

Commentary

Climate warming and environmental sex determination in tuatara: the Last of the Sphenodontians?

Consider the plight of tuatara—reptiles seemingly pre-adapted for extinction. Today only two species survive—paltry remnants of a lineage (order Sphenodontia) that originated over 200 Myr ago (figure 1). They currently live only on some small islands off New Zealand. Their populations are small, sometimes male-biased, and genetically homogeneous (Hay *et al.* 2003). Moreover, tuatara take at least 10 years to mature and then reproduce only every few years (Cree 1994); hatchlings do not emerge for more than a year after egg laying. Now a new study (Mitchell *et al.* 2008) on *Sphenodon guntheri* predicts that climate warming will add to tuatara's vulnerability. These reptiles have temperature-dependent sex determination (TSD) during embryonic stages; continued warming may result in all-male clutches.

Not surprisingly, most studies of the biological 'fingerprints' of climate warming focus on adult organisms (Parmesan 2006). But developing organisms may be even more sensitive to environmental warming and extremes than are adults. They often cannot use behaviour to evade stressful environments (or to seek thermally favourable ones), because they are immobile, or relatively so. Shifting temperatures during development can alter offspring sex ratios in species with TSD, with profound demographic consequences (Schwanz & Janzen *in press*).

The demographic vulnerability of tuatara to climate warming has been noted previously (e.g. Nelson *et al.* 2002a). In the new study, Mitchell *et al.* (2008) build on prior physiological and behavioural data (e.g. choice of nesting sites and depths), and add a complex mechanistic model (Porter *et al.* 2002). Such models are not for the faint of heart, but they are able to predict nest temperature profiles over time and space. They require topographic input from a digital terrain model, microclimate input from a biophysical model, plus physiological data (empirically determined). The model first predicts nest-temperature profiles by solving heat and mass balance equations under current versus projected climate regimes. Next it predicts hatchling sex ratio from nest temperatures predicted for the sex-determination phase. In addition, these models can predict the impact of climate change on time of hatching as well as neonate energy reserves.

Mitchell *et al.* (2008) predicted how offspring sex ratios should change under climate-change scenarios (from now to the 2080s) expected for the region. If the air temperature change is at the low end of projections (<1°C), the sex ratio will become increasingly male biased. But if the change is at the high end (4°C), nests

will produce only males. A demographic model is not needed to predict the population consequences.

So the future looks grim for tuatara. But is there hope? In principle, TSD species can survive climate change in several ways (Janzen & Paukstis 1991).

- (i) A species could adapt to warming temperatures either by shifting the thermal sensitivity of sex determination (thus changing sex ratios associated with specific temperatures) or by shifting from TSD to genotypic sex determination (GSD, thus stabilizing sex ratio). Modest geographical variation in the temperature thresholds of sex determination occurs in a few turtles (e.g. Ewert *et al.* 2005), and phylogenetic analyses reveal that GSD and TSD have arisen independently multiple times in amniotes (Janzen & Krenz 2004). Thus adaptation is theoretically feasible, but seems unlikely to save tuatara, given their low genetic variation and long generation times.
- (ii) Species can use behaviour to buffer climate warming. For example, they could shift geographical ranges (e.g. move to higher altitudes, colonize cooler islands). Tuatara do not have this option, as they survive only on low-altitude islands. However, they could shift nest sites: in fact, if tuatara select nest sites based on temperature, they might 'autocorrect' for climate warming. Females of several species of lizards and turtles with TSD do shift nest sites geographically, selecting relatively cool nests in warmer climates (Ewert *et al.* 2005; Doody *et al.* 2006). This result is remarkable since nesting behaviour is sex-limited in expression and, hence, should evolve more slowly than a trait expressed in both sexes. However, tuatara females have few thermoregulatory options when choosing nests, at least on the island studied by Mitchell *et al.* (2008).

Analyses of other TSD taxa may add perspective. Few long-term studies have monitored TSD species, but some intriguing—if disturbing—clues are emerging. In most studies of turtles, nesting phenology and offspring sex ratios have changed moderately in response to warming (e.g. Schwanz & Janzen *in press*). However, in one population of turtles, females are nesting three weeks earlier than they did only a decade ago. Such earlier nesting might seem a useful means to sidestep elevated nest temperatures, but in fact soil temperatures at the new nest times are still relatively cool. And because cool incubation temperatures



Figure 1. Female *Sphenodon punctatus* at a nest on Stephens Island, New Zealand. Photograph courtesy N. Nelson.

induce males in this species (just the opposite of the pattern of TSD in tuatara), this population is increasingly male biased (Tucker *et al.* in press).

Other compensatory options rely not on adaptive adjustments by tuatara, but on those by humans. Transferring tuatara to other islands is feasible (Nelson *et al.* 2002b). However, as Mitchell *et al.* (2008) caution, the favourability of those islands should first be checked with microclimate simulations. One possible intervention is familiar to gardeners: use shade cloth to lower nest temperatures (Mitchell *et al.* 2008).

The mechanistic–physiological approach developed by Mitchell *et al.* (2008) is a major step beyond correlational approaches that attempt to predict the impacts of climate warming. It provides a ‘first-principles’ understanding of the mechanistic bases of observed (or predicted) patterns: correlation and climate-envelope models cannot do that. Moreover, mechanistic models permit a rigorous evaluation of what-if scenarios. What if air temperature increases by 4°C? What if tuatara shift laying month or nest depth? What are the odds of successful reproduction in a population (re)introduced to another island?

Of course, mechanistic models make many assumptions and rely on data with inherent error. Thus a sceptic might charge that model predictions will have wide confidence intervals at best, or be completely off target at worst. Sensitivity analyses and model evaluations can mute such criticisms. (In the present study, one validation test suggests that the model underestimates the negative influence of warming on sex ratio.) Moreover, mechanistic approaches can identify key model parameters, helping direct research efforts towards those parameters. But mechanistic models require lots of input data, only some of which can be simulated. They are also complex, which means that anyone interested in applying these models faces a steep learning curve. Still the pay-offs (above) make the effort worthwhile, and the inherent complexities of mechanistic processes even make these models necessary.

What is the bottom line? Are we witnessing the Last of the Sphenodontians? And might warming also be a liability for other species with TSD? We and Mitchell *et al.* (2008) take some solace in remembering

that the tuatara lineage—and in fact many lineages with TSD—have ‘weathered the storm’ of temperature change for over 200 Myr (Janzen & Krenz 2004). Moreover, lineages with TSD do not show evidence of elevated extinction rates during periods of substantial environmental upheaval in deep time, such as at the K–T boundary (Rage 1998).

So does this paradox of long-term survival by species with TSD suggest that the warnings raised by Mitchell *et al.* (2008) and others are inflammatory? Not necessarily. Relative to the past, tuatara now have few places to hide; if anything their genetic inertia is now elevated. Moreover, they face a rate of temperature change that is unprecedented over the last 50 Myr and perhaps deeper into Earth’s biotic history. Thus, anthropogenic climate warming may doom tuatara, unless anthropogenic interventions—hopefully guided by mechanistic models—can somehow compensate.

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