

**The Effects of a Long-Term Male-Biased Sex Ratio on Population
Dynamics and Viability of Tuatara (*Sphenodon punctatus*)**

by

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Abstract

Sex ratio is a critical parameter in the population dynamics and ecology of a species. Changes in population sex ratio can influence sexual selection and individual behaviour, which ultimately impact reproductive rates and population viability. For territorial species, sex ratio variation can influence territorial behaviour, and thus, the pattern of activity areas where animals acquire critical resources to perform biological processes. However, empirical studies addressing population consequences of sex ratio through behaviour and patterns of activity are rare. A biased sex ratio has been recognized as a major factor contributing to extinction in small populations, due to the vulnerability to environmental, demographic, and genetic stochasticity.

Species with temperature-dependent sex determination (TSD) are prone to sex ratio biases because hatchling sex ratios are influenced by thermal conditions during embryonic development. A warming climate poses an increasing concern for the population viability of species with TSD, because rapidly shifting temperatures may strongly skew offspring sex ratios. Tuatara (*Sphenodon punctatus*) are long-lived reptiles endemic to New Zealand. They are particularly at risk based on their rare pattern of TSD, where males hatch at higher nest temperatures.

Since the late 1990s, there has been an increasing male bias in a small, isolated tuatara population on North Brother Island. Survival and body condition of adult tuatara have declined, with a steeper rate of decline in females. Population viability analyses predicted the extinction of this population under the previous demographic parameters. However, longer term studies are needed to examine whether the sex ratio ultimately fluctuates around a more balanced sex ratio despite fluctuations based on the climate, or if the male bias becomes more extreme under climate warming.

I explored the effects of a male biased sex ratio on population dynamics and viability of tuatara on North Brother Island using updated survey data over 30 years. I estimated the current sex ratio, body condition, survival rates, and population size and temporal trends in these parameters. In addition, I quantified tuatara activity areas on North Brother Island and in two translocated populations, which can reflect resource competition and the effects

of sex ratio and population density. Then, I performed behavioural observations on captive populations to investigate how dominance is associated with intra-specific interactions to understand the implications of a male bias for population viability. Lastly, I updated the population viability of North Brother tuatara population based on the recent population parameters.

There has been a continual male bias over 30 years in the North Brother Island tuatara population. Survival and body condition have declined over time, with a steeper rate of decline in females. In my recent data, I found a decrease in population size, as well as a further lengthening of the female breeding cycle. By contrast, the male bias has become less skewed over time in new cohorts of this population after 2005. Also, there has been an increase in male body condition and in survival of both sexes in new cohorts. The activity areas in males are larger than females, and activity areas became larger more recently under a smaller population size. Behavioural observations on captive tuatara showed larger males had an advantage in accessing females based on smaller distances to females, males had dominance over females through maintaining larger activity areas, and males and larger individuals had dominance in aggressive interactions. Based on the updated population parameters, the population viability analysis predicted a lower probability of extinction for this tuatara population than previous studies. However, the low female fecundity and the likely further skewed male bias under a warming climate could drive this population to extinction at a rapid rate if demographic parameters further shift.

This project revealed how a male bias can influence individual behaviour and patterns of activity areas, and impact parameters, such as body condition, survival and population size, and ultimately, influence population viability. As more new cohorts enter this population, the population could experience a less skewed sex ratio and improved survival over time. Therefore, longer-term monitoring of the North Brother Island tuatara population is needed to investigate the lagged impact of environmental temperature on sex ratio and other population parameters, as well as population viability. Changes in sex ratio can be an early indicator of decline due to the effects of climate warming for species with TSD, an issue that thus far has not been detected in other tuatara populations. This study provides implications for the conservation and management of other species with TSD, which can also be prone to skewed sex ratios in a warming climate.

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This thesis is dedicated to my son, who makes me ever stronger.



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Chapter 1

Consequences of temperature-dependent sex determination in a warming climate: an introduction

Introduction

Sex ratio is a crucial parameter for population dynamics and the evolutionary ecology of a species (Ancona et al., 2017; Emlen & Oring, 1977; Le Galliard et al., 2005; Sykes et al., 1974). This ratio of the number of males to females in a population can indicate the relative survival rate of each sex (Skalski et al., 2010). The sex ratio of a population can influence individual behaviour, including male-male competition and female mate choice, which can have profound effects on demographic parameters such as reproductive success and survival, and ultimately, affect population viability (Ancona et al., 2017; Clutton-Brock et al., 1984; Dale, 2001; Gwynne, 1990; Heinsohn et al., 2019; Jirotkul, 1999; Le Galliard et al., 2005). For example, a strong male bias in swift parrots (*Lathamus discolor*) may cause high interference from unpaired males on nesting females, resulting in a decline in female nest success (Heinsohn et al., 2019). Similarly, in an empirical study on the common lizard (*Zootoca vivipara*, formerly *Lacerta vivipara*), a male bias triggered male aggression towards females, with negative impacts on female survival and fecundity (Le Galliard et al., 2005).

Population sex ratio can be affected by differing factors at each life stage, such as, mechanisms of sex determination during the embryonic period (e.g., genetic sex determination and environmental sex determination), differential mortality at each life stage from embryonic to post-reproduction, and differential maturation times, dispersal rates and life expectancies by sex (Ancona et al., 2017; Donald, 2007; Székely et al., 2014).

For example, in an ortolan bunting (*Emberiza hortulana*) population, females are more dispersive than males during the breeding season, which is thought to lead to a strong male bias of the population (Steifetten & Dale, 2006). Swift parrots (*Lathamus discolor*) have female-biased mortality during nesting season due to predation by an introduced mammal, resulting in strongly male-skewed populations (Heinsohn et al., 2019).

Although the sex ratio of a population can shift due to a number of drivers, offspring sex ratio at birth has a significant influence on population sex ratio patterns, and as such, offspring sex ratios have been a focal topic in evolutionary and population biology (Douhard, 2017). Given offspring sex ratio can vary substantially among species or among populations of the same species, many sex ratio theories have been proposed to explain variation in population sex ratio for species with genetic sex determination (GSD). Fisher's principle assumes the equal investment in the production of male and female offspring, therefore the balanced sex ratio in sexually reproducing species is considered an evolutionarily stable strategy (Fisher, 1930; Shaw & Mohler, 1953). This theory proposes that natural selection would favour individuals of the rarer sex, as they would have higher reproductive success than the other sex due to having more potential mate choice. As such, individuals of the rarer sex would produce a higher proportion of offspring, leading to a re-balancing of the sex ratio. Fisher's principle is considered as the foundation of adaptive sex ratio theories and has been supported by many empirical studies across a wide range of taxonomic groups including invertebrates and vertebrates (Bosch & Vicens, 2005; Conover & Van Voorhees, 1990; Slagsvold, 1990). For example, in an experiment on the Atlantic silverside (*Menidia menidia*), a fish with sex determination through an interaction between temperature and sex-determination genes, a constant experimental temperature produced an initial strongly skewed sex ratio. However, there was an increased proportion of the rarer sex in subsequent generations until a balanced sex ratio was achieved (Conover & Van Voorhees, 1990).

The local mate competition model was proposed to explain the prevalent female-biased sex ratio in a wide range of animals (e.g., insects and arthropods), where mating occurs at the natal patch (Foster & Benton, 1992; Macke et al., 2011; Schrempf et al., 2005; Werren, 1980; West & Herre, 1998). Under local competition for mates between related males, mothers tend to bias the offspring sex ratio towards females as only a small number

of males are necessary to fertilize all the females. An excess of males could result in some males being unable to mate, which would be a waste of the mother's resources. By investing more resources in producing female offspring, a mother can increase her fitness compared to one who produces fewer female offspring (Hamilton, 1967; Taylor & Bulmer, 1980; Werren, 1987; West et al., 2002). Empirical evidence for this theory arises in a flightless ant species, *Cardiocondyla batesii*, where over 83% of matings occurred between siblings at the natal patch. Driven by the local competition for mating, there was an extremely female-biased sex ratio, with over 85% of sexuals being young queens (Schrempf et al., 2005).

The Trivers–Willard hypothesis proposes that where environmental conditions have differential impacts on the fitness of male and female offspring, parents would manipulate the sex of their offspring to better adapt to the environmental conditions (Trivers & Willard, 1973). This model has been used to explain sex-biased parental investment in many mammals, where parents in good condition produce more sons and parents in poor condition produce more daughters (Cameron et al., 1999; Clutton-Brock et al., 1984; Douhard et al., 2016; Roche et al., 2006; Ryan et al., 2012; Thomas et al., 1989). For example, in Richardson's ground squirrels (*Urocitellus richardsonii*), mothers in good condition (with high levels of fecal cortisol during gestation period) were more likely to produce male-biased litters than mothers in poor condition (Ryan et al., 2012). This is presumed to be because male offspring produced by parents in good condition are more likely stronger in male-male competition for mates in the future and thereof have greater reproductive success (Clutton-Brock et al., 1984). The Trivers–Willard hypothesis can also explain the sex ratio patterns in response to mate quality in birds (Burley, 1981; Pike & Petrie, 2005; Romano et al., 2015; Sheldon et al., 1999; Taff et al., 2011). The concept argues that if a female has a high-quality mate, with elaborate ornaments, for example, she is more likely to produce more sons than daughters. Inheritance of these features is expected to confer greater fitness advantages to sons than daughters (Fawcett et al., 2007). In an experiment on a captive population of peafowl (*Pavo cristatus*), females produced more male offspring when they mated with males having full complement of feathers than when they mated with the same males with reduced attractiveness after the removal of prominent eyespot feathers (Pike & Petrie, 2005).

Despite the great success that sex ratio theory has achieved in understanding variation in offspring sex ratios, the physiological mechanisms that species with genetic sex determination (GSD), such as mammals and birds, use to adjust the offspring sex ratio are still elusive (Cameron, 2004; Schindler et al., 2015; West et al., 2002). The increasing evidence on parental ability to adjust offspring sex ratio in species with GSD indicates that the sex chromosome may not constrain an adaptive sex ratio despite its significant role in sex determination (Douhard, 2017; West & Sheldon, 2002). Compared to species with GSD, whose sex is primarily determined by sex chromosomes, the sex of some species is determined by various environmental factors such as light, pH, nutrition, or temperature during a specific period of embryonic development (Korpelainen, 1990). For example, pH conditions were found to have effects on sex determination in some fish species (e.g., the genera *Apistogramma* and *Pelvicachromis*), where increasing male broods were hatched at higher pH conditions (Römer & Beisenherz, 1996; Rubin, 1985). Temperature-dependent sex determination (TSD) is a prevalent form of environmental sex determination (ESD), where incubation temperatures influence gonadal differentiation during a specific portion of embryonic development (Bull, 1980, 1983; Janzen & Paukstis, 1991). To date, TSD has been observed across many taxonomic groups, including fish, reptiles, insects and crustaceans (Bull, 1980; Devlin & Nagahama, 2002; Korpelainen, 1990).

Sex ratio of reptiles with TSD in a warming climate

About one quarter of reptiles have been found with TSD, including crocodiles, sea turtles, lizards and tuatara (Mitchell & Janzen, 2010; Valenzuela & Lance, 2004), and gonadal differentiation broadly occurs in the middle third of incubation (Andrews, 2004; Bull, 1983). There are three types of TSD based on the effect on offspring sex ratio as the incubation temperature increases (Valenzuela & Lance, 2004). To date, all species of sea turtles have shown the pattern of male-female (MF), where males hatch at lower temperatures and females hatch at higher temperatures (Hays et al., 2010). The female-male-female (FMF) pattern is prevalent in crocodylian species, where lower and higher temperatures produce females and intermediate temperatures produce males (González et al., 2019; Lang & Andrews, 1994). In the female-male (FM) pattern, females are produced at lower temperatures and males are produced at higher temperatures. Tuatara (*Sphenodon*

punctatus) are the only known species with the rare FM TSD pattern (Cree et al., 1995; Mitchell et al., 2006).

Charnov-Bull proposed that ESD is favoured by natural selection when environmental factors have differential impact on the fitness of each sex (Charnov & Bull, 1977). This model has been supported by some studies on reptiles with TSD, such as, lizards and turtles (Bobyne & Brooks, 1994; Valenzuela, 2021; Warner & Shine, 2008). Jacky dragons (*Amphibolurus muricatus*) are short-lived lizards (~3-4 years) with TSD, where female offspring are produced at lower and higher temperatures and both sexes are produced at intermediate temperatures (Warner & Shine, 2008). Warner & Shine (2008) used hormone manipulations to produce embryos of both sexes from all incubation temperatures, and demonstrated sex-biased fitness at differing incubation temperatures. Incubation temperatures naturally producing one sex maximized the fitness of this sex by producing more offspring than the other sex, providing the empirical evidence for the Charnov-Bull model. Similarly, in a long-lived pleurodiran turtle (*Podocnemis expansa*), warm and dry years produced high food availability and female-biased hatchlings, while cold and wet years produced low food availability and male-biased hatchlings (Valenzuela, 2021). This is hypothesised to be because a rapid growth rate due to food abundance benefits female fitness more than males, and slow growth rates due to food shortages have less influence on male fitness than females (Valenzuela, 2021).

Offspring sex ratios in reptiles with TSD can vary dramatically from clutch to clutch in natural nests based on habitat heterogeneity and female nesting behaviour. Consequently, reptiles with TSD are prone to considerable variation in sex ratio (Bull, 1983; Mitchell & Janzen, 2010). Green sea turtles (*Chelonia mydas*) hatching from differing thermal conditions among beaches resulted in moderate female-biased sex ratios in some populations and extremely female-biased hatchlings or even 100% female hatchlings in other populations (Jensen et al., 2018). Furthermore, a warming climate poses an increasing challenge for species with TSD and the concept of an evolutionarily stable strategy of an even sex ratio, because increasing temperatures can cause overproduction of one sex or even populations with single sex (Janzen, 1994; Mitchell & Janzen, 2010; Valenzuela et al., 2019).

The ancestry of current reptiles (i.e., turtles, crocodiles, lizards, snakes and tuatara) originated between the early Permian and the late Triassic (Fastovsky & Weishampel, 2009). Therefore, these lineages have survived historical climate shifts including the drastic climate change at the end of the Permian, which caused one of Earth's largest mass extinction events, and a series of glacial and interglacial periods with cold and warm climates alternating many times (Huey & Ward, 2005; Savin, 1977). However, sex determining systems of these lineages may not have been stable throughout this period. Increasing evidence indicates that GSD and TSD do not necessarily exclude each other, where sex determination can be affected by the interaction between genes and environmental temperatures (Sarre et al., 2004). For example, although Eastern three-lined skinks (*Bassiana duperreyi*) have strongly differentiated sex chromosomes, more males hatch at lower temperatures (Shine et al., 2002). Moreover, phylogenetic studies indicate that evolutionary transitions between GSD and TSD have occurred many times in reptiles (Ewert et al., 1990; Janzen & Krenz, 2004; Sarre et al., 2011), and an empirical study showed this transition can occur rapidly (Australian bearded dragon, *Pogona vitticeps*, Holleley et al., 2015). These transitions indicate there is a trade-off between the costs and benefits of different sex determination systems in response to thermal conditions (West et al., 2002), and that reptiles may have some capacity for adaptation to climate shifts. However, the current rate of climate warming is unprecedented (Intergovernmental Panel on Climate Change, 2023), and the capability of modern reptiles to adapt to rapid climate change in the landscape of the Anthropocene is unknown. As such, current sex ratio patterns and the ensuing population consequences for reptiles with TSD are of significant conservation concern.

In the current climate, there are apparent female biases in many sea turtle populations arising from the MF pattern (Jensen et al., 2018; Laloë et al., 2016; Patino-Martinez et al., 2012). Crocodylian species with the FMF pattern demonstrate various results in the sex ratio of wild populations (e.g., a male bias, Charruau, 2012; a female bias, Espinal & Escobedo-Galván, 2011), but the population sex ratios are predicted to become strongly female biased in the future as the temperature increases (Charruau, 2012; Escobedo-Galván et al., 2016). To some extent, a female bias can benefit population growth because more breeding females can produce more offspring, unless extreme temperatures cause all-female

populations or high embryonic mortality (Hays et al., 2017; Wedekind, 2002). By contrast, the FM pattern is more problematic in a warming climate because overproduction of males can directly lead to fewer offspring, and subsequently, population decline (Mitchell & Janzen, 2010). Tuatara are endemic reptiles in New Zealand, inhabiting offshore islands and sanctuaries on the main islands (Cree, 2014). Studies in different populations of tuatara have provided insights on how current climates are impacting a reptile species with the FM pattern of TSD. A previous study on a large tuatara population showed a balanced sex ratio (Moore, Daugherty, & Nelson, 2009), while there has been an increasing male bias since the late 1990s in a small tuatara population nearby (Grayson et al., 2014; Mitchell et al., 2010; Nelson, Keall, Pledger, et al., 2002). Regardless of the TSD pattern, rapid shifts in climate and reproductive phenology may result in highly skewed offspring sex ratios for a wide range of species.

Effects of male bias

Sex ratio is a major driver for population dynamics through its influence on individual behaviour and resource competition (Clutton-Brock et al., 1984; Gwynne, 1990; Jirotkul, 1999; Kappeler et al., 2022). Empirical studies have shown that a biased sex ratio can change competition for mates and mate choice. A male bias in guppies (*Poecilia reticulata*) caused increased interference behaviours among males, and female preference for males with more orange colour (Jirotkul, 1999). In a sex ratio manipulation experiment on the rosy bitterling (*Rhodeus ocellatus*), females showed aggression towards other females and took a more active role in courtship under female-biased sex ratios, while these behaviours were not observed under a balanced sex ratio (Liao et al., 2014). Although an excess of either females or males can create mating limitation, and subsequently limit population growth, a male bias is more problematic because of intensified male-male competition and male aggressiveness to females, which can incur costs on individual survival and female fitness (Dale, 2001; Heinsohn et al., 2019; Holveck et al., 2015; Le Galliard et al., 2005; Owens, 2002). Under a male-biased sex ratio, male squinting bush browns (*Bicyclus anynana*) showed increased intrasexual competition and a smaller proportion of females rejected male mating attempts (Holveck et al., 2015). Similarly, a male bias in common lizards (*Zootoca vivipara*, formerly *Lacerta vivipara*) caused male aggressiveness toward

females, resulting in a decline of female survival and fecundity and an ensuing population decline (Le Galliard et al., 2005). For tuatara populations with the FM pattern of sex determination, behavioural overlays on a male-biased sex ratio, and likely increases in the proportion of males in populations as the temperature increases are major concerns for population viability (Mitchell et al., 2008; Nelson, Keall, Pledger, et al., 2002).

Previous behavioural observations of tuatara indicate sex and size have significant effects on social behaviours, where males outcompete females in competition for space and food, and large males have an advantage in male-male agonistic interactions and female access (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009; Moore, Daugherty, Godfrey, et al., 2009; Wörner, 2009). These studies were performed on the Takapourewa (Stephens Island) tuatara population where there is a balanced sex ratio, or on captive juvenile tuatara with the origin of Takapourewa (Moore, Daugherty, & Nelson, 2009; Wörner, 2009). Social behaviour of tuatara has not been studied under a male-biased sex ratio. Moreover, although it is widely acknowledged that sex ratio can influence territorial behaviour and resource competition (Kodric-Brown, 1988; Spence & Smith, 2005), empirical studies investigating sex ratio as a driver for space use (a measure of resource acquisition, Adams, 2001; Perry & Garland, 2002) are lacking. In addition, studies on space use of territorial vertebrates often cover a short time span (several days to months) and are mostly conducted on birds and mammals (Silva et al., 2020). Terrestrial reptiles have more sedentary movement patterns and subsequently limited dispersal abilities. As such, long-term data may provide better insights into space use of terrestrial reptiles, especially for species with extended lifespans.

