**0.001**
Males	Intercept	0.033	0.024	0.161
	Active season length	**-0.174**	**0.030**	**<0.001**

Population size	-0.076	0.023	0.001

Discussion

The study population underwent a sudden transition from an apparently stable size of around 150 adult individuals to a new abundance of around 600 individuals. The main aim of this study was to understand the drivers of this massive and rapid shift, with a focus on vital rates (i.e., survival, recruitment, and breeding probability). The Jolly-Seber model showed that the increase in the number of captured individuals from 2013 onwards is mainly due to a sharp increase in recruitment. This increase occurred initially in males, peaking in the period between 2013 and 2016, and again more recently in 2023. In females the peak is smaller, and is found during the period 2016-2020. The concurrent slightly decreasing trend observed in survival (especially in females), consistent with previous studies (Lenzi et al., 2024), further strengthens the finding that recruitment is the main responsible for the observed demographic changes. The increase and stabilisation of the probability of resuming breeding Ψ^{NB_B} in females from 2015 onwards can partly explain the observed increase in the number of captured individuals (Figure 1) as there will be more females at the breeding site, but it cannot explain the increase in the total population size estimated from the Jolly-Seber model (Figure 8; black dots), as it includes both breeding and non-breeding females. Changes in breeding probability affect in fact only the ratio of breeding and non-breeding females. The estimated breeding population size (i.e., not including female non-breeders) shows a similar temporal pattern to the total estimated population size (Figure S7), with only minor differences. This confirms that the increase in the probability of resuming breeding can affect the number of breeders at the breeding site, but only to a minor degree.

To understand why recruitment strongly increased in recent years we tested if relevant environmental conditions during key early stages of the life cycle could drive changes in recruitment. Notably, we found that the temperature during the egg phase is positively correlated with female recruitment. This finding suggests that at warmer temperatures egg survival might be higher and the hatching time faster, possibly resulting in an increased survival in the first year and consequently in an increased number of individuals entering the breeding population in the following years. The same trend is observed in males, although the effect was not strictly significant. Moreover, we find indications of a positive effect of temperature during the first-year juvenile phase (July-October) for both males and females (Table 2). Warmer temperatures during this period could lead to higher survival due to lower physiological stress, increased food availability, and faster development, which might be beneficial for surviving the first winter. The importance of early life-stage conditions for amphibians has been previously described, especially in experimental settings, with a generally recognised role of density and environment on tadpole growth and survival (e.g., Semlitsch & Caldwell, 1982; Reading & Clarke, 1999; Altwegg, 2003), with a cascading effect at the population level (e.g., Berven, 1990). Also juvenile (i.e., the stage between metamorphosis and maturity) survival has been identified as a key vital rate for amphibian populations (Vonesh & De la Cruz, 2002; Petrovan & Schmidt, 2019), whereas egg survival might play a minor role, as the stronger regulating effect is found on the tadpole stage due to density dependence (Vonesh & De la Cruz, 2002; but see Lampo & de Leo, 1998, for the role of egg survival). The fact that we find a significant correlation of temperature during the egg phase and female recruitment might mean that the role of conditions during the egg phase can be context-dependent, especially at higher elevations where temperature might be more relevant in determining egg survival, as freezing temperatures could compromise egg survival or hatching.

If warmer temperatures during the egg or first-year juvenile phases are driving recruitment then we should observe a parallel increase in temperatures in the study area in recent years, to match the increasing recruitment. This does not seem to be the case (Figures S3 and S5, Appendix S1), hinting at the fact that these effects might actually be quite weak, and other factors are the main drivers of the increasing recruitment.

One of these drivers could be the behaviour of a single above-average cohort, which either was the result of an exceptional breeding year or survived better than expected until adulthood, due to factors that we have not identified. We have reason to believe that this is a possibility since the observed difference of 4-5 years between peak entry in males (in 2014) and females (in 2019) matches with the difference in sexual maturity age known for this population (Hemelaar, 1988), indicating that the new breeders entering the adult population might have been born in the same year. Of this cohort we would initially observe few precocial males which reached sexual maturity at a younger age and smaller size (sexual maturity age is not fixed; Hemelaar, 1988; Schmidt et al., 2012). In ectotherms especially, trajectories of body size in relation to age at maturity can vary depending on conditions during growth. For instance, there can be delayed maturity at both smaller and larger sizes (Berrigan & Charnov, 1994), but also earlier maturity at smaller sizes (Stearns & Koella, 1986; Roff, 2001), which could be the case in our population. The precocial males would then be followed first by a larger portion of bigger first-time breeding males, as they had one more year to grow. Then by the first few precocial smaller (relatively speaking) females, and finally by a larger number of bigger first-time breeding females. This pattern is exactly what is observed from both the trend of new individuals entering the population (Figure 8), and the body-size temporal trend (Figure 9), thus providing support for the hypothesis that a single cohort might be largely responsible for the observed increase in the number of breeding adults. The beginning of a similar pattern might be observable for the years 2020-2023, hinting at a second, more recent, cohort behaving similarly. Following this line of thought, we can speculate that populations in harsh environments can persist and even thrive thanks to sporadic good years due to stochastic environment or events, resulting in particularly successful cohorts (Pechmann & Wilbur, 1994; Alford & Richards, 1999; Turgeon et al., 2024a; but see Green, 2003).

