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A Threat to New Zealand's Tuatara Heats Up

This unique outlier in the reptile class produces excess male offspring when temperatures rise, presenting a confounding conservation challenge.

Kristine L. Grayson, Nicola J. Mitchell, and Nicola J. Nelson

No matter how many times we head to one of New Zealand's offshore islands, the feelings are always a mix of sheer awe at the beauty and biodiversity preserved in these special refuges and lingering nerves. Did we remember all the gear? Do we have enough food and water in case we get stuck? Can the helicopter land on the side of a cliff in these winds? These epic journeys are in pursuit of a lone remnant of the reptile evolutionary tree, with a unique ecology that has big implications under climate change.

One of our most visited sites is North Brother Island, a small reserve in the Cook Strait between the North and South Islands. The most direct route is by helicopter from the wharf in downtown Wellington, where we load field gear and supplies while business people rush by in their suits. We leave the center of New Zealand's capital city and in mere moments are flying over green hills and through the array of wind turbines that provide supplemental power to the city. After crossing the churning water of the Cook Strait, we reach a small rock outcrop to conduct our survey. North Brother Island is only 4 hectares in size, topped by a lighthouse and a few vacant structures from the days when lighthouse keepers were residents. Often buffeted by sea spray and intense gale winds of Antarctic air, dubbed "southerlies," the sparse vegetation on the island clings to shallow soil and rarely reaches waist height.

This location seems like an unlikely refuge for 200 million years of evolutionary history resting in a single endemic species. North Brother Island is one of approximately 40 offshore islands home to populations of the last remaining reptile from the Order Rhynchocephalia: the tuatara. The population on North Brother Island serves as a bellwether of a particular risk that tuatara populations face because of climate change: There are too many male tuatara on this small island.

Despite appearances, tuatara are not lizards. Living reptiles sit within four orders: crocodilians, turtles, squamates (lizards and snakes), and tuatara. The tuatara lineage separated from squamates 250 million years ago, and the single species remaining today has several unique morphological characteristics, such as the structure of the skull and dentition, not seen in any other living animal.

The biology of the tuatara is unusual for a reptile, partly due to physiological and behavioral adaptations for New Zealand's cool climate. For example, egg development occurs at much cooler temperatures and requires much longer than most reptiles. Even in comparison to some species of turtles, tuatara take life in the extreme slow lane. Adults mature in 15 to 20 years and are primarily nocturnal. The longevity of tuatara is thought to exceed 100 years, with wild individuals thus far known to reach 70 years old. Tuatara inhabit burrows, in which they can cohabitate with other animals such as seabirds. They are carnivorous and active predators, eating a variety of prey ranging from insects to lizards and sea bird chicks. Males are highly territorial of the area surrounding their burrows, which they defend against other males, and these territories can be stable for decades. Females breed every two to five years and clutches of eggs can be fertilized from multiple males.

Our work is part of the Tuatara Research Program at Victoria University of Wellington (one of us, Nicola Nelson, is the current lead investigator). Biologists in this group conduct long-term monitoring and research to understand the ecology and population viability of this endemic species of evolutionary significance and cultural importance to the Māori people. Risks for tuatara include its restricted range, susceptibility to environmental modification, and threats from introduced predators.

As with many species, particularly for isolated populations that lack options to migrate, climate change poses concerns about how these animals and their habitat will respond. Added to all these risk factors is another complication. For tuatara, a fundamental component of their reproductive biology places the species at particular risk of population collapse under climate change: the dependence of offspring sex on temperature.

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The tuatara population on North Brother Island serves as a bellwether for the risks climate change poses to the New Zealand reptile. As nest temperatures rise, more male offspring develop, and the warming climate could spell the end for this small population of unusual long-lived animals, unless conservationists intervene.

Tuatara at Risk

Tuatara conservation is representative of the larger challenge of saving isolated species. Their story is a common one in the history of remote islands, where endemic biodiversity has been decimated following the introduction of non-native predators. Polynesians arrived on the two main islands of New Zealand around 1,000 years ago and brought with them the Pacific rat, causing the extinction of many species of ground-nesting birds and severely reducing mainland tuatara populations.

