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Variation in amphibian maturation rates influences population vulnerability to disease-induced declines

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Abstract

Understanding factors that influence population-level responses to emerging threats in declining species is crucial for informed conservation action. In amphibian species impacted by the chytrid fungus (*Batrachochytrium dendrobatidis*), a pathogen that has caused amphibian declines globally, a commonly reported pattern is that more severe population declines tend to occur at higher elevations. Previous research has suggested that this pattern could be driven by reduced environmental suitability for chytrid fungus at lower elevations. However, delayed amphibian maturation, which is common in cold, high elevation populations, could also increase vulnerability to population decline. Here, we tackle this key knowledge gap, focusing on the critically endangered corroboree frogs (*Pseudophryne corroboree* and *P. pengilleyi*), which have experienced a pattern of extirpation at higher elevations, with remnant populations persisting at lower elevations. First, we quantify the age structure of two extant low elevation *P. pengilleyi* populations and museum specimens (both species) collected before the emergence of chytrid fungus in Australia. Male age to maturation varied from 1 to 3 years, with the extant population with higher chytrid prevalence displaying severe age structure truncation. Second, we use population simulations to calculate elasticity values under a range of scenarios with varying ages to maturation and chytrid-associated mortality. When the population growth rate was fixed at 1, adult survival became increasingly important as age to maturation increases, particularly under a scenario of high chytrid-associated mortality. Our simulation results indicate that delayed maturation could be a previously underappreciated factor associated with an increased risk of amphibian population decline and that earlier maturation could contribute to population persistence. Our study highlights the importance of examining variation in life history traits to better understand population-level responses to novel threats and guide the development of appropriate conservation actions.

Introduction

Growing awareness of the emerging extinction crisis has triggered a major research effort to identify the characteristics of species most at risk of extinction. Decades of research across vertebrates has identified a range of factors, such as small geographic range size and large body size (Pimm, Jones, & Diamond, 1988; Purvis *et al.*, 2000; Cazalis *et al.*, 2022). Of particular interest are species life history traits, such as longevity and age to maturation, which can shape species responses to novel threats (Purvis *et al.*, 2000; Reynolds *et al.*, 2005; Hutchings *et al.*, 2012; Hutchings, 2021). While the role of interspecific differences in shaping species-level vulnerability to decline is relatively well documented, much less attention has been paid to the role of variation between populations in shaping population-level responses (Hutchings, 2021). Examining life history variation across populations with contrasting responses to novel threats could lead to an improved understanding of how life history traits shape population-level vulnerability to decline and subsequently inform conservation actions.

Different populations can exhibit substantial variation in life history traits in response to environmental conditions, with trait differences underpinned by genetic variation and/or phenotypic plasticity (Moran, Hartig, & Bell, 2016). In ectotherms, temperature is a key constraint on individual growth rates, particularly in temperate regions (Morrison & Hero, 2003). At large scales, temperature is strongly influenced by latitude and elevation, with increased time to sexual maturity in ectotherm populations at high elevations or latitudes due to slow growth rates (Morrison & Hero, 2003). For example, in European populations of the common toad (*Bufo bufo*), age at maturation varies from 2 to 3 years at low elevations to 6 to 8 years at high elevations (Hemelaar, 1988). At local scales, temperature can also be influenced by site-specific factors such as canopy cover (Skelly, Freidenburg, & Kiesecker, 2002). For example, in pond-breeding amphibians, larval development rates are strongly linked with temperature, with colder temperatures associated with increased time to metamorphosis and/or smaller body size at metamorphosis (Newman, 1998), which can subsequently translate into increased time to maturity (Berven, 1990). Understanding variation in maturation rates is important as time to maturation is a key determinant of population growth rates (Stearns, 1992), and increased time to maturation is a predictor of extinction risk at the species level (Hutchings *et al*., 2012).

Amphibians are the most threatened vertebrate group, with approximately 40% of species at risk of extinction (Luedtke *et al*., 2023). One of the key drivers of amphibian endangerment globally is the chytrid fungus (*Batrachochytrium dendrobatidis*, hereafter *Bd*) (Scheele *et al*., 2019), which causes the disease chytridiomycosis (Berger *et al*., 1998). A notable characteristic of *Bd*-associated amphibian declines is that they tend to be more severe in higher elevation populations (Young *et al*., 2001; La Marca *et al*., 2005; Scheele *et al*., 2017b; Brannelly *et al*., 2021; Scheele *et al*., 2023). Previous research has established that this pattern is in-part driven by higher environmental suitability for *Bd* in some montane and mountainous regions, which tend to be cooler and wetter (Bell *et al*., 2020; Fisher & Garner, 2020). Furthermore, temperature can influence the efficacy of the amphibian immune system, with cold temperatures appearing to reduce functionality (Fisher & Garner, 2020; Brannelly *et al*., 2021). Although cold temperatures below the optimal range for *Bd* could also theoretically limit the pathogen, research to date has failed to support this hypothesis (Knapp *et al*., 2011). Another potential mechanism is that high elevation populations with slow growth rates may be more vulnerable to decline due to increased time to maturation and subsequent slower population growth rates. Life history theory predicts that delayed age to maturation can increase vulnerability to extrinsic sources of mortality (Stearns, 1992) and increased time to maturation has been associated with population-level responses to threats in other taxa. For example, slow-maturing Atlantic cod (*Gadus morhua*) populations are more vulnerable to overexploitation (Hutchings, 2021). However, the role of delayed age at maturation in increasing decline risk in high elevation populations of *Bd*-impacted species has not been thoroughly examined (but see Hardy *et al*., 2022).

