

Investigating climate change extinction risks of  
amphibians by simulation: the importance of life  
history and thermal performance traits

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## **Abstract**

The biological traits of species may be used as indicators of heightened vulnerability to climate change. Current methods for the prediction of species' extinction risks from climate change do not explicitly use interspecific variation in biological traits. Simulation of population abundances under climate change provides an approach to build an understanding of the importance of variation in biological traits on climate change extinction risk.

Here, I investigate the effect of variations of life history and thermal performance traits on the climate change extinction risks for amphibians. I expand on the work by Dickinson (2012) using a stage-based matrix model with climate dependent survival rates and evaluating the relative changes in extinction risk are by elasticity and limitation analysis. To deliver robust conclusions, the model was parameterised with a range of baseline life history strategies and thermal performance characteristics that represent a variety of amphibian species.

I find that variations in biological traits have a strong effect on climate change extinction risk, with the later life stages' survival rates and age at first reproduction showing the greatest impact. The model predicts that species currently living close to their optimal performance temperature with narrow thermal tolerances are vulnerable to warming temperatures. These findings support the need to have species' biology integrated into the methodology of assessing climate change extinction risk.

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## **Introduction**

The biology of a species can be an indicator of extinction risk. Aspects of ecology, genetics, life history and physiology have been shown to be predictors of relative extinction risks for various vertebrates from anthropogenic threats (Bennett & Owens 1997; Collen et al. 2006; Purvis et al. 2000).

The prediction of species' extinction risks from climate change is currently dominated by methods based on climate envelope modelling (Pearson & Dawson 2003). The level of extinction risk is determined using the change in distribution of the climate envelope (the conditions thought to be suitable for the species to persist) under projected climate change (Araújo et al. 2006; Thomas et al. 2004). These methods do not explicitly include interspecific variation in biological traits.

Given that specific traits have been shown to heighten extinction risk in general (Bennett & Owens 1997; Collen et al. 2006; Purvis et al. 2000), it follows that it is likely that a species' vulnerability to climate change can be associated with the underlying biology. Possible traits that indicate susceptibility to climate change extinction risk have been determined, including narrow climatic tolerances (Tewksbury et al. 2008) and a dependence on climatic cues to commence a life history event (Foden et al. 2009). Particular life history traits, including high reproductive rates and short life spans, have been shown to promote resilience to disturbances (McKinney 1997). There is a need for greater understanding of the relative importance of the traits, or trait combinations, on climate change extinction risk. The potential importance of the underlying biology has led to suggestions of a new 'whole ecology' approach to assessing climate change extinction risk (Brook et al. 2009; Williams et al. 2008). Simulation of population abundances under climate change provides a possible method to build a sense of the biological traits that promote extinction risk.

### **The Dickinson model**

Here, I report on my expansion of the work by Dickinson (2012), who developed a model to investigate the effect of variation of life history and thermal performance traits on climate change extinction risk. The Dickinson model simulates a typical amphibian

population (excluding caecilians) using a stage-based matrix model, with climate dependent survival rates.

It is of critical importance to build an understanding of extinction risks faced by amphibians as they are among the most threatened vertebrate taxa (Stuart et al. 2004). Several factors have been the cause of this status, including climate change (Hof et al. 2011). This vulnerability to climate change is likely enhanced because amphibians' physiological functions and fitness depend on temperature (Angilletta et al. 2010; Deutsch et al. 2008; B. Huey & Stevenson 1979).

The life cycle of a typical amphibian can be described in four stages: premetamorphic aquatic stage (eggs and tadpoles), metamorph, juvenile, and adult. Eggs develop into tadpoles, metamorphose and progress into juveniles all within one year. Based on Vonesh & De la Cruz's (2002) model, the annual time step stage-based matrix model applied therefore comprises of two states, with the premetamorphic aquatic and metamorph survival being included within fecundity as follows:

$$\begin{bmatrix} J \\ A \end{bmatrix}_{t+1} = \begin{bmatrix} \left( \frac{1-\sigma_j^{(1-d)}}{1-\sigma_j^d} \right) \sigma_j & c\sigma_p\sigma_m\sigma_a py \\ \frac{\sigma_j^d(1-\sigma_j)}{1-\sigma_j^d} & \sigma_a \end{bmatrix} \begin{bmatrix} J \\ A \end{bmatrix}_t \quad (1)$$

Where: J is the number of juveniles, A is the number of adults, t is the year,  $\sigma_j$  is the annual juvenile survival rate, d is the number of years spent as a juvenile, c is the clutch size,  $\sigma_p$  is the premetamorphic aquatic survival rate,  $\sigma_m$  is the metamorph survival rate,  $\sigma_a$  is the annual adult survival rate, p is the proportion of females breeding in a given season, and y is the population sex ratio. Within one breeding season males can fertilise multiple females and are unlikely to limit population growth (Harper et al. 2008), therefore only females are modelled with y as a constant 1.

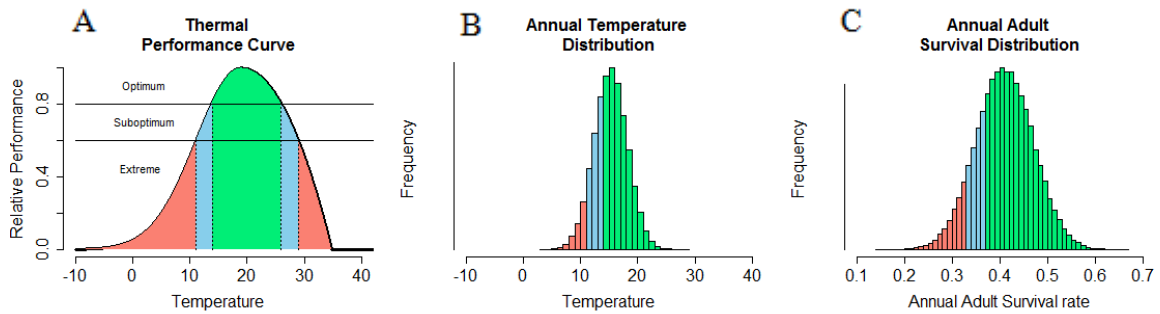
The Dickinson model combines published empirical thermal performance, vital rates and climate data to generate climate dependent survival rates. Drought dependence is integrated in the aquatic stage survival rate and temperature dependence is integrated in the terrestrial survival rates. As zero premetamorphic aquatic survival has been observed in low rainfall years (Berven 2009; Carey et al. 2002), Dickinson's model applies a binary classification of drought year or non-drought year with zero aquatic stage survival in drought years.

The effectiveness of ectotherms to accomplish various functions necessary for survival at different temperatures can be described by thermal performance curves. These curves are asymmetric and unimodal, gradually increasing from a critical minimum temperature ( $CT_{min}$ ) to an optimal temperature ( $T_{opt}$ ) and then sharply dropping to a critical maximum temperature ( $CT_{max}$ ) (Angilletta et al. 2002). The thermal performance curve function applied in the Dickinson model was based on Deutsch et al. (2008) as follows:

$$P(T) = \begin{cases} \exp\left(-\left(\frac{T-T_{opt}}{2s}\right)^2\right), & T \leq T_{opt} \\ 1 - \left(\frac{T-T_{opt}}{T_{opt}-CT_{max}}\right)^2, & T > T_{opt} \end{cases} \quad (2)$$

Where: P is relative performance, T is temperature,  $T_{opt}$  is the optimal temperature, s dictates the breadth of the thermal performance at temperatures below  $T_{opt}$ , and  $CT_{max}$  is the critical maximum temperature.

Thermal performance curves provide a relationship between temperature and survival related functions. However, it is unlikely that temperature is the only determinant of annual survival. The Dickinson model directly links survival and temperature by implementing the following. Firstly, using the amphibian's thermal performance curve, the temperature ranges that fall within arbitrary thresholds of relative performance are determined and categorised as optimum (>80%), suboptimum (<80% and >60%), and extreme conditions (<60%) (see Fig. 1A). Secondly, the proportion of current temperatures experienced by the amphibian that are within these temperature ranges is determined (Fig. 1B). Finally, the survival rate distributions of the terrestrial stages are segmented by the frequency of current optimum, suboptimum and extreme temperatures, assuming that highest survival rates occur at optimal temperatures and lowest survival rates occur at extreme temperatures (see Fig. 1C). The survival rate for each terrestrial stage, applied in the model for a given year, is the mean survival rate of the corresponding segment of the distribution to the simulated annual temperature.



**Fig. 1: *Rana sylvatica*'s thermal performance curve, annual temperature distribution and annual adult survival distribution.** (A) The thermal performance curve is segmented into three zones (green depicting optimum, blue depicting suboptimum and red depicting extreme). The temperature bounds for these segments are determined from the intersection of the thermal performance curve and each threshold. (B) The frequency of current annual temperatures that occur within these temperatures bounds, segments the annual temperature into the three zones. (C) The annual adult survival rate is segmented by the frequencies that the temperatures occur in the three zones. This is completed by assuming that the highest survival rates occur at optimal temperatures, while lowest survival rates occur at extreme temperatures.

Dickinson projected the population for an initial 20 years under current climate conditions, to give suitable starting values, before projecting for 50 years under seven climate scenarios (See Appendix subsection 'Climate parameters and climate change simulations' for further details). A population ceiling on adult population numbers was applied. If the adult abundance of any year exceeded a carrying capacity ( $K$ ), adult numbers were reduced to  $K$  and juvenile abundances were lowered by the same proportion. The extinction risk was determined by calculating the cumulative probability of extinction (CPE), defined as the proportion of 1000 model runs in which the population was considered extinct by the final time step.

Dickinson's model was parameterised with the life history and thermal performance trait values of the wood frog (*Rana sylvatica*), a species that is considered to have a 'typical' life history on basis of a median clutch size and body size. The parameter space boundaries for each life history trait were defined with reference to the life history trait values of two distinct species: the boreal toad (*Bufo boreas*) and the spotted salamander (*Ambystoma maculatum*).