Another possible reason contributing to an increased abundance is that toads might be reaching sexual maturity at a younger age, with younger individuals thus contributing to the breeding population. This shift towards a younger age of sexual maturity might be visible in body-size changes, if we assume an associated lower body size, as some studies predict (Stearns & Koella, 1986; Roff, 2001). This could especially be the case in males, as first-time breeders since 2010 are generally smaller than in the 25 years before, while in females the trend is less evident. As theory predicts, earlier sexual maturity could be due to a plastic response to better environmental conditions (Stearns & Koella, 1986) such as warmer temperatures, which could increase food availability and metabolism (Stearns & Koella, 1986; Amat & Meiri, 2018). Our linear regressions suggest that population density and the length of the active season might be partly responsible for driving body size of first-time breeders, although the low r-squared values indicate that there are probably more factors at play.

To summarise, we propose two most reasonable explanations for the four-fold increase and stabilisation of the adult population post-2013. The first reason is that there can be cohorts that survive exceptionally well, perhaps in part due to better conditions for egg, tadpoles, and first-year juveniles with more individuals surviving the most critical initial life stages. The related vital rates (in particular survival of tadpoles and juveniles) have been previously identified as being of critical importance for population dynamics (e.g. Biek et al., 2002; Vonesh & De la Cruz, 2002; Petrovan & Schmidt, 2019). Although our study could not find strictly significant positive effects of environmental conditions during tadpole and first-year juvenile stages on recruitment, we can still observe a trend, thus cannot exclude their importance for population persistence. Future analyses fully dedicated to the study of egg, tadpole, and juvenile success are required to confirm if early life-stages success indeed contributes importantly to recruitment into the adult population. Such analyses are very complex but provide valuable knowledge (Berven, 1990) and might benefit from new technologies (Ringler et al., 2015). The second reason is the possible shift in sexual maturity age, which could be confirmed by obtaining age data on first-time breeders and comparing them to previous studies (Hemelaar, 1988).

Overall, the analysis of this long-term study reveals that this population was for at least 30 years held fluctuating around a return point due to density dependence, but interestingly, it has escaped this tendency due to a massive increase in recruitment. We ascribe this shift partly to beneficial environmental conditions during the early life-stages, but mainly to a single cohort surviving exceptionally well. Future studies on the focal population should attempt to verify the latter hypothesis, while also clarifying if the massive increase in abundance is a temporary situation (i.e., surviving temporarily beyond the carrying capacity) with a return to lower abundances, or if it will stabilise around a new carrying capacity.

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.

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 will be made available online on the open repository Zenodo upon submission of the manuscript.

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Supporting information

Appendix S1 - Temporal patterns of environmental covariates and breeding population size

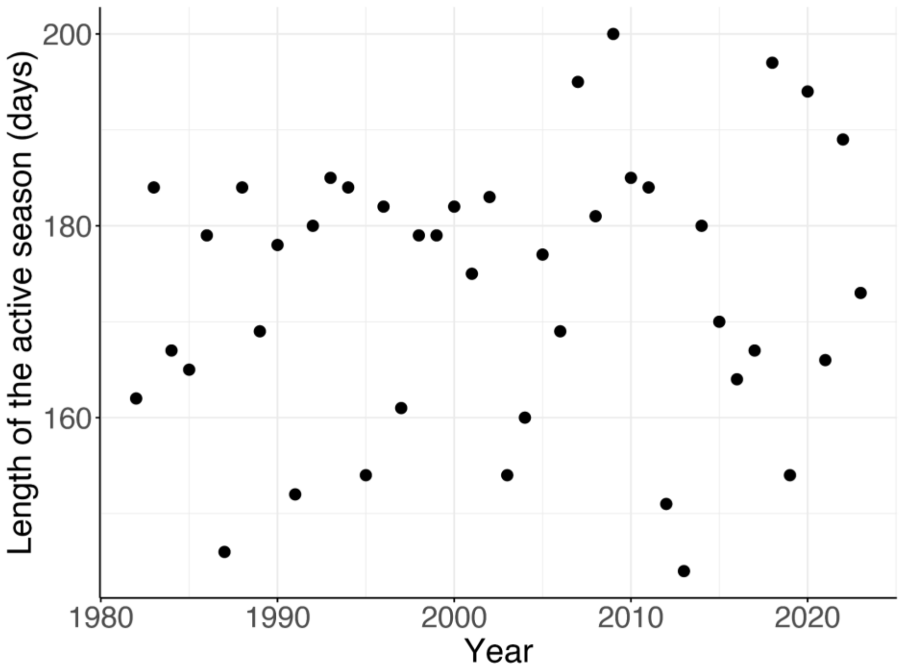


Figure S1. Temporal pattern of the length of the active season over the period 1982-2023.