In this study, we tackle the key knowledge gap surrounding how variation in age at maturation influences amphibian population-level vulnerability to decline when challenged by *Bd*. Our study focused on the critically endangered corroboree frogs (*Pseudophryne corroboree* and *P. pengilleyi*) or Gyack, to the people of the Wolgalu Aboriginal Nation (Connolly, Williams, & Williams, 2017). Corroboree frogs provide an ideal opportunity to investigate the potential role of variation in age at maturation in shaping population responses to *Bd* as: (1) they occur across a large elevational range (850 to 1800 m asl) and previous research indicates substantial variation in age to maturation across elevations (Pengilley, 1966; Hunter, 2000), (2) breeding sites occur in open and closed canopy wetlands, providing potential fine scale variation in temperature regimes which could affect maturation rates, (3) population declines have been more severe at high elevations (Scheele *et al*., 2022), and (4) *Bd* prevalence does not appear to be strongly associated with elevation (i.e., there is no evidence that environmental conditions at the lower end of the species' elevational range limit *Bd*) (Scheele *et al*., 2017a).

We first use skeletochronology to quantify age at maturation and population age structures for two extant, low elevation populations as well as for museum specimens collected before the emergence of *Bd* in southeastern Australia. We then estimate baseline mortality rates from museum specimens and the impact of *Bd* infection on frog mortality rates using published data. Finally, we use population simulations to calculate elasticities to survival probabilities under a range of different maturation ages and levels of *Bd*-associated mortality.

Materials and methods

Study region, species and populations

Our study was conducted in the Snowy Mountains in south-eastern Australia. The climate is temperate with an average annual rainfall of 1200–1800 mm, with snow persisting for several months during winter at higher elevations, while only remaining at low elevations for several days per year. Corroboree frogs (*P. pengilleyi* and *P. corroboree*) are small (snout–urostyle length 23–31 mm) terrestrial frogs with restricted distributions in montane and subalpine meadows, woodlands and forests. *Pseudophryne pengilleyi* was described in 1985 after being split from *P. corroboree* (Wells & Wellington, 1985), and the species are similar morphologically and ecologically, and in terms of maturation rates across different elevations, we consider the two species analogous. Breeding occurs from February to mid-March and fertilized eggs are deposited in nests located in dense grass, moss or litter surrounding the edges of small seasonal pools that are typically dry when eggs are laid (Pengilley, 1973). Eggs hatch following pool filling in autumn, and tadpoles are free swimming and feeding until metamorphosis begins in November (Pengilley, 1966). During the non-breeding season, adults utilize woodland and forest habitat (Pengilley, 1966).

Both corroboree frog species were historically common within their naturally restricted ranges but experienced major declines commencing in the 1980s associated with the emergence of *Bd* (Osborne, Hunter, & Hollis, 1999; Hunter *et al.*, 2010; Scheele *et al.*, 2017a) and *P. corroboree* is now functionally extinct in the wild (Hunter *et al.*, 2018; Kosch *et al.*, 2019). *Pseudophryne pengilleyi* historically occurred across an elevational range of 850 to 1800 m a.s.l., while *P. corroboree* occupied a narrower and higher elevational range (1350 to 1800 m a.s.l.). Declines in *P. pengilleyi* have been most severe at higher elevations, while *P. corroboree* has declined across its range (Osborne, Hunter, & Hollis, 1999; Hunter *et al.*, 2010; Scheele *et al.*, 2017a). *Pseudophryne pengilleyi* is now restricted to several locations, which have been the focus of research to understand mechanisms of persistence and inform translocation/reintroduction efforts from captive breeding colonies (Scheele *et al.*, 2022).

Previous work has examined maturation rates in both *P. pengilleyi* and *P. corroboree*. In a *Bd*-infected population at an elevation of ~1500 m a.s.l., the majority of *P. corroboree* males attain sexual maturity in four years post-metamorphosis, with a small proportion taking three years (Hunter, 2000). Females, which attain larger body sizes, appear to take four to five years to reach sexual maturity (Hunter, 2000). At an elevation of ~1030 m a.s.l., male *P. pengilleyi* were estimated to mature at two to three years post-metamorphosis (Pengilley, 1966).

