Spatial and demographic consequences of genotypic and thermosensitive sex determination in stable and changing climates

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Abstract

For many species of reptile, crucial demographic parameters such as juvenile survival and individual sex (male or female) depend on ambient temperature. This suggests that population persistence and, hence, geographic range could be determined by local climate and be strongly impacted by climate change. Unfortunately we know little about these factors empirically or how they might interact in continuous populations with or without dispersal. Furthermore, although not temperature linked, the adult sex ratio may influence female fecundity through the effects of the strength of male limitation and, hence, population persistence. This thesis has been a first step in quantifying the relative importance of juvenile survival, juvenile sex ratio, male limitation and dispersal in determining reptile population persistence, range limits and range change in stable and warming climates using plausible and testable models.

Recent models of climate warming have predicted major consequences (local population extinctions) for populations with temperature-dependent sex determination (TSD) arising from biased juvenile sex ratios. In many TSD reptiles females are produced at warmer temperatures and increasingly feminised populations are occurring. Juvenile survival may also be affected by temperature, because eggs successfully incubate only at certain temperatures. In Chapter 2, the population dynamics of theoretical female-biased populations of reptiles with TSD were compared to populations with genotypic sex determination (GSD) using an analytical approach. The effects of climate (ambient air temperature) on juvenile survival, juvenile sex ratio and male limitation on population size and persistence were evaluated in populations of females. A population growth equation was used to estimate population sizes of females in ecological equilibrium, along three gradients of stable environmental temperatures (i.e. 16 – 31^{o}C, 18 – 33^{o}C and 20 – 35^{o}C). Included in the equation were cohort

sex ratios (CSR) response curves (to model skews in the sex ratio) and ‘normal’ (wider) and ‘left-skew’ (narrower) curves to model temperature-dependent embryonic survival. There were three levels of male limitation: none, moderate and strong.

Warmer climates producing female-biased sex ratios in populations of reptiles with TSD resulted in larger effective population sizes of females in the short-term. However, reduced fecundity in female-biased populations when fecundity was limited by the abundance of males resulted in smaller population sizes and reduced population persistence across a narrower range of temperatures. The effects of the moderate and stronger levels of male limitation were qualitatively similar, except that the stronger level resulted in greater reductions in population sizes. The shape of the temperature–dependent juvenile survival curve influenced the number of surviving TSD and populations of reptiles with GSD, and the wider curve resulted in greater population persistence. For populations of reptiles with TSD, despite short-term increases in population sizes in female-biased populations the decrease in males and reduction in juvenile survival as a result of climate warming are likely to offset any short-term gains.

Reptiles with limited climatic range, or not able to change their range are at risk of population declines from climate warming. Species located at range edges live closer to their physiological limits and experience greater stress than those located towards the centre of their ranges. Male-biased dispersal is thought to be the main dispersal tendency in reptiles. As climates warm, if populations become increasingly female-biased recruitment of male hatchlings through dispersal may facilitate population persistence at range edges. In Chapter 3, population persistence in reptiles in a stable climate (temperature gradient 18 – 33^{o}C) was explored further with the introduction of dispersal. The role of dispersal in determining population persistence and range limits was explored extensively in continuous populations of males and females.

A matrix of 10,000 populations were distributed along a temperature gradient (100 temperatures, the columns of the matrix), and replicated with 100 populations per temperature (the rows of the matrix). A simulation model was developed that incorporated both demographic (Chapter 2) and dispersal models. The dispersal model was a probability density function based on a fat-tailed dispersal kernel including three levels of dispersal (none, small and large). There were four dispersal tendencies (none, male, female and both sexes). Simulations proceeded in 1000 discrete time steps (years), and there were 10 replicates for each combination of TSD and, separately GSD with each dispersal level and tendency.

Dispersal tendency was found to be more influential in determining population persistence and range limits in TSD than in populations of reptiles with GSD. Populations of reptiles with GSD were more influenced by temperature-dependent embryonic survival. Hence, populations of reptiles with TSD were able to persist beyond the limits of populations of reptiles with GSD through dispersal. This is a key and novel finding. Under climate warming these effects were exacerbated.

TSD reptiles are considered to be very vulnerable to climate warming as they have biased juvenile sex ratios. Furthermore, imbalanced sex ratios in marginal habitats determine the limit of range expansion, in stable climates. As climates warm it has been predicted that imbalanced sex ratios at the leading (colder) edge of the range of a species will become more equal resulting in more rapid population growth. As a consequence, a new pool of dispersers will be produced and this will facilitate range expansion. In Chapter 4, the population model and simulation details were similar to Chapter 3. The main differences were: there were 15 replicates for each dispersal condition; dispersal levels of none, very small and small were used; and there were two simulations, one for a scenario of no climate warming and the other for a scenario of climate warming. A 3^{o}C increase in ambient temperature across 100 years was chosen. Simulations were run for 1100 years in a stable climate (temperature gradient 18

– 33°C) (no climate warming scenario), and separately for 1000 years, followed by 100 years where temperature increased in equal increments until a 3°C increase was reached (climate warming scenario).

Populations with female-biased primary sex ratios did not become extinct following climate warming by 3°C. As climates warmed the effects of the interaction of juvenile survival, juvenile sex ratios and male limitation were further exacerbated and a number of populations were lost at the warmer edge of the range. Nevertheless, the loss of populations was less than would have occurred on the basis of theoretical predictions about the effects of climate warming on populations of reptiles with TSD. Dispersal level was found to be most effective in increasing population persistence in populations of reptiles with TSD when dispersal occurred at a relatively ‘large’ level. Populations showed little capacity for range shift, or range expansion following climate warming. Populations of reptiles with TSD with increasingly female-biased (and not equal) adult and juvenile sex ratios reached the largest sizes, following climate warming, at the colder edges of the range.

Populations of reptiles with TSD with temperature-linked juvenile sex ratios and juvenile survival as well as limited dispersal capacity and limited behavioural or evolutionary compensatory mechanisms may be vulnerable to future declines in population persistence. However, the rate of local population extinctions from climate warming may not be as great as previously thought.

Certificate of Authorship of Thesis

Except where clearly acknowledged in footnotes, quotations and the bibliography, I **Maria Boyle**, certify that I am the sole author of the thesis submitted today entitled –

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I further certify that to the best of my knowledge the thesis contains no material previously published or written by another person except where due reference is made in the text of the thesis.

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Date: …13-Feb-14…………………………..

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President John F. Kennedy.

> **"***But in a very real sense, it will not be one man going to the Moon. If we make this judgment affirmatively, it will be an entire nation. For all of us must work to put him there***".**

Table of Contents

Abstract .... **iii**

Certificate of Authorship of Thesis .... **vii**

Acknowledgements .... **ix**

Table of Contents .... **xi**

List of Figures .... **xv**

List of Tables .... **xix**

Chapter 1: Under what conditions do climate-driven sex ratios enhance versus diminish population persistence in reptiles? **1**

- 1.1. Thesis Aims and Structure 16
  - 1.1.1. Aims: 17
  - 1.1.2. Structure 17

Chapter 2: Modelling effects of climate on reptile populations **23**

- 2.1. Introduction 23
  - 2.1.1. The TSD reaction norm 24
  - 2.1.2. Cohort sex ratio (CSR) 24
  - 2.1.3. Temperature-dependent embryonic survival 26
  - 2.1.4. Male limitation 28
  - 2.1.6. Aims 31
- 2.2. Methods 32
  - 2.2.1. Model description 32
  - 2.2.2. Population size 32
  - 2.2.3. Cohort sex ratio and temperature 35
  - 2.2.4. Juvenile survival and temperature 37

2.2.4. Juvenile survival and temperature 40

2.2.5. Male limitation 41

2.2.6. Combined effects of juvenile survival, cohort sex ratio, temperature, and of male limitation 42

2.3. Results 44

2.3.1. Model behaviour and sensitivity 44

2.3. Results 45

2.3.1. Model behaviour and sensitivity 45

2.3. Results 46

2.3.1. Model behaviour and sensitivity 46

2.3.2. Population size 46

2.3.3. Cohort sex ratio and temperature 49

2.3.4. Juvenile survival and temperature 51

2.3.5. Male limitation 51

2.3.6. Combined effects of juvenile survival, cohort sex ratio, temperature, and male limitation 54

2.3.6.1. Populations of reptiles with GSD 54

2.3.6.2. Populations with TSD 54

2.3.6.2.1. Populations of reptiles with TSD with no male limitation on female fecundity (b=0) 54

2.3.6.2.2. Populations of reptiles with TSD with a moderate level of male limitation on female fecundity (b=0.01) 56

2.3.6.2.3. Populations of reptiles with TSD with a strong level of male limitation (b=0.1) 59

2.4. Discussion 63

2.4.1. Summary 69

Chapter 3: The role of dispersal in determining range limits in reptiles. 71

3.1. Introduction 71

3.1.1. Range limits in temperature-dependent sex determination (TSD) species 71

3.1.2. Potential for local adaptation 73

3.1.3. Role of dispersal 75

3.1.4. Rationale 78

3.2. Methods 79

3.2.1. Model description 79

3.2.1.1. Population model 79

3.2.1.2. Dispersal model 80

3.2.1.3. Simulation 85

3.3. Results 87

3.3.1. Dispersal in populations of reptiles with GSD 87

3.3.2. Dispersal in populations of reptiles with TSD 91

3.3.3. Results summary 93

3.4. Discussion 96

3.4.1. Conclusions 101

Chapter 4: The effects of climate warming on population persistence and abundance in reptiles 103

4.1. Introduction 103

4.1.1. Aims 110

4.2. Methods 111

4.2.1. Simulation 111

4.2.2. Population model 112

4.2.3. Spatial analysis and correlation of sex ratios in populations of reptiles with TSD113

4.2.4. Dispersal 114

4.3. Results 115

4.3.1. GSD Populations 115

4.3.2. Populations of reptiles with TSD 117

4.4. Discussion 129

4.4.1. Conclusions 135

Chapter 5: Synopsis 139

5.1. Contribution of my thesis 139

5.2. Role of empiricists in data collection 142

References 149

List of Figures

Figure 1.1: Temperature-dependent sex determination (TSD) reaction norms for sex determining patterns (a) TSD1A, (b) TSD1B, and (c) TSDII.. 12

Figure 1.2: Thesis outline and structure 21

Figure 2.1: Logistic growth curves for varying population sizes.. 36

Figure 2.2: Cohort sex ratio (CSR) response curves and baseline juvenile survival curves. .. 38

Figure 2.3: The female fertilisation probability as a function of adult sex ratio (ASR).. 43

Figure 2.4: Incorporation of the effects of juvenile survival (*a*), cohort sex ratio (*p*), temperature, and of male limitation.. 43

Figure 2.5: Simple logistic population growth for a single population generated using equation 1 at 24.5°C. 48

Figure 2.6: Population sizes of females for cohort sex ratio (CSR) response curves.. 50

Figure 2.7: Female population size without male limitation.. 52

Figure 2.8: Populations of females for genotypic sex determination (GSD) and temperature-dependent sex determination (TSD) and no temperature-dependent embryonic survival (TS) with varying levels of male limitation, for temperature gradient 2. 53

Figure 2.9: Populations of females for various combinations of temperature-dependent sex determination (TSD) and genotypic sex determination (GSD) with and without temperature-dependent juvenile survival (TS). Males do not limit female fecundity (*b*=0). 57

Figure 2.10: Populations of females for various combinations of temperature-dependent sex determination (TSD) and genotypic sex determination (GSD) with and without temperature-dependent embryonic survival (TS). Moderate level of male limitation on female fecundity (*b*=0.01).. 60

Figure 2.11: Populations of females for various combinations of temperature-dependent sex determination (TSD) and genotypic sex determination (GSD) with and without temperature-

dependent embryonic survival (TS). Strong level of male limitation on female fecundity (b=0.1).. 62

Figure 3.1: Demographic and dispersal processes in the simulation model 81

Figure 3.2: The female fertilisation probability as a function of adult sex ratio (ASR= M:F) 83

Figure 3.3: Normal temperature-dependent baseline juvenile survival parameter, *a* distributed along a temperature gradient from 18 to 33°C. 84

Figure 3.4: Actual probability of an individual moving a certain number of cells across a population matrix,according to two fat-tailed dispersal kernels (equation 8).. 86

Figure 3.5: Population persistence by temperature interval for genotypic sex determination (GSD) populations.. 90

Figure 3.6: Population persistence by temperature interval for temperature-dependent sex determination (TSD) populations. 94

Figure 4.1: Actual probability of an individual moving a certain number of cells (dispersal distance) across a population matrix for two fat-tailed dispersal kernels (equation 8). 116

Figure 4.2: Population persistence by temperature interval for genotypic sex determination (GSD) populations without and with climate warming.. 118

Figure 4.3: Average population sizes and standard errors, for populations of reptiles with GSD with very small dispersal, for each individual column of the population matrix. 119

Figure 4.4: Population persistence by temperature interval for temperature-dependent sex determination (TSD) populations without and with climate warming.. 124

Figure 4.5: Average population sizes and standard errors, for temperature-dependent sex determination (TSD) populations with very small dispersal, for each individual column of the population matrix 125

Figure 4.6: Contour maps of adult sex ratios (proportion male, from 0 to 1, right column) for populations of reptiles with TSD, with the very small level of two-sex dispersal (a) without climate warming, and (b) with climate warming. 126

Figure 4.7: Contour maps of juvenile sex ratios (proportion males, from 0 to 1, right column) for populations of reptiles with TSD, with the very small level of two-sex dispersal (a) without climate warming, and (b) with climate warming.. 127

Figure 4.8: The effect of different adult sex ratios on average population sizes in temperature-dependent sex determination (TSD) populations with the very small level of two-sex dispersal, with no climate warming and climate warming. 128

List of Tables

Table 2.1: Details of cohort sex ratio (CSR) response curves for the snow skink, painted turtle and loggerhead turtle. 39

Table 2.2: A description of the parameter space of baseline juvenile survival (*a*) and the proportion of male offspring (*p*) used to estimate the effects on population size (N)........ 47

Table 3.1: Total numbers of surviving genotypic sex determination (GSD) populations by dispersal level for all temperatures. N.B**.** Total surviving populations were averaged based on ten replicates per dispersal level. 89

Table 3.2: Total numbers of surviving temperature-dependent sex determination (TSD) populations by dispersal level for all temperatures. N.B. Total surviving populations were averaged based on ten replicates per dispersal level. 95

Table 3.3: Chi-square analysis (χ^2) of the differences between the numbers of surviving populations for GSD and populations of reptiles with TSD. 95

Table 4.1: Percentage of genotypic sex determination (GSD) populations with larger average population sizes with no climate warming compared with climate warming. The majority of populations had larger average population sizes with no climate warming. 123

Table 4.2: Percentage of temperature-dependent sex determination (TSD) populations with larger average population sizes with no climate warming, compared with climate warming. The majority of populations had larger average population sizes with no climate warming. 123

Chapter 1: Under what conditions do climate-driven sex ratios enhance versus diminish population persistence in reptiles?

Climate change presents major challenges for both species and ecosystems (Andrewartha and Birch 1954;Walther *et al.* 2002;Krebs 2009). Empirical evidence suggests that climate change has already had considerable ecological impact on the Earth's biota, and as climate change progresses the impact is likely to increase (Stenseth *et al.* 2002;Walther *et al.* 2002; IPCC 2013). Ecological impacts include: changes in the abundance and distribution of species; in their patterns of migration; shifts in species ranges; increases in invasive species; disease outbreaks (Krebs 2009); changes in phenology (the timing of seasonal activities, such as reproduction in animals and plants (Walther *et al.* 2002; Visser and Both 2005)); in physiology; and decoupling of trophic interactions (Parmesan *et al.* 2000; McCarty 2001; Stenseth *et al.* 2002; Walther *et al.* 2002; Hughes 2003; Visser and Both 2005; Parmesan 2006; Schwanz and Janzen 2008; Krebs 2009). The extent to which species respond to climate change will depend largely on their biological traits, including behavioural, physiological, genetic and life history traits (Walther *et al.* 2002).

As climates warm, species with phenological or physiological traits that strongly depend on ambient temperature and those with limited geographical range, are at risk of declines in population persistence and possible local extinctions. The survival of these species is often linked with their physiological tolerance to environmental temperatures (Hughes 2003; Visser and Both 2005; Sinervo *et al.* 2010). Phenology is important in the context of climate change, as many species rely on environmental cues, such as temperature for the timing of spring activities, for example flowering, nesting, breeding and migration (Stenseth *et al.* 2002; Walther *et al.* 2002).

Alterations in phenology could potentially have either positive or negative outcomes for species and even entire ecosystems (Hughes 2003). A positive outcome might include realignment of breeding with temperature and abundance of food. Negative outcomes might include incongruity between these factors and decoupling of species interactions. The associated cascading of effects could destabilise entire ecosystems (Hughes 2003). Hence the ecological consequences of global warming could be either a ‘match’ or ‘mismatch’ between trophic levels, or consumers and resources (Hughes 2003; Visser and Both 2005; Krebs 2009). The trend over the past several decades has been towards earlier occurrences of spring activities linked to climate warming (Hughes 2000; McCarty 2001; Stenseth *et al.* 2002; Walther *et al.* 2002; Visser and Both 2005; Krebs 2009; Chambers *et al*. 2013).

Over the past several decades large changes in the phenology of plants and animals have been associated with a trend of increasing average winter temperatures (Walther *et al.* 2002). Mean laying date of 20 (of 65) bird species in the United Kingdom is around 9 days earlier in 1995 than in 1971. No significant changes in the other 45 bird species were recorded (Crick *et al.* 1997). Earlier breeding has been reported in some amphibians to occur around 1 to 3 weeks earlier per decade since the 1960s (Beebee 1995). Several bird species have shifted the timing of breeding in response to climate warming (Nussey *et al.* 2007) but no evidence from bird studies supports compensation from changes in the microhabitat, such as making alternative nest site choices (e.g. nesting in shadier and cooler areas).

Species with physiological traits that make them very dependent on environmental temperatures are likely to be at increased risk as climates warm. Ectothermic animals, such as invertebrates and reptiles, may be vulnerable as many of their life history traits are strongly linked with environmental temperatures. For example, in invertebrates, various species of porcelain crabs (genus *Petrolisthes*), from both tropical (Panama) and temperate (California) latitudes that were tolerant of high temperatures were found to be at high risk from climate warming (Somero 2010). This is because these species are already living near the current maximum habitat temperature (MHT) and further increases in MHT owing to climate warming may exceed lethal temperatures. Porcelain crabs have little capacity to acclimatise to warmer temperatures and were especially vulnerable in tropical areas (Somero 2010).

For many species of insects, notwithstanding that warming in tropical areas is relatively low in magnitude compared to temperate regions, tropical insects are typically very sensitive to temperature changes. These insects are currently living close to their thermal maxima (Deutsch *et al.* 2008; Tewksbury *et al.* 2008; Bonebrake and Deutsch 2012). In contrast, insect species located at higher latitudes have wider thermal tolerance as they are living in climates that are cooler than their thermal maxima, and so are likely to display the largest responses (Deutsch *et al.* 2008; Tewksbury *et al.* 2008; Bonebrake and Deutsch 2012). For these species warming may enhance their capacity to persist. Deutsch *et al.* (2008) argue that terrestrial vertebrate ectotherms will show similar patterns in their responses to temperature change as insects. In the absence of immigration and adaptation the greatest risks of extinction from climate warming are faced by tropical insects, compared with insects in temperate areas. The same may be true for vertebrate ectotherms (Deutsch *et al.* 2008).

A review of the historical records of 48 species of lizard at 200 Mexican sites (Sinervo *et al.* 2010), show that 12% of local populations have become extinct. Viviparous (production of live offspring) reptile populations are most at risk at low latitudinal and elevational range limits where species are limited by thermal physiology (Sinervo *et al.* 2010). To be more explicit, viviparity is thought to be a thermal adaptation to cold climates. Thus, when high physiologically active body temperatures exceed a temperature threshold, the impact on embryonic development may be negative and extinction risk higher (Sinervo *et al.* 2010).

Species with limited climatic range or an inability to respond appropriately to climate warming through dispersal are also highly vulnerable to climate warming (Sinervo *et al.* 2010). Range contraction, expansion or shift is one of the most widely studied biological responses by species to climate change (Andrewartha and Birch 1954; McCarty 2001). Central to range change is the concept of *niche*. The niche has been defined as the set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes (Hutchinson 1957; Wiens and Graham 2005). The *fundamental niche* describes the abiotic (climate) conditions for species persistence in the presence of competitors, and the *realised niche* describes the conditions in which a species persists given the presence of other species (for example, competitors, prey and predators) (Hutchinson 1957; Wiens and Graham 2005). The realised niche is a subset of the fundamental niche, and the range of a species is the spatial projection of realised niche (Brown 1984; Wiens and Graham 2005; Davies *et al.* 2009). The edges of a species range (range limits) are often characterised by more hostile environments (e.g. environments that are either hotter or colder at the margins) where habitats are more marginal than in the interior of the range. Species at range edges are often living close to their physiological limits and may be subject to greater environmental stress than those located towards the centre of the range (Andrewartha and Birch 1954; Caughley *et al.* 1988).

Geographical ranges of species are not static and may change in response to climate change (Davis and Shaw 2001; Davies *et al.* 2009). The range of a species has been defined as having a ‘trailing’ (warmer) and a ‘leading’ (colder) edge under climate warming (Brown and Kodric-Brown 1977; Kallimanis 2010). The trailing edge of the range is of lower habitability and may become more marginal as climates warm (Davies *et al.* 2009; Kallimanis 2010). The leading edge of a species range is also of lower habitability (Caughley *et al.* 1988) but in contrast to the trailing edge may become more habitable as climates warm (Brown and

Kodric-Brown 1977; Parmesan *et al.* 1999; Davis and Shaw 2001; Davies *et al.* 2009; Kallimanis 2010).

As climates warm populations located at trailing edges are assumed to be more at risk of local extinction. However, this may occur concomitant with population growth and range expansion at the leading edges as habitats become more favourable (Davis and Shaw 2001; Kallimanis 2010). Given relative mobility and some dispersal propensity, species may be able to shift their geographical ranges to cooler latitudes (for example, towards the poles or higher elevations) and establish new populations, under climate warming (Parmesan *et al.* 2000; Hughes 2003; Parmesan 2006).

Evidence of range shift in response to climate warming (warmer average spring temperatures) from southern to locations further to the north exists for North American and European bird, butterfly and mammal species. In the United Kingdom, 59 bird species with a southern distribution were found to have shifted north (despite no changes in density) by around 19 km over a 20 year period between 1988 – 1991 compared with 1968 – 1972 (Thomas and Lennon 1999). Northward movements (and range shifts to higher elevations) of butterfly species in Northern Europe are documented by Parmesan (2006). A survey of small mammals in the southern United States of America found northward range shift in 19 species in response to climate warming (Davis and Callahan 1992). The shift into cooler latitudes and consequent population growth in numerous species may be accompanied by local population extinctions at warmer or lower latitudes in other species (Hughes 2000, 2003).

Many plant, passerine bird, butterfly and some amphibian species have shifted their geographical ranges to cooler latitudes (for example, towards the poles or higher latitudes) in response to climate warming and established new populations (Parmesan 2006). Amphibians are reported to be the least successful of these species in their ability to respond to climate change (Lawler *et al.* 2010). Reptiles are one of the better studied vertebrate taxa in terms of their potential responses to increases in temperature. Not surprisingly climate warming is considered a major extinction threat to many local populations (Janzen 1994; Girondot *et al.* 2004; Hawkes *et al.* 2009; Sinervo *et al.* 2010). Reptile species that have been described as especially vulnerable are those with limited geographical ranges (Sinervo *et al.* 2010) and temperature-dependent sex determination (TSD) (Janzen 1994; Hawkes *et al.* 2009; Mitchell and Janzen 2010; Doody and Moore 2011).

There are two main types of sex determining mechanisms in vertebrates: genotypic sex determination (GSD) (Ohno 1967) and environmental sex determination (ESD) (Bull 1980). Sex determination in vertebrates usually involves some type of GSD (Ohno 1967), where the sex of the offspring is determined at conception by the chromosomal contributions of each parent (for example, XX/XY chromosomes, or ZZ/ZW chromosomes). The sex ratio of GSD species is well described as a binomial process generated by variation of meiotic segregation of sex chromosomes (Freedberg and Taylor 2007). ESD is a form of phenotypic plasticity in which environmental factors experienced during embryonic development permanently determine the sex of the offspring after fertilisation (Bull 1980).

In species with ESD, sex may be determined by a number of environmental factors, of which temperature is the most common. Dependence of sex determination on temperature may lead to severe demographic perturbations under climate change owing to increasingly biased sex ratios (Janzen 1994; Hawkes *et al.* 2007; Mitchell *et al.* 2008; Mitchell and Janzen 2010). In some species TSD appears to be the sole sex determining factor (Ewert and Nelson 1991; Valenzuela 2001) while in others temperature and genetic factors interact to determine sex (Shine *et al.* 1997). TSD occurs widely in reptiles: all crocodilians, marine turtles, and the tuatara, most freshwater turtles and some lizards (Bull 1980; Ewert and Nelson 1991; Janzen and Paukstis 1991; Cree *et al.* 1995; Valenzuela and Lance 2004). There are several patterns of TSD identified in reptiles. These are TSD1A, TSD1B and TSDII (Ewert and Nelson 1991) (Figure 1.1).

1) TSD1A (Male-Female) is the most common pattern in reptiles, and males are produced at lower incubation temperatures, females at higher temperatures and both sexes at intermediate temperatures. TSD1A is present in many turtles (Ewert *et al.* 1994).

2) TSD1B (Female-Male) produces females at lower incubation temperatures, males at higher temperatures and both sexes at intermediate temperatures. TSD1B occurs in some lizards (Viets *et al.* 1994), some crocodiles (Ferguson and Joanen 1983) and the tuatara (Cree *et al.* 1995; Mitchell *et al.* 2008).

3) TSDII (Female-Male-Female) produces females at both high and low temperatures and males at intermediate temperatures. This pattern occurs in many crocodile, most lizard and some turtle species (Ewert *et al.* 1994). In some fish the reverse pattern (Male-Female-Male) may be observed. For example, in the Atlantic silverside (*Menidia menidia*) (Conover *et al.* 1992).

In TSD reptiles, the sex of the offspring is irreversibly determined by incubation temperature during embryonic development. The crucial period of thermal sensitivity occurs around the middle third of development of the embryo (Charnov and Bull 1977; Bull 1980). The relationship between the probability of an individual (or a single clutch) developing as either male or female and the incubation temperature of the individual (or clutch) is considered a physiological *reaction norm* (Hulin *et al.* 2009). Mathematically, the reaction norm of TSD reptiles (Figure 1.1) can be described across a group of individuals by sigmoidal equations (as a first approximation) incorporating the incubation temperatures and sexual outcomes (Hulin *et al.* 2009).

There are two parameters that are important in defining the TSD reaction norm. The first is the *pivotal temperature*, defined as the temperature at which males and females are produced in equal proportions (50:50 sex ratio) (Girondot *et al.* 2004). The other is the *transitional range of temperatures* (TRT) defined as the range of constant temperatures that produce both sexes in variable proportions (Georges *et al.* 1994; Hulin *et al.* 2009). Outside of the TRT all males or all females are usually produced. Both the pivotal temperature and TRT may vary considerably among reptile species (Ewert *et al.* 2005). Ewert *et al*. (2005) argue that populations of the American snapping turtle (*Chelydra serpentina*) in cold environments adapt to the shorter nesting season by laying eggs under shaded environments, producing warmer nest temperatures and faster embryonic development than populations in lower latitudes. Thus warmer pivotal temperatures are expected in these populations due to the warmer nest temperatures.

Fisher (1930) is recognised as having produced the most important work on the subject of sex ratios, and its basic principle is central to sex ratio dynamics in natural systems. According to Fisherian frequency-dependent selection, the primary sex ratio should be 1:1 as each sex is restricted to providing half of the genetic contribution to the next generation. If there is a greater abundance of one sex, frequency-dependent selection should favour the production of the rare sex, readjusting the sex ratio to 1:1(Fisher 1930). In populations of reptiles with TSD the primary sex ratio (sex ratio of offspring) is largely controlled by the interaction of the environment (temperature) and the response of the species to the environment (Charnov 1982; Charnov and Bull 1989). Hence, biased sex ratios should be adjusted under Fisherian frequency dependent selection, adapting the phenotypic expression of TSD towards a 1:1 sex ratio in local climates (Fisher 1930).

In contrast, Charnov and Bull (1989) demonstrated that in populations of reptiles with TSD sex ratios are unlikely to be 1:1. Primary and secondary sex ratios in reptiles with TSD were found to range from approximately balanced to female (or male) biased (Charnov and Bull 1989). Predominantly female (or male) biases should result in greater relative fitness for males (or females) and the sex ratio should tend back towards 1:1. According to Charnov and Bull (1989) there is still an equilibrium sex ratio on which frequency-dependent selection operates but not necessarily towards 1:1. The primary sex ratio will be equal to the ratio of lifetime fitness resulting from female incubation temperatures to the fitness resulting from incubation at male producing temperatures (Charnov and Bull 1989).

Alterations in temperature may potentially have direct impacts on several important demographic parameters in reptiles including juvenile sex ratio in species with TSD. Reduced juvenile survival owing to extreme environmental temperatures may also cause obvious reductions in population growth parameters. In oviparous (egg laying) reptiles most of the embryonic development occurs outside of the maternal environment, usually in the nest (Girondot *et al.* 2004). Hence egg or juvenile survival is strongly linked with environmental temperatures and will be greatly reduced if temperatures become too hot or too cold (Girondot *et al.* 2004). Irrespective of this there are relatively few data available on the limits of egg survival in reptiles (Birchard 2004).

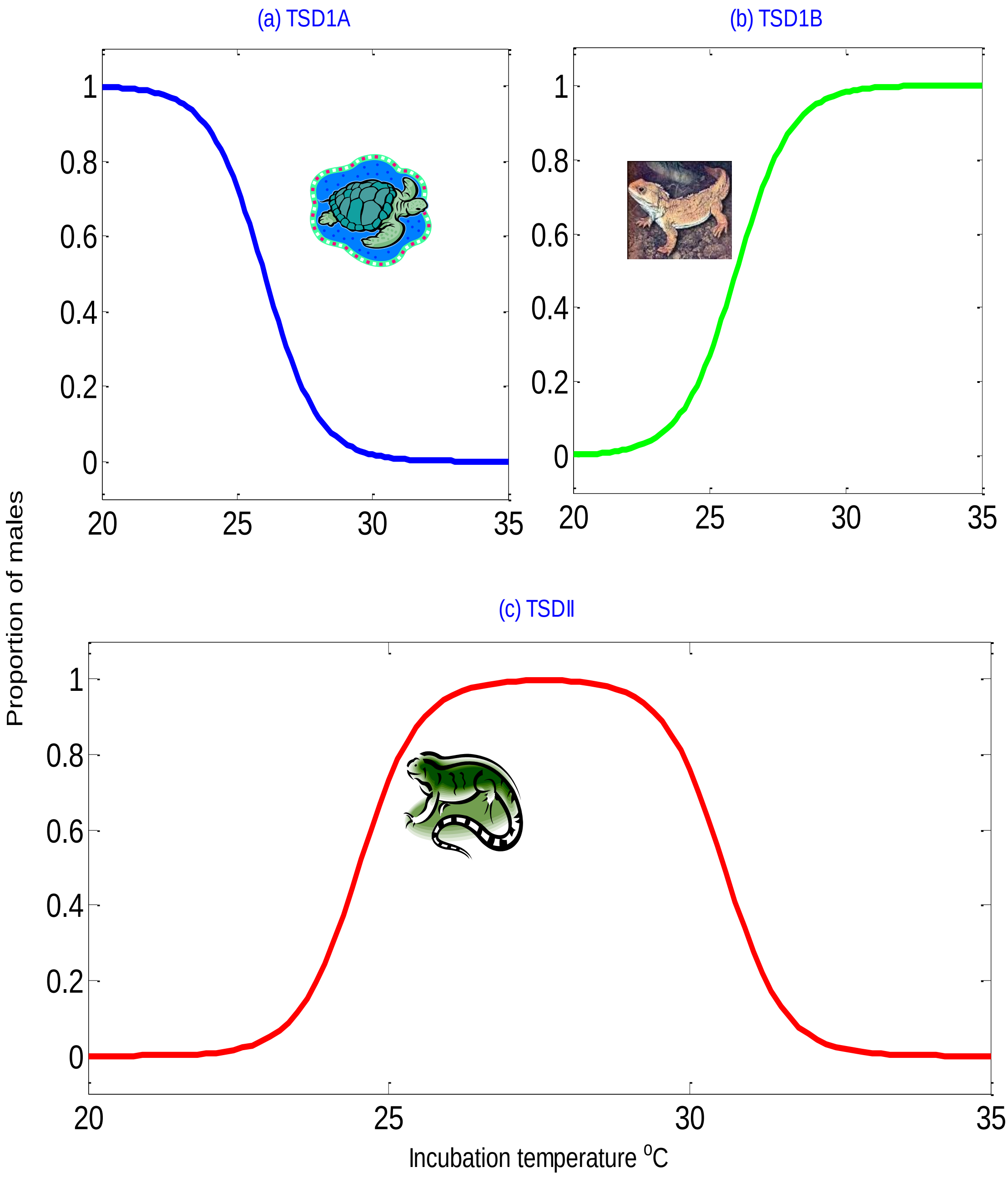
Populations of reptiles with TSD are considered to be very vulnerable to climate warming as the primary sex ratio (sex ratio of hatchlings) is determined by ambient temperature and is predicted to become very biased in extreme climates (Janzen 1994; Hays *et al.* 2003; Hawkes *et al.* 2007; Hawkes *et al.* 2009; Witt *et al.* 2010). There is some evidence of the relationship between cohort sex ratio (CSR) (proportion of juvenile males in a population) and ambient air temperature from field studies (Wapstra *et al.* 2009; Schwanz *et al.* 2010). A 1^{o}C increase in air temperature from 17 ^{o}C to 18^{o}C in a population of the snow skink (*Niveoscincus ocellatus*) living at low elevation, resulted in the juvenile sex ratio shifting from a 0.7 to 0.3 proportion of males (Wapstra *et al.* 2009). An increase in July air temperatures resulted in a shift from male to female biases in the juvenile sex ratios of freshwater painted turtles (*Chrysemys picta*) (Schwanz *et al.* 2010). Janzen (1994) undertook a rigorous quantitative analysis of heritable sex determining factors and empirical data from a natural population of freshwater painted turtles and concluded that a 4^{o}C temperature increase may eventually eliminate males.

The link between adult and juvenile sex ratios has been examined in marine turtles, but not in many other taxa (Stabenau *et al.* 1996; Braun-McNeill *et al.* 2007). Data from marine turtle studies suggest, that female-biased primary sex ratios are maintained at older life stages for loggerhead turtles (*Caretta caretta*) (Braun-McNeill *et al.* 2007), and Kemp's Ridley turtles (*Lepidochelys kempi*), green turtles (*Chelonia mydas*) and leatherback turtles (*Dermochelys coriacea*) (Stabenau *et al.* 1996). Hence, a climate induced increase in female-biased primary sex ratios could result in declines in population persistence and reproductive failure owing to male shortages (Witt *et al.* 2010; Wright *et al.* 2012).

Low numbers of males may generate the *Allee effect*, which refers to a decrease in per-capita growth rate at low population numbers (Courchamp *et al.* 1999). One of the factors that may generate the Allee effect is demographic stochasticity, in this instance sex-ratio fluctuation. Low numbers of males may result in difficulties for females in finding mates, and this is particularly the case when populations are small (Courchamp *et al.* 1999).