Dickinson conducted elasticity and limitation analysis on the model parameters to assess the importance of the life history and thermal performance trait values on extinction risk. The traits investigated included the survival rate at each lifecycle stage, the clutch size, the age at maturity (age at first reproduction), the breadth of the thermal performance curve and the thermal position (the difference between the  $T_{opt}$  and the mean annual temperature of the habitat). The CPE values over each life history trait

parameter space were fitted with a least square logistic curve to remove variation by the stochasticity of the model. The life history trait elasticity and limitation analysis was conducted on these fitted curves. The gradients of linear models between the thermal parameters and scenario to CPE were used to determine the bearing of their variation on extinction risk.

Dickinson's investigations led to a number of conclusions. Firstly, variations in life history traits strongly influence extinction risk, with annual adult survival and age at sexual maturity showing the greatest impact. Secondly, populations living in a habitat with a mean temperature below  $T_{opt}$  have a greater risk of extinction due to climate change. Thirdly, populations with a broad thermal performance breadth have a reduced risk of climate change extinction. Finally, populations that have a broad thermal performance breadth and are living in a habitat with mean temperature below  $T_{opt}$  are at greater climate change extinction risk.

For further details on the Dickson model, including data sources and rationale for the methods, please refer to the appendix where I have included an extract of Dickinson's thesis.

### **Progression from the Dickinson model**

Dickinson's model is a novel approach to identify species that are likely to be particularly sensitive to climate change. The modelling method aims to be a balance between an abstract theoretical model and a detailed model of a particular species. However, I believe the model tends to be over influenced by the trait values of one species and requires further modelling and analysis to determine if the conclusions are robust. Therefore, I have modified the model structure and parameterisation to test the generality of the outputs.

Dickinson only parameterised her model with baseline values based on the life history traits and thermal performance characteristics of one species, *R.sylvatica*. There is a need to clarify whether the relative gradients of the CPE-to-parameter value curve would be dramatically different if the baseline values were altered to represent a species with a different life history strategy e.g. a long lived species. With regards to thermal performance characteristics, *R.sylvatica*'s mean annual temperature is categorised in the optimal condition zone, however, it is several degrees below its  $T_{opt}$ . Consequently the



majority of its annual temperatures are within the optimal temperature conditions and warming climate change reduces the extinction risk. It would therefore be valuable to determine if the model's outputs would be different if the baseline thermal performance characteristics were differed. To come to robust conclusions, I parameterised the model with a variety life history strategies and thermal performance characteristics.

In addition, I have investigated aspects of the model setup to determine if the biological conclusions stand when they are altered. These included varying the relative performance bands' threshold values and the carrying capacity.

By conducting this analysis I determine biological traits that are likely to increase species climate change extinction risk that are generalizable for a variety of amphibian species. I show that variation in biological traits strongly influence climate change extinction risk and therefore suggest interspecific trait variation should be included in species risk assessment of climate change.

## Materials and Methods

To be able to complete additional modelling through adjustments of the Dickinson model, it was necessary to rewrite it. Dickinson's model was sound, however the coding style did not allow for simple adjustments of its setup or parameters. This rewritten version of the Dickinson model is further referred to as the original model (OM).

### Model modifications

#### *Threshold analysis*

The Dickinson model's methodology of segmenting the survival distribution based on the frequency of temperature ranges is crucial to build in the temperature dependence of the stage survival rates. To test the robustness of the arbitrary relative performance bands' threshold levels on the biological conclusions I developed several variants of the OM with differing thresholds. I increased and decreased the threshold values as well the number of relative performance bands, introducing four and five bands, corresponding to three and four threshold levels, respectively.

#### *Correcting model parameter base values*

The parameterisation of the Dickinson model was based on published data. When exploring the sources and derivation of the parameters, I found some minor oversights. The  $CT_{max}$  parameter value of 34.8°C used for *R.sylvatica*, sourced from Brattstrom (1968), was incorrectly copied from a table. The model was updated to use the corrected *R.sylvatica*  $CT_{max}$  parameter value from Brattstrom (1968) of 33.6°C. The Dickinson model's parameter value for K of 4,500 originated from the carrying capacity reported for a *R.sylvatica* adult population in Berven (2009) of 3,263 males and 1,151 females. However, the Dickinson model is only modelling the female population. Therefore, the updated model used the female only reported value (1,151). This updated version of OM is referred to here as the updated original model (UOM).

#### *K sensitivity*

It is likely that the carrying capacity of 1,151 females is dependent on the availability of resources and therefore not a universal value for all populations. To test the robustness of the biological conclusions of the Dickinson model, UOM's K parameter value was

increased from the base value of 1,151 to 2,000 and then in perturbations of 1,000 until 10,000.

## Varying the life history strategy

### *Life history parameters*

The OM was parameterised with the same values used in the Dickinson model. The life history trait parameters of this model, based on *R.sylvatica*, represent the life history strategy for short lived, early maturing amphibians with median clutch sizes. The life history trait values for two additional distinct species, *B.boreas* and *A.maculatum*, had been sourced from published data for Dickinson’s model (see Table 1). I leveraged on this information and used these values to parameterise the life history trait parameters of the model to represent long lived, late maturing amphibians with large and small clutch sizes respectively.

**Table 1: The life history trait parameters of the three distinct species and the minimum and maximum values used to define the parameter space.**

Life History Trait	Baseline value for <i>Rana sylvatica</i>	Baseline value for <i>Bufo boreas</i>	Baseline value for <i>Ambystoma maculatum</i>	Minimum value of parameter space	Maximum value of parameter space
Aquatic stage survival	0.17	0.24	0.28	0.1	0.9
Metamorph stage survival	0.38	0.32	0.44	0.1	0.9
Annual juvenile survival	0.22	0.28	0.64	0.1	0.9
Annual adult survival	0.41	0.55	0.73	0.1	0.9
Clutch size	1,162	9,591	172	100	10,000
Age at maturity	2	5	5	2	7

### *Life history trait analysis*

Elasticity and limitation analysis was conducted on the life history trait parameters of the model variants to determine the life history traits’ relative importance on extinction risk. The elasticity analysis was conducted by increasing each life history trait value by 5% in isolation and examining the proportional change in CPE. The limitation analysis was conducted by numerical perturbation of each life history trait value from the minimum and maximum value of its parameter space (see Table 1) and comparing the

proportional change in CPE. To independently understand the impact of the life history strategy from thermal performance characteristics, the model was parameterised for each of the three life history example species with a variety of thermal performance characteristics.

### Varying the thermal performance characteristics

#### *Thermal performance curve parameters*

Additional thermal performance data was obtained from published sources for two distinct amphibians: *B.boreas* with a broad thermal tolerance and a pipid frog *Xenopus tropicalis* with a narrow thermal tolerance (see Table 2). To estimate the current climate conditions for these two species, their geographical range within a 100km radius of each of the study sites was determined by using the IUCN shape files (IUCN 2012). The temperature and rainfall distribution for these geographical ranges were estimated from the Climate Research Unit TS 2.10 dataset (Mitchell et al. 2004) from 1961-1990 over the spring/summer months (March-August) using tcclim (<http://code.google.com/p/tcclim/>).

**Table 2: The thermal performance trait values of three species and the basic statistics of the corresponding temperature distributions.**

Species	Mean (°C)	SD (°C)	T <sub>opt</sub> (°C)	T <sub>opt</sub> (°C) source	CT <sub>max</sub> (°C)	CT <sub>min</sub> (°C)	CT <sub>max</sub> and CT <sub>min</sub> (°C) source
<i>Rana sylvatica</i>	15.3	2.9	19.0	Dickinson model/(Freidenburg & Skelly 2004)	33.6	<0	Dickinson model/(Brattstrom 1968; Costanzo & Lee 1994; Manis & Claussen 1986)
<i>Bufo boreas</i>	12.3	1.6	27	(Lillywhite et al. 1973)	38.1	-2	(Brattstrom 1968)
<i>Xenopus tropicalis</i>	25.1	1.4	25	(Herrel & Bonneaud 2012)	34	12	(Herrel & Bonneaud 2012)

#### *Thermal performance trait analysis*

The conclusions of Dickinson's linear model about thermal position and breadth on extinction risk were tested by parameterising the UOM with the thermal performance trait values of species with differing thermal performance characteristics. In my analysis I altered the breadth of the thermal performance curve by the warming tolerance (difference between CT<sub>max</sub> and mean annual temperature of the habitat) and the value

of  $s$ , the breadth of the curve below  $T_{opt}$  (see equation 2). To explore the impact of the thermal position on extinction risk the UOM was updated to be *X.tropicalis*' thermal position while the remaining parameters being based on *R.sylvatica*'s life history traits, climate distribution and thermal performances traits. The impact of narrower thermal breadth, and narrower thermal breadth with small thermal position on extinction risk was analysed similarly; refer to Table 3 for details of the thermal parameter changes. The impact of the alterations of the thermal performance characteristics on extinction risk was assessed by comparing the predicted change in extinction risk from current conditions and the temperature warming climate scenarios.