Captain James Cook arrived in 1769, with 11 new species establishing shortly thereafter, and European settlers started arriving in the 1840s. By this time, tuatara were almost if not completely extinct on the two main islands. During these arrivals and in the coming decades, Europeans introduced more than 50 mammal species; today, approximately 30 species are still established and generally found in prolific numbers. Major predators include brushtail possums, black and Norwegian rats, stoats, ferrets, and domestic cats. These predators had catastrophic effects on native populations of birds, insects, reptiles, and frogs. Despite legal protection of tuatara beginning as early as 1895, populations on offshore islands continued to decline due to habitat modification and incursions from predators.

The most pristine remnants of New Zealand's biodiversity occur on offshore islands that were never colonized by rats, followed by islands where complete eradication of introduced predators and ecological restoration by the Department of Conservation have been successful in recent decades. Tuatara survived in the wild on 32 of these islands, with 5 islands located in the Cook Strait between the main South and North Islands and 27 off the northern coast of the North Island. Several translocations and reintroductions to restored islands and fenced mainland sanctuaries have been successful. A few islands have dense populations of tuatara, and overall the species is not listed as endangered. For example, the population on Stephens Island is estimated between 30,000 and 50,000 individuals, and at least five other islands are thought to have populations in the thousands.

The concern for the tuatara is the inherent risks of isolation and the potential for local extinctions from natural disasters, inbreeding, disease, or incursion from a non-native predator. Thus, understanding the population dynamics of

Tuatara are distributed across 32 offshore islands in New Zealand, although they also once lived on the mainland islands. Recent translocations to other islands and to mainland sanctuaries bring the total number of populations to more than 40. The population on North Brother Island, pictured at left, was first monitored in the 1950s. (Photograph courtesy of Jo Monks.)

these isolated populations and their viability in the future becomes critical for ensuring the persistence of the species.

The North Brother Island population in the Cook Strait became a focus of conservation efforts after revisions to the taxonomy of tuatara. Tuatara were first described by John Edward Gray of the British Museum in 1831 and named *Sphenodon punctatus*. In 1877, the population on North Brother Island was first described as a separate species based on morphological differences and named *S. guntheri*, but this distinction was overlooked and North Brother tuatara were considered a subspecies until the early 1990s. At this time, protein markers called *allozymes* indicated genetic divergence that supported full species status for the North Brother population and the name *S. guntheri* was reinstated (with *Nature* running a tuatara cover photo with the headline "Bad Taxonomy Can Kill").

After this distinction was made for the North Brother population, conserving this lineage was made a high priority and several translocations occurred as part of a national tuatara recovery plan. These efforts both founded additional populations and ensured that the North Brother tuatara lineage would be present in other locations. However, work in 2009 led by Jennifer Hay at Massey University, New Zealand, used mitochondrial DNA and microsatellite markers to show that North Brother tuatara are not as genetically distinct as the original analyses indicated. The new genetic markers and re-analysis of the previous data with more powerful methods supported that the primary genetic differences are between the Cook Strait and Northern populations, grouping the North Brother population with the rest of the Cook Strait.

The current consensus is to describe tuatara using a single scientific name, *S. punctatus*, with recognition of distinct genetic variation between island groups. This genetic variation is an important component of conservation management plans for tuatara across its entire range and when considering the future of the North Brother Island population.

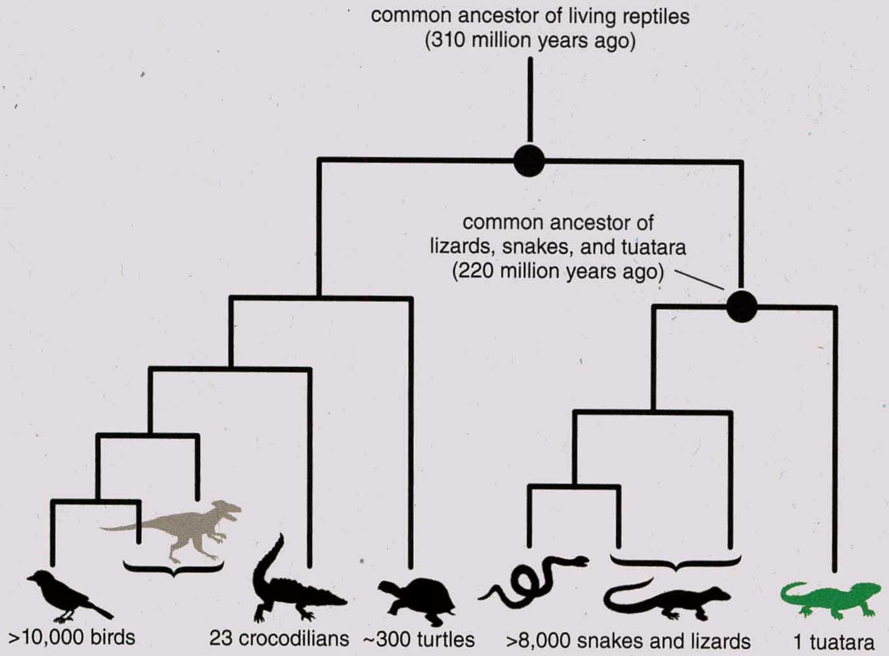
Another important component of tuatara conservation is their position as a *taonga*, or cultural treasure, to the indigenous Māori people. Tuatara are featured in Māori stories and carvings, often representing guardians signifying knowledge, forewarnings, or sacred boundaries. Māori tribes or *iwi* actively work with the New Zealand Department of Conservation in the protection of sacred flora and fauna and conservation areas. From its cultural significance and iconic status in New Zealand to its evolutionary history and sex determination, the tuatara is truly unique.