Given the potential direct effects of a warming climate on juvenile survival and sex ratios, the longer-term persistence of populations with TSD at the trailing edge will depend on plastic compensatory responses or evolutionary responses that prevent reductions in juvenile survival and biases in primary sex ratios. The mechanisms that may be used by TSD reptiles to respond or adapt to ongoing climate change include micro-evolutionary changes, and plasticity in physiological and behavioural traits. Micro-evolutionary changes regulated by genetics or heritable factors (Hulin *et al.* 2009) may allow for *in situ* adjustments to the pivotal temperature or nesting behaviours in response to changing environmental conditions at nesting sites or beaches (Davenport 1989; Poloczanska *et al.* 2009). A major effect of climate change on nesting beaches are sea level rises, resulting in habitat destruction and this may reduce the availability of nesting sites (Witt *et al.* 2010; Fuentes *et al.* 2011).

TSD reptiles may also respond to climate warming through altered nesting behaviour (evolutionarily or plastically) through: changing nest site choice (Hays *et al.* 2003; Fuentes *et al.* 2011); shifting nests to cooler microhabitats (Doody and Moore 2011); or shifting nesting to cooler months (timing) (Hays *et al.* 2003; Weishampel *et al.* 2004). Earlier nesting has been observed in several populations of turtles in response to climate warming (Weishampel *et al.* 2004; Tucker *et al.* 2008). Nesting plasticity may prevent increases in nest temperature that would otherwise reduce juvenile survival or generate imbalances in primary sex ratios. However several studies of the painted turtle (Morjan 2003; Schwanz and Janzen 2008; Telemeco *et al.* 2013) have suggested that phenotypic plasticity in female nesting behaviour in response to rising temperatures is not sufficient to ameliorate the effects of climate warming. For example, Telemeco *et al*. (2013) suggest that females are not able to protect their offspring from the negative effects of sustained climate warming, solely by adjusting nesting date. The study predicted that nests will produce primary sex ratios that are 100% female, with a considerable increase in juvenile mortality, due to prolonged exposure of eggs to temperature increases (Telemeco *et al.* 2013). The water dragon (*Physignathus lesueurii*) chooses different nesting sites at different temperatures across its range (Doody *et al.* 2006).


(a) TSD1A

(b) TSD1B

(c) TSDII

Figure 1.1: Temperature-dependent sex determination (TSD) reaction norms for sex determining patterns (a) TSD1A, (b) TSD1B, and (c) TSDII. Equations used to generate the plots are from Hulin *et al*. (2009).

Observed variation in nesting among water dragon populations may result from either behavioural plasticity or local adaptation (Doody *et al.* 2006). Three-lined skinks (*Bassiana duperreyi*) have shown behavioural plasticity by adjusting nest depth in response to environmental temperature (Telemeco *et al.* 2009).

Local adaptation in nesting may not occur fast enough to restore balances in primary sex ratios or increase the probability of juvenile survival, in particular in long-lived or late-maturing reptiles (Morjan 2003). The evolution of nest site choice and threshold temperature (above which females are produced) is not expected to be able to occur at the same rate as contemporary climate warming, and imbalanced sex ratios resulting from climate warming will not be redressed (Morjan 2003). Furthermore shifts in nesting phenology resulting from individual plasticity may have moderate compensatory effects on primary sex ratios for climate warming reducing selective pressure (Schwanz and Janzen 2008).

Notwithstanding that TSD taxa have survived climate warming and cooling over evolutionary timeframes (Mitchell and Janzen 2010), it remains unclear if TSD reptiles are able to respond quickly enough to contemporary climate warming through evolutionary compensatory mechanisms, or if they have scope to respond through phenotypic plasticity (Morjan 2003; Schwanz and Janzen 2008; Mitchell and Janzen 2010). If microevolution of the reaction norm, and plasticity or evolution in nesting are unable to adequately compensate for temperature induced primary sex ratio imbalance or reduced juvenile survival, then the demographic effects of a mismatch between life history traits and climate warming is likely to result in local population extinctions (Tuljapurkar *et al.* 2003). The ability of TSD species to change or shift geographical range becomes of fundamental importance, yet there have been few attempts to describe the response of reptile species to recent climate warming, at the edges and centres of their geographical ranges.

Kallimanis (2010) proposed a model describing the geographical distribution of sex ratios as follows. The model assumes that imbalanced sex ratios in marginal habitats limit population growth and set the limit of range expansion at range edges under stable climatic conditions. Kallimanis' (2010) model as described applies to species with the male-female (Type 1A) pattern of TSD and TSD pattern II. The TSD 1A pattern is also the focus of my thesis. TSD species have balanced sex ratios at the centre of ranges and biased sex ratios at the edges. The leading edges of the geographical ranges of some TSD species are characterised by low temperatures and have male-biased sex ratios. In contrast, the trailing edges are characterised by environments of high temperatures and have female-biased sex ratios. This model predicts that cool leading edge populations may grow under climatic warming because as sex ratios will change from male biased to equal, increasing population growth will produce a new pool of dispersers and, hence, enable range expansion into previously cooler areas. Conversely, the trailing edge populations may become extinct as ranges become too hot and sex ratios become 100% female (Kallimanis 2010; Escobedo-Galvan *et al.* 2011). In contrast, Freedberg and Taylor (2007) argue that increases in reproduction and population growth are associated with female-biased sex ratios, and not balanced sex ratios. Hence, a trailing edge that becomes female-biased, as climates warm, may not retract, and conversely a leading edge that becomes balanced, may not grow as well as assumed. For example, many populations of marine turtles persist at thermal range limits with heavily female biased sex ratios, at least in the short-term (Hawkes *et al.* 2007).

The number of juveniles produced in many TSD species may be directly linked with the number of sexually mature females (Girondot *et al.* 2004). Many models of reproduction consider the contribution to the next generation to be relatively unresponsive to the number of sexually mature males. This has been termed *female dominance* (Girondot *et al.* 2004). In contrast Kallimanis (2010) assumes that males and females both play an important role in determining the number of offspring contributing to the next generation and hence population persistence. Escobedo-Galvan *et al.* (2011) criticised the model proposed by Kallimanis (2010) as an oversimplification of ecological and evolutionary processes and considered more complex responses of TSD species to climate change. One of the criticisms is that TSD species are unlikely to benefit widely under climate warming, building pools of dispersers to colonise new ranges (Escobedo-Galvan *et al.* 2011). Range expansion is not only a matter of population growth at range margins, but also of dispersal, and many TSD species are thought to be poor dispersers (Escobedo-Galvan *et al.* 2011). Range expansion (or range shift) and population growth at the leading edge of the range is not guaranteed as climates warm, unless dispersal is effective.

Dispersal tendencies in birds and mammals have been widely studied (Greenwood 1980), but little is known about dispersal tendencies in reptiles. Male recruitment through dispersal is thought to be essential to facilitate population persistence in increasingly female-biased populations of reptiles with TSD (Doody and Moore 2011). This may be fortuitous as male-biased dispersal is thought to be the dominant dispersal tendency in many reptiles with TSD (Karl *et al.* 1992; Limpus 1993; Casale *et al.* 2002; Roberts *et al.* 2004; Freedberg *et al.* 2005; Bowen and Karl 2007) and GSD (Doughty *et al.* 1994; Rassmann *et al.* 1997; Rivera *et al.* 2006; Keogh *et al.* 2007; Dubey *et al.* 2008). However, little is known about the role dispersal may have in determining range limits and range expansion in stable and warming climates.

In summary, for many reptile species, vital demographic parameters such as individual sex (male or female) and juvenile survival depend on ambient temperature. This suggests that population persistence and, hence, geographic range could also be determined by local climate and strongly influenced by climate change. Although not dependent on temperature, the adult sex ratio may influence female fecundity through the strength of male limitation and, hence, population persistence. Dispersal may also be strongly influential in population persistence, determining range limits, and range change as climates warm.

1.1. Thesis Aims and Structure

Unfortunately, our empirical knowledge is lacking on dispersal tendencies in reptiles, and on how juvenile survival, juvenile sex ratios, male limitation and dispersal may interact in continuous populations (with or without dispersal), and affect population persistence. It is particularly important for empiricists to understand the relative importance of these parameters and their influence on population persistence in order to recommend priorities for future research. My thesis is a first step in elucidating the relationships between juvenile survival and juvenile sex ratios, male limitation and dispersal and the relative importance of these factors in determining population persistence, range limits and range change in reptile species with temperature-dependent sex determination (TSD) and genotypic sex determination (GSD). I use analytical and simulation approaches to examine how the interaction of these factors affects population persistence across climatic gradients of stable and warming climates.

The responses of populations with TSD and GSD under stable climatic conditions and short-term climate warming are explored theoretically. My thesis does not address long-term evolutionary responses to climate warming, but rather focuses on the short-term effects of stable and warming climates on population persistence and range change. Climate in this thesis is represented by ambient air temperature. There is no density dependence in annual fecundity, annual adult survival and age at first reproduction. There are density effects in juvenile survival only. This thesis does not study TSD 1B and TSDII, but TSD1A only. Parthenogenesis (females producing individuals from an unfertilised egg) is not included in this thesis.

1.1.1. Aims:

1) To explore how climatically-linked juvenile survival, juvenile sex ratio and male limitation interact in continuous populations without dispersal and how they affect population persistence across a range of stable climates (**Chapter 2**).

2) To explore the interactions between dispersal and the factors described in 1) on population persistence in continuous populations with dispersal distributed across stable climates. Furthermore, to examine the role of dispersal in determining range limits in a stable climate (**Chapter 3**).

3) To explore the influence of dispersal, juvenile survival and juvenile sex ratio on population size and range change in a warming climate (**Chapter 4**).

4) To identify those life history parameters that have the greatest impact on population persistence and species range change with the aim of recommending priorities for empirical research. Such research could directly guide and inform empiricists and conservation managers' decisions regarding TSD and GSD reptiles as climates warm.

A schematic summary of this thesis outline and structure is shown below in Figure 1.2.

1.1.2. Structure

In **Chapter 2** an analytical model of population growth and persistence (Figure 1.2) is established to compare and contrast the population dynamics (especially population persistence) of TSD and GSD reptile populations across a range of constant environmental (ambient air) temperatures. It moves beyond speculation and using a simple analytical model, evaluates how climatically-linked juvenile sex ratios and juvenile survival affect population persistence across a range of climates using a plausible and testable model.

In **Chapter 2** the following questions are posed for populations of reptiles with TSD and GSD.

1) How does climate (ambient air temperature) influence population persistence?
2) What are the effects of the interaction between temperature-linked juvenile sex ratios and juvenile survival on population persistence across a range of climates?
3) How does the degree of male limitation on female fecundity affect population persistence when numbers of males (through effects on sex ratio) are influenced by climate?

In **Chapter 3** the response of species to climate at the interior and edges of geographical ranges are evaluated. The role of dispersal in determining range limits is explored extensively, in continuous populations with dispersal (Figure 1.2). **Chapter 2** incorporated temperature, juvenile survival, sex ratio and male limitation in continuous populations without dispersal. In **Chapter 3**, populations living at different climates are linked on a geographic temperature gradient. Similar to **Chapter 2** in the absence of dispersal, the distributions of surviving populations (population persistence) for TSD species would be expected to differ from GSD species, as TSD species have biased juvenile sex ratios. The distribution of populations of reptiles with GSD would be expected to be determined by temperature-linked juvenile survival and the distribution of populations of reptiles with TSD by both temperature-linked juvenile survival and juvenile sex ratio. The adult sex ratio is also expected to influence female fecundity through the effects of the strength of male limitation, such that stronger levels of male limitation reduce female fecundity and ultimately population persistence.

I explore population persistence as a function of temperature, with multiple populations of males and females on a temperature gradient, using simulation modelling. I introduce four levels of dispersal tendency: no dispersal; male only; female only; and two-sex dispersal.

Male biased dispersal is thought to be the predominant pattern of dispersal in reptiles. However, the effects of female dispersal or both sexes dispersing on TSD (and GSD) populations are largely unknown, or undocumented.

The following questions are posed for populations of reptiles with TSD and separately, GSD:

1) How do the parameters of juvenile survival, juvenile sex ratio and male limitation explored in **Chapter 2** in combination with dispersal tendency influence population persistence when dispersal is included in a simulation model?
2) What is the role of dispersal in determining the range limits of species in a stable climate assuming no local adaptation?

The main aim of **Chapter 4** is to evaluate the effects of climate warming (Figure 1.2) on range change or range shift in TSD and populations of reptiles with GSD. The role of climate in determining geographical range changes of species is evaluated using a simulation model.

In **Chapter 4** the following question is posed for TSD and populations of reptiles with GSD:

1) How do dispersal and temperature effects on juvenile sex ratio and juvenile survival influence range change under a warming climate?

In **Chapter 5** the major findings from **Chapters 2, 3**, and **4** are analysed and the major contributions to existing knowledge of this research are evaluated. The shortfalls in data on the parameters analysed in this thesis are identified and the need for empiricists to collect this data to inform research is emphasised. There have been speculations that TSD species with biased primary sex ratios will be adversely impacted by climate warming, but this is the first model to quantify the interaction between climate-linked juvenile survival, juvenile sex ratios and dispersal and their impacts on population persistence as climates warm. A model of the range limits and distributions of persisting TSD and populations of reptiles with GSD is presented for the first time.

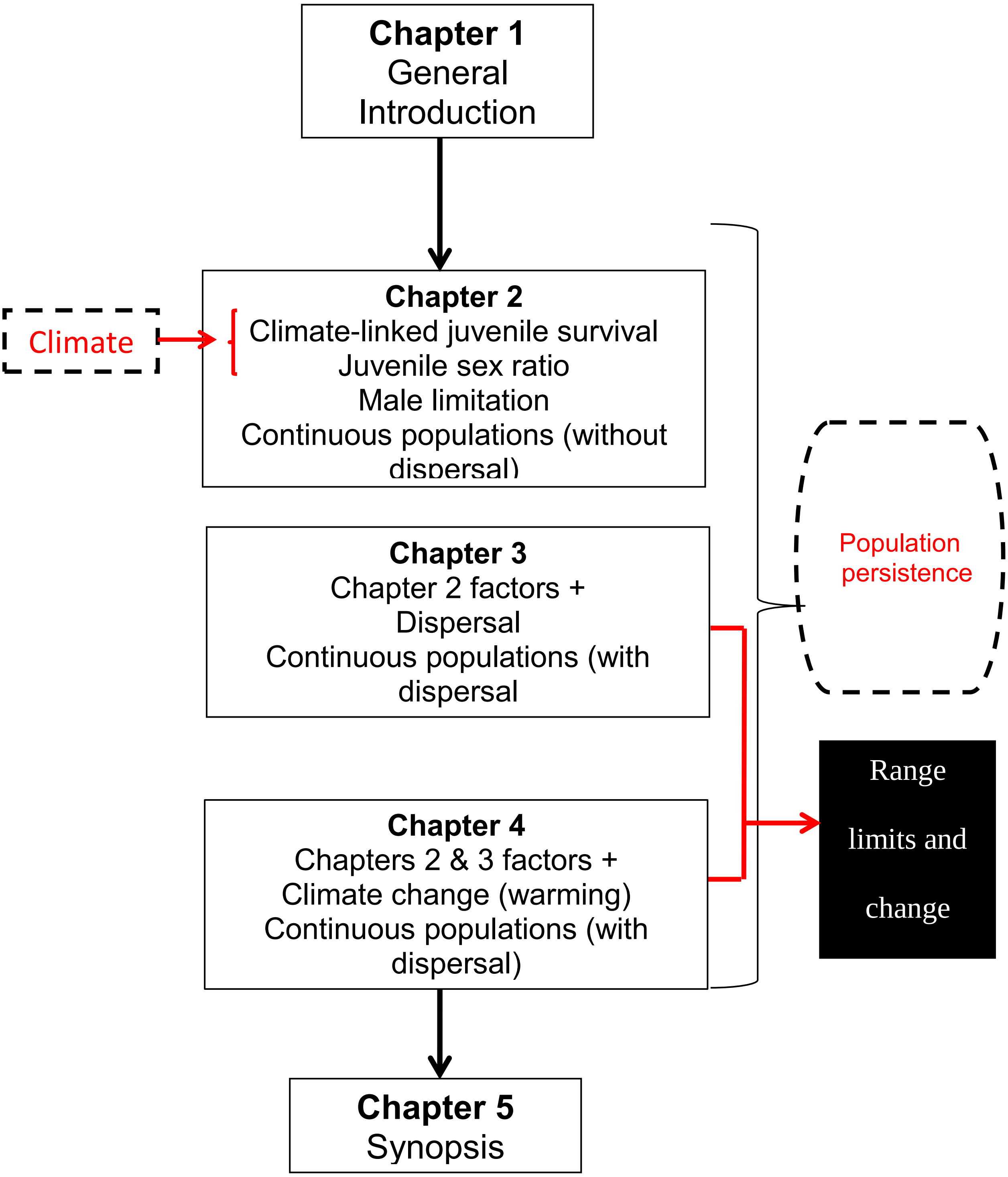


Figure 1.2: Thesis outline and structure

Chapter 2: Modelling effects of climate on reptile populations

2.1. Introduction

Reptiles with TSD are considered to be particularly vulnerable to climate warming, owing to the production of biased primary sex ratios (sex ratios of offspring) (Hays *et al.* 2003; Hawkes *et al.* 2007; Mitchell *et al*. 2008; Hawkes *et al.* 2009; Wapstra *et al.* 2009; Witt *et al.* 2010). Reduced juvenile survival is also anticipated as climates warm in reptile populations with both TSD and genotypic sex determination (GSD) (Hawkes *et al.* 2007; Telemeco *et al.* 2013).

Many populations of reptiles with TSD currently have primary sex ratios that are biased towards the sex produced in warmer climates (Mitchell and Janzen, 2010). Tuatara have primary sex ratios strongly biased towards males at higher temperatures (Mitchell *et al.* 2008; Mitchell *et al.* 2010), but more typically primary sex ratios are biased towards females at higher temperatures (Janzen 1994; Hawkes *et al.* 2007). Such female bias has been demonstrated for all species of marine turtle (Mrosovsky 1983; Georges *et al.* 1994; Wibbels *et al.* 1999; Broderick *et al.* 2001; Poloczanska *et al.* 2009; Patino-Martinez *et al.* 2012) and some freshwater turtles (e.g. *Chrysemys picta*) (Schwarzkopf and Brooks 1987; Janzen 1994). Very minor increases in nest or incubation temperature close to pivotal temperatures (the constant temperature at which both sexes are produced in equal proportions) (Hulin *et al.* 2009) can skew the sex ratio of hatchlings towards females (Yntema and Mrosovsky 1982; Mrosovsky 1988; Janzen 1994; Mrosovsky 1994; Godfrey *et al.* 1999) or towards males in the tuatara (Mitchell *et al.* 2008; Mitchell *et al.* 2010).

Nest temperatures are determined by the interplay of solar radiation and air temperatures. The interaction between climate, soil and topography has also been demonstrated to be influential on nest temperatures (Mitchell *et al*. 2008). Rising air temperatures will increase minimum and mean temperatures, at depth for a given soil type. From this it follows that nest and incubation temperatures will also increase (Godley *et al.* 2002; Hays *et al.* 2003; Georges *et al.* 2005) and primary sex ratios and juvenile survival will be impacted (Mrosovsky *et al.* 1984; Janzen 1994; Hawkes *et al.* 2009; Poloczanska *et al.* 2009; Telemeco *et al.* 2013).

2.1.1. The TSD reaction norm

Theoretically, populations of reptiles with TSD of reptiles with TSD may adapt to warmer climates through phenotypic plasticity in female nesting behaviours or micro-evolutionary changes in the reaction norm (Mitchell and Janzen 2010) (refer to Chapter 1 for more details). The TSD reaction norm describes the relationship between the probability of an individual (or a single clutch) developing as either male or female, and the incubation temperature of the individual (Hulin *et al.* 2009).

Of central importance to the reaction norm are the transitional range of temperatures (TRT), the narrow range of temperatures at which both males and females are produced (Bull 1980). The TRT for the reaction norm is based on data collected from the incubation of mixed samples of eggs (containing both males and females) from various nests at constant incubation temperatures (Hulin *et al.* 2009). The TRT is defined at the population level and does not predict the sex ratio of individuals or single clutches (Hulin *et al.* 2009).

2.1.2. Cohort sex ratio (CSR)

Although much is known about how individual or clutch sex varies with incubation temperature (Bull 1980; Janzen and Paukstis 1991) less is known about the influence of air temperature on the cohort sex ratio (CSR). The CSR is defined as a distribution of p, the proportion of hatchlings that develop as male (Schwanz *et al.* 2010). The CSR response curve describes the relationship between CSR and ambient air temperature in one year and is a population level relationship (Schwanz *et al.* 2010). Hence, the slope of the CSR response curve could range theoretically from very steep, to relatively shallow, depending on the ambient air temperature change required for the transition from a 100% male to 100% female CSR.

There are two reasons that populations could vary with the slope of this curve: differences in how strongly incubation temperature influences individual sex determination (the reaction norm); and plasticity in female nesting behaviours in response to climate (refer to Chapter 1 for extensive details). The pivotal temperature for an individual or single clutch is usually higher than ambient air temperature (Girondot *et al.* 2004). For example the pivotal temperature for the painted turtle (*Chrysemys picta*) is about 28.5^{o}C (nest temperature). By contrast the CSR for the painted turtle is at equity around 24.5^{o}C (ambient air temperature) (Schwanz *et al.* 2010).

The CSR response curve has been described in only a limited number of studies (Wapstra *et al.* 2009; Schwanz *et al.* 2010) and hence lacks empirical data. However, there is some compelling evidence from field studies that warrant further investigations into the relationship between CSR and air temperature (Wapstra *et al.* 2009; Schwanz *et al.* 2010). The snow skink (*Niveoscincus ocellatus*) has an interesting sex ratio pattern. In one population existing at a low elevation a ‘TSD-like’ sex ratio response has been observed. However the bias does not reach the extremes of either all males or all females (Wapstra *et al.* 2009).

In the low elevation population, for the few degrees of mean yearly air temperature (around 16.9 to 18^{o}C) for which data for the CSR (proportion males) were available, the CSR was male biased at lower temperatures, and female biased at higher temperatures (Wapstra *et al.* 2009). The relationship between CSR and temperature has been described by a linear equation with a relatively shallow slope. A 1^{o}C increase in temperature from around 17^{o} to 18^{o}C results in the CSR changing from a 0.7 to 0.3 proportion of males (Wapstra *et al.* 2009).

One of the most detailed descriptions of the relationship between CSR and air temperature is for a population of painted turtles, existing on an island in the Mississippi River near Illinois, USA (Janzen 1994; Schwanz *et al.* 2010). The cohort sex ratios of offspring were highly correlated with mean July air temperature. Painted turtles produce females at higher temperatures and, as July air temperatures increased, CSRs became more heavily female biased. Reduced juvenile recruitment was also found in painted turtles, following a protracted summer with high temperatures in 1988 (Janzen 1994; Schwanz *et al.* 2010). Janzen (1994) postulated that an increase in mean July air temperature of 4^{o}C in the longer term could eventually eliminate males. The CSR response curve may prove to be a useful predictive tool for local population growth, decline and extinction as climates warm.

2.1.3. Temperature-dependent embryonic survival

Whereas much attention has been given to the effects of climate on biased primary sex ratios, far less has been given to juvenile survival and the interaction with CSRs. This is probably because experiments resulting in the death of animals (such as exposing embryos to maximum lethal temperatures) are unlikely to gain approval from animal ethics committees. As detailed in Chapter 1, most of the embryonic development in oviparous (egg laying) reptiles occurs outside of the maternal environment and in the nest, and hence, juvenile survival is strongly linked with environmental temperatures and if temperatures rise (or fall) rapidly then juvenile survival will be adversely impacted.

For empiricists interested in predicting the persistence of species with TSD, these changes in temperature could have multiple adverse effects on CSR and juvenile survival. For example, many nests produce a few males and increasing temperatures are likely to skew primary sex ratios even further towards females. Primary sex ratios are currently around 95% female in many marine turtle species (Hawkes *et al.* 2009). Furthermore, if temperatures exceed the threshold for embryonic development (around 33°C) in marine turtles for sustained periods, embryonic and hatchling mortality will increase (Witt *et al*. 2010).

Throughout this thesis the range of temperatures of climatically-linked juvenile survival is referred to as temperature-dependent embryonic survival. Temperature-dependent embryonic survival has not been extensively researched, but research is imperative as many TSD species (for example, marine turtles) are listed as critically endangered, or endangered (Poloczanska *et al.* 2009; IUCN 2012).

For many reptiles, juvenile survival is reported to occur between temperatures of approximately 17 and 40°C. Juvenile survival in some reptiles is reported to follow a ‘bell-shaped’ (or approximately normal) distribution (Birchard 2004). However, juvenile survival occurs along a much narrower range of temperatures for individual species. Juvenile reptiles are reported (Birchard 2004) to be able to survive better in colder than in warmer temperatures. In contrast, juvenile bearded dragons (*Pogona vitticeps*) are not likely to survive at colder temperatures (Quinn *et al.* 2010). In some reptiles, temperatures above the higher end of the temperature range (for example, greater than 40°C) may be lethal to embryos (Birchard 2004).

There seem to be relatively few studies that report ranges of temperatures for egg or juvenile survival in reptile species. The range of developmental temperatures for juvenile survival in marine turtles has been reported as approximately 24 to 35°C (Yntema and

Mrosovsky 1982; Hawkes *et al.* 2007), 22 to 32°C for the painted turtle (Schwarzkopf and Brooks 1987) and 20 to 30°C for the snapping turtle (Steyermark and Spotila 2001). The differences in these temperature ranges may occur as a consequence of local adaptation in thermal tolerances between TSD species. Sustained exposure during the incubation period to temperatures beyond the critical incubation range may lead to considerable juvenile mortality (Broderick *et al.* 2001).

2.1.4. Male limitation

Temperature-dependent embryonic survival and CSR may strongly influence population persistence in many reptile species. Although not directly temperature-linked, the adult sex ratio may influence female fecundity, through the effects of the strength of male limitation and, hence, also affect population growth and persistence.

Studies of non-reptile species with female biased sex ratios (not temperature-dependent) have found varying results with respect to the effect of reduced numbers of males on female fecundity and population viability. In the saiga antelope (*Saiga tatarica*) (Milner-Gulland *et al.* 2003) male limitation had a negative effect on population growth as males were trophy hunted, and adult sex ratios became very biased towards females as a consequence. Females were unable to find mates and fecundity and population viability declined considerably (Milner-Gulland *et al.* 2003).

In the butterfly *Hypolimnas bolina,* an inherited infection passed from females to males (but not affecting other females) results in ultra-biased female juvenile sex ratios, where the ratio of males to females is around 1 to100. In *H. bolina* populations, very small numbers of males can fertilise large numbers of females successfully and population viability is largely unaffected (Dyson and Hurst 2004). However, there is a lack of data on how primary and adult sex ratios affect population viability and persistence in many species

(Rankin and Kokko 2007) and studies that quantify population growth and density even at the most basic levels are also lacking (Sibly and Hone 2002).

The effects of male limitation where female fecundity is limited by the abundance of males are largely unquantified in reptile species. In single sex (female) population models, female fecundity is not considered to be limited by the number of males (Rankin and Kokko 2007). Monogamous populations are thought to be very sensitive to changes in the sex ratio, and a large decrease in numbers of males may result in reduced population growth (Sibly and Hone 2002; Rankin and Kokko 2007; Wright *et al.* 2012). Low numbers of males may not always adversely affect female biased populations. In marine turtles some nesting beaches have been able to retain viable populations with strong female biases for at least several decades (Godfrey *et al.* 1999; Hays *et al.* 2003; Hawkes *et al.* 2009; Poloczanska *et al.* 2009). There is no evidence that low numbers of male hatchlings limit female fecundity and population viability in larger populations of marine turtles (Broderick *et al.* 2000; Hawkes *et al.* 2009). However, in smaller populations with strong female biases the low numbers of males could reduce female fecundity (Wright *et al.* 2012).

Females require sperm to produce viable eggs, so female fecundity is eventually limited by males. However, there are several reasons why the level of male limitation may be low in female biased populations of marine turtles. Firstly, males mate with multiple females (Broderick *et al.* 2001; Pearse *et al.* 2002). Secondly, female turtles can store viable sperm for up to four years (Pearse *et al.* 2002). Reproductive intervals in female marine turtles are typically between 2 and 4 years (Pearse *et al.* 2002). An advantage of sperm storage in long-lived organisms is that females can produce offspring without having any contact with males for a number of years. This is beneficial if there are low numbers of males, or after males are deceased (Zamudio and Sinervo 2000; Pearse and Avise 2001; Pearse *et al.* 2002).

Sperm storage also enables sperm competition, an extension of mate competition, without males directly competing, or coming into contact with each other at all, and may lead to greater 'fitness' (for example, larger size and greater mobility) in offspring, given that there are enough males to ensure the successful insemination of females (Pearse and Avise 2001; Pearse *et al.* 2002). Finally, age at first reproduction and frequency of mating can also affect the population dynamics of female biased populations. Populations that reproduce earlier and more frequently have the advantage of greater potential population growth and viability (Ferrer *et al.* 2004). These populations are likely to be able to withstand the impacts of low numbers of males as more offspring are produced (Calsbeek *et al.* 2002; Ferrer *et al.* 2004; Wright *et al.* 2012). A recent study of mating patterns in the endangered green turtle (*Chelonia mydas*) indicated that despite a 95% female biased primary sex ratio there were around 1.4 adult males for every adult female at the nesting beaches studied (Wright *et al.* 2012). This indicates that male reproductive patterns may be shorter than the 2 to 4 year interval of females, and/or males frequently move between female biased nesting beaches. The later explanation was supported by satellite tracking of male movements between assemblages of females (Wright *et al.* 2012). Hence, the mating patterns of male green turtles may have the potential to reduce some of the effects of potentially reduced female fecundity owing to male shortages (Wright *et al.* 2012).

For many reptile species, important life history parameters such as juvenile sex-ratio and juvenile survival depend on ambient temperature. This suggests that population size and population persistence could be strongly influenced by local climate. Furthermore, the adult sex ratio may influence female fecundity through the effects of the strength of male limitation and also affect population persistence. There are large gaps in our knowledge of these factors empirically, or how temperature-dependent embryonic survival, juvenile sex ratio and male limitation interact in continuous populations and affect population persistence. This chapter is a first step towards elucidating the nature of the relationships between these factors, and how they interact in determining population persistence in theoretical populations of females in stable climates, using a population model.

2.1.6. Aims

In this study the population dynamics of female biased populations of reptiles with TSD are compared and contrasted with the dynamics of genotypic sex determination (GSD) populations with balanced sex ratios in stable climates. This is the first known attempt to estimate the effects of temperature on both juvenile survival and CSR, and the effects of male limitation, and the combined effects of these on continuous populations without dispersal.

The relationship between CSR and ambient air temperature was investigated through the CSR response curve (a distribution of the proportion of hatchlings that develop as male against ambient air temperature). The relationship between juvenile survival and ambient air temperature was investigated through the temperature-dependent embryonic survival (TS) curve. A sensitivity analysis of temperature, CSR, juvenile survival and male limitation will be undertaken on population dynamics.

The model is a first step in understanding how CSR interacts with TS and male limitation. It allows investigation of these interactions on population dynamics, in particular on population size and population persistence. The study will assist in identifying the data that are needed by empiricists interested in studying the persistence of TSD species in an environment with ongoing climatic change using a general non-species-specific model. Four theoretical CSR response curves of varying slope in combination with three temperature-dependent embryonic survival (TS) curves for juvenile females and three levels of male limitation (none, moderate and strong) were used to investigate the relative effects of temperature-dependent embryonic survival, the CSR response curve and the interaction between these and male limitation on population growth and persistence (number of surviving populations) in a range of stable climates. It is important to note that these relationships are for single-sex populations (of females) and not individuals.

2.2. Methods

2.2.1. Model description

Theoretical populations of females with GSD (genotypic sex determination), GSD+TS (genotypic sex determination combined with temperature-dependent juvenile survival), TSD (temperature dependent sex determination) and TSD+TS (temperature -dependent sex determination combined with temperature- dependent juvenile survival) were evaluated. These populations were collectively referred to as populations of reptiles with TSD, or GSD. For populations of reptiles with GSD, the CSR was not influenced by ambient air temperature and the proportion of females was 0.5. Temperature-dependent survival of juveniles was referred to as juvenile TS, or more simply TS. Distributions used to model TS were referred to as TS curves. For populations of reptiles with TSD, sex ratios were biased towards males at the lower temperatures and females at the higher temperatures i.e. TSD 1A. The code for the analytical model was developed using the object-oriented programming language Matlab version 2012b.

2.2.2. Population size

Deterministic population growth is density dependent, i.e., it tracks the number of females (N_f) in a population. The population equation (Equation 1) was developed by Professor Jim Hone, and describes logistic population growth. The left-hand side of the equation relates to growth and the right-hand side to recruitment, incorporating demographic parameters A small level of density dependence in juvenile survival has been incorporated, in accordance with models developed by Professor Hone.

$$\mathrm{N_f}(t+1) = \mathrm{N_f}(t)s + \mathrm{N_f}(t)B(1-p)a\mathrm{e}^{-c\mathrm{N_f}(t)} \qquad \text{eqn 1}$$

where,

N(t) = population size at time t

s = adult survival, (0.95) (Congdon *et al*. 1994)

B = number of offspring (eggs laid) per adult female, (with male limitation, 0 to 10)

p = proportion of hatchlings that develop as male (and 1-p, the proportion of hatchlings that develop as female), (TSD: 0 to 1, depending on temperature. GSD: 0.5) (Bull 1980)

a = baseline juvenile survival, (0 to 0.015, depending on temperature) (Heppell 1998)

c = parameter for density dependence in juvenile survival, (0.001) (Jim Hone, *pers.comm*)

T = temperature (^{o}C) (Birchard, 2004).

These parameters are for a long-lived animal consistent with average life expectancy for many turtles of around 20 years (Congdon *et al.*1994; Heppell 1998), for example the painted turtle (Schwanz *et al*. 2010). Baseline juvenile survival (a) is modified by c, and the further c is away from zero, the stronger the effect of density on juvenile survival. If c=0, there is no effect of density and baseline juvenile survival remains at a. For the purpose of modelling, baseline juvenile survival was either held constant (a=0.015; no TS) or depended on environmental temperature, described by a normal or left-skewed curve with a maximum baseline juvenile survival (a_{max}=0.015; TS, see below for more details) (Heppell 1998). Age at first reproduction was set at one year (Lande 1988) and the maximum number of offspring (number of eggs laid) per adult female was set at B_{max}=10. B was a function of the adult sex ratio and, in some scenarios could decline as males became rarer (i.e., male limitation, see below). Each time step is equivalent to one year. Models were parameterised based primarily on painted turtles (Schwanz *et al*. 2010).

Equation 1 can be re-arranged to estimate the population size of females at equilibrium ($N(t+1) = N(t)$), when $N_f^* = K$ (carrying capacity) (Equation 2).

$$N_f^* = -\left(\frac{1}{c}\right) log_e \left(\frac{1-s}{a \times B \times (1-p)}\right) = \mathrm{K} \qquad \text{eqn 2}$$

Equation 1 represents a discrete model of population growth. Equation 1 was used to estimate population growth over time in Figures 2.1 (a) to (c). Equation 2 was used to estimate population sizes of females at equilibrium.

