West, M., Todd, C. R., Gillespie, G. R., & McCarthy, M. (2020). Recruitment is key to understanding amphibian's different population-level responses to chytrid fungus infection. *Biological Conservation*, Vol. 241, 108247.

DOI: https://doi.org/10.1016/j.biocon.2019.108247

West, M., Todd, C. R., Gillespie, G. R., & McCarthy, M. (2020). Recruitment is key to understanding amphibian’s different population-level responses to chytrid fungus infection.

Recruitment is key to understanding amphibian's different population-level responses to chytrid fungus infection.

Running Head: Understanding amphibians differing responses to *Bd* infection

Key-words: deterministic discrete-time matrix model; disease; chytridiomycosis; introduced predator; population growth rate; pathogen

Word count: 6993 (all text from the first word of the Abstract through the last word of the Literature Cited including table or figure legends or the body of tables

Authors: West, M., Todd, C. R., Gillespie, G. R., & McCarthy, M.

Author's Addresses:

Correspondence to: Matt West, matthew.west@unimelb.edu.au

Abstract

Understanding why related species have differing population-level responses to threats can be key to identifying conservation options for declining populations. However, this is difficult when multiple threats are implicated. Chytrid fungus (*Batrachochytrium dendrobatidis: Bd*) is implicated in at least 500 amphibian population declines globally, although few tangible options exist to mitigate pathogen impacts. Other threatening processes also invariably operate on most amphibians. Non-native fish, for example, can contribute to amphibian declines and may exacerbate *Bd* impacts. We disentangled the impacts of *Bd* and non-native fish upon two stream breeding frog species with differing conservation statuses to reveal vital rates that are crucial for species persistence. *Litoria spenceri* are threatened and historically occurred at elevations between 300 - 1100m asl in southeastern Australia. *Litoria lesueurii* are non-threatened and sympatric with *L. spenceri* at some sites. Using mark-recapture derived demographic rates known to correlate with climate and elevation, discrete-time deterministic population models were constructed for each species at high, moderate and low elevation sites, and multiple management scenarios. Our study reveals that age to maturation, clutch size and egg-year 1 survival influenced interspecific and intraspecific population-level responses of the two frogs to *Bd* impacts. Importantly, our results highlight that an amphibian population's capacity to counteract *Bd*-mediated adult mortality is clearly constrained by other threats and environment interactions that moderate species recruitment. Furthermore, understanding limits to recruitment may help identify *Bd* mitigation strategies. In our study, disease mitigation may be best achieved at some sites by enhancing recruitment through non-native fish management.

Introduction

Understanding why amphibians have differing population-level responses to chytrid (*Batrachochytrium dendrobatidis: Bd*) infection is a key priority to identify conservation strategies for species threatened by the pathogen (Collins 2010; James et al. 2015). *Bd* is implicated in at least 500 amphibian population declines globally (Scheele et al. 2019) and causes a disease known as chytridiomycosis in susceptible individuals (Berger et al. 1998). The response of individuals and populations to *Bd* can vary both between and within species (Blaustein et al. 2005; Briggs et al. 2005; Tobler and Schmidt 2010). Crucially *Bd* can cause rapid population declines and extinctions of some species at some sites (e.g. Gillespie et al. 2015; Lips et al. 2006) but other species can experience slower rates of population decline or may persist despite *Bd* presence (Phillott et al. 2013; Scheele et al. 2015).

Variation in disease outcomes at the population-level can be influenced by numerous individual-level intrinsic and extrinsic factors, especially involving site-specific interactions between the host, environment, and pathogen (James et al. 2015). Notably, microclimate and microhabitat conditions, immune defenses and pathogen virulence can all influence an individual's risk of infection and ability to survive or recover from infection (Daskin et al. 2014; Doddington et al. 2013; Gahl et al. 2012; Gervasi et al. 2014; Heard et al. 2014; Tobler and Schmidt 2010). The same site-specific microclimatic conditions (particularly temperature) can influence pathogen growth and survival (Piotrowski et al. 2004), and amphibian demographic rates including age to maturation, clutch size and longevity (Morrison et al. 2004). Populations may persist despite *Bd* infection as long as sufficient adult frogs survive and successfully reproduce (Briggs et al. 2005). Several studies have hypothesized that an amphibian population's extinction risk may be determined by their ability to compensate for *Bd*-induced mortality through recruitment (Muths et al. 2011; Phillott et al. 2013; Scheele et al. 2015; Tobler et al. 2012). These factors, and others, can all lead to differing outcomes for species exposed to *Bd*.

Bd infected populations may be at greater risk of extinction if impacted by other threats (Phillott et al. 2013) and most amphibians are invariably influenced by multiple threats (Bielby et al. 2008; Heard et al. 2011). The combined impacts of multiple threats on species can be complex (Blaustein and Kiesecker 2002) but must be clarified to identify species management requirements. The implications for species are most serious if threats combine to have additive or synergistic effects (Brook et al. 2008; Wake 2012) although management requirements may differ if threats combine to have antagonistic (opposing) effects (e.g. Gahl et al. 2011).

Introduced fish (such as trout species) can severely affect amphibians and are implicated in species declines (Gillespie 2001; Knapp 2005; Matthews et al. 2001; Vredenburg 2004). The impacts of introduced fish could be particularly severe for species that are also influenced by *Bd*, as the threats may simultaneously affect different amphibian life stages. Introduced predatory fish can reduce amphibian larval survival (Gillespie 2001; Hunter et al. 2011), whereas the impacts of *Bd* upon survival may be most severe following metamorphosis (Berger et al. 1999). The threats could therefore be additive and accelerate a species decline. Alternatively, the threats may have antagonistic effects; *Bd* impacts may be reduced if disease dynamics are influenced by population density (e.g. Rachowicz and Briggs 2007), and fish predation may limit a species' population density (e.g. Vredenburg 2004). An understanding of these effects and interactions is therefore crucial to developing sound conservation strategies for amphibians where multiple threats are operating and potentially interacting.

Here, we examine the population-level responses of a threatened and a non-threatened frog species to two threats, *Bd* and introduced trout. *Bd* can reduce the apparent annual survival of both the Critically Endangered spotted tree frog (*Litoria spenceri*) (Hero et al. 2004) and non-threatened Lesueur's frog (*Litoria lesueurii*) at an individual-level (West 2015). Although, whilst introduced trout (*Salmo trutta* and *Oncorhynchus mykiss*) can significantly reduce the survival of *L. spenceri* tadpoles they appear to have little effect on the survival of *L lesueurii* tadpoles (Gillespie 2001). We suspected that differences in the species population-level outcomes to these threats may be due to different impacts of trout or different consequences of Bd infection due to demographic variation between sites correlated with temperature and elevation. Using recent demographic parameter estimates we developed a multistate matrix model to examine conditions that influence each frog species' population viability in different environmental settings, to evaluate management options for threat mitigation.

Methods

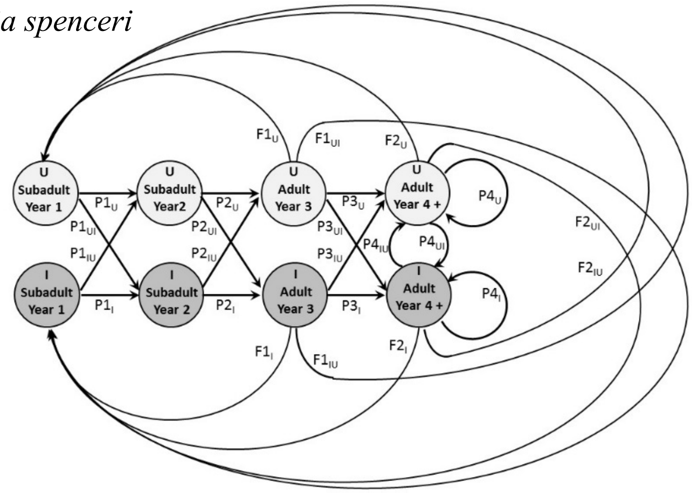
Case Study

Litoria spenceri and *L. lesueurii* both breed annually in mountain streams between 300-1110 m elevation during late spring and summer (November – January) in southeastern Australia. Eggs hatch and tadpoles metamorph into frogs within a single season, prior to April when both species become inactive, due to onset of cooler temperatures. Activity generally resumes in mid-late October. *Litoria spenceri* matures less quickly and breeds at a later age than *L. lesueurii* (minimum maturity ages: *L. spenceri*: 3 -5 years versus *L. lesueurii*: 2-4 years) (Gillespie 2010). Age to maturity for both species is expected to vary with site-specific climatic conditions and skeletochronology indicates both species reach maturity earlier at low elevations compared to higher elevations (Table 1) (Gillespie 2010; Author 3 unpublished data). Skeletochronology also indicates that *L. spenceri* can live longer than *L. lesueurii*, (Gillespie 2010; Author 3 unpublished data). Longevity estimates for both species (Gillespie 2010; Author 3 unpublished data) and the general observed pattern in other amphibians

(Morrison and Hero 2003) suggests that mean survivorship of *L. spenceri* and *L. lesueurii* is longer at cooler high elevations compared to warmer low elevations.