Sex Determination & Climate Change

The fact that tuatara sex is determined by nest temperature is what makes this animal both fascinating and challenging to conserve. It is one of many animals that develops sex in this way, but its relationship between temperature and the sexes produced is unique.

In humans, as well as other mammals and birds, the sex of our offspring is determined by sex chromosomes at fertilization. However, some vertebrates have no consistent genetic differences between males and females, and sex determination occurs after fertilization according to the environmental conditions. Temperature-dependent sex determination, where sex is determined by incubation temperature, is found in some species of fish but is most prevalent in reptiles. Although not found in snakes, temperature-dependent sex determination is common in crocodilians and turtles, and is found in some species of lizards.

In species that have temperature-dependent sex determination, sex is determined during a window in development called the thermosensitive period. In tuatara this critical period occurs during a one- or two-week window at approximately a third of the way through development from egg-laying until hatching. The sex that results from



Tuatara are not lizards, despite their similar appearance. Their lineage diverged from a common reptilian ancestor during the late Triassic Period, and tuatara are the only remaining species of this ancient lineage (Image adapted from Winter, D., 2013. http://sciblogs.co.nz/tuataragenome/2013/6/17/why-sequence-the-tuatara-genome.)

the incubation temperature during this period depends on the temperature-dependent sex determination pattern.

Three categories have been described based on the sex ratio produced as temperature increases. In the first scenario, low temperatures produce males and higher temperatures result in female offspring. The reverse pattern is produced in the second scenario. In a third scenario, females are produced at both low and high temperatures, and intermediate temperatures result in males. Sex ratio skew in hatchlings is common in species with temperature-dependent sex determination, but extreme cases that result in sex ratio skew in the adult breeding population can lead to mate limitation, reduced reproduction, and effects on population viability.

Given the dependence of sex on environmental conditions, temperature-dependent sex determination seems an unlikely reproductive mode to be maintained by evolution across all reptile orders. Many hypotheses have been proposed to explain the prevalence of temperature-dependent sex determination. One possibility is that it is an evolutionary remnant from the early diversification of reptiles and may not have any current adaptive significance. However, using a phylogenetic approach to examine the evolution of this trait, Fred Janzen of Iowa State University has shown that there is a high degree of variability in sex determining systems. For example, this reproductive mode has been lost at least five times in the evolutionary history of turtles and evolved independently in at least three different lineages of lizards.

These patterns suggest an adaptive hypothesis for the origin and maintenance of temperature-dependent sex determination, and a broad variety of ideas have been put forward. The challenges of testing adaptive hypotheses have resulted in little empirical data to date (with some notable exceptions), and the topic remains an active area of research. In the context of tuatara conservation, we are interested in whether the temperature-dependent sex determination system has the potential to become maladapative under rapid climate change because of a tendency toward male-biased sex ratios.

Several studies across multiple taxa have demonstrated that hatchling sex ratios are skewed in years of climatic extremes and highlighted the potential for rapid, directional changes in climate to bias offspring sex ratio and pose a threat to species with temperature-dependent sex determination. The most extensively studied system is the painted turtle (*Chrysemys picta*). Researchers from Iowa State University are combining long-term data and experimental studies to determine if changes in maternal nesting behavior or shifts in phenology can compensate for the potential of female-biased offspring sex ratios in this species under a warmer climate. Thus far, unlike the situation in the tuatara on North Brother Island, changes in painted turtle offspring sex ratio have yet to result in strong directional biases in adult populations.

