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# Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara?

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How will climate change affect species' reproduction and subsequent survival? In many egg-laying reptiles, the sex of offspring is determined by the temperature experienced during a critical period of embryonic development (temperature-dependent sex determination, TSD). Increasing air temperatures are likely to skew offspring sex ratios in the absence of evolutionary or plastic adaptation, hence we urgently require means for predicting the future distributions of species with TSD. Here we develop a mechanistic model that demonstrates how climate, soil and topography interact with physiology and nesting behaviour to determine sex ratios of tuatara, cold-climate reptiles from New Zealand with an unusual developmental biology. Under extreme regional climate change, all-male clutches would hatch at 100% of current nest sites of the rarest species, *Sphenodon guntheri*, by the mid-2080s. We show that tuatara could behaviourally compensate for the male-biasing effects of warmer air temperatures by nesting later in the season or selecting shaded nest sites. Later nesting is, however, an unlikely response to global warming, as many oviparous species are nesting earlier as the climate warms. Our approach allows the assessment of the thermal suitability of current reserves and future translocation sites for tuatara, and can be readily modified to predict climatic impacts on any species with TSD.

**Keywords:** climate change; global warming; temperature-dependent sex determination; reptile; *Sphenodon*

## 1. INTRODUCTION

The ecological impact of increasing air temperatures on terrestrial animals is mediated by complex interactions between climatic variables, terrain and vegetation, as well as the animal's morphology, behaviour and physiology. Translating a predicted air temperature increase into a survival probability for a species ideally requires a mechanistic understanding of these underlying processes. For oviparous species, the most vulnerable part of an animal's life cycle is often the embryo, since eggs are typically left unattended in fixed locations throughout their development (e.g. Feder 1997). Elevated nest temperatures can cause death, but, more subtly, can also influence hatchling sex ratios in species with temperature-dependent sex determination (TSD). TSD is widespread in reptiles (Valenzuela & Lance 2004) with recent discoveries including viviparous species (Robert *et al.* 2003), making it increasingly important that we develop mechanistic, spatially explicit approaches for predicting the impact of global warming on sex ratios.

Most forms of TSD result in the production of female offspring above a temperature threshold (Valenzuela & Lance 2004). Tuatara (*Sphenodontia*), from New Zealand,

are the only survivors of one of the four orders of reptiles, and have a rare form of TSD (FM or type IB), where male hatchlings are produced at higher constant incubation temperatures and in hotter natural nests (Nelson *et al.* 2004a; Mitchell *et al.* 2006). Other features of tuatara biology are also unusual; they are nocturnal and active at low temperatures, slow to mature and long-lived and females reproduce every 2–5 years (Bogert 1953; Cree 1994; Nelson *et al.* 2002b). Nesting occurs in the austral spring and early summer, and young hatch around one year after oviposition (Dendy 1899).

Like much of New Zealand's fauna, tuatara evolved in the absence of mammalian predators. The introduction of mammals by human colonizers drove tuatara to extinction on the mainland islands (Towns & Daugherty 1994), but two species, *Sphenodon punctatus* and *Sphenodon guntheri*, survived on offshore islands and are now protected. The largest population (estimated at 30 000 individuals) occurs on Stephens Island in Cook Strait, but most of the remaining 34 populations consist of 10–300 individuals on islands less than 5 ha in size (Gaze 2001) and have low levels of genetic variation (Hay *et al.* 2003; MacAvoy *et al.* 2007).

Tuatara earned their status as 'living fossils' due to their morphological similarity to their Mesozoic ancestors (Apesteguía & Novas 2003). Their lineage evolved on

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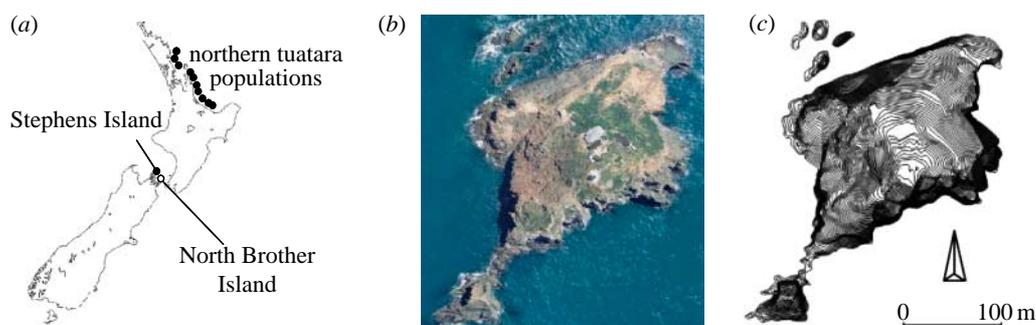


Figure 1. (a) Distribution of extant natural tuatara populations, (b) aerial photograph and (c) the digital terrain model of North Brother Island used in our projections. North Brother Island is the southernmost island supporting a naturally occurring tuatara population, and has a rugged topography typical of smaller tuatara reserves. Four translocations of Cook Strait tuatara (*S. punctatus* and *S. guntheri*) to islands south and west of their natural range have occurred since 1995.

the Pangean supercontinent that was characterized by rapid and severe fluctuations in air temperature (Fastovsky & Weishampel 2005), and the survival of tuatara and other basal reptiles (crocodilians and chelonians) suggests that either TSD evolved later or that these reptiles were able to adapt to past climate change. However, contemporary rates of climate change threaten the survival of tuatara because their isolation on islands prevents southward migration that could counter the effects of increasing air temperatures on sex ratios, and the capacity of tuatara to adapt to increasing air temperatures via evolutionary mechanisms is further limited by their long generation time and low genetic diversity in the surviving populations. Climatically imposed biases toward males in tuatara populations will increase the chance of demographically driven extinctions, and are likely to be particularly deleterious in smaller populations due to the additional burden of stochastic and/or Allee effects (Nelson *et al.* 2002b).