The population size at one step forward $N(t+1)$ depends on the current population size $N(t)$ (May 1981). Models for population growth in a limited environment are based on two fundamental premises. Firstly, that populations have the potential to increase exponentially; and secondly that there is density-dependent feedback that progressively reduces the maximum rate of population increase (r_m) (May 1981). There are issues surrounding population stability for populations with varying life spans (Figures 2.1(a) to (c)). The populations in this chapter are long-lived (i.e., around 20 years) and the issues affecting relatively short-lived populations (such as stochastic fluctuations and short-term population ‘crashes’) are unlikely to affect them as the maximum rate of population growth (r_m) is unlikely to be greater than 2.00 (May 1981). Maximum annual population growth rate (r_m) is 0.10 per annum, given that maximum parameter values (listed above) are assuming density-independence (c=0) and all offspring are female (p=0). When $2.00 < r_m < 2.50$ the population approaches K with damped oscillations (Figure 2.1(b)).

2.2.3. Cohort sex ratio and temperature

Cohort sex ratio (CSR) response curves are a distribution of p (the proportion of hatchlings that develop as male) against ambient air temperature. Four CSR curves were developed to explore the relationships between p (sex ratio) and air temperature for populations with TSD.

The slopes of several CSR response curves (Hawkes *et al.* 2007; Wapstra *et al.* 2009) were explored to determine if there were variants with a steeper (shallower) slope than for the painted turtle (Schwanz *et al.* 2010) in populations of reptiles with TSD (Figure 2.2(a)). The slopes of the CSR response curves for the painted turtle (Schwanz *et al.* 2010) and snow skink (Wapstra *et al.* 2009) were identical. In contrast, the slope for the loggerhead turtle (*Caretta caretta*) was more shallow (Hawkes *et al.* 2007) (Table 2.1).

I chose to use the data for the painted turtle as the basis of my explorations of parameter space due to the wealth of data available (Schwanz *et al.* 2010). Sex ratio was reported to be negatively related to mean July (summer in the northern hemisphere) air temperature through a linear equation with a slope of -0.147 and T is the long-term mean value for July temperature at 23.9^{o}C predicting a male biased cohort (sex ratio=0.63) (Schwanz *et al.* 2010). Although empirical data were not available for alternative CSR response curves, I also explored results for species that have steeper (or shallower) CSR response curves than the painted turtle (Figure 2.2(a)).

The first CSR response curve was for populations of reptiles with GSD, where the offspring sex ratio was 0.5 for all air temperatures. Curve 1 (Figure. 2.2(a)) represents GSD with corresponding parameters for the slope (β=0.0) and intercept (α=0.5). Because the CSR curve is likely to vary across populations of reptiles with TSD and is known for only a few species, we considered results for several different CSR response curves (Hawkes *et al.*, 2007;

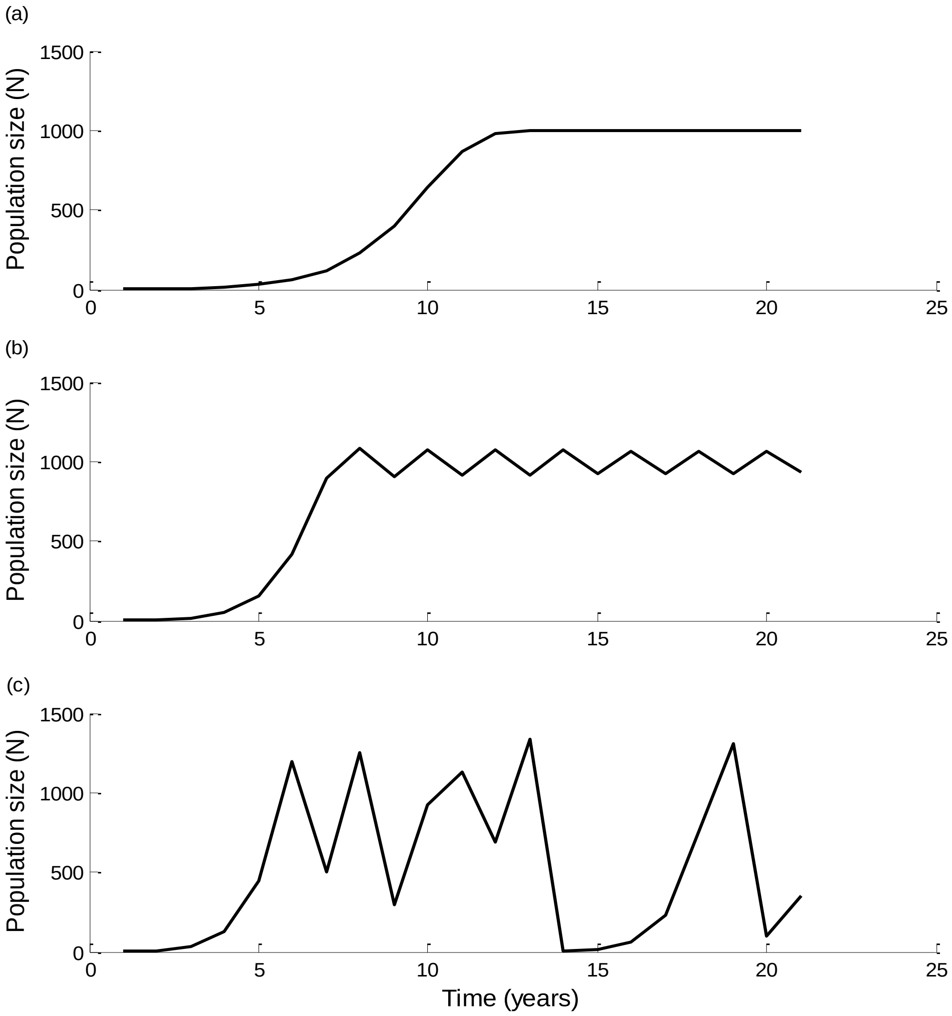


Figure 2.1: Logistic growth curves for varying population sizes. (a) When r_m <2.00 for example (r_m =1) for longer-lived populations (e.g. 20 years). (b) When 2.00< r_m <2.50 for example (r_m =2) for populations with a 'medium' life span (e.g. 8 years). (c) When r_m >2.50 for example (r_m =3) for very short-lived populations (e.g. 1 to 2 years) large fluctuations occur and the population doesn't converge on carrying capacity (adapted from May (1981), Figure 2.2).

Wapstra *et al.,* 2009; Schwanz *et al.,* 2010) (Table 2.1, Figure 2.2(a)). CSR response Curve 2, the first TSD curve (Figure 2.2(a)) represents a species with a shallow slope (β=-0.069) and an intercept of α=2.28. Curve 3 (Figure 2.2(a)) uses the parameters derived for the painted turtle (Schwanz *et al.,* 2010) with intercept α =4.14 and slope β=-0.147. CSR response Curve 4 (Figure 2.2 (a)) represents a species with a steeper slope (β=-0.454, α=11.48) relative to the painted turtle. The curves cross at approximately 0.6 proportion male offspring because this was the sex ratio produced at the long-term average air temperature for painted turtles (Schwanz *et al.,* 2010). Because we calculated population size for stable air temperatures, p did not fluctuate across years.

2.2.4. Juvenile survival and temperature

For GSD and TSD (no TS) juvenile survival (ae^{-cNf}) depended only on density from a at the lowest density and tending towards zero near $N_f(t+1)=N_f(t)$. For GSD+TS and TSD+TS, baseline juvenile survival (a) of females depended on temperature according to a normal or a 'reverse' chi square (left-skew) distribution and these are referred to as TS curves (Figure 2.2(b)). TS curves apply to both male and female juveniles. However, in this chapter, population growth and persistence for female populations only are evaluated. The identification of 'bell shaped' distributions of hatchability detailed by Birchard (2004) provided a basis for selecting a 'normal' distribution to model juvenile TS. A left-skew distribution may also occur where there is a 'long-tail' of low probabilities of juvenile survival at the 'cold' end and a relatively steep decline to zero at the 'hotter' end (lethal temperature) of the temperature distribution.

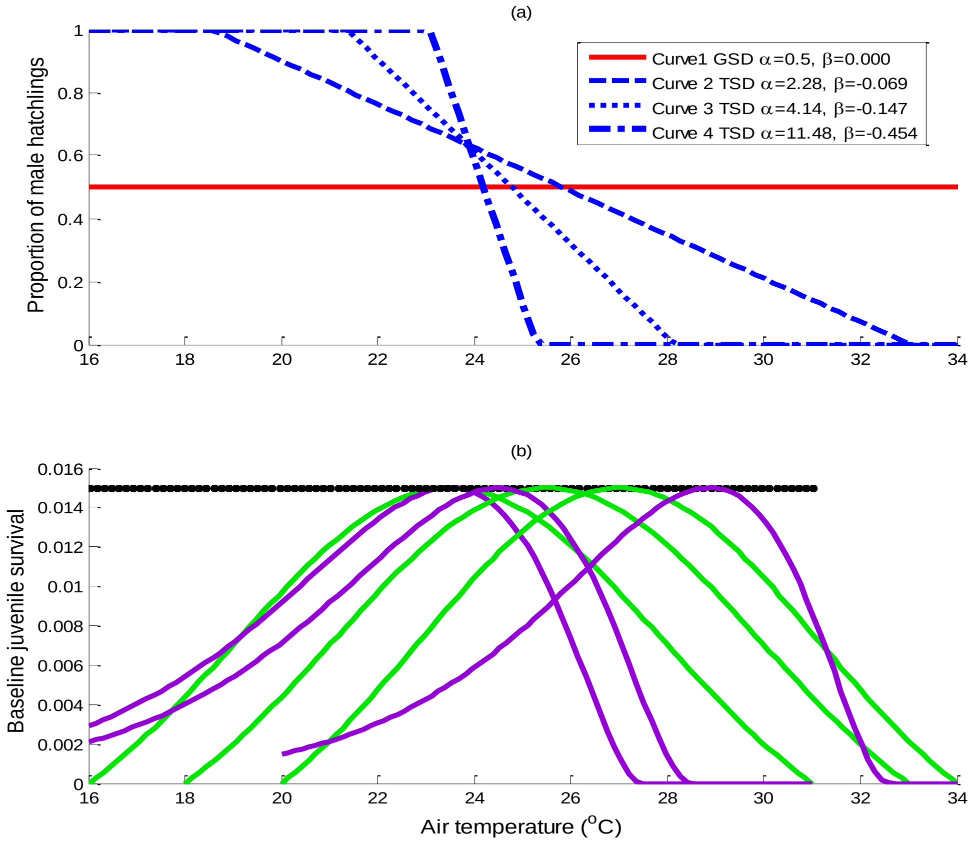


Figure 2.2: Cohort sex ratio (CSR) response curves and baseline juvenile survival curves. (a) CSR response curves for GSD (or perfectly plastic TSD) (Curve 1). TSD (Curve 3) uses the regression equation parameters for the slope and intercept estimated from data on the painted turtle (Schwanz *et al.* 2010). TSD (Curves 2 and 4) use parameters for hypothetical species with shallower and steeper slopes for CSR response curves, respectively. The left-skew curves were truncated before they became negative as the values of juvenile survival are positive (*α* = the intercept, *β* = the slope). (b) Normal (green) and left-skew (purple) distributions (TS curves) of baseline juvenile survival *a* distributed along temperature gradients 1, 2 and 3. Maximum baseline juvenile survival (a_{max}=0.015) is denoted by the black line.

Table 2.1: Details of cohort sex ratio (CSR) response curves for the snow skink, painted turtle and loggerhead turtle.

Species	**Slope (*β*)**	**Range of temperatures with intermediate CSR**	**Source**
Painted turtle (*Chrysemys picta*)	-0.147	21 to 27^{o}C	(Schwanz *et al.* 2010)
Snow skink (*Niveoscincus ocellatus*)	-0.147	17 to 18^{o}C	(Wapstra *et al.* 2009)
Loggerhead turtle (*Caretta caretta*)	-0.069	24 to 29^{o}C	(Hawkes *et al.* 2007)

2.2.4. Juvenile survival and temperature

For GSD and TSD (no TS) juvenile survival (ae^{-cN_f}) depended only on density from a at the lowest density and tending towards zero near $N_f(t+1)=N_f(t)$. For GSD+TS and TSD+TS, baseline juvenile survival (a) of females depended on temperature according to a normal or a ‘reverse’ chi square (left-skew) distribution and these are referred to as TS curves (Figure 2.2(b)). TS curves apply to both male and female juveniles. However, in this chapter, population growth and persistence for female populations only are evaluated. The identification of ‘bell shaped’ distributions of hatchability detailed by Birchard (2004) provided a basis for selecting a ‘normal’ distribution to model juvenile TS. A left-skew distribution may also occur where there is a ‘long-tail’ of low probabilities of juvenile survival at the ‘cold’ end and a relatively steep decline to zero at the ‘hotter’ end (lethal temperature) of the temperature distribution.

Both distributions were ‘scaled’ such that the maximum height of the curves was equal to $a=a_{\max}=0.015$ and $a=0$ at both ends of the distribution, at the minimum or maximum survival temperature. The range of temperatures determines how the temperature of the maximum baseline juvenile survival relates to CSR, and may influence the results. Hence, TS curves were modelled using three gradients of environmental temperatures (16 – 31°C, 18 – 33°C and 20 – 35°C), with respective peaks of 23°C, 25°C and 27°C (Figure 2.2(b)). The TS curves distributed along each of the three temperature gradients are shown in Figure 2.2(b). The gradients of environmental temperature were based on temperature ranges for juvenile survival reported for some GSD turtles (Birchard 2004) and TSD turtles (Yntema and Mrosovsky 1982; Schwarzkopf and Brooks 1987; Steyermark and Spotila 2001; Hawkes *et al.* 2007).

2.2.5. Male limitation

For populations exhibiting TSD (GSD) there were three levels of male limitation on female fecundity: none, moderate and strong. The probability of fertilisation of a female (Pr(*fert)*) is described as a function of adult sex ratio (ASR) and estimated using equation 3.

$$\Pr(fert) = \frac{ASR}{ASR + b} \qquad \text{eqn 3}$$

The shape parameter for equation 3 is *b* (Rankin and Kokko 2007), and represents the relative strength of male limitation on female fecundity. If *b*=0, males do not limit female fecundity, and, if b=1, males strongly limit female fecundity. Three levels of male limitation on female fecundity in accordance with Rankin and Kokko (2007) were:

b=0, no male limitation on female fecundity;

b=0.01, a moderate level of male limitation on female fecundity and;

b=0.1, a strong level of male limitation on female fecundity.

The effect of parameter *b* on the relationship between the fertilization and the sex ratio is illustrated in Figure 2.3.

The adult sex ratio (ASR) is the proportion of males in the population, and was estimated from the CSR of the population as:

> ASR=The number of adult males in the population/ (the number of adult males in the population+the number of adult females in the population).

CSR does not directly correspond to ASR as 1) there is a time lag and 2) differential survival of male and female juveniles occurs when TS applies. Ideally, male population size would be calculated using a separate growth equation. However ASR may be estimated from the cohort sex ratio in the population given the following assumptions.

1. There are no fluctuations in temperature over time.
2. Juvenile survival and separately adult survival were equal for males and females.

Fecundity was thus estimated using equation 4.

$$B = B_{max} \times \Pr(fert) \qquad \text{eqn 4}$$

When males are never limiting (b=0), female fecundity is always at its maximum (B=B_{max}=10). As the proportion of adult males declines in combination with greater sensitivity of fertilisation probability (b) to ASR, the probability of female fertilisation decreases with a consequent decrease in the number of female offspring.

2.2.6. Combined effects of juvenile survival, cohort sex ratio, temperature, and of male limitation

Each of the effects outlined in the previous sections of the Methods are modelled using equation 1 and the place in which they act in equation 1 is shown below (Figure 2.4). Equation 1 can then be rewritten to show the specific incorporation of the effects and becomes equation 5.

$$\mathrm{N_f}(t+1) = \mathrm{N_f}(t)s + \mathrm{N_f}(t)B(b, ASR)\big(1 - p(T)\big)a(T)\mathrm{e}^{-c\mathrm{Nf}(t)} \qquad \text{eqn 5}$$

where $B(b$, ASR) is the effect of male limitation on fecundity (B), $p(T)$ is the effect of temperature on CSR and $a(T)$ is the effect of temperature on juvenile survival.

The population equation used to calculate equilibrium population sizes in the results was equation 6. The parameters and values are identical to equation 1.

$$N_f^* = -(\frac{1}{c})\, log_e\left(\frac{1 - s}{a(T) \times B(b, ASR) \times (1 - p(T))}\right) = \mathrm{K} \qquad \text{eqn 6}$$

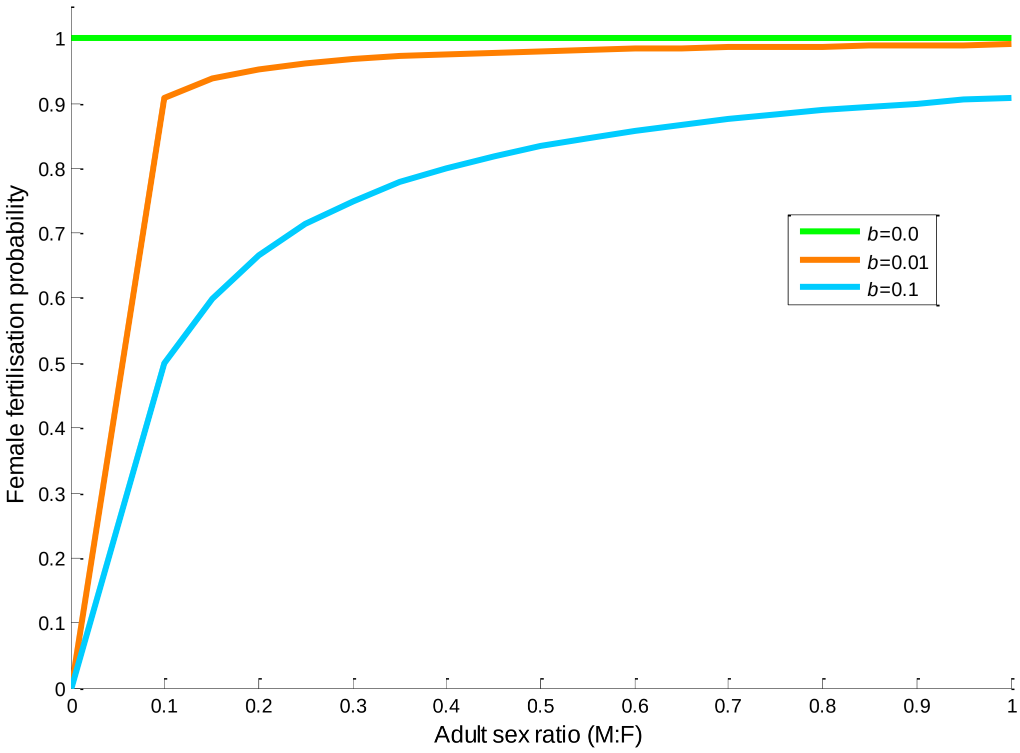


Figure 2.3: The female fertilisation probability as a function of adult sex ratio (ASR). The different lines represent different sensitivities of fertilisation probability to changes in the ASR (after Rankin and Kokko (2007)).

$$N_f(t+1) = N_f(t)s + N_f(t)\overset{\substack{\text{Male limitation}\\ \text{acts on } B\\ \downarrow}}{B}(1-\underset{\substack{\uparrow\\ \text{Cohort sex ratio}}}{p})\overset{\substack{\text{Juvenile survival}\\ \downarrow}}{a}e^{-cN_f(t)} \qquad \text{eqn 1}$$

Figure 2.4: Incorporation of the effects of juvenile survival (*a*), cohort sex ratio (*p*), temperature, and of male limitation.

The response of population size (*N)* at equilibrium (*N**) to variation in baseline juvenile survival (*a,* Table 2.2) and CSR (*p*) due to climate (air temperature) was investigated. Hence N_f was explored over *T* parameter space (Table 2.2). In equations 1 (and 5) and 2 (and 6), the two variables that may depend on *T*, *a* and *p*, are multiplicative. As described above, the parameter space that relates both *a* and *p* to *T* was explored by varying the CSR and TS curves. The interaction between male limitation and these parameters was also evaluated. The separate effects of density dependence, juvenile survival and temperature, CSR and temperature and male limitation are outlined using a single example for GSD and, separately TSD species. This will enable greater clarification of how each effect is individually modelled through equation 6 (the equation used to estimate population size). Subsequently all contingencies of the combined and interactive effects will be described in detail, as follows below.

2.3. Results

2.3.1. Model behaviour and sensitivity

The parameters used to estimate population size in equation 6 are all equal to the values listed below equation 1, unless otherwise specified. If baseline juvenile survival is constant at *a*=0.015 and males do not limit female fecundity, only density limits population size (Figure 2.5).

For populations of reptiles with TSD, the CSR curve used is the medium slope (β=-0.147) unless otherwise specified. To illustrate the effects separately, only the temperature gradient from 18 to 33^{o}C will be used. The combined effects will be evaluated across all temperature gradients.

Each line in a particular distribution (Figures 2.6 to 2.11) represents the population sizes of females in ecological equilibrium along a gradient of temperatures (calculated from equation 6). Hence the line can be interpreted to represent comparative population sizes of 1) populations distributed across different climates (population growth occurred at around 23.9^{o}C) or 2) a single population with a changing climate over time (for example, one usually at 23.9^{o}C). The former interpretation was taken with respect to the results (Figures 2.6 to 2.11).

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2.3.2. Population size

A simple example of logistic population growth over time generated using equation 1 is shown in Figure 2.5. The equilibrium population size is 1000.

Table 2.2: A description of the parameter space of baseline juvenile survival (*a*) and the proportion of male offspring (*p*) used to estimate the effects on population size (N).

Parameter	**Definition**	**Range**
Slope(β), $p[T]$	Relationship between p and air temperature	[0, -0.069, -0.147, -0.454]
$a[T]$	Relationship between a and air temperature	None, normal and left-skew
$a_{max}\,[T]$	Peak of '$a_{\max}$' occurs at three air temperatures (T)	23, 25, 27^{o}C

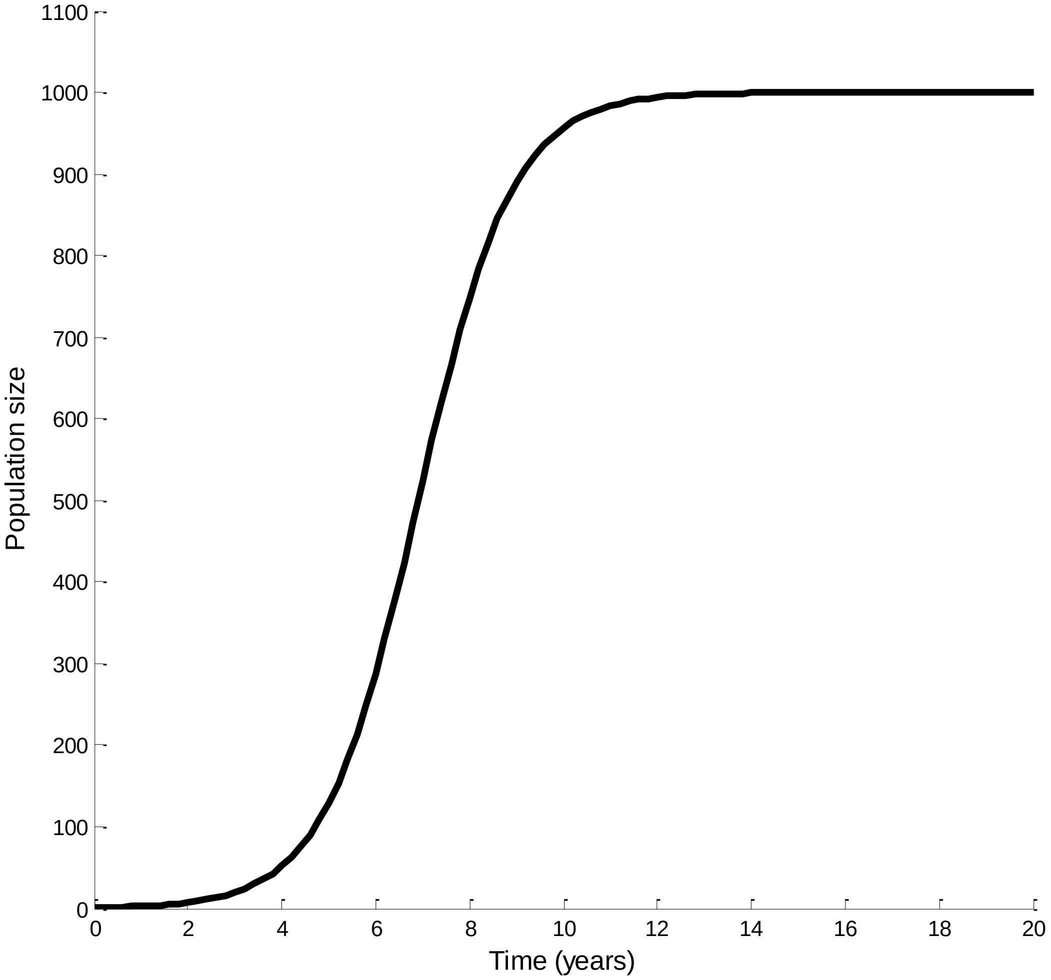


Figure 2.5: Simple logistic population growth for a single population generated using equation 1 at 24.5^{o}C.

2.3.3. Cohort sex ratio and temperature

This example illustrates the population sizes reached for GSD (no TS) and TSD (no TS) populations if baseline juvenile survival is constant at a=0.015 and in the absence of male limitation (i.e. only density limits population growth). Equilibrium populations are sustainable indefinitely at the same size across temperatures for GSD (K=400, Figure 2.6) and at temperature-dependent sizes for TSD (maximum K=1099, Figure 2.6). The difference between populations of reptiles with GSD and TSD is that temperature acts on p (or sex ratio) for TSD, resulting in sex ratios that range from 0 (100% female) to 1(100% male). Populations are size zero if 100% males are produced. In the absence of male limitation, populations are at maximum size when 100% females are produced.

In contrast, for populations of reptiles with GSD, the sex ratio is at equity and hence has constant equilibrium population sizes (Figure 2.6). Populations have greater growing potential when female-biased than when the sex ratio is at equity. The greater potential for growth in female-biased populations leads to a greater K.

The following example for TSD (no TS) populations demonstrates the effect of changing the slope parameter of the CSR response curve from shallow β=-0.069 (curve 2) to medium β=-0.147 (curve 3) to steep at β=-0.454 (curve 4) (Figure 2.6). The steeper slope indicates that a smaller change in temperature is needed to switch from a CSR of 100% male to 100% female. When males don’t limit female fecundity, curve 4 results in populations with larger numbers of female offspring produced, surviving and recruited in the middle temperature ranges than for the other CSR curves (Figure 2.6). Hence, curve 4 produces larger populations at intermediate temperatures but still reaches the same maximum population size as the other CSR response curves, for populations of reptiles with TSD.

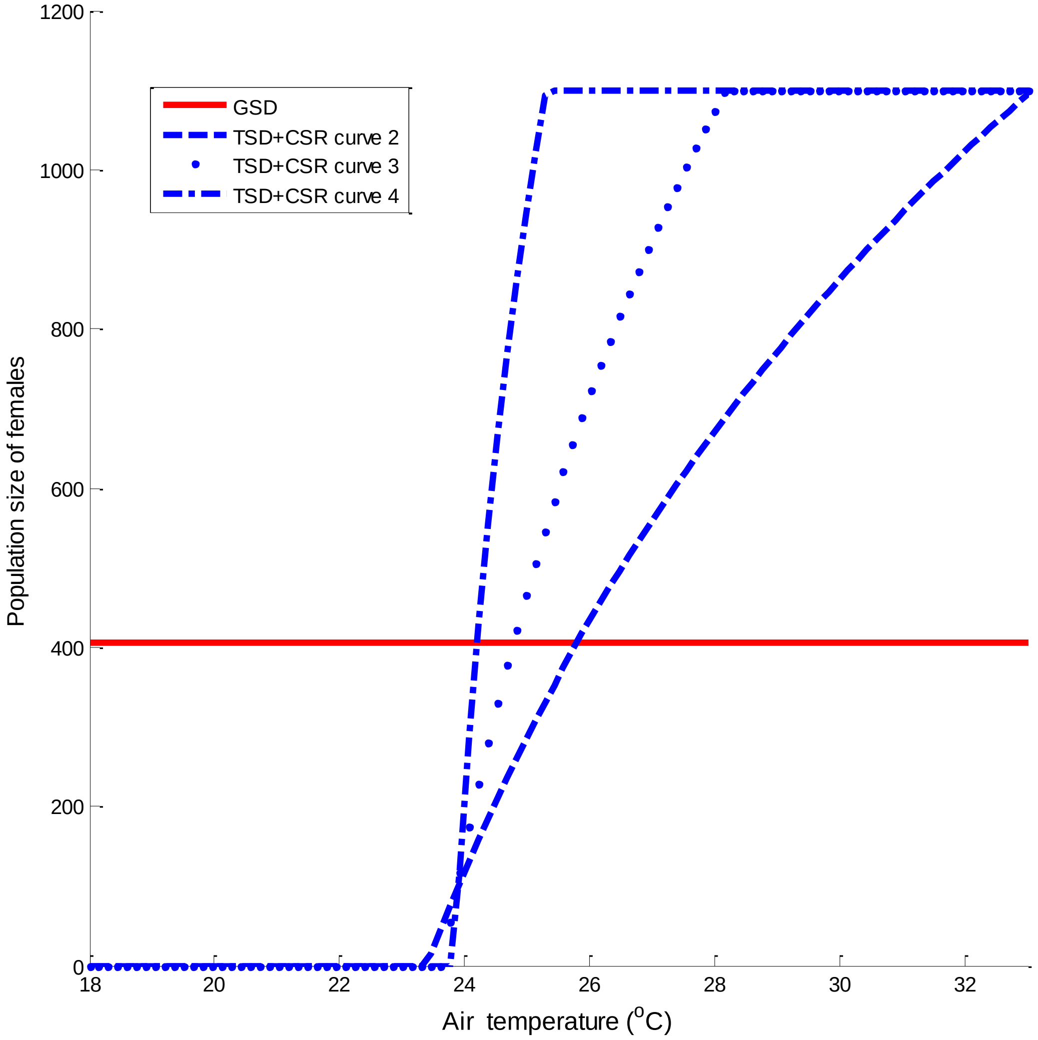


Figure 2.6: Population sizes of females for cohort sex ratio (CSR) response curves. Populations of females for GSD with CSR curve 1 (zero slope) and TSD (no TS) with CSR curve 2 (shallow slope) and separately CSR curves 3 (medium slope) and 4 (steep slope). CSR curves are shown for temperature gradient 2 (18 to 33°C).

2.3.4. Juvenile survival and temperature

The following examples for GSD and populations of reptiles with TSD are used to illustrate how temperature acts on juvenile survival (*a*), through equation 6, using the TS normal curve for juvenile survival. For populations of reptiles with GSD and for populations of reptiles with TSD the effect of normally distributed TS on respective CSR curves 1 and 2 are shown, and populations are no longer sustainable indefinitely for GSD+TS (Figure 2.7). For GSD+TS populations, the CSR was at equity across all temperatures and levels of juvenile survival. In contrast, the CSR was biased towards females at the temperature of maximum juvenile survival ($a=a_{\max}$ at 25°C) for TSD + TS populations in temperature gradient 2. In the absence of male limitation for populations of reptiles with TSD, greater numbers of female offspring were produced, survived and were recruited than in GSD+TS populations where the CSR was around equity (Figure 2.7).

2.3.5. Male limitation

The strong effects of female bias on population growth are reduced with the introduction of male limitation on female fecundity. This is described in greater detail in the section of the results that follows on combined effects. As an example of the effect of male limitation on GSD (no TS) and TSD (no TS) populations, population sizes are shown with the three levels of male limitation i.e., none (b=0), moderate (b=0.01) and strong (b=0.1) (Figure 2.8). Thus, the effect of male limitation on population size in populations of reptiles with TSD varies across temperatures because sex ratio varies across temperatures (Figure 2.8).

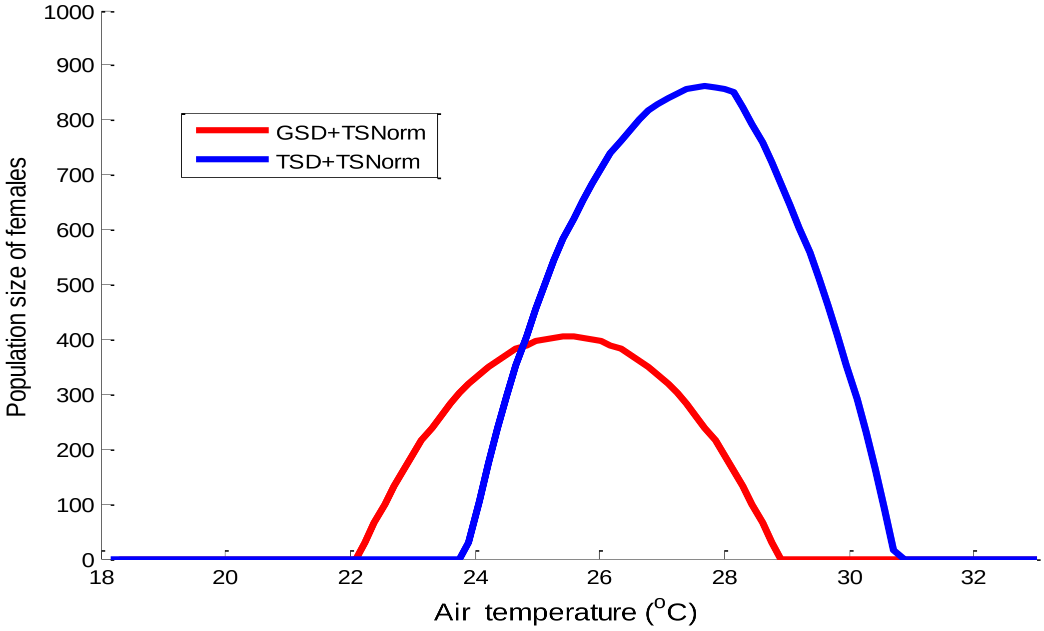


Figure 2.7: Female population size without male limitation. Populations of females for GSD and TSD (with TS) and without male limitation on female fecundity, for temperature gradient 2. TSD is shown with CSR curve 3 (slope β=-0.147). Population size is limited by TS as well as density dependence. Note: TSD+TS peaks at a higher temperature than GSD+TS.