The risks from climate change for species with temperature-dependent sex determination depends on the sex determining pattern and the degree of sex ratio bias expected. Environmental changes that result in production of a single sex (100 percent males or females) have obvious implications for population viability. A skew in sex ratio toward males is the most worrisome outcome for population viability due to reduced mating opportunities, higher male–male competition, and the production of fewer offspring.

Ecological theory predicts that an overabundance of one sex should lead to mechanisms to correct the imbalance, such as lower survival or emigration of the more common sex. Counter to this theory, in some cases a male-biased sex ratio can create feedbacks that magnify the negative consequences to female fitness and population growth and result in further skews in sex ratio. For example, research by Jean-François Le Galliard, currently at France's National Center for Scientific Research, and his colleagues demonstrated that male aggression in the common lizard (*Lacerta vivipara*) intensifies under male-biased

Male tuatara are bigger than females and sport a more prominent spiny crest along the head, back, and tail. (Photograph courtesy of Tom Lynch, Foris Eco-tours, NZ.)

Tuatara live in burrows and dig nests for their eggs. The temperature of the nest during a critical developmental window determines the sex of the offspring. (Photograph at left courtesy of Anna Carter, at right courtesy of Susan Keall.)

sex ratios and becomes damaging to females, amplifying the sex-ratio bias toward males and creating a downward spiraling cycle that results in fewer and fewer females until the population declines to extinction. This situation can be described as an *extinction vortex*, where cumulative effects further compound extinction risk as the effective population size becomes smaller.

Fortunately for the conservation of most reptile species with temperature-dependent sex determination, the patterns that result in more females at higher temperatures are by far the most prevalent. It is worth noting that it can be difficult to predict how reproductive timing, nest temperatures, and climate change will interact. Sex ratio skew may occur in unexpected directions with changes in the timing of egg laying and shifts in the climatic conditions that occur during the thermosensitive period. However, the pattern where higher temperatures result in more males is most concerning in the face of climate change. The tuatara is one of the only known species of reptiles that has this rare pattern, placing the potential for male-biased offspring sex ratios as one of the many risks facing its isolated island populations.

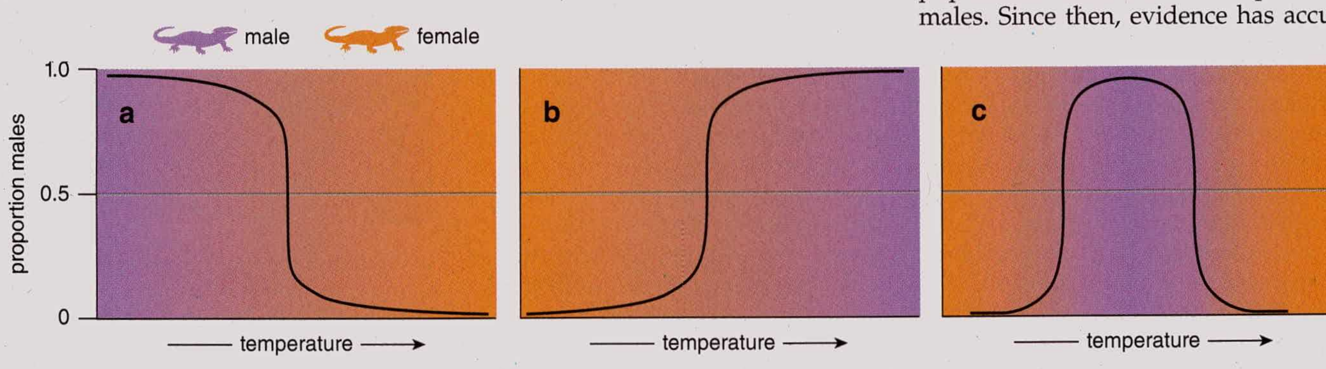
Too Many Males

Conserving threatened populations can be a challenging endeavor, often with limited data to inform complex management decisions. The tuatara of North Brother Island serve as a valuable case study of conserving a species with temperature-dependent sex determination threatened with sex ratio skew from climate change. Our detailed understanding of this one population illustrates how microclimate modeling can be used to predict offspring sex ratio. The North Brother case has also been applied to a recently developed framework for making decisions about assisted colonization, the conservation strategy of relocating species threatened by climate change to more suitable habitats.