The few attempts to assess the impact of past and future climates on reptiles with TSD have been based on correlations between air or nest temperatures and hatchling sex ratios (Janzen 1994; Hays *et al.* 2003; Glen & Mrosovsky 2004; Nelson *et al.* 2004a; Hawkes *et al.* 2007). In general, the approach has been to (i) correlate measured nest temperatures with air temperature, (ii) interpolate this relationship to predict nest temperatures using either historical air temperature records or predicted future increases in air temperature, and (iii) to estimate sex ratios based on the relationship between nest temperatures and sex ratios measured in nature. This approach is useful when long-term correlative data are available, but cannot be used to reliably predict the impacts of global warming when environmental conditions vary outside the range used to generate the correlative model. Moreover, behavioural mechanisms that could counter the effects of global warming on sex ratios, such as changing nest depth or location (*sensu* Bartholomew 1964), are not easily modelled. Given that intervention (e.g. translocation) may be required to save species with TSD from extinction, models that can account for the complexity of TSD and nesting behaviours, and that use data collected over a relatively short time frame, will be of greatest use in predicting translocation sites that are likely to be successful.

Here we integrate physiological data on development with a first-principles model of microclimate (Niche Mapper; Porter *et al.* 2002; Kearney & Porter 2004; Porter & Mitchell 2006) to make the first mechanistic assessment of nest-site suitability for a species with TSD,

the endangered North Brother Island tuatara (*S. guntheri*; figure 1). We used high-resolution digital terrain data for North Brother Island and applied the microclimate model to predict daily thermal cycles at specific locations and soil depths on the island, under current and future climates. We then used published data on the thermal sensitivity of development rate and sex ratios for tuatara (Mitchell *et al.* 2006) to translate predicted thermal environments into development times and sex ratios. In particular, we assessed the extent to which changes in female nesting behaviour—laying month and nest depth—would allow female *S. guntheri* to behaviourally compensate for the impact of global warming on hatchling sex ratios.

## 2. MATERIAL AND METHODS

### (a) Study site and population

North Brother Island (41° 06' S, 174° 26' E) is a wildlife reserve and light station in Cook Strait, New Zealand and hosts the only natural population of *S. guntheri* (figure 1). The 4 ha island rises steeply to 66 m above sea level. Approximately half of the island's surface is weathered rock, cliff faces or human-made structures, with deeper soils on the broad northeastern face resulting from extensive burrowing and nesting by tuatara and seabirds. The adult population of *S. guntheri* numbers approximately 350 adults and has a 60% male bias (Nelson *et al.* 2002b) and the lowest genetic diversity recorded for any tuatara population (Hay *et al.* 2003; MacAvoy *et al.* 2007). The typical nesting season spans four to six weeks in November and December (austral late spring/early summer) and nest sites are concentrated on the northern and northeastern face of the island (figure 2). Females deposit three to eight soft-shelled eggs in unshaded sites, usually in a single layer near the soil surface (Cree *et al.* 1991). Nest depth ranges between 50 and 250 mm and depends to a large extent on the compaction of the soil. The females take several days to several weeks to excavate a nest, and may guard the nest for a couple of nights once oviposition has occurred and the nest has been backfilled (Nelson *et al.* 2004a). Embryos develop relatively rapidly over the austral summer and autumn and then overwinter in the nest, hatching in the following spring or summer after a total incubation period of approximately 11–14 months.

### (b) Digital terrain model

We obtained a high-resolution digital terrain model (DTM) of North Brother Island (0.5 m contours; GeoSmart, New Zealand), onto which we overlaid an orthographically