**Table 3: The thermal performance variations of the updated original model (UOM) to test the impact of thermal position and breadth on extinction risk.**

Model Name	Life history traits based on	Thermal Position (°C)	Warming Tolerance (°C)	$s$
UOM	<i>Rana sylvatica</i>	3.7	18.3	5.5
UOM with <i>Xenopus tropicalis</i> TP	<i>Rana sylvatica</i>	-0.1	18.3	5.5
UOM with <i>Xenopus tropicalis</i> $s$ and WT	<i>Rana sylvatica</i>	3.7	8.9	3
UOM with <i>Xenopus tropicalis</i> thermal	<i>Rana sylvatica</i>	-0.1	8.9	3

## Results

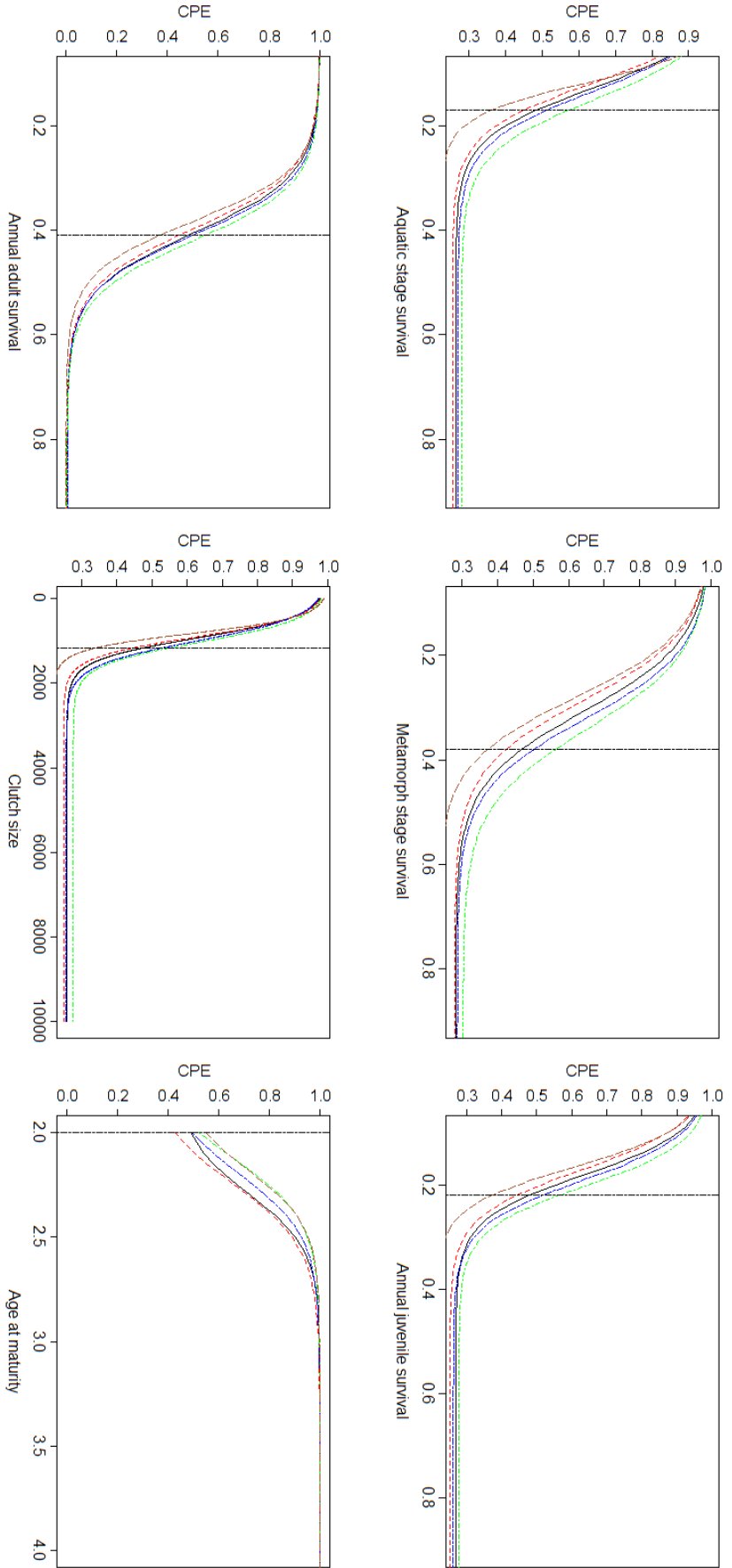
### Model modifications

#### *Threshold analysis*

The threshold values and number of relative performance bands used to segment the survival rate distributions did not affect the biological conclusions of the model. The estimated level of extinction risk altered for each variant of the model (see Fig. 2). However, the gradients of the relationship between CPE and the life history trait value were relatively consistent at the baseline values. The elasticity and limitation analysis showed that the annual adult survival rate and the age at maturity have the strongest effect on extinction across all climate scenarios (see Table 4). This result is in agreement with the conclusions by Dickinson (2012).

**Table 4: The life history traits that equate to the largest and second largest proportional change in cumulative extinction risk (CPE) under the elasticity and limitation analysis of the original model (OM) with varying thresholds.**

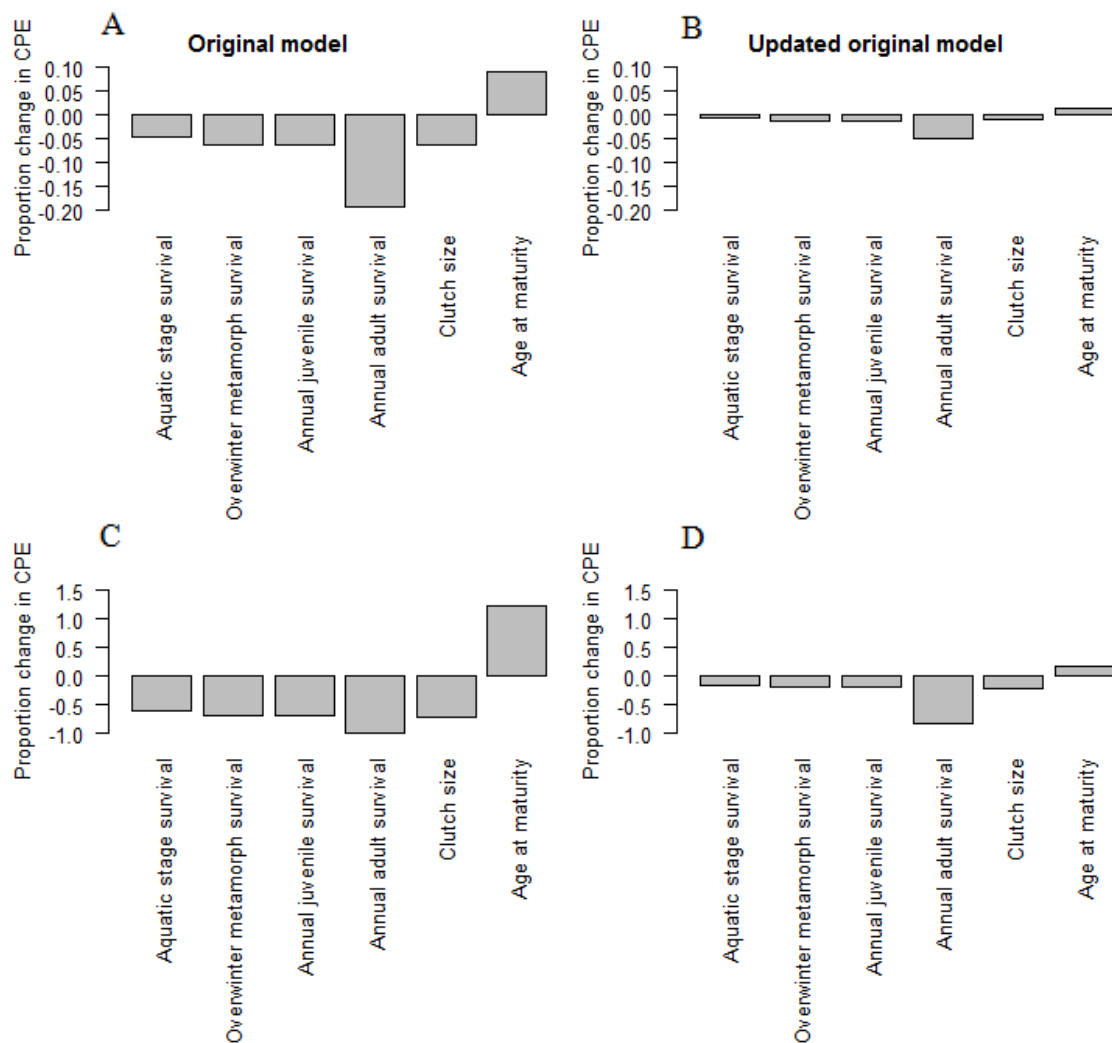
	<b>OM with thresholds 60/80</b>	<b>OM with thresholds 55/75</b>	<b>OM with thresholds 65/85</b>	<b>OM with thresholds 60/80/90</b>	<b>OM with thresholds 60/80/90/95</b>
<b>Most elastic life history parameter</b>	Annual adult survival	Annual adult survival	Annual adult survival	Annual adult survival	Annual adult survival
<b>Second most elastic life history parameter</b>	Age at maturity	Age at maturity	Age at maturity	Age at maturity	Age at maturity
<b>Life history parameter with the largest change in CPE for limitation analysis</b>	Age at maturity	Age at maturity	Age at maturity	Age at maturity	Age at maturity
<b>Life history parameter with the second largest change in CPE for limitation analysis</b>	Annual adult survival	Annual adult survival	Annual adult survival	Annual adult survival	Annual adult survival



**Fig. 2: The fitted curves of the cumulative extinction risk (CPE) values over each life history trait parameter space from models with varying thresholds (the current climate scenario). The solid black curve represents the fitted curve for the OM with thresholds 60% and 80%. The various coloured curves represent the fitted curves for the model variants with different thresholds. The vertical black dot-dash line represents the baseline value of each life history trait.**

*Correcting model parameter base values*

By using the UOM, with corrected values of  $K$  and  $CT_{max}$ , the calculated proportional change in extinction risk was reduced with the largest mean determined by the UOM being  $5.04\% \pm 1.04\%$  SD compared to  $19.13\% \pm 2.38\%$  SD for the OM. Nonetheless, the annual adult survival rate continued to have the largest effect on CPE for small changes in the trait value, as determined by elasticity analysis (see Fig. 3A and Fig. 3B). The impact of age at maturity on CPE reduced when using the UOM such that it was no longer strongly influential.