North Brother Island is unique in that detailed demographic data have been collected on the tuatara population over the past three decades. This concerted effort has resulted from the taxonomic interest in the population, its relatively easier access compared to more rugged and further offshore islands, and the support of the guardian Māori tribe (*Te Atiawa Manawhenua ki te Tau Ihu*). The first surveys were conducted by Dick Barwick in the 1950s, who marked animals we continue to find 40 years later. More extensive surveys began in the late 1980s, with the founding of the tuatara research group at Victoria University of Wellington by Charles Daugherty and the research efforts of Alison Cree and Mike Thompson. The consistency of our surveys has been spearheaded by Susan Keall, who has been part of every survey on the island since 1991.

A male-biased sex ratio was first noticed in the late 1990s, with the adult population estimated at 60 percent males. Since then, evidence has accu-

There are three patterns of temperature-dependent sex determination seen in the animal kingdom. As nest temperatures increase, either more females (a) or more males (b) may develop. In the third scenario (c), more females are produced at extreme temperatures, while males are produced at intermediate temperatures.



mulated regarding the consequences of the male bias on female fitness and population health. Our recent analysis of population trends over the last decade indicates that the male bias is now approaching more than 70 percent.

Despite the small size of the island, North Brother hosts four other species of reptiles. In addition to the population of 300 to 500 tuatara, two species of gecko combine to number over 5,000, and the combined populations of two skink species number over 8,000. With this very high density of reptiles, resource competition is intense on this sparse island. Spray-bearing winds constrain vegetative growth, and depletion of invertebrate prey is a concern. Male tuatara are larger than females and are socially dominant.

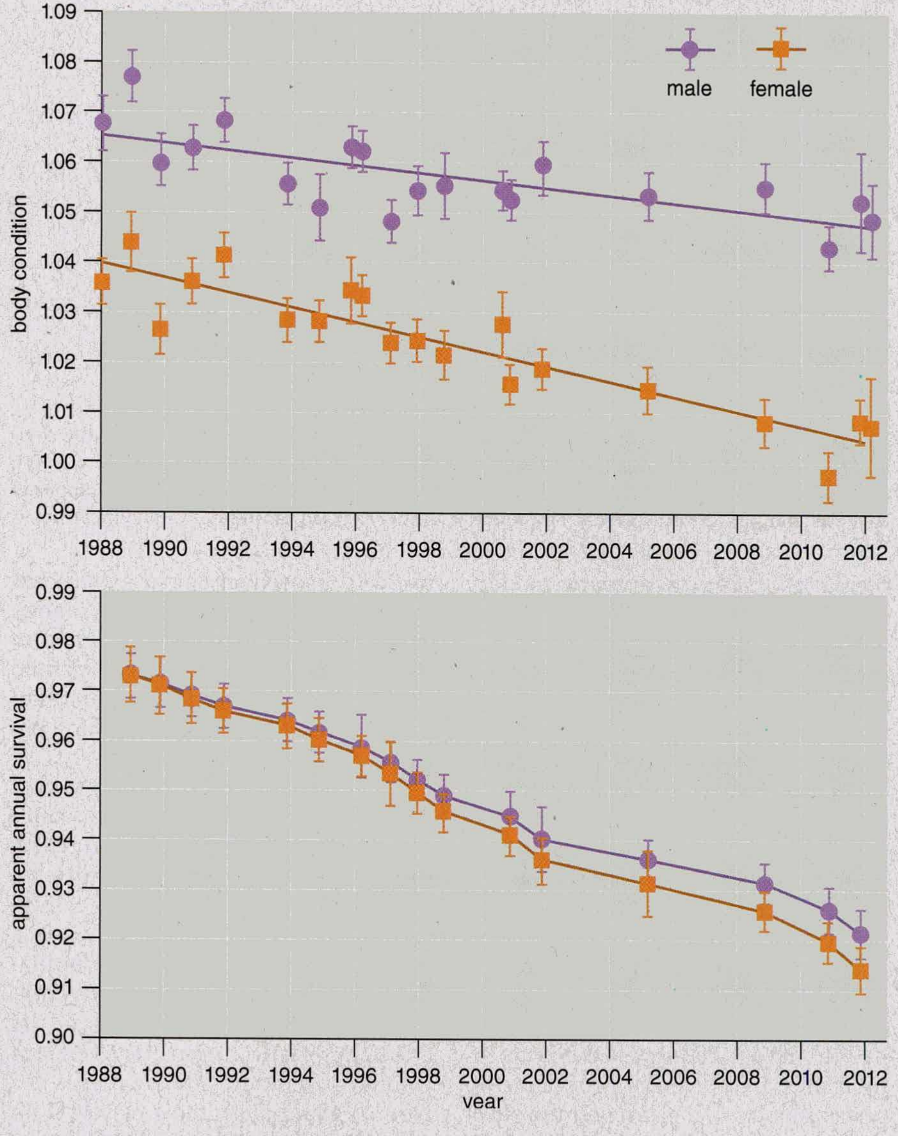
Trends in body condition over time have shown a decline in body mass relative to body size for both male and female tuatara, but with more steep declines for females. Even more dramatic are the reductions in female reproductive output. On a neighboring island, females breed every two to five years and produce an average of nine eggs per clutch. On North Brother Island, females only breed every nine years and produce an average of six eggs per clutch.