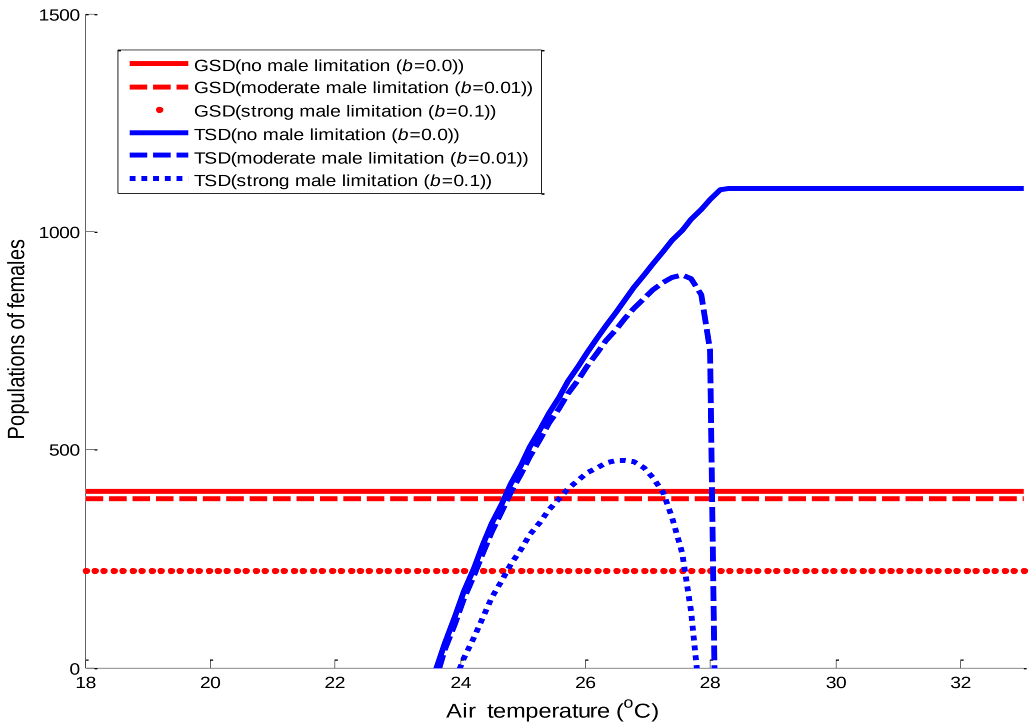


Figure 2.8: Populations of females for genotypic sex determination (GSD) and temperature-dependent sex determination (TSD) and no temperature-dependent embryonic survival (TS) with varying levels of male limitation, for temperature gradient 2.

2.3.6. Combined effects of juvenile survival, cohort sex ratio, temperature, and male limitation

2.3.6.1. Populations of reptiles with GSD

For GSD+TS populations, population persistence (range of temperatures at which populations persisted above size zero) and population sizes were linked to the relationship between baseline juvenile survival (a) and air temperature (Table 2.2, Figures 2.9 to 2.11). The normal temperature-dependent embryonic survival (TS) curve was wider than the left-skew TS curve (Figure 2.2(b)) and resulted in larger population sizes, over a wider range of temperatures (compare dashed and dotted red lines in Figures 2.9 to 2.11).

The moderate level of male limitation had little or no effect on population growth and persistence (Figure 2.10). In contrast, at the strong level of male limitation, the reduction in female fecundity led to much smaller population sizes across the temperature range and population persistence over a narrower range of temperatures (Figure 2.11). This is not surprising as there is a substantial reduction in fertilization even with a 1:1 sex ratio when b=0.1. Hence, a drop in population size should be expected under GSD (Figure 2.3). However, the effects of male limitation on fecundity resulted in the production of fewer females and, hence, a smaller number survived and were recruited (Figure 2.11).

2.3.6.2. Populations with TSD

2.3.6.2.1. Populations of reptiles with TSD with no male limitation on female fecundity (*b*=0)

Warmer climates or higher ambient air temperatures producing female-biased sex ratios resulted in larger population sizes and persistence of females (Figure 2.9) relative to populations of reptiles with GSD. However, a continued reduction in the number of males through male limitation reduced population sizes (Figures 2.10 and 2.11).

For TSD (no TS) populations, all CSR response curves eventually resulted in strongly biased female CSRs and populations of the same relatively large sizes at high enough temperatures (comparing columns in Figure 2.9). However, populations of reptiles with TSD, with CSR response curve 4 resulted in larger populations for a much smaller change in temperature (within 1^{o}C) (Figures 2.9(c), 2.9(f) and 2.9(i)). When baseline juvenile survival (a) was invariant with temperature population size was limited only by density dependence and hence populations persisted indefinitely irrespective of temperature (Figure 2.9). When baseline juvenile survival (a) varied with temperature the population persistence was influenced by the relationship between baseline juvenile survival (a) and air temperature, through the width of the TS curves.

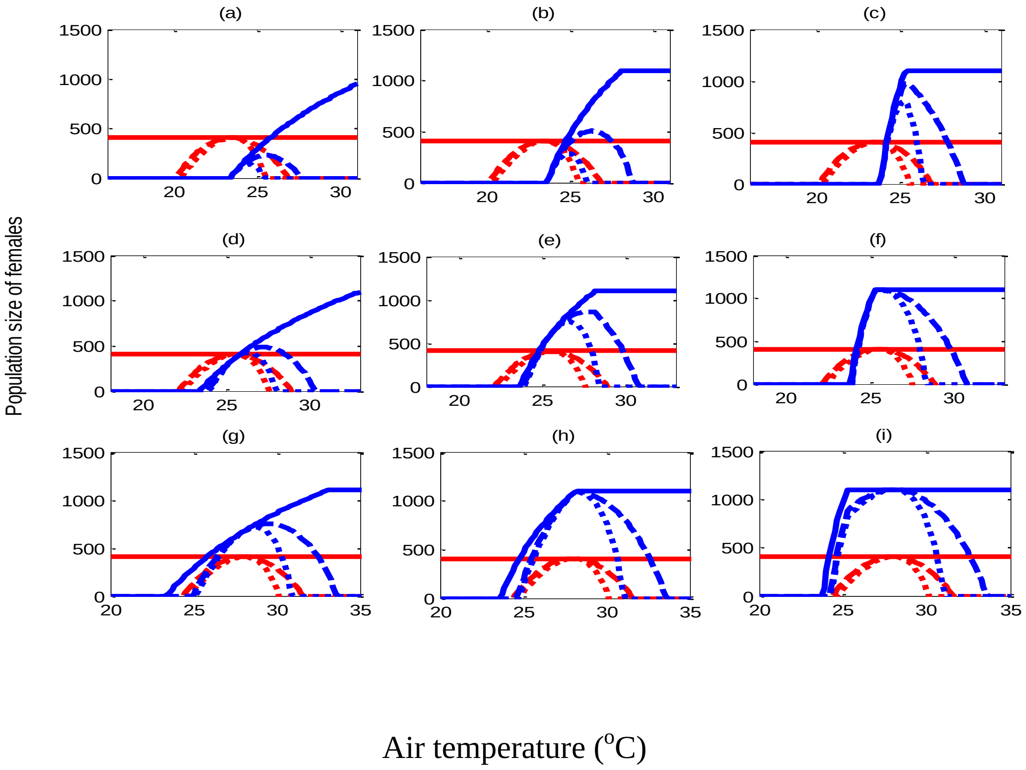
The relative importance of the temperature-dependent embryonic survival curve did not change as the slope of the CSR curve changed (Figure 2.9). The CSR curve with the steeper slope resulted in populations of larger sizes, but the underlying distribution of surviving populations ‘mirrored’ the shape of the TS and CSR curves. The shape of the TS curve was important for numbers of persisting populations as the TS ‘normal’ curve in all instances resulted in a greater number of persisting populations, than the TS ‘left-skew’ curve (Figure 2.9). TS interacted with the slope of the CSR curve, such that the curve 4 (steepest slope) produced TSD+TS populations of relatively larger sizes than curves 2 or 3 (Figure 2.9). Hence the slope of the CSR curve affected population sizes, but not the numbers of surviving populations, or population persistence, which increased as a more strongly female biased CSR coincided with maximum juvenile survival (a_{max}) in the higher temperature gradients (Figure 2.9).

For TSD+TS ‘left-skew’ populations (with CSR curve 2) (Figure 2.9(a)) produced extremely small population sizes. In ‘nature’ it is very unlikely that populations of this size would persist or grow to relatively large sizes, if juvenile survival had an extreme value distribution, i.e., the left-skew TS curve, at temperatures in the lower range.

For populations of reptiles with TSD with TS, if the CSR was more biased towards females at temperatures near maximum baseline juvenile survival (a_{max}), greater numbers of female offspring were produced, survived and recruited (Figures 2.9(c), 2.9(f) and 2.9(i)) than if the CSR was at equity at around a_{max} (Figures 2.9 (a), 2.9(d) and 2.9(g)). Juvenile female survival and recruitment increased with both temperature and the steepness of the slope of the CSR response curve (Figure 2.9). The smaller the change in temperature between a 100% male to 100% female CSR the larger the numbers of female offspring that were recruited (Figure 2.9). In temperature gradients 2 and 3 this effect was particularly evident in populations that became 100% female within a degree of temperature change (Figures 2.9(f), and 2.9(i)).

2.3.6.2.2. Populations of reptiles with TSD with a moderate level of male limitation on female fecundity (b=0.01)

If we examine the independent effect of male limitation on population size and persistence in populations of reptiles with TSD (comparing Figures 2.9 & 2.10, solid black lines of the same panels between figures), we found that high air temperatures, which led to female-biased sex ratios, no longer resulted in large population sizes. The narrower the transitional range of temperatures (TRT) of the CSR response curve (CSR curve 4) the smaller the range of temperatures for persistent populations. Populations became extinct as they approached 100% females (Figures 2.10(c) to 2.10(i)). TSD (no TS) populations (solid blue lines in figures) were no longer only limited by density effects on juvenile survival, but also by access to rare males and its effect on female fecundity. Hence, populations did not



GSD (——), GSD+TSnormaldist (----), GSD+TSleftskew (....)

TSD (——), TSD+TSnormaldist (----), TSD+TSleftskew (....)

Figure 2.9: Populations of females for various combinations of temperature-dependent sex determination (TSD) and genotypic sex determination (GSD) with and without temperature-dependent juvenile survival (TS). Males do not limit female fecundity (*b*=0). Temperature gradient 1 (a) to (c). Temperature gradient 2 (d) to (f). Temperature gradient 3 (g) to (i). TSD is shown with (a), (d) and (g) CSR response curve 2 (slope β=-0.069), (b), (e) and (h) CSR response curve 3 (slope β =-0.147) and (c), (f) and (i) CSR response curve 4 (slope β =-0.454).

persist indefinitely when the CSR was 100% female as they had in the absence of male limitation (Figure 2.10). populations of reptiles with TSD with CSR response curve 4 (right column of Figure 2.10) showed peak population sizes at much lower temperatures than other curves, but population persistence did not occur beyond a degree or two of temperature, owing to loss of males. Populations of reptiles with TSD with CSR curve 4 changed little. Male limitation at the smallest level changed the relative influence of TS on population size and in particular the range of temperatures for population persistence, in some instances but not in others. For CSR curve 3, the shape of the TS curve was influential on population persistence in temperature gradient 1 (Figure 2.10(b)), similar to when males did not limit female fecundity (Figure 2.9(b)). However as temperature increased, population persistence was ‘curbed’ by the interaction of male limitation with the slope of CSR curve 3, such that the shape of the TS curve became increasingly less influential (or not influential) on population persistence at different temperature gradients (Figures 2.10(e) and 2.10(h)).

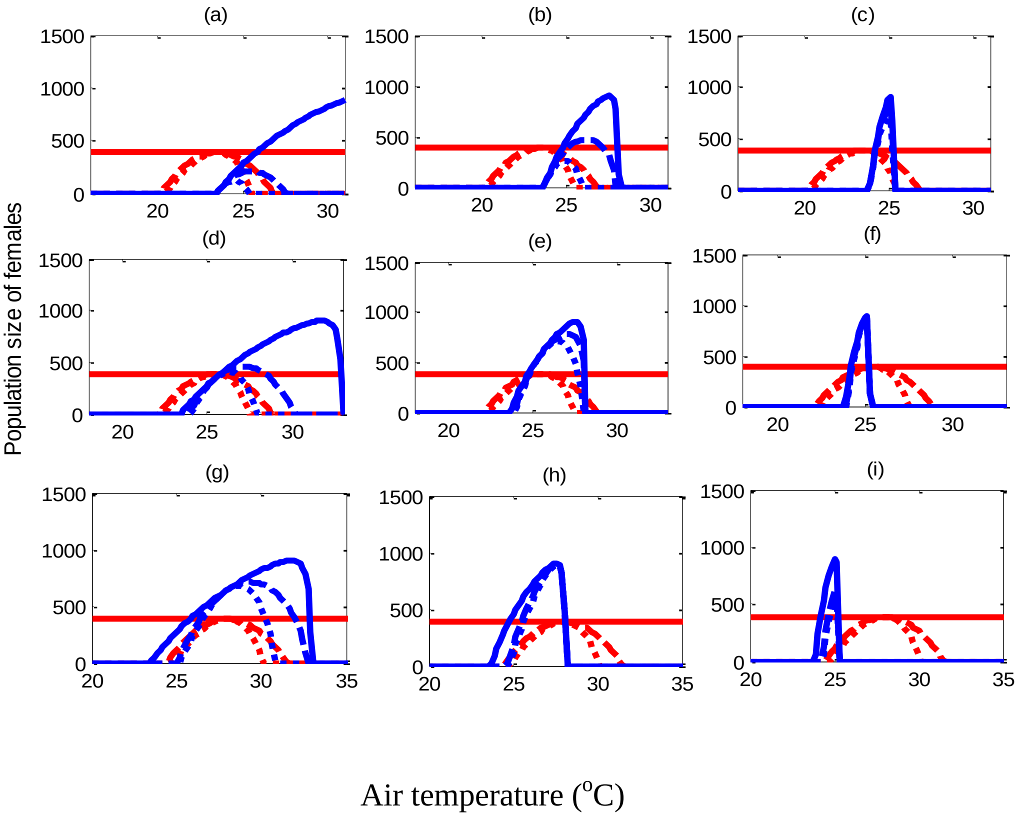
The relative positions of the peaks of TSD +TS population curves did not change with respect to maximum juvenile survival (a_{max}). In temperature gradient 1, the peak of the TSD+TS population curves (Figure 2.10, top row) was located around 2^{o} to 3^{o} C above the peak of the TS curve (23^{o}C for temperature gradient 1). This is towards the upper end of the range of juvenile survival. In temperature gradients 2 and 3, the peaks of the TSD+TS population curves were located within a degree of the peaks of the TS curves (25^{o}C and 27^{o}C, respectively). The peaks of the TSD+TS population curves shift substantially in the transition between lower and higher temperature gradients (Figures 2.10(a), (d) and (g)). In contrast, in the right column the peaks don’t move at all across gradients. In the absence of male limitation the position of a_{max} was advantageous for population size if it coincided with more female biased populations and resulted in a greater number of females produced, surviving and recruited into the breeding population (Figure 2.9).

The occurrence of larger population sizes and numbers of persisting populations at higher temperatures, where female biased sex ratios are produced, was negated with the introduction of male limitation on fecundity. Female fecundity obviously relied on the presence of some males in the population (Figure 2.10). In contrast, when males did not limit female fecundity, the shape of the TS curve was strongly influential on population persistence (Figures 2.9(e) and 2.9(h)). The interaction between male limitation, the slope of the CSR curve and baseline juvenile survival (a) is best seen by comparing the shallow and moderate CSR curve to the steep CSR curve (curve 4). The shape of the TS curve was no longer influential on population persistence and these did not persist for more than a degree of temperature (Figures 2.10 (c), (f) and (i)). This was because as populations tended towards 100% female, populations collapsed due to the complete loss of males, resulting in populations of zero size.

2.3.6.2.3. Populations of reptiles with TSD with a strong level of male limitation (b=0.1)

A strong level of male limitation on female fecundity resulted in similar trends to the moderate level of male limitation. There were stronger negative effects on population size and population persistence than for the smaller level of male limitation (Figures 2.10 and 2.11). Intemperature gradient 1 for TSD+TS populations the stronger effect of male limitation on populations than at the peak of the TSD+TS (Figure 2.11(a)) population curve are only around 50% female. Maximum juvenile survival occurs around 3^{o}C before the peak of the population curve and this results in very few females being recruited into populations (Figure 2.11(a)).

Population size increases in temperature gradients 2 and 3 for TSD+TS populations (Figures 2.11(d) and 2.11(g)) as the peak of the TSD+TS population curves and a_{max} are closer together, as the sex ratio is also at equity and so the same numbers of offspring were



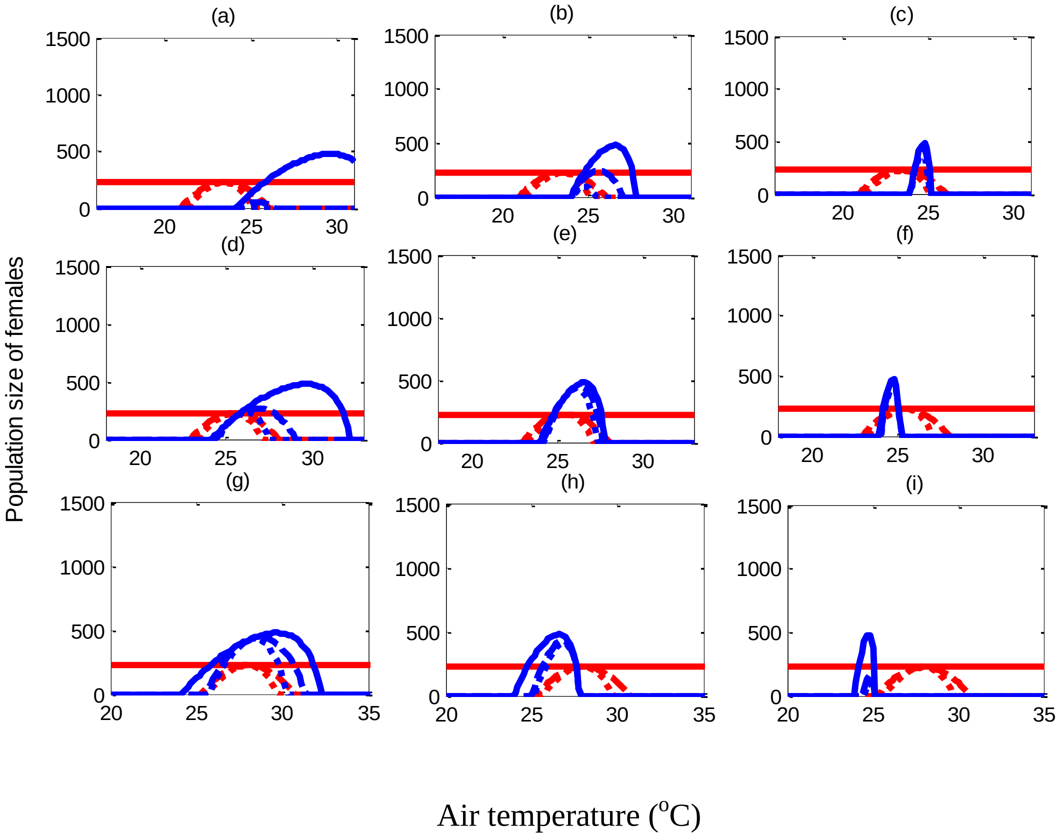
GSD (——), GSD+TSnormaldist (----), GSD+TSleftskew (....)

TSD (——), TSD+TSnormaldist (----), TSD+TSleftskew (....)

Figure 2.10: Populations of females for various combinations of temperature-dependent sex determination (TSD) and genotypic sex determination (GSD) with and without temperature-dependent embryonic survival (TS). Moderate level of male limitation on female fecundity (*b*=0.01). Temperature gradient 1 (a) to (c). Temperature gradient 2 (d) to (f). Temperature gradient 3 (g) to (i). TSD is shown with (a), (d) and (g) CSR response curve 2 (slope β =-0.069), (b), (e) and (h) CSR response curve 3 (slope β =-0.147) and (c), (f) and (i) CSR response curve 4 (slope β =-0.454).

produced, but more survived and hence were recruited. It seems unlikely that some populations of females subject to the strong level of male limitation resulting in very small sizes (Figures 2.11(c), 2.11(f) and 2.11(i)) would occur in natural populations. Population persistence in populations of reptiles with TSD increased as a result of the interaction between the CSR response curve with the medium slope and temperature-dependent embryonic survival in Figures 2.9 (b), 2.10 (b) and 2.11 (b) relative to 2.9 (a), 2.10 (a) and 2.11(a).

Populations of reptiles with TSD persisted in warmer areas than their GSD counterparts. In Figures 2.9 (i), 2.10 (i) and 2.11 (i) populations of reptiles with TSD persisted in similar areas. The interaction between TS and the CSR curve with the medium slope (Figure 2.9(h)) produced populations of reptiles with TSD of larger sizes, relative to the interaction between TS and the CSR curve with the shallow slope (Figure 2.9(g)). In contrast, in Figures 2.10 (g) and 2.10 (h) the response curve and temperature-dependent embryonic survival had only marginal effects on populations of reptiles with TSD. The strength of male limitation had the strongest effects on population growth in populations of reptiles with TSD (Figures 2.10 and 2.11). However, in populations of reptiles with GSD the strong level of male limitation reduced population sizes to a considerable extent (Figure 2.11).



GSD (——), GSD+TSnormaldist (----), GSD+TSleftskew (....)

TSD (——), TSD+TSnormaldist (----), TSD+TSleftskew (....)

Figure 2.11: Populations of females for various combinations of temperature-dependent sex determination (TSD) and genotypic sex determination (GSD) with and without temperature-dependent embryonic survival (TS). Strong level of male limitation on female fecundity (*b*=0.1). Temperature gradient 1 (a) to (c). Temperature gradient 2 (d) to (f). Temperature gradient 3 (g) to (i). TSD is shown with (a), (d) and (g) CSR response curve 2 (slope β=-0.069), (b), (e) and (h) CSR response curve 3 (slope β=-0.147) and (c), (f) and (i) CSR response curve 4 (slope β=-0.454).

2.4. Discussion

There have been many studies of the potential effects of extreme female biases in offspring sex ratios on the population dynamics of TSD species in warming climates (Hays *et al.*, 2003; Hawkes *et al.*, 2007, 2009; Poloczanska *et al.*, 2009; Janzen, 1994; Mitchell *et al.*, 2008; Mitchell & Janzen, 2010; Wapstra *et al.*, 2009; Witt *et al.*, 2010; Patino-Martinez *et al.*, 2012). However, we still have little understanding of how important the strength of male limitation or climatically-linked juvenile survival are for population persistence compared to biased sex ratios as climates warm. While it is intuitive that specifying male limitation and temperature-dependent juvenile survival will limit that capacity for population growth in female-biased populations, we also uncovered unpredictable results arising from the interactions of these factors.

In this chapter a model of the interaction between these three crucial demographic parameters has been developed for the first time. Hence, a first step has been taken towards elucidating the nature of the relationships between these factors and in determining population persistence in theoretical populations of reptiles with GSD and TSD.The major results are summarised as follows. Warmer climates producing female-biased sex ratios in populations of reptiles with TSD resulted in larger population sizes of females (Figure 2.9). Female-biased populations of reptiles with TSD with no male limitation resulted in short-term population growth (Figure 2.9). However, when fecundity was limited by the abundance of males, smaller population sizes resulted (Figures 2.10 and 2.11). The strongest level of male limitation resulted in greatly reduced population sizes in both populations of reptiles with GSD and TSD (Figure 2.11).

Strong female biases in the primary and adult sex ratios are thought to potentiate short-term population growth, as long as males are not limiting fecundity and temperatures do not increase to the extent that significant loss or elimination of males occurs (Freedberg and Taylor 2007; Mitchell and Janzen 2010). Warmer climates (higher temperatures) which produced female biased CSRs resulted in larger female populations for populations of reptiles with TSD with temperature-dependent embryonic survival and no male limitation (Figure 2.9). However, this positive effect was greatly diminished by incorporating male limitation. The steeper the slope of the CSR curve, the shorter the temperature transition to population collapse (Figures 2.10 and 2.11). The effects of moderate and stronger male limitation were qualitatively similar, except that the stronger level resulted in further reductions in population sizes (Figures 2.10 and 2.11).

In populations of reptiles with TSD and GSD, the shape of the temperature-dependent embryonic survival curve influenced the number of surviving populations, to varying degrees, depending on the interaction with the CSR response curve. Despite short-term increases in population sizes and persistence in female biased populations the decrease in males and reduction in juvenile survival as a result of climate warming are likely to offset any short-term gains.

In GSD (with temperature-dependent embryonic survival) there was no effect of temperature on CSR and temperature effects on juvenile survival were the sole determinant of the range of temperatures on population persistence (Figures 2.9 to 2.11). If temperature-dependent embryonic survival was normally distributed this resulted in greater population persistence over a wider temperature range than if TS was left-skewed (Figures 2.9 to 2.11). In populations with TSD, the probability of female fertilisation decreased as males became rare (equation 3). Female fertilisation probability was very sensitive to changes in the ASR (proportion of males), and this sensitivity increased at the stronger levels of male limitation (Figure 2.3).

Male limitation meant that females had reduced access to males, resulting in population collapse as populations tended towards 100% female (Figures 2.10 and 2.11). Populations of reptiles with TSD with the shallowest CSR curve persisted across a wider range of temperatures following the inclusion of male limitation (Figures 2.10 and 2.11). This findings supports the proposal by Hulin *et al.* (2009) that TSD species with a wider transitional range of temperatures (TRT) (the narrow range of temperatures at which both males and females are produced) should more likely be able to adapt and subsequently evolve to new thermal regimes and, hence, be able to withstand rapid and ongoing climate change (Hulin *et al.* 2009). As a caveat, this will only occur if males become limiting to a considerable extent, otherwise populations with female-biased sex ratios are more likely to reach larger sizes.

At the moderate level of male limitation, the slope of the CSR response curve appears to have a stronger effect than male limitation (Figures 2.9 to 2.11). The strongest level of male limitation seems to override the ‘resilience’ to male limitation of the shallower slope. At the strongest level of male limitation, the interaction between male limitation, the slope of the CSR curve and temperature-dependent embryonic survival was so strong that populations could not exist at any temperature. Hence male limitation at the strongest level was considered to have a stronger effect on population size and persistence than interactions between the slope of the CSR curve and juvenile survival (Figure 2.11). It is unlikely that the strong level of male limitation would occur in populations of marine turtles. This is because males mate with multiple females in most instances (Broderick *et al.* 2001; Pearse *et al.* 2002), and females are able to store viable sperm for up to 4 years. Hence, contact with males during that time may not be necessary for successful reproduction to occur (Pearse *et al.* 2002).

It is very difficult, and perhaps even not possible to obtain experimental data on male limitation on females in populations of marine turtles, given their wide scale distribution and movements across oceans (Miller 1997; Wright *et al.* 2012). Males are also thought to reproduce more frequently than females, and move considerable distances between assemblages of females in order to reproduce. Male limitation on female fecundity is thought to be low in these populations (Broderick *et al.* 2000; Poloczanska *et al.* 2009).

Populations of reptiles with GSD were equally as sensitive to male limitation as TSD as the male limitation parameter was the same (equation 3) but males did not become rare as sex ratios were equal. In populations of reptiles with GSD as there was no change in the adult sex ratio (proportion of males), reduced female fertilisation probability with increasing male limitation may reflect other factors such as competition among males for females. Female fertilisation probability was very sensitive to changes in the adult sex ratio and this increased at the strong level of male limitation (Figures 2.3 and 2.11). Hence, there was a discernible effect of male limitation on populations of reptiles with GSD, at the strong level (Figure 2.11).

In the absence of male limitation, the shape of the distribution of the temperature-dependent embryonic survival curve is important in determining the range of temperatures over which populations persist irrespective of the steepness of the slope of the CSR curve. The temperature-dependent embryonic survival curve interacts with CSR curves with steeper slopes to facilitate population growth in 100% female biased populations, in particular in warmer climates. This effect could potentially have assisted very female biased populations to survive historical short-term temperature increases, and possible consequent shortfalls in the numbers of males, owing to the production of female biased primary sex ratios at higher temperatures. As males became limiting this advantage was negated, and the CSR with the shallow slopes resulted in greater population sizes, and persistence.

Recruitment of male hatchlings through immigration into very female-biased populations may increase the number of persisting populations, population sizes and reduce the likelihood of local extinctions (Doody and Moore 2011). The CSR response curves in this study were designed to capture a wide range of slopes to reflect variation across populations of reptiles with TSD. Among the known species, the painted turtle (Schwanz *et al.* 2010) and snow skink (Wapstra *et al.* 2009) have identical slopes of the CSR response curves despite being very different species, existing at different temperatures (Table 2.1). In contrast, the loggerhead turtle has a much shallower slope of the CSR response curve (Table 2.1) (Hawkes *et al.* 2007).

CSR curve 3 incorporated the ‘medium’ slope of the CSR response curve from the painted turtle (Schwanz *et al.* 2010) and the snow skink (Wapstra *et al.* 2009) (Figure 2.2(a)). CSR curve 2 had a ‘shallow’ slope similar to the loggerhead turtle (Hawkes *et al.* 2007) (Figure 2.2(a)). CSR curve 4 with the steepest slope was for a theoretical TSD species, as there are no empirical data which support CSR response curves with slopes as steep as curve 4 (Figure 2.2(a)). However, it is possible that they exist for some species, depending on the amount of variation in nest temperatures within a population. It is likely that a CSR response curve with a very steep slope resulting in either the production of 100% males or 100% females may result in population sinks. A population sink occurs where the number of offspring produced are below replacement level and without sufficient recruitment through immigration the population will become extinct (Krebs 2009). Knowledge of the CSR is very important in predicting population persistence as populations that shift from all male to all female clutches within a degree or two of temperature are likely to be more vulnerable to local extinctions.

In the absence of population level data, it would be useful to be able to infer the slope of the CSR response curve from the TSD reaction norm (for individuals or single clutches), as there is much more empirical data available on the reaction norm. However, it is unlikely that the slope of the CSR response curve could be inferred from the reaction norm without detailed knowledge on distributions of nest temperatures across climates. The CSR response curve may potentially capture the effects of female plasticity in nesting behaviour in the response to climate, but could also reflect differences in the reaction norm for single clutches across nests. The shape of the CSR curve is probably not easily inferred from the reaction norm. When more data are available for both CSR curves and reaction norms such inference may be possible.

The temperature-dependent embryonic survival curve is also of value to empiricists as it can be used to estimate the range of temperatures that apply to juvenile or hatchling survival, ideally at the population level. Data are available for many TSD species on the ranges of temperatures for survival of individuals (Yntema and Mrosovsky 1982; Schwarzkopf and Brooks 1987; Steyermark and Spotila 2001; Hawkes *et al.* 2007), but there have been far fewer formal attempts to plot the distributions of juvenile survival against climate for populations (reviewed in Birchard (2004)). The relationship has been qualitatively defined at the population level. Even the limited descriptions of the distributions of juvenile survival (reviewed in Birchard (2004)) would probably not be sufficient to model the distribution of temperature-dependent embryonic survival, and far more data are needed.

The collection of accurate data on environmental temperatures (air and sand or nest) is also vital in developing CSR response curves for populations with TSD. Air temperatures have been described as directly influential on nest or incubation temperatures (Poloczanska *et al.* 2009). Recently in a study of leatherback turtles (*Dermochelys coriacea*) a significant positive linear relationship (R^2=0.61, $P<0.05$) between ambient air and sand (incubation temperature) was found (Patino-Martinez *et al.* 2012). Patino-Martinez *et al*. (2012) used air temperatures to predict current and future sand temperatures and from this predicted that towards the end of the 21st Century temperatures would have become lethal for egg incubation, leading to local population extinctions. This type of data is vital in establishing links between individual nest temperatures, primary sex ratios and cohort sex ratios of nests, although Patino-Martinez *et al.* (2012) did not investigate sex ratios. A more sophisticated approach to predicting nest temperatures than relying on correlations between air and sand/or soil temperatures, is through the use of mechanistic models (e.g. Mitchell *et al*; Fuentes and Porter 2013).

The collection of data for both the CSR response curve and temperature-dependent embryonic survival curve are important as they can assist in understanding and predicting the size and viability of future reptile populations as climates warm. Temperatures, or compensatory mechanisms for temperatures (for example, plasticity in female nesting behaviours) need to be appropriate for the production of two sexes to facilitate population growth in the longer term (Hawkes *et al.* 2009). A model of the potential impacts of climate change on a sea turtle population, has predicted that extreme temperature increases in excess of 6°C are likely to result in almost 100% hatchling mortality (Hawkes *et al.* 2007). Similar outcomes have recently been reported for the painted turtle with climate warming (Telemeco *et al.* 2013). These findings were consistent with the results of this study as all populations (with temperature-dependent embryonic survival) went to extinction with approximately a 6 to 9°C increase in temperature (Figures 2.9 to 2.11).

2.4.1. Summary

There have been many papers on the effects of extreme female biases in the sex ratio on the population dynamics of populations of reptiles with TSD in warming climates (Hays *et al.* 2003; Hawkes *et al.* 2007; Hawkes *et al.* 2009; Poloczanska *et al.* 2009; Witt *et al.* 2010;

Patino-Martinez *et al.* 2012). However, there is a large amount of empirical data needed and the sensitivity of our predictions to potential variation in these data, are largely unknown.

In this chapter I have developed a novel non-species-specific model to estimate how a warming climate (ambient air temperature) will impact on the population dynamics of TSD and GSD through CSRs and juvenile survival. Equation 6 was used to estimate population sizes at equilibrium for TSD and GSD species with varying CSR response curves and distributions of juvenile survival. CSR response curves were designed or based on curves described in Wapstra *et al*. (2009) and Schwanz *et al*. (2010), and TS curves were based in part on distributions of juvenile survival in studies reviewed in Birchard (2004). The interaction between CSR, TS and male limitation was also explored.

My approach is ‘novel’ as it investigates the population dynamics of populations of reptiles with TSD and GSD through the combination of CSR response curves, TS curves and male limitation through population equations. This model will be an effective tool for empiricists in estimating the underlying population dynamics of TSD reptiles tending towards extreme female bias in a changing climate, and will have practical applications in conservation management.

Chapter 3: The role of dispersal in determining range limits in reptiles.

3.1. Introduction

3.1.1. Range limits in temperature-dependent sex determination (TSD) species

Populations with temperature-dependent sex determination (TSD) have wide geographical distributions across mostly tropical, subtropical and warmer temperate areas (Davenport 1997; Hawkes *et al.* 2009). As sex is determined by temperature in TSD reptiles, primary sex ratios (sex ratios of offspring) may show wide geographical variation if associated climatic variation determines nest temperatures. There has been at least one attempt (Kallimanis 2010) to describe the geographical distribution of sex ratios, of TSD species, with balanced sex ratios at the 'centre' of ranges and skewed sex ratios at the edges of ranges. In the model proposed by Kallimanis (2010) imbalanced sex ratios and marginal habitats are assumed to limit population growth and determine range limits. Escobedo-Galvin et al. (2011) criticises Kallimanis (2010) arguing that TSD species do not exhibit balanced sex-ratios at the centre of their distributions, and biased sex-ratios at range margins. Escobedo-Galvin et al. (2011) argues that local temperature variation is uncorrelated with offspring sex ratio for the various patterns of TSD, across wide geographical locations.

The range limits of a species reflect the abiotic (climate) and biotic conditions that define their realised niche (Brown 1984;Wiens and Graham 2005; Davies *et al.* 2009). The edges of a species range (range limits) are often characterised by more hostile environments (environments that are either hotter or colder at the extremes), where habitats are marginal than in the interior of the range (Caughley *et al.* 1988). The trailing edges are environments of high temperatures and therefore may become more marginal as climates warm. In contrast, the leading edges are environments of low temperatures that may become more favourable under climate warming (Parmesan *et al.* 1999;Davis and Shaw 2001; Davies *et al.* 2009; Kallimanis 2010).

As climates warm, populations located at trailing (warmer) edges are more at risk of extinction, but this is assumed to be accompanied by population growth and range expansion at the leading (colder) edges, as habitats become more ‘favourable’ (Davis and Shaw 2001; Kallimanis 2010). Given relative mobility and dispersal propensity, species may be able to shift their geographical ranges to cooler latitudes, for example, towards the poles or higher elevations, and establish new populations (Parmesan *et al.* 2000;Hughes 2003;Parmesan 2006).