Our field sampling focused on two *P. pengilleyi* 'populations': Micalong Swamp, at an elevation ~976 m asl and Waragong-Cotterill, at an elevation ~1000–1100 m a.s.l. We use the term 'population' to refer to a series of nearby breeding sites occupied by *P. pengilleyi*. Although the two populations occupy similar elevations, the environmental characteristics of each are highly divergent, and we anticipate that different thermal regimes between the sites could influence age to maturity. The Waragong-Cotterill population utilizes areas with dense forest canopy cover in both the breeding and non-breeding habitats, whereas the Micalong population breeds in open wetlands (no canopy cover) and the non-breeding habitat is woodland with more open canopy cover than forested areas.

Field and museum sampling

To examine population age structure and age to maturity, we sampled adult males from the Micalong and Waragong-Cotterill populations and museum specimens (*Pseudophryne pengilleyi* and *P. corroboree*) collected from four populations (elevation range: 1053–1732 m a.s.l.) before the emergence of *Bd* in the study region. The populations from which museum specimens were collected are now extirpated. We used a total of 56 adult specimens from the Australian Museum collection (species, museum identification numbers, year and collection locations are provided in Table S1). The sex of museum specimens is unknown. All specimens were originally fixed in formalin and stored in ethanol.

In the Micalong population, sampling was conducted from mid-February to early March during the 2012, 2018, 2019 and 2020 breeding seasons (samples for skeletochronology were not collected in 2012). In the Waragong-Cotterill population, sampling was only conducted in February 2018. Sampling involved collecting a single digit (removed at the base of the second phalange and stored in 70% ethanol) and a skin swab to test for *Bd* (using sterile swabs, MW 100–100, Medical Wire & Equipment Co., U.K.). Each swab was collected in a standardized way, with three strokes on each side of the abdominal midline, the inner thighs, hands, and feet. Samples were analysed in triplicate with real-time quantitative polymerase chain reaction following the method of Hyatt *et al.* (2007). We considered a sample positive if all three wells returned a positive reaction. Sampling focused exclusively on calling adult males, as non-calling individuals are rarely encountered. Each individual was handled with a new pair of gloves. Field work was conducted under the New South Wales government scientific licenses SL102035 and SL100436 and approved by the Australian National University animal ethics committee (protocols: A2011/19 and A2018/04).

Skeletochronology and age at maturation

We used skeletochronology to determine the age of our field-collected samples and museum specimens. Accurate age determination using skeletochronology is dependent on the presence of clearly discernible lines of arrested growth and relies on the assumption that these lines are consistently deposited annually (Smirina, 1994). Skeletochronology is a reliable method for aging amphibians in regions that experience strong, consistent seasonal variations in climate (Smirina, 1994), such as the range of both corroboree frog species, and has been cross-validated with mark-recapture in *P. corroboree* (Hunter, 2000).

Skeletochronology involved decalcifying whole digits in 10% formic acid for 14 h, followed by rinsing in running water for 3 h. After standard histological processing, samples were vertically embedded in paraffin wax and sectioned using a rotary microtome to cut 10 µm sections. The entire second phalange was sectioned to ensure that the mid-diaphysis region, which contains the best sections for ageing, was identified. Sections were mounted on slides, stained for 30 min using Harris's haematoxylin, rinsed and mounted with a 60 -mm cover slip using Pertex mounting fluid to create a permanent mount. Lines of arrested growth were counted under 400× magnification using a light microscope. To improve age estimation, each individual was aged twice without reference to the previous result. For seven individuals, there was a discrepancy of 1 year between the two age estimates, and in such cases, we reinterrogated the samples and conservatively used the number of unambiguous lines of arrested growth as the age. We excluded one museum sample that could not be aged. We assume age was estimated accurately, but caution that the age of older frogs could be underestimated as growth in this species is minimal post-maturation, potentially making lines of arrested growth increasingly difficult to discern as individuals age.

Consistent with previous research, we refer to frog ages in years post-metamorphosis, noting that eggs are fertilized and deposited in February/March and individuals do not metamorphose until November or December. As such, an individual sampled during the breeding season with one line of arrested growth is approximately 14 months post-metamorphosis, or 2 years post-egg fertilization. Given sampling at extant populations focused exclusively on calling males in breeding habitats, we take the age of the youngest individual in each population to represent the minimum age to maturity of males in that population.

Statistical analyses

Parameter estimation

We fit our models in a Bayesian framework using nimble 0.13.1 (de Valpine *et al*., 2017; de Valpine *et al*., 2022) in R 4.3 (R Core Team, 2023) using default Markov chain Monte Carlo (MCMC) algorithms to sample from posterior distributions of model parameters. For all models, we ran four chains for 50 000 iterations after discarding 10 000 as burn-in, saved every 10th sample, and assessed convergence and MCMC behaviour using Gelman-Rubin ($\hat{R}$) diagnostics and visual inspection of chain histories. We used vague or weakly informative priors unless specified otherwise. We summarized posterior distributions with medians and 95% highest posterior density intervals (HDPI). Code to recreate the analyses is available at https://github.com/mhollanders/anu-corroboree.