**Fig. 3: Comparison between the original model (OM) and the updated original model (UOM) of the life history parameters relative effects on the mean cumulative probability of extinction (CPE) across climate scenarios. (A) Elasticity analysis on the life history traits parameters of the OM. (B) Elasticity analysis on the life history traits parameters of the UOM (C) Limitation analysis on the life history traits parameters of the OM (D) Limitation analysis on the life history traits parameters of the UOM.**

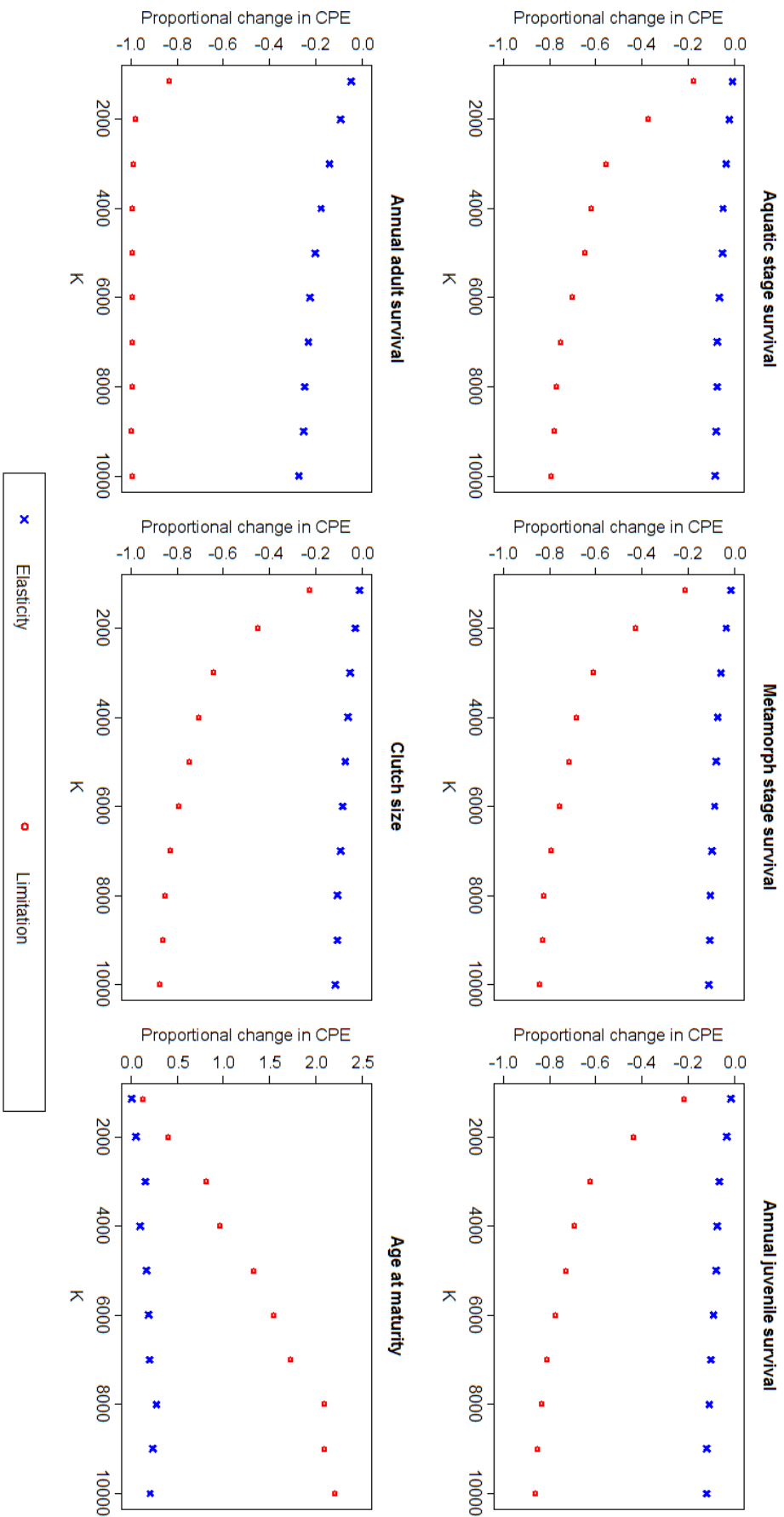


### *K sensitivity*

When the value of  $K$  was increased the proportional change in CPE increased in magnitude for both the elasticity and limitation analysis, remaining as a positive change for age at maturity and a negative change for the other life history traits (see Fig. 4). The model therefore predicts that small changes in life history traits will have a greater influence on the extinction risk for populations with larger carrying capacities.

By comparing the proportional change in CPE determined by elasticity analysis for each of the life history traits at specific value of  $K$ , the annual adult survival rate has the greatest impact on extinction risk for small changes in the trait value. For example for  $K=4,000$ , the mean proportional change in CPE across climate scenarios for aquatic stage survival is -4.91%, metamorph stage survival is -7.23%, annual juvenile survival rate is -7.37%, annual adult survival rate is -17.69%, clutch size is -6.10% and age at maturity is 9.90%. This conclusion is independent of the value of  $K$ .

By conducting similar comparisons, the limitation analysis shows that the age at maturity has the greatest impact on CPE for large changes in the trait value but only when  $K$  is greater than 4,000. For  $K$  values 4,000 and below the annual adult survival rate has the greatest impact on CPE for large changes in the trait value.

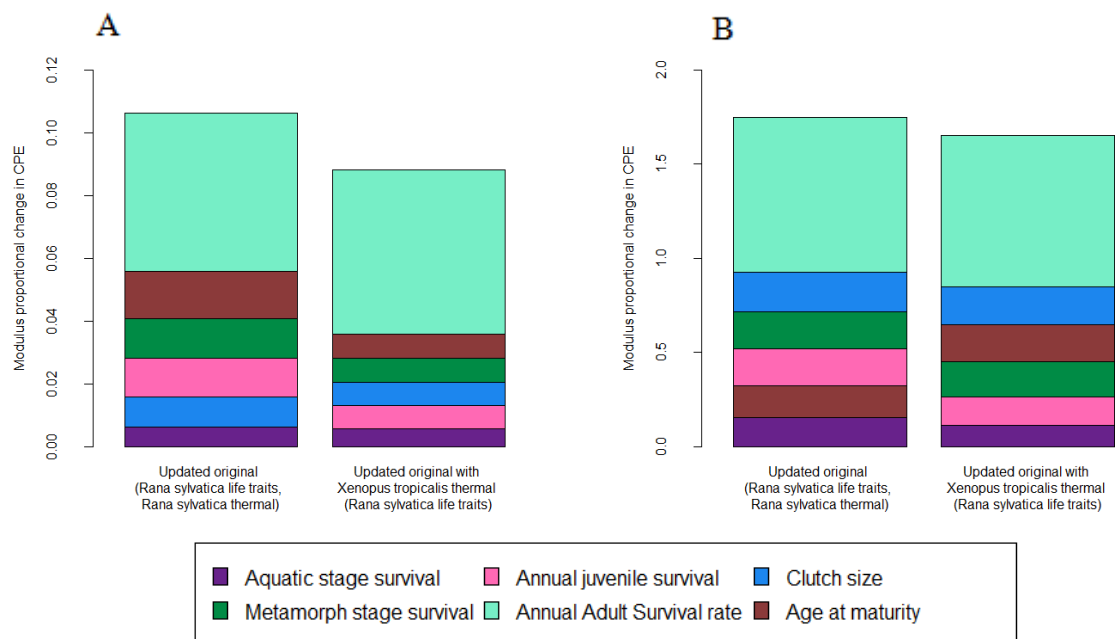


**Fig. 4: The mean proportional change in cumulative probability of extinction (CPE) across climate scenarios from the elasticity and limitation analysis over a varying carrying capacity value (K).**

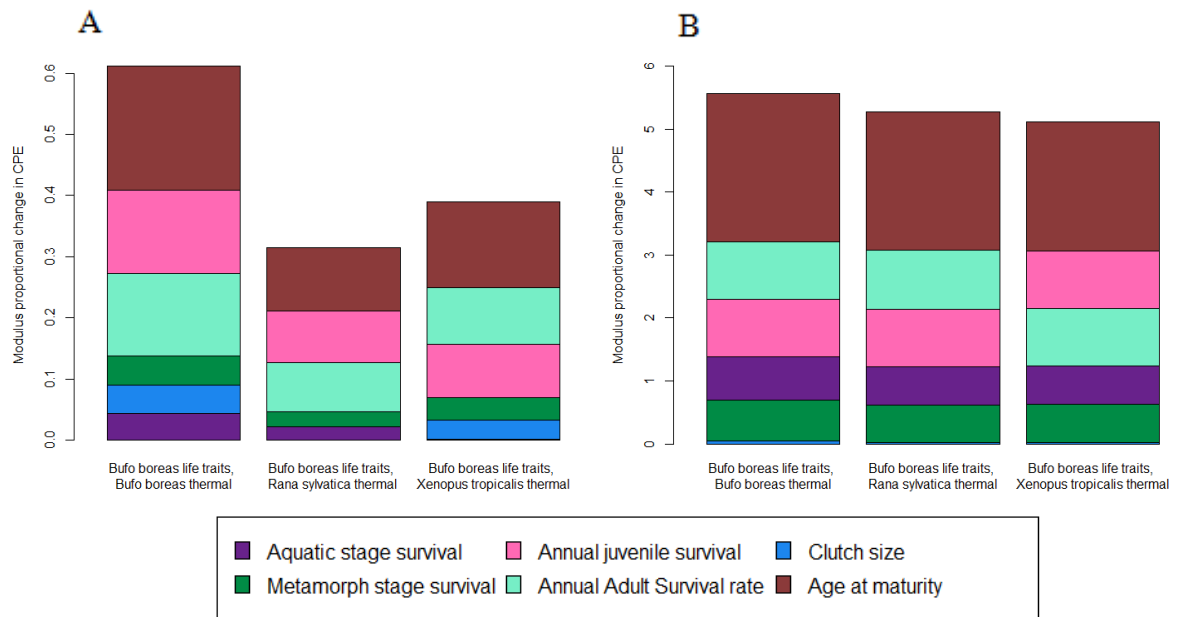
## Varying the life history strategy

Applying *X.tropicalis*' thermal performance characteristics to the UOM model (which was parameterised with *R.sylvatica*'s life history strategy) did not alter which life history traits largely impacted on CPE i.e. the annual adult survival rate (see Fig. 5). Similarly, applying different thermal performance characteristics to models parameterised with *B.boreas*' or *A.maculatum*'s life history strategy did not alter which life history traits largely impacted on CPE (see Fig. 6 and Fig. 7, respectively).