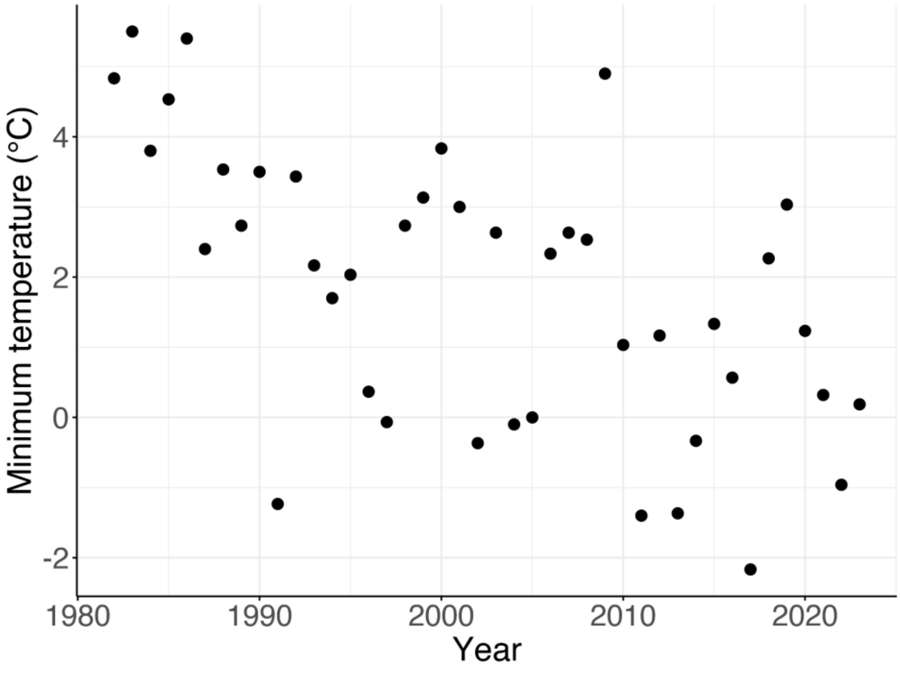


Figure S2. Temporal pattern of the two-weeks mean minimum temperature before breeding over the period 1982-2023.

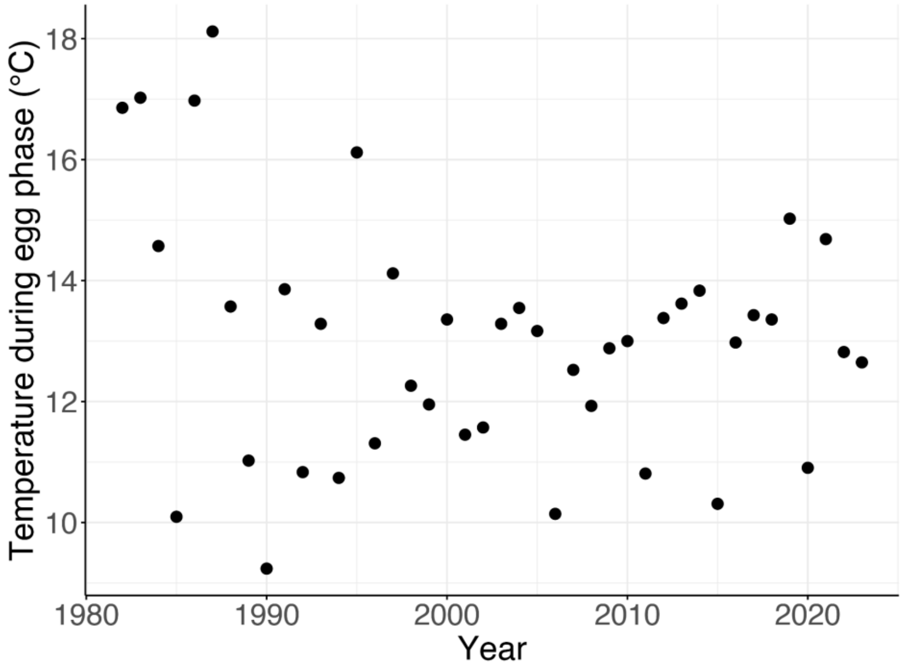


Figure S3. Temporal pattern of the temperature during the egg phase for the period 1982-2023.

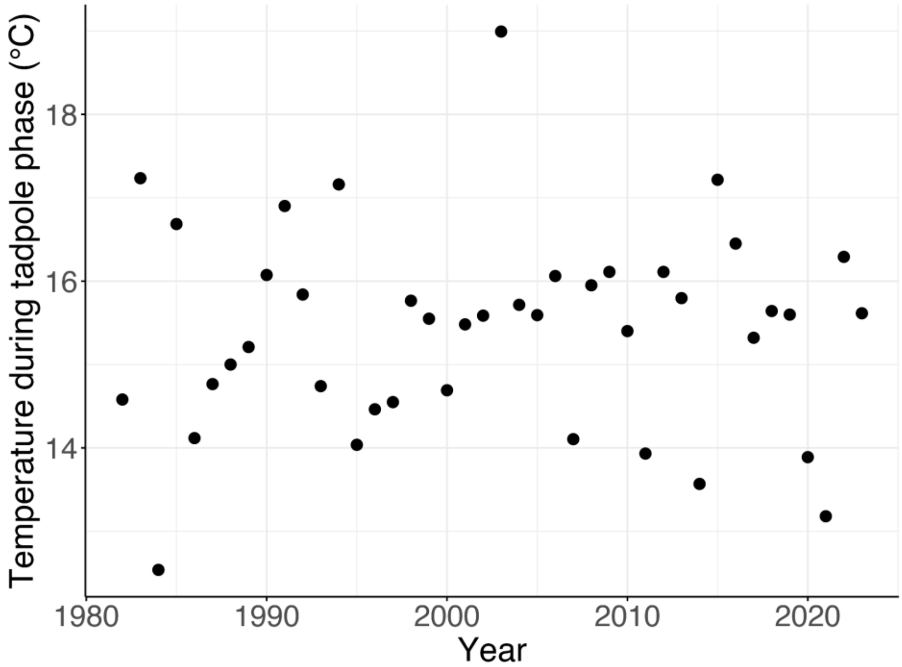


Figure S4. Temporal pattern of the temperature during the tadpole phase for the period 1982-2023.