Age structure in extant populations and museum specimens

To examine whether there were differences in age structure between the two extant populations and pre-*Bd* museum specimens, we modelled their age distributions with two negative binomial distributions fitted to the observed individual ages of animals from the Micalong and Warogong-Cotterill populations and the museum specimens (due to small sample sizes, museum specimens collected at four sites were combined). We used a negative binomial distribution as it is consistent with integer responses and features a dispersion parameter, making it more flexible than a Poisson distribution when accounting for different distribution shapes. We placed weakly informative priors on the two parameters of each negative binomial distribution, with Beta (1, 1) priors on the success probability (p) and Exponential (rate = 0.5) priors on the number of successes (r). We then calculated the mean ages of the extant populations and museum specimens, computed as $r(1-p)p^{-1}$, and compared the difference of the mean ages. We considered differences in age structure notable when the 95% HPDI of the mean differences between sites did not contain 0.

Batrachochytrium dendrobatidis prevalence in extant populations

We compared differences in *Bd* prevalence in *P. pengilleyi* sampled from the Micalong population in 2012 and 2018–2020 ($n = 149$) and the Warogong-Cotterill population (2018 $n = 40$) using logistic regression with site-specific intercepts and random year effects (shared across sites). We computed the site-specific marginal means of infection prevalence by averaging the predicted infection prevalence per year and computed an odds ratio of these marginal means to compare their differences.

Estimation of survival

We specified a model incorporating two separate datasets to estimate (1) annual survival probabilities for *Bd*-naïve corroboree frogs and (2) the effect of *Bd* infection on corroboree frog survival. The two datasets were the age data derived using skeletochronology from the pre-*Bd* museum specimens and the *Bd*-challenge experiment reported in Kosch *et al.* (2019). For the latter, 76 individuals were exposed to 1×10^6 zoospores (with 17 unexposed controls) and monitored for 103 days. We analysed these datasets jointly because there was no information in the Kosch *et al.* (2019) dataset to estimate baseline survival, as all control animals survived the experiment.

First, for the museum specimens, we assumed a stable age structure, meaning the age structure can be modelled with a geometric distribution where the success probability is the individual annual mortality probability. However, while the sex of museum specimens is unknown, given the cryptic nature of female and sub-adult corroboree frogs and the lack of young individuals, we assume breeding males were the focus of specimen collection efforts. To account for this, we only modelled the observed ages of frogs >3 years old, which yielded a monotonically declining observed distribution of ages. For the ith individual, we subtracted 4 from its age y_i to model it as a random draw from a geometric distribution supported on the set $\{0, 1, 2, \cdots\}$, and parameterized the mortality probability ϕ_y as a function of the annual mortality hazard rate α (Ergon *et al*., 2018):

$$\begin{aligned} y_i &\sim \text{Geometric}(\phi_y) \\ \phi_y &= 1 - \exp(-\alpha) \end{aligned} \tag{1}$$

Then, for the Kosch *et al.* (2019) experimental data, we modelled the days survived (minus 1) until morbidity (and subsequent euthanasia) of the jth individual x_j, as a random draw from a geometric distribution where the daily mortality probability $\phi_{x[j]}$ was parameterized as a function of the daily mortality hazard rate $h_{x[j]}$, which was modelled as a log-linear function of *Bd* exposure inf_j:

$$\begin{aligned} x_j &\sim \text{Geometric}\left(\phi_{x[j]}\right) \\ \phi_{x[j]} &= 1 - \exp\left(-h_{x[j]}\right) \\ h_{x[j]} &= \exp\left(\log(\alpha/365) + \beta \times \text{inf}_j\right) \end{aligned} \tag{2}$$

Thus, we estimated two parameters for the two datasets: a baseline annual mortality rate in the absence of *Bd* α and the effect of *Bd* infection on the mortality rate β. We performed prior predictive checks to select suitable priors. For α, we used a Gamma (2, 1) prior, as this skews the prior annual survival probability away from 1 and places a roughly 5% probability on individuals living beyond the age of 10 and a 1% probability that they live beyond the age of 15. For β, given that *Bd* infection has a strongly positive effect on mortality, we selected a Normal (0, 1.5) prior, which places roughly 2.5% of the prior probability that mortality could be increased 20-fold or more.

Elasticity analyses

To investigate the effect of time to maturation under different levels of *Bd*-associated mortality, we calculated the elasticities of adult survival and fecundity from population projection models. Elasticity analyses are a useful method to evaluate the relative contribution of vital rates, such as survival, to population growth rates (De Kroon, Van Groenendael, & Ehrlén, 2000; Heppell, Caswell, & Crowder, 2000). We built 7-age population matrices and populated survival probabilities (S) for *Bd*-naïve populations using the posterior median of the mortality hazard rates (α) estimated from the museum specimens (Equation 1) as $S = \exp(-\alpha)$. We generated four scenarios with varying levels of *Bd*-associated mortality (0, corresponding to no *Bd* in the system, and the predicted mortality associated with 0.2, 0.4 and 0.6 prevalences of *Bd* in the system) using the posterior median of the effect of *Bd* on mortality hazard rates estimated above (β) (Equation 2). We simulated matrices with four ages of maturation (2, 3, 4 and 5 years old). We set annual fecundity probabilities (to the nearest two decimal points) to the value that yielded population growth rates of 1 to simulate hypothetical scenarios of stable age structures. We conducted these hypothetical simulations under the assumption of stable age structure to enable comparison of populations with different ages to maturation. We then used the popbio R package to calculate the elasticities of adult survival for each scenario (Stubben & Milligan, 2007). We summarized the scenario-specific elasticities of fecundity and survival by averaging the age-specific elasticities of each vital rate over the 7 years.