How this situation arose in the North Brother tuatara population is an open question. We have evidence that the population was severely reduced in the late 19th century due to habitat destruction associated with building the lighthouse and over-collection. Research at Victoria University of Wellington by Jo Monks, currently of the New Zealand Department of Conservation, put forth the hypothesis that after this population crash the tuatara population rebounded to its carrying capacity and the current dynamics are a delayed density-dependent response. The current male bias could have initiated due to demographic stochasticity as the population grew or due to past climatic conditions. With density-dependent competition, the expectation is that as a population reaches its carrying capacity survival will decline and the size of the population will go down.

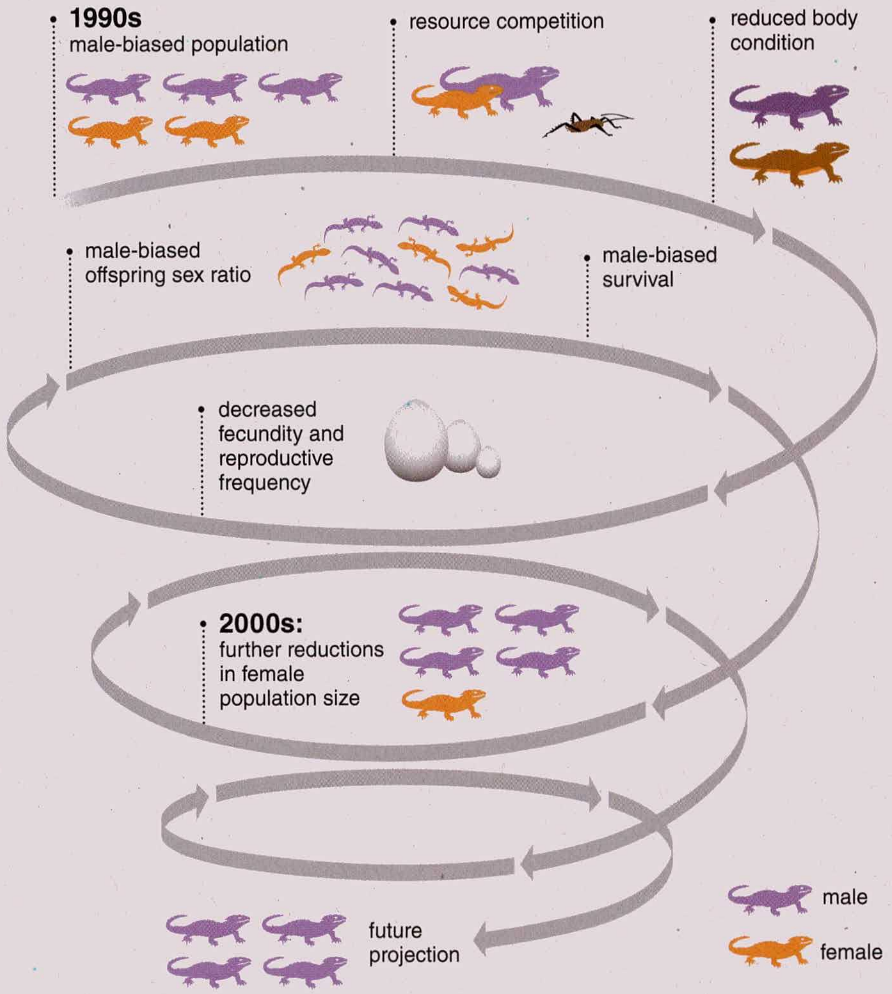
Indeed, the population size of the tuatara is dropping. When we analyzed our survey records using mark-recapture analyses, we found that annual adult survival has declined from approximately 96 percent to about 91 percent, with females beginning to have lower survival estimates compared to males. We are concerned that even a reduction in population size will not be sufficient to ease the impacts to females and reverse the increasing male-biased trend the population is experiencing. In addition to the compounding effects on adult females from increasing competition with adult males, our work indicates that the offspring sex ratio is also likely skewed toward males, resulting in male-biased cohorts reaching adulthood.

