



Dispersal and climate warming determine range shift in model reptile populations



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ABSTRACT

Average air temperature is predicted to rise by at least 3 °C across the 21st century. As individual sex (male or female) is determined by temperature in many reptiles, there are concerns that climate warming will skew offspring sex ratios and local species extinctions will follow. Range shift away from hotter areas through dispersal may prevent species extinctions in many reptiles with temperature-dependent sex determination (TSD), and could be facilitated or impeded by sex-biased populations at the expanding edge. We used a simulation model to examine the role of sex-determining mechanism [TSD and genotypic sex determination (GSD)], climate warming and dispersal in determining range shift and population growth in reptiles. Dispersal influenced range shift (after climate warming) in TSD species to a greater extent than in GSD species. Our novel finding is that biased sex ratios may influence range shift, through the mixing of the rare sex (females) with males located at the colder range edges, as both sexes disperse. However, if faced with climate warming of 3 °C over the next 100 years many TSD reptiles will show limited capacity for range shift.

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1. Introduction

Global average air temperature has increased by approximately 0.8 °C during the 20th century and is predicted to rise an additional 2 to 6 °C during the 21st century (IPCC, 2013). Reptiles with temperature-dependent sex determination (TSD) are considered to be especially vulnerable to climate warming as offspring sex ratios are determined by temperature. There have been numerous predictions that warming climates will skew offspring sex ratios towards females, resulting in local population extinctions, in the absence of dispersal or in situ changes in nesting behaviour (Grayson et al., 2014; Hawkes et al., 2007; Hawkes et al., 2009; Hays et al., 2003; Janzen, 1994; Witt et al., 2010). In the tuatara climate warming may skew the sex ratio towards males resulting in local population declines or extinctions (Mitchell et al., 2008). However, TSD reptiles have existed for hundreds of millions of years and persisted despite historical climatic changes involving both warming and cooling (Silber et al., 2011). To elaborate, if projections of around 6 °C are reached in the 21st century, then the Earth will have reached the same amount of mean global warming as it did following a period

of around 5000 years at the end of the last glacial maximum (IPCC, 2013).

One potential advantage of climate warming for TSD reptiles is the creation of more favourable microclimates in areas that were unfavourable. Changes in habitat favourability may allow species to shift or expand their geographical ranges in cooler latitudes, and in warmer latitudes altitudinal shifts may occur (Hughes, 2003; Parmesan et al., 2000). Hence, population growth may occur if colonisation of the expanded range is successful. However, range expansion relies on the ability of a species to successfully disperse, and many TSD reptiles are thought to be poor dispersers (Escobedo-Galvan et al., 2011). Furthermore, some terrestrial (Olsson and Shine, 2003) and aquatic (Brown and Brooks, 1993; Mockford et al., 2005; Morreale et al., 1984) reptiles only disperse short distances.

In addition to the importance of dispersal distances for range expansion, the sex of the dispersers may be crucially important for TSD populations at range edges (Boyle et al., 2014a). Kallimanis (2010) proposed a model describing the geographical distribution of sex ratios in TSD reptiles, and their importance for range boundaries. In this model, unbalanced sex ratios in marginal habitats are assumed to limit population growth and set the limit of range expansion under stable climatic conditions. The sex ratios of TSD reptiles vary with geography, with balanced sex ratios occurring in the core regions, and male- or female-biased sex ratios at the edges or limits of thermal ranges (Kallimanis, 2010). Under warming

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scenarios, the ‘leading’ (colder) edges of ranges are environments of historically low temperatures containing male-biased sex ratios, and the ‘trailing’ (warmer) edges are environments of high temperatures with female-biased sex ratios. Kallimanis (2010) argued for TSD pattern 1A that at the colder edge, warming climates will change sex ratios from male biased to even (1:1), and population growth will increase, producing a ‘pool’ of dispersers to expand their ranges into previously cooler areas. Conversely, the warmer edge populations will become extinct as ranges become even hotter and sex ratios reach 100% female bias (Escobedo-Galvan et al., 2011; Kallimanis, 2010).

Spatial variation in sex ratios may not occur as over time the increased population sizes that occur as a result of biased sex ratios would disappear as frequency dependent selection favours unbiased sex ratios by allowing adaptation to local temperatures (Fisher, 1930). Morjan (2003) and McGaugh and Janzen (2011) demonstrated that the heritability of sex determining factors enables sex determining mechanisms and maternal behaviour to adapt to local temperatures. This adaptation would in principle reduce the relationship between geography and local population sex ratios. However, Morjan (2003) allowed the pivotal temperature (the temperature at which male and female offspring are produced in 50:50 sex ratios) to evolve to any temperature, but in natural systems the pivotal temperature varies little between populations (Harts et al., 2014). Harts et al. (2014) demonstrated that local adaptation in pivotal temperature is limited by demographic dominance in females.