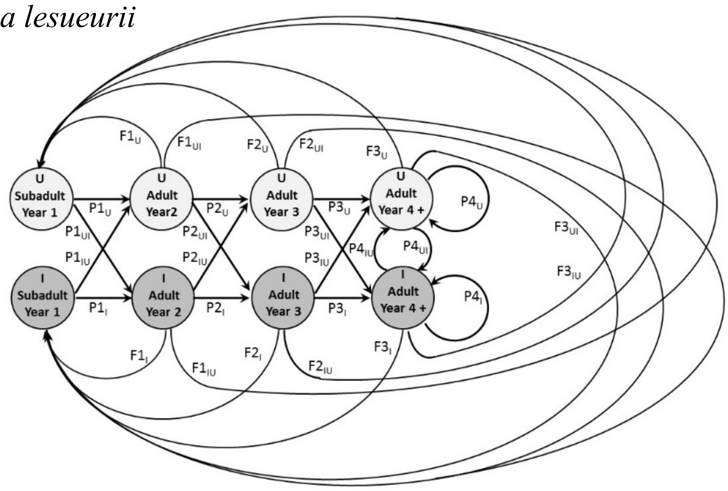
Bd is known to occur at all but two *L. spenceri* sites, where the pathogens presence is uncertain (West 2015; Authors 1 and 3 unpublished data). During the frog active season temperatures at all sites are frequently within known optimal growth condition for Bd (e.g. Stevenson et al. 2013). When *Bd* is present, individual frogs are assumed to exist in one of two disease states: uninfected or infected. For each species, the disease dynamics for individuals at low elevation sites can be approximated as shown in Figure 1, assuming an annual time step and a pre-birth census. At moderate and high elevation sites, both species spend longer periods in a subadult state (Supplementary Material).

Litoria spenceri



$$\boldsymbol{A} = \left[\begin{array}{cccc|cccc} 0 & 0 & F1_U & F2_U & 0 & 0 & F1_{IU} & F2_{IU} \\ P1_U & 0 & 0 & 0 & P1_{IU} & 0 & 0 & 0 \\ 0 & P2_U & 0 & 0 & 0 & P2_{IU} & 0 & 0 \\ 0 & 0 & P3_U & P4_U & 0 & 0 & P3_{IU} & P4_{IU} \\ \hline 0 & 0 & F1_{UI} & F2_{UI} & 0 & 0 & F1_I & F2_I \\ P1_{UI} & 0 & 0 & 0 & P1_I & 0 & 0 & 0 \\ 0 & P2_{UI} & 0 & 0 & 0 & P2_I & 0 & 0 \\ 0 & 0 & P3_{UI} & P4_{UI} & 0 & 0 & P3_I & P4_I \end{array}\right]$$

Litoria lesueurii



$$\boldsymbol{A} = \left[\begin{array}{cccc|cccc} 0 & F1_U & F2_U & F3_U & 0 & F1_{IU} & F2_{IU} & F3_{IU} \\ P1_U & 0 & 0 & 0 & P1_{IU} & 0 & 0 & 0 \\ 0 & P2_U & 0 & 0 & 0 & P2_{IU} & 0 & 0 \\ 0 & 0 & P3_U & P4_U & 0 & 0 & P3_{IU} & P4_{IU} \\ \hline 0 & F1_{UI} & F2_{UI} & F3_{UI} & 0 & F1_I & F2_I & F3_I \\ P1_{UI} & 0 & 0 & 0 & P1_I & 0 & 0 & 0 \\ 0 & P2_{UI} & 0 & 0 & 0 & P2_I & 0 & 0 \\ 0 & 0 & P3_{UI} & P4_{UI} & 0 & 0 & P3_I & P4_I \end{array}\right]$$

Figure 1 Multi-state life-cycle graphs and coresponding population matrices for L. spenceri and L. lesueurii at low elevation sites. In our life-cycle graphs indidivuals can exisit in a sub-adult or one of three adult life stages (each represented by circles) and in each stage they can occur in either an uninfected (U; white circles) or infected (I; grey shaded circles) disease state. Frogs can transition (represented by lines) between life stages and disease states. The coresponding population matrices describe the probabilities of transitions between each life stage and disease state. In the graphs and matrices P represents the probability of survival and probability of transition between states, and F represents fecundity. Numbers are used to index fecundity and probabilities of survival plus transition relative to the life stage. UI represents a transition from an uninfected-infected disease state and IU represents a transition from an infected-uninfected disease state.

Table 1. Annual demographic parameters of *L. spenceri* and *L. lesueurii* at low, moderate and high elevation sites. Parameter estimates are generally based on mean published data derived during mark-recapture studies (West 2015; Author 2 unpublished data), counts of egg clutches (Gillespie 2011a) or skeletochronology (Gillespie 2010). Some parameters are based on expert opinion or unpublished data*. Mortality, infection and recovery parameter values are extrapolated for moderate and high elevation sites-based parameter estimates derived at low elevations sites.

		L. spenceri			***L. lesueurii***			
symbol	**parameter**	**low**	**moderate**	**high**	**low**	**moderate**	**high**	**Refs.**
sr	sex ratio	0.5	0.5	0.5	0.5	0.5	0.5	1.
$b1$	probability females breed in first adult year	0.5	0.5	0.5	0.5	0.5	0.5	2.*
b	probability females breed in subsequent years	1	1	1	1	1	1	2.
f	fecundity (mean clutch size)	720	599	477	1602	1501	1400	2.*
S_e	survival probability of eggs-year1	0.011	0.011	0.011	0.052	0.052	0.052	4. /1.
M_1	baseline mortality of subadults year1-year2	0.463	0.391	0.339	0.296	0.226	0.203	4. /5.
M_2	baseline mortality of subadults year2-year3	0.445	0.376	0.326	0.271	0.209	0.188	4. /5.
M_3	baseline mortality of subadults year3-year4	0.361	0.309	0.270	0.160	0.131	0.120	4. /5.
M_A	baseline mortality of adults	0.358	0.306	0.268	0.157	0.128	0.118	5.
a_1	added mortality of subadults year1-year2 due to chytridiomycosis	0.184	0.257	0.309	0.578	0.648	0.671	4. /5.
a_2	added mortality of subadults year2-year3 due to chytridiomycosis	0.191	0.260	0.309	0.598	0.661	0.682	4. /5.
a_3	added mortality of subadults year3-year4 due to chytridiomycosis	0.220	0.272	0.310	0.689	0.719	0.730	4. /5.
a_A	added mortality of adults due to chytridiomycosis	0.221	0.272	0.310	0.692	0.720	0.731	5.
pI	probability of apparent infection	0.694	0.694	0.694	0.996	0.996	0.996	5.
pR	probability of apparent recovery	0.956	0.956	0.956	0.949	0.949	0.949	5.
-	female earliest age at maturation	3	4	5	2	3	4	1.*
-	female longevity	12	14	16	9	11	12	1.*
D	coefficient to manipulate disease impact on all age classes	1	1	1	1	1	1	-
C	coefficient to manipulate M_1	1	1	1	1	1	1	-

1. Gillespie (2010); 2. Gillespie (2011a); 3. Gillespie (2011b); 4. Author 1 unpublished data; 5. West (2015); * Author 3 unpublished data.

Parameter estimation

A series of intensive mark-recapture and life history studies provided demographic parameter estimates for *L. spenceri* (Table 1). Apparent annual survival probabilities and population growth rates were estimated following a 21 to 23-year mark-recapture study at two low elevation sites (~330m) (see Supplementary Material). Mean estimates of stage-specific survival, using a Cormack-Jolly-Seber model, were very similar at both sites. To address this, disease state-specific apparent annual survival probabilities of adult *L. spenceri* were estimated during a 6-year multi-state mark-recapture study (West 2015). Estimates for probabilities of apparent annual infection of uninfected frogs and apparent annual recovery of infected frogs were derived using a Bayesian multi-state mark-recapture analysis (West 2015). A comparison of the species life history at low (~330m) versus high elevation (~1110m) sites indicates an equal sex ratio in terrestrial life stages and relative high mortality in juvenile compared to adult age-classes (Gillespie 2010). Adult females at high elevations reach maturity approximately two years later than females at low elevation sites (Gillespie 2010, 2011a; Gillespie 2011b). Additionally, within a site, regardless of elevation, approximately half of females reach maturity a year earlier than other females within each cohort (Gillespie 2010, 2011a; Gillespie 2011b).

Litoria lesueurii produce larger clutches (mean eggs/female: 1510.2) than *L. spenceri* (mean eggs/female: 527.9) (Gillespie 2011a), however the clutch sizes of both species can vary and are larger at lower elevation sites. A linear model was fitted to clutch sizes determined from field and museum specimens of individual collected across and elevational gradient (supplementary material). Mean clutch sizes at high (1100m), moderate (735m) and low (350m) elevations sites were derived using the estimated linear model intercept and co-efficient values for each species (Table 1). Disease state-specific apparent annual survival probabilities of adults, and probabilities of apparent annual infection and recovery were estimated for *L.*

lesueurii during a 4-year multi-state mark-recapture study (West 2015). Stage-specific survival estimates were not available for earlier *L. lesueurii* life stages, so survival of subadults in each year was assumed to equal that for *L. spenceri*.