Although our field sampling focused on males (few females were observed), we used female-based models and assumed a 1:1 sex ratio and equivalent vital rates between sexes. However, females have larger body sizes, and previous work has suggested that under the same conditions, females take an additional year compared to males to reach maturity (Hunter, 2000), and hence we evaluated maturation ages ranging from 2 to 5 years (see Table S2 for a summary of the different ages at maturation observed in this study and previous research). This range was chosen to represent the ages at which females likely mature across the elevational range of *P. pengilleyi* and *P. corroboree*.

Results

Population age structure, age at maturity, and *Bd* prevalence

We determined the age of 126 adult male *P. pengilleyi* from two extant populations (86 from Micalong, 40 from Warogong-Cotterill) and 55 museum specimens (*P. pengilleyi* and *P. corroboree*) collected before the emergence of *Bd* in Australia. The estimated mean ages in the two extant populations, Micalong and Warogong-Cotterill, were 1.98 (95% HPDI: 1.67–2.3) and 3.69 (95% HPDI: 3.04–4.38), respectively (Fig. 1). The mean estimated age in the *Bd*-naïve museum specimens was 4.42 (95% HPDI: 3.78–5). The 95% HPDI of the difference in mean ages at Micalong compared to Warogong-Cotterill did not contain 0, suggesting these sites were notably different in mean ages. For the museum specimens, 77% of the posterior distribution of the mean age was above that of the Warogong-Cotterill population, suggesting the museum specimens were generally older.

The youngest observed age of breeding males (assumed to represent age at maturation) in the Micalong population was one-year old (Fig. 1). However, the high frequency of 2-year-old individuals suggests that most individuals mature and enter the breeding population at age two. The Warogong-Cotterill population and museum specimens both contained a single 2-year-old (Fig. 1, Table S1). However, in the Warogong-Cotterill population, most individuals appear to mature at three years old. In the museum specimens, while some individuals mature at three, the higher proportion of four-year-old individuals indicates that most individuals mature at four (Fig. 1).

The proportion of individuals infected with *Bd* in the Micalong population (0.313, 95% HPDI: 0.240–0.390) was 4.77 times higher (expressed as an odds ratio) than in the Warogong-Cotterill population (0.0874, 95% HPDI: 0.0193–0.181) (Fig. 2). In the Micalong population, there was substantial variation in *Bd* prevalence across years (Figure S1).

Estimating *Bd*-associated mortality

Using the truncated geometric age structure model, we estimated the annual mortality hazard rate of the *Bd*-naive population to be 0.59 (95% HPDI: 0.43–0.78), corresponding to an annual survival probability of 0.55 (95% HPDI: 0.46–0.65). The effect of *Bd* exposure was strong, with a log hazard increase of 2.4 (95% HPDI: 2.02–2.77), corresponding to a hazard ratio of 11.01 (95% HPDI: 7.23–15.53).

Elasticity analyses

Using population matrices, we examined how age to maturity influenced elasticity values for survival and fecundity under a range of hypothetical *Bd* impacts. Adult survival had higher average elasticities than fecundity for all scenarios (Fig. 3a). As age to maturity increased, the elasticity of