Kallimanis (2010) proposed that the ‘leading’ edges of the geographical ranges of TSD species are environments of low temperatures and marginal habitats that are further limited by imbalanced sex ratios. The model predicts the reverse scenario for the trailing edge of the population, where in an environment of already high temperatures, further increases in temperature may increase sex ratio imbalances and reduce available habitat, leading to local population extinctions. The leading edge populations will grow under climatic warming because as sex ratios approach 1:1 consequent population growth will produce more dispersers to colonize the habitats created by climate warming (Kallimanis 2010).

Dispersal may have a major role in population persistence, and has the potential to ‘rescue’ populations from local extinctions. Local extinctions may occur because of demographic or environmental stochasticity (Brown and Kodric-Brown 1977). Demographic stochasticity involves random changes in birth and death rates and the resulting fluctuations in populations due to processes such as variation in sex ratios, survival and age structure (Brown and Kodric-Brown 1977). The potential rescue effects of dispersal are described by

Kallimanis (2010) in the context of climate change, but not the role of dispersal on population persistence and range limits in stable climates. At the edges of geographical ranges, both extreme temperatures and dispersal may affect adult sex ratios and influence population growth, survival and persistence in TSD species. Under climate change, the leading (colder) edge of the range will grow as biased sex ratios will become more balanced (Kallimanis 2010).

3.1.2. Potential for local adaptation

Whereas extreme nest temperatures can have dramatic effects on early-life demography in TSD species, populations at extreme climates (for example, at range edges) may exhibit behavioural (for example, nesting behaviour) or physiological (changes in pivotal temperature) compensation for extreme climate, in ways that prevent extreme nest temperatures or prevent demographic perturbations. Nesting behaviour, pivotal temperature (the constant temperature at which both sexes are produced in equal proportions) and embryonic tolerance of extreme temperatures, may prevent demographic perturbations (Hulin *et al.* 2009).

Changes in nesting behaviour may involve plasticity and evolution. Some examples include nest site choice, nest depth and timing of nesting. The water dragon (*Physignathus lesueurii*) has been observed to choose different nesting sites across its range, in a manner that leads to similar nest temperatures (Doody *et al.* 2006). Observed variation among water dragon populations may be due to either behavioural plasticity or local adaptation (Doody *et al.* 2006). Behavioural plasticity has been observed in three lined skinks (*Bassiana duperreyi*) (Telemeco *et al.* 2013). Three lined skinks shift nest depth and timing of nesting in response to environmental temperature (Telemeco *et al.* 2009). Behavioural plasticity has also been observed in the timing of nesting of painted turtles (Schwanz and Janzen 2008). However the shifts in timing of nesting were not strong enough to compensate for climate (Schwanz and Janzen 2008). The outcome of nesting plasticity and evolution in the timing of nesting is to prevent changes in nest temperatures that may reduce the probability of hatchling survival, or biased primary sex ratios.

Embryonic or hatchling survival may also increase as a result of local adaptation to temperature in green turtle (*Chelonia mydas*) embryos (Weber *et al.* 2012). Two different populations a few kilometres apart on Ascension Island (United Kingdom) but experiencing different sand temperatures differed in thermal tolerance. Specifically, eggs from the black sand (warmer) beaches were able to tolerate higher incubation temperatures than the eggs from the pale sand (cooler) beaches. The differences were attributed to local adaptation to thermal temperatures and not plasticity in maternal nesting behaviour (Weber *et al.* 2012).

Micro-evolutionary changes regulated by genetics or heritable factors (Hulin *et al.* 2009) may allow for *in situ* adjustments to pivotal temperature in response to changing environmental conditions at nesting sites or beaches (Davenport 1989; Poloczanska *et al.* 2009). In contrast, Ewert *et al*., (2005) demonstrate that changes in nesting behaviour and not pivotal temperatures, allow for local sex ratio adaptation in different thermal environments. Populations in cold environments adapt to the shorter nesting season by laying their eggs in un-shaded environments, producing warmer nest temperatures and faster embryonic development than populations in lower latitudes. Hence, warmer pivotal temperatures are expected in these populations due to warmer nest temperatures (Ewert *et al.* 2005).

Local adaptation can occur as a consequence of dispersal as gene flow into a population increases (Garant *et al.* 2007). However, local adaptation from gene flow may not occur as numerous factors may prevent gene flow across the landscape. Some examples include: dispersal related mortality due to predation; physical exhaustion; reduced survival and reproductive success due to maladaptation to the new environment. Furthermore, dispersal from high quality source to low quality sink environments may increase population density above carrying capacity in the population sinks, and conversely reduce population density in the source populations (Garant *et al.* 2007).

3.1.3. Role of dispersal

Dispersal is a major driving force in the population dynamics and genetic structure of many taxa. There are many definitions of dispersal, however the definition used in this thesis is consistent with Clobert *et al*. (2001), who broadly defined dispersal as the movement of an individual from the natal area (birth place) to the area where the first successful reproduction occurs (natal dispersal). When an individual disperses it may either move a short distance to the nearest suitable area, or it may move a considerable distance to establish a home range (Caughley and Sinclair 1994).

Sex-biased dispersal is widespread in vertebrate populations and usually involves one sex dispersing further than the other and the opposite sex showing philopatry (the tendency for an individual to stay in or return to the natal site to breed) (Greenwood 1980). There are a wealth of dispersal data for mammals and birds (Greenwood 1980) however for reptiles data are sparse and dispersal tendencies are less well known (Olsson and Shine 2003; Dubey *et al.* 2008). Male-biased dispersal (a larger proportion of males move) has been demonstrated in lizards, iguana, and snakes including; the side blotched lizard (*Uta stansburiana*) (Doughty *et al.* 1994), the Galapagos marine iguana (*Amblyrhynchus cristatus*) (Rassmann *et al.* 1997) and the argentine boa constrictor (*Boa constrictor occidentalis*) (Rivera *et al.* 2006), the small-eyed snake (*Rhinoplocephalus nigrescens*) (Keogh *et al.* 2007) and an Australian tropical snake (*Stegonotus cucullatus*) (Dubey *et al.* 2008).

Dispersal is considered to be largely male-biased in all marine turtles (Laurent *et al.* 1998; Casale *et al.* 2002; Roberts *et al.* 2004; Bowen and Karl 2007) and in the diamondback terrapin (*Malaclemys terrapin*) (Sheridan *et al.* 2010). There is also some evidence for male-biased dispersal in freshwater turtles (e.g. Morreale *et al*. 1984; Brown and Brookes 1993; Mockford *et al*. 2005). Laurent *et al.* (1998) hypothesised that the Atlantic pelagic juvenile movement of loggerhead turtles (*Caretta caretta*) is male-biased. This is thought to partly explain the low matriarchal gene flow observed between Mediterranean and Atlantic populations (Laurent *et al.* 1998). Results from genetic analyses of micro-satellite loci in marine turtles suggest that gene flow between nesting beaches is male-mediated and supports male-biased dispersal (Karl *et al.* 1992; Casale *et al.* 2002; Roberts *et al.* 2004; Bowen and Karl 2007). Karl *et al*. (1992) and Limpus (1993) describe male-mediated gene flow as occurring between geographically distant populations of green turtles (*Chelonia mydas*) that are unlikely to share foraging areas, or overlapping home ranges. Male-mediated gene flow is important in maintaining genetic relatedness and demographic connections among geographically distant green turtle populations (FitzSimmons *et al.* 1997b; Roberts *et al.* 2004).

Casale *et al*. (2002) found in loggerhead turtles that juvenile male turtles disperse further than female juvenile turtles and gene flow among nesting beaches from the Atlantic to the Mediterranean was male-mediated. This is not to say that females do not disperse, however, males disperse further (Casale *et al.* 2002). Roberts *et al*. (2004) describe male-mediated gene flow in green turtles as occurring widely across both the Pacific and Atlantic oceans. The results of these genetic analyses suggest that male marine turtles disperse far from their natal sites to breeding sites (Bowen and Karl 2007). There is also evidence for male-biased dispersal from a behavioural study of mating patterns in the green turtle. The data from satellite tracking indicated that males disperse frequently among nesting beaches and this is likely to be related to mating opportunities (Wright *et al.* 2012).

By contrast, FitzSimmons *et al*. (1997a) found evidence that philopatry exists in both males and females, for a population of green turtles. Mitochondrial DNA ($_{mt}$DNA) haplotype frequencies were found not to differ for males and females among study sites. This indicates that both females and males may mate at or near the beach where they hatched. The results of this study suggest that the evidence for directional or sex-biased dispersal towards males is not unequivocal, and males and females may both show philopatry and/or disperse (FitzSimmons *et al.* 1997a).

Very few documented cases of female dispersal in reptiles exist. Female dispersal has been demonstrated in the alpine lizard (*Niveoscincus microlepidotus*) (Olsson and Shine 2003). Natal dispersal (a shift in the home range over the lizard's first year of life) and adult dispersal (shifts in home ranges between breeding attempts) were investigated. Female neonates and adult females were found to disperse further (around twice the distances) of males (Olsson and Shine 2003). There are several studies of lizard dispersal between habitat patches, for example, Cunningham's skink (*Egernia cunninghami*) (Stow *et al.* 2001) and a lizard (*Egernia whitii*) (Chapple and Keogh 2005), but no clear patterns of dispersal were established.

However, many populations rely on dispersal for gene flow and ultimately population persistence (Kawecki 2003). In a theoretical analysis of gene flow between populations (general species) and the role of gene flow in maintaining populations, two sex dispersal was found to be beneficial for population persistence in marginal habitats as gene flow through dispersal occurred in both directions (Garant *et al.* 2007). Dispersal can have many positive benefits on population persistence as it may increase juvenile fitness and reduce the costs of inbreeding (Garant *et al.* 2007).

Unfortunately, knowledge is lacking on dispersal tendencies in most reptiles. There is also a paucity of data on other vital demographic parameters such as juvenile survival, primary sex ratio and male limitation, and these are important parameters in recommending priorities for empirical research.

3.1.4. Rationale

In populations of reptiles with TSD, vital demographic parameters such as juvenile survival and primary sex ratio of individuals depend on ambient temperature. From this it follows that population persistence and range limits may be determined by local climatic conditions and potentially be strongly affected by climate change. There are very few empirical data on juvenile survival, sex determination, male limitation and dispersal and how they interact in connected populations with dispersal. Furthermore, the factors that are most influential in determining the range limits of TSD and genotypic sex determination (GSD) reptile species are unknown.

In this Chapter, I used a theoretical approach to examine the effects of juvenile survival, sex ratio, male limitation and dispersal on population persistence and in determining range limits in a gradient of stable climatic conditions (climate change is addressed in Chapter 4).

3.1.5. Aims

My main aim is to explore the effects of climate and dispersal on population persistence and in determining range limits in species with temperature-dependent embryonic survival and temperature-dependent and genotypic sex determining mechanisms, in a gradient of stable temperatures. The role of the aforementioned demographic parameters in determining population persistence and range limits will also be assessed.

3.2. Methods

3.2.1. Model description

3.2.1.1. Population model

A matrix of 10,000 populations were distributed along a temperature gradient (100 temperatures, the columns of the matrix), and replicated with 100 populations per temperature (the rows of the matrix). Population persistence is defined as the range of temperatures at which populations exist with non-zero population size. Each population in the matrix was initiated with 100 males and 100 females. Temperatures were constant and identical to the middle temperature gradient (18 to 33^{o}C) in Chapter 2, Figure 2.2(b). The demographic and dispersal processes in the simulation model (Figure 3.1) are described in detail below.

The population modelling in this thesis is non-species specific and based on reptiles with TSD pattern 1A, including sea turtles (Hawkes et al. 2007), the painted turtle (Schwanz *et al*., 2010) and the snow skink (Wapstra et al. 2009). The number of juveniles produced depends on the number of adult females in the population and female fecundity (Figure 3.1). Female fecundity, the number of offspring (eggs laid) per adult female, was a function of the adult sex ratio in the population, asymptoting to a maximum level (B_{max}=10) when males are common, and moving towards zero when males become rare.

$$B = B_{max} * (ASR / (ASR + b)) \qquad \text{eqn 7}$$

A moderate level of male limitation on female fecundity (b=0.01) was chosen as in most instances no male limitation (b=0) and the stronger level of male limitation (b=0.1) used in Chapter 2 seem unlikely for populations in nature (Figure 3.2).

The number of offspring in each population that were male was sampled using a random binomial distribution, given the total number of offspring and the population-specific sex ratio probability of producing a male, p) (Figure 3.1).

The number of female offspring was the total number minus the number assigned to be male. For populations of reptiles with GSD, the sex ratio was at equity. That is, a flat cohort sex ratio (CSR) response curve (Methods section, Chapter 2) was used, with an intercept of α=0.5 and a slope of β=0 (Figure 2.2(a)). For populations of reptiles with TSD, p (the proportion of hatchlings that develop as male) was a function of population temperature (temperature gradient 18 – 33°C, Figure 3.1) (Methods section, Chapter 2, Figure 2.2(b)), described by CSR response curve 3 (Methods section, Chapter 2). CSR curve 3 has the parameters derived for the painted turtle (Schwanz *et al.* 2010) with intercept α=4.14 and slope β=-0.147 (Figure 2.2(a)). The number of adults surviving to the next time step was sampled using a random binomial distribution with the initial number of adults and a probability of survival (s=0.95 for both males and females) (Figure 3.1). The number of offspring that recruited into the adult population in the next time step (survived to and bred at age 1) depended on temperature-dependent embryonic survival followed by dispersal. A normal distribution of baseline juvenile survival probabilities was distributed along a temperature gradient (18 – 33°C), with a maximum baseline juvenile survival a_{max} =0.015 and a minimum baseline survival value of zero (Figure 3.3). Realised juvenile survival also decreased as the effects of density increased.

3.2.1.2. Dispersal model

Several dispersal scenarios were evaluated as insufficient empirical information is available to accurately parameterise dispersal in reptile species and species may vary in their dispersal tendencies. There were three levels of dispersal: none, ‘small’ and ‘large’. However, these terms are relative as there is no available information to estimate what small or large

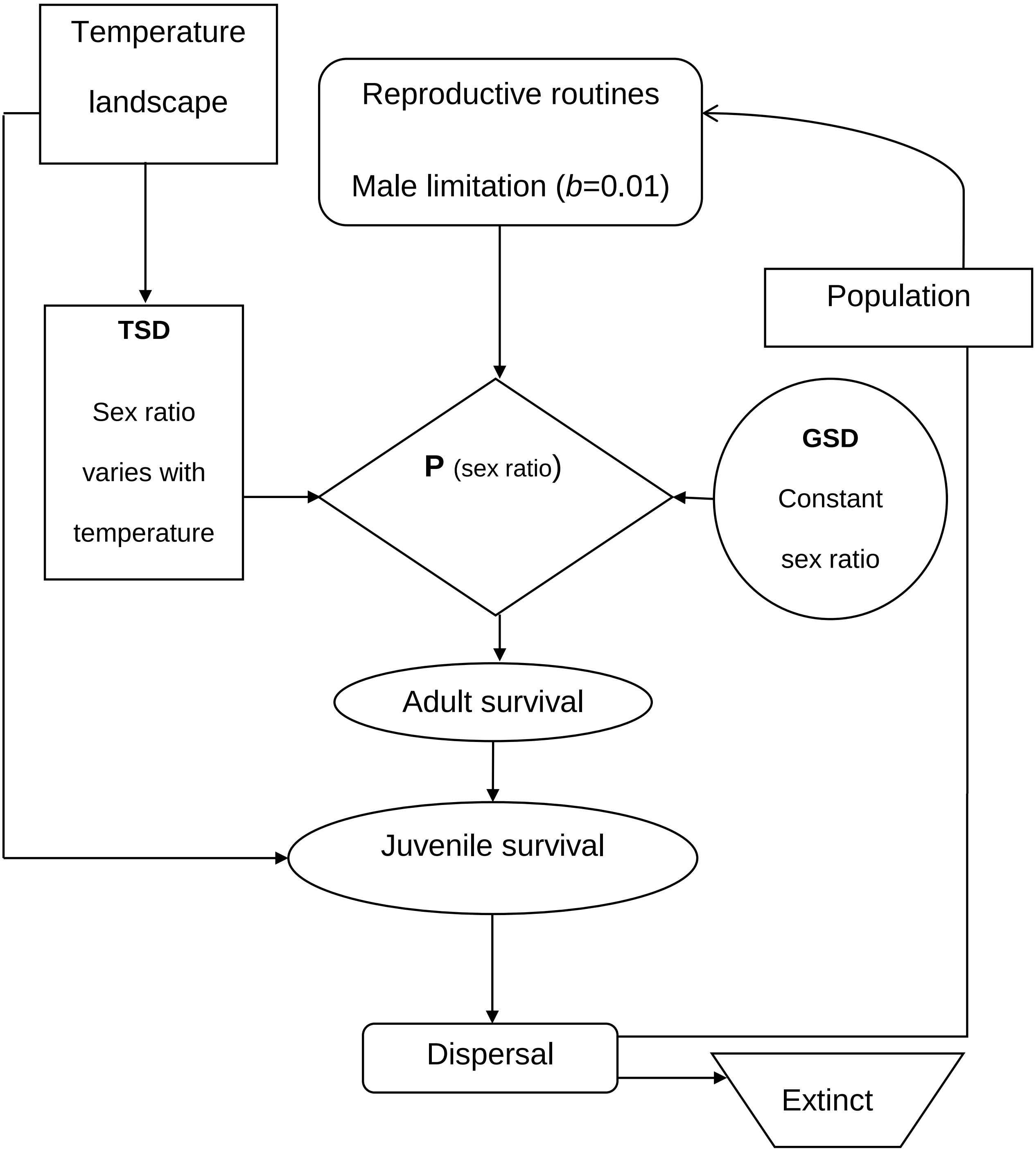


Figure 3.1: Demographic and dispersal processes in the simulation model

dispersal would be in these species. For relatively small dispersal, juveniles have a higher probability of not dispersing and a lower probability of travelling large distances relative to juveniles with relatively large dispersal (Figure 3.4). Small and large dispersal had three separate dispersal tendencies, i.e., male only, female only and two sex dispersal. Juveniles either remained in the place they were born (a population cell) or dispersed. Adults did not disperse. The dispersal model consisted of a probability density function (PDF) based on a fat-tailed (FT) dispersal kernel, which is thought to best approximate dispersal in real animals compared to other dispersal kernels (Chapman *et al.* 2007). The FT dispersal kernel is leptokurtic and right skewed to describe a scenario where most individuals disperse a short distance or do not disperse at all. A small number of individuals disperse a long distance. This kernel also describes a higher proportions of long-distance dispersers than the negative exponential and Gaussian kernels (Chapman *et al.* 2007).

$$\Pr(dispersal\ distance) = 1/(1 + A * (\mathrm{D}_{\mathrm{ij}}^{Z})) \qquad \text{eqn 8}$$

Pr(*dispersal distance*) is the probability that an individual moves a certain distance, D_{ij}. D_{ij} is the distance moved between cells or populations, where *i* represents any row, and *j* any column in the dispersal matrix. Parameter A defines the distribution of dispersal differences, and 1/A is the average dispersal distance (Moilanen 2004). Z is a shape parameter for the dispersal curve (Moilanen 2004).

Distances were calculated between cells as a von Neumann neighborhood. The von Neumann neighborhood comprises the four cells orthogonally surrounding a central cell on a two-dimensional square lattice (Menard and Marceau 2005). Dispersal from the cell in which the individual was born occurred in any direction with equal probability. Firstly, dispersal distance was chosen at random, then a cell that corresponded to that distance (including the natal cell) was chosen, and the individual dispersed to that cell. If a distance of zero was

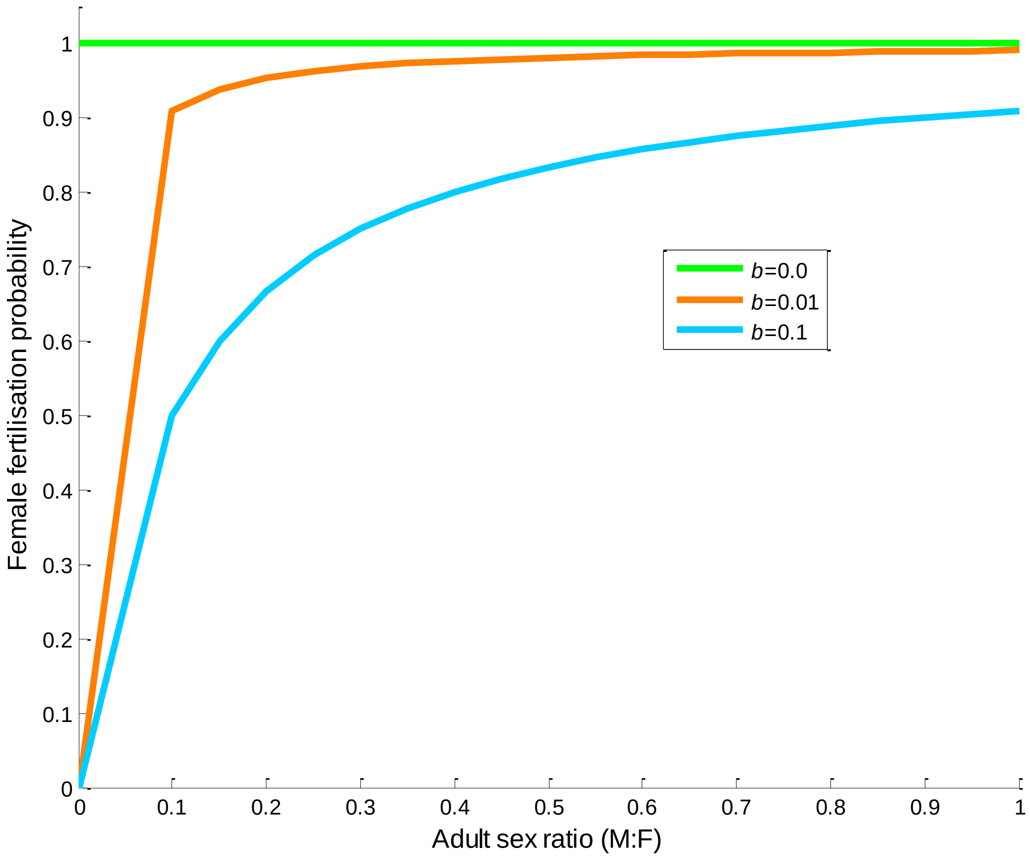


Figure 3.2: The female fertilisation probability as a function of adult sex ratio (ASR= M:F). The different lines represent different sensitivities of fertilisation probability to changes in the ASR (after Rankin and Kokko 2007). N.B. As the ASR approaches 1 if there are any females remaining in the population there is a very high probability that they will be fertilised.

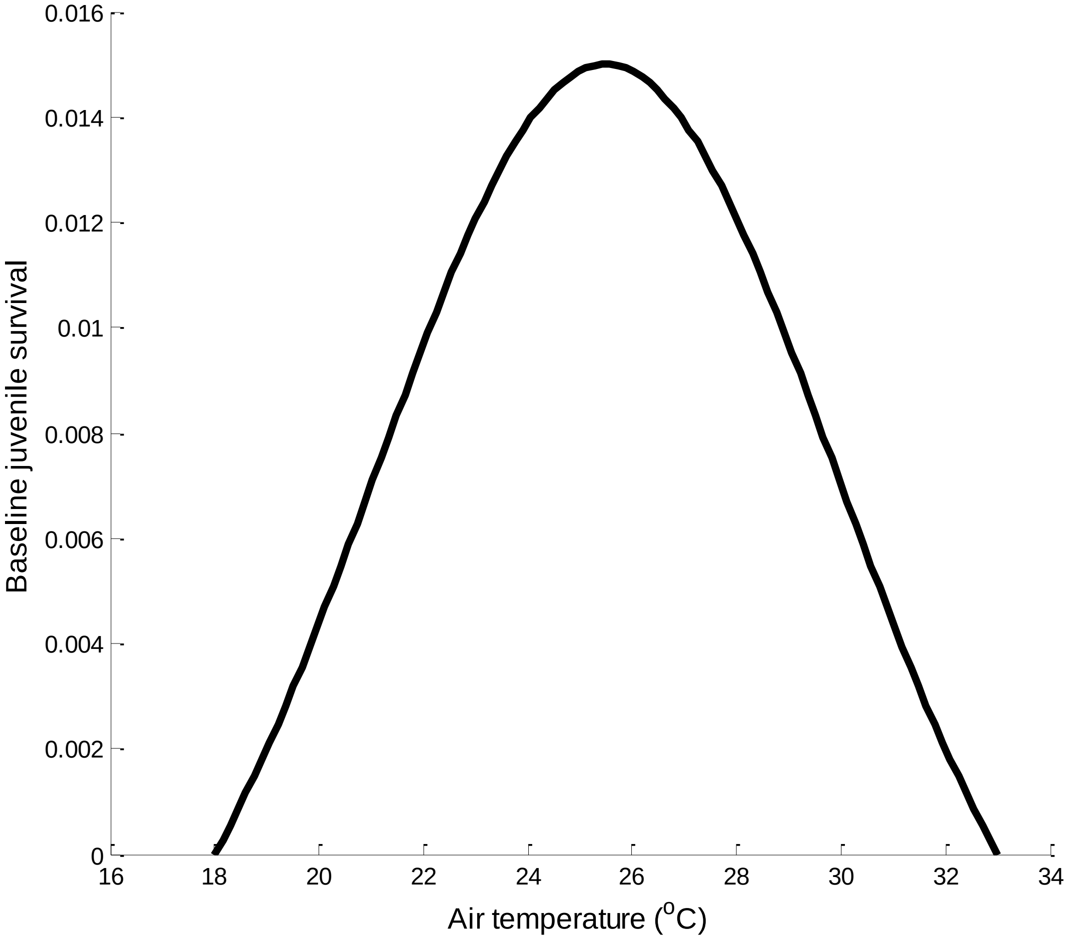


Figure 3.3: Normal temperature-dependent baseline juvenile survival parameter, *a* distributed along a temperature gradient from 18 to 33^{o}C.

chosen the individual did not disperse. The edge cells of the matrix were defined as the ‘boundaries’ beyond which an individual could move no further. If a dispersal distance was chosen to which no cells corresponded, a new distance was chosen. There was a small probability (0.1) for dispersal related mortality in juveniles. Dispersal related mortality, however, did not increase with distance moved. After adult survival, juvenile survival and dispersal, populations were counted as extinct if they had either zero adult males or zero adult females. The temperature gradient (18 – 33^{o}C) was across 100 columns in the matrix. Hence a dispersal distance of 10 cells was equivalent to a change of 1.5 ^{o}C and a dispersal distance of 20 cells was equivalent to a change of 3^{o}C. The latter temperature change as climate warming over 100 steps (years) is used in Chapter 4.

Populations with both adult males and females were counted as ‘surviving’. Thus populations can be counted as surviving even if they did not produce any viable offspring, as long as males and females immigrate to the population. Similarly, populations could persist while producing offspring of a single sex if individuals of the other sex immigrate to the population.

3.2.1.3. Simulation

The code for the simulation was co-developed by me and Dr Lisa Schwanz using Matlab 2012b. Professor Arthur Georges provided the conceptual framework for the simulation. I also developed code to average the results and produce plots using R version 3.0.2. The only standard R packages used throughout the thesis were plotrix and lattice. Simulations proceeded in discrete ‘time’ steps, for 1000 iterations. Iterations were not synonymous with a ‘breeding’ generation as generations are overlapping. At each step in each population, males and females ‘breed’ (Figure 3.1). Each simulation was replicated ten times and the averaged results were plotted in ten temperature intervals (Figures 3.5 and 3.6).

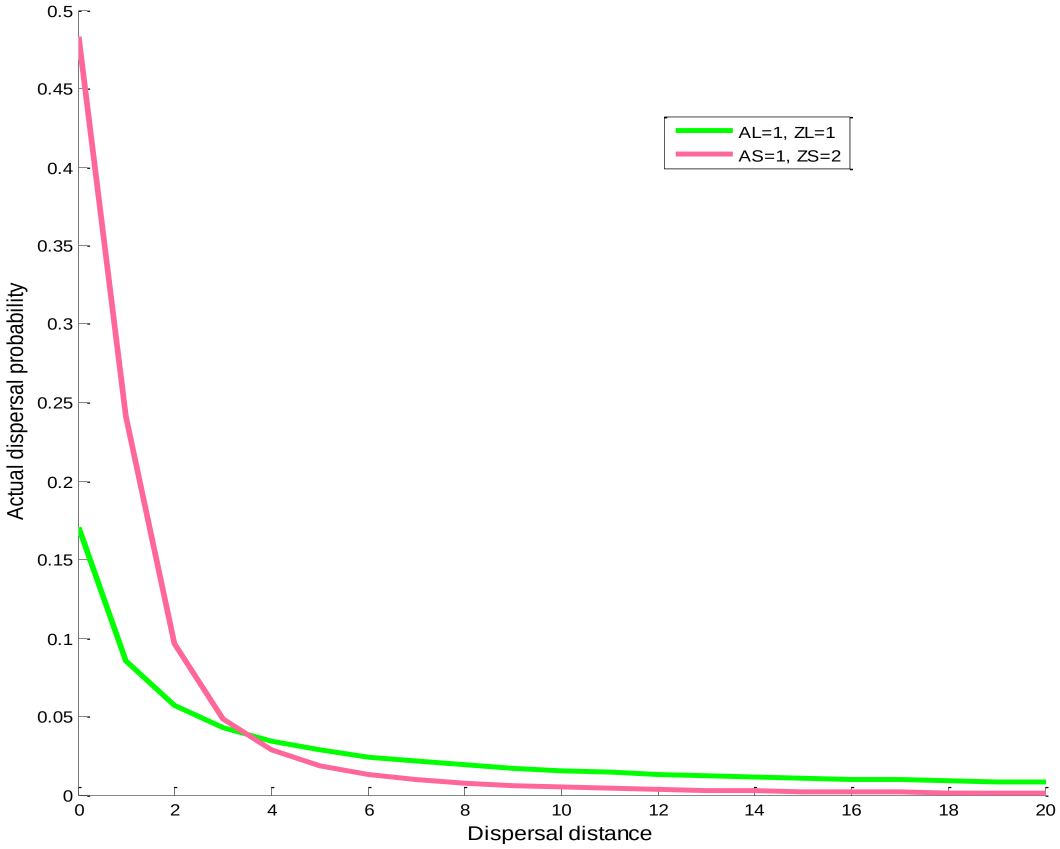


Figure 3.4: Actual probability of an individual moving a certain number of cells (dispersal distance) across a population matrix, according to two fat-tailed dispersal kernels (equation 8). Relatively large dispersal has parameters A_L=1 and Z_L=1 and relatively small dispersal had parameters A_S=1 and Z_S=2, where L=relatively large, and S=relatively small.

3.3. Results

3.3.1. Dispersal in populations of reptiles with GSD

For populations of reptiles with GSD, the normally-distributed temperature-dependent embryonic survival curve (black solid line), and cohort sex ratio (CSR) response curve (black dashed line) are shown in Figure 3.5(a). For populations of reptiles with GSD, the relationship between CSR and temperature is invariant, and hence the primary sex ratio is at equity along the temperature gradient. The number of surviving populations of reptiles with GSD is shown in Table 3.1.

The distributions of surviving populations of reptiles with GSD (Figure 3.5) (with the exception of relatively large two sex dispersal (Figure 3.5(h)) seem largely determined by the shape of the temperature-dependent embryonic survival curve. As $a=a_{max}$ at 25°C, and baseline juvenile survival is normally distributed, the greatest number of surviving populations should be distributed within a few degrees each side of 25°C. Most surviving populations of reptiles with GSD are distributed between 22.5 and 30°C (Figure 3.5).

The extent to which surviving populations of reptiles with GSD are influenced by dispersal varies. The shapes of the distributions of surviving populations of reptiles with GSD with no dispersal (Figure 3.5(b)), small (Figure 3.5(c)) and large (Figure 3.5(d)) amounts of male dispersal are the same and the limits of the range are largely determined by the shape of the temperature-dependent embryonic survival curve.

The range limits of populations of reptiles with GSD with small (Figure 3.5(e)) and a large amount of female dispersal (Figure 3.5(f)) were also largely determined by the shape of the temperature-dependent embryonic survival curve. However, dispersal had modest effects on populations of reptiles with GSD with female dispersal, but the effects differed between small (Figure 3.5(e)) and large (Figure 3.5(f)) dispersal. In populations of reptiles with GSD with a small amount of female dispersal a relatively large proportion of females did not disperse and the proportion that did disperse moved relatively small distances compared with relatively large dispersal. Either of these factors may have resulted in greater recruitment of females into the 22.5 to 24^{o}C and 28.5 to 30^{o}C temperature intervals (Figure 3.5(e)), relative to large dispersal (Figure 3.5(f)).

In contrast, for large female dispersal, a larger proportion of females dispersed larger distances and fewer females were recruited into the 22.5 to 24^{o}C and 28.5 to 30^{o}C temperature intervals (Figure 3.5(f)). For both small and large dispersal if females moved into the colder or warmer edges of the temperature distribution the chances of them encountering males were reduced because of the constraints of temperature-dependent embryonic survival. That is, in populations of reptiles with GSD the sex ratio is 50% male at all temperatures and there is a reduced chance of male survival at both the lowest and highest edges of the range (Figure 3.3). If females dispersed to populations at the extreme edges of the range where there were few surviving males the chances of reproducing decreased, and populations did not persist. There was also a reduction in female recruitment into viable populations, and this in turn decreased population persistence. This effect is highlighted by comparisons between female dispersal (Figures 3.5(e) and 3.5(f)) and two sex dispersal (Figures 3.5(g) and 3.5(h)).

Dispersal by both sexes greatly expands the range of temperatures and number of populations persisting at most temperatures compared to other dispersal scenarios (Figure 3.5(g)). Indeed, for relatively large two-sex dispersal (Figure 3.5 (h)) the effects of dispersal are so large that most of the starting populations are maintained, except at the highest and lowest temperatures.

Table 3.1: Total numbers of surviving genotypic sex determination (GSD) populations by dispersal level for all temperatures. N.B**.** Total surviving populations were averaged based on ten replicates per dispersal level.