Introduced brown trout (*Salmo trutta*) can significantly reduce the survival of *L. spenceri* tadpoles (Gillespie 2001). An assessment of the *L. spenceri* population age structure suggests survival of eggs, tadpoles and metamorph frogs to year 1 (eggs-year 1) is approximately 4.75–times lower at sites when trout are present compared to when trout are absent (Gillespie 2010). The survival of *L. lesueurii* eggs-year 1 is not known but was assumed to equal the survival of *L. spenceri* in the absence of trout, given that trout appear to have little effect on the survival of *L. lesueurii* tadpoles (Gillespie 2001).

Probabilities of survival that had been derived at low elevation sites (West 2015; Author 2 unpublished data) were scaled to medium and high elevation sites as actual parameter estimates were not available. Survival at these elevations was calculated relative to the ratio of maximum longevity at low elevation sites (long_{low}) compared to the maximum longevity at either the moderate or high elevation sites ($\text{long}_{\text{elev}}$):

$$Su_{y,\text{elev}} = Su_{y,\text{low}} \text{ x } (\text{long}_{\text{low}} / \text{long}_{\text{elev}}) \qquad \text{eqn 1}$$

$$Si_{y,\text{elev}} = Si_{y,\text{low}} \text{ x } (\text{long}_{\text{low}} / \text{long}_{\text{elev}}) \qquad \text{eqn 2}$$

where $Su_{y,\text{elev}}$ and $Si_{y,\text{elev}}$ respectively represent the annual survival probability of subadults in age-class (y : year 1, 2, or 3) when uninfected or infected with *Bd* at either a moderate or high elevation; $Su_{y,\text{low}}$ and $Si_{y,\text{low}}$ represent annual survival probability of uninfected and infected subadults in age-class 1, 2, or 3 and at a low elevation.

The same calculations were made to convert probabilities of survival of adults in uninfected ($Su_{A, low}$) or infected ($Si_{A, low}$) disease states derived at low elevation sites to state-specific survival estimates at moderate and high elevations.

$$Su_{A, elev} = Su_{A, low} \times (long_{low} / long_{elev}) \qquad \text{eqn 3}$$

$$Si_{A, elev} = Si_{A, low} \times (long_{low} / long_{elev}) \qquad \text{eqn 4}$$

The survival of frogs following metamorphosis was assumed to be influenced by their *Bd* infection status. Disease state-specific estimates of survival for each species have only been derived for adult frogs (West 2015). The relative influence of disease upon survival of individuals in other age-classes was assumed to be proportional to the difference in disease state-specific adult survival. Probabilities of survival of subadults when either uninfected ($Su_{y, elev}$) or infected ($Si_{y, elev}$) with *Bd* were as assumed to be:

$$Su_{y, elev} = (S_{y, elev}/S_{A, elev}) \times Su_{A, elev} \qquad \text{eqn 5}$$

$$Si_{y, elev} = (S_{y, elev}/S_{A, elev} \times Si_{A, elev} \qquad \text{eqn 6}$$

where subadult survival in each disease state was calculated as the ratio of subadult survival ($S_{y, elev}$) to adult survival ($S_{A, elev}$) ignoring disease state and proportional to either the probability of survival of uninfected adults ($Su_{A, elev}$) or infected adults ($Si_{A, elev}$). Disease state-specific survival was calculated in the same manner for each age-class (*y*: years 1, 2, or 3) and at each elevation ($_{elev}$). The survival of *L. lesueurii* in each subadult age-class was assumed to be equal to the survival of *L. spenceri* in each subadult age-class when disease state was unknown. Disease state specific estimates of subadult survival were then calculated relative to those of adults (West 2015). Age-specific baseline mortality probabilities for subadults in each age class ($M_{y, elev}$) and adults ($M_{A, elev}$) for each elevation (*elev*) were:

$M_{y,\ elev} = 1 - Su_{y,\ elev}$ eqn 7

$M_{A,\ elev} = 1 - Su_{A,\ elev}$ eqn 8

The added mortality probabilities due to chytridiomycosis for subadults in each age class ($a_{y,\ elev}$) and for adults ($a_{A,\ elev}$) at each elevation were:

$a_{y,\ elev} = Su_{y,\ elev} - Si_{y,\ elev}$ eqn 9

$a_{A,\ elev} = Su_{A,\ elev} - Si_{A,\ elev}$ eqn 10

Population Models

Three multistate age-structured population projection matrices were constructed for each frog species to represent their population dynamics at a low, medium and high elevation site (Table 1). Each projection matrix **A** was composed of four submatrices:

$$\mathbf{A} = \left[\begin{array}{c|c} \mathbf{A}_1 & \mathbf{A}_3 \\ \hline \mathbf{A}_2 & \mathbf{A}_4 \end{array}\right] \qquad \text{eqn 11}$$

where submatrices described the survival and disease transition probabilities and reproduction of individuals that either remain uninfected (**A**$_1$) or infected (**A**$_4$), or transition from an uninfected to infected disease state (**A**$_2$), or from an infected to uninfected disease state (**A**$_3$) in each time step.

Submatrices for each species were constructed using lower level demographic parameters. The reproduction elements (F: in Figure 1) were calculated as a function of the sex ratio (*sr*), probability of breeding in first (*b*1) or subsequent adult year (b), clutch size (*f*: fecundity) and survival probability of eggs-year 1 (S_e). The survival and transition elements (*P*: in Figure 1) were calculated for each age class as a function of the baseline mortality, added mortality due to *Bd*, and disease impact coefficient (*D*). Reproduction and survival elements were also a function of T_i, the probability of an individual remaining in a current disease state or transitioning to another disease state.

The matrix construction for each species at other elevations was modified so the dimensions of each submatrix represented the number of age classes prior to female maturation and timing of first breeding (See Supplement A).

The construction and analysis of matrix population models was performed in R using the popbio package (Version 2.4.4) which is a R translation of Matlab code found in Caswell Caswell (2001) and Morris and Doak (2002) (Stubben and Milligan 2007). Population growth rates were evaluated as the dominant eigenvalue for each population projection matrix **A.** Sensitivity analysis was performed to evaluate the sensitivity of growth rates to perturbations in the species' demographic parameters/vital rates. The sensitivity analysis also examined the change in growth rate with respect to changes in key demographic parameters across a biologically plausible range. Mortality was manipulated using coefficients; changes in mortality of subadults in year 1-year 2 (M_1) were examined by varying coefficient *C*, and the added mortality due to *Bd* across all life stages was manipulated by varying a disease coefficient *D*.

Population growth rates were compared under seven management scenarios; including: 2 scenarios that eliminated trout impacts, 4 scenarios that reduced or eliminated Bd impacts, and 1 scenario that eliminated both trout and Bd impacts. This was achieved by modifying key demographic parameter values that were likely to be influenced by each management scenario, whilst holding all other parameter values constant. The assumptions for each management scenario are listed in table 2. Management activities to mitigate the impacts of trout are likely to influence the probability of survival of eggs-year 1. Management activities to mitigate the impacts of *Bd* are likely to influence the probability of added mortality due to *Bd* fungus and/or the probabilities of infection and recovery. If *Bd* management activities effected frog survival, the added mortality due to *Bd* across all life stages was manipulated by varying a disease coefficient (D).

For *L. spenceri* at a low elevation site, submatrices $\mathbf{A_1}$ and $\mathbf{A_2}$ were:

$$\mathbf{A_i} = \begin{bmatrix} 0 & 0 & sr \times b1 \times f \times S_e \times T_i & sr \times b \times f \times S_e \times T_i \\ (1 - (M_1 \times C)) \times T_i & 0 & 0 & 0 \\ 0 & (1 - M_2) \times T_i & 0 & 0 \\ 0 & 0 & (1 - M_3) \times T_i & (1 - M_A) \times T_i \end{bmatrix} \qquad \text{eqn 12}$$

for *i*=1,2 where $T_1 = 1 - pI$, the probability of an uninfected individual remaining uninfected and $T_2 = pI$, the probability of an uninfected individual becoming infected. *Litoria spenceri* submatrices $\mathbf{A_3}$ and $\mathbf{A_4}$ at low elevations were:

$$\mathbf{A_i} = \begin{bmatrix} 0 & 0 & sr \times b1 \times f \times S_e \times T_i & sr \times b \times f \times S_e \times T_i \\ \big(1 - (M_1 \times C + a_1 \times D)\big) \times T_i & 0 & 0 & 0 \\ 0 & \big(1 - (M_2 + a_2 \times D)\big) \times T_i & 0 & 0 \\ 0 & 0 & \big(1 - (M_3 + a_3 \times D)\big) \times T_i & \big(1 - (M_A + a_A \times D)\big) \times T_i \end{bmatrix} \qquad \text{eqn 13}$$

for *i*=3,4 where $T_3 = pR$, the probability of an individual recovering from an infection and $T_4 = 1 - pR$, the probability of an individual remaining infected.