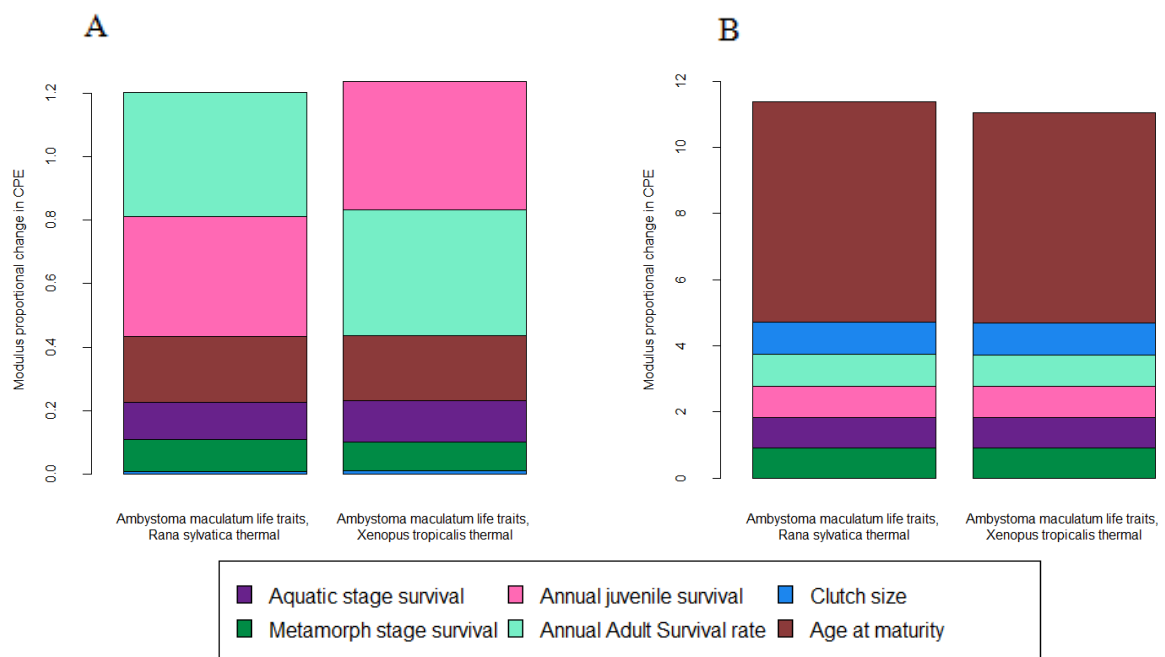
The age at maturity, annual juvenile survival rate, and annual adult survival rate had the greatest impact on extinction risk for the models parameterised with the life history trait values based on *B.boreas* and *A.maculatum* (see Fig. 6 and Fig. 7, respectively). This demonstrates the heightened importance of the annual juvenile survival rate on the extinction risk for long lived, late maturing species (*B.boreas* and *A.maculatum*) compared with the short lived, early maturing species (*R.sylvatica*, see Fig. 5 for the lower relative impact of annual juvenile survival rate).



**Fig. 5: The stacked ranked mean modulus value of the proportional change in cumulative probability of extinction (CPE) across climate scenarios for models parameterised with *Rana sylvatica* based life history trait values. (A) Elasticity analysis on the life history traits parameters on models parameterised with *Rana sylvatica* and *Xenopus tropicalis* based thermal performance traits. (B) Limitation analysis on the life history traits parameters on models parameterised with *Rana sylvatica* and *Xenopus tropicalis* based thermal performance traits.**



**Fig. 6: The stacked ranked mean modulus value of the proportional change in cumulative probability of extinction (CPE) across climate scenarios for models parameterised with *Bufo boreas* based life history trait values. (A) Elasticity analysis on the life history traits parameters on models parameterised with *Bufo boreas*, *Rana sylvatica* and *Xenopus tropicalis* based thermal performance traits. (B) Limitation analysis on the life history traits parameters on models parameterised with *Bufo boreas*, *Rana sylvatica* and *Xenopus tropicalis* based thermal performance traits.**



**Fig. 7: The stacked ranked mean modulus value of the proportional change in cumulative probability of extinction (CPE) across climate scenarios for models parameterised with *Ambystoma maculatum* based life history trait values. (A) Elasticity analysis on the life history traits parameters on models parameterised with *Rana sylvatica* and *Xenopus tropicalis* based thermal performance traits. (B) Limitation analysis on the life history traits parameters on models parameterised with *Rana sylvatica* and *Xenopus tropicalis* based thermal performance traits.**

Fig. 5, 6 and 7 demonstrate that changing the life history strategies used to parameterise the model produces a considerable change in the calculated impact that different life history traits have on CPE, as determined by elasticity and limitation analysis. For the UOM (parameterised with *R.sylvatica*'s life history traits, climate performance, and thermal performance), a 5% increase in the annual adult survival rate through elasticity analysis resulted in a mean proportional change of CPE of 5 % (mean 5.04 %  $\pm$  1.04 % SD) (see Fig. 5A). Whereas, when the model was parameterised with *A.maculatum*'s life history traits and *R.sylvatica*'s climate and thermal performance, elasticity analysis of the annual adult survival showed a mean proportional change of CPE of 39 % (mean 39.05 %  $\pm$  4.18 % SD) (see Fig. 7A).

The limitation analysis of life trait values also showed vast differences in the level of impact on extinction risk between life history strategies. The change from 0.1 to 0.9 in annual adult survival rate, for the UOM (parameterised with *R.sylvatica*'s life history traits, climate and thermal performance) produced the largest mean proportional change of 82% to CPE (see Fig. 5B) (mean 82.27%  $\pm$  1.46% SD). In comparison, the change of 2 to 7 in age of maturity for models parameterised with *B.boreas* and *A.maculatum*'s life history traits (with *R.sylvatica*'s climate and thermal performance parameters), brought their largest mean proportional changes of 220% and 666% to CPE respectively (see Fig. 6B and Fig. 7B) (*B.boreas* mean 219.71%  $\pm$  29.96% SD and *A.maculatum* mean 666.04%  $\pm$  110.50% SD).

### **Varying the thermal performance characteristics**

The UOM projected the level of extinction risk for the climate scenarios with increased mean temperatures is lower than the baseline risk of the scenario with current conditions (see Table 5 column (1), negative values). This is consistent with the results of the Dickinson model. When the thermal position of UOM was altered to be very low, such that the population's mean annual temperature almost equals  $T_{opt}$ , the relative level of extinction risk increased (see Table 5 column (2), negative values closer to zero than column (1)). This is contradictory to Dickinson's linear model conclusion that populations living in a habitat with a mean temperature below its  $T_{opt}$  have a greater risk of extinction.

The relative extinction risk is also slightly increased when the UOM’s thermal breadth is reduced (see Table 5 column (3), negative values closer to zero than column (1)). This is consistent with the conclusions from Dickinson’s linear model, that populations with a broader thermal performance breadth have a reduced risk of extinction.

The UOM with *Xenopus tropicalis* thermal is the combination of these two thermal characteristics changes. The combined result equates to an increase in baseline risk (see Table 5 column (4), positive values) which is larger than the sum of the two individual increases. Contrary to Dickinson’s conclusions this suggests that populations with narrow thermal performance breadths that live in a habitat with a mean temperature near  $T_{opt}$ , are at greater extinction risk than populations that have a broad thermal performance breadth and are living in a habitat with a mean temperature below  $T_{opt}$ .

**Table 5: The change in extinction risk from the baseline current conditions to the warming climate scenarios for the thermal performance variations of the updated original model (UOM).**

Climate scenario	UOM (1)	UOM with <i>Xenopus tropicalis</i> TP (2)	UUOM with <i>Xenopus tropicalis</i> s and WT (3)	UOM with <i>Xenopus tropicalis</i> thermal (4)
1°C increase to mean temperature with current drought frequency	-5.40%	-2.09%	-4.17%	0.47%
2°C increase to mean temperature with current drought frequency	-7.88%	-1.77%	-7.51%	5.51%

## Discussion

The variation in biological traits had a strong effect on climate change extinction risk in the simulations. There are specific biological traits and trait combinations that showed an increase risk for extinction from climate change. These traits include low later stage survival, late age of first reproduction, small clutch sizes, and living close to optimal performance temperature with narrow thermal tolerance.

The impact of trait variation on extinction risk differed among traits and between different life history strategies. Variation in the annual adult and juvenile survival rates and in the age at sexual maturity had the largest effects on extinction risk. A small increase in the annual adult survival rate peaked beyond 7 fold in its reduction of extinction risk. This emphasizes the need for conservation efforts to concentrate on the adult and juvenile stages supplementing Vonesh & De la Cruz (2002) call for the focus of efforts to explain amphibian declines to be on the later life stages. The juvenile survival rate was predicted to be less important in short lived, early maturing species. This is a rational dissimilarity because of the shorter length of time in the juvenile stage.

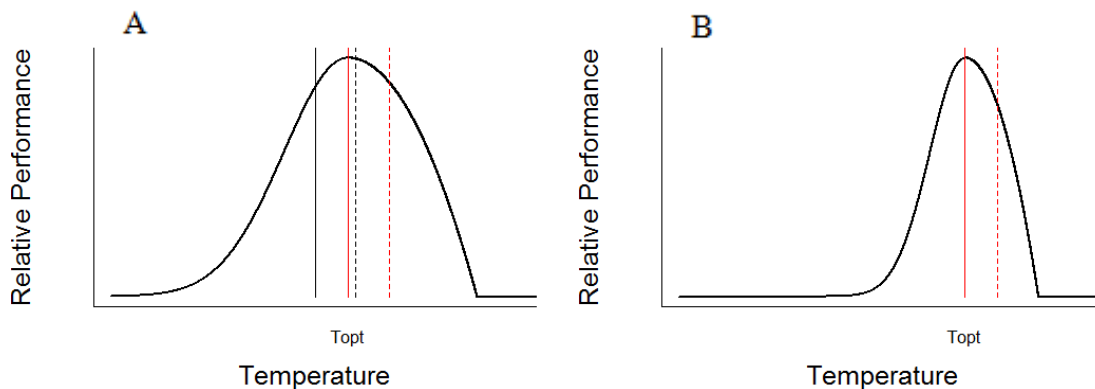
The changes to extinction risk from variation in trait values were greater for the long lived, late maturing species with small clutch sizes compared with long lived, late maturing species with large clutch sizes across all life history traits. The initial smaller number of eggs produced by each breeding attempt intensifies the effects of changes to the vital rates in the model. This suggests that species that have small clutch sizes are more vulnerable to climate change as vital rate changes are a likely consequence of climate change (Grafe et al. 2004; Pounds et al. 2006).