Directly measuring offspring sex ratio on North Brother Island is complicated by numerous factors. Only 13 percent of the female population breeds in a given year, nests are hard to locate, and eggs take 12 to 15 months to develop. Hatchlings are extremely difficult to find and require a laparoscopic procedure to visualize the gonads to determine sex, because secondary sexual characteristics do not develop until maturity and no genetic differences exist between males and females.

The absence of field data on offspring sex ratio was not for lacking of trying. The most determined of us (Nicola Mitchell) spent parts of two summers in 2000 and 2001 living on North Brother Island searching for nests and gleaning all possible information from the few females she observed. Her solution to these challenges was to combine the available in-



Both male and female tuatara on North Brother Island are declining in body condition and survival, but the decline for the females is higher. These declines are attributed to resource competition and a male-biased sex ratio. Note that body condition is a unitless measure calculated from several size variables and apparent annual survival is a proportion calculated using mark-recapture techniques. (Figures adapted from K. L. Grayson et al., *PLoS ONE* 9:e94214.)



The consequences of the current male bias on North Brother Island are expected to be compounded over time as the declining number and condition of females, combined with warming nest temperatures, exacerbates the problem until the population becomes entirely composed of males, long-lived but unable to reproduce. (Graphic adapted courtesy of Chantalle Foster.)

formation with two computer models: a spatially explicit microclimate model to describe soil temperatures at typical nest depths and a biophysical model to estimate development rates and predict the sex of hatchlings. Together these models not only allowed us to predict the current offspring sex ratio produced from the environmental conditions on the island, but also enabled us to make predictions under climate change scenarios. This framework allows the estimation of nesting conditions from habitat data and can be applied to many systems where field data are unavailable or inaccessible.

Our model estimates that typical nest sites are currently producing 56 percent males. We examined the effect of both minimum and maximum climate change scenarios from the New Zealand Climate Change Office (0.1 to 0.8 degree Celsius or 3.3 to 4 degrees Celsius air temperature increase by 2080, respectively) on the predicted offspring sex ratio. The small change in air temperature under the minimum scenario only raised offspring sex ratio to 57 percent males, but the maximum scenario results in nests producing entirely male offspring by 2080.

Together these compounding factors create a bleak scenario for the viability of the tuatara population on North Brother Island. Further increases in the male-biased sex ratio create a downward spiral that will likely result in a functionally extinct, all-male population. Even if density-dependent competition and male dominance in the adult population eases, the current trends in temperature increases for New Zealand align most closely with projections from maximum warming scenarios. Thus, without a massive adjustment in nesting behaviors, the sex ratio of hatchlings entering the population will continue to be further biased towards males, with a very real possibility of the island only producing male hatchlings in the future.

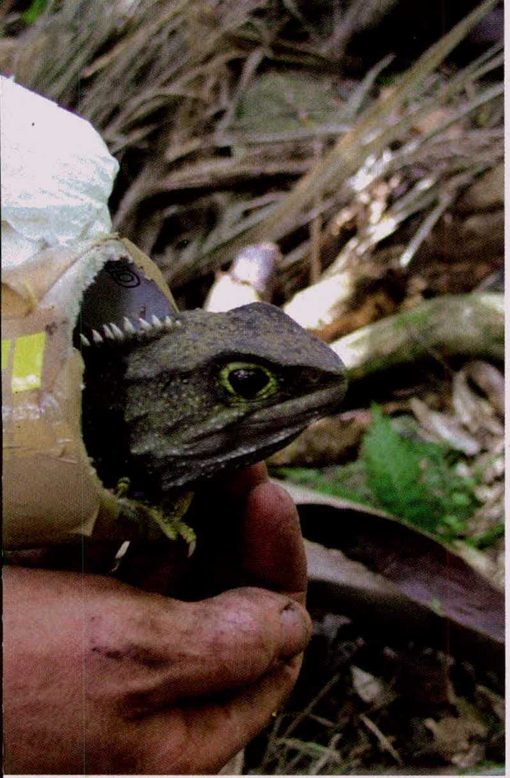
Can Tuatara Adapt?