For *L. lesueurii* at a low elevation site, submatrices $\mathbf{A_1}$ and $\mathbf{A_2}$ were:

$$\mathbf{A_i} = \begin{bmatrix} 0 & sr \times b1 \times f \times S_e \times T_i & sr \times b \times f \times S_e \times T_i & sr \times b \times f \times S_e \times T_i \\ (1-(M_1 \times C)) \times T_i & 0 & 0 & 0 \\ 0 & (1-M_2) \times T_i & 0 & 0 \\ 0 & 0 & (1-M_3) \times T_i & (1-M_A) \times T_i \end{bmatrix} \quad \text{eqn 14}$$

for i=1,2 where $T_1 = 1 - pI$, the probability of an uninfected individual remaining uninfected and $T_2 = pI$, the probability of an uninfected individual becoming infected. *Litoria lesueurii* submatrices $\mathbf{A_3}$ and $\mathbf{A_4}$ at low elevations were:

$$\mathbf{A_i} = \begin{bmatrix} 0 & sr \times b1 \times f \times S_e \times T_i & sr \times b \times f \times S_e \times T_i & sr \times b \times f \times S_e \times T_i \\ \left(1-(M_1 \times C + a_1 \times D)\right) \times T_i & 0 & 0 & 0 \\ 0 & \left(1-\ (M_2 + a_2 \times D)\right) \times T_i & 0 & 0 \\ 0 & 0 & \left(1-(M_3 + a_3 \times D)\right) \times T_i & \left(1-(M_A + a_A \times D)\right) \times T_i \end{bmatrix} \quad \text{eqn 15}$$

for i=3,4 where $T_3 = pR$, the probability of an individual recovering from an infection and $T_4 = 1 - pR$, the probability of an individual remaining infected.

Results

Variation in the survival of eggs-year 1 (S_e) had the greatest impact on estimated growth rate of *L. spenceri*, which was relatively insensitive to changes in other parameters (Figures 2 and 3). The growth rate of *L. lesueurii* was sensitive to changes in the survival of eggs-year 1 age-class (S_e), the baseline mortality of year 1 subadults (M_1), the added mortality of year 1 subadults due to *Bd* (a_1), the added mortality due to disease (D) of all age classes, and the probability of infection (pI) (Figures 2 and 3). Under all scenarios examined (Table 2), population growth rates (λ) of both species decreased with elevation despite increased longevity.

Under current conditions, *L. spenceri* populations at high (λ=0.88) and moderate (λ=0.95) elevation sites and *L. lesueurii* at high elevations sites (λ=0.98) were all nonviable. Population viability increased at lower elevations for both *L. spenceri* (λ=1.06 at low elevation sites) and *L. lesueurii* (with λ=1.37 and λ=2.13 respectively at moderate and low elevation sites).

A reduction of trout impacts upon the eggs-year 1 age-class could most improve the growth rate of *L. spenceri* at low elevation sites. This was true even if the *Bd* infection rate increased. Trout management was only beneficial to *L. spenceri* at higher elevations if *Bd* impacts did not change. Under *Bd*-only management scenarios, the greatest benefit to *L. spenceri* could be achieved by preventing disease transmission (i.e. reducing the infection probability; *pI*) or increasing survival of infected frogs (i.e. preventing the added mortality due to chytridiomycosis). Increasing the recovery probability of infected frogs was unlikely to improve the population growth rate. The best outcome, however, was produced by eliminating both *Bd* and trout threats which increased *L. spenceri* growth rate by 55 to 69% (Table 2), depending on elevation.

Population growth rates of *L. lesueurii* were predicted to increase under all *Bd* management scenarios, with the greatest benefit for high elevation populations (Table 2). As with *L. spenceri*, increasing the probability of recovery of infected frogs was unlikely to increase the growth rate of *L. lesueurii*. Surprisingly, *L. lesueurii* growth rates declined ($\lambda<1$) at moderate elevations in the trout management scenario (B) if the probability of infection increased and the probability of recovery dropped to zero. However, *L. lesueurii* growth rates at moderate elevations were equal to or greater than 1 if the probability of recovery was at least 0.3 (Figure 3).

Table 2. Estimated deterministic population growth rates of *L. spenceri* and *L. lesueurii* at low, moderate and high elevation sites, under current conditions seven management scenarios that mitigate the impacts of introduced trout and/or *Bd* fungus. Management was assumed to influence *L. spenceri*'s probability of survival of eggs-year1 (S_e), species probability of infection (pI) or recovery (pR), or the added mortality across all terrestrial life stages due to disease (D). Mean vital rates are assumed unless listed. Percentage change from current conditions is shown in parenthesis.

Management Scenario	**Assumptions**	**Estimated Population Growth Rates**					
		L. spenceri			***L. lesueurii***		
		low	moderate	high	low	moderate	high
Current (no management)	Mean vital rates	1.06	0.95	0.88	2.13	1.37	0.98
Trout management A (no change to *Bd* impacts)	*L. spenceri* $S_e = 0.052$; *L. lesueurii* S_e = no change	1.56 (46.2%)	1.27 (33.2%)	1.11 (25.6%)	2.13 (0%)	1.37 (0%)	0.98 (0%)
Trout management B (but increased *Bd* impacts)	*L. spenceri* $S_e = 0.052$; *L. lesueurii* S_e = no change; Both species $pI = 1$, $pR = 0$.	1.32 (24.4%)	1.00 (5.6%)	0.84 (-4.8%)	1.75 (-18.0%)	0.78 (-43.0%)	0.53 (-45.6%)
***Bd* management A** (no change to trout impacts)	Both species pI = mean, $pR = 1$	1.07 (0.3%)	0.95 (0.4 %)	0.89 (0.5 %)	2.15 (1.0%)	1.39 (1.6%)	0.99 (1.1%)
***Bd* management B** (no change to trout impacts)	Both species $pI = 0$, $pR=1$	1.23 (15.8%)	1.15 (20.7%)	1.09 (23.8%)	4.52 (112.3%)	2.83 (106.2%)	2.21 (126.1%)
***Bd* management C** (no change to trout impacts)	Both species 50% reduction in added mortality due to disease ($D = 0.5$)	1.15 (8.3%)	1.05 (11.0%)	0.99 (12.7%)	3.57 (67.5%)	2.26 (64.8%)	1.72 (76.0%)
***Bd* management D** (no change to trout impacts)	Both species 100% reduction in added mortality due to disease ($D = 0$)	1.23 (15.8%)	1.15 (20.7%)	1.09 (23.8%)	4.52 (112.3%)	2.83 (106.3%)	2.21 (126.1%)
Trout and *Bd* management (complete threat elimination)	*L. spenceri* $S_e = 0.052$; *L. lesueurii* S_e = no change; Both species $pI = 0$, $pR = 1$, $D = 0$	1.80 (69.5%)	1.52 (60.4%)	1.37 (55.1%)	4.52 (112.3%)	2.83 (106.3%)	2.21 (126.1%)

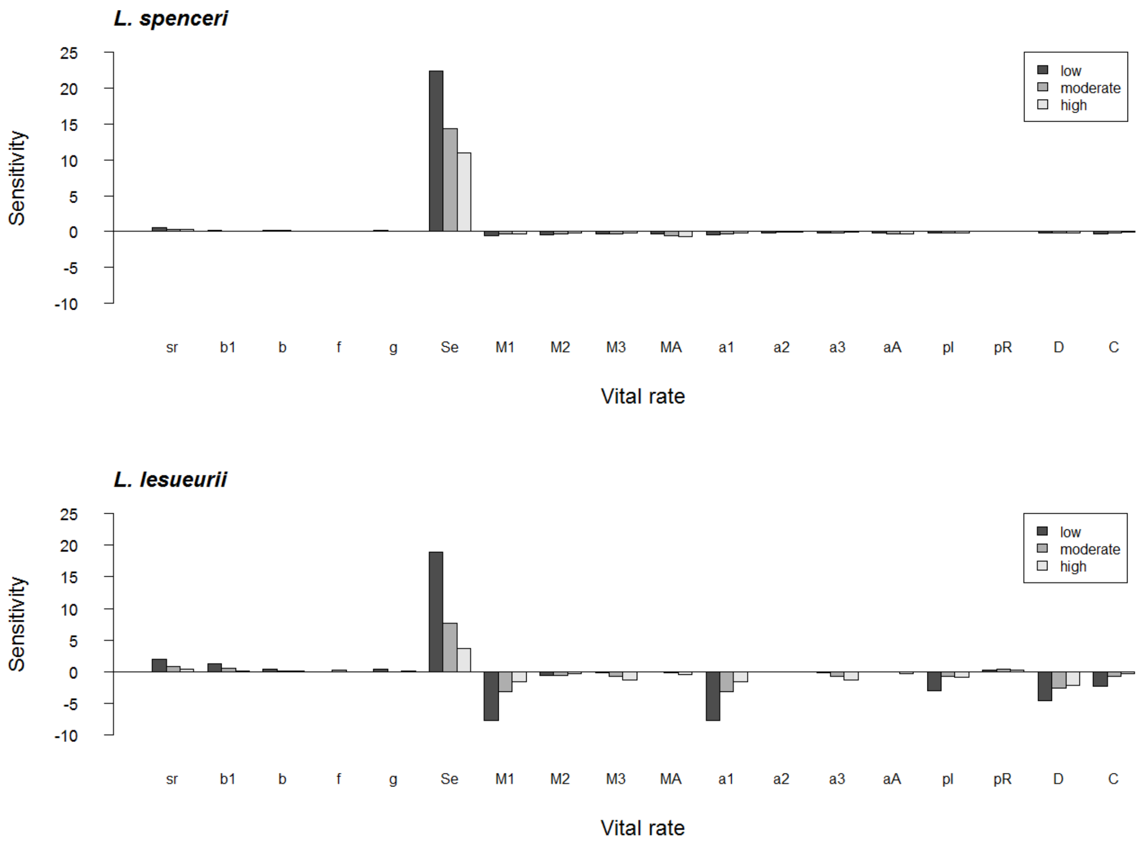


Figure 2. Sensitivity of population growth rate ($d\lambda/dp$, where p is the vital rate) to each of the vital rates of a) *L. spenceri* and b) *L. lesueurii* for multistate age-structured models constructed to represent populations at low, moderate or high elevation sites. Symbol definitions listed in Table 1.