Dispersal	Number of surviving populations of reptiles with GSD
None	4119
Male small	4157
Female small	4976
Two sex small	7934
Male large	4092
Female large	3450
Two sex large	9403

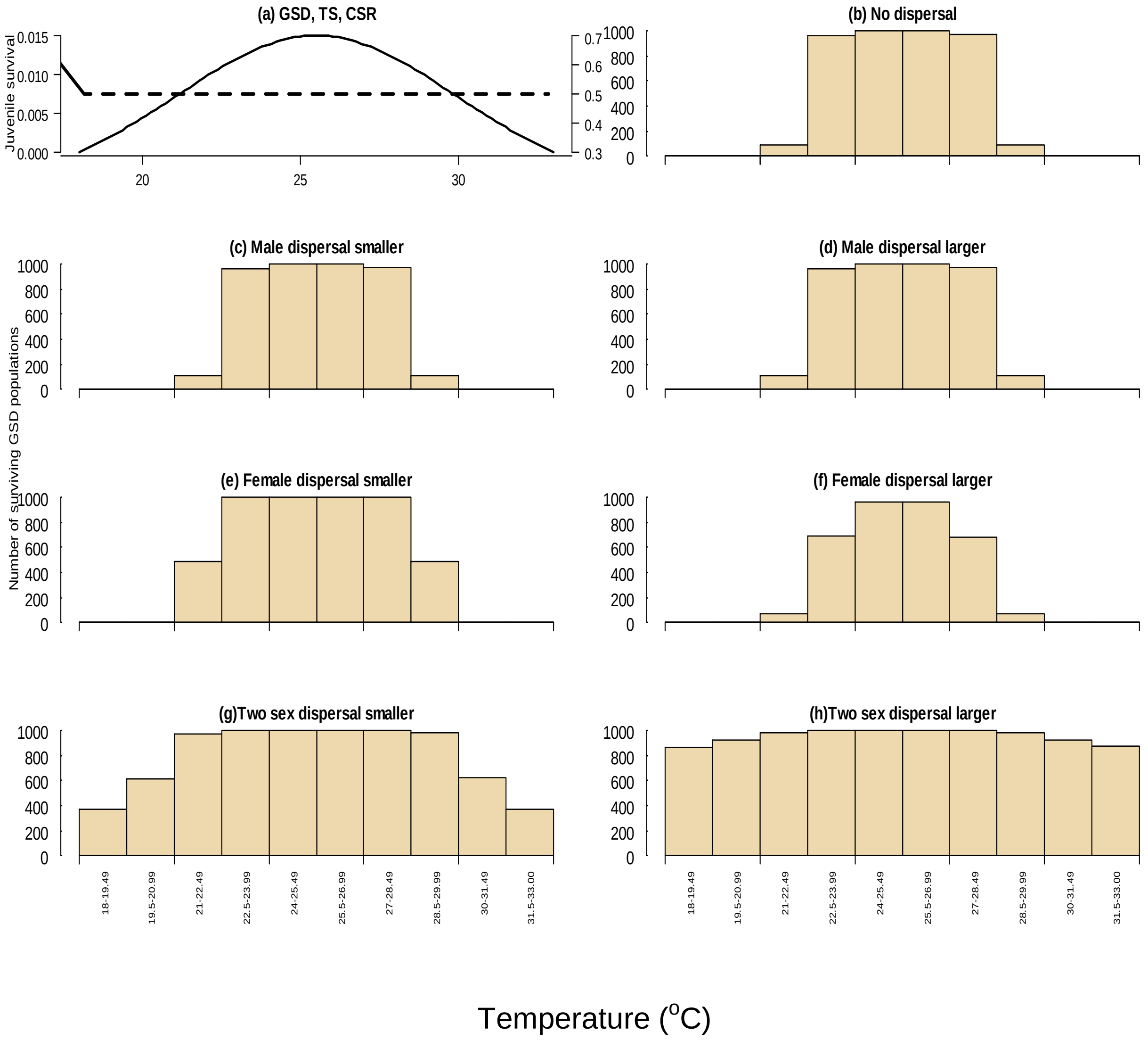


Figure 3.5: Population persistence by temperature interval for genotypic sex determination (GSD) populations. (a) Temperature-dependent embryonic survival curve (TS) (black solid line) and cohort sex ratio (CSR) (black dashed line) with intercept and slope parameters (α = 0.5, β=0.0), for populations of reptiles with GSD. The unlabelled right y-axis represents the proportion of male hatchlings. (b) to (h) shows distributions of surviving populations of reptiles with GSD by temperature (°C) for dispersal conditions. The maximum population in each temperature interval is 1000.

The total numbers of surviving populations of reptiles with GSD distributed across all temperatures are shown in Table 3.1. Populations of reptiles with GSD with two-sex dispersal had the largest number of persisting populations and populations with large female dispersal had the smallest number of persisting populations (Table 3.1).

3.3.2. Dispersal in populations of reptiles with TSD

For populations of reptiles with TSD the temperature-dependent embryonic survival (TS) curve and cohort sex ratio (CSR) response curve are shown in Figure 3.6(a). The relationship between CSR and temperature varies along the temperature gradient from 100% males at the ‘colder’ edge to 100% female at the ‘warmer’ edge of the temperature range (Figure 3.6(a)).

When the effect of temperature on primary sex ratio is added into the model, the results share some similarities with the GSD results, but also have several important differences. For both TSD and populations of reptiles with GSD, there are relatively large numbers of surviving populations between 24 and 28.5^{o}C (Figures 3.5 and 3.6). Hence, the majority of surviving populations are concentrated around the central temperature intervals. In populations of reptiles with TSD this 4.5^{o}C temperature range (between 24 and 28.5^{o}C) represents a transition from around equity in the sex ratio to a very female biased sex ratio (less than 20% males produced).

As TSD dispersing males moved into the warmer temperature ranges they encountered increasingly larger numbers of females and when sex ratios are 100% female, populations are no longer male limited. The importance of male limitation on female fecundity is evident by comparing Figure 3.6(b) with Figures 3.6(c) and 3.6(d). In the absence of dispersal (Figure 3.6(b)) warm populations were limited by the absence of males. Male dispersal resulted in considerably greater population persistence (Figures 3.6(c) and 3.6(d)). Populations in the temperature intervals between 28.5 to 32.5^{o}C (Figures 3.6(c) and 3.6(d)) benefited most from male dispersal, as very-female biased populations survived in temperature ranges where they had not without dispersal (Figure 3.6(b)).

The distributions of populations of reptiles with TSD with male dispersal (Figures 3.6(c) and (d)) were shifted more to the right towards the warmer edge of the range than populations of reptiles with GSD with male dispersal which were more centrally located in range (Figures 3.5(c) and (d)). This is because males dispersing to warmer climates encountered more females, and greater recruitment occurred.

Secondly, in populations of reptiles with TSD at the coldest edges of the temperature range only males are produced and the primary sex ratio is 100% male. By contrast, in populations of reptiles with GSD the primary sex ratio is not determined by temperature and is 50% male at the coldest temperatures. There is a reduced chance of juvenile survival at the lowest (and highest) edges of the temperature range and the probability of a single male surviving is higher in a 100% male (TSD) population than a population that is 50% male (GSD). The total numbers of surviving populations of reptiles with TSD distributed across all temperatures are shown in Table 3.2. Populations of reptiles with TSD with two-sex dispersal, had the largest number of persisting populations, and populations with the large female dispersal had many more persisting populations, than their GSD counterparts (Table3.1). Comparisons between populations of reptiles with GSD without dispersal (Figure 3.5(b)) and populations of reptiles with TSD without dispersal (Figure 3.6(b)) reveal that populations of reptiles with TSD without dispersal are more limited by biased sex ratios (females at higher temperatures and males at lower temperatures) relative to populations of reptiles with GSD because they show less persistence at the extremes of the temperature ranges (Figures 3.5(b) and 3.6(b)). A chi-square analysis (Table 3.3) indicated significantly more surviving GSD than populations of reptiles with TSD with no dispersal a small level of male dispersal, female dispersal and two sex dispersal. For the large dispersal levels (male, female and two sex) there were significantly more surviving TSD than populations of reptiles with GSD. Both relatively smaller and relatively larger two sex dispersal (Figures 3.6(g) and 3.6(h)) had a large ‘rescue’ effect on populations, similar to populations of reptiles with GSD (Figures 3.5(g) and 3.5(h)). The shapes of the distributions of TSD and GSD with relatively small and large two sex dispersal are very similar. In both instances for large dispersal equilibrium populations are almost maintained. This suggests that the level of dispersal may be too large for aquatic and terrestrial reptiles, but possibly not marine turtles. The issue of dispersal level is addressed in Chapter 4.

3.3.3. Results summary

In a qualitative sense, population persistence and range limits were more strongly influenced by temperature-dependent embryonic survival in populations of reptiles with GSD, and by dispersal in populations of reptiles with TSD. Sex determining mechanisms were also influential as female-biased populations of reptiles with TSD at the hotter, and male-biased populations of reptiles with TSD at the colder edges of the range, benefited more from dispersal by the opposite sex than populations of reptiles with GSD, with balanced sex ratios. The results indicated that TSD species through dispersal were able to persist theoretically at the hotter and colder range margins, and hence, live in larger ranges where populations of reptiles with GSD could not. The extent to which the adult sex ratio influenced female fecundity through the effects of the strength of male limitation also strongly affected the results. The strength of male limitation was also influential, in particular on female-biased populations of reptiles with TSD as populations that were moderately female biased (around 80%) experienced only a moderate level of male limitation (Figure 3.2) and this contributed to an increase in population persistence and range expansion (Figures 3.6(c) and (d)).

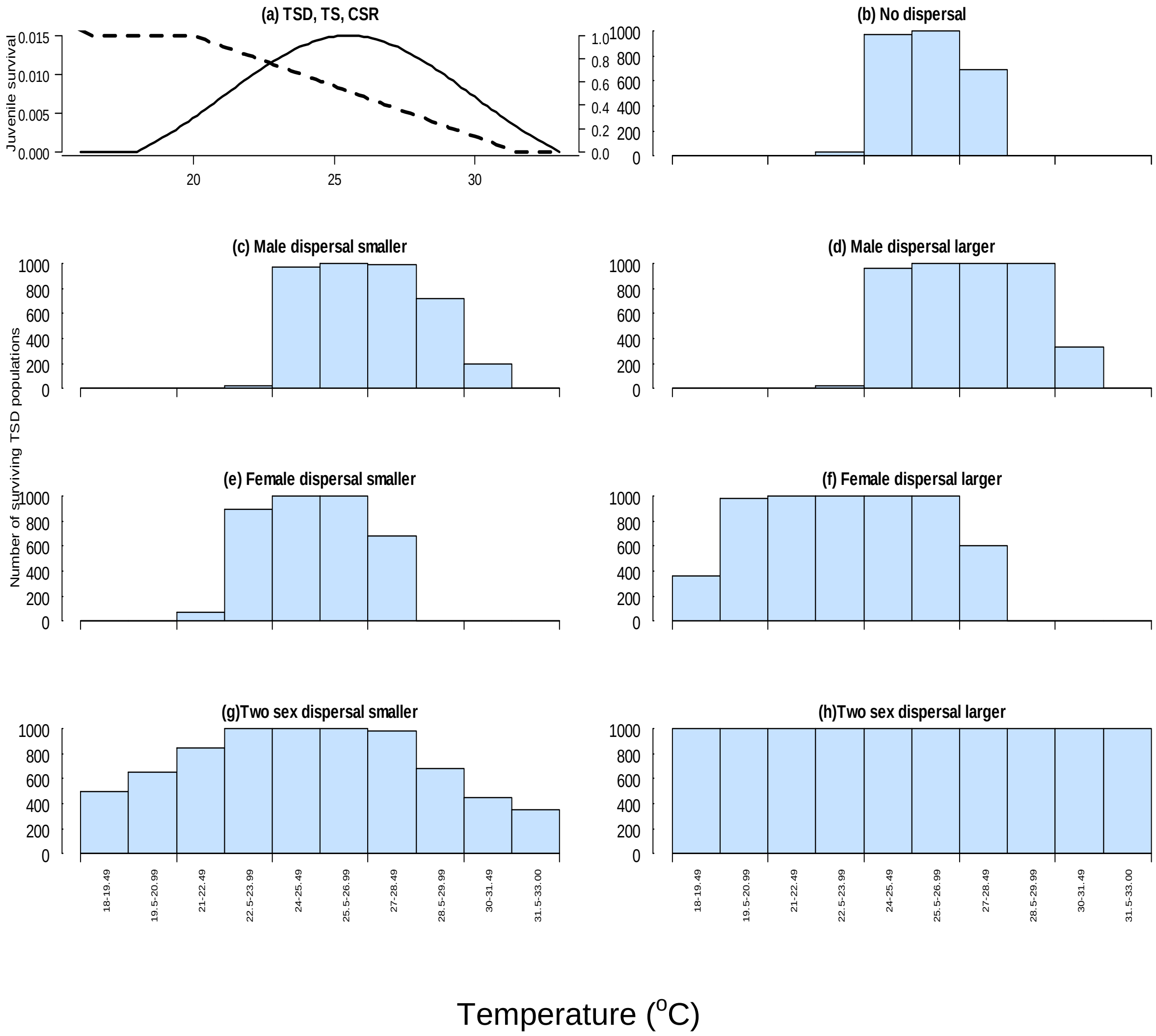


Figure 3.6: Population persistence by temperature interval for temperature-dependent sex determination (TSD) populations. (a) Temperature-dependent embryonic survival curve (TS) (black solid line) and cohort sex ratio (CSR) (black-dashed line) with intercept and slope parameters (α = 4.14, β=-0.147), for populations of reptiles with TSD. The unlabelled right axis represents the proportion of male hatchlings. (b) to (h) shows distributions of surviving populations of reptiles with TSD by temperature (^{o}C) for dispersal conditions. The maximum population in each temperature interval is 1000.

Table 3.2: Total numbers of surviving temperature-dependent sex determination (TSD) populations by dispersal level for all temperatures. N.B. Total surviving populations were averaged based on ten replicates per dispersal level.

Dispersal	**Number of surviving populations of reptiles with TSD**
None	2691
Male small	3905
Female small	3658
Two sex small	7475
Male large	4316
Female large	5957
Two sex large	10000

Table 3.3: Chi-square analysis (χ^2) of the differences between the numbers of surviving populations for GSD and populations of reptiles with TSD.

GSD compared with TSD		
Small dispersal	χ^2	**P**
None	299.4	<0.001
Male	7.9	0.005
Female	201.2	<0.001
Two sex	13.7	<0.001
Large dispersal	χ^2	**P**
Male	6.0	0.015
Female	668.1	<0.001
Two sex	18.4	<0.001

3.4. Discussion

In this chapter dispersal tendencies were found to be more influential in determining population persistence and range limits in TSD than GSD species, in a qualitative sense. To be more explicit, populations of reptiles with TSD with biased sex ratios were demonstrated to have the capacity to persist in areas where populations of reptiles with GSD with balanced sex ratios could not (Figures 3.5 and 3.6). This was especially the case at the temperature extremes (warmer or cooler) of the range, where populations of reptiles with TSD had the strongest persistence, relative to populations of reptiles with GSD. Population persistence and range limits in GSD species were largely determined by the shape of the temperature-dependent embryonic survival curve (Birchard 2004).

This result provides a clear distinction between GSD and TSD species in their responses to dispersal at range boundaries, and by inference their responses to climate change (explored further in Chapter 4). This is the most important finding of this chapter. An important distinction has also been made between the effects of juvenile survival at range limits (Figure 3.5) and the effects of biased sex ratios (Figure 3.6) at range limits, given dispersal. TSD species with biased sex ratios are able to persist beyond the limits of juvenile survival.

Dispersal has a major role in population persistence and has the potential to facilitate population persistence and reduce the probability of local extinctions due to demographic or environmental stochasticity (Brown and Kodric-Brown 1977). One source of demographic stochasticity in TSD species are imbalances in the sex ratios, specifically for many species female-biased sex ratios occurring at warmer temperatures (Janzen 1994; Hawkes *et al.* 2009; Mitchell and Janzen 2010). Dispersal by male hatchlings has been hypothesised to have an important role in facilitating population persistence in increasingly feminised populations of reptiles with TSD (Doody and Moore 2011). My thesis has taken this a step further by demonstrating for theoretical populations of reptiles with TSD that male dispersal does have a rescue effect on female-biased populations located at the warmer edge of the range (Figures 3.6(c) and (d)). Furthermore, populations of reptiles with TSD with male dispersal are able to persist outside of the range limits of populations of reptiles with GSD (Figures 3.5(c) and (d)), but with a consequent loss of many populations of reptiles with TSD at the colder edge of the range.

Populations of reptiles with TSD with the large level of female dispersal (Figure 3.6(f)) had the larger ranges but lost more surviving populations at the warmer edge of the range than GSD populations with the large amount of female dispersal (Figure 3.5 (f)). There were likely two reasons why this occurred. Firstly, in populations of reptiles with TSDthat are female biased there are many more females dispersing from warmer areas into the colder edge of the range, especially for large female dispersal where females may disperse relatively larger distances. If females dispersed to the warmer edge of the temperature distribution they would encounter only other females and hence populations did not persist at the warmest temperature intervals.

A surprising finding was that female dispersal in populations of reptiles with TSD also has the potential to increase population persistence in male-biased populations distributed towards the colder edge of the range. There was a consequent loss of populations from the warmer edge of the range (Figures 3.6(e) and (f)) relative to populations of reptiles with GSD (Figures 3.5(e) and (f)). It is unknown whether populations of reptiles with TSD can persist in colder areas, and if the limits of any ‘real’ populations of reptiles with TSD are concentrated towards the colder edge of the range. For populations to persist in colder areas evolution of tolerance for lower physiological temperatures, or towards lower pivotal temperatures would have to occur (Ewert *et al.* 2005). Another complication is that population persistence at the colder edge of the range occurs through female dispersal (Figures 3.6(e) and (f)). Dispersal by females has only been demonstrated in one reptile species, the alpine skink (Olsson and Shine 2003). Dispersal in GSD skinks is very different to dispersal in TSD species, such as marine turtles. Skinks are considered to be relatively ‘poor’ dispersers, and dispersal may occur over very short distances of a few metres (Olsson and Shine 2003). By contrast male marine turtles are considered to be very effective dispersers and may travel across oceans (Karl *et al.* 1992; Laurent *et al.* 1998; Casale *et al.* 2002; Bowen and Karl 2007). In future empirical research the distribution of populations of reptiles with TSD towards the colder edge of the range, or the potential of reptile species to push range limits for range shift under warming climates towards colder edges of the range due to female dispersal, could be further explored. Currently, the literature strongly supports male-biased dispersal in reptiles, but other dispersal tendencies remain largely uninvestigated.

Male-biased dispersal has been found to be the main dispersal tendency in GSD and TSD reptiles (Olsson and Shine 2003). The evidence for male-biased dispersal may not be as unequivocal as it seems. For example, female turtles move large distances across the Pacific or Atlantic Oceans during their lives, between foraging and nesting areas (Bowen and Karl 2007). This suggests that females are not restricted to encounters with males on nesting beaches, but also in the open ocean, and have the potential to shift to new nesting grounds or disperse. Opportunities for gene flow may arise due to overlapping adult populations in foraging areas and overlapping home ranges (Bowen and Karl 2007). Evidence from one study (FitzSimmons *et al.* 1997a) suggests that both males and females have dispersal tendencies.

Populations of reptiles with TSD with male dispersal (Figures 3.6(c) and 3.6(d)) showed population persistence and, hence, range limits that seemed to broadly correspond with the reported ranges of thermal tolerances for egg incubation of 25 to 35^{o}C in marine turtles (Yntema and Mrosovsky 1982; Hawkes *et al.* 2007; Hawkes *et al.* 2009) and 22 to 32°C in painted turtles (Schwarzkopf and Brooks 1987). These thermal limits for egg survival also seem to broadly apply also to a GSD turtle, the smooth soft shell turtle (*Apalone mutica*) (Birchard 2004). There are no known or documented studies of the degree of overlap between the range limits of TSD turtles and the limits of egg survival. The lack of information of the limits of egg survival restricts the inferences that can be made about male-biased dispersal as the predominant mode of dispersal TSD turtles, despite broad correspondence between the range limits of populations of reptiles with TSD with male dispersal and reported tolerances for egg incubation. Although population persistence and range limits for populations of reptiles with TSD with male dispersal (Figures 3.6(c) and (d)) seem quite realistic for marine turtles, the results cannot be extrapolated to apply to all TSD reptiles.

Dispersal of both sexes resulted in largest ranges or greatest potential to expand their ranges for both GSD and populations of reptiles with TSD (Figures 3.5(g) and (h) and 3.5(g) and (h)). However, this large capacity to push range limits through dispersal was considered to be somewhat ‘unrealistic’ in reptile species. Populations located at range edges may actually be *sinks*, where the rate of production is below replacement level, and without sufficient immigration will ultimately become extinct (Krebs 2009). Hence, it remains unknown how far range limits are extended by TSD reptile species through dispersal.

There is only one documented study of the green turtle that supports dispersal in both males and females (FitzSimmons *et al.* 1997a). Furthermore, if two-sex dispersal is the most effective dispersal tendency for maintaining gene flow in populations located at marginal habitats (Garant *et al.* 2007) in TSD reptiles then by implication the evolutionary mechanisms that select for sex-biased dispersal may be inefficient. Once again the importance of collecting relevant data on dispersal is emphasised to contribute towards understanding the role of dispersal in determining population range limits.

Some populations of reptiles with TSD may persist in the short-term with biased sex ratios at range margins, for example, female-biased populations at warmer edges of the range persisting through male dispersal. As a caveat, across evolutionary timeframes populations at range margins with biased sex ratios may evolve in response to frequency-dependent selection and this may move the sex ratio back to an equilibrium (Charnov and Bull, 1989). As a caveat, these considerations are evolutionary, and my thesis focuses on the population dynamics and demography of sex determination in a spatial context and I have not addressed evolutionary responses at all by design.

Frequency-dependent selection operates to favour development in the rare sex and may operate in populations of reptiles with TSD through local adaptation. Local adaptation has not been taken into consideration in this study, given the broad scale distributions, and the non-species specific nature of these theoretical populations (Weber *et al.* 2012).

In this Chapter populations of reptiles with GSD and TSD were mostly distributed towards the centres of the temperature range closer to where sex ratios were at equity rather than at range margins. Populations of reptiles with TSD without dispersal (Figure 3.6(b)) were limited by biased primary sex ratios (female bias at the warmer edge, male bias at the colder edge) relative to populations of reptiles with GSD (Figure 3.5(b)) resulting in fewer surviving populations at ‘extreme’ temperatures. Thus in the absence of dispersal GSD (Figure 3.5(b)) populations have stronger persistence than their TSD counterparts (Figure 3.6(b)). This is a good illustration of how in the absence of dispersal, population persistence and range are determined by local climate which is influential on both juvenile survival and sex ratios, in populations of reptiles with TSD.

In a model of the geographical distributions of sex ratios Kallimanis (2010) describes range expansion in some TSD species as regulated [*sic*] by low population growth at range margins, and this is due in part to biased sex ratios. However, Kallimanis (2010) doesn't consider the role of dispersal in 'stable' climates to establish new home ranges and population range limits. TSD species that don't disperse, or are 'poor' dispersers at risk of local population extinctions as climates warm (Kallimanis 2010). There were no theoretical spatial distributions of populations of reptiles with TSD at the interior or edges of their ranges presented for scenarios before or after climate change in the model proposed by Kallimanis (2010).

Theoretical models, empirical data and an understanding of demographic parameters are needed to inform research on the response of TSD and GSD species to climate change. It is imperative to understand the relative importance of demographic parameters, in particular juvenile survival, sex ratios and dispersal, in population persistence and range change in order to recommend priorities for future empirical research. Hence it will be imperative for empiricists to collect data on these parameters which affect thermal tolerances, the limits of egg survival and range limits. While data on dispersal are harder to collect, inferences about dispersal can be made from genetic analyses. Genetic analyses of sea turtles suggest that gene-flow is male-mediated and hence male-biased dispersal is the likely pattern (Karl *et al.* 1992; Casale *et al.* 2002; Roberts *et al.* 2004; Bowen and Karl 2007). Collecting data on dispersal tendencies, frequency, rates and relative distances will enable the empiricist to study responses to climate change of reptile species.

3.4.1. Conclusions

Dispersal was influential in determining range limits in TSD, and not populations of reptiles with GSD. In stable climates, populations of reptiles with TSD with biased primary sex ratios were shown to have larger ranges, through dispersal, and persist beyond the limits of populations of reptiles with GSD, with balanced primary sex ratios (Figures 3.5 and 3.6).

Population persistence and range limits in GSD species were largely determined by the shape of the temperature-dependent embryonic survival curve (Birchard 2004). This is a new and important finding as it will enhance our knowledge of the role dispersal may have in determining range limits and facilitating population persistence in reptiles.

An important distinction has also been made between the effects of juvenile survival at range limits (Figure 3.5) and the effects of biased sex ratios (Figure 3.6) at range limits. TSD species with biased sex ratios are able to persist beyond the range limits determined by juvenile survival, given dispersal. If dispersal does not occur (Figure 3.6(b)) then population persistence already limited by temperature is further reduced due to biased sex ratios, relative to populations of reptiles with GSD (Figure 3.5(b)). The importance of dispersal in facilitating population persistence and determining range limits has been demonstrated using a theoretical approach.

This is the first known study which has attempted to model population persistence and spatial distributions (ranges) of TSD and GSD reptiles in stable climatic conditions. Climatically-linked juvenile survival, climatically-linked sex ratios, dispersal and male limitation were all influential to varying degrees on population persistence and in determining range limits. It is anticipated that in Chapter 4 under climate warming these effects will be exacerbated, and indicate for populations of reptiles with TSD s that potential range change will be strongly influenced by dispersal, and in populations of reptiles with GSD by climatically-linked juvenile survival, in a qualitative sense.

Chapter 4: The effects of climate warming on population persistence and abundance in reptiles

4.1. Introduction

Global average air temperatures have increased by around 0.8°C during the 20th Century and are predicted to rise between 2 and 4.5°C during the 21st Century (IPCC 2013). Accompanying these increases in air temperature are an increase in sea level of 1 to 2 mm per annum, and an increase in sea surface temperature of between 1 and 3°C during the 21st Century (IPCC 2013). A recent revision of the estimates of rising global air temperatures indicates that the Earth may warm more slowly across the 21st Century, consistent with a 2°C increase (Otto *et al.* 2013). However, caution is urged about interpreting this as positive, as global air temperatures are still rising faster than in the past 11,000 years (Otto *et al.* 2013). Extreme weather phenomena (for example, considerably warmer summers, colder winters, and increases in bush fires, floods and cyclonic activity) are predicted to occur more frequently and with greater intensity with temperature increases (IPCC 2013). Over the millennia the Earth has experienced considerable climatic warming and cooling, but the current and projected rates of climate warming are considered to be far greater than any previous changes, considering the 100 year timeframe (Hughes 2003; IPCC 2013).

Many reptiles have a trait, known as temperature-dependent sex determination (TSD) that is considered to make them especially vulnerable to climate change (Janzen 1994; Hays *et al.* 2003; Hawkes *et al.* 2007; Hawkes *et al.* 2009; Witt *et al.* 2010). In these species, the sex of an individual is determined permanently by incubation temperature during the middle third of embryonic development (Bull 1980;Janzen and Paukstis 1991;Georges *et al.* 2005). The consequences of increases in incubation temperature are biased primary sex ratios (mostly towards females) (Janzen 1994) and a reduction in juvenile survival. Reptiles with genotypic sex determination (GSD) also exhibit a reduction in juvenile survival as temperatures exceed the thermal tolerances for egg survival (Bull 1980; Birchard 2004).

TSD species have existed for hundreds of millions of years (Silber *et al.* 2011) and it follows that they have survived and persisted despite historical climatic changes involving both warming and cooling (Mitchell and Janzen 2010). The precise mechanisms by which TSD taxa survived climate change in the past are largely unknown (Silber *et al.* 2011). It has been hypothesised that non-avian dinosaurs had TSD (Ferguson and Joanen 1982; Miller *et al.* 2004) and climatic warming resulted in male-biased populations which contributed to consequent population extinctions (Ferguson and Joanen 1982; Miller *et al.* 2004). Broad-scale volcanic eruptions occurring at the Cretaceous-Palaeogene (K-Pg) boundary around 65.6 million years before the present (*bp*), released large quantities of carbon dioxide (CO_2) into the atmosphere and this may have triggered a global warming event. This global warming event may have contributed to the extinction of many taxa (McLean 1985).

Silber *et al*. (2011) argue that the hypothesis that Cretaceous period non-avian dinosaurs with TSD experienced more extinctions due to global warming than their GSD counterparts may not be quantifiable. The TSD hypothesis for non-avian dinosaurs is argued (Silber *et al.* 2011) not to be directly testable as closely related birds have GSD and closely related crocodilians have TSD patterns of sex determination. Hence, it would be equally parsimonious to infer either GSD or TSD in non-avian dinosaurs (Silber *et al.* 2011). The TSD in non-avian dinosaurs hypothesis was indirectly tested by Silber *et al*. (2011) using 62 (of 68) late Cretaceous period non-dinosaur taxa, for which sex-determining mechanisms could be inferred. Of this fossil taxa located at Hell Creek Formation, Montana, USA, GSD was inferred for 46 of 62 (or 74%) of taxa (mammals, reptiles and amphibians) and in 16 of 62 (or 26%) of taxa (turtles and crocodilians). Of the TSD taxa, two of 16 (or 13%) and of the GSD taxa, 28 of 46 (or 61%) (including all mammals) went extinct at this location (Silber *et al.* 2011). Several explanations have been proposed by Silber *et al*. (2011) for the apparent resilience of TSD taxa to climate warming. These were: (1) only a small amount of climate change occurred at the K-Pg boundary; (2) TSD species were able to adjust pivotal temperatures (Janzen and Paukstis 1991), or demonstrate nesting plasticity (Doody *et al.* 2006) preventing skewed sex-ratios; and (3) TSD taxa had primary sex ratios that were skewed towards females and not males at higher temperatures (Silber *et al.* 2011), that allowed for increasing population growth.

TSD species commonly have biased primary sex ratios, usually skewed towards females (Janzen 1994). One way that biased sex ratios in a breeding population may be prevented is through dispersal among populations of different sex ratios. Dispersal may have been influential in the survival of ancient TSD taxa, in a changing climate, as it may be in more modern TSD taxa. Male-biased dispersal is hypothesised to have a rescue effect on modern populations of reptiles with TSD with female-biased primary sex ratios (Doody and Moore 2011). Nothing is known about dispersal tendencies in ancient TSD species, or if dispersal may have had a rescue effect on ancient clades with TSD, preventing their extinction due to climate warming. However, much more recently, marine turtles (an extensively studied TSD group) have shown the ability to respond to the effects of climate change including, climatic warming or cooling, and rising sea levels (Hawkes *et al.* 2009; Poloczanska *et al.* 2009; Fuentes *et al.* 2011).

Nesting grounds near the continental shelf of the Great Barrier Reef, Queensland, Australia that existed 12,000 years ago and previously in time were presumably accessed by flatback turtles (*Natator depressus*) have long since flooded and are no longer accessible (Limpus 1987; Fuentes *et al.* 2011). Flatback turtles may have been able to respond to climatic change and, hence, continue to exist today, by redistributing nesting sites and changing their geographical ranges. This demonstrates that flatback turtles had the capacity to respond to historical climate change, through a combination of microevolution *in situ* (for example, female nest site choice or physiology) and dispersal to more favourable nesting sites (Fuentes *et al.* 2011).

However, in the context of contemporary climate change, TSD reptiles are faced with a suite of anthropogenic activities, in addition to more rapid climate warming. Currently, for many populations of turtles, human-related destruction of habitats is restricting female nesting site choices and resulting in reduced reproductive rates and ultimately less successful dispersal (Poloczanska *et al.* 2009; Fuentes *et al.* 2011). Thus, the potentially ameliorating effect of dispersal in response to historical climate change cannot be extrapolated to future events.

One of the most widely measured types of biological response to climate change is geographical range change or range shift. There is increasing evidence that suggests species are responding to contemporary climate warming by shifting their ranges towards cooler latitudes (for example, towards the poles) or to higher elevations (Parmesan *et al.* 2000; Walther *et al.* 2002; Hughes 2003). A species range may be limited by abiotic factors, notably climate (Andrewartha and Birch 1954). The range limits of a species are described as reflecting the *realised niche* (Wiens and Graham 2005; Davies *et al.* 2009), as defined in Chapter 1.

The edges of a species range are often characterised by more hostile environments, than in the interior of the range (environments are either hotter or colder at the margins). Where habitats are marginal and species are living close to their thermal limits or physiological tolerances, they may be subject to greater environmental stress (Andrewartha and Birch 1954; Caughley *et al.* 1988). Climatic warming may result in the creation of more favourable habitats in previously colder and more hostile areas and species may be able to shift their geographical ranges to cooler latitudes (Parmesan *et al.* 2000; Hughes 2003).

The combination of biased primary sex ratios (sex ratios of offspring) (Janzen 1994) and reduced juvenile survival (Girondot *et al.* 2004) renders TSD species especially vulnerable to climate warming. Warming environments can simultaneously reduce juvenile survival and lead to biased primary sex ratios (Hawkes *et al.* 2009). This is an issue of concern, especially if juvenile sex ratios are maintained in the population into later life stages, due to the loss or elimination of the opposite sex (Janzen 1994; Wright *et al.* 2012). The few available data on the relationship between juvenile and adult sex ratios in TSD reptiles come primarily from studies of marine turtles. The results largely support the maintenance of juvenile sex ratios in later stages of life (Stabenau *et al.* 1996; Braun-McNeill *et al.* 2007) (refer to Chapter 1 for further details).

In the absence of dispersal or *in situ* changes in nesting behaviour local population extinctions are probable. There have been relatively few attempts to model the relationship between climate warming and range shift in TSD species with biased primary sex ratios. Kallimanis (2010) proposed a model describing the geographical distribution of sex ratios (refer to Chapter 3, Introduction). Imbalanced sex ratios in marginal habitats are assumed to limit population growth and set the limit of range expansion under stable climatic conditions (Kallimanis 2010).

Kallimanis (2010) suggests that equal sex ratios will result in the highest population growth. In contrast, Freedberg and Taylor (2007) argue that increases in reproduction and population growth are associated with female biased sex ratios, and not balanced sex ratios. Male recruitment through dispersal is thought to be essential to facilitate local population persistence in increasingly female biased populations (Doody and Moore 2011). This may be fortuitous as male-biased dispersal is thought to be the dominant dispersal tendency in many reptiles with GSD (Doughty *et al.* 1994; Rassmann *et al.* 1997; Rivera *et al.* 2006; Keogh *et al.* 2007; Dubey *et al.* 2008) and TSD (Karl *et al.* 1992; Limpus 1993; Casale *et al.* 2002; Roberts *et al.* 2004; Freedberg *et al.* 2005; Bowen and Karl 2007). Dispersal and recruitment of male hatchlings into female-biased populations may influence the persistence of populations vulnerable to climate warming. However, many populations may actually be sinks, where the rate of production is below replacement level, and without sufficient immigration will ultimately become extinct (Krebs 2009).

Kallimanis (2010) assumed that the sex ratios of TSD species vary with geography, and balanced sex ratios occur in the interior, and biased sex ratios occur at the edges of ranges. The ‘leading’ edges of ranges are environments of low temperatures and male-biased sex ratios and the ‘trailing’ edges are environments of high temperatures and female-biased sex ratios. Kallimanis (2010) argued that at the leading edge as sex ratios change from male biased to equal, as climates warm, population growth will increase and range expansion into previously cooler areas, will occur. Conversely, the trailing (hotter) edge populations will become extinct as ranges become too hot and sex ratios become all female (Kallimanis 2010; Escobedo-Galvan *et al.* 2011).

Escobedo-Galvan *et al*. (2011) criticise the model proposed by a Kallimanis (2010) as an oversimplification of ecological and evolutionary processes that may produce more complex responses of TSD species to climate change. For example, range expansion is not only a matter of population growth at range margins, but also of dispersal and many TSD species are thought to be poor dispersers (Escobedo-Galvan *et al.* 2011). Population growth in TSD species may not be at the maximum when sex ratios are equal (Freedberg and Taylor 2007). Hence, a trailing (hotter) edge that becomes female-biased may not retract and conversely a leading (colder) edge that tends towards equal sex ratios and may not grow as well as assumed by Kallimanis (2010).

Wedekind (2002) demonstrated theoretically that a continuous manipulation of the adult sex ratio of species away from equal and towards female-bias leads to enhanced population growth over time in terms of the absolute population numbers. In a few generations populations were able to overcome the initial genetic disadvantage of a biased adult sex ratio. Hence, female-biased populations lead to enhanced growth, as long as there were at least some males, of course.