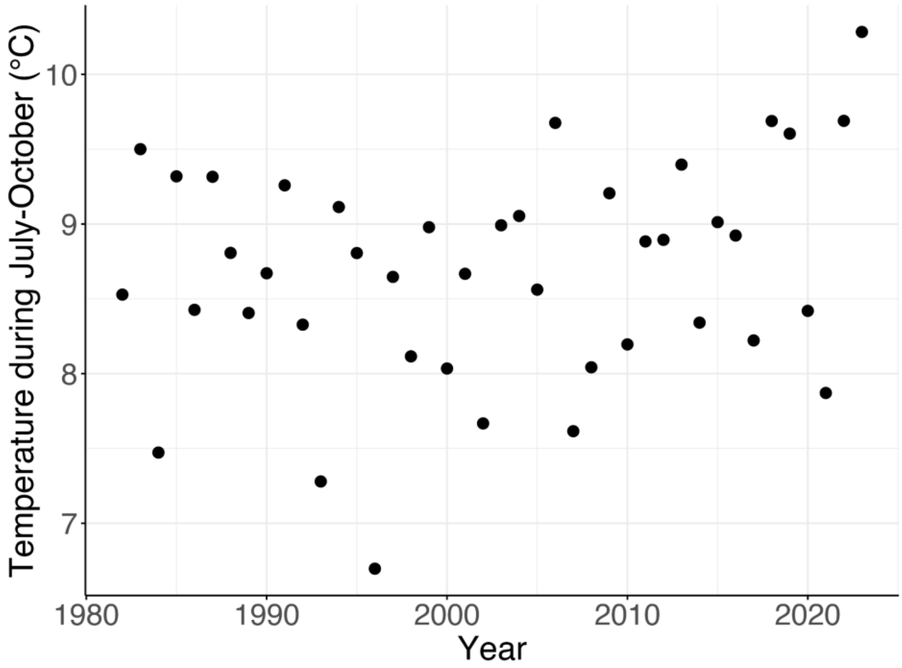


Figure S5. Temporal pattern of the temperature during late summer and early autumn (July-October) for the period 1982-2023.

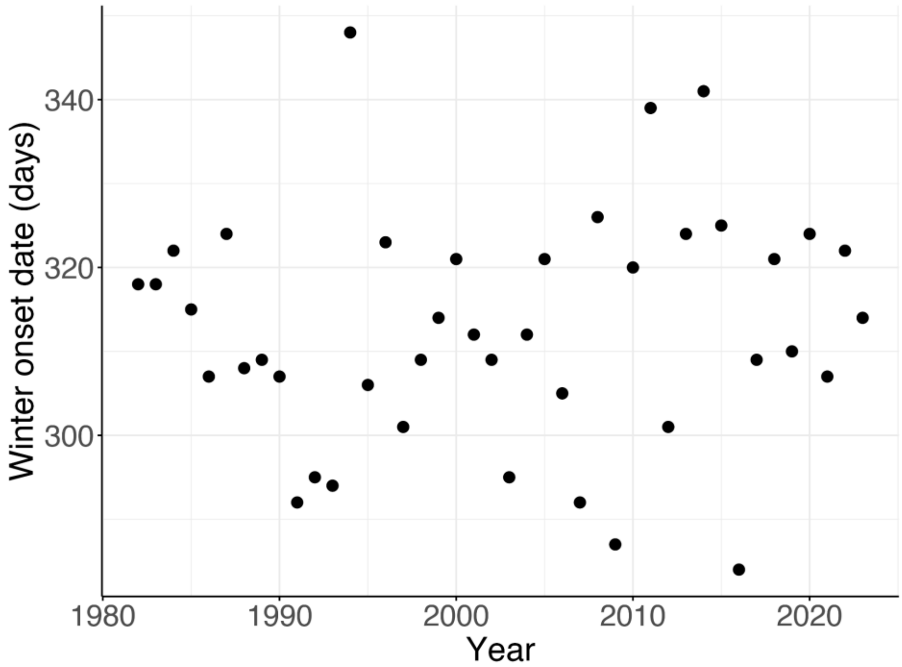


Figure S6. Temporal pattern of the winter onset date for the period 1982-2023.