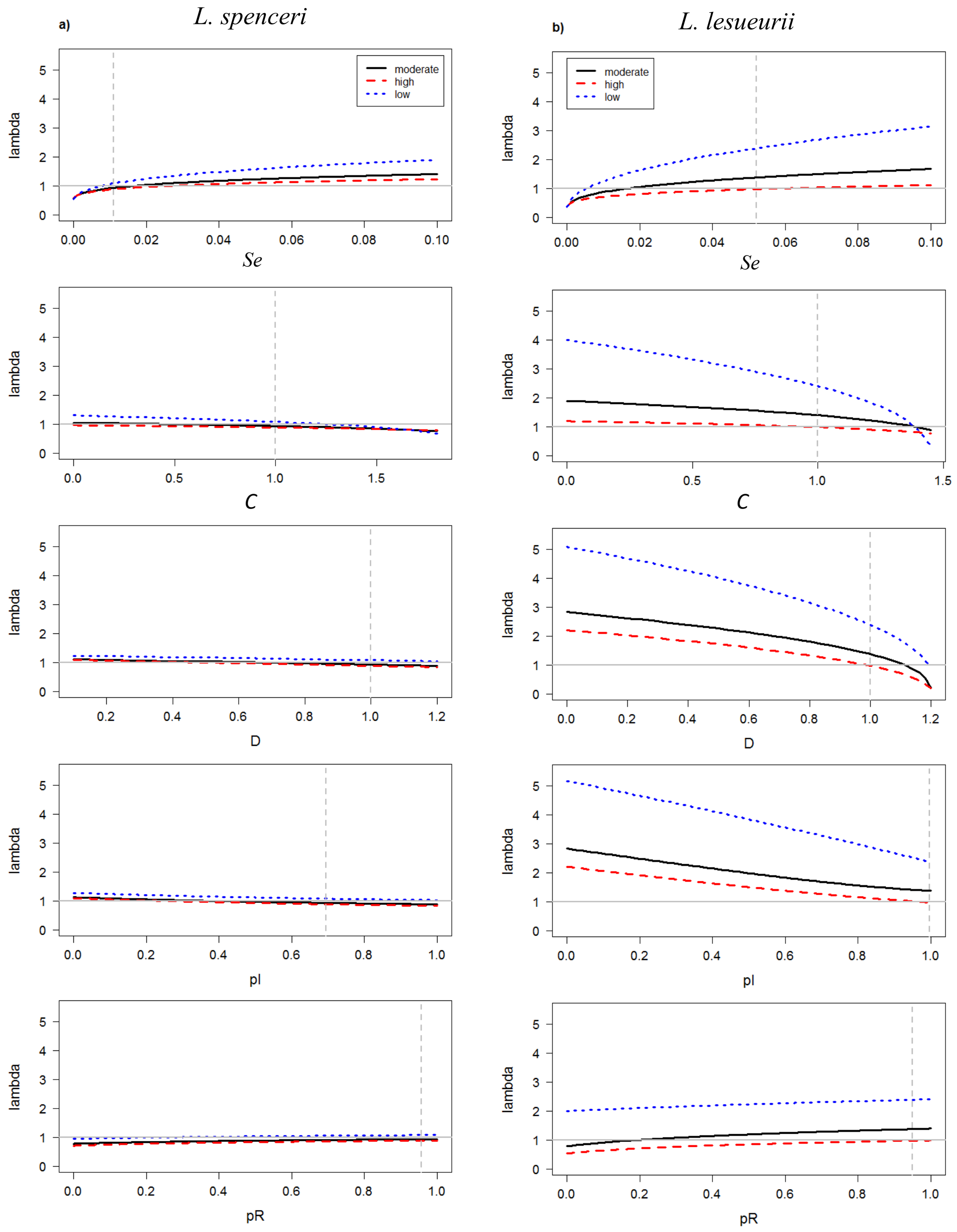


Figure 3 The potential change in deterministic population growth rates (lambda) of *Litoria spenceri* and *L. lesueurii* if vital rates vary from current mean parameter estimates (shown at grey vertical dashed line). Vital rates examined: survival of eggs-year1 (S_e); proportional change in baseline mortality of year1 subadults (C); proportional change in added mortality due to chytridiomycosis (D) on all life stages; apparent probability of infection (pI) of uninfected frogs; apparent probability of recovery (pR) of infected frogs. Population growth rates were estimated for populations at low (blue dotted line), moderate (black solid line) or high (red dashed line) elevation sites.

Discussion

Our results support the hypothesis that species can persist if recruitment can compensate for *Bd*-induced mortality (Muths et al. 2011; Phillott et al. 2013; Scheele et al. 2015; Tobler et al. 2012). Interspecific differences in the age at maturity, clutch size and survival of individuals between egg-year 1 account for the differences in the capacity of *L. spenceri* and *L. lesueurii* to compensate for *Bd*-induced adult mortality. *Litoria lesueurii* populations cope with *Bd* infection better at low and moderate elevations despite individuals having a slightly lower survival probability when infected and a higher infection probability than *L. spenceri*. Importantly, *L. spenceri* cannot compensate for *Bd*-induced mortality of adults via recruitment due to predation of their eggs and tadpoles by introduced trout (Gillespie 2001, 2010). *Litoria lesueurii* has a competitive advantage over *L. spenceri* as trout do not consume *L. lesueurii* tadpoles (Gillespie 2001) and our results support this conclusion.

This case study highlights that the impact of threats upon species can vary spatially when species' vital rates vary between sites. Populations with shorter activity times or growth seasons tend to mature later, live longer and produce larger eggs and these traits often vary across an elevation and climatic gradient (Morrison and Hero 2003). Interspecific variation in the clutch size of amphibians has been both positively and negatively correlated across elevational gradients but has been most strongly linked to differences in species body size across sites (Cvetković et al. 2009; Leskovar et al. 2006; Liao et al. 2016; Miaud et al. 2000; Morrison and Hero 2003). Both species in our case study are considered to mature later, produce less eggs and live longer at cool high versus warm low elevations (Gillespie 2011b). We found that age of maturity, clutch size and egg-year 1 survival were more important for species persistence than longevity. *Litoria spenceri* populations were predicted to be non-viable ($\lambda<1$) at moderate and high elevation sites but may be able to persist at low elevation sites ($\lambda=1.07$) in the absence of adverse stochastic events. The earlier maturation age and increased number of eggs produced by *L. lesueurii* compared with *L. spenceri* also appears to buffer *L. lesueurii* against the impact of *Bd* at low (λ=2.39) and moderate (λ=1.38) elevation sites. Although the later age of maturity and smaller number of eggs produced mean that *L. lesueurii* was nonviable at high (λ=0.97) elevation sites. These results supports the hypothesis that high-elevation, range-restricted, aquatic amphibian species with low fecundities are generally at greatest risk of *Bd* associated declines (Bielby et al. 2008). The risk of extinction is clearly higher for *L. spenceri* than *L. lesueurii* as it has a more restricted distribution, smaller population sizes and a lower growth rate and capacity to recover.

In the absence of effective strategies to directly mitigate *Bd* an alternative strategy for conserving *L. spenceri* may be to increase recruitment by managing introduced trout. Admittedly the benefits of trout management to *L. spenceri* populations are currently uncertain, particularly as the anticipated increased frog population density could lead to an increase in *Bd* transmission between individuals. High population density may have contributed to the rapid decline and extirpation of *L. spenceri* at a high elevation site during an epidemic *Bd* infection (Gillespie et al. 2015). Despite this, our results suggest that at low elevations that populations' may be able to compensate for an increase in *Bd* infection and associated adult mortality through recruitment. Experimental fish management is technically feasible and has benefited other frog populations known to be threatened by introduced trout (Knapp et al. 2007; Vredenburg 2004). Experimental management trials are warranted to evaluate the benefits and consequences of mitigating introduced fish predation to conserve L. spenceri populations. Careful comparative monitoring and evaluation of such trials is required to compare population responses of target species and other ecological changes that may have unforeseen ecological consequences.