In Chapter 3, populations of reptiles with TSD with biased sex ratios were found to have the capacity for expanded ranges compared to populations of reptiles with GSD, through dispersal, enabling population persistence outside of the ranges of GSD. Population persistence and expanded ranges was found in GSD to be more strongly influenced by temperature-dependent embryonic survival, than by dispersal, at least in a qualitative sense. Although the very large effect of two-sex dispersal in enhancing population persistence at all temperatures (Chapter 3), indicates that the level of dispersal may be too high for some aquatic or terrestrial reptiles, as these species are known to either disperse small very distances (sometimes only a few metres) (Olsson and Shine 2003; Freedberg *et al.* 2005) or not at all (Escobedo-Galvan *et al.* 2011).

While the large or small levels of dispersal may be of relevance for reptile species that are effective dispersers such as marine turtles (Casale *et al.* 2002; Roberts *et al.* 2004), a very small level of dispersal was introduced in this chapter to broaden the simulation model to be as non-species specific as possible. In Chapter 3, dispersal, juvenile survival, sex determining mechanisms and male-limitation were found to be influential on population persistence to varying degrees. Hence, it is expected that the effects of these factors will be exacerbated by climate warming. In this chapter the effects of rapid, short-term climate change across 100 years, and dispersal on range expansion in TSD and GSD species are evaluated.

Biased primary sex ratios may have detrimental effects on local population growth and persistence, although their impact has been poorly explored. Kallimanis (2010) argued that geographical ranges (and range expansion) are limited by poor population growth at the range boundary due to biased sex ratios, but growth may be facilitated through dispersal as climates warm, at the leading edge of the range. In contrast, Freedberg & Taylor (2007) argue that population growth is enhanced by female-biased sex ratios. Kallimanis (2010) was not specific about whether biased adult or juvenile sex ratios were limiting population growth at range margins. As adult and juvenile sex ratios are highly correlated in marine turtles (Wright et al. 2012), I tested both to cover both contingencies. The degree of association between adult and juvenile sex ratios will be tested in accordance with the secondary aim.

4.1.1. Aims

My primary aim is to explore the effects of climate warming and dispersal on population persistence and range change in species with temperature-dependent embryonic survival and temperature-dependent and genotypic sex determining mechanisms, using a gradient of increasing temperatures. Climate warming is represented by a 3^{o}C increase in ambient air temperatures across a 100 year period. My secondary aim is to evaluate the degree of association between juvenile and adult sex ratios for populations of reptiles with TSD without and with climate warming.

4.2. Methods

4.2.1. Simulation

The code for the simulation was developed using Matlab 2012b. Code was developed to average the results and produce plots using R version 3.0.2. The only standard R packages used were plotrix and lattice. A matrix of 10,000 populations were distributed along a temperature gradient (100 temperatures, the columns of the matrix), and replicated with 100 populations per temperature (the rows of the matrix). Each population in the matrix was initiated with 100 males and 100 females. There were two climate scenarios: (1) no climate change; and (2) climate change. A 3^{o}C increase in ambient air temperature was selected as it is consistent with 'medium' projected temperature increase (IPCC 2013). Under the 'no climate change' scenario, the temperatures were identical to the middle temperature gradient (18 to 33^{o}C) used in Chapter 2, Figure 2.2(b), and Chapter 3 for the 'stable' climate (Figure 3.3) and maintained thus for 1100 iterations (or years). Under the 'climate change' scenario, a 3^{o}C increase in temperatures across the final 100 years of the simulation (iterations 1000 to 1100 inclusive) resulted in temperatures ranging from 21 to 36^{o}C, representing a new temperature gradient for climate change.

Simulations were run for 1100 years with no climate change to estimate range limits under constant climate (refer to Chapter 3). Separate simulations with the same parameters were run for 1100 years, 1000 years with no climate change and for the last 100 years temperatures increased in equal increments until a 3^{o}C increase was reached. Each simulation was replicated 15 times and the averaged results were plotted in adjacent bins, approximately 1.5^{o}C in width, or 10 cells, the columns of the matrix, representing fixed geographical locations of modelled populations. The first set of bins represented the number of surviving populations without climate warming and the second the number of surviving populations following climate warming. Thus, the bins may be thought of as constant places on a landscape (for example, latitude). Range limits were measured by determining the proportion of populations that persisted at each temperature. Simulations proceeded in discrete ‘time’ steps. At each step in each population, adult males and females reproduced. Refer to Chapter 3 for further details of the simulation.

In addition, average population sizes (and standard errors) for each column of the matrix were plotted, for conditions of no climate change and following climate change. Each column in the population matrix corresponds to an individual temperature on the temperature gradient, between 18 – 33^{o}C and 21 – 36^{o}C at time=1100. Plotting average population sizes by column in the population matrix instead of temperature enables the direction of range shift to be visualised, and shows how average population sizes differ between dispersal tendencies and the sex determining mechanism.

4.2.2. Population model

Extensive details of the population model are outlined in Chapters 2 and 3.

The number of juveniles produced depended on the number of adult females in the population and female fecundity. Female fecundity, the number of offspring (eggs laid) per adult female, was a function of the adult sex ratio in the population, asymptoting to a maximum level (B_{max}=10) when males were common, and moving towards zero when males become rare.

$$B = B_{max} * (ASR / (ASR + b)) \qquad \text{eqn 7}$$

See Chapter 2 (equation 4) for more details. A moderate level of male limitation on female fecundity (b=0.01) was chosen (refer to Chapter 3).

The number of offspring in each population that were male was sampled using a random binomial distribution, given the total number of offspring and the population-specific sex ratio (probability of producing a male, p or female ($1-p$); Figure 3.1). The number of female offspring was the total number of offspring minus the number assigned to be male. For populations of reptiles with GSD, the sex ratio was equal, in all populations. For populations of reptiles with TSD, p (the proportion of hatchlings that develop as male) was a function of the population temperature at that time step. The cohort sex ratio (CSR) response curve 3 (refer to Methods section, Chapter 2) with parameters derived for the painted turtle (Schwanz *et al.* 2010) with intercept $\alpha=4.14$ and slope $\beta=-0.147$ (Figure 2.2(a)) was used.

After offspring production, the number of adults surviving to the next time step was sampled using a random binomial distribution given the initial number of adults in the population and a probability of survival ($s=0.95$ for both males and females) (Figure 3.1). The number of offspring that were recruited into the adult population in the next time step (survived to and bred at age 1) was based on population temperature and dispersal functions (refer to Chapter 3 Methods section). A normal distribution of juvenile survival probabilities was distributed along the ‘no climate change’ temperature gradient scenario (18 – 33^{o}C) with a maximum juvenile survival a_{max} =0.015 and a minimum survival value of zero (Figure 3.3). The relationship between juvenile survival rates and temperature was not allowed to evolve. The pivotal temperature was also not allowed to evolve.

4.2.3. Spatial analysis and correlation of sex ratios in populations of reptiles with TSD

The analysis in this section is related to my secondary aim. The population matrices of populations of reptiles with TSD with the two sex dispersal tendency (very small level) of the adult sex ratio (ASR) and juvenile sex ratio (p, the proportion of hatchlings that develop as male a function of the population temperature at a time step) were represented spatially for scenarios of no climate and climate warming. If female-biased juvenile sex ratios were maintained into adulthood, then this is an issue of concern because of the loss or elimination of the opposite sex. Male shortages have obvious implications for female fecundity, and population growth and persistence. However, there seems to be a paucity of data available on the extent of male limitation on reptile populations. To investigate this further a Spearman's rank correlation test was performed to test if there were significant differences between juvenile and adult sex ratios, without and with climate warming. The adult sex ratio (ASR) is the proportion of adult males in the population, and was estimated as:

ASR=The number of adult males in the population/ (the number of adult males in the population+the number of adult females in the population).

4.2.4. Dispersal

There were three levels of dispersal none, small and very small. The small level of dispersal was the same as in Chapter 3, and was selected over large dispersal as many reptile species are considered to disperse relatively small distances (Olsson and Shine 2003), or not disperse at all (Escobedo-Galvan *et al.* 2011). The very small level of dispersal was introduced as it is also considered to represent a more realistic level of dispersal for many reptile species (Figure 4.1). In the Methods section of Chapter 3 extensive details are given of the dispersal model. In this chapter small and very small dispersal levels were each divided into four dispersal scenarios, as in Chapter 3: no dispersal; male dispersal; female dispersal; and two-sex dispersal. In the very small level of dispersal juveniles have a higher probability of not dispersing (around 63%) and dispersing to the next cell (around 33%), and a lower probability of dispersing further (around 4%) than in the small level of dispersal (around 48%, 24% and 28%, respectively) (Figure 4.1).

4.3. Results

4.3.1. GSD Populations

After 1100 steps (years) of stable climatic conditions, the distributions of populations of reptiles with GSD (Figure 4.2, yellow bars) (with the exception of two-sex dispersal) seem largely determined by the shape of the temperature-dependent embryonic survival (TS) curve, in a qualitative sense. After climate warming, the number of surviving populations of reptiles with GSD decreased marginally at the warmer edge of the range (Figure 4.2, red bars). populations of reptiles with GSD without dispersal (Figure 4.2 (b)), with male dispersal (Figures 4.2 (c) and (d)), and with very small female dispersal (Figure 4.2 (f)), showed very similar patterns of population persistence. Hence, male dispersal and very small female dispersal had no effect on population persistence. The small decline in populations of reptiles with GSD at the warmer edge of the range (Figures 4.2 (b), (c), (d) and (e)) with climate warming occurred because juvenile survival rates declined to a level where population growth rates fell below replacement level. Populations with the small level of female dispersal (Figure 4.2 (e)) showed higher range, compared with the other dispersal tendencies (except for two-sex dispersal) (Figures 4.2 (b), (c), (d) and (f)). In populations with two-sex dispersal, populations persisted at almost all temperatures (Figure 4.2). A very modest amount of range shift occurred towards the colder edge of the range as climates warmed for populations of reptiles with GSD with two-sex dispersal (Figure 4.3(d)).

The direction of range shift towards colder temperatures is evident with climate warming (red lines) relative to no climate warming (gold lines) (Figure 4.3(d)). Although range contraction

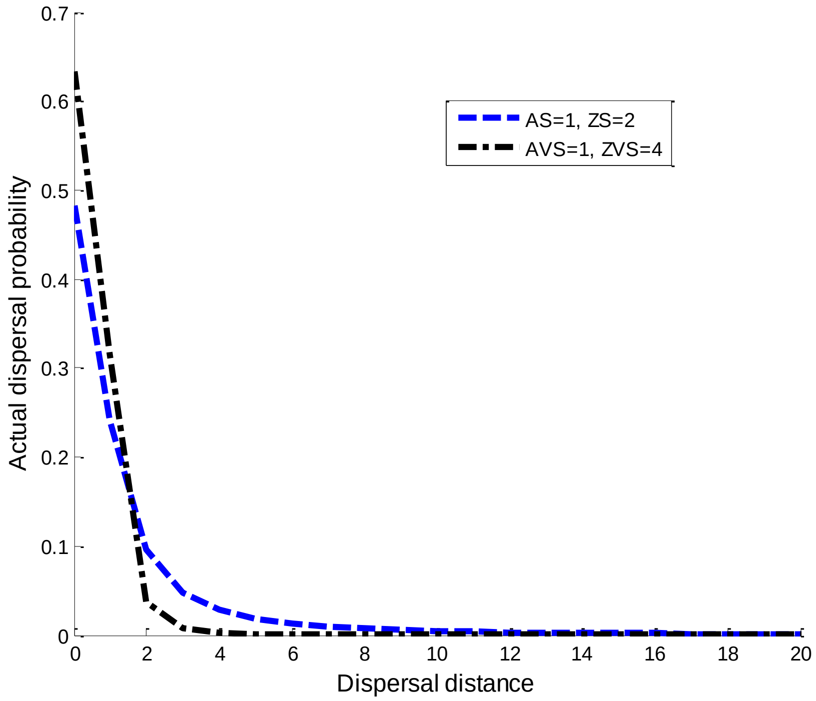


Figure 4.1: Actual probability of an individual moving a certain number of cells (dispersal distance) across a population matrix for two fat-tailed dispersal kernels (equation 8). Small dispersal has parameters A_s=1 and Z_s=2, and very small dispersal has parameters A_{vs}=1 and Z_{vs}=4. where, s =small and vs= very small.

at the warm edge of the range was observed in all instances, range expansion at the colder edge of the range was not observed in any of the modelled populations of reptiles with GSD (Figures 4.2 and 4.3). Average population sizes (and standard errors) are not shown by temperature, but by column (for each of 100 columns) of the population matrix (Figure 4.3). populations of reptiles with GSD with very small two-sex dispersal (Figure 4.3(d)) have populations that are much larger on average, than populations of reptiles with GSD with the other dispersal tendencies (Figures 4.3 (a), (b), (c)). The majority of populations had larger average sizes without climate warming relative to climate warming (Table 4.1). The distributions of populations with climate warming were skewed towards a decrease in average population sizes at the warmer edge of the range (Figure 4.3, red lines). Populations grew to larger sizes at colder edge of the range (Figure 4.3, red lines), compared to those without climate warming (Figure 4.3, gold lines).

4.3.2. Populations of reptiles with TSD

As climates warmed the number of surviving populations of reptiles with TSD (Figure 4.4, red bars) decreased at the warmer edge of the range compared to no climate warming (Figure 4.4, grey bars). The main reason for the decline in the number of surviving populations at the warmer edge of the range was an increase in female bias in the sex ratios, and consequent reductions in determining the range limits of populations of reptiles with TSD. This is because at the warmer (or colder) edges of the range sex ratios are strongly female (or male) biased, and fecundity is reduced, in the absence of immigration. This effect increased following climate warming, and there was a reduction in the number of surviving populations of reptiles with TSD, at the warmer edge of the range compared with no climate warming (Figure 4.4(b)).

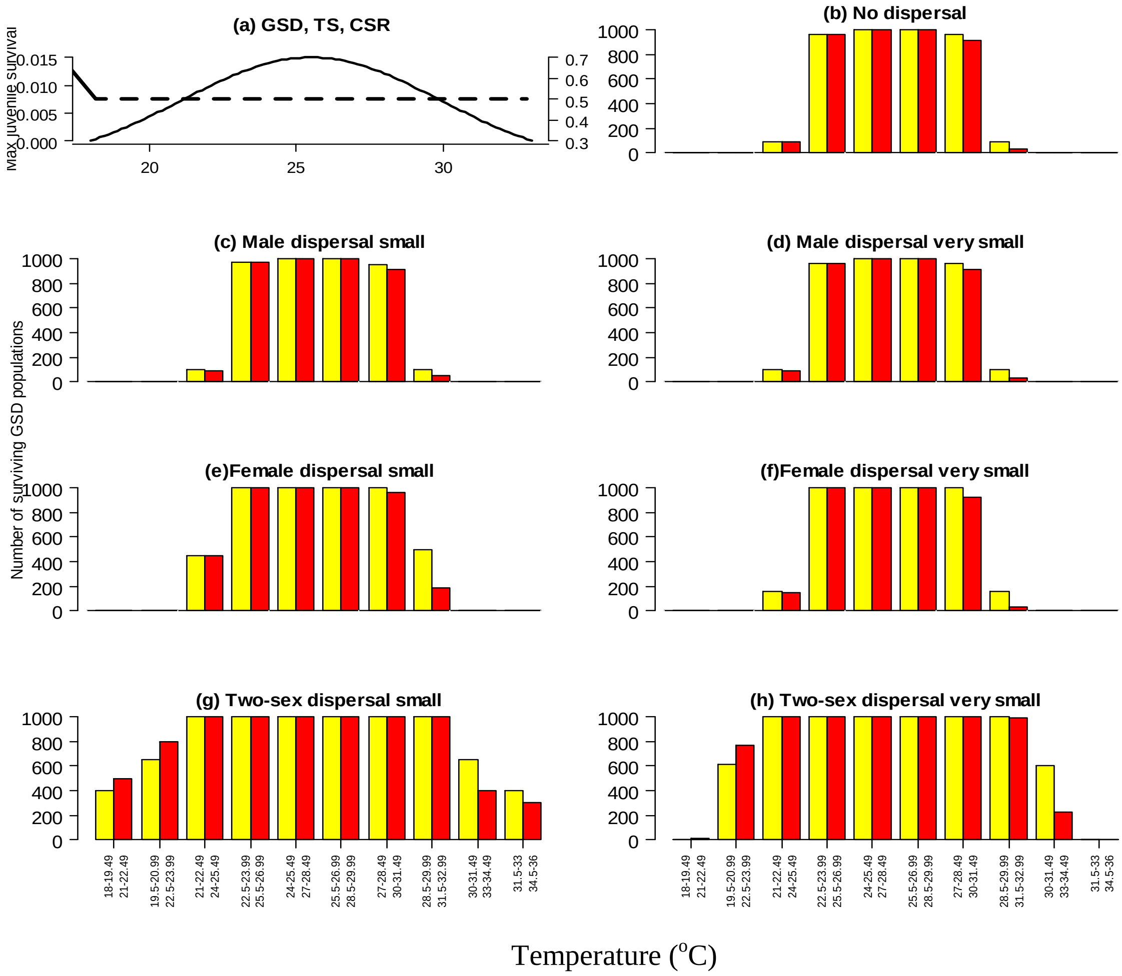


Figure 4.2: Population persistence by temperature interval for genotypic sex determination (GSD) populations without and with climate warming. (a) Temperature-dependent embryonic survival curve (TS) (black solid line) and cohort sex ratio (CSR) (black dashed line) with intercept and slope parameters (α = 0.5, β = 0.0), for populations of reptiles with GSD. The unlabelled right y-axis represents the proportion of male hatchlings. (b) to (h) show distributions of surviving populations by temperature (°C) for dispersal levels none, small and very small. Populations with no climate warming (yellow bars) and with climate warming (red bars) are shown. Climate warms by 3°C over 100 steps (years). The maximum number of surviving populations in each temperature interval is 1000.

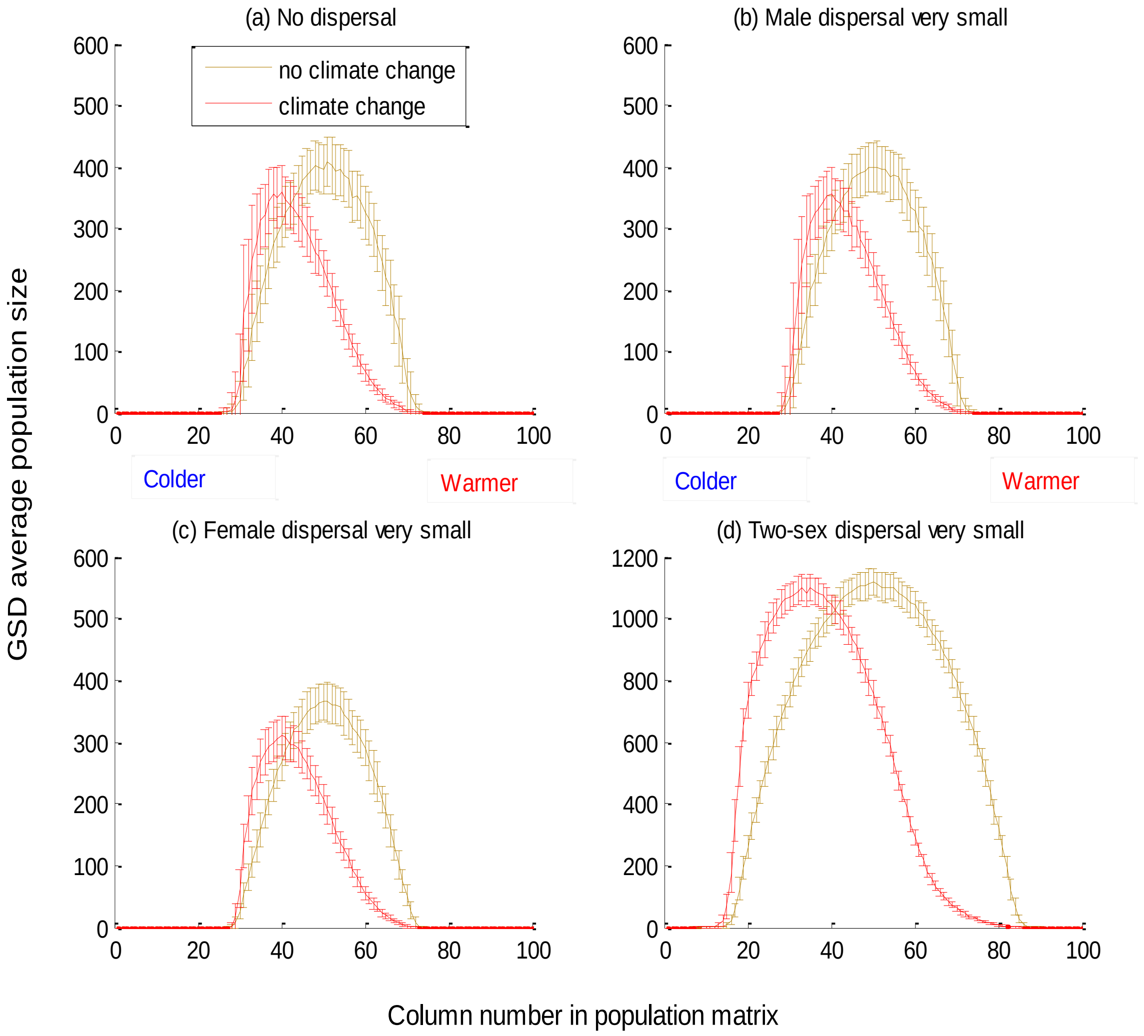


Figure 4.3: Average population sizes and standard errors, for populations of reptiles with GSD with very small dispersal, for each individual column of the population matrix. Each column in the matrix corresponds to an individual temperature, either before or following climate warming. Each column corresponds to an individual temperature which increases along the gradient (starting at 18°C with no climate warming and 21°C following climate warming). (a) No dispersal, (b) male dispersal, (c) female dispersal and (d) two-sex dispersal. Note: Populations with two-sex dispersal reach much larger average sizes, and, hence, the scale on the y-axis is twice that of the other plots.

The decline in the number of surviving populations at the warmer edge of the range was because of an increase in female bias in the sex ratios, and reductions in the proportion of males, female fecundity, as well as juvenile survival. Hence cohort sex ratio (CSR), temperature-dependent embryonic survival, and male limitation were all influential in determining the range limits of populations of reptiles with TSD.

The very small amount of male dispersal (Figure 4.4 (d)) had no effect on population persistence, or in determining range limits, which were determined primarily by baseline juvenile survival (*a*) and CSR, similar to no dispersal (Figure 4.4(b)). Populations with a very small amount of female dispersal persisted at the colder edge of the range and the number of surviving populations increased marginally following climate warming (Figure 4.4(f)). The distribution of surviving populations as a result of a very small amount of female dispersal was similar to populations of reptiles with TSD with no dispersal (Figure 4.4(b)), and a very small amount of male dispersal, with both no climate warming and climate warming (Figure 4.4(d)).

A small amount of female dispersal (Figure 4.4(e)) resulted in greater population persistence at the colder edge of the range (with no climate change and climate change) compared with a very small amount of female dispersal (Figure 4.4(f)). More populations with a small amount of male dispersal persisted at the warmer edge of the range (Figure 4.4 (c)), than populations with a very small amount of male dispersal (Figure 4.4(d)). The larger numbers of females produced and/ or dispersing further were able to increase population persistence towards the colder edge of the range, for the small amount of dispersal (Figure 4.4(e)). Climate warming resulted in the production of a greater proportion of females and a reduced proportion of males. If more females dispersed to populations with fewer males (due to climate warming) then the rates of reproduction may be higher as there is more dispersal related recruitment of females, and no cost to males associated with dispersal. However, there was a 10% risk of dispersal related mortality, and hence, reduced juvenile survival for the dispersing sex. Only populations of reptiles with TSD with a very small amount of dispersal showed evidence of range expansion (Figure 4.4(h)). All populations of reptiles with TSDchanged in population size as climates warmed (Figure 4.5). Range shift towards colder temperatures occurred only for populations with a very small amount of two-sex dispersal with climate warming (red lines), compared to no climate warming (blue lines) (Figure 4.5). Overall, there was a decrease in average population sizes with climate warming (Figure 4.5). The distributions of populations were skewed at the warmer edge, towards the overall decrease in average population size at the warmer edge of the range, with climate warming (Figure 4.5). At the colder edge of the range average population sizes increased with climate warming (Figure 4.5). The majority of populations had smaller average sizes with climate warming than in a stable climate (Table 4.2).

The largest average population sizes (average size greater than 1000) in populations of reptiles with TSD with two-sex dispersal, at a very small amount and no climate warming occurred between population matrix columns 45 to 65 (Figure 4.5 (d), blue line). This corresponds to adult sex ratios of 0.1 to 0.45 (proportion males) (Figure 4.6 (a)) and juvenile sex ratios approximately 0.15 to 0.5 (proportion males) (Figure 4.7 (a)). In populations of reptiles with TSD, with two-sex dispersal and climate warming, populations of the largest average size (average size greater than 1000) occurred between population matrix columns 34 to 50 (Figure 4.5(d), red line). This corresponds to an adult sex ratio of between 0.05 and 0.4 (proportion males) (Figure 4.6(b)) and juvenile sex ratios approximately 0.05 to 0.4 (proportion males) (Figure 4.7(b)). In populations of reptiles with TSD with the very small amount of two-sex dispersal, adult and juvenile sex ratios for persisting populations (of size greater than zero), changed from around equity without climate warming (Figures 4.6(a) and 4.7 (a)), to increasingly female biased with climate warming (Figures 4.6(b) and 4.7 (b)).

Populations of reptiles with TSD in columns 28 to 48 (colder edge of range) with no climate warming (Figure 4.5(d), blue lines) that had male-biased (0.5 to 0.8, proportion males) adult sex ratios (Figure 4.6(a)), grew to larger sizes with climate warming (Figure 4.5(d), red lines), as the proportion of females in the population increased (0.15 to 0.4, proportion males) (Figure 4.6(b)). Populations declined at the warmest, most female-biased part of the range (Figure 4.5(d), red lines).

At column 55 with climate warming (Figure 4.5(d), red line) populations had large average sizes despite having adult sex ratios of around 0.05 (proportion males) (Figure 4.6 (b)). However, with no climate warming (Figure 4.6 (a)) populations in column 55 had adult sex ratios of around 0.4 (proportion male). The gradual transition across 100 years from adult sex ratios of around 0.4 (proportion male) to 0.05 (proportion male) seemed to delay the decline in population sizes, that would be expected given a reduction in female fecundity owing to the loss of males.

Spearman's rank correlation test, comparing adult and juvenile sex ratios, for populations of reptiles with TSDwith two-sex dispersal, without climate warming (r = 0.999, df=9998, P<0.0001) and with climate warming (r = 0.824, df=9998, P<0.0001) were highly significant. This result indicates highly significant positive correlations and hence a high degree of positive association between adult and juvenile sex ratios without and with climate warming. The largest average population sizes occurred in populations of reptiles with TSD,with a very small amount of two-sex dispersal at an adult sex ratio at around 0.15 (proportion male), with no climate warming and 0.2 (proportion male), with climate warming (Figure 4.8). Following climate warming, populations with even sex ratios or male-biased adult sex ratios had smaller average population sizes than expected compared to the static scenario without climate warming (Figure 4.8).

Table 4.1: Percentage of genotypic sex determination (GSD) populations with larger average population sizes with no climate warming compared with climate warming. The majority of populations had larger average population sizes with no climate warming.

GSD	Percentage of populations
No dispersal	68%
Male dispersal	68%
Female dispersal	71%
Two-sex dispersal	61%

Table 4.2: Percentage of temperature-dependent sex determination (TSD) populations with larger average population sizes with no climate warming, compared with climate warming. The majority of populations had larger average population sizes with no climate warming.

TSD	Percentage of populations
No dispersal	62%
Male dispersal	67%
Female dispersal	52%
Two-sex dispersal	55%

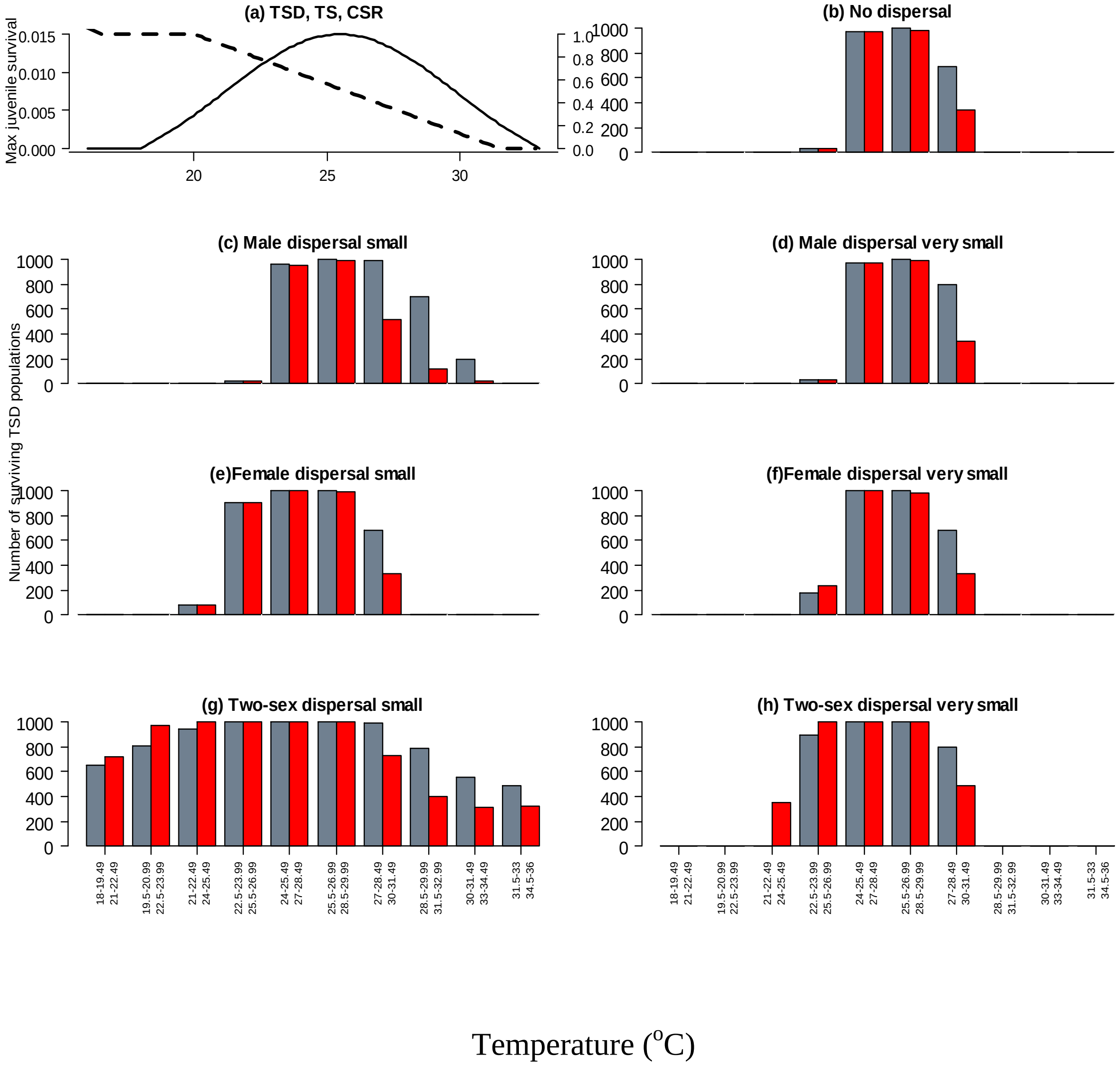


Figure 4.4: Population persistence by temperature interval for temperature-dependent sex determination (TSD) populations without and with climate warming. (a) Temperature-dependent embryonic survival curve (TS) (black solid line) and cohort sex ratio (CSR) (black dashed line) with intercept and slope parameters ($\alpha = 4.14$, $\beta = -0.147$), for populations of reptiles with TSD. The unlabelled right axis represents the proportion of male hatchlings. (b) to (h) shows distributions of surviving populations of reptiles with TSDby temperature (^{o}C) for dispersal tendencies none, small and very small. Populations with no climate warming (grey bars) and with climate warming (red bars) are shown. Climate warms by 3^{o}C over 100 steps (years). The maximum number of surviving populations in each temperature interval is 1000.

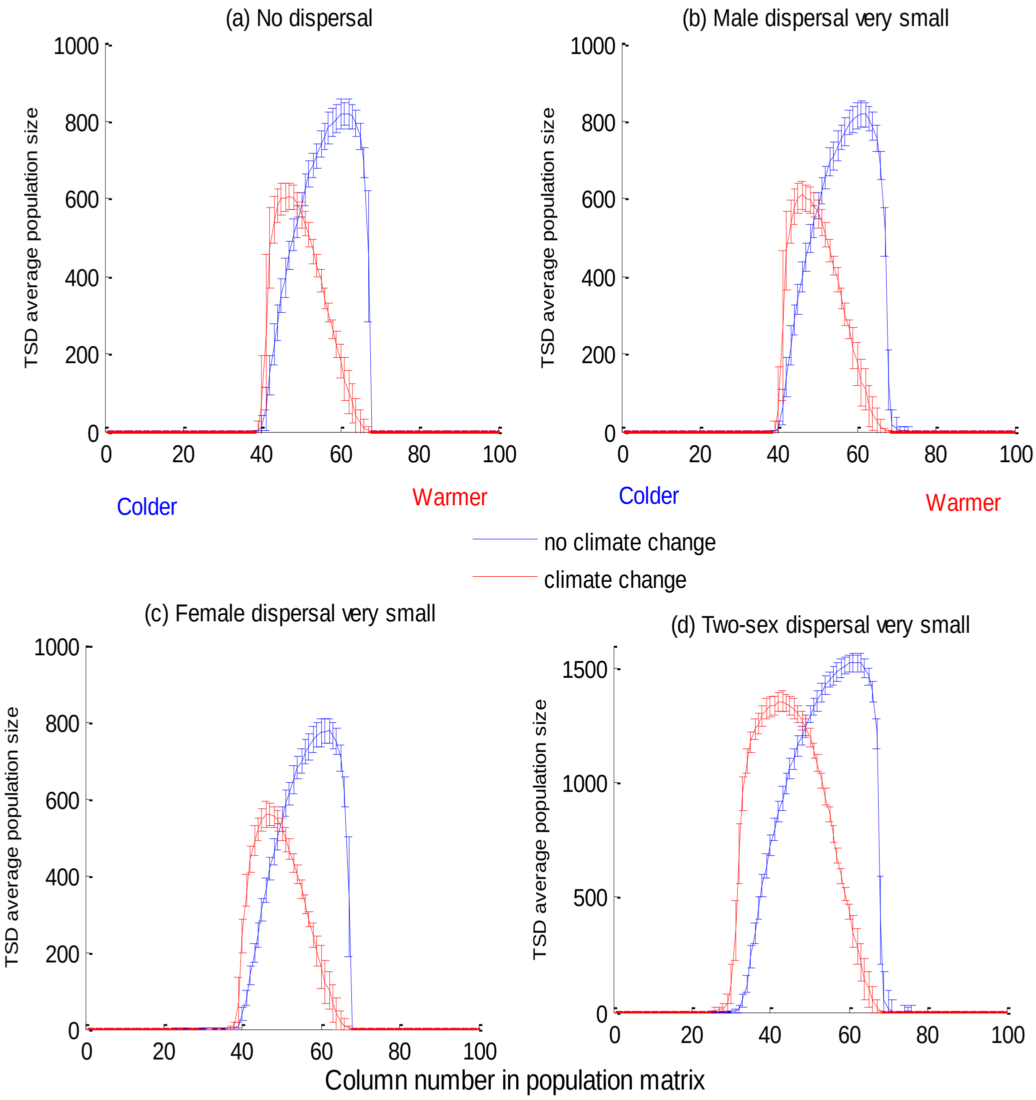


Figure 4.5: Average population sizes and standard errors, for temperature-dependent sex determination (TSD) populations with very small dispersal, for each individual column of the population matrix. Each column in the matrix corresponds to an individual temperature which increases along the gradient (starting at 18°C with no climate warming and 21°C following climate warming). (a) No dispersal, (b) male dispersal, (c) female dispersal and (d) two-sex dispersal. Note: Populations with two-sex dispersal reach much larger average sizes and, hence, the scale on the y-axis is 1.5 times the size of the other plots.