There has been a male bias in the North Brother Island tuatara population since the 1990s, which makes this population an ideal case to examine the effects of a male bias on space use with regard to resource competition. Recording tuatara behaviour in natural populations is challenging, because tuatara have low detectability from being nocturnal and inhabiting underground burrows (Ussher, 1999). By contrast, behavioural observations of captive tuatara populations allow for repeated behavioural data collection on the same individual, which can help understand intra-specific interactions. Such understanding can provide implications of a male bias for population viability.

Tuatara

Tuatara are medium-sized reptiles endemic to New Zealand (Figure 1.1). They have high taxonomical importance and conservation value as the only extant species of the Order Rhynchocephalia, which split from the lineage that forms the modern squamates (lizards and snakes) around 250 million years ago in the Triassic (Cree & Butler, 1993; Gemmell et al., 2020; Jones et al., 2013). The ancestors of modern tuatara have been on the landmass of New Zealand that split away from the rest of Gondwana about 80 million years ago (Hay et al., 2003; Jones et al., 2009). Tuatara were widespread throughout New Zealand based on the subfossil records in Holocene, but they disappeared from the mainland due to habitat destruction and introduced mammalian predators (e.g., rats, cats, dogs, and mustelids) after the arrival of Māori and European settlers (Cree, 2014; Cree & Butler, 1993; Wood, 2009; Worthy & Holdaway, 2002). Tuatara are currently limited to 32 natural populations on offshore islands and 14 translocated populations on offshore islands or at sanctuaries (Cree, 2014). Most of these tuatara populations are in a small population size (few tens - low thousands) except for the Takapourewa population which supports at least 30,000 tuatara



Figure 1.1 Tuatara in New Zealand. Tuatara are sexually dimorphic reptiles, with males (upper individual) having more developed crest and larger body size and head measurements than females (lower individual).

(Cree, 2014). By 2021, the conservation status of tuatara was assessed as 'Relic' in New Zealand Classification System (Hitchmough et al., 2021), and as 'Least Concern' in the IUCN Red List of Threatened Species (IUCN, 2021).

Tuatara are a long-lived species where longevity is over 100 years, and the mean generation interval is around 32 – 44 years in the wild (Cree, 2014; Mitchell et al., 2010; Reinke et al., 2022). Tuatara reach sexual maturation at about 13-15 years of age and females breed typically every 4-5 years (Cree, 2014). Although there is a lack of intermittent organ in males, tuatara are sexually dimorphic with males having more developed crest and larger body size and head measurements than females (Cree, 2014; Gillingham et al., 1995; Herrel et al., 2010) (Figure 1.1). Tuatara mate in austral summer and females are gravid for a long period and nest in austral spring of the following year (Cree, 2014; Cree et al., 1991). Tuatara eggs incubate for 11-16 months, but less than half of them can be successfully hatched in the wild (Cree et al., 1991; Thompson et al., 1996). The clutch size of tuatara is positively correlated to the female size, but the mean weight of each egg is similar between populations (Cree et al., 1991). For example, in the North Brother Island population where females are smaller, the mean clutch size is 6.5 ± 0.6 eggs, while the mean clutch size is 9.9 ± 1.2 eggs in the Takapourewa population where females are larger (Cree et al., 1991).

Tuatara are adapted to cool climates where they are more active in emerging and thermoregulating at much lower temperatures (5 – 6 °C) than other reptiles living in the same region such as geckos and skinks (Saint-Girons, 1980; Vermunt et al., 2014). Most research on tuatara and their sex determination has been carried out on Takapourewa (Cree, 2014). Besides the rare TSD pattern of tuatara where males hatch at higher temperatures (Cree et al., 1995; Mitchell et al., 2006), the pivotal temperature (T_{piv}) producing a balanced sex ratio of hatchlings is around 22 °C and the transitional range of temperature (TRT) producing hatchlings of both sexes is less than 1 °C (Mitchell et al., 2006; Nelson et al., 2004b). Takapourewa is a relatively large island (150 ha) supporting the largest tuatara population ($N > 30,000$) with heterogeneous nesting habitat and substrate (Cree & Butler, 1993). The adult sex ratio on Takapourewa based on a mark-recapture survey in 2003 was approximately even (53% males; 47% females) (Moore, Daugherty, & Nelson, 2009). The hatchling sex ratio over the nesting season of 2002/2003 based on the thermal conditions in the nest was also predicted to be even, even though 2002 was the second warmest year on record at the time

(Nelson et al., 2004a). In the near future, behavioural variations in nesting phenology may offset a male bias in offspring, because if female tuatara nest earlier after warm winters, the resulting thermosensitive period (when the sex of species with TSD is determined) will occur earlier than the hottest months, potentially producing a female bias from those nests (Nelson et al., 2018). However, climate warming may threaten the population viability of Takapourewa tuatara if temperatures increase by 4 °C when the earlier phenology will be unable to offset the male bias of hatchlings (Carter, 2015; Nelson et al., 2018).

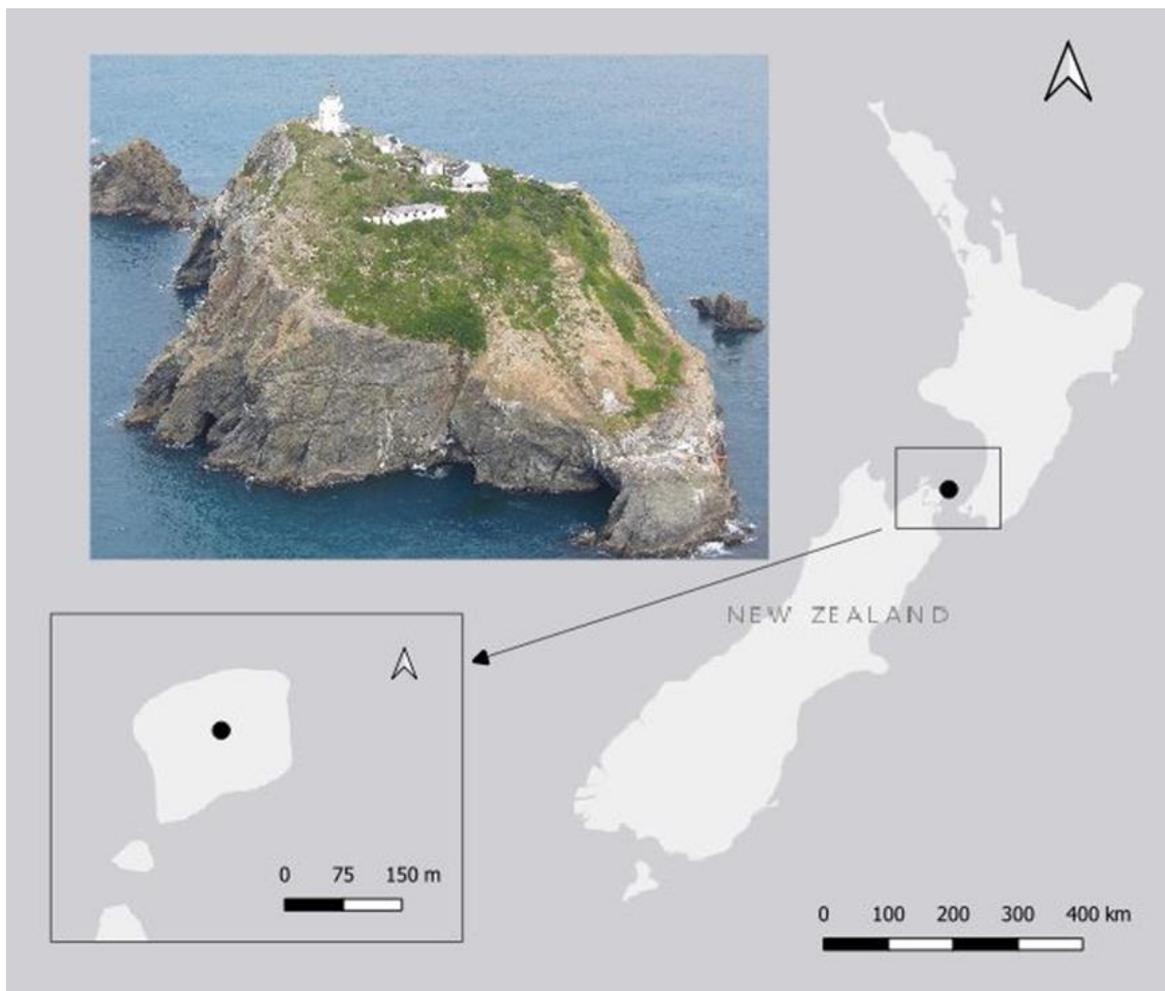


Figure 1.2 North Brother Island in Cook Strait, New Zealand. North Brother Island is a 4-ha wildlife sanctuary, supporting a natural tuatara population. Rising to 66m above sea level, this island is mainly weathered rock. Tuatara largely inhabit and nest on the northern face which is covered by low vegetation and shallow soil.

Not all tuatara populations are likely to be in the same situation as on Takapourewa. North Brother Island is a 4-ha wildlife sanctuary in Cook Strait, New Zealand (41° 07' S, 174°

27' E) supporting a small tuatara population ($N = 473$, Mitchell et al., 2010). The island rises to 66m above sea level, with steep cliffs on three sides and a relatively gentle slope on the northern face (Figure 1.2). The island is mainly weathered rock, with only the northern face is covered by shallow soil and low vegetation, such as taupata (*Coprosma repens*) and horokaka (*Disphyma australe*) (Grayson et al., 2014), providing limited resources and nesting habitat for tuatara (Hoare et al., 2006). This tuatara population experienced a rapid decline in the late 19th century due to habitat modification from the construction of the light house and harvest (Buller, 1877; Newman, 1878), followed by a rapid population growth. By 2001, there were an estimated 473 tuatara in the population (Mitchell et al., 2010), a density similar to other tuatara populations, but likely over carrying capacity for North Brother Island (Cree & Butler, 1993; Gibbs, 1999; Keall et al., 2001; Markwell, 1999). Driven by the resource depletion on North Brother Island, tuatara of this population are smaller in body and clutch size than tuatara in most other populations (Cree et al., 1991). Tuatara on North Brother have extremely low genetic diversity and a small effective population size (Aitken et al., 2001; Hay et al., 2003; MacAvoy et al., 2007). Since the late 1990s, there has been an increasing male bias (Grayson et al., 2014; Mitchell et al., 2010; Nelson, Keall, Pledger, et al., 2002), and a consistent decline in body condition and survival (Grayson et al., 2014; Hoare et al., 2006). The hatchling sex ratio was estimated as 56% males in 2011 based on the thermal conditions in the nest and predicted to become extinct in 1183 years. However, under a maximum climate warming scenario (an increase of 3.3–4°C by 2080), there would be 100% male hatchlings produced at this site, indicating the population extinction may occur sooner (Grayson et al., 2014; Mitchell et al., 2010). Furthermore, as a small population, this tuatara population is at high risk of extinction because of the vulnerability to environmental, demographic, and genetic stochasticity, such as, extreme weather events, random variations in sex ratio and survival, and inbreeding (Dale, 2001; Lande, 1993; Shaffer, 1981).

There is an urgent need to investigate the current sex ratio and other population parameters (survival, body condition and population size) of the North Brother Island tuatara population to understand the implications of sex ratios for population viability under climate warming. A male bias could have implications for behaviour of individuals, affecting their access to resources, as males are proposed to be the dominant sex (Moore, Daugherty, & Nelson, 2009; Wörner, 2009). Empirical evidence of how dominance from a male biased sex

ratio affects other population parameters will inform population viability modelling. Furthermore, it is important to estimate tuatara sex ratio patterns over the long term to gain insights into mechanisms regulating sex ratios. Based on the circumstances of North Brother Island tuatara population, there are two possibilities of sex ratio patterns over the long term (Figure 1.3). One possibility is the male bias will be more evident due to an increasing percent of male hatchlings at nests in a warming climate (Janzen, 1994; Mitchell & Janzen, 2010). Another possibility is there will be a generally balanced sex ratio despite irregular fluctuations. When the population size is around the carrying capacity, intense resource competition will exacerbate the disadvantage of resource acquisition for females, leading to lower female condition and survival and thereby a sex ratio towards more male-biased. The intense resource competition under carrying capacity drives a decline in population size, which in turn lessens the intensity of resource competition and may improve female condition, survival and fecundity. Over generations, the sex ratio may tend to fluctuate around evolutionarily stable 1:1 sex ratio (Fisher, 1930). To date, the monitoring of tuatara population size and sex ratio has not yet covered one generation of tuatara evolution. Through an extended term of population surveys of North Brother Island tuatara population, this thesis contributes empirical data to investigate mechanisms of population dynamics and risks of a sex ratio bias in a species with temperature-dependent sex determination.

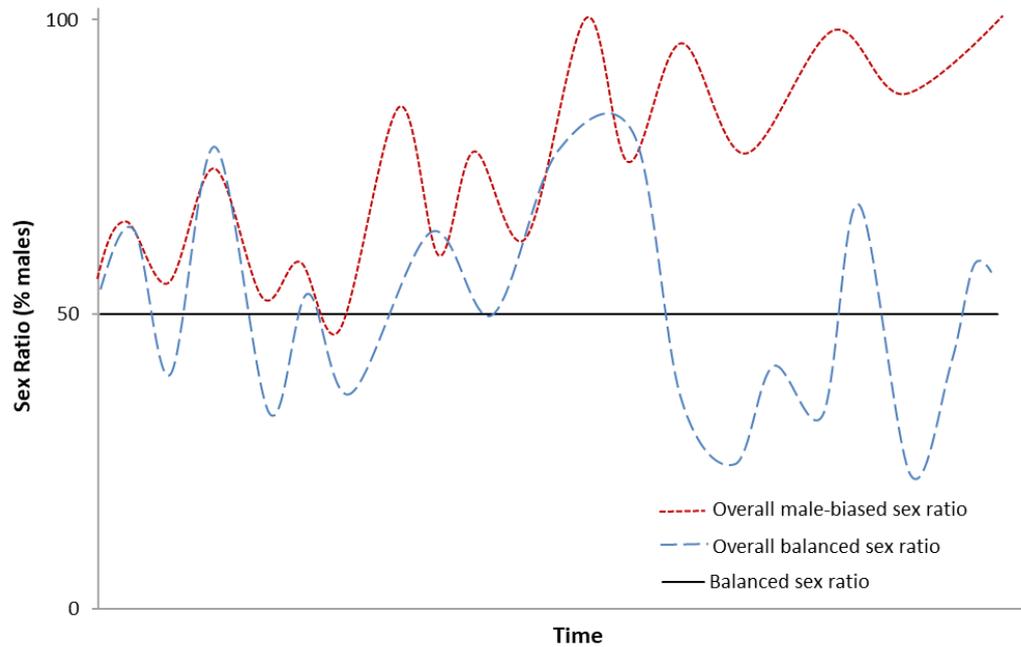


Figure 1.3 Two hypothesised possibilities of the temporal trend of sex ratio in North Brother Island tuatara population in a warming climate. Red dashed line shows the sex ratio bias will become more evident. Blue dashed line shows there will be an overall balanced sex ratio.

Thesis aim and structure

Driven by the concern for tuatara population viability in a warming climate, and considering tuatara's survival through historic climates and their long lifespans, my thesis uses the North Brother Island tuatara population as a case study to investigate the effects of a long-term male bias on population viability. I examine the temporal trend of sex ratio, which was previously male-biased, and other major population parameters based on the 30-year tuatara survey data on North Brother Island. I investigate the activity area patterns of tuatara on North Brother Island to evaluate the implications of a male bias on resource competition. I conduct behavioural observations on captive tuatara to investigate the nature of interactions and dominance to understand consequences of a male bias. With the updated population parameters, I predict the probability of extinction for tuatara on North Brother Island and discuss the implications of a male bias for population viability. This

research contributes vital data to inform conservation management decisions for tuatara on North Brother and implications for other populations of tuatara and other species with TSD.

Main questions

- What is the temporal trend of the adult sex ratio and other major population parameters (survival, body condition and population size) in the North Brother Island tuatara population? Is there a different temporal trend for sex ratio and other major population parameters in new cohorts (recruits) entering the adult population?
- What are the activity area patterns of tuatara on North Brother Island and how do individuals interact and experience social dominance in captive tuatara populations? What are the implications for access to females in a male-biased environment?
- Under the current parameters, is the North Brother Island tuatara population viable for the long-term?

Thesis outline

This thesis is comprised of three stand-alone chapters that are formatted for peer-reviewed publications. As such, there is some repetition of information, particularly in the introductory sections, to facilitate publication and keep coherence among chapters.

In Chapter Two, I collect and update the population survey data for the North Brother Island tuatara population to now include 30 years of captures, examining whether the previously observed male bias is still evident or more balanced. I also examine the temporal trend of survival, population size, and body condition to evaluate demographic consequences of a male bias. In Chapter Three, I investigate the activity area patterns of tuatara on North Brother Island to see the implications of a long-term male bias. Based on the records of capture locations over 30 years, I estimate the activity areas by sex and by decade and examine the drivers for spatial interactions including body size and sex. In Chapter Four, I perform observations of tuatara behaviour in captive facilities to investigate the role of dominance on individual interactions with regard to competition for resources such as space, food and mate access. In Chapter Five, I summarise the main research findings of previous three data chapters. I use the updated population parameters from Chapter Two to predict the population viability of the North Brother Island tuatara population. The implications of a male bias are discussed based on the male dominance over females found in Chapter Three

and Chapter Four. Finally, I outline the limitations of this study paired with recommendations for future research.

Contributions to research

All study design, data collection and analyses, mapping, and writing were conducted by me under the supervision of Professor Nicola Nelson in the School of Biological Sciences at Victoria University of Wellington, NZ and Associate Professor Kristine Grayson in the Biology Department at the University of Richmond, US. I acknowledge the following contributions to the completion of this thesis:

- **Data collection:** Tuatara population survey data on North Brother Island used in Chapter Two and Chapter Three were provided by Nicola Nelson (surveys prior to 2018) and were collected by me with the assistance of Nicola Nelson, Sue Keall, Kristine Grayson, Sarah Lamar, and Peter Martin (surveys in 2018 and 2019). The data of activity area patterns used in Chapter Three were collected in collaboration with Department of Conservation on Long Island and with the assistance of lots of volunteers on Matiu Somes Island. Tuatara individual measurements in Chapter Four were provided by the Otorohanga Kiwi House, Auckland Zoo, Wellington Zoo and Sue Keall in the School of Biological Sciences at Victoria University of Wellington. Otorohanga Kiwi House and Sue Keall provided the plans of Otorohanga Kiwi House and Victoria University of Wellington tuatara enclosures. I also thank Te Ātiawa and Taranaki Whānui for their support of this project.
- **Statistical advice:** Dr Lisa Woods in the School of Mathematics and Statistics at Victoria University of Wellington provided advice on statistical analyses of sex ratio and body condition estimation in Chapter Two.

Permits and ethics

This research was granted by the Victoria University of Wellington Animal Ethics Committee (27041, Conservation of New Zealand reptiles) and conducted under permits of the New Zealand Department of Conservation (Authorisation Number: 50568-FAU). Iwi consultation was obtained as part of permission to work on the island.

Chapter 2

The effects of a long-term male bias on an isolated tuatara (*Sphenodon punctatus*) population

Introduction

Sex ratio is a crucial parameter in population dynamics and evolutionary ecology of a species (Ancona et al., 2017; Emlen & Oring, 1977; Le Galliard et al., 2005; Sykes et al., 1974). It is the ratio of the number of males to females in a population, indicating the relative survival rate of the two sexes (Skalski et al., 2010). Although sex ratio is usually considered as a relatively stable population parameter, variations in sex ratio commonly exist in natural populations. For instance, significant sex ratio differences were found among natural guppy (*Poecilia reticulata*) populations at the same sampling time, and within the same population among differing seasons (Pettersson et al., 2004). Skews in population sex ratio can influence sexual selection and individual behaviour (Glutton-Brock & Parker, 1992; Gwynne, 1990; Jirotkul, 1999), and ultimately have impacts on population viability (Heinsohn et al., 2019; Le Galliard et al., 2005). For example, a study on wild swift parrot (*Lathamus discolor*) populations showed a strong male bias can change the mating system from monogamy to polyandry and drive a decline in individual fitness and population viability (Heinsohn et al., 2019).