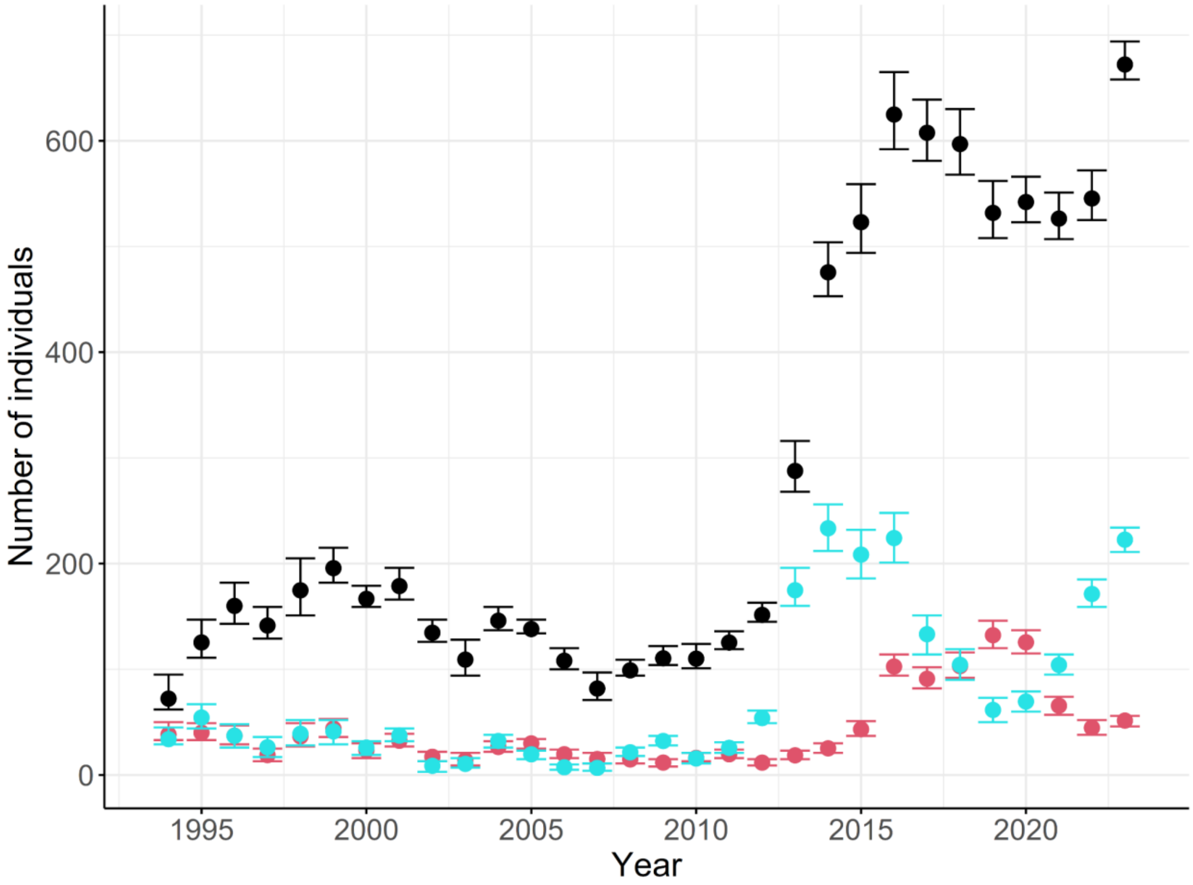
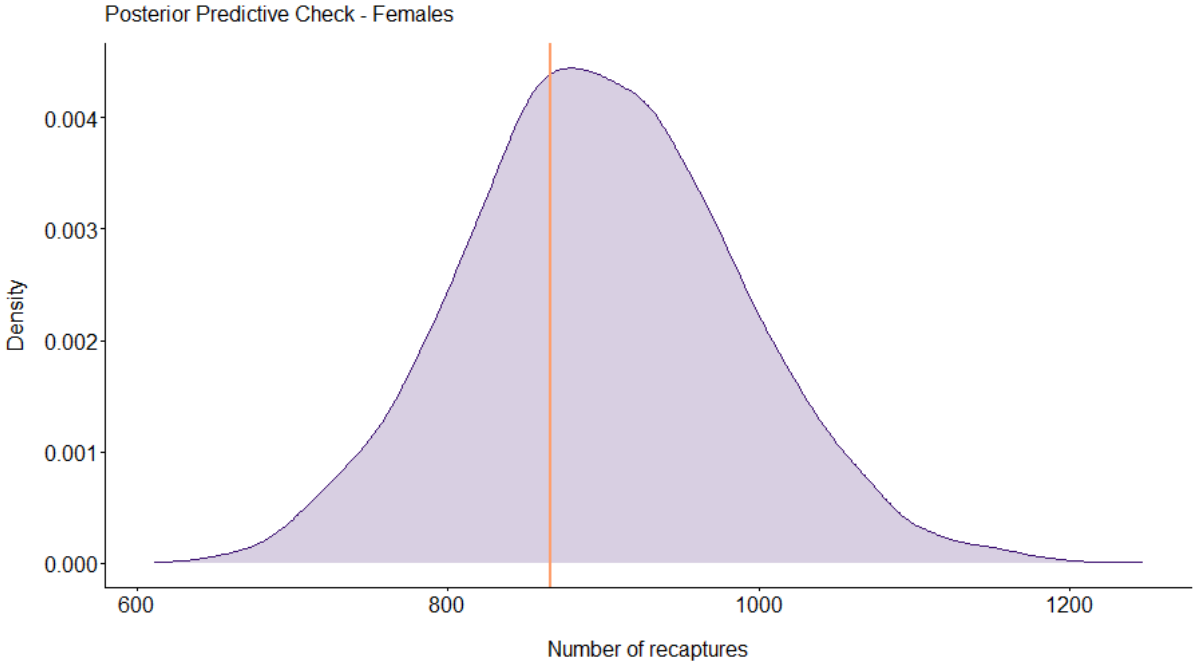


Figure S7. Temporal pattern of the estimated breeding population size (males + breeding females; black dots), new male recruits (blue dots), and new female recruits (red dots) for the period 1982-2023.