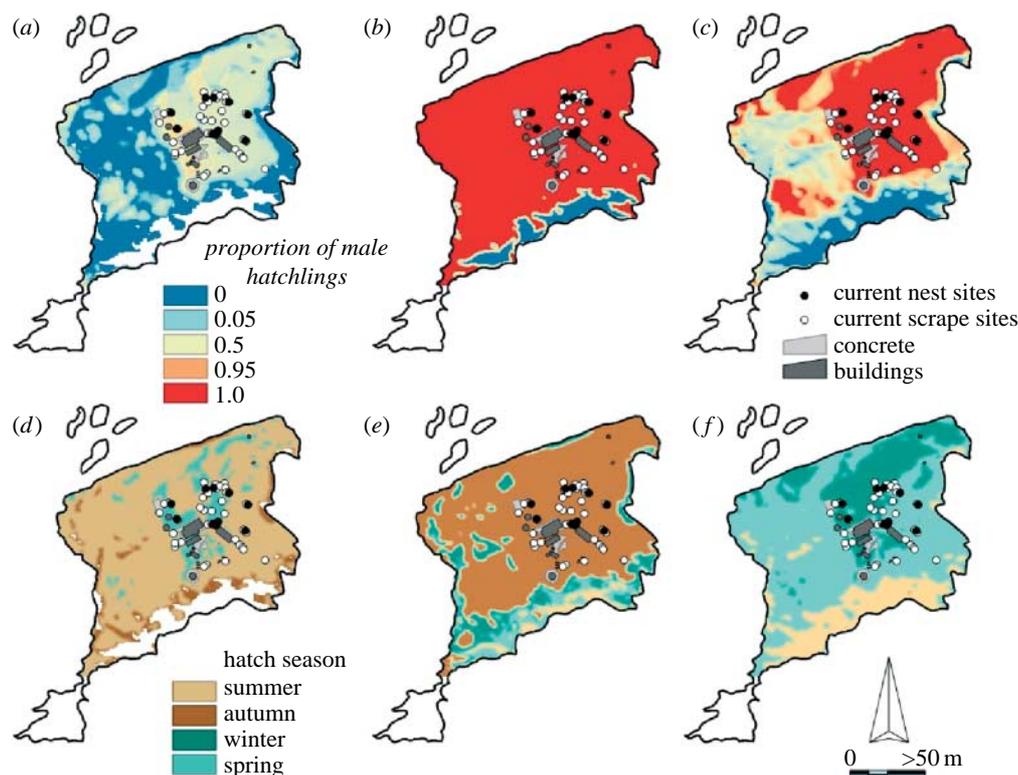


Figure 2. Example of the spatial distribution of (a–c) sex ratios and (d–f) hatching season under (a,d) current climatic conditions and two maximum warming simulations (b,e) November nesting and (c,f) January nesting. These models assumed that eggs were deposited in unshaded sites 100 mm below the soil surface. White regions in the current climate maps indicate sites where development times exceed 1.5 yr and no projections were made for the outlying islands.

corrected aerial photograph using a GIS software (Manifold, CDA International Ltd). We then generated the latitude, longitude, elevation, slope and aspect for 52 tuatara nests and scrapes (nest attempts) observed on North Brother Island during two five-week visits in the 2000 and 2001 nesting seasons which we plotted onto the aerial photograph. Similarly, we overlaid a 0.5 m grid onto the DTM to generate a database of 27 058 points from which we could predict monthly soil temperatures across the whole island. This grid was subsampled at 2 m intervals to produce a smaller database (1806 points) for sensitivity analyses.

#### (c) Microclimate model

We used a microclimate model (McCullough & Porter 1971; Porter *et al.* 2002; Porter & Mitchell 2006) to estimate soil temperatures on North Brother Island under the current climate and under two warmer climates projected for the mid-2080s (New Zealand Climate Change Office 2004). The microclimate model includes a one-dimensional finite-difference algorithm that simultaneously solves heat- and mass-balance equations for the ground surface and specified depths below. It includes a subroutine for computing clear-sky solar radiation given a specific time, latitude, longitude, elevation, slope and aspect (McCullough & Porter 1971), and requires climate maximum and minimum data for arbitrary time intervals, e.g. monthly, weekly or daily, and physical properties of the soil as major input variables.

We obtained records of daily variation in shaded air temperature from an automated weather station established on North Brother Island in 1997, while monthly mean maximum and minimum cloud cover values were calculated from 4 to 12 daily observations made by lighthouse keepers between 1970 and 1990. Relative humidity (RH) was recorded only at 09.00,

so RH was assumed not to vary during the day. Air RH does not impact soil RH, since the water vapour mass balance in the soil is controlled by matric potential and other variables so that even desert soils typically have soil humidities well above 95% at 1–2 cm depths (Van Haveran & Brown 1972). Mean daily maximum and minimum wind speeds were calculated for each month from hourly records collected between 1997 and 2007. Climate data are freely available at <http://cliflo.niwa.co.nz/>, and an example data input file used for current climate simulations is shown in the electronic supplementary material, table S1.

To simulate global warming, we increased mean monthly minimum and maximum air temperatures by seasonal increments projected for Wellington, New Zealand by the 2080s (New Zealand Climate Change Office 2004; Wellington is 30 km to the east of North Brother Island). For the minimum warming scenario, we added between 0.1 and 0.8°C to air temperatures, and for maximum warming we added 3.3–4.0°C to air temperatures, with the largest increase occurring in the austral winter. The minimum warming scenario is similar to the 0.7°C warming detected for the South Island of New Zealand over the period 1940–1990 (Salinger & Mullan 1999).

#### (d) Biophysical model

We assumed a uniform soil type on the island and set the microclimate model to predict hourly soil temperatures at depths between 50 and 300 mm on the middle day of each month for specified sets of unshaded sites. Cycling soil temperatures were converted to a constant temperature equivalent (CTE) for each month, rather than a mean temperature, because CTEs are better predictors of offspring sex (Georges *et al.* 2005). In brief, a CTE is calculated by first computing the amount of development completed at small,

equally spaced intervals (e.g. minutes) during a fluctuating temperature cycle, from a previously established relationship between temperature and development rate. The temperatures and their corresponding developmental weightings are then ranked to determine a 'developmental median'—the temperature above which exactly half of the predicted development occurred (the CTE). We improved the resolution of our CTE calculations by integrating our hourly temperature predictions using a cubic spline, and we used a nonlinear development rate function (see §2f) to predict development rates (refer to Georges *et al.* 2005 for a detailed methodology).