The success of any mitigation strategies could be influenced by other species interactions. For instance, extinction risk of *L. spenceri* may increase when both *L. lesueurii* and *Bd* are present at sites. Pathogen host reservoirs can form when species have different responses to disease (Fisher et al. 2009). The ability of *L. lesueurii* populations to persist at sites despite the impacts of *Bd* could increase *Bd* transmission rates through *L. spenceri* populations when the species are sympatric. Previously research found that the presence of both *Bd* and *L. lesueurii* are correlated with a decline in occupancy of *L. spenceri* (West 2015). In contrast, *L. lesueurii* may now occupy more *L. spenceri* sites despite *Bd* (West 2015). These observations suggest that *L. lesueurii* may be an important pathogen host reservoir for *L. spenceri*.

The deterministic discrete-time model approach used in this study provides simple but important insights into the potential population-level impacts of multiple-threats upon frog species with contrasting population dynamics. This type of information is generally lacking for most amphibian species (Biek et al. 2002; Gillespie 2011b). The utility of our predictions may be strengthened by examining potential density or frequency–dependent effects and consequences of environmental and demographic stochasticity. For example, both species are vulnerable to stochastic events that can reduce recruitment (i.e. flood or bushfire Gillespie and West 2012) or age of maturity (i.e. a series of cool summers *sensu* Morrison and Hero 2003). Furthermore, disease dynamics may need to be modelled on a continuous scale or shorter discrete time step and with interactions between species when sympatric at a site. Our results are sensitive to the selected parameter values, particularly estimates of eggs-year 1 survival, although the parameter estimates are broadly consistent with those derived for other species. For instance, survival from hatching to metamorphosis in other species is considered generally less than 10% (Wells 2010). Additional research to evaluate the components of the egg-year 1 period most sensitive to mortality could provide further insight into the mechanisms of decline.

Similarly, additional research is required to clarify age-specific survival of *L. lesueurii* which was assumed to be equivalent to *L. spenceri* in this study.

Conclusions

Numerous factors can influence epidemiological outcomes and species population-level responses to chytridiomycosis including site-specific environmental conditions, a hosts susceptibility to the Bd, pathogen virulence and interactions with co-occurring host-reservoir species (James et al. 2015). This case study provides clear evidence that an amphibian population's capacity to cope with *Bd* is influenced by environmental processes and other threats (such as non-native predators) that can restrict recruitment. Furthermore, these factors can explain spatial variation in the two species population-level responses to Bd.

Currently few options exist to mitigate *Bd* impacts upon amphibian populations (Scheele et al. 2014), particularly for lotic systems. However, strategies that increase recruitment to offset mortality caused by *Bd* could benefit declining amphibian populations and be achieved for *L. spenceri* by managing non-native fish. In contrast to *Bd*, fish mitigation options are technically feasible (i.e. piscicide use, removal via electrofishing). At warmer low elevation sites, fish management may be the optimal approach, but strategies to manage *Bd* or both threats concurrently may be required at cooler, higher elevation sites. Due to the current uncertainty in the species responses to intervention, management options should be examined in an experimental framework to avoid exacerbating the impacts of either threat. Our results indicate that spatially-explicit knowledge of species demography and population-level impacts of interacting threats is important when designing effective management strategies for threatened species.

Acknowledgements

Funding was provided by University of Melbourne (MW), Zoos Victoria (MW), Holsworth Wildlife Research Endowment (MW), Alfred Nicholas Fellowship (MW), National Environmental Science Program (NESP) Threatened Species Recovery (TSR) Hub (MW) and the Australian Research Council (ARC) Centre of Excellence for Environmental Decisions, ARC Future Fellowship (MM). Discussions with O. Gimenez, M. Oli, J.D. Leberton during the development of models and comments from D. Hunter, C. Visintin and G. Ryan have helped to improve this manuscript.

Supporting Information

Supplementary Material

References

Berger, L., Spear, R., Hyatt, A.D., 1999. Chytrid Fungi and Amphibian declines: Overview, Implications and Future Directions, In Declines and Disappearances of Australian Frogs. pp. 23-33. Environment Australia.

Berger, L., Speare, R., Daszak, P., Green, D., Cunningham, A., Goggin, C., Slocombe R. Ragan, M., Hyatt, A., McDonald, K., Hines, H., Lips, K., Marantelli, G., Parkes, H., 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. P Natl Acad Sci USA 95, 9031 - 9036.

Berger, L., Speare, R., Hines, H.B., Marantelli, G., Hyatt, A.D., McDonald, K.R., Skerratt, L.F., Olsen, V., Clarke, J.M., Gillespie, G., Mahony, M., Sheppard, N., Williams, C., Tyler, M.J., 2004. Effect of season and temperature on mortality in amphibians due to chytridiomycosis. Australian Veterinary Journal 82, 434-439.

Biek, R., Funk, W.C., Maxell, B.A., Mills, L.S., 2002. What Is Missing in Amphibian Decline Research: Insights from Ecological Sensitivity Analysis. Conservation Biology 16, 728-734.

Bielby, J., Cooper, N., Cunningham, A.A., Garner, T.W.J., Purvis, A., 2008. Predicting susceptibility to future declines in the world's frogs. Conservation Letters 1, 82-90.

Blaustein, A., Romansic, J., Scheessele, E., Han, B., Pessier, A., Longcore, J., 2005. Interspecific variation in susceptibility of frog tadpoles to the pathogenic fungus *Batrachochytrium dendrobatidis*. Conserv Biol 19, 1460 - 1468.

Blaustein, A.R., Kiesecker, J.M., 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters 5, 597-608.

Briggs, C.J., Vredenburg, V.T., Roland, A.K., Rachowicz, L.J., 2005. Investigating the population-level effects of chytridiomycosis: an emerging infectious disease of amphibians. Ecology 86, 3149-3159.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23, 453-460.

Caswell, H., 2001. Matrix population models, Second edition edn. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Collins, J.P., 2010. Amphibian decline and extinction: What we know and what we need to learn. Diseases of Aquatic Organisms 92, 93-99.

Daskin, J.H., Bell, S.C., Schwarzkopf, L., Alford, R.A., 2014. Cool temperatures reduce antifungal activity of symbiotic bacteria of threatened amphibians–implications for disease management and patterns of decline. Plos One 9, e100378.

Doddington, B.J., Bosch, J., Oliver, J.A., Grassly, N.C., Garcia, G., Schmidt, B.R., Garner, T.W.J., Fisher, M.C., 2013. Context-dependent amphibian host population response to an invading pathogen. Ecology 94, 1795-1804.

Fisher, M.C., Garner, T.W.J., Walker, S.F., 2009. Global Emergence of *Batrachochytrium dendrobatidis* and Amphibian Chytridiomycosis in Space, Time, and Host, In Annual Review of Microbiology. pp. 291-310.

Gahl, M.K., Longcore, J.E., Houlahan, J.E., 2012. Varying Responses of Northeastern North American Amphibians to the Chytrid Pathogen *Batrachochytrium dendrobatidis*. Conservation Biology 26, 135-141.

Gahl, M.K., Pauli, B.D., Houlahan, J.E., 2011. Effects of chytrid fungus and a glyphosate-based herbicide on survival and growth of wood frogs (*Lithobates sylvaticus*). Ecological Applications 21, 2521-2529.

Gervasi, S.S., Hunt, E.G., Lowry, M., Blaustein, A.R., 2014. Temporal patterns in immunity, infection load and disease susceptibility: understanding the drivers of host responses in the amphibian-chytrid fungus system. Functional Ecology 28, 569-578.

Gillespie, G., Hunter, D., Berger, L., Marantelli, G., 2015. Rapid decline and extinction of a montane frog population in southern Australia follows detection of the amphibian pathogen *Batrachochytrium dendrobatidis*. Animal Conservation 18, 295-302.

Gillespie, G.R., 2001. The role of introduced trout in the decline of the Spotted Tree Frog (*Litoria spenceri*) in south-eastern Australia. Biological Conservation 100, 187-198.

Gillespie, G.R., 2010. Population Age Structure Of The Spotted Tree Frog *Litoria spenceri*: insights into population declines. Wildlife Research 37, 1-8.

Gillespie, G.R., 2011a. Egg compliment variation between temperate stream-breeding hylid frogs in south-eastern Australia. Proceedings of the Royal Society of Victoria 132, 153-160.

Gillespie, G.R., 2011b. Life history variation in the Spotted Tree Frog, *Litoria spenceri* (Anura: Hylidae), from south eastern Australia. Herpetologica 67, 10-22.

Gillespie, G.R., Hines, H.B. eds., 1999. Status of Temperate Riverine Frogs in South-Eastern Australia. Enivironment Australia, Canberra.

Gillespie, G.R., West, M., 2012. Evaluation of Impacts of Bushfire on the Spotted Tree Frog *Litoria spenceri* in the Taponga River, Northeast Victoria, In Rebuilding Together.

Heard, G.W., Scroggie, M.P., Clemann, N., Ramsey, D.S.L., 2014. Wetland characteristics influence disease risk for a threatened amphibian. Ecological Applications 24, 650-662.

Heard, M., Smith, K.F., Ripp, K., 2011. Examining the Evidence for Chytridiomycosis in Threatened Amphibian Species. Plos One 6, 1-4.