Low predicted extinction risk was associated with high adult and juvenile survival and early age at first reproduction. However, this combination of traits is unlikely to occur as amphibian species with high terrestrial survival usually display slow sexual development (Duellman and Trueb 1994). The short lived, early maturing species with median clutch sizes displayed slightly higher extinction risk than the long lived, late maturing species with large clutch sizes. To determine the trade-off of lower adult and juvenile survival to later age at first reproduction on extinction risk, future work could model a long lived, late maturing species with median clutch sizes to compare the extinction risk with a short lived, early maturing species.

The number and level of thresholds applied to segment the survival distribution, did not change the biological conclusions. Thus, the testing of this aspect of the Dickinson model methodology displayed satisfactory robustness.

The model predicted that populations with higher carrying capacities are more responsive to changes in their life history trait values. This is likely due to the higher carrying capacity imposing less pressure on the population numbers and therefore, the full extent of the change in the life history trait is realised.

The model also predicts that thermal performance characteristics of species alter the climate change extinction risk. Under climate warming scenarios, species living in a habitat with mean temperature at  $T_{opt}$  are predicted to be at increased extinction risk compared to those living below  $T_{opt}$ . To rationalise this contrary prediction to Dickinson, Fig. 8A depicts the change of the mean temperatures relative to the thermal performance curve for a given increase of mean temperature. The population currently living at  $T_{opt}$  (see Fig. 8A current mean at solid red line) will have a mean temperature hotter than  $T_{opt}$  after climate warming (see Fig. 8A dashed red line) whereas the population currently living below  $T_{opt}$  (see Fig. 8A current mean at solid black line) will have a mean temperature closer to  $T_{opt}$  (see Fig. 8A dashed black line). Therefore the model's conclusion follows theoretically, as any warming will cause the population living currently at  $T_{opt}$  to be further to right of  $T_{opt}$  and therefore have a lower mean performance. This is consistent with Deutsch et al.'s (2008) study which expresses damaging consequences from climate change for insect species living near their  $T_{opt}$ .



**Fig. 8: The change of the mean temperatures relative to thermal performance curve for a given increase of mean temperature.** The solid lines indicating the current mean temperature and the dashed lines indicated the new warmer mean temperature. (A) Comparison of change in mean temperature relative to the thermal performance curve for species currently living below  $T_{opt}$  (black lines) to species currently living at  $T_{opt}$  (red lines). (B) A species currently living at  $T_{opt}$  with a narrow thermal performance curve.



The model predicts species with broader thermal performance curves to have lower climate change extinction risk than species with narrow thermal tolerances which is in line with recent studies by Calosi et al. (2008) and Tewksbury et al. (2008).

Species possessing the two vulnerable thermal performance traits, of living in a habitat with mean temperature at  $T_{opt}$  and having narrow thermal tolerances, are predicted to be at greater extinction risk than the aggregate risks of each trait. The reduction in mean performance for species currently living at  $T_{opt}$ , caused by the increase of mean temperature, is exaggerated by the sharper drop in performance of the narrow thermal performance curve (see Fig. 8B and compare drop in performance of species represented with red lines in Fig. 8A). These two thermal performance traits are typical of low-altitude tropical species (Deutsch et al. 2008; Ghalambor et al. 2006; Huey et al. 2009). With high projected land use change being concentrated in the tropics (Hof et al. 2011), these species are likely to be confronted with a synergy of threats.

The models used here did not include any evolution with the thermal tolerance curves remaining static throughout the projection. Future work could develop the model further to incorporate the potential for modifying species' thermal tolerance. This addition is likely to compound the extinction risk for tropical species due to associated poor acclimatory ability (Calosi et al. 2008) and low potential for desiccation tolerance adaption (Hoffmann et al. 2003) and so has merit for future investigation.

## **Conclusions**

In this paper, I have demonstrated that variations in biological traits have a strong impact on climate change extinction risk. I conducted an investigation on the impact of variation of life history and thermal performance traits on climate change extinction risks for amphibians by analysing simulated population abundances under differing parameters. The later life stages' survival rates and age at sexual maturity showed the strongest effects on extinction risk. Elevated climate change extinction risks are predicted to be associated with low adult and juvenile survival and late age at first reproduction. The model predicts that species currently living close to their optimal performance temperature with narrow thermal tolerances are vulnerable to warming temperatures.

My results indicate that variations in biological traits are a key factor influencing species vulnerability to climate change, consistent with work by Dickenson (2012). As a consequence, I believe that predictions on species extinction risk that ignore the underlying biology have the potential to mislead conservation prioritisation. These findings give further justification for the need to develop a new approach to assessing climate change extinction risk that integrates species' biology.

## **Acknowledgements**

I would like to show my gratitude to my supervisor, Prof. Georgina Mace for your enthusiasm and initial ideas for the project, and your guidance throughout it. I would also like to thank Maria Dickinson for her patience in her explanations of her work and always making time for my questions. Finally, I would like to thank my fiancé, Adrian, and both our families for your encouragement and financial support for me to go back to study.

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## Appendix

### Extract from Dickinson (2012) ‘Climate change impacts on species: a trait-based approach’, methods section of chapter 4

#### METHODS

##### *Life history parameters and the model matrix*

I developed a stage-based stochastic matrix model with a time step of one year to describe the life cycle of a typical amphibian (see Figure 4.1) based on that of Vonesh and De la Cruz (2002). Egg, tadpole and metamorph stages occur within one year, but juvenile and adult survival are usually estimated annually. Therefore, the life cycle was collapsed to two stages, adults and juveniles, and premetamorph and metamorph survival rates included within fecundity. Only females were included in the model, as males can fertilise multiple females in a breeding season so are unlikely to be limiting to population growth (Harper et al. 2008).

The model thus takes the general form:

$$\begin{pmatrix} J \\ A \end{pmatrix}_{N_{t+1}} = \begin{pmatrix} \text{Juvenile to juvenile} & \text{Fecundity * adult survival} \\ \text{Juvenile to adult} & \text{Adult survival} \end{pmatrix} * \begin{pmatrix} J \\ A \end{pmatrix}$$

and population growth is modelled by the resulting Leftkovich matrix:

$$\begin{pmatrix} J \\ A \end{pmatrix}_{N_{t+1}} = \begin{pmatrix} \left( \frac{1 - \sigma j^{(1-d)}}{1 - \sigma j^d} \right) * \sigma j & \frac{c * \sigma p * \sigma m *}{\sigma a * p * s} \\ \left( \frac{\sigma j^d (1 - \sigma j)}{1 - \sigma j^d} \right) & \sigma a \end{pmatrix} * \begin{pmatrix} J \\ A \end{pmatrix}$$

where the matrix element for fecundity was calculated as the product of premetamorph ( $\sigma p$ ) and metamorph survival rates ( $\sigma m$ ), clutch size ( $c$ ), proportion of females breeding in a given season ( $p$ ) and the population sex ratio ( $s$ , to exclude males, assumed to be 1:1). As the model is a post-breeding model, individuals must survive to the next time step in order to reproduce, so adult survival ( $\sigma j$ ) is included within the matrix element

for fecundity. Matrix elements giving the probabilities of a juvenile remaining in that stage or maturing to adult stages were derived from the annual juvenile survival rate ( $\sigma_j$ ) and the number of years spent as a juvenile ( $d$ ), following (Crouse et al. 1987). Means and standard deviations for the above vital rates were obtained from the literature (see Table 4.1 for values of vital rates and Appendix 3, Part 1 for details of their derivation).

To place a realistic cap on population size I applied a simple ceiling model of density dependence in the terrestrial stages: where population size at a given time step exceeded carrying capacity ( $K$ ), adult abundance was reduced to  $K$  and juvenile abundance reduced by the same proportion. Density dependence was assumed to affect adults and juveniles equally, as they generally use similar resources and are subject to similar predation and desiccation risks (Duellman and Trueb 1994).

I generated stochastic simulations of climate change over a 50 year period. Simulated values of temperature and rainfall were used to describe each year as one of six environmental states: three temperature states, optimal temperature, suboptimal temperature and extreme temperature, and two rainfall states, drought or non-drought conditions. Six different Leftkovich matrices determined population growth under each of these environmental states. the sampled climate values for each time step dictated which matrix was applied in simulating population growth.

**Table 4.1: Vital rate estimates applied in the stochastic matrix model: (A) for the typical amphibian *Rana sylvatica* and the range of values over which the mean traits values were varied; and (B) for the species used in limitation analysis.**

A				
Parameter	Mean	SD	Source	Range
Aquatic survival*	0.17		(Berven 1990)	0.1-0.9
Metamorph survival	0.38	0.12	(Berven 1990)	0.1-0.9
Juvenile survival	0.22	0.08	(Berven 1990)	0.1-0.9
Adult survival	0.41	0.06	(Bastien and Leclaire Jr. 1992, Berven 2009)	0.1-0.9
Clutch size**	1162	-	(Berven 1982a, Stebbins 1951)	100-10,000
Age at first breeding (years)	2	-	(Berven 2009, Berven 1982a)	2-7
$K$	4500	-	(Berven 2009)	-
Drought frequency	1 in 5 years		(Berven 2009)	Up to +20% frequency
Mean temperature	15.27	2.91		Up to +2°C/
$T_{opt}$ (°C)	19.00	-	(Freidenburg and Skelly 2004)	±25%



<i>CTmax</i> (°C)	34.80	-	(Brattstrom 1963)	±25%
<i>CTmin</i> (°C)	<0	-	(Costanzo 1994,Manis and Claussen 1986)	±25%

## B

Species	Parameter	Mean	SD	Source
<i>Bufo boreas</i>				
	Aquatic survival*	0.24	-	(Brockelman 1969)a
	Metamorph survival	0.32	0.08	(Clarke 1977)b
	Juvenile survival	0.28	0.04	(Clarke 1977)b
	Adult survival	0.55	0.07	(Fretey et al. 2004)
	Clutch size**	9591	-	(Carey et al. 2002,Samollow 1980)
	Age at first reproduction	5	-	(Carey et al. 2002)
<i>Ambystoma maculatum</i>				
	Aquatic survival*	0.28	-	(Petranka 1989,Shoop 1974)
	Metamorph survival	0.44	0.11	(Russell et al. 1996)c
	Juvenile survival	0.64	0.03	(Russell et al. 1996)c
	Adult survival	0.73	0.02	(Blackwell et al. 2004,Madison 1997,Whitford and Vinegar 1966)
	Clutch size**	172	-	(Howard and Wallace 1985,Shoop 1974)
	Age at first reproduction	5	-	(Flageole and Leclair Jr 1992,Wilbur 1977a)

*a Bufo americanus*

*b Bufo woodhousei*

*c Ambystoma macrodactylum*

\*Aquatic stage survival was modelled as a fixed value, as the variation in survival rate was determined in the model by drought or non-drought conditions, with survival in drought conditions being 0.