Because averaged monthly climate data were used to predict soil temperatures, we assumed a stable CTE for each month, from which we calculated daily development using the nonlinear development rate function described in §2f. The integration of daily developmental increments allowed us to predict the month of hatching and other critical points of development, such as the thermosensitive period (TSP) for sex determination. The TSP in tuatara encompasses 0.5–0.55% of embryonic development (Mitchell *et al.* 2006), hence the CTE for the month when half embryonic development was completed was converted into a sex ratio (sr) according to the equation

$$\text{sr}(\text{CTE}) = \left(1 + \left(2^{e^{3.3}} - 1\right) \exp(1/0.0398 \cdot (21.57 - \text{CTE}))\right)^{-1/e^{3.3}}.$$

This sex ratio function is the best fit to the sex ratio data produced from constant incubation experiments on *S. guntheri* (Mitchell *et al.* 2006), and has a pivotal temperature (sr 1 : 1) of 21.6°C and a transitional range of temperatures (TRT<sub>0.05</sub>), where both sexes are produced, of 3.2°C (refer to fig. 1 in Mitchell *et al.* 2006). We therefore assumed that mixed-sex nests would result for sites with CTEs within the boundaries of the TRT<sub>0.05</sub> (19.1–22.3°C), and that only females would be produced below the TRT<sub>0.05</sub> boundary and only males above this boundary.

We made provision for predicting temperature-induced mortality in our biophysical model by excluding sites where an hourly soil temperature exceeded 35°C in any month, but this condition was not violated, even in our hottest simulations (50 mm, maximum warming). However, in our hottest simulations, CTEs exceed 25°C in some months (14% of sites in December, 62% of sites in January and 46% of sites in February; all CTEs ≤ 27°C). Constant temperature incubation at 25°C was unsuccessful in the early experiments on *S. punctatus*, but recent experiments at 24.5°C have produced viable hatchlings (Mitchell *et al.* 2006), hence there is still uncertainty over the upper temperature limits tolerated by tuatara embryos. When these data become available, temperature-induced mortality can be further incorporated into the biophysical model.

#### (e) Testing the microclimate model

On North Brother Island, soils are strongly weathered on exposed ridges and enriched and homogenized by seabird activity on the northeastern face, and hence the physical properties of soils would vary across the island and with depth. As we did not have samples of North Brother Island soils, we selected values for their physical properties that were similar to those of related New Zealand soils (soils below 200 m in the Marlborough Sounds of New Zealand are mostly silty or clay loams derived from siliceous rock or greywacke; Walls & Laffan 1986). We then compared the soil temperatures predicted by the microclimate model for the middle day of each month with average monthly soil temperatures that we had measured in duplicate in 2001 at

the same depths (100 and 200 mm) at four experimental sites on the island (Hobo/StowAway temperature loggers; hourly measurements for 10 months). To make this comparison relevant, we replaced the average (1997–2007) monthly temperature and wind speed data with the data from 2001 only, and we used the turbulent velocity profile in Niche Mapper (Porter & Mitchell 2006) to predict surface wind speeds based on those measured at 10 m (the height of the anemometer near the summit of North Brother Island). However, we reduced daily minimum and maximum wind speeds by 50% for two reasons: (i) boundary-layer effects due to wind shear across the island itself would reduce wind speeds near the ground considerably more than predicted by the turbulent velocity profile used in Niche Mapper (since the latter assumes level ground), and (ii) large regions of the island are sheltered from wind at any point in time due to local topographic effects.

The impacts of wind on soil temperatures could be directly addressed using the fluid dynamics program FLUENT (<http://www.fluent.com>) to estimate local velocity fields specific to the shape and orientation of the island relative to wind direction, but this was beyond the scope of the current study. However, we conducted a sensitivity analysis on the effect of wind speed on two outputs from the biophysical model at 100 mm depth (CTE and development per month), where we varied maximum and minimum wind speeds between 25 and 75% of their monthly averages. These analyses were conducted for both the current climate and the maximum warming scenario. At most, in the hottest months, there was a 1.2°C difference in the CTE from the CTE predicted at 50% wind speeds, which made a 0.03% difference to the development completed per month. The CTEs and development times showed negligible differences in winter months, because temperatures are too cold for appreciable development. Hence, we are confident that varying the maximum and minimum wind speeds has only a small influence on the outputs of the biophysical model. Soil temperatures predicted using 50% wind speeds were very similar to the actual temperatures measured at the experimental sites; on average, the model overestimated soil temperatures by 0.22°C at 100 mm depth and underestimated soil temperatures by 0.34°C at 200 mm depth (table S2 in the electronic supplementary material).