Appendix S2 - Posterior predictive checks



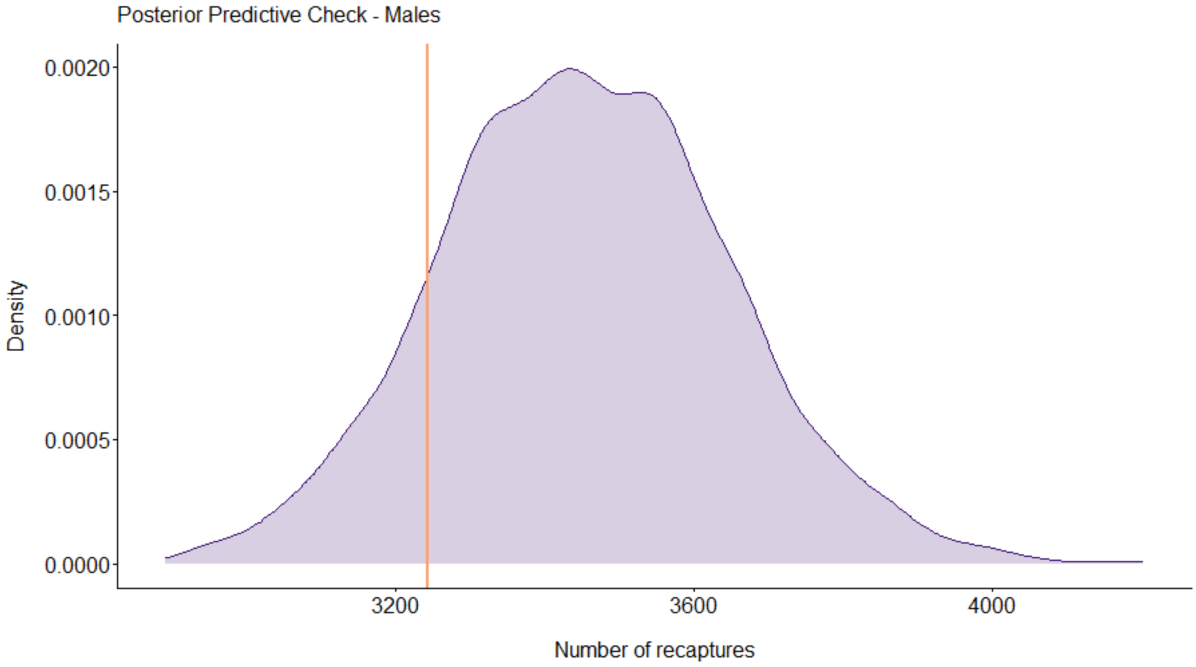


Figure S1. Posterior predictive check plots, showing the distribution of the number of recaptures for the simulated datasets (purple line) and for the original dataset (orange vertical line). The plot above shows a very good fit for the model on females (Bayesian p-value = 0.63), while the plot below shows a moderately good fit for the model on males (Bayesian p-value = 0.86).

General Discussion

Population ecology is a fundamental discipline aiming to understand the dynamics of populations, based on the study of underlying processes such as birth, mortality, immigration, and emigration. It is therefore a much-needed discipline to understand how species are organised in terms of abundance and distribution, while providing the scientific basis for conservation and management actions. Modern population ecology dates back to the second half of the 19th century and the early decades of the 20th (Egerton, 2015), and tremendous advances in this field were made in the past 150 years. The main reasons have been the constant development of mathematical tools and statistical methods coupled with the development of new technologies, resulting in increased computational power and constantly refined techniques and devices (e.g., individual marking techniques, camera traps, GPS loggers, satellites, drones…), which enabled ecologists to address some of the most fundamental questions in the field of population ecology. Currently, a majority of populations of most taxa are facing multiple threats such as global climate change and anthropogenic influence. As ecologists, we have a responsibility to conduct comprehensive analyses based on sound methods and appropriate data and, when needed, provide reliable suggestions to ensure that the most effective measures are implemented.

This thesis focuses on the scientific aspect rather than the applied one. It consists of a comprehensive analysis of a marginal population of common toad living at the edge of its elevational range, with each chapter focusing on complementary aspects of its ecology and its demography, thus providing a complete overview on the role of individual traits, the environment, and population density in influencing this population. Combined, these chapters significantly contribute to our knowledge of alpine amphibian populations, which are seldom studied, and provide useful information to ecologists whose interests lie outside of this narrow niche. In fact, this thesis can potentially serve as a basis to comprehensively study other populations and to illustrate what data is needed, thanks to the methodology that I showcase. In the text that follows, I summarise each chapter and provide a broader outlook into potential perspectives and limitations.

In **Chapter 1**, I investigated the temporal changes in breeding phenology and its drivers. The environment plays a significant role in determining the individual timing of arrival, while genetics (in the form of repeatability) only plays a minor role, although it could in part contribute to the general timing of breeding alongside environmental conditions. The implication of an earlier breeding in spring is that toad eggs might face an increased risk of disturbance due to late frost events, leading to compromised tadpoles. On the other hand, early metamorphosed juveniles might have more time to fully develop and grow before the first hibernation, increasing their survival chances.

The phenology of hibernation was not the focus of this chapter but could be particularly relevant, since hibernation is a key event in the annual life cycle of toads. The start of the hibernation period is unknown for our population and can only be presumed from the meteorological data. Indeed, the start of hibernation is probably due to environmental factors such as snowfall, colder temperatures, reduced daylength, and others. Investigating how the timing of hibernation is changing is key to understanding how much time toads have in summer to grow and prepare for winter. It also enables us to assess how much time they spend in hibernation, which is a sensitive period with potential consequences on their fitness upon emergence in spring.

A feasible way to obtain more precise individual-level information on phenology for both breeding and hibernation periods could consist of telemetry monitoring by using radio transmitters or GPS trackers. Tracking individuals and their movements would enable a much more refined understanding of the activity of toads during their annual life cycle. Additionally, if we extend our interest beyond phenology, we would also be able to understand how toads navigate their environment. Importantly, it would provide information on how toads partition their daily activity schedule, for instance when feeding, or when coping with particularly hostile conditions (e.g., droughts or storms), which can occur frequently and less predictably at higher elevations. This detailed look into the daily life of toads would enable us to better understand how they interact with their environment, and ultimately the consequences for their survival.

Aside from the intrinsic value of investigating phenology changes in the context of climate change in this population, this study represents a valuable asset for future comparative studies, such as evidence syntheses and meta-analyses focused on phenological changes across taxa. The uniqueness of the context (i.e., alpine ecosystem) and the length of the study would help fill knowledge gaps and contribute to a more comprehensive overview of how phenology is shifting, both in intensity and direction, and why.