\*\*Clutch size was modelled as a fixed value, as the factors determining clutch size are often dependent on individual body condition, which depends on a number of factors such as such as age and whether the individual bred in the previous year (Reading 1998,Reading and Clarke 1995).

### *Climate parameters and climate change simulations*

Means and standard deviations for baseline (1961-1990) temperature and rainfall were obtained from the Climate Research Unit TS 2.10 dataset (Mitchell et al. 2004) using *tcclim* (<http://code.google.com/p/tcclim>). I used values for parts of *R. sylvatica*'s geographic range (using polygons shapefiles obtained from IUCN)(IUCN 2009) within a 100km radius of the study sites used to derive that species' vital rates (see Table 4.1 for climate parameter values). Only values for spring/summer months (March-August) were used, as many species are not active over winter (Duellman and Trueb 1994).

Climate change predictions are spatially explicit, meaning that the predicted climate change at a given location is unlikely to be representative of the nature and extent of anticipated global climate change. Rather than applying the change predicted across the geographic range of a particular species, I applied two temperature change scenarios (+1°C and +2°C), two rainfall change scenarios with changing drought frequency rather than rainfall amount (+10% and +20% drought frequency) (Stevens and Baguette 2008) and two combined temperature and rainfall change scenarios (1°C and +10% drought frequency; 2°C and +20% drought frequency) intended to broadly encompass global climate change likely to be experienced by the majority of terrestrial species based on the ensemble forecasts from the IPCC's Fourth Assessment Report (IPCC 2007).

Mean temperature and drought frequency were changed incrementally at each time step between current climate and future climate. The changing value of mean temperature at each time step was used to generate a normal distribution from which a value of temperature for that time step was sampled. Rainfall at each time step was sampled from a truncated normal distribution (bounded at 0 to prevent negative values of rainfall) based on mean and standard deviation of baseline climate. The quantile of the rainfall distribution determining whether the sampled value represented drought conditions was changed incrementally, resulting in changes to drought frequency. Sampling from temperature and rainfall distributions was weighted at each time step such that years with above average temperature or rainfall were more likely to be followed by above average years. Cycles lasted on average every 7 time steps, simulating the autocorrelation in climate that is caused by oscillations such as the North Atlantic Oscillation and El Niño.

#### *Climate dependence of life history traits and generating Leftkovich matrices*

There were two layers of life-stage specific climate dependence built into the model: drought effects on aquatic (egg and larval) stages and temperature effects on terrestrial (metamorph, juvenile and adult) stages. Six Leftkovich matrices corresponding to the six environmental states reflect these dependencies.

Based on observed zero survival in low rainfall years (Banks and Beebee 1988, Berven 2009, Carey et al. 2002), drought was assumed to inflict catastrophic mortality on

aquatic stages. I applied a very simple binary model of rainfall dependence of aquatic stage survival to reflect this. Each year was described as a drought or non-drought year based on the sampled value of rainfall and the expected drought frequency for that time step. Survival was zero in years where drought occurred and was equal to the maximum value reported, assumed to be the survival rate in the absence of predation, in non-drought years.

Temperature was assumed to affect survival rates only in terrestrial stages. Parameters for these effects were derived from three sources: (i) mean and variation in terrestrial survival rates; (i) mean and variation in current climate; and (ii) thermal performance curves, which described the relationship between temperature and performance; these were used to link together the distributions of terrestrial survival rates and current climate to generate values for use in Leftkovich matrices.

Means and standard deviations for terrestrial survival rates (see Table 4.1 for values and data sources) were used to generate survival rate distributions. Survival rates were bounded by 0 and 1 using a truncated normal distribution, the exact shape of which could vary depending on its mean (mean values near 0 yielded a different distribution from mean values near 1).

Means and standard deviations for current temperature and rainfall were used to generate distributions of each parameters under baseline climate conditions, applying normal and truncated normal distributions to temperature and rainfall respectively, as described above.

Thermal performance curves were used to define temperatures that represent optimal, suboptimal and extreme conditions with respect to organism performance. Curves are laboratory-derived measures of the dependence of a given activity (e.g. locomotion, jumping or digestion) on temperature. They define the range of temperatures over which performance of activities directly relevant to survival in the wild is possible, with direct consequences for survival rates (Huey and Stevenson 1979). the exact function used to describe the relationship between performance and temperature varies, but is generally agreed that to be asymmetric (Angilletta et al. 2002,Huey and Stevenson 1979,Navas et al. 2008). Performance is zero at the critical minimum temperature ( $CT_{min}$ ) and increases gradually as temperature approaches the optimum ( $T_{opt}$ ). Above  $T_{opt}$ , performance

declines sharply to zero at a critical maximum temperature ( $CT_{max}$ ). Values of  $CT_{max}$ ,  $CT_{min}$  and  $T_{opt}$  were taken from the literature and were based on *R. sylvatica* (see Table 4.1). I followed Deutsch et al. (2008) and applied the following function for performance at a given temperature  $P(T)$ :

Equation 4.1:

$$P(T) = \begin{cases} \exp\left\{-\left(\frac{T - T_{opt}}{2s}\right)^2\right\}, & T \leq T_{opt} \\ 1 - \left(\frac{T - T_{opt}}{T_{opt} - CT_{max}}\right)^2, & T > T_{opt} \end{cases}$$

Where:

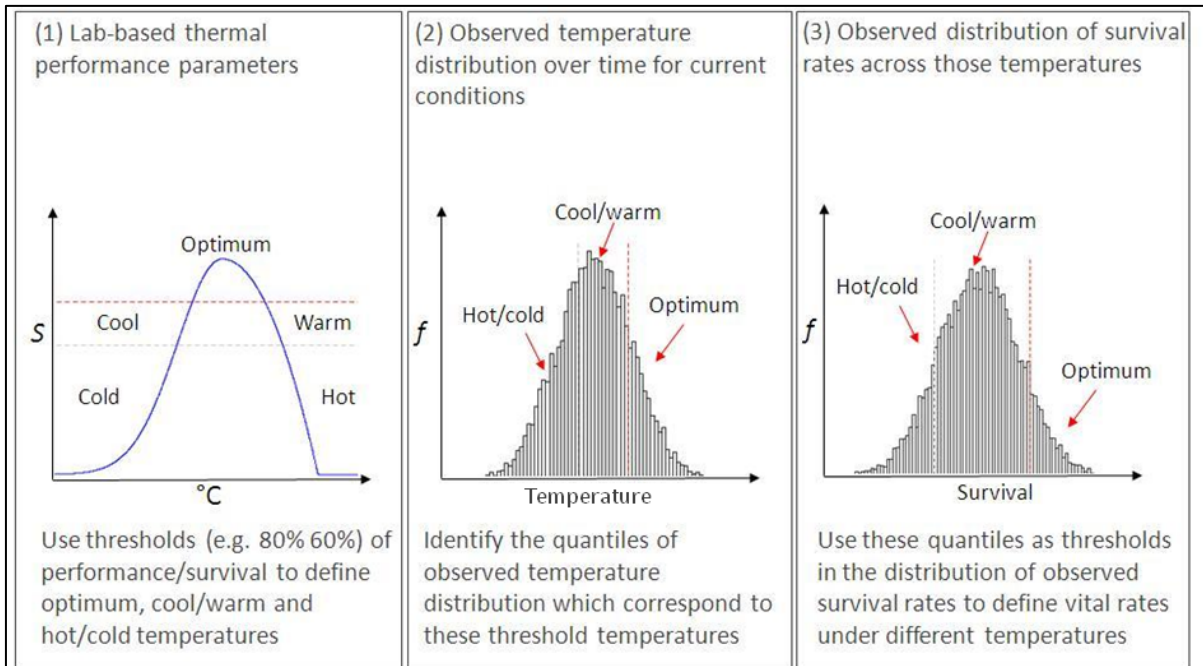
$T$  is the continuous variable, temperature;

$T_{opt}$  is the optimum or preferred temperature;

$s$  dictates the breadth of the thermal performance curve at temperatures below  $T_{opt}$ , indirectly determining  $CT_{min}$ ; and

$CT_{max}$  is the upper critical temperature at which performance is 0.

The thermal performance curve was used to define optimal, suboptimal and extreme temperatures by applying two thresholds of performance. Optimal temperatures were defined as those leading to performance within 80% of maximal performance at  $T_{opt}$  (the 80% performance breadth or B80) (Angilletta et al. 2002). Outside of this region, suboptimal temperatures lead to performance within 60% of maximal performance (B60). Extreme temperatures lead to performance of less than 60% of maximal performance.



**Figure 4.2 Temperature dependence of survival rates.** (1) The thermal performance curve was used to define optimum (> dashed red line), cool/warm (>dashed grey line but < dashed blue line) and hot/cold (< dashed grey line) conditions. (2) The quantiles of the distribution of current temperatures corresponding to each of the three temperature ranges, optimum, cool/warm, hot/cold were determined. (3) These quantiles were applied to the distribution of survival rates. Mean values for the three divisions of the survival rate distribution were used as the survival rate for the three temperature states.