#### (f) Testing the development rate function

Development rates at constant temperatures are similar for *S. punctatus* from Stephens Island and *S. guntheri* (refer fig. 2 in Mitchell *et al.* 2006), so we chose to use data for *S. punctatus* to generate development rate functions, as the data have been collected over a broader range of temperatures (15–25°C). Moreover, there are extensive data on natural nest temperatures, hatch times and sex ratios for the large *S. punctatus* population (Nelson *et al.* 2004a), which allowed us to test the various predictions of our biophysical model.

The relationship between temperature and development rate is approximately linear between 15 and 25°C (Mitchell *et al.* 2006), but because tuatara can survive transient exposure to nest temperatures between 1 and 38°C, we needed to make assumptions about development rates beyond the linear limits. Degree-day functions do not produce realistic CTEs when temperatures cycle beyond the linear region of the temperature/development rate function, so we developed a nonlinear function as recommended by Georges *et al.* (2005). We used the programs DEVAR and DEVARA (Dallwitz & Higgins 1992) to

Table 1. Proportions and development times of all-female, mixed-sex and all-male clutches predicted from late spring nesting under current and two future climates. (Percentages were calculated from the combined results of simulations at four nest depths (50, 100, 150 and 200 mm—nests at 300 mm depth are unknown) for 52 current nesting locations, assuming oviposition in mid-November or mid-December.)

	current climate	minimum warming 2080s	maximum warming 2080s
percentage of all-female nests	51.7	44.0	0.0
percentage of mixed-sex nests	24.7	32.4	0.0
percentage of male nests	23.6	23.6	100.0
sex ratio (female : male)	0.64 : 0.36	0.60 : 0.40	0 : 1
<i>mean development time in yr (n nests)</i>			
all-female nests	1.16 (215)	1.15 (183)	—
mixed-sex nests	0.98 (103)	1.00 (135)	—
all-male nests	0.82 (98)	0.76 (98)	0.44 (416)

respectively fit a linear-with-threshold (degree-day) function and various nonlinear (Dallwitz Higgins) functions to the *S. punctatus* data, with starting parameters  $b_1=0.06$  and  $b_2=12.5$  (DEVAR) and  $b_1=0.8$ ,  $b_2=13.0$ ,  $b_3=25$ ,  $b_4=6$  and  $b_5=0.4$  (DEVARA). In the latter case, parameter  $b_1$  is the maximum development rate possible and  $b_2$  the temperature at which the development rate approaches zero. Parameters  $b_4$  and  $b_5$ , which control the asymmetry and steepness of the curve, were fixed at 6 and 0.4, respectively, which is recommended when data at extreme temperatures are scarce (Dallwitz & Higgins 1992). Because parameter  $b_3$ , the temperature at which the development rate peaks, is unknown, we systematically fixed  $b_3$  at 1°C intervals between 25 and 35°C to produce 11 nonlinear development rate functions (see figure S2 in the electronic supplementary material). The 12 development rate functions (one linear-with-threshold and 11 nonlinear) were then applied to predict development rates from temperatures recorded in 14 natural *S. punctatus* nests where hatch dates were known (Nelson *et al.* 2004b), with the aim of selecting the function that was the best predictor of total incubation time.

For all the 14 nests, we integrated the hourly development predicted using each development rate function to estimate the percentage of development completed on the mean hatch date. We then compared the residual sum of squares (where completed development  $y=100\%$ ) for each development rate function. All nonlinear functions produced better estimates of the percentage of development completed on the hatch date than the single linear function, and the function with parameters  $b_1=0.985$ ,  $b_2=13.79$ ,  $b_3=30$ ,  $b_4=6$  and  $b_5=0.4$  was the best overall predictor of development rate (SSE=862.2, mean development predicted on the hatch date=98.9% and range=87–112%).

#### (g) Testing sex ratio predictions

Using temperatures from 16 *S. punctatus* nests where hatchling sex had been determined by laparoscopy (Nelson *et al.* 2004b), we compared the sex ratio predicted by the biophysical model with the sex ratio of offspring from each nest. We applied the sex ratio function for *S. punctatus* that has a pivotal temperature of 22°C and a TRT<sub>0.05</sub> of 1.1°C (Mitchell *et al.* 2006), and predicted mixed-sex nests for sites with CTEs between 21.2 and 22.25°C, all-female nests for CTEs below 21.2°C and all-male nests for CTEs greater than 22.25°C. Our predictions were accurate for all-female ( $n=5$ ) and mixed-sex nests—those producing at least two hatchlings of each sex ( $n=2$ )—but we predicted only 67% of all-male nests ( $n=9$ ), indicating that our developmental model is slightly conservative in its prediction of males.

### 3. RESULTS

We first examined sex ratios and development times estimated at five representative nest depths (50–300 mm) and five potential laying months (September–January) at current nest sites under the current climate. For a typical scenario (oviposition of eggs at 100 mm depth in November or December), mostly female offspring (64%; table 1) were predicted to hatch in the following austral spring or summer (figures 2 and 3; table S3 in the electronic supplementary material). Male-producing nests were predicted at shallower sites and all-female nests were overwhelmingly predicted at depths greater than 150 mm, irrespective of laying date (figure 4). An animated map showing the changes in hatchling sex ratios with increasing nest depth for the current mid-November nesting season is available as electronic supplementary material (figure S3).