In **Chapter 2**, I assessed direct and indirect (i.e., trait-mediated) effects of extrinsic (i.e., the environment) and intrinsic (i.e., population density) factors on survival and breeding probability. We obtained valuable and interesting findings, such as the presence of density dependence effects on adult survival, a novel insight for natural amphibian populations. We also showed the importance of individual traits, in our case body size, not only in potentially affecting vital rates, but in mediating their response to extrinsic and intrinsic factors as well, suggesting that including indirect effects leads to a more accurate depiction of the underlying processes affecting vital rates. For instance, we could show that there are negative associations between population size and body size, and between body size and survival (thus globally a positive indirect effect), indicating that density might buffer the negative effect of body size on survival while still maintaining itself a direct negative effect. The framework applied in this paper is quite flexible and can be applied to various species across different contexts.

While I specifically focused on body size, there might be other important physiological traits also mediating the effects of the environment and population density on demographic rates, such as metabolism. Ideally, one would analyse a suite of traits to fully understand the underlying processes involved, although increased complexity must not always be the end goal if it hinders interpretability. For instance, having focused only on body size in our study, any indirect effect of an ecological variable on a vital rate acting through another individual trait would instead be interpreted as a direct effect. Thus, an even more detailed study on how various individual traits can mediate extrinsic and intrinsic factors, and their interplay, while simultaneously also investigating more extrinsic factors, could be beneficial to truly understand the mechanisms responsible for vital-rate variation.

In **Chapter 3**, Daniel and I investigated the mating system of the study population, with a particular focus on the association between body size and successful mating attempts in males (i.e., being in amplexus with a female). This study serves as an important reference for studies on reproductive events of natural amphibian populations by combining an impressive dataset with a comprehensive and detailed analysis. It also helps bridging the gap between experimental analyses and the reality of natural populations, by highlighting the importance of body size in successfully entering amplexus and resisting displacement as previously shown in experimental studies. Moreover, we could also show that males were less successful with increasing age, despite technically benefitting from a larger size, as individual growth never truly stops over their lifetime. Combining these findings and the results of Chapter 2, where I found a negative correlation between body size and survival in males, we can conclude that there is probably a senescence effect. Older males are bigger but have lower survival and breeding success than younger individuals, hinting at a decline in general performance at older age.

An interesting question that could be investigated in a follow-up study on the mating system is to determine which individuals actually reproduce. For adult females, data suggests that all or most of them reproduce successfully, given the strong male-biased sex-ratio observed at the breeding pond. Regarding males, we rarely know which toad was actually in amplexus during spawning, since data collection does not take place every night, and displacements between males could lead to new pairs during the unsampled nights. Sampling daily is problematic due to the excessive disturbance and stress for the toads. To solve this issue, one would need to establish relatedness and build a pedigree, using genetic samples. Such data would let us not only determine with accuracy who is producing offspring, with follow-up analyses about the drivers of fitness, but also estimate the effective population size, a key metric that population geneticists often calculate when investigating population resilience and persistence.

In **Chapter 4**, I investigated the sudden and rapid increase in the number of breeders in the population and explored the possible proximate mechanisms that have caused this increase, and ultimate consequences for the population. The fact that this population could increase four-fold in a short timespan after being rather stable for at least 30 years is very interesting and unexpected. I could find indications of density dependence limiting population growth in the period before this strong increase, suggesting that rare events such as particularly successful breeding years can push a population beyond the current capacity and lead to a new equilibrium. This finding also implies that there must be a new, and higher, carrying capacity, perhaps due to changing conditions in the ecosystem which can now sustain a larger population. Given the unexpected dynamics shown by the population, I am curious to observe how it will behave in the future. In the near future, if conditions do not change excessively, we might expect the population to fluctuate around the new carrying capacity. The distant future might look less favourable, especially considering the high sensibility of alpine environments to climate change (Diaz et al., 2003), and the high dependence of toads to their native water habitat. The breeding pond is rather small, and thus probably less buffered against changing abiotic and biotic conditions (e.g., drought, vegetation change, water acidity…), which could prove problematic for population persistence.

A limitation of this study consists in not knowing the age of individuals. Having the age structure of this population would make almost trivial understanding if the increase in abundance is the result of a single cohort surviving exceptionally well, as hypothesised. For this reason, I tried to obtain the age of a subset of 100 toads through skeletochronology. Skeletochronology is a method consisting in determining the age of vertebrates (especially reptiles and amphibians) based on the number of lines of arrested growth (LAG) visible in cross-sections of bones, akin to dendrochronology for trees. LAGs are formed during phases when the individual does not grow (i.e., hibernation) and thus each LAG corresponds to a year. Skeletochronology has been widely used before (see Castanet & Smirina, 1990; Sinsch, 2015), but recently its accuracy and validity have come under scrutiny (Schucht et al., 2021). In my case, the outcome of the skeletochronology analysis was disappointing. Most cross-sections were not showing LAGs, and in the cases where LAGs were visible, there were strong intra-individual differences in their number, causing uncertainty in age assignment. The lack of reliable age estimates has not been so problematic, since I could adopt valid alternatives, such as the von Bertalanffy growth model Bayesian framework which does not require age (Chapter 2), or using age since first capture as a proxy (Chapter 3). Nevertheless, knowing the age of individuals would have facilitated certain analyses and would have allowed for more direct comparisons with other studies. It could also have provided an answer to the question of shifting age at sexual maturity. Another way to obtain reliable age information consists in marking juveniles, enabling lifelong monitoring and knowledge on the exact age of individuals. This would probably require smaller PIT tags, as well as a bigger financial and manpower effort, but the information that could be obtained would be worthwhile.