Sex ratio can be influenced by various biological and environmental factors that can influence the proportion of both sexes in a population at certain life stages. Sex ratio at hatching is dependent on the sex determination mechanism that controls the timing and development of sexual characteristics of biological organisms. Species with genetic sex

determination (GSD) usually have an approximately balanced sex ratio of hatchlings or offspring because of the Mendelian segregation of sex chromosomes in heterogametic systems, and therefore sex is determined at the fertilization stage (Muller, 1932). In species with environmental sex determination (ESD), the sex of offspring is determined by various environmental factors such as temperature, nutrition, pH, humidity, photoperiod, social factors and oxygen levels. Temperature-dependent sex determination (TSD) is widely present in reptiles in which thermal conditions during a critical period of embryonic development influence sex determination and hatchling sex ratios (Bull, 1980). For example, incubation temperatures during the second third of embryonic development determine the sex of sea turtles, where males hatch at lower temperatures and females hatch at higher temperatures (Santidrián Tomillo & Spotila, 2020).

The sex determining systems are not always neatly classified into ESD or GSD. There are exceptions where the sex ratio of species with GSD at birth deviates from 1:1 due to environmental factors such as parental condition. For example, maternal body condition can skew offspring sex ratios in many mammal species, where females in better body condition are more likely to produce more sons than daughters (Cassinello, 1996; Kojola & Eloranta, 1989; Wauters et al., 1995). Furthermore, sex determination is just the beginning of sex-biased effects on later population sex ratios. For example, sex-biased embryo survival can influence the hatchling sex ratio of egg-laying species. In an artificial incubation experiment on Australian brush-turkey (*Alectura lathami*), female embryo survival was greater at higher incubation temperatures while male embryo survival was greater at lower incubation temperatures (Eiby et al., 2008). A considerably lower survival of juvenile female Magellanic penguins (*Spheniscus magellanicus*) than males, which may result from greater vulnerability to food shortage in females, was a major driver for an increasing male bias and population decline (Gownaris & Boersma, 2019). In adult populations, sex-based differences in survival can skew numbers of reproductive adults. For example, male-biased sex ratios in freshwater turtle populations have been associated with road mortality where female turtles are at higher risk of mortality during nesting migrations (Steen & Gibbs, 2004). In adult mallards (*Anas platyrhynchos*), female survival was lower than that of males during breeding season probably due to their increased vulnerability to predation during nesting, contributing to a male-biased sex ratio (Brasher et al., 2006). During the mating season, male aggression

towards females in Hawaiian monk seals (*Monachus schauinslandi*) caused higher female mortality and ensuing strong male bias (Johanos et al., 2010).

Reptiles exhibit multiple forms of sex determination: Male-Female (MF; males hatch at lower temperatures and females hatch at higher temperatures), FMF (males hatch at medium temperatures and females hatch at higher and lower temperatures), FM, or GSD. Because offspring sex of reptiles with TSD is determined by environmental temperatures, the sex ratio can vary dramatically from clutch to clutch in natural nests. As such, reptiles with TSD are prone to considerable sex ratio variations (Bull, 1983; Mitchell & Janzen, 2010). For example, a study on green sea turtles (*Chelonia mydas*) showed differing thermal conditions among beaches can cause moderate female-biased sex ratios in some populations and extreme female-biased hatchlings or even 100% female hatchlings in other populations (Jensen et al., 2018). Increasing evidence suggests that GSD and TSD are not mutually exclusive, where sex determination can be affected by the interaction between genes and environmental temperatures (Sarre et al., 2004). For example, although Eastern three-lined skinks (*Bassiana duperreyi*) have strongly differentiated sex chromosomes, more males hatch at lower temperatures, indicating the co-occurrence of the two sex determination systems (Shine et al., 2002). This is probably because there is a trade-off between the costs and benefits of different sex determination systems in response to thermal conditions (Sarre et al., 2004; Shine et al., 2002).

Under climate warming scenarios, extremely skewed sex ratios for some reptile populations are predicted, which can lead to one-sex populations and population extinction (Mitchell & Janzen, 2010). For example, a recent study showed extremely female-biased sex ratios in all age classes of a green sea turtle (*Chelonia mydas*) population in a warming climate (Jensen et al., 2018), which may threaten population viability (Blechs Schmidt et al., 2020). To some extent, female-biased sex ratios can increase the number of breeding females and population size despite the increased inbreeding depression and reduced genetic diversity (Hays et al., 2017; Wedekind, 2002). By contrast, tuatara (*Sphenodon punctatus*), the only known species having the rare FM TSD pattern (Mitchell et al., 2006), are most at risk of extreme male biases (Cree et al., 1995; Mitchell et al., 2010). An overabundance of males, despite also having consequences for increased inbreeding depression and reduced genetic

diversity, can also lead to production of fewer offspring as a function of fewer breeding females, and ensuing population decline in a warming climate (Grayson et al., 2014).

Sex ratio bias has been recognized as a major factor contributing to population extinction in small populations (Dale, 2001; Lacy, 2000; Steifetten & Dale, 2006). Small isolated populations are more likely to be vulnerable due to stochasticity in demographic parameters, for example, random variations in sex ratio and survival, as well as environmental and genetic effects, such as, extreme weather events and inbreeding (Dale, 2001; Lande, 1993; Shaffer, 1981). However, studies addressing how a sex ratio bias interacts with other demographic parameters are still limited, particularly in the natural populations of long-lived species, which have delayed responses to demographic variations. In this study, I explored the effects of a long-term male bias on other population parameters in a well-studied tuatara population based on a 30-year data set.

Since the late 1990s, a male bias has been observed in a small tuatara population on North Brother Island (Grayson et al., 2014; Mitchell et al., 2010; Nelson, Keall, Pledger, et al., 2002). Tuatara are characterized by their longevity (~100 years) and late maturation (~13-20 years) (Cree, 2014; Reinke et al., 2022), likely leading to delayed demographic responses to sex ratio variations that arise at hatching. However, in this population, a decline in body condition and survival are already evident, potentially arising from a population at carrying capacity (Grayson et al., 2014; Hoare et al., 2006; Mitchell et al., 2010). Tuatara have survived climate shifts over at least 100,000 years (Cree, 2014; Miller et al., 2012), although the effects of historical and current climates on their sex ratio fluctuations and population demography are unknown. Recent research from another tuatara population proposes how behavioural variations in nesting phenology could potentially balance the sex ratio in the medium term within an increase of about 2°C (Nelson et al., 2018). Therefore, there is an increasing need to investigate the sex ratio of this small male-biased tuatara population over a longer term, examining whether the degree of sex ratio bias can fluctuate over time, despite the climate-mediated effects on sex determination, or whether the male bias continues to become more evident under climate warming. In addition, sex ratio patterns of this population may be an early indicator of issues related to climate warming that are yet to be detected in other

tuatara populations. Consequences for other demographic parameters and an understanding of the interactions between them are crucial to understand population trajectories.

I investigated whether the previously observed male sex ratio bias was still evident with 30 years of data as predicted using climate warming scenarios, or whether a new cohort of recruits into the population demonstrated a population response towards a more even sex ratio bias based on theoretical principles. I also calculated survival, population size and body condition estimates to evaluate demographic consequences of a male bias and small population size for population viability.

Methods

Study species and site

Tuatara are medium-sized reptiles endemic to New Zealand. As the only surviving species of the Order *Rhynchocephalia*, they have high taxonomical importance and conservation and cultural value (Cree & Butler, 1993; Ramstad et al., 2007). Tuatara are long-lived species with a lifespan of approximately 100 years (Cree, 2014; Reinke et al., 2022). They reach sexual maturation at about 13-15 years of age, and females breed typically every 4-5 years (Cree, 2014). They are adapted to cool climates and have FM pattern of TSD, where males hatch at higher temperatures (Cree et al., 1995; Mitchell et al., 2006). Prior to the arrival of humans, tuatara were widespread throughout New Zealand, but currently they are limited to 32 natural populations on offshore islands and 14 translocated populations on offshore islands or at sanctuaries, due to habitat destruction and predation by introduced mammals (Cree, 2014).

The small male-biased population of tuatara is on North Brother Island in Cook Strait, New Zealand (41° 07' S, 174° 27' E; Figure 2.1). This 4-ha wildlife sanctuary supported a natural tuatara population of at least 473 individuals in 2001 (Mitchell et al., 2010). The island rises to 66m above sea level, with steep cliffs on three sides and a relatively gentle slope on the northern face (Figure 2.1). The island is mainly weathered rock, and only the northern face is covered by low vegetation and shallow soil. Tuatara largely inhabit and nest in this 2.2-ha

area, including a 0.2-ha area inaccessible for searching, and tuatara are rarely captured in the remaining 1.8 ha of the island (Thompson et al., 1992).

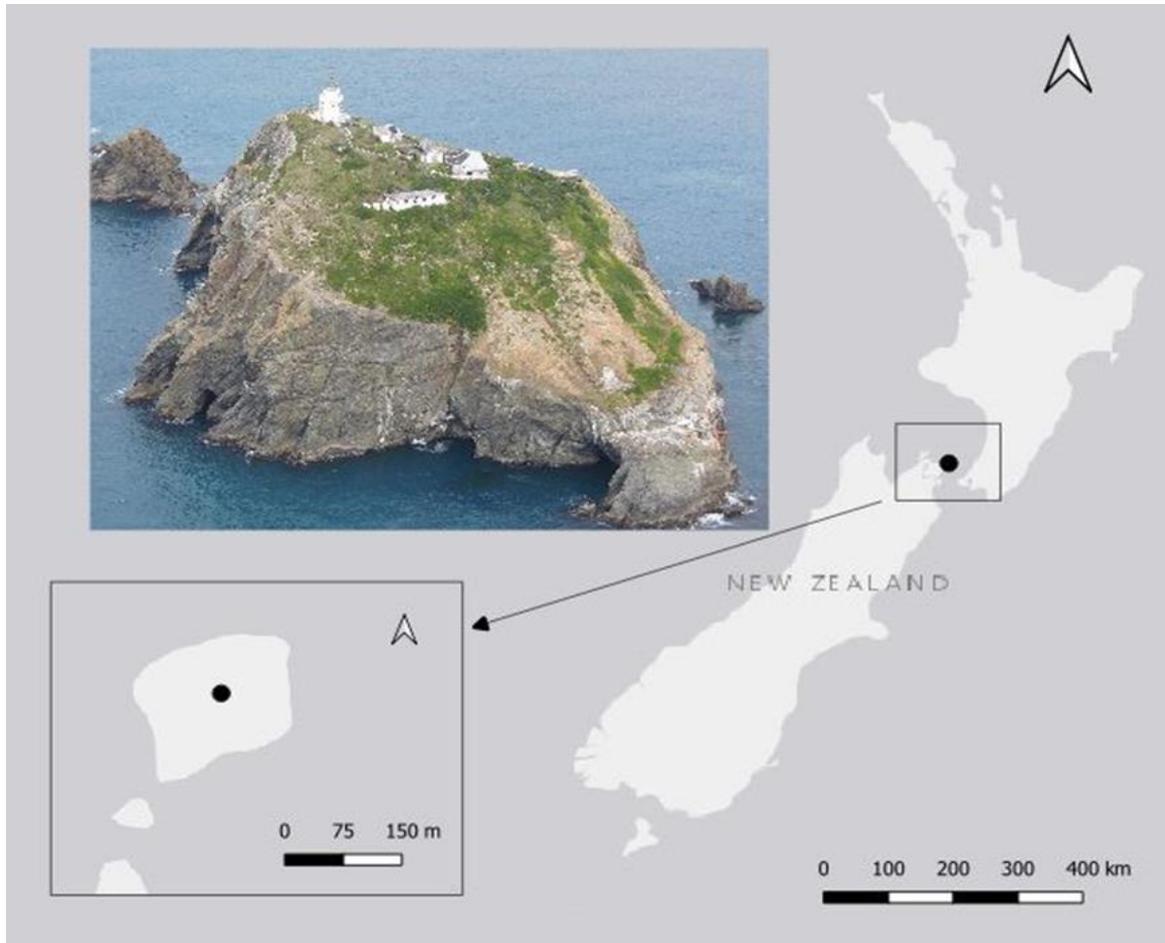


Figure 2.2. North Brother Island in Cook Strait, New Zealand. North Brother Island is a 4-ha wildlife sanctuary, supporting a natural tuatara population. Rising to 66m above sea level, this island is mainly weathered rock. Tuatara largely inhabit and nest on the northern face which is covered by low vegetation and shallow soil.

Data collection

Data for this study were collected on 24 trips between January 1988 and November 2019, including complete surveys in 2000 and 2001 over 52 nights and 32 nights respectively, and short surveys in the other 22 trips ranging from one to seven nights (Table 2.1). From the late 1990s, we performed each short survey for five consecutive nights with five people if possible, to provide a consistent methodology over surveys for improving the accuracy of estimates of population parameters. Tuatara were captured by hand at night over the 2-ha accessible area.

Tuatara were given permanent marks when first captured by toe-clipping prior until 2000 and by passive integrated transponder from 2001 (PIT tags, Allflex, ISO FDX-B, Dallas, Texas, USA). During each survey, we identified individuals on the first capture, recorded their sex and location on a grid system, and measured their snout-vent length (SVL; mm), vent-tail length (VT; mm) and weight (WT; g), then released them back at their capture site. A unique number was written on the side of each animal with non-toxic markers to identify recaptures during each survey. The identity and location of each recapture were also recorded.

Data analyses

Only adult data were used for estimating population parameters in this study due to very low capture numbers of juvenile tuatara (Dawbin, 1982) (Table 2.1). Demographic estimates generated from Program Mark (version 9.x) were presented with standard errors (SE) derived from the Delta method (Cooch & White, 2019), or 95% profile likelihood confidence intervals (PLI), which are more appropriate for mark-recapture study estimates than the traditional standard error or symmetric confidence intervals (Cormack, 1992).

Survival

Annual survival rates of tuatara over time were estimated with open model analyses in Program MARK. Five surveys were not included in open model analyses due to unusually low capture numbers in 1995, 2000 (August) and 2019 surveys, the short interval between surveys in 1990 (October survey removed), and a male manipulation experiment during the 2012 survey, which could influence female capture probability (Table 2.1). Nineteen surveys between January 1988 and November 2019 were selected for an open model analysis to estimate the survival rate of the population over 30 years (Table 2.1). A second open model analysis was performed using six surveys between March 2005 and November 2019 to estimate the survival rate of the emerging new cohort within the population (Table 2.1). The new cohort is defined as new recruits into the population after the two complete surveys in 2000 and 2001, where each individual was caught. These recruits are subadults which have not been marked in earlier surveys because there were not detected as juveniles. Since each open model analysis spans multiple surveys, I selected individuals captured at least once across these surveys, and simplified the capture history of each individual to record captured or not for each survey.

Table 2.1. Tuatara capture data on North Brother Island and their use in demographic analyses.

Survey	Date	Number of survey nights	Number of researchers	Adult numbers	Male adult numbers	Female adult numbers	Juvenile numbers	Open model analysis of the population		Open model analysis of the new cohort		Closed model analyses of the population		Closed model analyses of the new cohort		Body condition analysis of the population		Body condition analysis of the new cohort	
								Surveys selected	Number of males used in the model	Number of females used in the model	Surveys Selected	Number of males used in the model	Number of females used in the model	Surveys Selected	Number of males used in the model	Number of females used in the model	Surveys selected	Number of males used in the model	Number of females used in the model
1	Jan-88	3	1	110	74	36	2	✓	67	32						✓	71	29	
2	Dec-88	3	1	67	48	19	0	✓	18	12						✓	20	13	
3	Nov-89	3	2	79	29	50	1	✓	21	15						✓	24	22	
4	Oct-90	7	1	54	32	22	0												
5	Nov-90	3	3	120	71	49	0	✓	60	37						✓	69	42	
6	Nov-91	3	3	114	67	47	0	✓	51	39						✓	58	40	
7	Nov-93	5	3	184	132	52	4	✓	122	45						✓	118	48	
8	Nov-94	3	3	209	135	74	2	✓	126	62						✓	131	68	
9	Nov-95	1	4	36	22	14	0									✓	19	14	
10	Mar-96	5	5	250	166	84	8	✓	151	68			✓	156 (3)	69 (4)	✓	149	66	
11	Feb-97	5	6	238	158	80	5	✓	154	72						✓	148	77	
12	Dec-97	5	5	188	120	68	15	✓	127	60			✓	122 (0)	61 (2)	✓	116	57	
13	Oct-98	2	5	71	43	28	0	✓	33	18						✓	42	27	
14	Aug-00	1	3	37	25	12	0									✓	23	11	
15	Nov-Dec 2000	52	3	431	260	171	11	✓	229	132						✓	205	114	
16	Nov-Dec 2001	32	2	288	163	125	1	✓	166	100						✓	151	90	
17	Mar-05	5	5	164 (23)	118 (18)	46 (5)	0	✓	121	42			✓	117 (4)	41 (1)	✓	112	39	
18	Nov-08	4	6	145 (37)	108 (27)	37 (9)	4	✓	109	40			✓	17 (1)	5 (0)	✓	102	34	
19	Nov-10	5	5	135 (36)	101 (26)	34 (10)	0	✓	100	34			✓	98 (2)	34 (0)	✓	93	29	
20	Nov-11	5	5	174 (43)	116 (29)	58 (14)	0	✓	117	57			✓	111 (6)	55 (2)	✓	105	53	
21	Mar-12	4	5	144 (32)	97 (24)	47 (8)	1						✓	28 (1)	14 (0)	✓	30	4	
22	Nov-16	5	5	204 (64)	135 (45)	69 (19)	1	✓	132	58			✓	44 (1)	19 (0)	✓	120	53	
23	Nov-18	5	5	206 (80)	130 (52)	76 (28)	2	✓	130	70			✓	126 (4)	67 (3)	✓	113	59	
24	Nov-19	5	5	115 (38)	72 (23)	43 (15)	0						✓	52 (0)	28 (0)	✓	66	31	

Data of this study were collected from 24 trips between January 1988 and November 2019, including two complete surveys in 2000 and 2001 and 22 short surveys. Subadults which could be sexed were included in adults. The numbers of adults, male adults, female adults and juveniles are the actual numbers of individuals caught in the field, and the numbers in brackets stand for the numbers of the new cohort. The numbers of individuals selected for open model analyses and closed model analyses on the same trip are different because of their differing model structures and the ensuing differing standards for data selection (see methods). In the columns of closed model analyses, the numbers in brackets stand for the individuals with high capture on each trip, which were not included in the closed model analyses but added back in later. In 1996 eighteen of 250 adults (seven males and eleven females) were removed from the island as founders for a new population on Titi Island; in 1998 twenty of 71 adults (ten males and ten females) were removed from the island as founders for a new population on Matiu Somes Island; in 2006 two males were removed from the island to Seahorse World in Picton.