Extending our analysis to include all potential locations on North Brother Island (including precipitous slopes and sites within the splash zone) revealed that current nesting sites occur in the warmer regions of the island (figure 2). Embryos developing on the south face would fail to complete development within 18 months, which we set as an arbitrary cut-off for defining a suitable nest site. As expected, suitable sites declined with nest depth; at 50 mm, 90–94% of the sites on the island would support nesting, decreasing to 46–73% at 200 mm (ranges depending on oviposition date). At 300 mm, predicted development times exceeded 18 months at more than 90% of sites (see table S4 in the electronic supplementary material).

Under minimum climate warming predicted for eastern Cook Strait by the 2080s (+0.1–0.8°C; New Zealand Climate Change Office 2004), we predicted small increases in the proportion of mixed-sex nests at the expense of all-female-producing sites (table 1; figure 4). However, under maximum climate warming, where seasonal air temperatures were increased by up to 4°C, our predictions are dramatically different (figure 3; animated figure S3 in the electronic supplementary material). If nesting locations and laying dates do not change, then all-male nests are predicted in 100% of simulations at depths between 5 and 200 mm (figure 4). Expanding our predictions across the whole island revealed that almost all locations produce males at shallow depths (see figure S1 in the electronic supplementary material) and at 100 mm depth, the only sites generating mixed sexes are in a narrow band along south-facing cliff tops (figure 2).

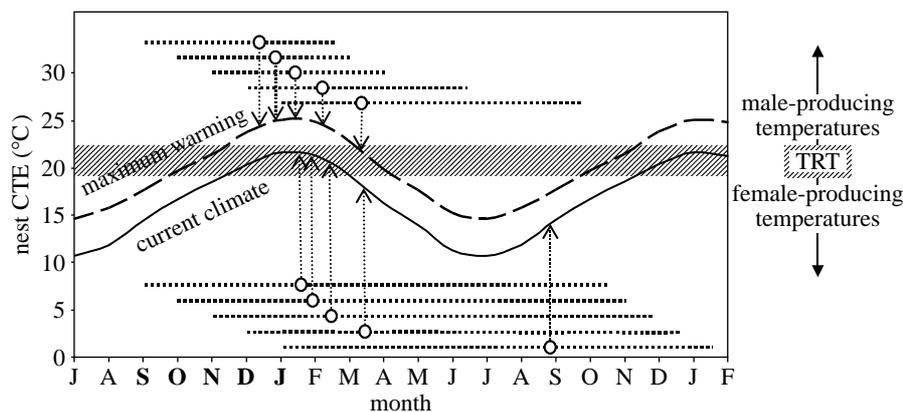


Figure 3. Example of how the date of oviposition affects the duration of embryonic development (horizontal dotted lines) and timing of the TSP (open circles) for nests 100 mm below the soil surface under current climatic conditions (lower horizontal dotted lines) and maximum warming (upper horizontal dotted lines). The cycling nest CTEs are the average monthly CTEs for current nest sites under the current climate (solid line) and maximum warming (dashed line), and the temperatures that would produce mixed-sex nests (the TRT) are indicated by hatching. The TSP falls at different positions along the development lines, depending on the date of oviposition and the temperatures that prevail thereafter. The oviposition months examined in our simulations are shown in bold, and tick marks indicate the middle day of each month. At this depth in the soil, it is clear that all-male nests would be predicted for most oviposition months under maximum warming, mixed-sex nests would be predicted for oviposition between September and November and all-female nests would be predicted for oviposition in December and January under the current climate.

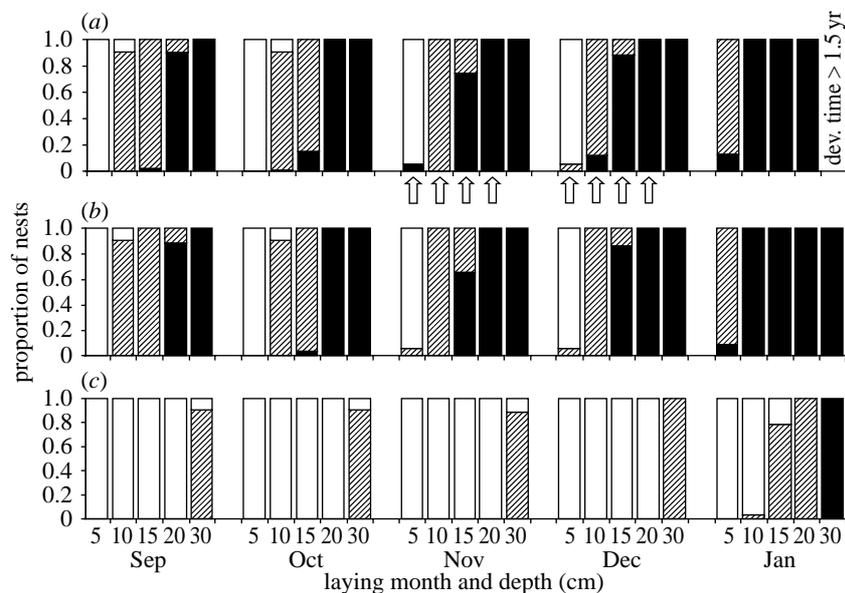


Figure 4. Proportion of all-male (open bars), mixed-sex (hatched bars) and all-female (filled bars) nests predicted at five depths and five laying dates for nesting locations currently used on North Brother Island, under (a) current climatic conditions, (b) minimum warming forecast for 2080s and (c) maximum warming forecast for 2080s. The models assumed that eggs were deposited in unshaded sites on the middle day of each month. Arrows show current nesting depths and dates for *S. guntheri*.