Overall, the four chapters of this thesis provide a comprehensive analysis of an alpine common toad population, with novel results and interesting insights, which go beyond the narrow focus on high-elevation amphibians. In Chapter 1, I show that breeding phenology advanced considerably over the study period, and in more recent years interannual variation has increased. In Chapter 2, I assessed direct and indirect effects of the environment and population density on vital rates, finding notably density dependence effects on adult survival, possibly a novel finding in natural amphibian populations. In Chapter 3, we focused on the mating system, finding support for the importance of body size also in natural populations, while also identifying a possible effect of senescence in males. Finally, in Chapter 4, I investigated the unusual population dynamics of the study population, with our findings hinting at the importance of early life stages and suggesting that rare events, leading to above-average cohorts, can push populations out of what could have appeared as a stable equilibrium.

One of the main reasons this thesis has been possible is the availability of a vast amount of data and its level of detail. Having more than 40 years of individual-level data is almost unheard of for amphibian populations. The length of the study enabled me to investigate processes over a period more representative of the changes happening in the population (Clutton-Brock & Sheldon, 2010; Reinke et al., 2019; Sheldon et al., 2022). For instance, with data covering only the past 20 years I would not have been able to identify the steep advancement of the breeding dates in the 1980s. With data only from the past 10 years, the large increase in the number of captured individuals would have never been observed, and the consequence would have been to assume that the population had been existing at a constant, high abundance. These examples show the importance of long-term studies. Obviously, short-term studies can provide very useful information as well, but the more we can follow a population, the more we are sure to capture a wider spectrum of processes and dynamics taking place (e.g., extreme environmental events), providing us with more reliable and informative data, which can then be valuable for research beyond the study itself. For instance, data on this population has been already used for multiple comparative studies (Cayuela et al., 2021, 2022; Reinke et al., 2022), and more are being prepared. My hope is that the findings of the chapters of this thesis can also be included in future comparative studies or meta-analyses, be it about phenology, mating behaviour, vital rates, or population dynamics. Given the rare context of this population, the findings would definitely represent an addition of quality. To conclude, I encourage the establishment of comprehensive long-term studies, especially of understudied locations or taxa. Starting new long-term studies is a massive investment, but I hope I could show why they are important and can contribute to the field of population ecology.

Acknowledgements

This thesis would not have been possible without the support from Info Fauna Karch, and the grant provided by the Federal Office of the Environment. I would like therefore to express my gratitude to both institutions for supporting my thesis.

I am very grateful to my main supervisor Benedikt Schmidt. First of all for accepting me for this project, and secondly for his continuous support during these four years. Thank you for your guidance, the feedback and comments on the various drafts, for answering my questions, sharing a lot of interesting papers, doublechecking my e-mails in German, and more.

I would also like to thank my co-supervisor and host here at UZH, Arpat Ozgul. Coming back to PopEcol after my master has been a real pleasure. Thank you Arpat for your presence, I knew I could count on you when needed, and thank you for the always constructive comments on my drafts. But most of all thank you for being a cool running (SOLA) and birding mate, I really appreciated all these out-of-office occasions. Despite what you have said multiple times, I am sure the PopEcol will be fine after I am gone and it will continue to run smoothly.

I am very thankful to all my other committee members, namely Michael Schaub, Silvia Zumbach, and both Hanna Kokko and Lukas Keller who shared the IEU representation duty. Thank you for your interesting and constructive comments during our three committee meetings, which have really helped shaping my thesis and guiding me. My gratitude also extends to Hugo Cayuela, for accepting to be my external examiner.

This thesis would have not been possible without the incredible and passionate work of countless volunteers collecting data in the field. They all performed an admirable work, withstanding often miserable weather conditions to catch and process thousands of toads over the study period. The dataset they created is really astounding and I am deeply grateful for having been able to work with such good data. Therefore, I would like to thank the ‘Scheideggleute’ for their amazing work, but also for their pertinent comments via email or during our in-person meetings: Kurt Grossenbacher, Silvia

Zumbach, Beatrice Lüscher, Sarah Althaus, Marco Thoma, Daniela Schmocker, and Helmut Recher. I extend my gratitude to all of their helpers as well.

I would also like to thank everyone in the PopEcol group, both past and present members, as well as the numerous associates. There are too many people to write down all of their names, and I enjoyed interacting with every one of them. The work environment in the past four years has been great and full of fun. I think everyone should be lucky enough to experience such an environment in their work life. Among the "popecollers" I would like to thank in particular Daniel Breitenmoser, the master student I was lucky to supervise. It is rare to find such an independent, curious, motivated, and capable student. I am sure you'll be successful no matter what you choose to do. And thank you for teaching me how to play Jass, while stuck in a snowstorm. Special mentions also go to Mo, for his patience and willingness to run many of my models on his computer in the last months, and to Louis for his precious feedback on parts of the thesis.

At Uni I would also like to thank the whole Admin/IT staff, for their help and kindness, in particular Ursina, Judith, Glauco, Debra, Michel, and Tina.

I am grateful to my family (the bros Vasco, Ivan, e Luca; as well as Mum and Dad) and my friends (in particular Benny, Gabs, Louis, Dilsad, Nino, Selin, Kevin, Lara, e "i soliti" Teo, Tom, e Pietro) for their presence. All moments shared, be it in the form of dog walks, playing (video)games, watching sport, outdoor activities, or relaxing weekends back home, have contributed massively to the completion of this PhD.

And finally, a special "merci beaucoup" of course goes to Eva and Moka. Having them by my side during this adventure made everything a bit easier. The amount of help I got from Eva is hard to quantify, and this thesis would have been impossible to complete without her. We grew a lot together during this shared adventure, and I am grateful for it.

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