The highest values in the distribution of survival rates were assumed to occur in optimal temperature conditions, the lowest values in extreme conditions and intermediate values in suboptimal conditions. the frequency with which optimal, suboptimal and extreme conditions occur in the baseline temperature distribution was used to define quantiles of the distribution of survival rates corresponding to survival in each of these temperature states, i.e. if 30% of baseline temperature values were within the optimal range of temperatures, the highest 30% of values in a survival rate distribution was assumed to correspond to survival under optimal conditions and the mean of those values used as the survival rate for that state; if 10% of the values for baseline temperature were within the extreme range of temperatures, the mean of the lowest 10% of values in a survival rate was used as the survival rate under extreme temperatures; remaining intermediate survival rate values were assumed to correspond to survival in suboptimal conditions (see Figure 4.2).

Variability in extinction risk under different model parameterisations was assessed as the effect on the cumulative probability of extinction (CPE, proportion of simulations in which the population was extinct by the final time step) based on 1000 model runs. a population was deemed extinct if the number of adults fell below a quasi-extinction threshold, set at 100 individuals, to avoid the need to account for demographic stochasticity. Quasi extinction was based on adults only as juvenile abundance was highly stochastic and published measures of abundance on which  $K$  was set were based on adults. Each simulation was run for an initial 20 years with current climate to generate a realistic starting age distribution and population size, with climate change being simulated for a further 50 years.

#### *Life history traits*

I applied two types of analysis to explore the relative effect of life history traits on extinction risk, elasticity analysis (Caswell 2001) and limitation analysis (Schmitt et al. 1999). Elasticity analysis assesses the effect of small perturbations in a life history parameter on the measure of interest, in this case cumulative probability of extinction, or CPE. Limitation analysis explores the effects of larger perturbations on CPE. Each of these analyses was applied to age-specific survival rates, clutch size and age at first reproduction.

Life history trait values were derived from studies of populations in different time periods and locations and determined using different methods. It is therefore uncertain to what extent the variability for individual vital rates represents sampling error or spatial rather than temporal variation in vital rates. To assess the robustness of results to potential error in estimates of vital rates, elasticities and limitations were recalculated with the value of individual life history traits increased by one standard deviation above the baseline values.

#### *Elasticity analysis*

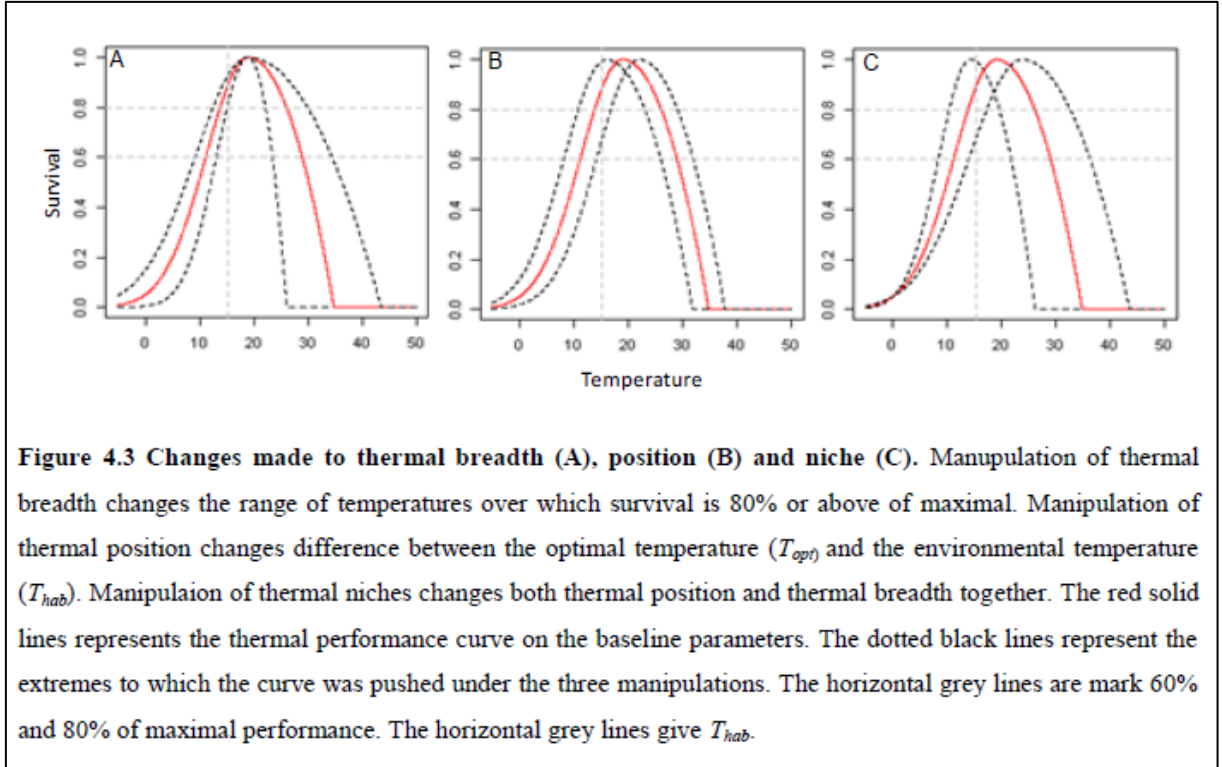
For the elasticity analysis, I examined the effect of a 5% increase in each life history trait in CPE. I also examined the level of variation in elasticity (expressed as the coefficient of variation to remove scaling) across climate change scenarios to identify traits that varied to a greater degree in their effect with climate change as these may also be traits important in predicting risk.

### *Limitation analysis*

The relative importance of a trait in predicting risk depends not only on the effect of changes to that trait, but also on the range of variation in that trait. If changing a trait has a large effect on extinction risk but inter-specific variation for that trait is low, it is of little use in identifying species sensitive to climate change. To explore the effect of larger perturbations I carried out limitation analysis within the parameter space of amphibian life history variation defined by the three example species (Schmitt et al. 1999). I applied a separate limitation analysis, quantifying the amount of change in each life history parameter required to increase extinction risk by 50% to explore the effect of changes outside the parameter space defined by the three example species.

### *Thermal performance traits*

The effect of temperature on survival within the model depends on both the breadth of the thermal performance curve (measured as the range of temperatures within B80) and on the thermal position (the difference between  $T_{opt}$  and environmental temperature). I varied both of these factors individually and together (for parameter values see Table 4.1; for an illustration of the perturbations, see Figure 4.3). I applied elasticity analysis to each of thermal breadth, thermal position and thermal niche (breadth and position combined). It was not possible to conduct a limitation analysis, as interspecific differences in the thermal performance curve depend not only on the parameter values for that curve, but also the environmental temperature of the species in question. I therefore varied the breadth and position of the thermal performance curve over a range of parameter values intended to represent realistic thermal performance curves (Brattstrom 1963).



Although preliminary testing (see Appendix 3, Part 2) suggested that 1000 runs was an appropriate number, elasticities and limitations calculated from the raw CPE values for initial testing runs were affected by variation in extinction risk due to the stochasticity in the model. Outputs from the final runs were therefore used to parameterise models of CPE as a function of parameter values and the fitted values from these models used to calculate elasticities and limitations.

For each life history trait, the CPE from simulations was fitted as logistic function of life history trait value (see Equation 4.2 and Figure 4.4) (Pinheiro and Bates 2000).

Equation 4.2:

$$CPE = minR + \frac{1 - minR}{1 + \exp\left[\frac{midR - x}{scale}\right]}$$

Where:

$x$  is the value of the life history parameter;

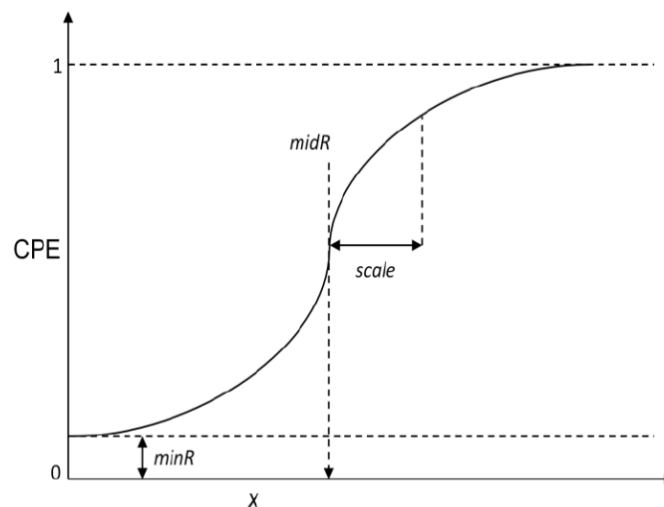
$minR$  is the value of the horizontal asymptote at low levels of risk;



$midR$  is the value of  $x$  at which CPE is halfway between  $minR$  and 1 and is the inflection point of the logistic curve; and

$scale$  is equal to the change needed in  $x$  to move three quarters of the distance from  $minR$  to 1.

A logistic model was chosen as preliminary runs indicated a logistic form of the relationship between parameter value and CPE, but also because the model conceptually captures the relationship between risk and parameter value. Risk asymptotes at a maximum value of 1 where all populations go extinct. the value of the lower asymptote of risk ( $minR$ ) is not necessarily 0, as some life history traits, even at their most extreme values, may not be sufficient to permit persistence of all populations. the  $scale$  parameter varies depending on the strength of the relationship between parameter value and extinction risk. Preliminary runs indicated that the relationship between thermal performance parameters and CPE was generally



**Figure 4.4 Four parameter logistic model describing the relationship between cumulative risk of extinction (CPE) and parameter values**, adapted from (Pinheiro and Bates 2000).  $MinR$  is the value of the horizontal asymptote at low levels of risk.  $MidR$  is the value of parameter where CPE is halfway between  $minR$  and the maximum level of extinction risk (always 1 for 100% extinction). It is the turning point between high risk and low risk parts of the curve.  $Scale$  is a measure of the slope of the relationship and is equal to the change needed in  $x$ , the value of life history parameter, to move three quarters of the distance from  $minR$  to 1. Values of  $scale > 0$  give increasing risk with increasing parameter values; values of  $scale < 0$  give decreasing risk with increasing value of parameter, the value of the life history trait.

described by a linear additive model (ANCOVA) with CPE as a function of thermal parameter values and scenario. There was some evidence of non-linearity in the relationship of extinction risk with both thermal position and thermal niche, but see Appendix 3, Part 3 for shape of curves and reasons for applying linear model.