Open model analyses in Program Mark estimate survival probabilities and capture probabilities simultaneously when fitting models, thus, I built up a model set including both parameters for each open model analysis. I tested whether survival probabilities could vary between sexes (sex), and either vary among surveys (time) or show a temporal linear trend over surveys (T). Therefore, I modelled adult survival (1) as combinations of time and sex, including time only (time), sex only (sex), additive effects (time+sex), and additive and interactive effects (time*sex), (2) as combinations of a temporal linear trend (T) and sex, including a linear trend only (T), additive effects (T+sex), and additive and interactive effects (T*sex), or (3) as a constant (.). Since capture probabilities could vary between sexes (sex) and among surveys (time), the capture probabilities were modelled either as combinations of time and sex, including time only (time), sex only (sex), additive effects (time+sex), and additive and interactive effects (time*sex), or as a constant (.). Therefore, for each open model analysis, there were 40 candidate models in the model set estimating survival and capture probability simultaneously (Table S2.1). As the final survival and capture probability are confounded in a fully time-dependent model (i.e., survival and capture probability simultaneously vary among surveys; Lebreton et al., 1992), I imposed the constraint on these models that the capture probabilities of last two surveys were equal. For each open model analysis, I tested goodness-of-fit of the most general model (i.e., the model with the most parameters in the model set) using the median \hat{c} approach to estimate overdispersion of the data. The most general model for the population fitted the data well ($\hat{c} = 0.98$) and required no corrections for overdispersion, whereas there was overdispersion of the data for the new cohort ($\hat{c} = 2.31$) based on the most general model, so the overdispersion was corrected. Candidate models of each open model analysis were ranked based on the corrected Akaike's Information Criterion (AICc) or the *quasi*-corrected Akaike's Information Criterion (QAICc; when overdispersion was corrected) values from the smallest to the largest, and model averaging was conducted over all models with weights to obtain more accurate estimates of survival and capture probability (Burnham et al., 2011).

Since candidate models selected for model averaging included all variables influencing annual survival, I assessed relative importance of each variable for explaining survival rate and capture probability (Burnham & Anderson, 2004). I summed weights over all models used for model averaging that included the same variable, and variables with high sum weights

were considered as important towards the estimation of survival rate and capture probability (Table S2.2).

Population size

Population size of each survey was estimated using a closed model analysis with the Huggins likelihood approach (Huggins, 1989) in Program MARK. For a small population, relatively higher capture probabilities ($p > 0.2$) and more occasions ($K > 5$) can effectively improve the precision of population size estimate in a closed model analysis (Cooch & White, 2019). Therefore, only surveys conducted by five people on five consecutive nights with usual (i.e., not unusually low) capture numbers were selected for closed model analyses (Table 2.1). The survey of 2019 was excluded from the closed model analysis because windy weather resulted in low captures. Seven surveys from March 1996 to November 2018 were selected for closed model analyses to estimate tuatara population sizes through this period, and five surveys from March 2005 to November 2018 were selected to estimate the population size of the new cohort by including all individuals captured during those surveys that were not known from earlier surveys (Table 2.1). Since each closed model analysis spans all survey nights within one survey, I selected individuals captured at least once within the survey, and simplified capture history of each individual to record capture or not on each survey night.

A closed model analysis generates the population size based on estimating individual capture probabilities. The capture probability could vary over differing survey nights (t) and vary between first capture and recapture (b). In addition, there were possibly unobservable sources of the heterogeneity in capture probabilities which can be modelled as either finite mixtures (h) or a continuous mixture (RE). Therefore, I constructed the candidate closed model set to test the variability in capture probabilities and estimate the population size with the null model (no variation in capture probability), and with the inclusion of one of these sources of heterogeneity, or combinations of them (Table S2.3). Two-mixture heterogeneity was selected where finite mixtures were considered as the source of heterogeneity, because two mixtures are generally supported by most data sets (Cooch & White, 2019). Some additive and interactive effects were not included in the model set when combining two or more of the sources of heterogeneity. For example, since the parameter for mixtures is a constant in a finite-mixture model, there is no interactive effect regarding the mixtures (h).

Continuous mixture models consider heterogeneity as a continuous infinite distribution and the variance of normal distribution of individual capture probability is a constant, thus, there were neither additive nor interactive effects regarding the continuous mixture (RE). In addition, interactions between behavioural responses to capture (b) and differing survey nights (t) were excluded because some parameters are inestimable when there is this behavioural heterogeneity and both first capture and recapture probabilities are fully time-dependent. Besides estimating the population size, I also estimated the population size of males and females with separate closed model analyses using the capture data of each sex, because there could be variations in capture probability between sexes which was supported by the open model analyses (see results of open model analyses). I constructed a closed model set of 12 candidate models on each survey estimating the population size and the sex-specific population size for the population and the new cohort (Table S2.3).

Although a unique goodness-of-fit test for a closed model is not available due to individual heterogeneity (Cooch & White, 2019), Fletcher \hat{c} was chosen to estimate the overdispersion of data in this study based on its good performance in detecting individual heterogeneity and estimating the population size (White & Cooch, 2017). I tested Fletcher \hat{c} on the most general model (Table S2.3) of each model set and corrected the overdispersion when Fletcher \hat{c} value was over 1. I ranked candidate models within each model set based on the AICc or QAICc values from the smallest to the largest. The rankings of candidate models varied largely among surveys, and some models in some surveys output unreliable estimates, which prevented me from selecting unanimous best models over surveys and performing model averaging. Therefore, the overall best model for all surveys was selected based on its relatively high and stable rankings as well as reliable estimates.

Since a few individuals (~8) were always captured (captures \geq 4) within the five-night survey, which may influence population estimates of heterogeneous models, such animals were removed from closed model analyses (Table 2.1). Therefore, the population size estimate was the sum of the estimate from the closed model analysis and the number of individuals of high captures, and the SE was that from the closed model analysis (Cormack, 1992). Also, some adult tuatara were removed from North Brother Island as founders for new populations in 1996 (seven males and eleven females), 1998 (ten males and ten females) and

2006 (two males). These individuals were not included in closed model analyses or population size estimation. Therefore, I added them back in manually where relevant for population estimates. We only captured animals in the search area of 2.0 ha, leaving an unsearched area of 0.2 ha. I estimated the population size of the whole 2.2 ha area based on the assumption that this unsearched area has the same tuatara density as the search area.

In addition, as a driver for the population size, female gravidity rate was estimated over differing periods. Mitchell et al. (2010) estimated the gravidity rate from 1989 to 2001 based on two research efforts: Cree et al. (1991) and Mitchell et al. (2010). In this study, I estimated the most recent gravidity rate using three surveys in 2011, 2016 and 2019 because of the detailed records on gravidity as established by abdominal palpation. Only sexually mature females were included in gravidity rate estimation.

Sex ratio

As long-lived individuals, wild tuatara reach a mean generation time around 40 years (32-44) (Mitchell et al., 2010). Tuatara population on North Brother Island is comprised of overlapping generations and a different subset of individuals were caught on each survey. Therefore, I used various methods to estimate and present the sex ratio of this tuatara population.

Firstly, I estimated the collated sex ratio of differing subsets of time, where I counted the total number of adults captured over a certain period of time, during which each individual was only counted once: (1) 24 surveys (January 1988- November 2019); (2) before complete surveys (January 1988- August 2000), (3) during complete surveys (November 2000 to December 2001), and (4) after complete surveys (March 2005- November 2019). Similarly, the collated sex ratio was estimated for the new cohort (March 2005- November 2019), that is, new unmarked animals captured during these surveys, in comparison with that of the total population over the same period. Secondly, I estimated the sex ratio of each survey for both the total population and the new cohort. I calculated the capture sex ratio based on the actual captures in the field (that is, minimum number alive).

General linear models were performed to explore the variation of capture sex ratios over time (the number of months since the first survey in the model) with differing subsets: the population over 24 surveys, and both the population and the new cohort between March 2005 and November 2019. Data were analysed in R (version 4.0.2) for model assumptions (linearity, homogeneity of variance and normality of residuals) and model analyses. Further, since previous research (Grayson et al., 2014; Nelson, Keall, Pledger, et al., 2002) and this study (see results of open model analyses) showed the difference in capture probabilities between sexes, I adjusted the sex ratio with the sex-specific capture probabilities to obtain more accurate sex ratio estimates. For each survey, I divided the number of each sex for the open model analysis by the sex-specific capture probabilities, then I added the translocated individuals of surveys 1996 and 1998 back. These adjusted population estimates were used to calculate the adjusted sex ratios, and the SEs were calculated using delta method based on the individuals used for the open model analyses. I also estimated the sex ratio from population estimates derived from the sex-specific closed model analyses.

Body condition

Body condition index was used as an indicator to assess individual condition of North Brother Island adult tuatara population. Body condition was estimated as the ratio of log-transformed WT to log-transformed SVL for a tuatara when first captured on a survey (Hoare et al., 2006). The temporal trend of individual body condition was estimated for the population from January 1988 to November 2019 and for the new cohort from March 2005 to November 2019, respectively. Because of the short interval between two surveys in 1990, the October survey was excluded (Table 2.1). Linear mixed models with three fixed factors, time (the number of months since the first survey), sex and VT, and one random intercept, individual, were used to evaluate factors influencing individual body condition. Model selection was performed using AIC values among the candidate model set: (1) sex and VT as main effects, and their interaction; (2) sex, VT and time as main effects, and interaction of sex with VT; and (3) sex, VT and time as main effects, and interactions of sex with both time and VT. Data were analysed in R for model assumptions (linearity, homogeneity of variance and normality of residuals), model analyses and model selection.

Further, I explored the temporal trend of SVL and WT to investigate how they drove the variations in body condition. General linear models were used to test the temporal trend of SVL and WT in the population (January 1988-November 2019) and the new cohort (March 2005-November 2019), including time (the number of months since the first survey in the model) and sex as well as their interaction. Data were analysed in R for model assumptions (linearity, homogeneity of variance and normality of residuals) and model analyses. In addition, I explored the temporal trend of SVL and WT of this population from January 1988 to November 2019 based on the raw data: (1) I summarised sex-specific descriptive statistics (mean, media, maximum and minimum) of each survey, and (2) I divided SVL and WT of each sex into differing subgroups based on measurements and calculated their percentage of each survey.

Results

Survival

The open model analysis for this population included 3027 captures (2034 males and 993 females) of 660 individuals (428 males and 238 females), and the open model analysis for the new cohort included 283 captures (197 males and 86 females) of 129 individuals (83 males and 46 females). In both open model analyses, models with survival included as a constant (\cdot), with a temporal trend (T), and with sex-based differences (sex) received support ($\Delta AICc \leq 2$), gaining approximately 90% of the weight within the candidate model set (Table 2.2; Table S2.2). Survey (time) and sex (sex) were dominant variables explaining capture probability in both open model analyses (Table 2.2; Table S2.2).

The annual survival of the population remained at a high rate between 0.95 and 0.96 from January 1988 to November 2018 for both sexes, with a slight downward trend. Females experienced a steeper decline in annual survival than males, with a slightly higher survival in January 1988 but a slightly lower survival in November 2018 than males (Figure 2.2A). The new cohort showed a similar high survival as the population, with the rate between 0.96 and 0.97 from March 2005 to November 2018. In contrast to the population, the new cohort showed an upward trend in annual survival over time, with males having a consistently higher survival and a more rapid increase than females through this period (Figure 2.2B). For each

sex, the survival of the new cohort was consistently approximately 1-2% higher than that of the population on the same survey (Figure 2.2C).

Both open model analyses showed considerable variations on capture probability among surveys, likely indicating a strong effect of weather factors such temperature, humidity, wind and rainfall. Estimates of capture probability were strongly sex-biased, with males 2%-11% higher than females on the same survey for both open model analyses.

Table 2.2. Model selection results on survival and capture probability using open model analyses in the population and in the new cohort.

Open model analysis of the population (January 1988 - November 2018)						Open model analysis of the new cohort (March 2005 - November 2018)					
Survival	Capture Probability	AICc	ΔAICc	AICc Weights	No. of Parameters	Survival	Capture Probability	QAICc	ΔQAICc	QAICc Weights	No. of Parameters
.	time+sex	7252.6	0	0.31	20	.	time	196.1	0	0.17	6
T	time+sex	7252.9	0.33	0.26	21	.	.	196.9	0.88	0.11	2
sex	time+sex	7254.6	2.03	0.11	21	sex	time	197.3	1.28	0.09	7
T+sex	time+sex	7254.9	2.37	0.1	22	T	.	197.4	1.34	0.09	3
time	time+sex	7255.7	3.11	0.07	36	.	time+sex	197.9	1.86	0.07	7
T*sex	time*sex	7256.2	3.63	0.05	23	T	time	198.2	2.14	0.06	7
.	time*sex	7257.6	5.04	0.03	37	.	sex	198.4	2.35	0.05	3
time+sex	time+sex	7257.7	5.1	0.02	37	T	sex	198.6	2.53	0.05	4
T	time*sex	7258.2	5.63	0.02	38	sex	.	198.6	2.59	0.05	3
sex	time*sex	7259.5	6.89	0.01	38	T+sex	.	199.3	3.28	0.03	4
time	time*sex	7260	7.42	0.01	52	sex	time+sex	199.5	3.41	0.03	8
T+sex	time*sex	7260.1	7.55	0.01	39	T+sex	time	199.5	3.45	0.03	8
time+sex	time*sex	7261.6	9	0	53	T*sex	.	199.9	3.87	0.02	5
T*sex	time*sex	7261.9	9.3	0	40	T	time+sex	200	3.99	0.02	8
time*sex	time+sex	7279.3	26.7	0	54	T*sex	time	200.3	4.28	0.02	9
.	time	7284.2	31.65	0	19	sex	sex	200.5	4.4	0.02	4
T	time	7284.4	31.86	0	20	T+sex	sex	200.6	4.51	0.02	5
sex	time	7285.9	33.35	0	20	time	time	200.9	4.86	0.01	9
T+sex	time	7286.1	33.51	0	21	time	.	201	4.95	0.01	6
time*sex	time*sex	7286.2	33.63	0	70	T+sex	time+sex	201.7	5.6	0.01	9
T*sex	time	7287.5	34.93	0	22	T*sex	sex	201.8	5.71	0.01	6
time	time	7288.7	36.14	0	35	time	sex	202.1	6.01	0.01	7
time+sex	time	7290.6	38	0	36	time+sex	time	202.3	6.2	0.01	10
time*sex	time	7309.2	56.61	0	53	T*sex	time+sex	202.5	6.47	0.01	10
time	sex	7873.9	621.33	0	20	time	time+sex	202.8	6.77	0.01	10
time+sex	sex	7875.8	623.2	0	21	time+sex	.	203.1	7.06	0	7
time*sex	sex	7897.3	644.69	0	38	time+sex	sex	204	7.96	0	8
time	.	7900.9	648.34	0	19	time+sex	time+sex	204.5	8.41	0	11
time+sex	.	7902.9	650.34	0	20	.	time*sex	205.5	9.46	0	11
time*sex	.	7924.4	671.8	0	37	sex	time*sex	207.6	11.55	0	12
.	sex	7946.3	693.74	0	3	T	time*sex	207.7	11.64	0	12
T	sex	7946.7	694.09	0	4	time	time*sex	208.2	12.15	0	13
sex	sex	7948.2	695.64	0	4	time*sex	.	209.5	13.41	0	11
T+sex	sex	7948.5	695.97	0	5	time*sex	time	209.5	13.47	0	14
T*sex	sex	7950.2	697.65	0	6	T+sex	time*sex	209.9	13.8	0	13
.	.	7973.2	720.59	0	2	time+sex	time*sex	210.5	14.44	0	14
T	.	7973.5	720.91	0	3	T*sex	time*sex	210.7	14.6	0	14
sex	.	7974.9	722.33	0	3	sex*time	sex	211.5	15.47	0	12
T+sex	.	7975.2	722.68	0	4	time*sex	time+sex	211.8	15.73	0	15
T*sex	.	7976.8	724.23	0	5	time*sex	time*sex	218.5	22.44	0	18

For both open model analyses, model averaging was performed among all models with weights (in bold) due to similarity of weights, to estimate survival and capture probability for each survey. Models in italics stand for the general model within the candidate model set which were tested for goodness-of-fit using the median \hat{c} approach to estimate overdispersion of the data. Candidate model sets for two open model analyses were ranked based on the AICc/QAICc values from the smallest to the largest.

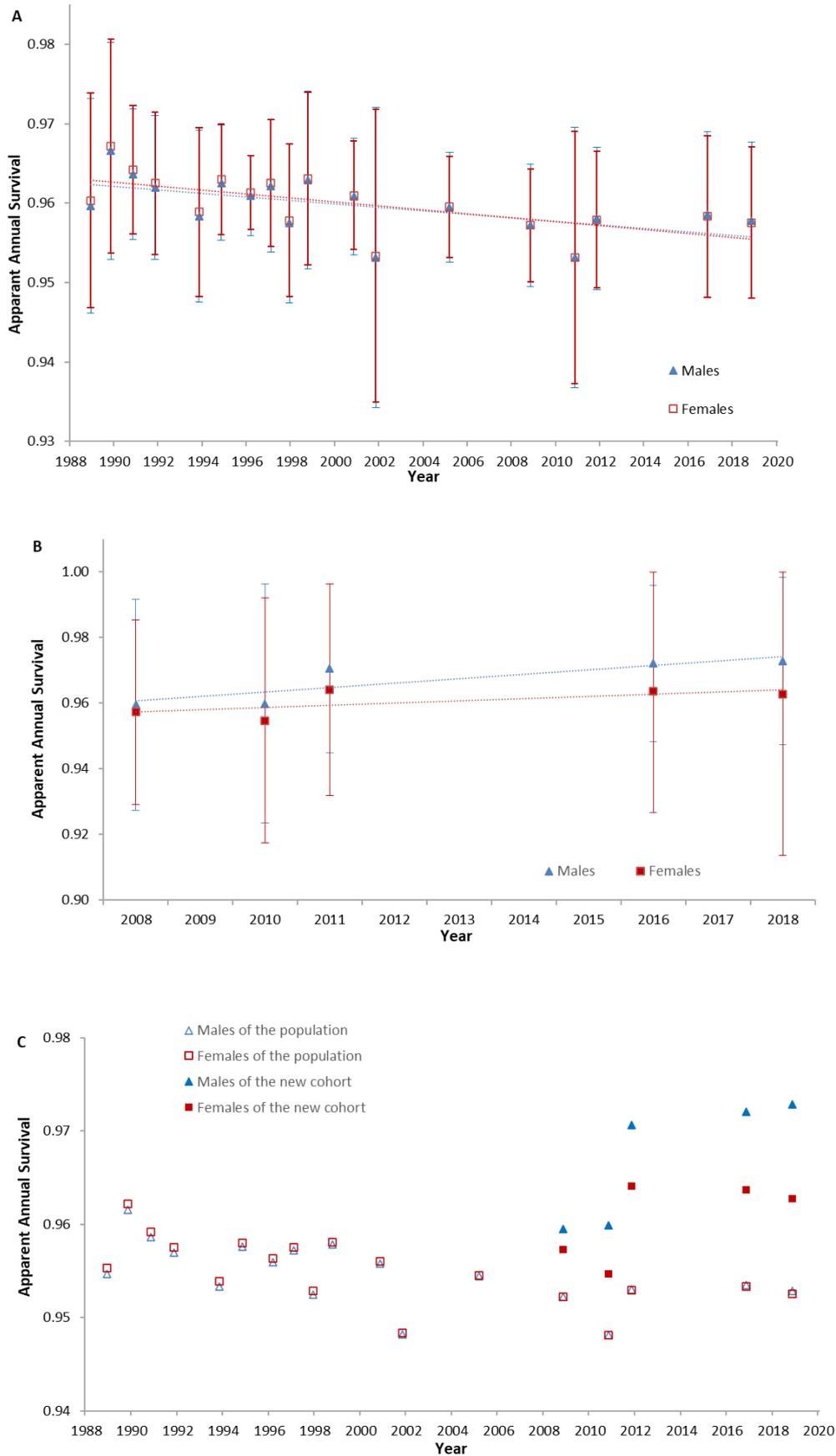


Figure 2.2. Annual survival of male and female tuatara of the population and the new cohort on North Brother Island. Estimates are shown with SEs in Figure 2A and 2B. Estimates and SEs were derived by model averaging. (A) The downward trend of survival rate of both sexes in this tuatara population from January 1988 to November 2018, with a more pronounced rate in females. (B) The upward trend of survival rate of both sexes in the new cohort from March 2005 to November 2018, with a greater rate in males. (C) The survival rate of the new cohort was consistently higher than that of the population on the same survey.