Hero, J.-M., Gillespie, G., Robertson, P., Littlejohn, M.J., Lemckert, F., 2004. *Litoria spenceri*. The IUCN Red List of Threatened Species 2004. IUCN, http://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T12154A3328048.en

Hunter, D.A., Smith, M.J., Scroggie, M.P., Gilligan, D., 2011. Experimental examination of the potential for three introduced fish species to prey on tadpoles of the endangered Booroolong Frog, *Litoria booroolongensis*. Journal of Herpetology 45, 181-185.

James, T.Y., Toledo, L.F., Rödder, D., da Silva Leite, D., Belasen, A.M., Betancourt-Román, C.M., Jenkinson, T.S., Lambertini, C., Longo, A.V., Ruggeri, J., Collins, J.P., Burrowes, P.A., Lips, K.R., Zamudio, K.R., Longcore, J.E., 2015. Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: lessons from the first 15 years of amphibian chytridiomycosis research. Ecology and Evolution 5, 4079-4097.

Knapp, R.A., 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. Biological Conservation 121, 265-279.

Knapp, R.A., Boiano, D.M., Vredenburg, V.T., 2007. Removal of nonnative fish results in population expansion of a declining amphibian (Mountain Yellow-Legged Frog, *Rana muscosa*). Biological Conservation 135, 11-20.

Lips, K.R., Brem, F., Brenes, R., Reeve, J.D., Alford, R.A., Voyles, J., Carey, C., Livo, L., Pessier, A.P., Collins, J.P., 2006. Emerging infectious disease and the loss of biodiversity in a neotropical amphibian community. Proceedings of the National Academy of Sciences of the United States of America 103, 3165-3170.

Matthews, K.R., Pope, K.L., Preisler, H.K., Knapp, R.A., 2001. Effects of nonnative trout on Pacific treefrogs (*Hyla regilla*) in the Sierra Nevada. Copeia, 1130-1137.

Morris, W.F., Doak, D.F., 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Morrison, C., Hero, J.M., 2003. Geographic variation in life-history characteristics of amphibians: a review. Journal of Animal Ecology 72, 270-279.

Morrison, C., Hero, J.M., Browning, J., 2004. Altitudinal variation in the age at maturity, longevity, and reproductive lifespan of anurans in subtropical queensland. Herpetologica 60, 34-44.

Muths, E., Scherer, R.D., Pilliod, D.S., 2011. Compensatory effects of recruitment and survival when amphibian populations are perturbed by disease. Journal of Applied Ecology 48, 873-879.

Phillott, A.D., Grogan, L.F., Cashins, S.D., McDonald, K.R., Berger, L.E.E., Skerratt, L.F., 2013. Chytridiomycosis and seasonal mortality of tropical stream-associated frogs 15 Years after introduction of *Batrachochytrium dendrobatidis*. Conservation Biology, 1-11.

Piotrowski, J.S., Annis, S.L., Longcore, J.E., 2004. Physiology of *Batrachochytrium dendrobatidis*, a chytrid pathogen of amphibians. Mycologia 96, 9-15.

Rachowicz, L., Briggs, C., 2007. Quantifying the disease transmission function: effects of density on Batrachochytrium dendrobatidis transmission in the mountain yellow-legged frog Rana muscosa. J Anim Ecol 76, 711 - 721.

Scheele, Scheele, B., Pasmans, F., Skerratt, L., Berger, L., Martel, A., Beukema, W., Acevedo, A., Burrowes, P., Carvalho, T., Catenazzi, A., De la Riva, I., Fisher, M., Flechas, S., Foster, C., Frías Álvarez, P., Garner, T.W.J., Gratwicke, B., Guayasamin, J., Hirschfeld, M., Kolby, J., Kosch, T., La Marca, E., Lindenmayer, D., Lips, K., Longo, A., Maneyro, R., McDonald, C., Mendelson, J., Palacios Rodriguez, P., Parra Olea, G., Richards Zawacki, C., Rödel, M.-O., Rovito, S., Soto Azat, C., Toledo, L., Voyles, J., Weldon, C., Whitfield, S., Wilkinson, M., Zamudio, K., Canessa, S., 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. Science 363, 1459-1463.

Scheele, B.C., Hunter, D.A., Grogan, L.F., Berger, L.E.E., Kolby, J.E., McFadden, M.S., Marantelli, G., Skerratt, L.F., Driscoll, D.A., 2014. Interventions for reducing extinction risk in chytridiomycosis-threatened amphibians. Conservation Biology 28, 1195-1205.

Scheele, B.C., Hunter, D.A., Skerratt, L.F., Brannelly, L.A., Driscoll, D.A., 2015. Low impact of chytridiomycosis on frog recruitment enables persistence in refuges despite high adult mortality. Biological Conservation 182, 36-43.

Stevenson, L.A., Alford, R.A., Bell, S.C., Roznik, E.A., Berger, L., Pike, D.A., 2013. Variation in Thermal Performance of a Widespread Pathogen, the Amphibian Chytrid Fungus Batrachochytrium dendrobatidis. Plos One 8.

Stubben, C.J., Milligan, B.G., 2007. Estimating and Analyzing Demographic Models Using the popbio Package in R. Journal of Statistical Software 22:11.

Tobler, U., Borgula, A., Schmidt, B.R., 2012. Populations of a susceptible amphibian species can grow despite the presence of a pathogenic chytrid fungus. Plos One 7.

Tobler, U., Schmidt, B.R., 2010. Within- and among-population variation in chytridiomycosis-induced mortality in the toad *Alytes obstetricans*. Plos One 5.

Vredenburg, V.T., 2004. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences of the United States of America 101, 7646-7650.

Wake, D.B., 2012. Facing extinction in real time. Science 335, 1052-1053.

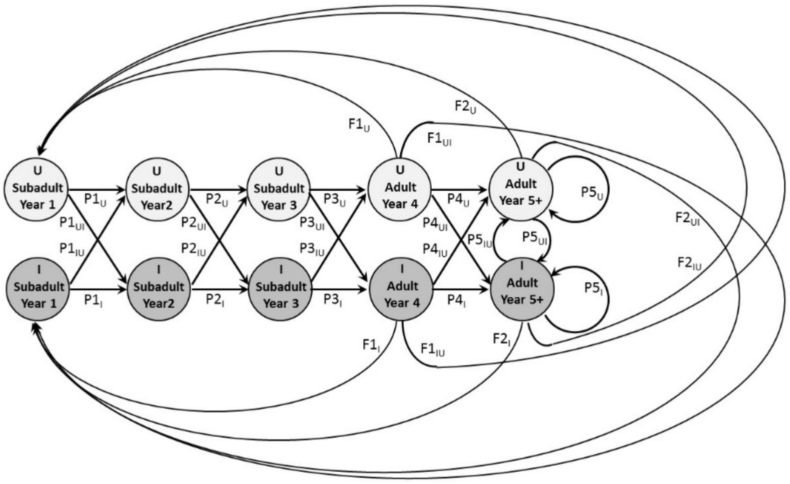
Wells, K.D., 2010. The ecology and behavior of amphibians. University of Chicago Press, United States of America.

West, M., 2015. Contrasting population responses of ecologically-similar sympatric species to multiple threatening processes, In School of BioSciences. p. 184. The University of Melbourne, Melbourne.

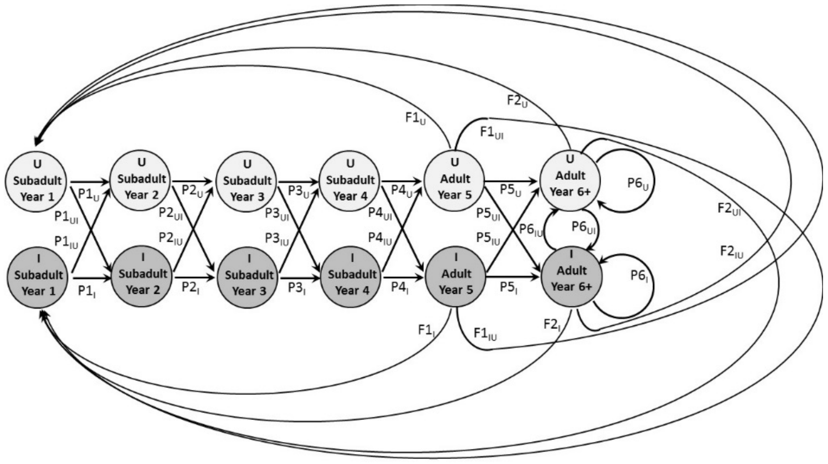
Supplementary Material

Life graphs for each species at moderate and high elevation sites.