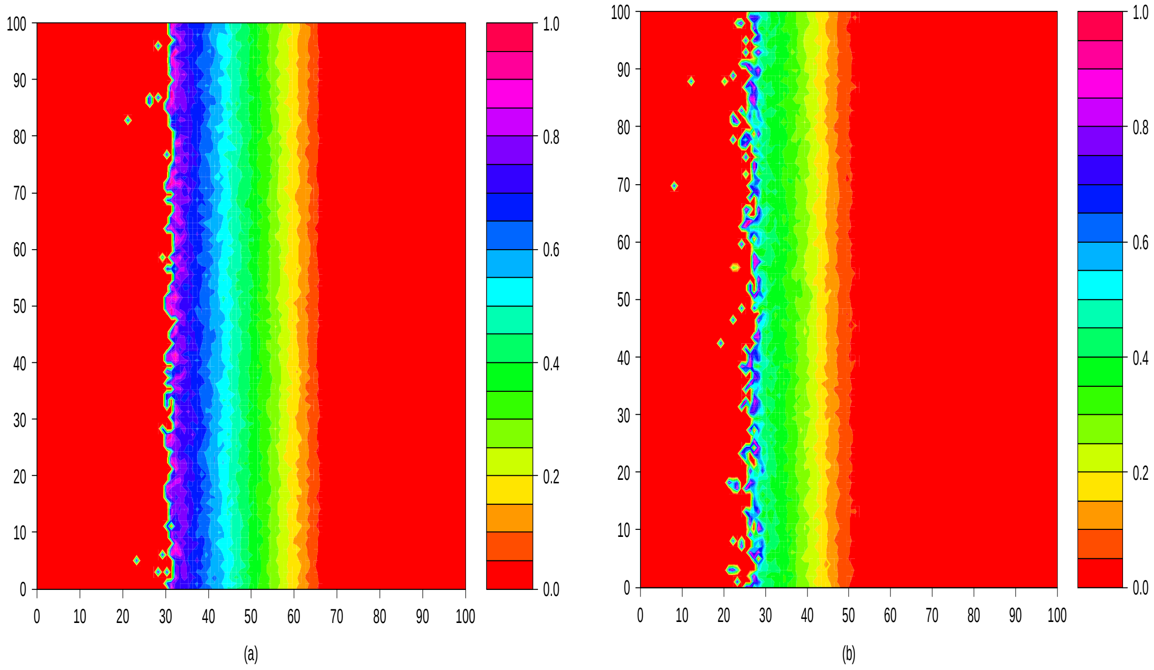


Figure 4.6: Contour maps of adult sex ratios (proportion male, from 0 to 1, right column) for populations of reptiles with TSD, with the very small level of two-sex dispersal (a) without climate warming, and (b) with climate warming. The y-axis represents rows in the population matrix and the x-axis represents columns. The red areas represent populations of size zero.

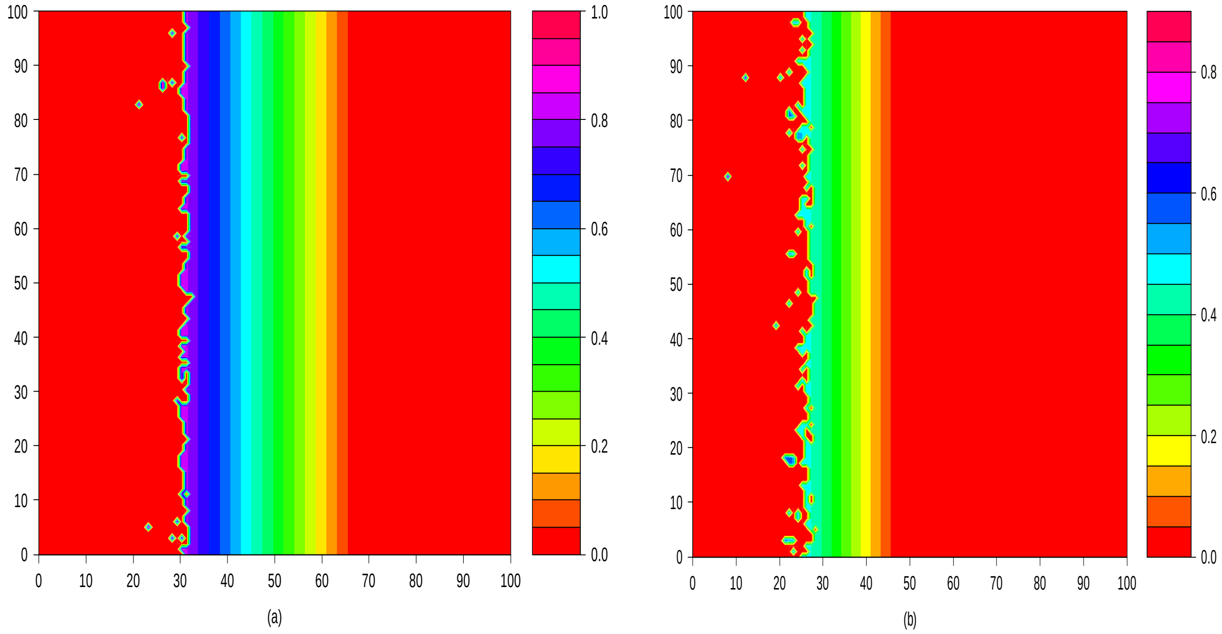


Figure 4.7: Contour maps of juvenile sex ratios (proportion males, from 0 to 1, right column) for populations of reptiles with TSD, with the very small level of two-sex dispersal (a) without climate warming, and (b) with climate warming. The y-axis represents rows in the population matrix and the x-axis represents columns. The red areas represent populations of size zero.

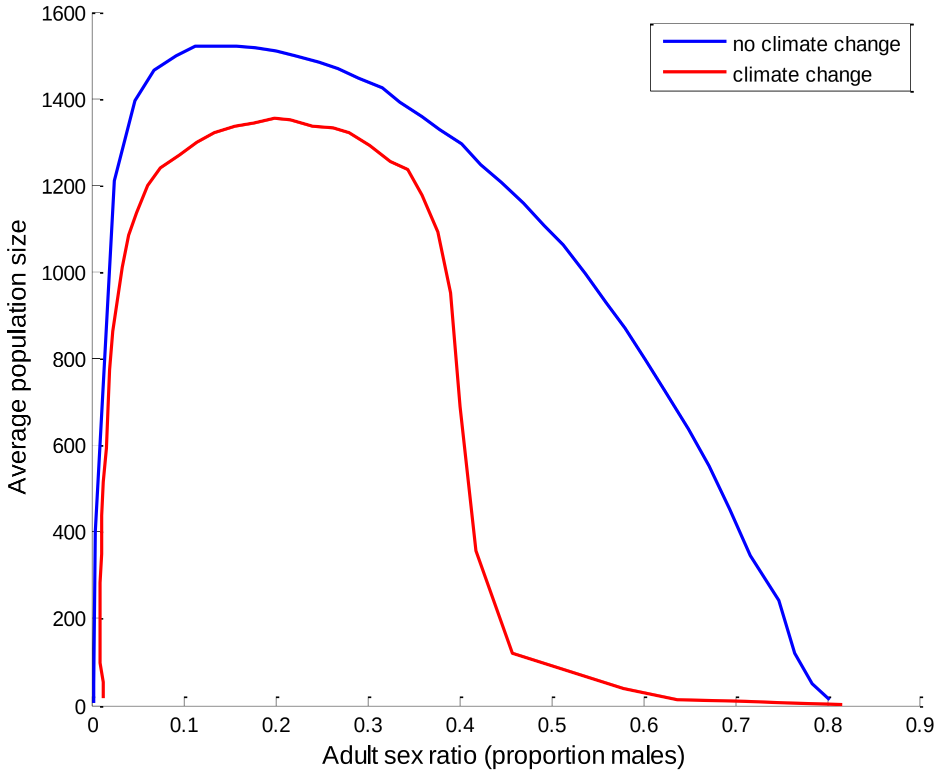


Figure 4.8: The effect of different adult sex ratios on average population sizes in temperature-dependent sex determination (TSD) populations with the very small level of two-sex dispersal, with no climate warming and climate warming.

4.4. Discussion

The effectiveness of dispersal in determining range limits and population persistence in TSD species was shown to depend on the amount of dispersal and dispersal tendency (Figure 4.4). Dispersal tendencies have been quite widely researched in reptiles (FitzSimmons *et al.* 1997b; Casale *et al.* 2002; Olsson and Shine 2003; Roberts *et al.* 2004) and assumed to have positive effects on population persistence given that dispersal is effective (Kallimanis 2010; Doody and Moore 2011).

As climates warmed dispersal had no effect on populations of reptiles with GSD, with the exception of two-sex dispersal (Figure 4.2). The results for GSD and populations of reptiles with TSD without climate warming are consistent with the findings in Chapter 3. In contrast, small dispersal facilitated population persistence in populations of reptiles with TSD (Figure 4.4). At the very small amount of dispersal (with the exception of two-sex dispersal), populations of reptiles with TSD no longer persisted outside of the ranges of populations of reptiles with GSD, but within contracted ranges inside of the range of population persistence for populations of reptiles with GSD (Figures 4.2 and 4.4). Hence, dispersal may only be effective if the dispersal level is large enough that there is sufficient recruitment through immigration so that population numbers do not fall below replacement level, and hence become potential population sinks (Brown and Kodric-Brown 1977; Krebs 2009). Two-sex dispersal at the small level in populations of reptiles with TSD (Figure 4.4(g)), and small and very small dispersal in populations of reptiles with GSD (Figures 4.2(g) and (h)) had relatively large numbers of persisting populations, and with exceptions of the coldest and warmest edges of the range, equilibrium populations were almost maintained. Populations of reptiles with TSD with the very small level of two-sex dispersal (Figure 4.4(h)), showed a very modest amount of range expansion.

Dispersal was considered to be effective at the small level; however, the magnitude of population persistence for two-sex dispersal in populations of reptiles with TSD indicated that it may be too large for some reptile species, especially aquatic and terrestrial species (Figure 4.4 (g)). Some terrestrial (Olsson and Shine 2003) and aquatic (Freedberg *et al.* 2005) reptiles may only disperse distances up to a few metres and many reptiles do not disperse (Escobedo-Galvan *et al.* 2011). Marine turtles are known to be very effective dispersers, and males may disperse across entire oceans for reproductive opportunities (Casale *et al.* 2002; Roberts *et al.* 2004; Wright *et al.* 2012). Nevertheless, for many other reptile species it is not known how far they are extending their ranges through dispersal. Furthermore, populations at range margins are more likely to be population 'sinks', given the loss of populations, than populations located at the interiors of ranges (Krebs 2009). The shortfall in our knowledge about dispersal creates opportunities for empiricists to collect dispersal data in reptile species.

In populations of reptiles with TSD, the small level of dispersal was more effective than the very small level of dispersal, but climate warming reduced the beneficial effects of small dispersal. However, the reduction in population persistence was not as large as would have been anticipated by some theoretical predictions of increasingly biased sex ratios as climates warm (Janzen 1994; Hawkes *et al.* 2007; Mitchell *et al.* 2010). This is explored and analysed in Chapter 5.

Average population sizes decreased at the warmer edge of the range, and increased at the colder edge of the range, with climate warming (Figures 4.3 and 4.5, red lines). These findings are consistent with the predictions of Kallimanis (2010), of population decrease at the warmer (trailing) edge of the range, and population increase at the colder (leading) edge of the range, as climates warm.

However, the explanations for population growth at the colder edge of the range differed from the predictions of Kallimanis (2010) of sex ratios tending towards equity as climates warm, resulting in rapid population growth. This study found that increasingly female-biased and not increasingly equal sex ratios as suggested by Kallimanis (2010) led to larger population sizes as climates warmed by 3°C (Figures 4.6 and 4.7). Populations of reptiles with TSD located at the colder edge of the range that had male-biased or equal sex ratios, (Figure 4.5, blue lines, Figures 4.6(a) and 4.7(a)) increased to large sizes as the proportion of females in the population increased with climate warming (Figure 4.5, red lines, Figures 4.6(b) and 4.7(b)).

Populations declined at the warmest, most female-biased part of the range, as accompanying an increase in the number of females was a decrease in the number of males produced and recruited, as well as a decrease in juvenile survival (Figure 4.4). In this study estimations of the adult sex ratios (Figure 4.6) and juvenile sex ratios (Figure 4.7) revealed that increasingly female-biased adult (and juvenile) sex ratios result in population growth at the colder edge of the range, as climates warmed. This is consistent with the findings of Freedberg and Taylor (2007) that female biases in the sex ratio will lead to rapid population growth, following climatic warming.

As a consequence of the population growth predicted by Kallimanis (2010), a new pool of dispersers will be produced to colonise newly created habitats due to climate warming and range expansion will occur. The results of this study also departed from this finding in relation to range expansion. While range contractions occurred in both GSD (Figures 4.2 and 4.3) and TSD (Figures 4.4 and 4.5) populations, range expansion at the colder edge of the range occurred in only one instance, for populations of reptiles with TSD following climate warming (Figure 4.4(h)). Range expansion is influenced by dispersal level and tendency, and seems to occur due to the high level of recruitment from dispersal by both sexes, in two-sex dispersal (Figure 4.4(h)). Furthermore, range expansion following climate warming resulted in populations that were largely male-biased and had smaller average sizes, and, hence, were likely to be sinks (Krebs 2009) (Figures 4.6(b) and 4.7(b)).

Escobedo-Galvan *et al*. (2011) criticised the model of Kallimanis (2010) as an oversimplification of the processes involved in the response of TSD species to climate change. The model proposed by Kallimanis (2010) considers only the effects of temperature on biased sex ratios, and assumes that dispersal is effective. I have incorporated a model of juvenile survival based on the empirical data of others, as well as male limitation into my models of population persistence, and this is novel as previous models have focused primarily on sex ratios. I have also looked at the interactions between these aforementioned demographic parameters and dispersal. However, dispersal is not necessarily effective, as shown herein, and is influenced by many factors, including the amount of dispersal and dispersal tendency.

The successful continuation of populations of reptiles with TSD has been argued (Doody and Moore 2011) to rely on male recruitment and ultimately male dispersal to facilitate population persistence in female-biased populations as climates warm. Assuming that dispersal is effective in reptile species, both male (Figure 4.4 (c)) and female (Figure 4.4(e)) dispersal at the small level increased the number of surviving populations. Female-biased sex ratios in combination with the small level of female dispersal increased population persistence in populations of reptiles with TSD. There is evidence for female dispersal from only one study (Olsson and Shine 2003). Hence, there is scope for empiricists to investigate female dispersal tendencies in reptiles located in colder climates.

There was also a small increase in population persistence for populations of reptiles with TSD with the very small level of female dispersal at the colder edge of the range (Figure

4.4(f)). Females are fundamental to population persistence and population growth. Population growth can occur with very few males, but many more females are needed (Freedberg and Taylor 2007). However, previous studies have not considered the influence of juvenile survival or male limitation on female fecundity, or on population growth. Populations of reptiles with GSD with very small female dispersal showed smaller average population sizes (Figure 4.3 (c)) than those with a very small amount of male dispersal. This may seem surprising, given balanced sex ratios in populations of reptiles with GSD; however, there is a 10% risk of mortality associated with dispersal. Although this applies to males and females if they disperse, the loss of females in the population results in a greater decline in fecundity, and population growth and persistence than the loss of males.

As climates warmed, the primary sex ratios of populations of reptiles with TSD became more female-biased and this in combination with lower male densities, meant that fewer males were produced and dispersed. Further, if males dispersed too far along the warmer edge of the temperature range they would encounter fewer surviving females. If females dispersed and males remained in their home ranges then males incurred no additional cost of dispersal related mortality. There were many more females produced than males in a warming climate for small dispersal in populations of reptiles with TSD, and a large number of females dispersing, or dispersing greater distances towards the colder edges of the ranges, were more likely to encounter surviving males and this would increase population persistence.

In a qualitative sense, a very small amount of female dispersal was shown to facilitate population persistence towards the colder limits of the range. Female dispersal at a very small amount was no longer effective (Figure 4.4 (d) and (f)). Female dispersal conveyed marginal benefits to population persistence at the colder edge of the range (Figure 4.4 (f)) and there were marginal gains to population persistence following climate warming.

There is wide support throughout the literature for male-biased dispersal in reptiles including TSD reptiles. However, as a caveat, most TSD studies of gene flow and dispersal between populations are based on research in marine turtles (Karl *et al.* 1992; Casale *et al.* 2002; Roberts *et al.* 2004; Bowen and Karl 2007). Male-biased dispersal may not be as effective a mechanism for facilitating population persistence in female-biased populations if male shortages occur as climates warm, as has been previously considered (Doody and Moore 2011). This emphasises the need for empiricists to collect vital information on life history traits and dispersal rates, as detailed in Chapters 3 and 5.

In some TSD species, namely marine turtles, males are excellent dispersers (Roberts *et al.* 2004), but there is a lack of information about dispersal tendencies or success for most other TSD species (Olsson and Shine 2003). Indeed, Escobedo-Galvan *et al*. (2011) argue that many TSD species are poor dispersers. Irrespective of the dispersal tendencies in TSD species, many contemporary populations are not only facing the impacts of anthropogenic climate warming and, hence, biased primary sex ratios (Janzen 1994; Hays *et al.* 2003; Hawkes *et al.* 2009), but also habitat destruction and fragmentation leading to a reduction in the number of nesting sites for females, reproductive rates and ultimately dispersal (Parmesan *et al.* 2000; Poloczanska *et al.* 2009; Fuentes *et al.* 2011).

Wedekind (2002) demonstrated that female-biased sex ratios result in larger population sizes, given that there are at least some males. In this study, maximum average populations size coincided with an adult sex ratio of 0.2 (proportion males) (Figure 4.8), and this finding is consistent with the results of Wedekind (2002). Following climate warming population sizes declined dramatically in populations with male-biased or equal sex ratios (Figure 4.8). This is because before climate warming most populations of non-zero size had adult sex ratios of 0.2 to 0.8 (proportion male), and following climate warming populations had adult sex ratios of 0.05 to 0.4 (proportion males). Following climate warming, there were few populations remaining with male-biased or equal sex ratios (Figure 4.8).

Mitchell *et al*. (2010) reported that under projections of extreme regional climate change, 100% male hatchlings could be produced for the tuatara (*Sphenodon guntheri*), in less than 100 years, leading to regional or local population extinctions by 2085. However, it was predicted that tuatara populations with 75% male hatchlings would be sustainable for around 2000 years, and in contrast 85% male hatchlings would be sustainable for around 300 years, after which populations would become extinct (Mitchell *et al.* 2010). This finding indicates that populations may persist for a number of generations, with biased sex ratios, as long as the bias is not too skewed.

If biased juvenile sex ratios are maintained into adulthood, as reported in some of the literature for marine turtles (Stabenau *et al.* 1996; Braun-McNeill *et al.* 2007;Mitchell *et al*. 2008; Wright *et al.* 2012), this could become problematic for TSD species with biased juvenile sex ratios, due to shortfalls in the opposite sex which may consequently result in a reduction in female fecundity, and ultimate population decline. In this study, a Spearman's rank correlation test comparing adult sex ratios with juvenile sex ratios in populations of reptiles with TSD with the very small level of two-sex dispersal showed that adult sex ratios and juvenile sex ratios were highly significant and positively correlated.

4.4.1. Conclusions

Kallimanis (2010) proposed that, for some TSD species, as climates warm population growth and range expansion will occur at the colder or 'leading' edge of species the range. In contrast, population growth will decline and populations of reptiles with TSD will be lost at the warming or 'trailing' edge of the species range. Furthermore, dispersal is assumed to be effective in rescuing populations from local extinctions (Kallimanis 2010). The results of this study showed that as climates warmed population persistence and average population sizes did indeed become smaller at the warmer edge, and grew to larger sizes at the colder edge of the range. While this was consistent with the predictions of Kallimanis (2010), population growth at the colder edge of the range occurred as a consequence of increasingly female-biased, rather than increasingly equal sex ratios as climates warmed. However, following climate warming, range expansion occurred only for populations of reptiles with TSD with the very small level of two-sex dispersal at the colder edge of the range. Hence, dispersal may not be effective in facilitating range expansion.

The results of this study suggest that if faced with climate warming of 3°C over the next 100 years without dispersal, or with the very small level of dispersal, populations of reptiles with TSD will be vulnerable to reductions in population persistence, at the warmer edge of their range. Having regard to the findings of previous studies (Janzen 1994; Hawkes *et al.* 2007; Mitchell *et al.* 2008; Mitchell *et al.* 2010), the reduction in population persistence found in this study was not as large as expected. For example, Mitchell *et al*. (2010) predicted the extinction of some tuatara populations with 85% male hatchlings after 300 years. Air temperatures increased incrementally by 3°C for 100 years in this study. It is possible that if climate warming stopped at 3°C, but simulations were run for a further 200 years that further declines in population persistence, or even local extinctions may have been observed.

Sex ratio bias may result in local population extinctions in the worst case scenario, but also of major concern is that the adaptive potential of populations may also be eroded by a consistent bias towards one sex (Mitchell and Janzen 2010). A greater loss of heterozygosity will occur in populations with unequal numbers of males and females, than the same sized populations with balanced sex ratios. Loss of heterozygosity is problematic if behavioural of physiological traits associated with TSD in a population are heritable rather than determined only by the environment (Mitchell and Janzen 2010). Populations with strong female (or male) biases in the adult sex ratio will have smaller effective population sizes than the ‘census size’ which has implications for the maintenance of genetic diversity.

Chapter 5: Synopsis

5.1. Contribution of my thesis

For many species of reptile, crucial demographic parameters such as juvenile survival and individual sex (male or female) depend of ambient temperature during incubation, and many populations are female biased. While much has been made of the role of climate on offspring sex ratios in populations of reptiles with TSD, the impact of variable sex ratio on populations is likely to depend on how limiting male numbers are to female fecundity in female-biased populations, and whether a climatic effect on juvenile survival overwhelms or interacts with offspring sex ratio.

The adverse impacts of climate warming on population persistence through biased primary sex ratios (Janzen 1994; Hays *et al.* 2003; Hawkes *et al.* 2007; Mitchell *et al.* 2008; Mitchell and Janzen 2010; Schwanz *et al.* 2010; Telemeco *et al.* 2013) and a reduction in juvenile survival (Hawkes *et al.* 2007; Telemeco *et al.* 2013) have been reported, but there have been no known attempts to quantify the effects of the interaction between juvenile survival and juvenile sex ratio on population persistence. The adult sex ratio may also influence female fecundity through the effects of the strength of male limitation (Rankin and Kokko 2007) and, hence, also affect population persistence. However, there are no known empirical studies that attempt to quantify the effects of male limitation on fecundity and population persistence. Furthermore there have been no attempts to quantify the role of these factors in determining range limits or the extent of range expansion following climatic warming.

I have addressed my four thesis aims (outlined in Chapter 1) and in doing so made several important contributions towards a greater understanding of population persistence, growth and range limits in reptile species, in the context of stable and warming climates. In addressing my four thesis aims I reach the following specific conclusions.

Aim 1) To explore how climatically-linked juvenile survival, juvenile sex ratio and male limitation interact in continuous populations without dispersal and affect population persistence across a range of stable climates. Warmer climates producing female-biased sex ratios in populations of reptiles with TSD resulted in larger population sizes and population persistence of females, relative to populations of reptiles with GSD. However, a continued reduction in the abundance of males through male limitation reduced population sizes and persistence across a range of stable climates.

Aim 2) To explore the interactions between dispersal, and the factors described in 1), on population persistence in continuous populations with dispersal distributed across stable climates. Furthermore, to examine the role of dispersal in determining range limits in a stable climate. Dispersal was more influential in determining range limits in TSD, than in populations of reptiles with GSD. In stable climates, populations of reptiles with TSD with biased primary sex ratios had larger ranges, through dispersal and were able to persist beyond the range limits of populations of reptiles with GSD, with balanced primary sex ratios. Juvenile survival was more influential than dispersal in determining the range limits of populations of reptiles with GSD. This is a new and important finding as it will enhance our knowledge of the role dispersal may have in determining range limits and facilitating population persistence in reptiles.

Aim 3) To explore the influence of dispersal, juvenile survival and juvenile sex ratio on population size and range change in a warming climate. Populations with female-biased primary sex ratios did not become extinct following climate warming by 3^{o}C across 100 years. As climates warmed the effects of juvenile survival, juvenile sex ratios and male limitation were further exacerbated and a number of populations were lost at the warmer edge of the range. Nevertheless, the loss of populations was less than would have occurred on the basis of some theoretical predictions about the effects of climate warming on populations of reptiles with TSD (Janzen 1994; Hawkes *et al.* 2007; Mitchell *et al.* 2010).

Populations showed little capacity for range shift, or range expansion following climate warming. populations of reptiles with TSD with increasingly female-biased adult and juvenile sex ratios reached the largest sizes, following climate warming, at the colder edges of the range. This is consistent with the theoretical prediction of Freedberg and Taylor (2007), but differs from the theoretical prediction of Kallimanis (2010) of populations reaching larger sizes at the colder edge of the range as sex ratios become more equal following climate warming. Following climate warming populations of reptiles with TSD grew larger at the colder edge of the range and decreased in size at the warmer edge of the range, and this is consistent with the theoretical prediction of Kallimanis (2010).

Theoretical (e.g. Charnov 1982; Charnov and Bull 1989) and empirical (e.g. Ewert *et al*. 2005) findings would seem to be at odds with my model. To be more explicit, local temperature variation should be uncorrelated with offspring sex ratio, and latitudinal trends are in opposite direction than anticipated in my theory and modelling. However, these considerations are evolutionary, and my thesis focuses on the population dynamics and demography of sex determination in a spatial context. I have not addressed evolutionary responses at all by design.

Aim 4) To identify those life history parameters that have the greatest impact on population persistence and species range change, with the aim of recommending priorities for empirical research. Such research could directly guide and inform empiricists and conservation managers' decisions regarding TSD and GSD reptiles as

climates warm. There are very few data available for reptiles on vital demographic parameters such as juvenile survival, juvenile sex ratio, male limitation and dispersal. However, research may have to be prioritised due to time and financial constraints, and identifying the most influential parameters is paramount. Predictions about population growth in this thesis were very sensitive to variations in male limitation and a continued reduction in the abundance of males through male limitation in populations of reptiles with TSD, resulted in reduced population sizes. It is recommended that the collection of data on the extent of male limitation on female fecundity is given a very high research priority. Dispersal was shown herein to have the potential to facilitate population persistence at range edges in populations of reptiles with TSD, relative to populations of reptiles with GSD. Gathering data on dispersal levels and tendencies in both TSD and populations of reptiles with GSD for comparative purposes is highly recommended.

5.2. Role of empiricists in data collection

Unfortunately, our knowledge is lacking of, and data are rarely available on, the parameters analysed in my thesis. I developed a population model to examine the effects of juvenile survival, juvenile sex ratio, male limitation and dispersal on population persistence and range change in stable and warming climates, in theoretical reptile populations. This creates an opportunity for empiricists to collect data for the model in order to address interesting questions about the extent to which in the field the demographic consequences of the above factors generate a reduction or increase in population persistence and determine range limits, and the extent of range expansion.

In relation to juvenile sex ratio, while much is known about how individual or clutch sex varies with incubation temperature (Bull 1980; Janzen and Paukstis 1991; Georges *et al.* 1994; Janzen 1994; Georges *et al.* 2005), far less is known about the influence of air temperature on cohort sex ratio (CSR). CSR is defined as the number of male hatchlings as a proportion of the total hatchlings of a population (Schwanz *et al.* 2010).

The CSR response curve has been described in a limited number of studies only (Hawkes *et al.* 2007; Wapstra *et al.* 2009; Schwanz *et al.* 2010) and, hence, knowledge for many TSD species is lacking. Due to logistical limitations CSR is typically calculated based on inferential nest temperature data or from measurement of a subset of nest temperatures. These could be biased if egg hormones change or nest temperatures are incorrectly estimated. Much more data needs to be collected on CSR and air temperatures to assess whether the CSR curve can be consistently and effectively described in a similar manner to the TSD reaction norm (Hulin *et al.* 2009).

Primary sex ratios, air temperatures and juvenile or egg survival, could be measured for each clutch in a population, at a nesting site, to ensure greater efficiency. These data may be obtained from counts and measuring abundance per unit time, and, hence, be easily measured. More complete data sets would inform research to enable more accurate predictions about population growth in reptile species, with biased sex ratios. In Chapter 2, the slope of the CSR curve affected population sizes, and in the absence of male limitation CSR response curves with the steepest slope resulted in the largest population sizes. Populations of reptiles with TSD with the shallowest CSR curve persisted across a wider range of temperatures with the inclusion of male limitation. This indicates the results of chapter 2 were very sensitive to accurately measuring the CSR response curve, otherwise the strength of the effects of male limitation could not be accurately measured.

There are very few data on the effects of male shortages on population persistence, especially at the population level (Rankin and Kokko 2007). Empirical data are lacking on critical levels of males needed to maintain viable populations. Furthermore the effect of low numbers of males on population persistence varies considerably between populations (Rankin and Kokko 2007). In future work it will be very important to measure male limitation parameters accurately. However the difficulty of this is appreciated in marine turtles as they may move across entire oceans, and also potentially have encounters with the opposite sex in the open ocean as well as on the nesting beaches. Male marine turtles often only come ashore to mate, and hence, are difficult to capture (Wright *et al.* 2012).

Wright *et al*. (2012) found at least equal numbers of adult males and females of green turtles present on nesting beaches that had 95% female biased cohort sex ratios. It was suggested that males mate and/or move more frequently between nesting beaches (Wright *et al*. 2012). Under current climate conditions males are thought not to limit female fecundity in some populations of marine turtles, as they are already greater than 90% female (Hawkes *et al.* 2009; Poloczanska *et al.* 2009; Wright *et al.* 2012). However, this may change as climates warm resulting in the primary sex ratio tending further towards 100% female.

Empiricists could measure adult sex ratios at nesting sites as a first step in trying to estimate the level of male limitation on female fecundity. The probability of fertilisation of a female as a function of ASR can be easily estimated (equation 3, Chapter 2), even if the estimate is not unbiased. However, estimating the male limitation parameter would prove more difficult. Empiricists could begin by investigating the length of time, or extent of sperm storage in females, or paternity analysis (how many fathers there are in a year). Furthermore, some observational studies could be made during mating periods of the access females have to rare males. In Chapter 2 predictions about population growth were very sensitive to variations in male limitation, as a continued reduction in the number of males through male limitation, especially in populations of reptiles with TSD, resulted in reduced population sizes (Figures 2.10 and 2.11). Hence, precise estimates of the male limitation parameter are highly desirable as predictions about population growth in TSD (and to a lesser extent GSD) populations were strongly affected by the extent of male limitation.

Male-biased dispersal is thought to be the main dispersal tendency in reptiles (Karl *et al.* 1992; Limpus 1993; Laurent *et al.* 1998; Casale *et al.* 2002; Roberts *et al.* 2004; Keogh *et al.* 2007; Velez-Zuazo *et al.* 2008). However little is known about female-biased or two-sex dispersal tendencies. Data on the level of dispersal needed to facilitate population persistence are rarely available. In Chapter 3 the results for populations of reptiles with TSD were greatly affected by dispersal level. That is, the large and to a lesser extent the small levels of dispersal facilitated the persistence of populations at range edges. This effect was greatly reduced with the introduction of the very small level of dispersal in Chapter 4, and populations of reptiles with TSD no longer persisted in larger ranges than their GSD counterparts. Hence, precise estimates of the level of dispersal are vital in making predictions about population persistence in TSD reptiles. Dispersal did not have strong effects on populations of reptiles with GSD, with the exception of dispersal by both sexes.

Male-biased dispersal has been described as having a ‘rescue’ effect on female-biased populations (Doody and Moore 2011), and in this thesis population persistence increased at the warmer edge of the range with male dispersal. A surprising finding of this thesis (Chapter 3) is that in some populations of reptiles with TSD, female-biased dispersal may also facilitate population persistence through recruitment into male-biased populations at the colder edge of the range. There are no available data on the effectiveness of female-biased dispersal at the colder edge of the range in reptile species. For these populations to persist, evolution of physiological tolerance towards colder temperatures, or towards lower pivotal temperatures would have to occur. This provides an interesting possibility for empiricists to investigate population persistence at the colder edges of the ranges, and to answer unaddressed questions about female dispersal in reptiles. Dispersal tendency has been effectively measured in marine turtles, primarily through genetic analyses (FitzSimmons *et al.* 1997b; Laurent *et al.* 1998; Casale *et al.* 2002; Roberts *et al.* 2004).

Dispersal level may range from being relatively easy to measure, for example in some lizard species, dispersing only a few metres, to very difficult in marine turtles, potentially dispersing across entire oceans. One study used satellite tracking, to trace the movements of adult male green turtles between nesting beaches or rookeries (Wright *et al.* 2012). Using this technology information about dispersal distance or level, and adult sex ratio (number of adult males in the population) could be captured in the one study, if both males and females were tracked.

Life history parameters for juvenile sex ratios, juvenile survival, male limitation and dispersal are all crucial, especially in vulnerable TSD reptile species. However, research may have to be prioritised due to time and financial constraints. If some parameters analysed in my thesis had to be selected above others, I would argue that male limitation on female fecundity is an essential parameter on which data should be gathered, in TSD reptiles. For example, there is already considerable available data on biased primary sex ratios, and concerns about male shortages (Janzen 1994; Mitchell and Janzen 2010), but there have been no formal analysis of the effects of male shortages on population persistence. Furthermore, in marine turtles dispersal tendency has been measured primarily through genetic analysis (FitzSimmons *et al.* 1997a; Laurent *et al.* 1998; Casale *et al.* 2002; Roberts *et al.* 2004), and if the male limitation parameter is estimated through paternity analysis, then there is scope for dispersal tendency to also be indirectly estimated. Dispersal has the potential to facilitate population persistence at the range margins in populations of reptiles with TSD. Gathering data on dispersal levels and tendencies is highly recommended. Juvenile survival is also very important, as so little is known about at which temperatures eggs successfully incubate in natural reptile populations or the thermal limits of juvenile or egg survival.

The importance of all of the parameters studied in this thesis is emphasised. Gathering data on one or two parameters only is not a panacea for our knowledge gaps. Many researchers with differing research priorities could focus on gathering a multitude of data from both experimental and observational studies. Data on vital life-history parameters included in the models developed herein, could be collected through a variety of techniques including: measurement of nest temperatures; observations and counts of juvenile sex ratios and adult and juvenile survival; radio telemetry; satellites; and genetic analysis. These are some of the techniques that empiricists have at their disposal to collect data on vital life history parameters, and to make more accurate predictions and address unanswered questions about the effects of climate warming on vulnerable TSD (and GSD) reptile populations, and ultimately to inform decision making in research and conservation management.

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