Population size

Model M(t) was selected as the overall best model across all surveys for estimating the population size of both the total population and the new cohorts (Table 2.3). Juveniles were not included in closed model analyses due to their low capture numbers, but they were captured on most of the surveys indicating recruitment is occurring in this population (Table 2.1). The estimate of population size fluctuated by survey and showed a downward trend from 445 (PLI 389-528) in March 1996 to 322 (PLI 292-368) in November 2018 (Figure 2.3). The sex-specific closed model analyses also showed a decrease in the population size of both males and females, from 293 (PLI 253-356) and 155 (PLI 122-221) to 204 (PLI 183-242) and 118 (PLI 101-151), respectively (Figure 2.3). The female population size estimate was consistently lower than that of males on each survey. The sum of population size estimates of both sexes on each survey was close to that of the population size estimate, with the exact same estimates in surveys of 2016 and 2018, indicating reliable results of the population size estimates as well as supporting sex ratio estimates presented later (Table S2.4).

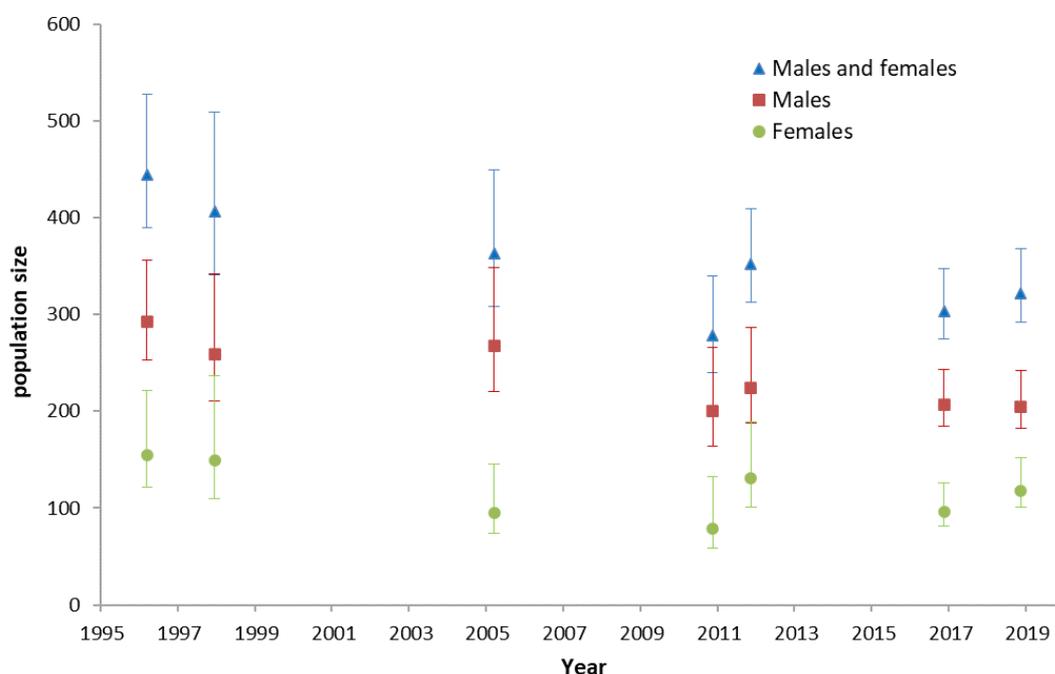


Figure 2.3. Estimates of the population size of males and females, males only and females only of North Brother Island tuatara population from March 1996 to November 2018. Estimates are showed with 95% PLI. There was a decline of the tuatara population size on North Brother Island, with a downward trend in both sexes.

Table 2.3. The rankings of candidate models in the model set of closed model analyses for population size estimation in the population and in the new cohort.

Surveys	The population												The new cohort																									
	Males and females						Males						Females						Males and females					Males					Females									
	Mar-96	Dec-97	Mar-05	Nov-10	Nov-11	Nov-16	Mar-96	Dec-97	Mar-05	Nov-10	Nov-11	Nov-16	Mar-96	Dec-97	Mar-05	Nov-10	Nov-11	Nov-16	Mar-05	Nov-10	Nov-11	Nov-16	Nov-18	Mar-05	Nov-10	Nov-11	Nov-16	Nov-18	Mar-05	Nov-10	Nov-11	Nov-16	Nov-18	Mar-05	Nov-10	Nov-11	Nov-16	Nov-18
M(0)	11	7	10	10	10	8	10	10	10	10	11	7	10	7	2	3	10	2	10	1	1	10	7	10	1	1	10	1	1	1	1	10	1	1	1	1	1	1
M(t)	4	1	1	3	3	2	4	4	3	2	2	1	4	7	2	5	5	1	4	1	7	7	1	7	7	7	7	7	7	6	2	1	1	7	7	7	7	7
M(b)	7	8	9	7	9	10	8	7	8	7	9	8	7	8	1	1	7	6	3	2	2	8	8	7	2	2	1	9	5	5	2	3	10	1	2	3	10	1
M(h)	10	11	12	12	12	7	12	12	11	12	10	10	12	11	7	9	12	1	12	5	5	12	12	5	5	5	12	10	12	5	4	12	11	7	7	7	7	7
M(RE)	12	9	11	11	11	9	11	11	9	11	12	9	11	4	6	6	11	5	11	3	3	11	9	11	3	3	11	8	11	3	3	2	7	7	4	4	7	4
M(tb)	3	2	2	1	5	4	3	3	2	1	5	2	3	5	1	8	7	4	3	4	3	4	3	4	8	8	4	3	2	2	8	4	3	2	8	9	5	3
M(th)	6	6	5	5	1	1	6	8	8	5	6	1	6	6	12	5	11	11	6	9	9	2	11	10	10	5	6	5	11	11	8	5	6	9	10	6	10	11
M(tRE)	5	3	3	4	2	3	5	5	5	4	3	3	4	5	10	3	9	7	5	9	9	5	9	9	9	9	5	2	3	3	10	8	1	9	6	11	9	8
M(bh)	9	12	6	9	7	12	9	12	9	9	7	12	9	8	12	6	4	9	11	9	6	11	9	6	6	6	6	6	6	6	6	6	11	9	9	9	9	9
M(bRE)	8	10	8	8	8	11	8	10	9	8	8	11	11	4	10	3	2	8	10	8	4	7	10	8	4	4	3	11	8	4	5	9	5	5	5	5	5	5
M(thh)	1	4	7	6	6	5	1	1	7	4	6	5	2	11	6	12	5	12	7	7	12	6	5	6	6	12	9	6	7	12	12	8	12	12	12	8	12	12
M(tbRE)	2	5	4	2	4	6	2	4	3	5	4	3	1	9	4	10	10	2	10	11	3	4	4	4	4	10	7	4	4	4	11	11	8	10	10	8	8	10

A candidate model set of 12 models was built up to test the capture probabilities and estimate the population size on each survey. The number stands for the ranking of the model in the model set based on the AICc or QAICc values from the smallest to the largest. The grey shade indicates there were inestimable estimates and/or SEs when fitting the model, or the model output produced unreliable estimates. M(t) was selected as the overall best model over all closed model analyses due to its relatively stable and high ranking as well as reliable estimates.

Table 2.4. Estimation of the gravidity rate of female tuatara on North Brother Island from November 1989 to November 2019.

Survey	1989	1990	1991	2000	2001	2011	2016	2019
Date	9-11 Nov	6-8 Nov	6-8 Nov	30 Oct-12 Dec	2 Nov-3 Dec	7-11 Nov	4-8 Nov	14-18 Nov
Number of survey nights	3	3	3	44	32	5	5	5
Number of researchers	2	3	3	3	2	5	5	5
# Number of females	41	40	37	139	139	53	59	34
[^] Number of gravid females	8	9	13	15	11	4	4	8
* Adjusted number of gravid females for short surveys	12	14	20	NA	NA	6	6	12
% gravid females	8.9	10.0	14.4	10.8	7.9	5.2	5.2	10.4
% average gravid females over a time span		11.1		9.4			7	
Reproductive cycle estimation (years)		9		10.7			14.4	

The gravidity rate of female tuatara on North Brother Island was estimated in the nesting season (November) from 1989 to 2019. Eight surveys (six short surveys and two complete surveys) were selected. Data between 1989 and 2001 were from the previous research by Cree et al. (1991) and by Mitchell et al. (2010). Three surveys after 2001 were selected because of the detailed records on gravidity. Based on the complete surveys in 2000 and 2001, Mitchell et al. (2010) calculated that on average 65% of gravid females would be captured during a three-night short survey in early November in North Brother Island tuatara population. In this study, I assumed this percentage was also applicable to a five-night short survey. Then I adjusted ^{*}the number of gravid females of each short survey by dividing [^]the number of gravid females captured in the field by 65%, and estimated the percentage of gravid females of each survey by dividing the adjusted number of gravid females for short surveys and the capture number of gravid females for complete surveys- by the female population size estimates (139 females for surveys 1989-2001 by Mitchell et al. (2010) and 118 females for surveys 2011-2019 derived from the closed model analysis of 2018).

Females were captured in the field (subadults not included).

[^] Gravid females of captured females in the field.

The population size estimate of the new cohort fluctuated among surveys and ranged between 100 and 150 (Table S2.4). However, results of first three surveys were unreliable because low captures caused large SEs and PLIs, which prevented me from exploring temporal trend of population size. Only results of 2016 and 2018 surveys were reliable based on the small SEs and PLIs as well as the close agreement in population estimates between the two. Therefore, the population size of the new cohort was approximately 139 (PLI 114-191) by 2018, accounting for about 43% of the population size. Similarly, the reduced data set for each sex caused unreliable estimates through the first three surveys, including the inestimable problem with females in 2005. Surveys of 2016 and 2018 outputs had similar estimates with small SE and PLI. Therefore, there were about 89 (PLI 71-127) males and 50 (PLI 38-87) females in the new cohort by November 2018. Despite unreliable outputs in the first three surveys, the estimates of males were still consistently higher than females over all selected surveys (Table S2.4).

Previous study showed the average gravidity rate of female tuatara was 11.1% between 1989 and 1991, and 9.4% over 2000 and 2001, indicating females bred every 9 and 10.7 years through the two periods, respectively (Mitchell et al., 2010). New estimates from 2011 to 2019 indicate the average gravidity rate declined to 7% indicating females bred every 14.4 years (Table 2.4).

Sex ratio

Collated sex ratios over differing subsets of survey data showed a strong male bias. In this tuatara population, there was a collated sex ratio of 1.644 (444 males: 270 females) between January 1988 and November 2019, 1.658 (335 males: 202 females) before complete surveys (January 1988-August 2000), 1.743 (244 males: 140 females) during complete surveys (November 2000-December 2001), and 1.874 (268 males:143 females) after complete surveys (March 2005-November 2019). The new cohort showed a collated sex ratio of 1.623 (86 males: 53 females) between March 2005 and November 2019.

The capture sex ratio of the population from January 1988 to November 2019 fluctuated without a significant linear temporal trend ($t_{22}=-1.339$, $p=0.194$), but showed a male bias through all 24 surveys except for 1989 (Figure 2.4A). The 1989 survey was

considered an outlier because the method of selecting individuals was unclear and only 47 (24 males and 23 females) of 79 (50 males and 29 females) individuals were marked. Despite a consistent male bias, the capture sex ratio of the new cohort showed a significant decline between March 2005 and November 2019 ($t_6=-4.538$, $p=0.004$, Figure 2.4B), during which there was a similar decline in that of the population ($t_6=-3.285$, $p=0.017$, Figure 2.4A).

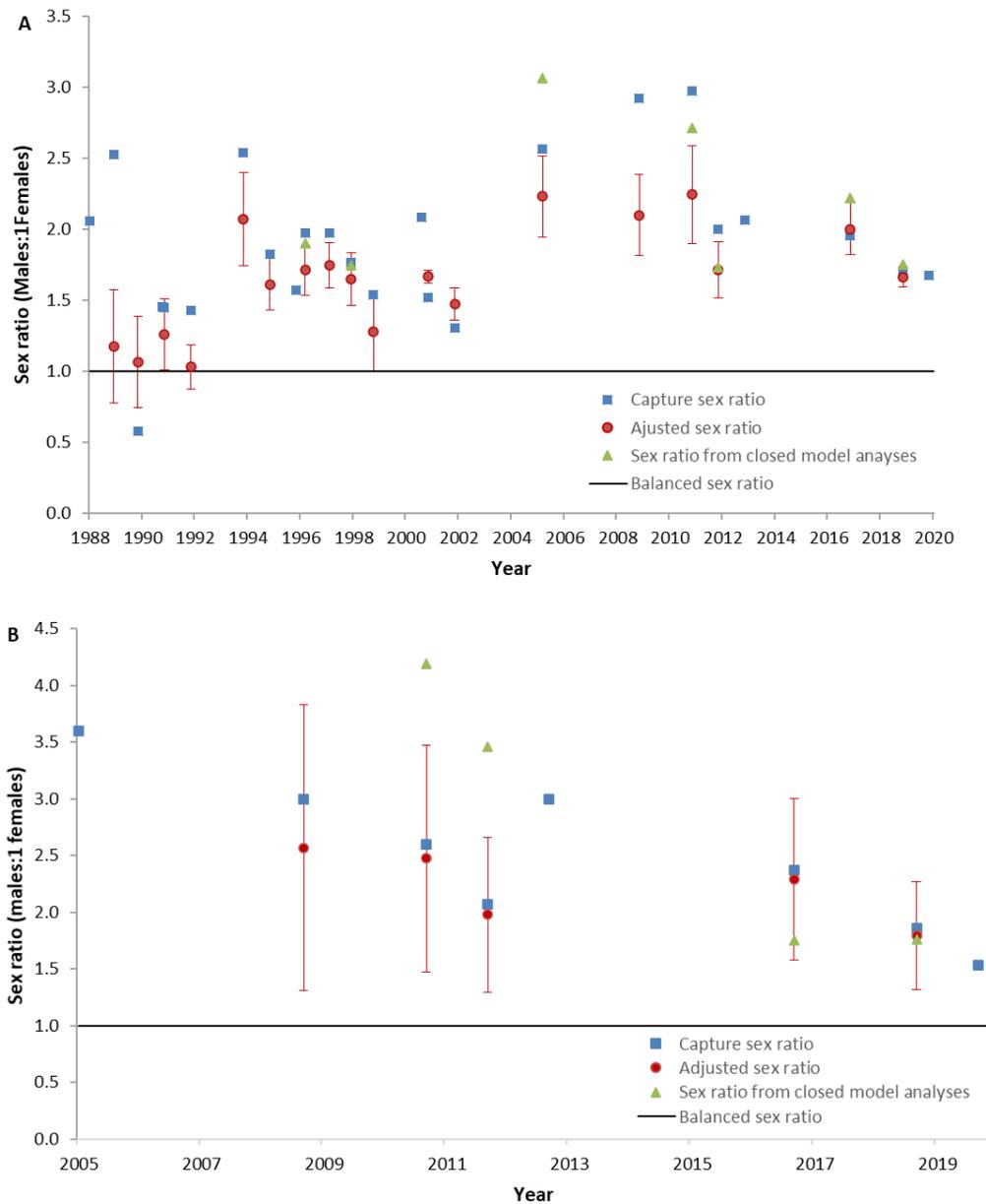


Figure 2.4. Sex ratio estimates of the North Brother Island tuatara population and the new cohort. (A) There was a long-term male-biased sex ratio of this tuatara population from January 1988 to November 2019 despite irregular fluctuations. (B) There was a decline in the sex ratio of the new cohort from March 2005 to November 2019. Estimates of the adjusted sex ratio are shown with SEs.

There was a close agreement in the temporal pattern between the adjusted sex ratio and that derived from closed model analyses in the population (Figure 2.4A) and the new cohort (Figure 2.4B), indicating the reliable results of sex ratio estimates. The adjusted sex ratio was selected to explore the temporal trend of sex ratio, because open model analyses spanned a longer period of time than closed model analyses. The adjusted sex ratio of the population showed a consistent male bias between January 1988 and November 2018 with substantial fluctuations among surveys (Figure 2.4A). With a slight male bias in the late 1990s, the adjusted sex ratio became further male-biased on the following surveys and the SEs never overlapped with a balanced sex ratio after 1998. Although consistently male-biased, the adjusted sex ratio of the new cohort showed a decline towards a more balanced sex ratio from March 2005 to November 2018, which was also supported by the sex ratio estimates from closed model analyses and the capture sex ratio (Figure 2.4B).

Body condition

The body condition analysis of the population included 3105 captures (2085 males and 1020 females) of 638 adults (407 males and 231 females) from January 1988 to November 2019 (Table 2.1). The mixed effects model incorporating sex, time and VT as main effects and interactions of sex with both time and VT was overwhelmingly supported (weight=1, Δ AIC for next best model=62.52, Table 2.5). Both sexes experienced a significant decline in body condition across 30 years ($t_{636}= 5.7516$, $P<0.001$), with consistently higher body condition in males than in females (Figure 2.5A). Female body condition declined at the annual rate of $12\times 10^{-4}\pm 9.0\times 10^{-5}$ gmm^{-1} ($t_{2459}=-13.2$, $P<0.001$), whereas male body condition declined at the annual rate of $3.1\times 10^{-4}\pm 6.1\times 10^{-5}$ gmm^{-1} ($t_{2459}=-5.1$, $P<0.001$). Body condition of adult females declined at a greater annual rate than that of males, with the annual difference in slopes of $8.9\times 10^{-4}\pm 1.1\times 10^{-4}$ gmm^{-1} ($t_{2459}=8.1$, $P<0.001$). The general linear model showed a significant decline in SVL in both sexes ($P<0.001$) of this tuatara population, with a steeper but non-significant ($p=0.278$) rate in males than in females (Figure 2.5C). Before complete surveys, the largest males and females were more than 250 and 220 mm respectively, whereas in the last decade the largest males and females were less than 240 and 220 mm respectively (Figure 2.6A). Similarly, there was a significant decline in WT in both sexes ($P<0.001$) with a greater rate in males ($P=0.0126$) (Figure 2.5E). The heaviest males and females captured around the late 1990s weighed more than 600 and 350 g respectively, while in the latest decade the

heaviest males and females weighted less than 450 and 250 g respectively (Figure 2.7A). The percentage of differing subgroups by measurements of SVL and WT over surveys in both sexes also indicated decline in SVL and WT over time in this tuatara population (Figure 2.6B, 2.6C, 2.7B, 2.7C).

The body condition analysis of the new cohorts included 229 captures (162 males and 67 females) of 92 adults (62 males and 30 females) from March 2005 to November 2019 (Table 2.1). The same model as the for the total population was selected as the best model (weight=1, Δ AIC for next best model=25.925, Table 2.5). The two sexes showed different temporal trends in body condition over time ($t_{131}= 5.5$, $P<0.001$). Males showed a significant increase with the annual rate of $25\times 10^{-4}\pm 3.0\times 10^{-4}$ gmm⁻¹ ($t_{131}= 8.3$, $P<0.001$), while females showed a slight but non-significant decline with the annual rate of $6.7\times 10^{-4}\pm 4.9\times 10^{-4}$ gmm⁻¹ ($t_{131}= -1.4$, $P=0.1757$) (Figure 2.5B). The general linear models showed a non-significant increase in SVL ($p=0.0815$) but a significant increase in WT ($p=0.00135$) of males, and a non-significant decline in both SVL ($P=0.0646$) and WT ($p=0.30016$) of females (Figure 2.5D, Figure 2.5F).

Table 2.5. The candidate model set and the result of model selection of the linear mixed model for body condition analyses in the population and in the new cohort.

Models	Number of parameters	The population		The new cohort	
		ΔAIC	AIC weights	ΔAIC	AIC weights
sex+VT+time+sex:VT+sex:time	8	0	1	0	1
sex+VT+time+sex:VT	7	62.52	0	25.925	0
sex+VT+sex:VT	6	191.31	0	51.333	0

The linear mixed model included sex, time and VT as fixed factors and individual as random factor. "+" and ":" stand for additive and interactive effects, respectively. VT was categorized into four categories based on the tail length. "time" was the number of months since the first survey of each linear mixed model.