#### 4. DISCUSSION

Despite increasing evidence that some species are adapting to contemporary climate change via genetically driven shifts in thermal traits (Bradshaw & Holzapfel 2006), long-lived and slow-reproducing reptiles with TSD are unlikely to adapt to the most extreme increases in air temperature, particularly when dealt the additional card of low genetic variation (Janzen 1994; MacAvoy *et al.* 2007). Our analyses demonstrate that without adaptation, extreme climate change will produce fast-developing all-male clutches, resulting in the extinction of smaller tuatara populations as operational sex ratios become increasingly male biased. The time frame over which extinctions could occur under global warming is difficult to predict given the longevity of tuatara (Nelson *et al.* 2002b) and that occasional cooler years would produce females.

Given that an evolutionary response to current rates of global warming is unlikely, could tuatara behaviourally compensate for the effects of extreme warming by altering the depth, location or time at which they lay their eggs? Mixed-sex nests are produced at 300 mm depth under maximum warming, but soils on North Brother Island are generally shallow and highly eroded and are likely to prevent females from digging deep nests. Alternatively, the female tuatara could nest on different regions of the island, but our analyses reveal that only limited portions of North Brother Island would produce mixed-sex offspring at current nest depths under maximum warming (5–34%; see figure S1 in the electronic supplementary material). At the typical nest depth of tuatara of 100 mm (Nelson *et al.* 2004a), mixed-sex-producing sites are restricted to the south-facing cliff tops, with only the southern face

Table 2. Proportions and development times of all-female, mixed-sex and all-male clutches predicted under maximum warming with either changed nesting phenology or selection of shaded nest sites. (Percentages were calculated from the combined results of simulations at four nest depths (50, 100, 150 and 200 mm—nests at 300 mm depth are unknown) for 52 current nesting locations. Current nesting season values incorporate predictions for oviposition in mid-November and mid-December.)

	earlier nesting (mid-October)	later nesting (mid-January)	current nesting season, each nest site 75% shaded	earlier nesting, each nest site 75% shaded
percentage of all-female nests	0.0	0.0	0.0	0.0
percentage of mixed-sex nests	0.0	45.7	100.0	100.0
percentage of all-male nests	100.0	54.3	0.0	0.0
sex ratio (female : male)	0 : 1	0.23 : 0.77	0.5 : 0.5	0.5 : 0.5
<i>mean development time in yr (n nests)</i>				
mixed-sex nests	—	0.76 (95)	0.91 (416)	0.88 (208)
all-male nests	0.42 (208)	0.62 (113)	—	—

generating females (figure 2). Generally, tuatara are scarce on south-facing slopes many of which are probably too steep to allow habitation; hence, females changing nesting locations to female-producing regions of the island is an unlikely response to maximum warming.

A more effective behavioural response to global warming would be to select nest sites that receive less solar radiation. The Australian agamid lizard *Physignathus lesueurii* has TSD and selects remarkably similar nest temperatures across a broad latitudinal distribution by preferring more shaded nest sites in warmer parts of its range (Doody *et al.* 2006). Although tuatara always nest in open areas (Nelson *et al.* 2004a), we simulated the effect of females nesting in partially (75%) shaded sites in response to maximum warming, and found that exclusively mixed-sex nests were produced at depths between 50 and 200 mm, hatching in just under one year (table 2). If female tuatara do not respond to global warming by selecting nest sites receiving relatively low levels of solar radiation, then balanced sex ratios and spring emergence of hatchlings could be achieved if humans cover nest sites with shade cloth after oviposition, but before the critical period for sex determination. Considerable disturbance of nesting females would be required to locate nests in large numbers, hence a more practical approach could be to shade entire rookeries at the completion of a nesting season.

A final mechanism for females to increase the proportion of mixed-sex and all-female offspring is to nest later, in January (table 2; table S3 in the electronic supplementary material). Later nesting means the TSP occurs when soil temperatures are cooler, and the hatching phenology currently seen in the tuatara is restored, with faster developing males hatching in spring, followed by female hatchlings in summer (figures 2 and 3). Notably, female tuatara from northern populations nest later than those from Cook Strait populations (Tyrrell *et al.* 2000), which may be adaptive in the warmer northern climate in ensuring that hatching occurs in the austral spring. It is therefore possible that selection on hatching times could move nesting seasons forward under global warming, but the strength of selection and heritability of the trait would need to be substantial to keep pace with increasing air temperatures. Conversely, warmer winters are predicted in New Zealand under climate change (New Zealand Climate Change Office 2004), which may lead to earlier vitellogenesis and calcification of eggs, and hence to earlier rather than later nesting. Several studies have documented earlier breeding in oviparous species in response to climate

change (Crick & Sparks 1999; Walther *et al.* 2002; Weishampel *et al.* 2004; Parmesan 2007), with one estimate suggesting an advance of 2.8 days per decade (Parmesan 2007). Our simulations show that earlier nesting by female tuatara would further bias sex ratios towards males and shorten development times (see table S4 in the electronic supplementary material), and may effectively eliminate recruitment of females into the breeding population. Again, partial shading of nest sites could correct the imbalance (table 2).