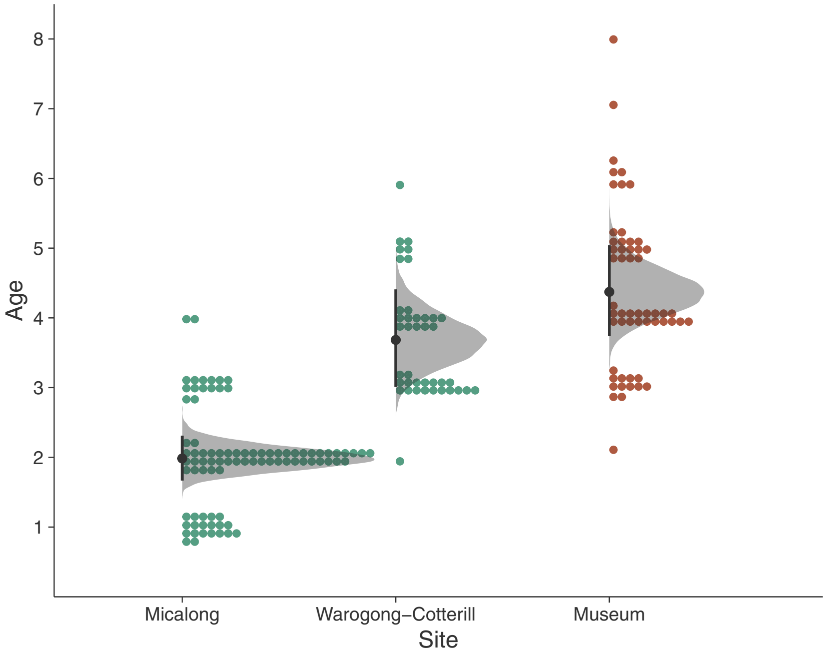

Figure 1 Observed ages and posterior distributions (with medians and 95% HPDI) of mean ages in the extant populations (*Pseudophryne pengilleyi*), Micalong and Warogong-Cotterill, and museum specimens (*P. pengilleyi* and *P. corroboree*). Frogs were aged to integer years, but for visual clarity, random noise was added to the ages for plotting.

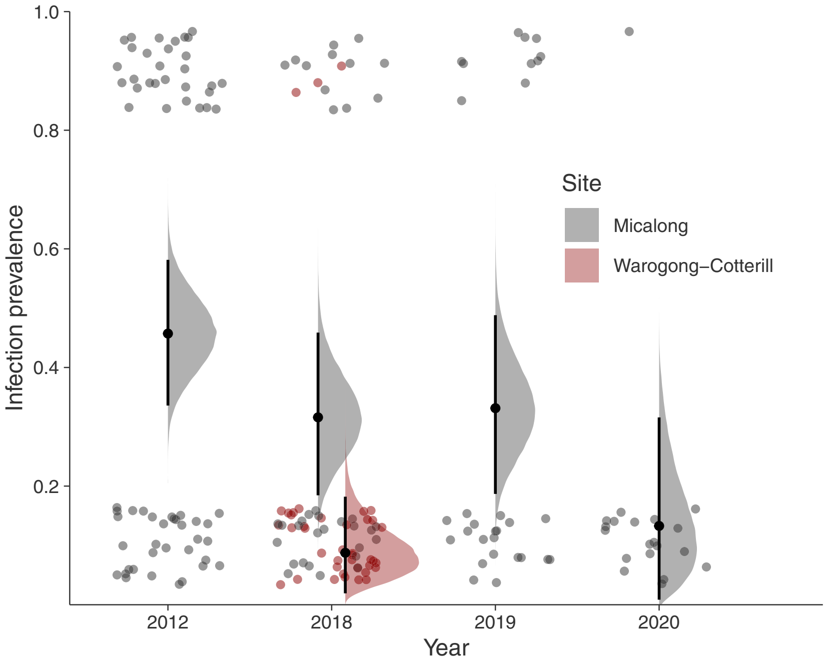

Figure 2 Posterior distributions (with medians and 95% HPDIs) of *Batrachochytrium dendrobatidis* infection prevalence. Points are individuals, clustered by being infected (top) or uninfected (bottom).

survival increased for all scenarios, indicating that adult survival is increasingly important with delayed maturation. At a given age of maturation, scenarios with higher *Bd*-associated mortality had lower elasticity values for adult survival and higher values for fecundity compared to scenarios with lower *Bd*-associated mortality. The simulations indicate that as age to maturation increases from 2 to 5 years, adult survival becomes increasingly important. In other words, delayed