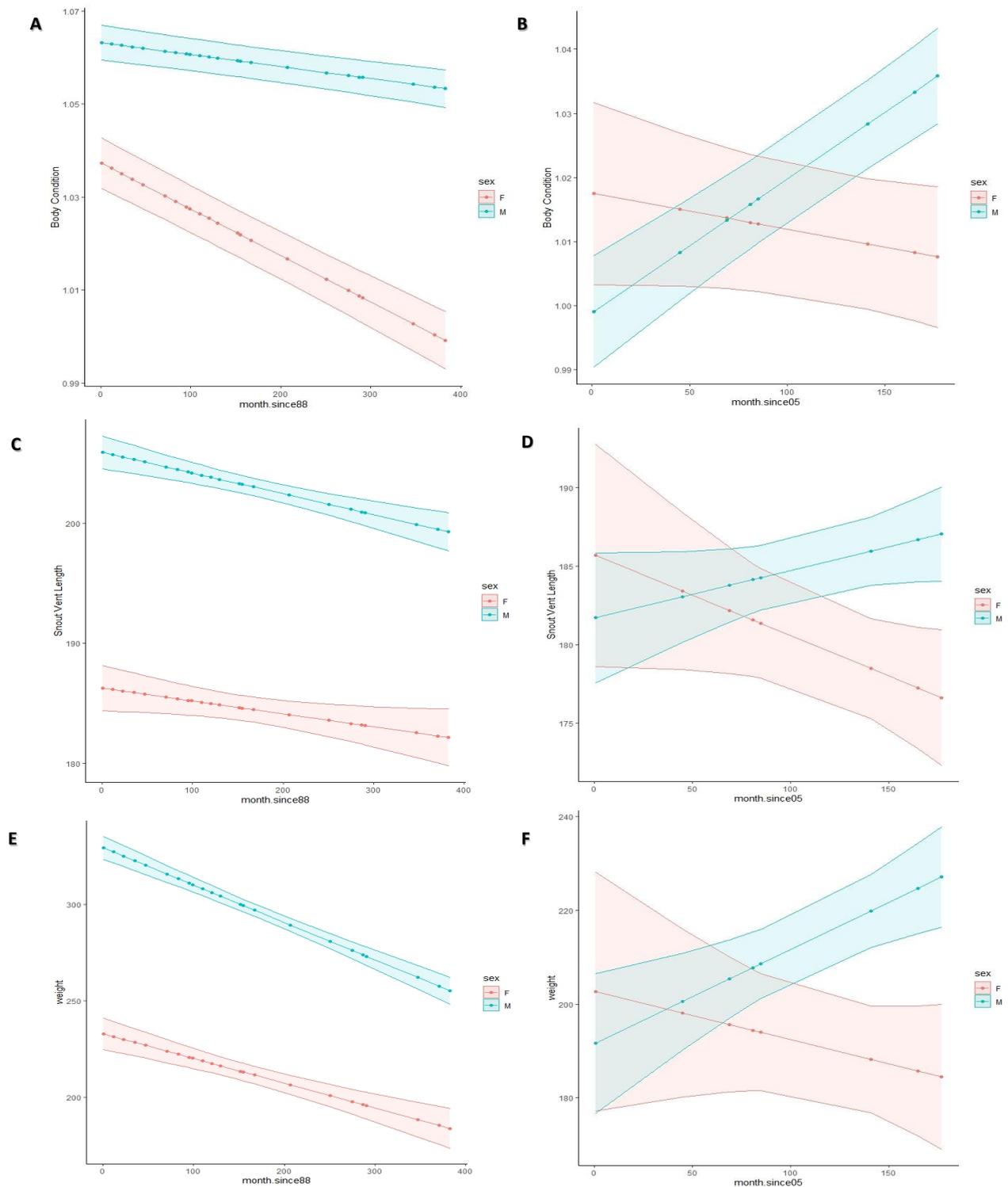


Figure 2.5. Sex-specific temporal trend of body condition, SVL and WT of tuatara population on North Brother Island from January 1988 to November 2019 and the new cohort from March 2005 to November 2019. (A) The body condition of two sexes of this tuatara population showed a significant decline over time, with a significant steeper rate in females. (B) The body condition of males in the new cohort showed a significant increase, while there was a slight but non-significant decline in the body condition of females. (C) Both sexes of this tuatara population showed a significant decline in SVL, with a steeper but non-significant rate in males compared to in females. (D) In the new cohort, there was a non-significant increase in SVL of males, and a non-significant decline in SVL of females. (E) Both sexes of the population showed a significant decline in WT, with a greater rate in males than in females. (F) In the new cohort, there was a significant increase in WT of males and a non-significant decline in WT of females. Estimates of body condition (Figure A and B) were derived from linear mixed models and shown as averaged estimated marginal means over the levels of VT with 95% CI. Estimates of SVL (Figure C and D) and WT (Figure E and F) were derived from general linear models and shown as estimated marginal means with 95% CI.

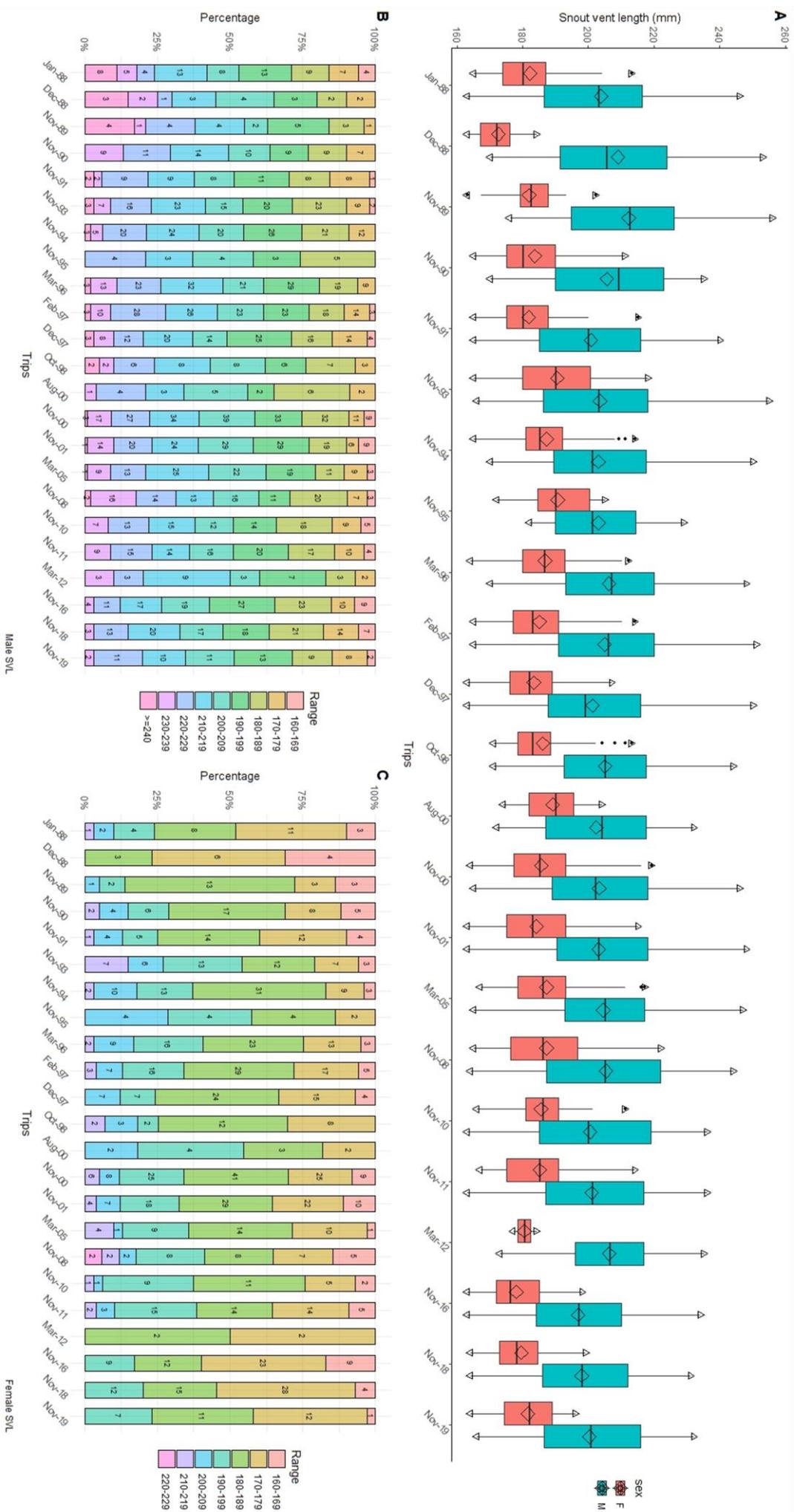


Figure 2.6. Temporal trend of SVL in the tuatara population on North Brother Island from January 1988 to November 2019. (A) Median (dash in the box), mean (diamond), maximum (triangle), minimum (upside down triangle) of SVL of each sex on each trip. Black dot: outlier; F: female; M: male. (B) The percentage of subgroups of SVL on each trip in males, and (C) in females. Numbers on bars are numbers of tuatara.

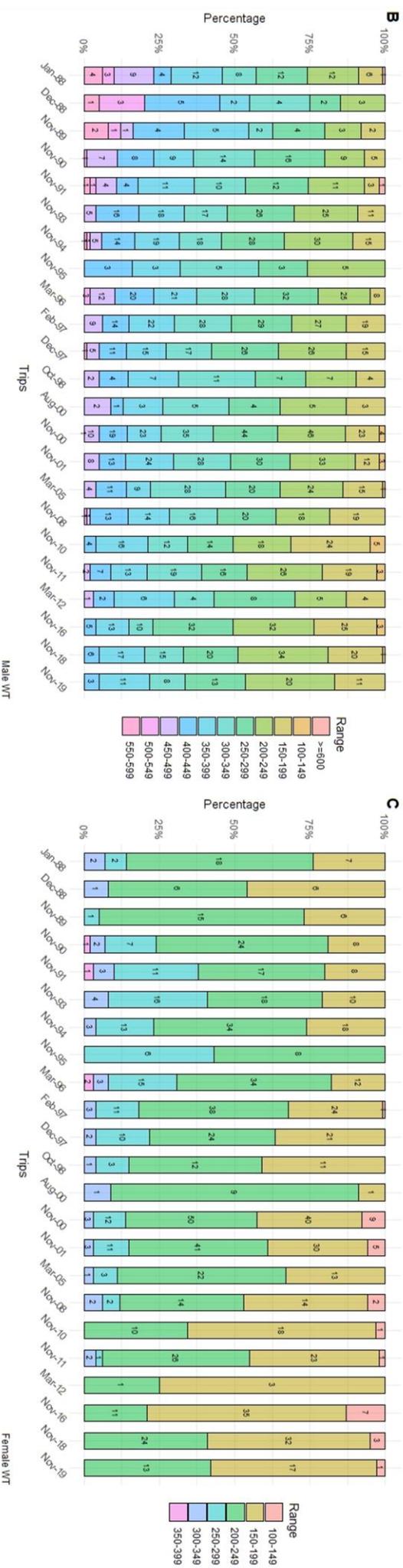
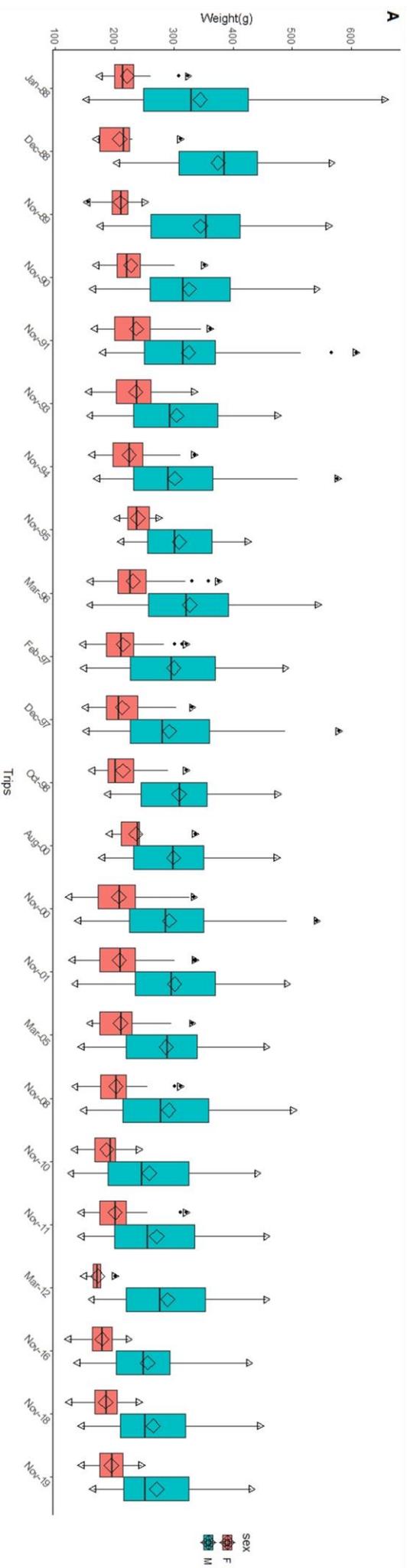


Figure 2.7. Temporal trend of WT in tuatara population on North Brother Island from January 1988 to November 2019. (A) Median (dash in the box), mean (diamond), maximum (triangle), minimum (upside down triangle) of WT of each sex on each trip. Black dot: outlier; F: female; M: male. (B) The percentage of subgroups of WT on each trip in males and (C) in females. Numbers on bars are numbers of tuatara.

Discussion

This research adds another decade of knowledge on the long-term demographic trends in an isolated, long-lived reptile population. Grayson et al. (2014), using the 20-year mark-recapture data of the North Brother Island tuatara population, theorised an extinction vortex for this population, based on an increasing male bias, as well as a consistent decline in body condition and survival, with a steeper rate of decline in females over time. With the inclusion of the most recent surveys, I confirmed the strong male bias as well as the decline in survival and body condition have continued over 30 years. Moreover, I found a downward trend of population size and a further extended breeding interval of females. However, there has been a less-skewed male bias in the new cohort, as well as an increase in male body condition and in survival of both sexes in more recent times.

By all methods of sex ratio estimation, despite fluctuations and some surveys with small samples sizes, I demonstrated a strong and long-term male bias in the North Brother Island tuatara population from January 1988 to November 2019. This finding confirmed the male bias identified in previous research (Grayson et al., 2014; Mitchell et al., 2010; Nelson, Keall, Pledger, et al., 2002) has continued over 30 years in this population. Although sexing subadults is challenging and occasionally we corrected their sex on our recapture records as dimorphic secondary sex characteristics became more evident (of 714 adults on our long-term capture records between January 1988 and November 2019, seven individuals were corrected from females to males and seven individuals were corrected from males to females), and some adults were removed from North Brother Island as founders for new populations, these factors cannot account for the strong male bias observed in this population.

The cause of the male bias in this population is still unclear. Small populations are vulnerable to shifts in population parameters through demographic, environmental and genetic stochasticity, and natural catastrophes (Lande, 1993; Shaffer, 1981). The skewed sex ratio of North Brother Island tuatara could arise from recruitment by chance among a finite number of individuals. The TSD pattern of tuatara can also contribute to a male-biased sex ratio in this population. Unlike species with GSD, which produce offspring in an approximately balanced sex ratio, the sex ratio of tuatara is subject to the incubation temperatures during

embryonic development. As the incubation temperatures increase, more male tuatara hatchlings are produced (Mitchell et al., 2006). While I am unable to continually monitor nests on North Brother due to the challenges of accessing the island, detailed microclimate modelling has demonstrated that increased incubation temperatures occur in warm years (Nelson et al., 2004a) or in the nests that experience more exposure to solar radiation or with shallow depths (Mitchell et al., 2008). Thus, a warm climate may cause a male bias in hatchlings of this population and further skew the male bias as it becomes warmer.

A significant decline in individual body condition of both sexes in this population, with a steeper rate of decline in females, was found in two earlier studies (Grayson et al., 2014; Hoare et al., 2006) over 14 years (1988-2001) and 24 years (1988-2012) respectively. I found this downward trend continues. Female body condition was consistently 2-6% lower than males and declined approximately four times as fast as males. The decline of both SVL and WT contributed to the downward trend of body condition, which may be related to the limited resources on the island. Based on the population estimate of 1996 survey in this study, the tuatara population density on North Brother Island was close to averages in other populations (Cree & Butler, 1993). However, North Brother Island has relatively limited plant and invertebrate resources (Gibbs, 1999), but supports dense populations of reptiles (Keall et al., 2001). Limited resources, especially food limitation, can lead directly to weight loss and limit individual growth. Tuatara on North Brother Island appear skinnier and smaller than individuals on Titi Island, Long Island and Matiu Somes Island (Figure 2.8), which were translocated populations from North Brother Island. These translocated populations showed an increase in SVL and WT following translocations (Nelson, Keall, Brown, et al., 2002; Nelson, unpublished data). The influence of food limitation on body condition has been observed in other species. For example, food shortage was found as a primary driver of body condition decline in black-legged kittiwakes, *Rissa tridactyla*, (Kitaysky et al., 1999) and in ovenbirds, *Seiurus aurocapilla*, (D. R. Brown & Sherry, 2006).



Figure 2.8. Tuatara of North Brother Island population are smaller and skinnier than those of translocated populations. Top: tuatara on North Brother Island. Bottom: tuatara on Matiu Somes Island.

Intersexual competition for resources can be common and intense (Leturque & Rousset, 2004; Li & Kokko, 2019), especially in a context of limited resources. Previous studies showed male tuatara are bigger than females (Dawbin, 1982) and have dominance over females in competition for resources (Moore, Daugherty, & Nelson, 2009; Wörner, 2009). For example, a study on juvenile tuatara showed males were more aggressive than females and

males outcompeted females in food competition (Wörner, 2009). Male tuatara on Takapourewa (Stephens Island) occupied territories more than twice as large as females even though there was a balanced sex ratio (Moore, Daugherty, & Nelson, 2009). Due to the social impact of dominant individuals, subordinates likely choose to avoid dominants to reduce unnecessary fights, which may influence their feeding behaviour. For example, a study on mares showed that in the presence of dominant horses, subordinates had significant shorter feeding time than dominants (Lisa Nash et al., 1987), which can have substantial influence on body condition of subordinates. Therefore, the dominance of males on resource competition may be a major driver of the lower female body condition compared to males in the North Brother Island tuatara population. In addition, male sexual harassment can also contribute to a more pronounced decline in body condition of female tuatara. Sexual harassment is widespread in animals and can incur substantial costs on females (Clutton-Brock & Parker, 1995). For example, frequent male harassment disturbed female feeding and thus caused compromised female condition in feral horses, *Equus caballus* (Rubenstein, 2018). Furthermore, a strong male bias can exacerbate the male harassment and aggression towards females (Clutton-Brock & Parker, 1995; Le Galliard et al., 2005) and compound females' disadvantage in resource acquisition, which likely further drives a more rapid decline of female body condition in this tuatara population. Meanwhile, a male bias can also incur costs to males. For example, repeated mating attempts of males can result in their loss of feeding time and poor body condition (Clutton-Brock & Parker, 1995), and a strong male bias could lead to excessive mating attempts. Furthermore, a male bias can exacerbate male-male competition (Holveck et al., 2015), which can incur more energy expenditure and influence body condition.