Our models highlight an additional consequence of extreme global warming for tuatara, in that males developing in all-male-producing nests would complete development five to six months early in autumn, rather than in spring/summer (figures 2 and 3). Incubation temperature has little effect on body size at hatching in tuatara (Nelson *et al.* 2004b), but the energetic consequences of early maturity will depend on whether hatchlings immediately emerge from the nest or overwinter in the nest cavity. Evidence from a review of emergence patterns in turtles that nest in spring and reach hatchling stage in autumn suggests that the phenomenon of overwintering in the nest may be adaptive in ensuring that hatchlings emerge in favourable spring conditions (Gibbons & Nelson 1978). If maximum warming promotes autumn maturity for tuatara, as our models suggest, then any hatchlings that overwinter will do so under much warmer nest temperatures than they do now, as the 4°C rise in winter air temperatures is predicted to be the most dramatic.

Warmer overwintering temperatures have been correlated with smaller yolk reserves in populations of red-eared slider turtles (*Trachemys scripta elegans*) emerging from the nest (Willette *et al.* 2005), which is a clear demonstration of a physiological change associated with climate. Using bioenergetic principles (Vleck & Hoyt 1991; Angilletta *et al.* 2000; Mitchell & Seymour 2000), we can estimate the energy cost of development to hatching stage by averaging the monthly 100 mm CTE for the 52 nest sites, predicting the proportion of development completed on each day using the nonlinear development rate function (figure S2 in the electronic supplementary material), and integrating age-specific rates of oxygen consumption at 20°C (Booth & Thompson 1991) corrected to the CTE using a  $Q_{10}$  of 3.01 (10–20°C) or 2.34 (20–30°C). The  $Q_{10}$  were calculated from mass-specific rates of carbon dioxide production in *S. punctatus* embryos (N. J. Mitchell & N. J. Nelson 2001, unpublished data). The energetic cost of development can

be estimated from the volume of oxygen consumed, using the conversion factor  $19.64 \text{ J ml O}_2^{-1}$  (Booth & Thompson 1991). Mean dry yolk mass of *S. guntheri* eggs is  $1.01 \text{ g}$  ( $n=9$ ; N. J. Mitchell 2002, unpublished data) and, assuming a similar yolk energy density to squamate reptiles ( $26.7 \text{ kJ g}^{-1}$ ; Booth & Thompson 1991), approximately  $27 \text{ kJ}$  of energy is present in a typical egg at oviposition.

On average, 72% (19.5 kJ out of 27 kJ) of yolk energy would be consumed during development to hatching under current nesting patterns (mid-November oviposition at 100 mm, hatching in 391 days), but this cost would decrease markedly under maximum warming to only 47% (12.7 kJ), because the embryos reach hatching stage in 153 days. If hatching stage is reached when relatively mild autumn weather prevails, then male hatchlings may emerge from the nest and begin their growing season in late autumn/early winter, at a time when the invertebrate prey that sustains juvenile tuatara is relatively scarce (Walls 1983). Conversely, if male hatchlings overwinter in the nest cavity, they would consume another 40% of their yolk energy if they emerge in mid-September (early spring), assuming that their metabolic rate remained the same as at hatchling stage, but varied with winter nest temperature. Importantly, under either scenario, the energy reserves of hatchlings from all-male nests under a warmer climate will differ from the reserves of those that hatch under the current climate. The same would apply to males and females completing development in mixed-sex nests in autumn and winter; yet females emerging from all-female-producing nests would retain the current hatchling phenology of spring emergence, and could take advantage of a long growing season. These energetic simulations demonstrate a largely male-biased disruption in emergence time and energy balance, which could have important consequences for sex-specific rates of juvenile activity, growth and mortality.

## 5. CONCLUSIONS

The greatest chance for the future survival of tuatara, other than reducing the magnitude of global warming, lies in their translocation to other islands or protected mainland areas predicted to have thermally suitable micro-sites for nesting (Nelson *et al.* 2002a). Several translocations aimed at restoring tuatara to parts of their former range have occurred since the mid-1990s, including three translocations of *S. guntheri*. Translocation sites have so far been selected on criteria such as security, predator-free status and ecotourism opportunities (Gaze 2001), rather than thermal suitability. Our spatially explicit modelling now provides the necessary tool to test potential translocation sites from the perspective of egg development. While we have only considered the influence of air temperature changes and shading of nest sites on development rates and sex ratios, our approach can also incorporate changes to other variables that affect soil temperature including rainfall, wind speed, humidity and cloud cover, and could incorporate physiological processes such as metabolic heating (Broderick *et al.* 2001). We have shown that mechanistic assessments are now possible for tuatara, and with appropriate physiological data our approach can be generalized to other species exhibiting TSD or other forms of environmental sex determination.

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