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

Populations with female-biased primary sex ratios did not become extinct following climate warming by 3^{o}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.

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> **“***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***”.**

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