In spite of the high survivorship of between 95-96% for both sexes over 30 years, there has been a consistent decline of survival with a greater rate of decline in females than in males. Tuatara are expected to have high survivorship and longevity based on their late sexual maturation and low reproductive output (Cree, 1994). Body condition is highly correlated to survival in mammals, birds, amphibians and reptiles (Aubry et al., 2013; Catlin et al., 2014; Civantos & Forsman, 2000; Morgan-Davies et al., 2008; Reading, 2007; Verhulst et al., 2004). For example, in a study on lesser snow geese (*Chen caerulescens*), the quality of colonies was identified as a driver of changes in gosling body condition, which ultimately influenced

juvenile survival (Aubry et al., 2013). Likewise, there were significant associations between body condition and survival in the Algerian sand racer (*Psammodromus algirus*), although such associations may differ based on sex and body size (Civantos & Forsman, 2000). Therefore, the decline of body condition of this tuatara population may be a direct driver for the decline of survival over 30 years, and the greater rate of decline in female body condition compared to males may contribute to a more rapid decline in female survival. This sex-specific difference in adult survival further skews the population towards male bias. Although I was not able to estimate survival of juveniles due to their low detection probabilities, lower survival in female juveniles was found in a semi-natural tuatara facility in another study (Gruber, 2007), which could only worsen the strong male bias in this population.

The downward trend of survival directly contributes to the decline in population size. From March 1996 to November 2018, this tuatara population experienced a decline of 28%. Population growth can be highly sensitive to adult survival (Souchay et al., 2013), particularly for long-lived species, because even a slight variation in survival can have substantial influence on population size due to their extended lifespan, slow maturation and low annual reproductive output (Péron et al., 2016). Therefore, a consistent decline in survival over 30 years, despite a low rate of decline, can have substantial influence on the population size. Besides survival rate, female fecundity can be another major driver for the variation in population size, especially when there is a decreasing adult survival rate (Sæther & Bakke, 2000). Based on the estimates of population size and survival rate in this study, there were around 380 adults in the population by 2001 (after two complete surveys), and approximately 200 of them has presumably died by 2018. However, there were 139 adults detected in the new cohort by 2018, indicating the recruitment only compensated for 70% of the mortality between 2001 and 2018, which reflects low female fecundity in this population. Tuatara typically breed every 4-5 years (Takapourewa; Cree, 2014), whereas Mitchell et al. (2010) found an extreme low female fecundity in the North Brother Island tuatara population over the period from 1989 to 2001, with females only breeding every 9 years. In this study, I found a further decline of female fecundity indicating that females reproduced only every 14.4 years from 2011 to 2019. Therefore, low female fecundity likely contributes to the rapid decline in population size for this tuatara population. This low female fecundity could directly arise from the decreased body condition. In an experiment of food availability manipulation on northern

grass lizards (*Takydromus septentrionalis*), females fed a low quantity of food showed lower body condition during the breeding season and subsequent lower seasonal reproductive output than those fed a high quantity of food (Du, 2006). Also, female body size in this tuatara population may have impacts on their fecundity where smaller females hold fewer eggs (Cree et al., 1991). This phenomenon is observed in many species of amphibians and reptiles. For example, fecundity (the follicle number) was positively correlated to female body size in four species of *Desmognathine* salamanders (Tilley, 1968), and similarly, large female grass lizards produced more clutches and more eggs per clutch than small ones within one breeding season (Ji et al., 2007; Luo et al., 2012). Moreover, a male bias can have an extra impact on female fecundity and survival through intensified male aggression to females (Le Galliard et al., 2005), consequently contributing to a further decline of population size. The decline of the population size of tuatara may also be a population response to carrying capacity. Together with the limited resources on the island, I hypothesize that the decline of the North Brother Island tuatara population is the response to intense resource competition at carrying capacity, which is compounded by a strong male bias.

Based on the 30-year survey data, the demographic pattern of the North Brother Island tuatara population seems in agreement with the prediction by Grayson et al. (2014) that this population could become a 100% male population and functionally extinct in the long-term. However, the different demographic pattern in the new cohort may signal a population-level response to the male bias. Tuatara have survived climate shifts over at least 100,000 years (Cree, 2014; Miller et al., 2012), although the effects of historical climates on their sex ratios are still unknown. Moreover, a recent study in another tuatara population has shown their potential for regulating their sex ratio to balance over time in a warming climate through behavioural variations in nesting phenology (Nelson et al., 2018). Therefore, further monitoring of the sex ratio pattern in this tuatara population is needed to investigate whether (1) the sex ratio generally fluctuates (long term) around 1:1 despite irregular fluctuations based on the climate-mediated sex determination, or (2) the male bias is becoming more evident under climate warming and will threaten population viability (Figure 2.9).

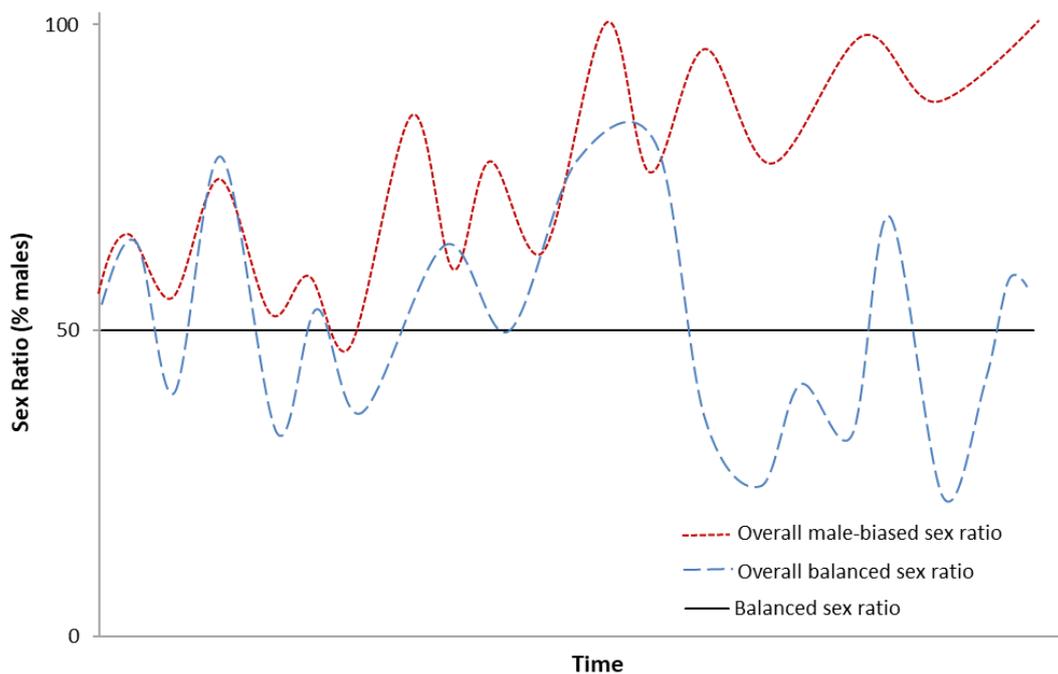


Figure 2.9. Two possibilities of the temporal trend of sex ratio in North Brother Island tuatara population in a warming climate. Red dashed line shows the sex ratio bias will become more evident. Blue dashed line shows there will be an overall balanced sex ratio despite irregular fluctuations

Regardless of the mechanism of sex ratio patterns, this less-skewed male bias in the new cohort may benefit individual body condition by reducing male harassment to females and male-male competition. Moreover, a substantial decline of the population size in this tuatara population could reduce the intensity of resource competition and subsequently improve individual body condition. Therefore, the new cohort have seen an improved temporal trend of body condition than the total population. An improved pattern of body condition in the new cohort can directly contribute to their higher and increasing survival over years, and ultimately boost their population size. By 2018, the new cohort have accounted for over 40% of the population size. As the percentage of the new cohort in this tuatara population increases, they have increasing influences on the pattern of the population. This could explain the downward trend of male bias in the population since the new cohort came into the population.

Despite the promising demographic pattern of the new cohort and its increasing influence on this population, there is still major concern for the population viability due to the low number of effective reproductive females. Based on the population size estimated in 2018, there were 118 female adults on the island. However, based on the low gravidity rate of 7%, only eight females on average are likely to be gravid each year. Moreover, a decline of population size and a continuous male bias can only worsen this situation through a further decreased female population size, and correspondently, a further smaller number of effective reproductive females. Taking into account their small clutch size (three to eight eggs) (Cree et al., 1991; Mitchell et al., 2010) and the potential impact of a prolonged incubation period in natural nests (approximately 365 days, Nelson et al., 2004b) on incubation success, there is an extremely low recruitment rate in this tuatara population, which may not be able to make up for the decline of the population size. In addition, a warming climate may exacerbate the male bias through overproduction of male hatchlings in the nest. Therefore, continued long-term monitoring, especially on the new cohort, is needed in this tuatara population to understand the mechanism of demographic changes and their effects on population viability.

Chapter 3

Activity area patterns for tuatara on North Brother Island under a long-term male bias

Introduction

Understanding activity area is critical for ecology and conservation biology of any species. Home range and territory are two descriptors of activity area (Dixon & Chapman, 1980). Home range is the area that animals traverse for purposes such as feeding, mating, or nesting (Burt, 1943). Territory is the area that animals actively defend for limited resources such as food, mates, or shelter (Maher & Lott, 1995; Noble, 1939). Although maintaining territories and home ranges can incur costs, animals acquire critical resources to perform biological processes in these activity areas that they may not have access to otherwise, which ultimately improves individuals' fitness (Hinde., 1956; Powell, 2000).

Although various features of activity areas can affect individual fitness, for example, habitat quality, the size of activity area is a significant measure of the resource acquisition and thereof the fitness of individual animals (Perry & Garland, 2002). Empirical studies indicate that activity area size is positively correlated with increased adult survival, mate access, reproductive success and offspring survival in vertebrates, such as reptiles (e.g. the common chuckawalla, *Sauromalus obesus*, reviewed by Simon, 1975), birds (e.g. great tits, *Parus major*, Both & Visser, 2000), and mammals (e.g. the American red squirrel, *Tamiasciurus hudsonicus*, Steury & Murray, 2003).

Intraspecific variation in activity area size can have significant effects on population demography and dynamics, because it is related to resource allocation (e.g., food and mate) among competitors through behavioural interactions, which can influence important

population parameters such as individual growth rate, survival and reproduction (Adams, 2001). Intensive studies showed a variety of drivers for intraspecific variation in activity area size, such as food availability, habitat features, season, local climate, population density, sex and body size across a range of taxonomic groups of invertebrates and vertebrates (Hyslop et al., 2014; Perry & Garland, 2002; Saïd et al., 2009; Schoener & Schoener, 1982; Van Beest et al., 2011; Wada, 1993; Wiens et al., 1985).

Sex-specific differences in activity area size are prevalent in vertebrates such as mammals, birds, reptiles and fish (Costa et al., 2011; Johansson et al., 2016; Perry & Garland, 2002; Rolando, 2002; Sprogis et al., 2016). In terrestrial reptiles, males normally maintain larger activity areas than females (Hyslop et al., 2014; Perry & Garland, 2002; Schoener & Schoener, 1982). For example, a study on eastern indigo snakes (*Drymarchon couperi*) showed males occupied annual home ranges 4.5 times and 6.6 times larger than females in two consecutive years (Hyslop et al., 2014). Similarly, there were larger home ranges in male sand lizards (*Lacerta agilis*) than females during the mating season (Wieczorek et al., 2020). By having larger activity areas, males can increase their female access, and ultimately, increase reproductive success (Perry & Garland, 2002; Schoener & Schoener, 1982).

Body size is also a major predictor of activity area size in vertebrates (Candolin & Voigt, 2001; Ottaviani et al., 2006; Perry & Garland, 2002; Tucker et al., 2014). For example, in an experiment on juvenile steelhead trout (*Oncorhynchus mykiss*), territory size increased with body size when food abundance and population density were controlled (Keeley, 2000). Likewise, iguanid lizards (*Sceloporus jarrovii*) of larger size class had territories more than twice as large as those of smaller class (Simon, 1975). This is probably because larger areas can provide more resources for larger animals to support their energetic requirements (Perry & Garland, 2002; Tucker et al., 2014).

In addition, activity area size can be regulated by population density (Hixon, 1980; Lott, 1984). Territorial animals are expected to reach an optimal size of activity area through the trade-off between costs and benefits for territory defence (Hixon, 1980; Schoener, 1971). An increasing population density can intensify intraspecific resource competition and correspondingly incur increasing costs on territorial defence, which can in turn influence the optimal activity area size (Owen-Smith, 2002). As such, population density is usually inversely

related to territory size or home range (Bengsen et al., 2016; Keeley, 2000; Norman & Jones, 1984; Trewhella et al., 1988).

It is widely acknowledged that sex ratio can regulate the intensity of sexual selection, and thus, territorial behaviour (Glutton-Brock & Parker, 1992; Gwynne, 1990; Kodric-Brown, 1988; Spence & Smith, 2005). However, empirical studies investigating sex ratio as a driver for activity area patterns and population viability are lacking. Besides, studies on activity areas of territorial vertebrates often cover a short time span (several days to months), and most on birds and mammals (Silva et al., 2020). Relative to birds and mammals, terrestrial reptiles have more sedentary movement patterns and subsequently limited dispersal abilities. As such, long-term data may provide better insights into activity area patterns of terrestrial reptiles and the ensuing population consequences, especially for species with extended lifespans.

Tuatara are long-lived reptiles (~100 years, Cree, 2014; Reinke et al., 2022). They are sexually dimorphic, with males being larger in body size and head size than females (Dawbin, 1982; Herrel et al., 2010). The detectability of tuatara is low in the wild as they are nocturnal and inhabit underground burrows (Ussher, 1999). Tuatara have long-term site fidelity where individuals were recaptured at the same locations over several decades (Moore, Daugherty, & Nelson, 2009). As social reptiles, tuatara defend spaces using a set of behaviours, such as body inflation, positioning, crest erection, head-shaking, chasing and biting (Gillingham et al., 1995; Gillingham & Miller, 1991). In the Takapourewa (Stephens Island) tuatara population where there is an even sex ratio, males maintain larger territories than females, and large males have dominance in overlapping with more females in their territories and excluding other males more effectively from their territories (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009). Since the late 1990s, there has been a continuous male bias in another tuatara population on North Brother Island, together with a decline in population size (Grayson et al., 2014; Mitchell et al., 2010; Nelson et al., 2002; Chapter Two). Therefore, North Brother Island tuatara population provides an ideal model to examine how a long-term male bias drives variation in activity area patterns in a long-lived reptile.

I investigated the activity area patterns of tuatara on North Brother Island based on the 30-year survey data. The following hypotheses were tested: (1) Males have larger activity areas than females; (2) with a decreasing population size, individual activity area increases;

and (3) larger males have the advantage in resource competition, including larger or more exclusive activity areas and more female access. Also, I compared these results to the factors that influence activity areas in two translocated tuatara populations, established with animals from North Brother Island, to understand the impact of different environmental contexts.

Methods

Study sites

Activity area patterns were explored in tuatara populations on North Brother Island and in translocated populations on Matiu/ Somes Island and Long Island (Kokomohua) in New Zealand (Figure 3.1; Table 3.1). North Brother Island, supporting a natural tuatara population, is mainly weathered rock, and the northern face is covered by low vegetation and shallow soil. Tuatara on Matiu/ Somes Island and Long Island are translocated populations established with animals from North Brother Island in 1998 and 1996, respectively. Relative to North Brother Island, Matiu/ Somes Island and Long Island are in much larger areas with more complex vegetation structure, providing tuatara with a variety of habitat as well as abundant food and shelter.

Data collection

Tuatara surveys on North Brother Island were performed over 24 surveys from January 1988 to November 2019 (Table 3.2). During each survey, tuatara were caught by hand at night and their locations were recorded manually based on a grid map. There were two versions of grid maps which were mapped based on two versions of an aerial photograph (the first version was used until 2000 and the second version has been use since 2001, Figure 3.2). Locations of tuatara were not recorded using GPS because the accuracy of handheld units was not high enough during the early surveys, and to continue the same methodology in more recent surveys. Tuatara were taken back to the field station and identified by their permanent marks (toe clips before 2001 or passive integrated transponder from 2001). Individuals were measured for weight (WT), snout-vent length (SVL), tail length (TL) and tail regeneration (R), and their sexes were recorded based on secondary sexual characteristics. Then all individuals were returned to the original capture locations. During each survey, each animal was marked with a unique number using a non-toxic marker when first captured. The identity and location of each recapture were also recorded but animals were not caught.

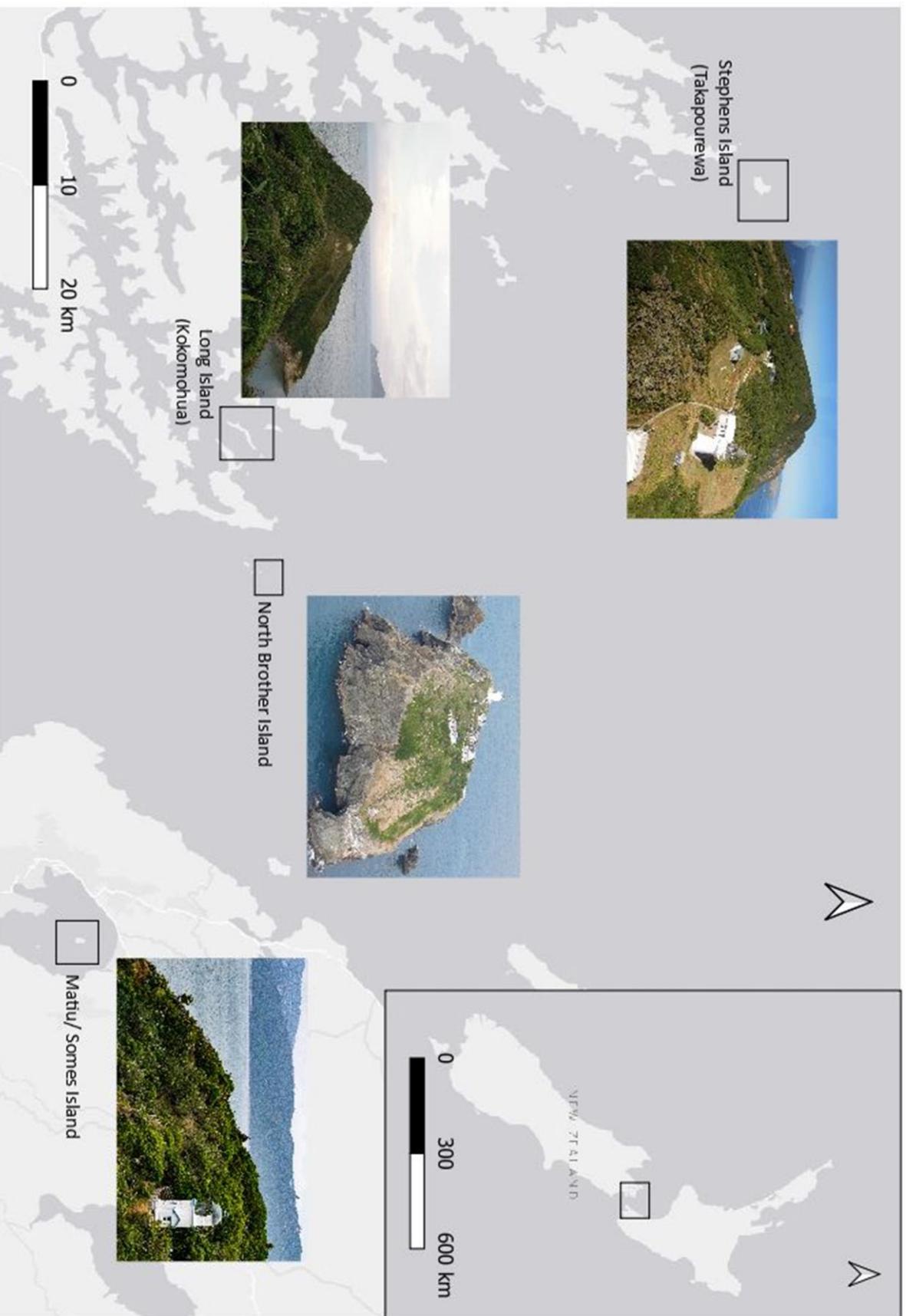


Figure 3.1. North Brother Island, Matiu / Somes Island, Long Island (Kokomohua) and Stephens Island (Takapourewa) of New Zealand. North Brother Island is mainly weathered rock, and only the northern face is covered by low vegetation and shallow soil. Matiu/ Somes Island, Long Island and Stephens Island are covered with dense vegetation and contain a substantially greater variety of habitat. Photos are by courtesy of Susan Kell (Long Island and Stephens Island) and Ian Blixt (Matiu/ Somes Island).