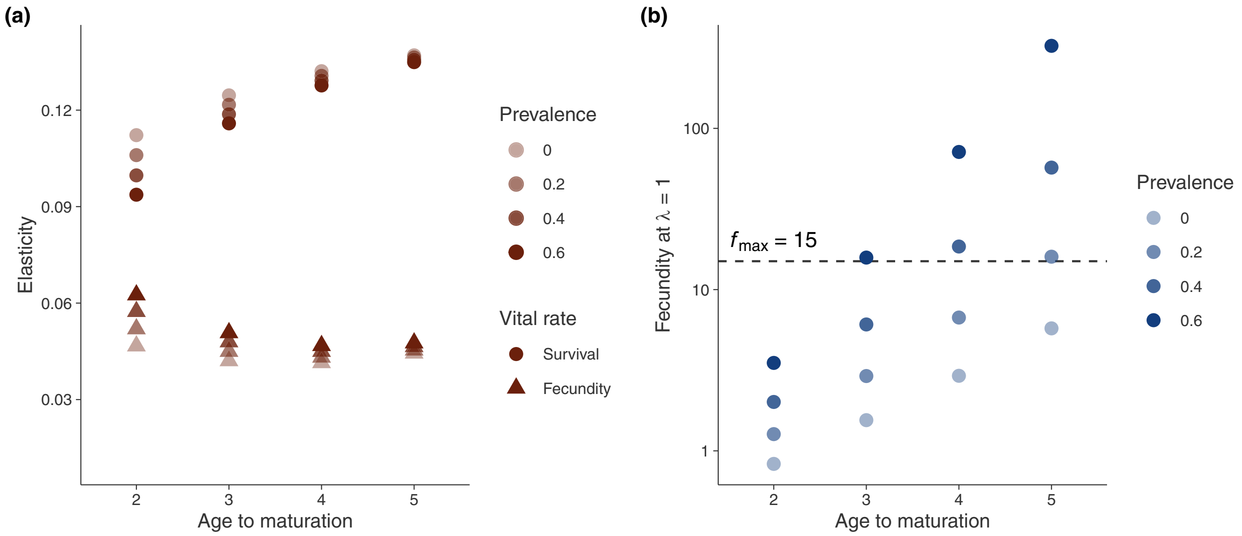

Figure 3 (a) Elasticities of fecundity and adult survival probabilities calculated for scenarios representing *Bd*-naive museum specimens (*Bd* prevalence = 0) and *Bd*-infected populations with varying *Bd* prevalence and associated mortality with four ages to maturation. Survival probabilities of uninfected and infected individuals were populated with the medians of the posterior distributions of model parameters (Equations 1 and 2). Fecundity values were chosen to maintain the population growth rate at 1 for each adult survival probability. (b) Fecundity rates (number of female offspring surviving to their first year per female) required to keep the population growth rate (λ) at 1 under the different age to maturation and prevalence scenarios. The horizontal line (f_{max}) gives the maximum possible fecundity assuming a clutch size of 30, a sex ratio of 0.5 and 100% survival to the first year.

maturity increases vulnerability to elevated rates of adult mortality, and this pattern is most pronounced under the high *Bd* mortality scenario. Fecundity rates (the number of female offspring surviving to their first year per female) indicated that as age to maturation increases, higher numbers of recruits are required to maintain a stable population, particularly under scenarios with high *Bd*-associated mortality (Fig. 3b).

Discussion

Variation in age to maturation is a potentially important but rarely investigated factor shaping population-level responses to novel threats. Here, we report that in the critically endangered corroboree frogs, earlier age at maturation is associated with decreased elasticity values for adult survival, indicating greater capacity to withstand higher rates of adult mortality. Conversely, populations with delayed age to maturity appear more vulnerable to increases in adult mortality. Furthermore, although fecundity rates in the wild are unknown, in our simulations, unrealistically high rates were required to maintain a stable population in scenarios with delayed age to maturation and moderate to high *Bd* impacts. These results indicate that slow maturation rates could be a previously unrecognized factor increasing vulnerability to declines in *Bd*-challenged populations.

A common pattern across *Bd*-impacted amphibian species is the tendency for declines to be more severe at higher elevations (Young *et al.*, 2001; La Marca *et al.*, 2005; Scheele *et al.*, 2017b; Brannelly *et al.*, 2021; Scheele *et al.*, 2023). Previous work has suggested that this pattern may be partially explained by increased environmental suitability for *Bd* and/or decreased amphibian immune efficacy (Fisher & Garner, 2020; Brannelly *et al.*, 2021). Our results indicate that delayed age to maturation could be an additional factor driving this pattern, with age at first reproduction strongly associated with maximum per-capita population growth rate (Stearns, 1992; Hutchings *et al.*, 2012), which in turn is associated with extinction risk (Lande, 1993; Mace *et al.*, 2008). Given that delayed maturation is common in high elevation amphibian populations (Morrison & Hero, 2003), this mechanism could operate across many declining amphibian species, with our findings complementing other recent research. For example, West *et al.* (2020) documented lower recruitment and a greater risk of extinction in high elevation spotted tree frog (*Litoria spenceri*) populations in southern Australia. Similarly, in western toad (*Anaxyrus boreas boreas*) populations in North America, compensatory recruitment is able to partially offset *Bd*-associated adult mortality at lower elevations (Muths, Scherer, & Pilliod, 2011), but not at higher elevations near the species' elevational limit (Hardy *et al.*, 2022).

Understanding mechanisms that facilitate persistence of declining species is crucial for informing conservation actions (Evans *et al.*, 2022). While the long-term viability of the two extant study populations is unknown, they have persisted for several decades, despite the presence of *Bd* (albeit while experiencing population declines). Previous research suggested that low *Bd* prevalence (associated with low reservoir host abundance) may be underpinning the persistence of the Waragong-Cotterill population (Scheele *et al.*, 2017a). Our age structure data support this notion, with a demographic profile consistent with adult survival across years and lower *Bd* impact. Notably, although this population is at a similar elevation to the Micalong population, breeding sites are characterized by high canopy cover, which could be associated with slower maturation rates. Slower growth rates have been observed in response to increased canopy cover in other amphibian species (Berven, 1990; Newman, 1998) and requires further investigation in *P. pengilleyi*. We suggest the slower maturation rates in this population mean persistence would be unlikely under a scenario of higher *Bd* impact. In contrast, the age structure of the Micalong population suggests a second distinct mechanism of persistence: early maturation, which appears to partially offset low apparent adult survival. These contrasting mechanisms are notable as they highlight different potential pathways to persistence – one associated with *tolerance* of threat impact and the other with *reduction* of threat impact – operating in populations of the same species that occur in close geographic proximity (<20 km apart). More generally, the contrasting responses across *P. pengilleyi* populations highlight the need for population-specific research to understand threat impacts and capacity for persistence (*sensu* Hardy *et al.*, 2022, Valenzuela-Sánchez *et al.*, 2022).