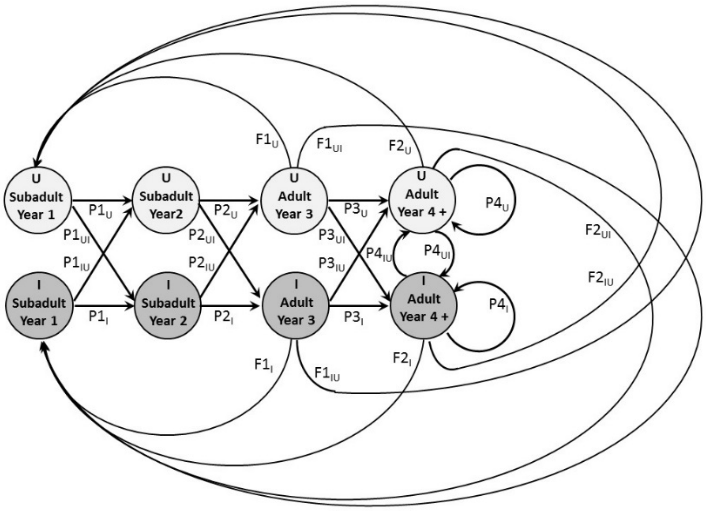
L. spenceri at moderate elevation sites



L. spenceri at high elevation sites



L. lesueurii at moderate elevation sites and corresponding matrix model



L. lesueurii at high elevation sites

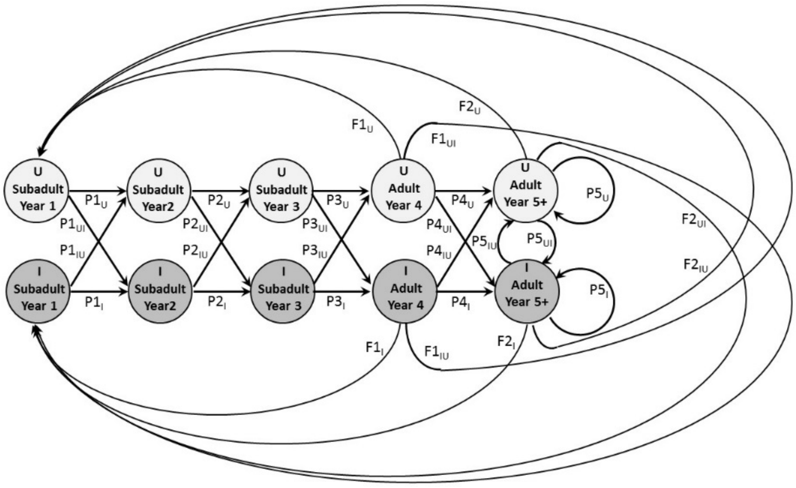


Figure S1 Multi-state life-cycle graphs and coresponding population matrices for *L. spenceri* and *L. lesueurii* at moderate and high elevation sites. In our life-cycle graphs indidivuals can exisit in a sub-adult or one of three adult life stages (each represented by circles) and in each stage they can occur in either an uninfected (U; white circles) or infected (I; grey shaded circles) disease state. Frogs can transition (represented by lines) between life stages and disease states. The coresponding population matrices describe the probabilities of transitions between each life stage and disease state. In the graphs and matrices P represents the probability of survival and probability of transition between states, and F represents fecundity. Numbers are used to index fecundity and probabilities of survival plus transition relative to the life stage. UI represents a transition from an uninfected-infected disease state and IU represents a transition from an infected-uninfected disease state

Unpublished Clutch Size Data for *L. spenceri* and *L. lesueurii*

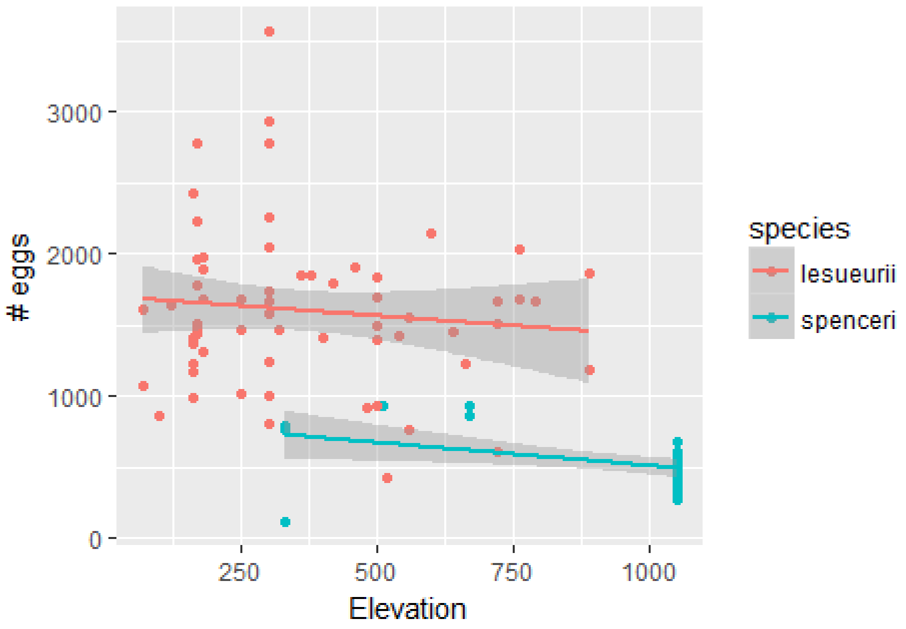


Figure S2: Egg clutch size data for *L. spenceri* (blue circles) and *L. lesueurii* (red circles) with respect to elevation (m above sea level). Lines represent the linear regression for each species (blue = *L. spenceri* and red = *L. lesueurii*) with shading representing the 95% confidence region. The linear regression equation for egg clutch size with respect to elevation for *L. spenceri* is Egg Clutch Size = 833.5 + (-0.32 x elevation) and for *L. lesueurii* is Egg Clutch Size = 1696.5 + (-0.27 x elevation).

Estimation of Population Growth rates at Low Elevation Sites

Field methods:

Litoria spenceri populations were examined studied on two streams located approximately 150 km north-east of Melbourne, Victoria, at an elevation of 330 - 340 m. Self-sustaining populations of brown and rainbow trout are present in both streams. Transects, 200 m in length, were established along Stream 1 in 1992 and Stream 2 in 1994. Censuses for frogs were conducted along these transects for frogs between October and March, the active season for the species. Censuses were conducted every 2 - 3 weeks during optimal conditions for locating the species (mild to -warm weather). During each visit, diurnal and nocturnal censuses were undertaken by two people slowly walking along each transect, examining all substrates (e.g. rocks, logs and vegetation) and potential sheltering sites (e.g. logs and stones) for frogs. All captured frogs were measured (snout-vent length, mm), their transect position recorded, and each was given an individual identification mark by toe clipping, (Hero 1989), if not previously marked.

Subsequent monitoring of growth and development through recapture of marked, known-aged juvenile frogs and skeletochronologically-aged adults and sub-adults allowed determination of age to sexual maturity and longevity.

Mark-recapture models and analyses

Understanding of the dynamics of animal populations and related ecological issues depends on the direct analysis of vital rates (Lebreton et al. 1992). In particular, the risk assessment of populations, often referred to population viability analysis, must rely on estimates of vital rates of a population, and often these can only be derived from the study of uniquely marked animals (White and Burnham 1999).

The capture histories of individual frogs from Site 1 and Site 2 were analyzed using MARK software using a Pradel Model (Pradel, 1996) for the estimation of parameters describing the distributions of survival rates and population growth. Males and females were combined in the analysis. Three age classes, juvenile, sub-adult and adult, were adopted for the population model. These age classes were defined as follows: Juveniles - individuals captured in their first summer season post metamorphosis, approximately 10 - 18 months post hatching; subadults - older individuals that had not reached sexual maturity; and adults - sexually mature individuals. Burnham and Anderson (1992) outline methods for multi-group models and model selection based upon Akaike (1985) Information Criterion (AIC). Lebreton et al. (1992) provides a unified view of mark-recapture theory with extensions for open population mark-recapture modelling, including AIC type model selection strategies.

Results in Brief

The mean growth rate (λ) for the two sites was estimated to be 1.07 (0.94 for Site 1 and 1.20 for Site 2), see Table S1.

Table S1 Estimates of growth rates from the analysis of the combined Site 1 and Site 2 mark-recapture data using the Pradel construction.

System	Model	Weight	Estimate	Standard Error
Site 1	{Phi(.)p(Pop*t)Lam(Pop)}	0.736	0.936	0.034
	{Phi(Pop)p(Pop*t)Lam(Pop)}	0.252	0.936	0.034
	{Phi(Pop)p(Pop*t)Lam(.)}	0.012	0.990	0.030
	Weighted Average		**0.937**	0.034
	Unconditional SE		0.034	
Site 2	{Phi(.)p(Pop*t)Lam(pop)}	0.736	1.201	0.090
	{Phi(Pop)p(Pop*t)Lam(pop)}	0.252	1.193	0.097
	{Phi(Pop)p(Pop*t)Lam(.)}	0.012	0.990	0.030
	Weighted Average		**1.197**	0.091
	Unconditional SE		0.094	
	Mean growth rate for both sites		**1.067**	

References for Supplementary Material

Akaike, H., 1985. Prediction and entropy, In Selected Papers of Hirotugu Akaike. pp. 387-410. Springer.

Burnham, K.P., Anderson, D.R., 1992. Data-based selection of an appropriate biological model: the key to modern data analysis, In Wildlife 2001: populations. pp. 16-30. Springer.

Hero, J.-M., 1989. A Simple Code For Toe Clipping Anurans. Herperological Review 20, 66-67.

Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62, 67-118.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird study 46, S120-S139.