To place our results in a broader context, we need to understand the threats to tuatara populations across all remaining islands and look for shared risk factors. Our predictions of extinction risk place the timeframe for becoming an all-male population quite far in the future, given the long generation time of tuatara.

Often conservation decisions need to be made quickly in the face of declining populations. In this particular case, managers have time to evaluate the science and logistics before making decisions. The skew in sex ratio on North Brother Island appears to be an isolated case in comparison to the other remaining island populations. Recent surveys of six islands across Northern and Cook Strait populations have not found evidence of sex ratio skew in other populations.

North Brother Island has several limitations that may explain why sex ratio bias has become magnified on this island in particular. These characteristics are also important in considering the potential for the tuatara population to make behavioral changes to alter the population sex ratio. The small size of North Brother Island along with the shallow soils and narrow range of nesting habitat provide very few opportunities for cooler nesting sites, as our modeling of the soil microclimate showed. Changes in reproductive timing, nest depth, or nest habitat to avoid more extreme temperatures could be possible when a population has access to more area with a variety of habitat (for example, shaded versus unshaded areas). The pivotal temperature at which sex is determined is unlikely to evolve in response to climate change due to the long generation time and the low genetic diversity of the North Brother population.

Given that the evolutionary history of Sphenodontian reptiles extends over 200 million years and because ancestors of modern tuatara have persisted through major shifts in climate, it is often suggested that the species should have the capacity to adjust in response to rapid climate change. Although this is true, we cannot determine the impact that past climatic changes had on specific populations



Captive-breeding programs, translocations, and releases into protected habitats are important current and future strategies for tuatara conservation. (Photograph courtesy of Susan Keall.)

and the distribution of Sphenodontids in New Zealand. From recent subfossil evidence, we know that tuatara were once widespread across the two main islands of New Zealand and spanned climates from the cooler southern tip of the South Island to the subtropical regions of the North Island.

Although this distribution suggests that tuatara can adapt to a wide range of climates, these populations could respond in ways that are not available to the North Brother population. These include migration to a different habitat or climate, sex ratio adjustment through immigration of the rarer sex or emigration of the excess sex, and access to a variety of habitat types providing thermal gradients for nest selection.

Just as past climate events likely affected some populations while others persisted or even grew, under current climate change North Brother Island is likely to be the most at risk of extinction of the current populations of tuatara. The potential for species to adapt under climate change is a pressing global question across all levels of biological organization. The decisions we face on North Brother Island are representative of the larger issues facing conservation managers today.

Presented with the latest information on the risks of extinction facing North Brother tuatara, managers must decide whether to intervene. Given the resource limitations that conservation organizations are facing, one option is to let the population continue on its current trajectory and observe the responses of the population. We have hypotheses about the scenarios that could occur, and very few empirically based studies on the dynamics of sex ratio bias in natural populations exist. Conversely, even though this is just one of many small island populations, each population is valuable given their ecological and cultural significance.

Potential management interventions could target nesting habitat by removing remnant structures associated with the lighthouse and restoring additional habitat for nesting on cooler faces of the island. The management of hatchling sex ratios could be achieved through captive incubation and supplementation with head-started juvenile females. Removal of adult males could temporarily relieve competition with females. Importantly, long-term solutions require addressing the skew in the offspring sex ratio produced from nests on the island, otherwise any efforts to manage the adult population are rendered ineffective as more and more male offspring are produced.

As biologists, we provide the best data we can to inform these difficult decisions, and the conversation with managers and policy makers continues. The story of the tuatara is notable for the cooperation that exists between stakeholders, from scientists and students to government managers and Māori tribes. For North Brother Island, the long-term discussion may revolve around the importance of maintaining a population on the island versus ensuring the lineage continues in other locations. Due to the longevity of the tuatara, we know the population will continue to persist for many decades on North Brother Island, even if it does become completely dominated by males and unable to sustain a population without intervention.

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