Furthermore there are several empirical studies suggesting sex ratios do not vary spatially over time. Escobedo-Galvan et al. (2011) argue that variation in local temperature is uncorrelated with offspring sex ratio in species with TSD 1A and II. Gibbons et al. (1988) that TSD species with wide variation in mean ambient temperatures [e.g. common snapping turtles (*Chelydra serpentina*) and painted turtles (*Chrysemys picta*)] show no latitudinal trends in population sex ratios. However, there is still relatively little empirical evidence to support the absence of sex ratio patterns across geographical ranges. Furthermore, there is considerable population variation in the sex-ratio of species described by Escobedo-Galvan et al. (2011) and these could be driven by variation in local climate.

There are two reasons to believe that population growth at the warm range margins could be enhanced by both female-biased sex ratios and by temperature-dependent increases in fitness. Demographic analyses have indicated that increases in reproduction and population growth are associated with female biased sex ratios, and not even sex ratios, as long as male density is not strongly limiting on female fecundity (Freedberg and Taylor, 2007). Moreover, higher temperatures have been shown to enhance the fitness of females in several lizard species (Warner and Shine, 2008; Holleley et al., 2015).

Notwithstanding, females at a warming range edge require males to fertilise their eggs. Dispersal by the rare sex is thought to be a driver of range limits in reptiles with TSD in stable climates (Boyle et al., 2014a). In many reptiles with TSD males are the rare sex and are more likely to disperse; thus, male recruitment through dispersal is thought to be essential to facilitate local population persistence in increasingly female-biased populations (Doody and Moore, 2011). However, other dispersal tendencies (i.e., female-biased or dispersal by both sexes) remain largely un-investigated. Sex-specific dispersal is more essential in maintaining populations of reptiles with TSD (through the mixing of the opposite sexes located towards either the warmer or colder range edges), than in reptiles with genotypic sex determination (GSD), in stable climates (Boyle et al., 2014a). To what extent will climate warming and dispersal determine the extent of range expansion in reptiles, and be more likely to lead to range expansion into previously cooler areas? In this paper, we develop a generalised model of reptiles with TSD

(and GSD) distributed across a theoretical landscape to establish how sex-determining mechanisms, dispersal and climate warming determine the extent of range expansion. In Boyle et al. (2014b), we found that warmer climates producing female-biased sex ratios in model reptile populations with TSD resulted in larger female population sizes, but population size was reduced by male limitation on female fecundity. In Boyle et al. (2014a), we established the relationship between dispersal and sex determining mechanism on range limits in stable and not warming climates. Specifically, immigration of the rare sex into a sex-biased edge population can rescue the population from extinction. However, little is known of the role of dispersal by the rare sex in range expansion and population persistence as climates warm.

The aims of this paper are to extend these findings in order to (1) establish the relationship between climate warming, dispersal and sex-determining mechanism in driving range expansion in reptiles under climate change. TSD 1A (where females are produced at higher temperatures) is the model system; (2) examine the effects of warming climates (3 °C increase in temperature across 100 years) on population growth in reptiles. The model does not include evolutionary changes in demographic (birth and death) rates or the effects of temperature on sex ratios. This is an area for further study.

2. Materials and methods

2.1. Simulation model

A matrix (100 rows by 100 columns) of 10,000 populations was distributed across a continuous air temperature gradient, with each column assigned a temperature from 18 °C to 33 °C. Population range limits were measured by determining the proportion of populations that persist at each temperature. Each population in the matrix was initiated with 100 males and 100 females. We projected these populations for 1000 years under constant climate in a simulation to determine range limits under three different scenarios of dispersal, temperature-dependence of sex ratios and climate. The GSD scenarios were null models so that we could separate the effects of temperature-dependent sex ratio and survival on persistence and range expansion. Within each population, simulated population operations approximated logistic growth, including density-dependent juvenile survival (Boyle et al., 2014b).

Following the initial 1000-year range establishment, we projected 100 additional years under one of two climate scenarios: no climate change, and climate change. A 3 °C linear increase in ambient air temperature was selected as it is within the range of projected temperature increase across the 21st century (IPCC, 2013). Under the ‘no climate change’ scenario, the distribution of temperatures was maintained as 18 to 33 °C. Under the ‘climate change’ scenario, temperatures ranged from 18 to 33 °C for the first 1000 years. A 3 °C increase in temperatures across the final 100 years of the simulation (from 1000 to 1100 years) resulted in temperatures ranging from 21 to 36 °C, representing a new continuous temperature gradient.

2.2. Male limitation (*B*)

Individual female fecundity, *B*, was an integer that was sampled using a random binomial distribution based on the probability of fertilisation of a female, $\text{Pr}\{\text{fert}\}$, with a maximum value of B_{max} :

$$B = B_{\text{max}} \times \text{Pr}\{\text{fert}\} \quad (1)$$

$\text{Pr}\{\text{fert}\}$ is a function of adult sex ratio (ASR), or the proportion of adults in the population that are male:

$$\text{Pr}\{\text{fert}\} = \frac{\text{ASR}}{\text{ASR} + b} \quad (2)$$

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