The age structure of the Micalong population is truncated towards young individuals, whereas the Warogong-Cotterill and museum specimens contain older individuals. We suggest this truncation is a result of high rates of *Bd*-associated adult mortality, consistent with the much higher prevalence of *Bd* in this population and the very high susceptibility of corroboree frogs to *Bd* under laboratory conditions (Kosch *et al.*, 2019). The loss of old individuals is consistent with demographic shifts reported in other *Bd*-challenged species (Scheele *et al.*, 2016; Lampo *et al.*, 2023), although in some cases *Bd* appears to disproportionately result in the loss of young individuals (Tessa *et al.*, 2023). Such differences may reflect variations in species ecology and the timing of high *Bd* exposure risk. Although population persistence appears to be influenced by time to maturation, the loss of individuals capable of reproducing across years could have a range of ecological, life history and evolutionary consequences (Hixon, Johnson, & Sogard, 2014; Scheele *et al.*, 2016; Scheele *et al.*, 2017c). Perhaps most importantly, truncation could reduce population capacity to withstand recruitment failure associated with drought and premature pond drying, which have been identified as threats to *P. pengilleyi* (Scheele *et al.*, 2012). As noted in other *Bd*-impacted amphibian species (Scheele *et al.*, 2016), age truncation may lead to a narrowing of the range of hydrological conditions under which species can persist. Notably, the Micalong population inhabits a series of large, interconnected wetlands that appear more robust to drought than small, isolated wetlands where the species has been extirpated. During droughts, breeding habitat selection shifts in the Micalong population from the wetland periphery to the centre, which better retains moisture. Another factor that could contribute to the persistence of the Micalong population is cohort iteroparity (Wilbur & Rudolf, 2006), where variation in development rates means that individuals that metamorphose in the same breeding season reach sexual maturity in different years. Although we cannot distinguish between return breeders and individuals maturing and entering the breeding population at 2-years old, the greater proportion of 2-year-old compared to 1-year-old males suggests that some individuals mature at 2 years, providing a degree of cohort iteroparity, which could increase resilience to periodic recruitment failure.

There are several caveats associated with our results, which stem from the critically endangered status of both species and their rarity in the wild, which precluded sampling additional sites (both species are now extirpated across much of their ranges). Due to the absence of extant high elevation *P. pengilleyi* populations, we used published information on *P. corroboree* maturation rates as an analogue for now extinct *P. pengilleyi* populations from high elevations. Use of information from both species, combined with only sampling two extant *P. pengilleyi* populations, means we must be cautious when interpreting the relationship between increasing elevation and age at maturation in corroboree frogs. Furthermore, we lack demographic information from the same populations pre- and post-*Bd* emergence, meaning we cannot definitively establish the role of *Bd* in truncating age structure in the Micalong population or rule out the potential for life history shifts associated with pathogen emergence, which could affect maturation rates. We note such challenges are common in studies on declining species where temporal datasets spanning the timing of threat emergence are lacking (Valenzuela-Sánchez *et al.*, 2022). Finally, the sex of the museum specimens we sampled is unknown, whereas only males were sampled from extant populations. Given females are thought to take an additional year to reach maturation (Hunter, 2000), if some of the museum specimens were females, our estimates of mean age and *Bd*-naïve survival may be slightly inflated relative to the male-only estimates from the extant populations.

Management implications

Due to the ubiquity of *Bd* and our inability to eradicate it, conservation actions for *Bd*-threatened species remain challenging (Scheele *et al.*, 2014; Fisher & Garner, 2020). The insights reported here on the role of maturation rates in shaping population-level responses to *Bd* have been used to redesign a translocation programme for captive-bred *P. pengilleyi*. Previously, frogs were unsuccessfully reintroduced to high elevation, historically occupied sites where they had become extirpated. However, our research has led to a shift towards identifying and evaluating lower elevation sites (between 800 and 1100 m a.s.l.) as candidates for assisted colonization, with the rationale that earlier maturation at lower elevation, warmer sites could enhance the chances of population establishment, despite the presence of *Bd* (Scheele *et al.*, 2022). Subsequently, a trial translocation to a site with characteristics similar to Micalong has commenced. More broadly, in planning translocations for *Bd*-threatened species, we urge consideration of how candidate site characteristics affect species vital rates, with a focus on identifying characteristics conducive to maximizing population growth rates (Hutchings *et al*., 2012; Scheele *et al*., 2021).

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Author contributions

BCS conceived the ideas and designed the methodology; BCS collected the data; RJW completed the skeletochronology; XH and MH analysed the data; BCS led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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Supporting information

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

Table S1. Specimen information and collection details for corroboree frogs sampled from The Australian Museum collection and aged using skeletochronology.

Table S2. Age of the youngest observed male across different populations.

Figure S1. Observed *Bd* infection status and posterior distributions (with mode and 95% HPDI) of the probability of infection over four years at Micalong.