Table 3.1. Demographic information of tuatara populations on North Brother Island, Matiu/ Somes Island, long Island and Stephens Island of New Zealand.

Tuatara population	Locations	Coordinates	Island size (ha)	Population estimates	Origins	Notes
North Brother Island	Cook Strait	41°06'13"S, 174°26'29"E	4	322 adults by 2018 (Chapter 2)	A natural population	
Matiu/ Somes Island	Wellington Harbour	41°15'30"S, 174°51'57"E	25	Unknown	North Brother Island	In 1998, 20 adults (10 females and 10 males) and 35 juveniles of uncertain sex were released to Matiu/ Somes Island to start the new population. Adults were directly from North Brother Island, and 35 juveniles were incubated in captivity from eggs collected from North Brother Island.
Long Island	Marlborough Sounds	41°06'57"S, 174°16'48"E	141	Unknown	North Brother Island	In 2007, 53 juveniles (19 males and 35 females) were released to Long Island to start the new population. They were incubated in captivity from eggs collected from North Brother Island. Their sex was assumed based on the incubation temperatures at which 100% males and 100% females hatch.
Stephens Island	Marlborough Sounds	40°40'13"S, 173°59'49"E	150	30,000-50,000 (Dawbin, 1982)	A natural population	The largest natural tuatara population.

Table 3.3. Tuatara population surveys on North Brother Island, Long Island and Maitiu/ Somes Island.

Tuatara populations	Surveys	Dates	Search effort	Number of researchers per day/night
North Brother Island	1	Jan-88	3 nights	Unknown
	2	Dec-88	3 nights	4
	3	Nov-89	3 nights	5
	4	Oct-90	7 nights	Unknown
	5	Nov-90	3 nights	3
	6	Nov-91	3 nights	3
	7	Nov-93	5 nights	3
	8	Nov-94	3 nights	3
	9	Nov-95	1 night	4
	10	Mar-96	5 nights	5
	11	Feb-97	5 nights	6
	12	Dec-97	5 nights	5
	13	Oct-98	2 nights	5
	14	Aug-00	1 night	3
	15	Nov-Dec 2000	52 nights	3
	16	Nov-Dec 2001	32 nights	2
	17	Mar-05	5 nights	5
	18	Nov-08	4 nights	6
	19	Nov-10	5 nights	5
	20	Nov-11	5 nights	5
	21	Mar-12	4 nights	5
	22	Nov-16	5 nights	5
	23	Nov-18	5 nights	5
	24	Nov-19	5 nights	5
Long Island	1	Jan-19	5 nights	5
Maitiu/ Somes Island	1	Nov-19	10 days and nights	4-6
	2	Mar-20	10 days and nights	3-7

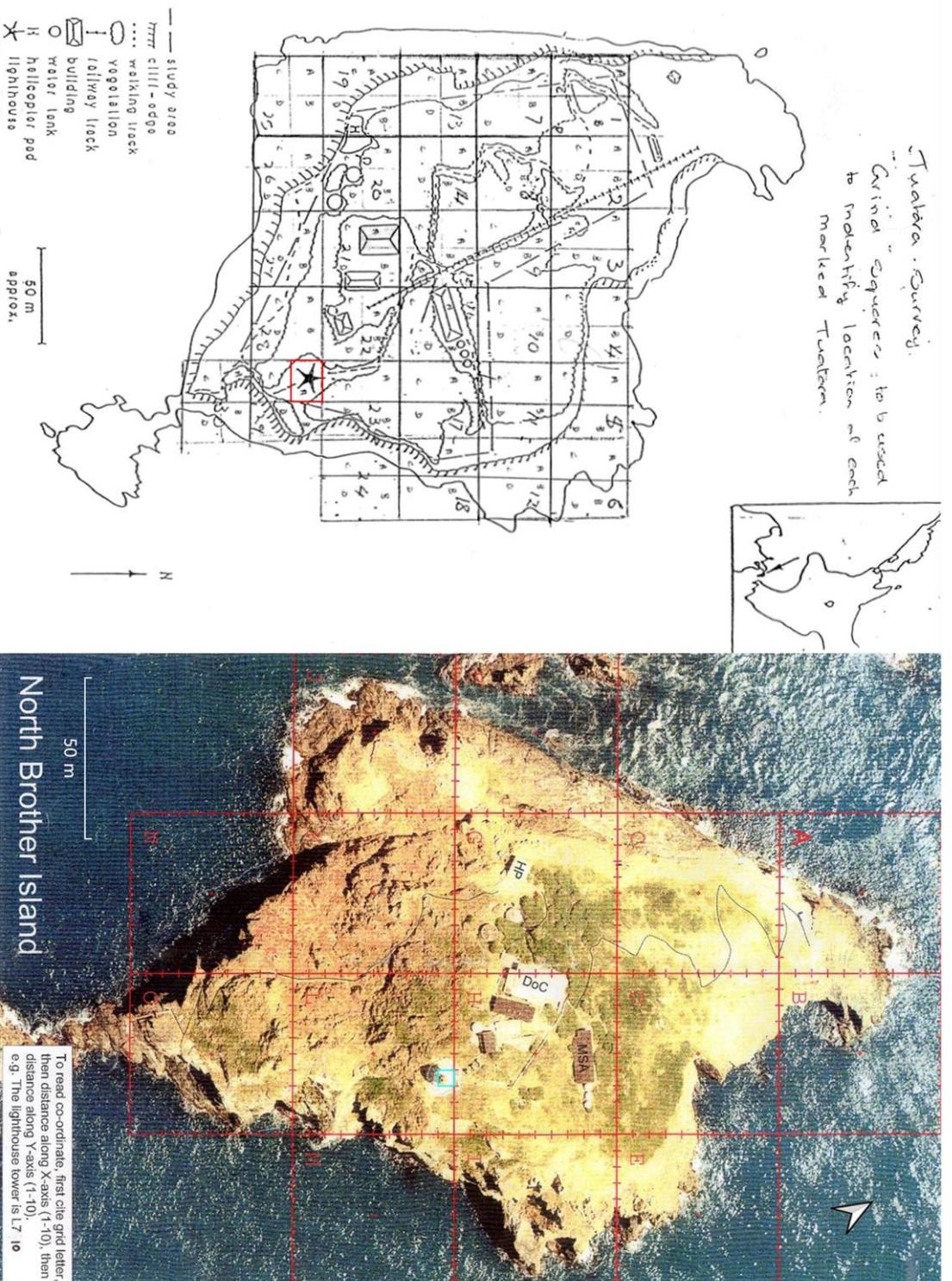


Figure 3.2. Two versions of grid maps of North Brother Island. The first version of grid map (left) was in use until 2000. The second grid map (right) has been in use since 2001. For each capture and recapture, the location on the grid map was recorded, then the coordinates of the centroid of each grid was allocated to all captures and recaptures that occurred in this grid. For example, the location of the lighthouse was recorded as 29 A on the first version of grid map (red square) and L7-10 on the second version of grid map (blue square). The approximate area of each grid is 100 m² (10 × 10m) for the first version of grid map and 25 m² (5 × 5m) for the second version of grid map.

For activity area estimates from translocated populations, I collected tuatara survey data in January 2019 for five consecutive nights on Long Island, and in November 2019 and March 2020 for ten days and nights respectively on Matiu/ Somes Island (Table 3.2). Tuatara were caught by hand at night on Long Island and in the afternoon and at night on Matiu/ Somes Island. I identified each individual by toe clips which were given prior to translocation, and recorded locations in coordinates using GPS (Garmin Rino 650), WT, SVL, TL and R and sex in the field. The method of marking animals when they were first captured and recording recaptures was the same as the surveys on North Brother Island.

Data analyses

For the North Brother Island tuatara population, several captures and recaptures were recorded as juveniles and subadults. An SVL of 163 mm is the minimum size for both sexes to reach sexual maturity (Mitchell et al., 2010). Due to the lack of knowledge on territoriality of tuatara at pre-adult stage, as well as their limited captures and recaptures, individuals which were considered as juveniles or subadults, or had an SVL of less than 163 mm were excluded. For North Brother Island, I performed georeferencing on both grid maps and extracted the coordinates of the centroid of each grid cell in QGIS (version 3.16.16). These coordinates were allocated to all captures and recaptures which occurred in each grid cell. Individual activity area was estimated by 95% minimum convex polygon (MCP) based on the coordinates of locations within specific time span (specified below). Activity areas were not estimated using kernel estimators due to their inaccuracy for herpetofauna (Row & Blouin-Demers, 2006). Due to the high site fidelity of tuatara (Moore, Daugherty, & Nelson, 2009), a small minimum number of locations (five locations) was selected for tuatara MCP estimation. Analyses were performed in R (version 4.1.2) except for overlap of activity areas that was analyzed in QGIS. Since data sets in this study did not meet assumptions for parametric statistical tests, non-parametric statistical tests were used to perform data analyses.

Activity area over 30 years

Activity area was estimated over 24 surveys from January 1988 to November 2019 for the North Brother Island tuatara population. I calculated the size of activity area of each adult based on all capture records for those captured five or more times. The number of locations is normally positively correlated with the size of convex polygon in lizard species (Rose, 1982).

As such, the relationship between tuatara activity area size and the number of locations was tested using a Spearman rank correlation test for each sex. The size of activity area was compared between sexes using a Kruskal-Wallis test. I examined whether covariates such as SVL, WT and body condition (BC, the ratio of log-transformed WT to log-transformed SVL) were correlated with individual activity area using Spearman rank correlation tests. For each tuatara, I used the mean (SVL, WT and BC respectively) over the records included in the MCP estimation. Based on sex-specific differences in activity area size detected in lizards (Aragón et al., 2004) and tuatara on Takapourewa (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009), the correlations between covariates and activity area size were performed for each sex respectively.

Activity area by decade

Temporal variation in activity area size was examined in the North Brother Island tuatara population. Activity area size of each tuatara was estimated by decade (January 1988-January 1998, August 2000-November 2008, November 2010- November 2019). The effects of sex on activity area size were analyzed within each decade and the effects of decade (as a categorical variable) on activity area size were analyzed using Kruskal-Wallis tests. However, the second decade only had a few individuals (four males and one female) with enough repeat captures for activity area estimation and was excluded from this analysis.

Spatial interactions and distributions

Spatial interactions of tuatara on North Brother Island were investigated by assessing the overlap between activity areas of individuals over a relatively short time span. Because few tuatara had enough recaptures for MCP estimation within each survey, I combined capture and recapture records over the latest three surveys (in 2016, 2018 and 2019) to estimate recent activity areas. The activity area size was compared between sexes using a Kruskal-Wallis test. I investigated male-male overlap (male-male competition) and male-female overlap (female access) of activity areas. For each focal male, I calculated the number of other males and the number of females that their activity area overlapped. I then calculated the cumulative percent of the activity area that each focal male overlapped other males and females respectively. Using Spearman rank correlation tests, I investigated whether SVL, WT, BC and activity area size of the focal male predicted the number of other males and the

number of females overlapped, as well as the cumulative percent of the activity area that other males and females overlapped. In addition, male tuatara were divided into two groups based on whether they overlapped other males and females or not, and the two groups were compared on their SVL, WT, BC and activity area size using Kruskal-Wallis tests.

The spatial distributions of tuatara were investigated based on activity areas over the last three surveys. I extracted centroids of activity areas as animals' activity centres (Dixon & Chapman, 1980; Winder et al., 2015) and performed the nearest neighbour analysis in QGIS, to test whether this population was dispersed versus randomly distributed. In theory, individuals, especially males, are supposed to be highly dispersed in a territorial population (J. L. Brown & Orians, 1970). Furthermore, for each male, I estimated the average distance to its nearest five males (male-male competition) and to its nearest five females (female access), then I explored how covariates of the focal male (WT, SVL and BC) were correlated to the distances to its five nearest males and to five nearest females using Spearman rank correlation tests.

Translocated populations

Since there were small numbers of captures and recaptures on Long Island and Matiu/ Somes Islands, all individuals were included in the analyses. Within each survey, the maximum travel distance was calculated for individuals having at least two capture and recapture records, and the 100% MCP was estimated for individuals having at least three capture and recapture records, representing activity area estimates.

Results

Activity area over 30 years

From January 1988 to November 2019, 609 adults (224 females and 385 males) were captured with 2851 capture records (929 female and 1922 male records). The average captures of each individual were 4.68 (range = 1-16), with 4.15 (range = 1-15) for females and 4.99 (range = 1-16) for males respectively. There were 259 individuals (82 females and 177 males) included in activity area estimation (Figure 3.3), with 2036 capture records (602 female and 1434 male records). For the individuals included in activity area estimation, the average captures were 8.10 (range = 5-16) for males and 7.34 (range = 5-15) for females, with no significant

difference between sexes (Kruskal-Wallis test; $P = 0.06$). Some individuals were repeatedly captured at the exactly the same locations, therefore, the size of their activity areas was estimated as zero. The activity area was significantly correlated with the number of locations in both females (Spearman rank correlation; $r_s = 0.51$, $N = 82$, $P < 0.001$) and males ($r_s = 0.51$, $N = 177$, $P < 0.001$). There were significantly larger activity areas in males than females (Kruskal-Wallis test; $P = 0.003$), with average size of $94.3 \pm 8.79 \text{ m}^2$ for males (range = 0-675) and $57.3 \pm 9.17 \text{ m}^2$ for females (range = 0-443). There was no significant correlation of activity area size with SVL, WT or BC in both sexes (Table 3.3).

Table 3.3. Sex-specific Spearman rank correlation tests between activity area size of tuatara and individual covariates on North Brother Island. Activity area size was calculated based on captures over all surveys from January 1988 to November 2019. SVL, WT and BC were the mean over the records included in the activity area estimation.

Sex	Covariate	Correlation coefficient (r_s)	Significance level (P)
Males ($N = 177$)	SVL	0.03	0.69
	WT	0.04	0.62
	BC	0.03	0.66
Females ($N = 82$)	SVL	-0.12	0.28
	WT	-0.08	0.47
	BC	-0.05	0.67



Figure 3.4. Activity areas of tuatara on North Brother Island over 24 surveys (January 1988 – November 2019). In total, 82 females (left) and 177 males (right) were included in activity area estimation. Polygons present activity areas; dots represent the locations of tuatara with activity areas as zero (i.e., repeated captures at exactly the same location). Male activity areas ($94.3 \pm 8.79 \text{ m}^2$) were significantly larger than females ($57.3 \pm 9.17 \text{ m}^2$) (Kruskal-Wallis test; $P = 0.003$).

Activity area by decade

During the first decade, 428 individuals (157 females and 271 males) were captured with 1161 capture records (381 female and 780 male records). The average captures of each individual were 2.71 (range = 1-7), with 2.43 (range = 1-7) for females and 2.88 (range = 1-7) for males. There were 54 individuals (13 females and 41 males) included for activity area estimation during the first decade, with 299 capture records (76 female and 223 male records). There was no significant difference in activity area size between males and females (Kruskal-Wallis test; $P = 0.51$), with means of $31.7 \pm 19.3 \text{ m}^2$ (range = 0-249) for females and $33.6 \pm 8.01 \text{ m}^2$ (range = 0-231) for males. During the third decade, 293 individuals (107 females and 186 males) were captured, with 835 capture records (263 female and 572 male records). The average captures were 2.85 (range = 1-6), with 2.46 (range = 1-6) for females and 3.08 (range = 1-6) for males. There were 53 individuals (10 females and 43 males) included for activity area estimation, with mean of $28.4 \pm 13 \text{ m}^2$ (range = 0-109) for females and $46.8 \pm 7.1 \text{ m}^2$ (range = 0-194) for males. There was no significant difference in activity areas between sexes (Kruskal-Wallis test; $P = 0.1268$) in the third decade. For the individuals included in activity area estimation, there was no significant difference in the number of individual captures between the first and the third decades (Kruskal-Wallis test; $P = 0.52$), with the average captures at 5.54 (range = 5-7) in the first decade and at 5.40 (range = 5-6) in the third decade. Comparing the size of activity areas between two decades, there were significantly larger activity areas in the third decade (Kruskal-Wallis test; $P = 0.006$), with means of $33.2 \pm 7.55 \text{ m}^2$ (range = 0-249) and $43.3 \pm 6.29 \text{ m}^2$ (range = 0-194) respectively (Figure 3.4). Therefore, individual activity areas increased over time in North Brother Island tuatara population.



Figure 3.4. Activity areas of tuatara on North Brother Island in the first decade and in the third decade. There were 54 individuals included in activity area estimation in the first decade (left; January 1988 - January 1998) and 53 individuals in the third decade (right; November 2010 - November 2019). Polygons represent activity areas; dots represent the locations of tuatara with activity area estimates as zero (i.e., repeated captures at exactly the same location). There were significant smaller activity areas in the first decade ($33.2 \pm 7.55 \text{ m}^2$) than in the third decade ($43.3 \pm 6.29 \text{ m}^2$) (Kruskal-Wallis test; $P = 0.006$).

Spatial interactions and distributions

Over three surveys of 2016, 2018 and 2019, there were 696 (225 females and 471 males) captures and recaptures of 237 individuals (85 females and 152 males). The survey with the highest capture number ($N = 172$ in 2018) was used to provide a visual distribution of captured tuatara on the island (Figure 3.5). The average number of captures and recaptures was 2.94 (range 1-11), with 2.65 (1-9) for females and 3.1 (1-11) for males. There were 42 individuals (12 females and 30 males) included for activity area estimation, with 261 capture and recapture records (75 female and 186 male records) (Figure 3.6). For the individuals included in activity area estimation, the average captures were 6.20 (range = 5-11) for males and 6.25 (range = 5-9) for females, with no significant difference between sexes (Kruskal-Wallis test; $P = 0.40$). The average activity area was $43.9 \pm 21.4 \text{ m}^2$ for females (0-259 m^2) and $70 \pm 13.7 \text{ m}^2$ (0 to 291 m^2) for males, with weakly significant larger activity area size for males (Kruskal-Wallis test; $P = 0.08$).

I removed four individuals with activity area estimate as zero (i.e., repeated captures at exactly the same location) and performed overlap analyses on 38 tuatara (28 males and 10 females). On average, males overlapped 0.93 ± 0.21 other males (range = 0-4). For each focal male, the average overlap size with another male was $11.84 \pm 2.41 \text{ m}^2$ (range = 0-56.47), accounting for $15 \pm 2.9 \%$ (range = 0-75.2%) of activity area of the focal male. Each male had the average cumulative overlap with other male(s) at $20.9 \pm 5.6\%$ (range = 0-100%) of its activity area. For each focal male, neither the number of other males overlapped nor the cumulative overlap with other males was significantly correlated with its SVL, WT or BC (Table 3.4). However, there was significant positive correlation between activity area size of the focal male and the number of other males overlapped (Spearman rank correlation test; $r_s = 0.57$, $N = 28$, $P = 0.002$), and cumulative overlap with other males (Spearman rank correlation test; $r_s = 0.42$, $N = 28$, $P = 0.02$) (Table 3.4). Thirteen of 28 males did not overlap any other males. There was no significant difference in WT, SVL and BC between overlapping males and non-overlapping males (Table 3.5). However, I found significant larger activity area sizes of overlapping males than non-overlapping males (Kruskal-Wallis test; $P = 0.001$), with $113 \pm 21.6 \text{ m}^2$ and $30.8 \pm 6.9 \text{ m}^2$ respectively.



Figure 3.5. Distribution of adult tuatara on North Brother Island in 2018 survey. There were 172 (59 females and 113 males) adult tuatara were captured in 2018 survey. Blue dots represent females; yellow dots represent males.



Figure 3.6. Activity areas of tuatara on North Brother Island over three surveys of November 2016, 2018 and 2019. In total, 12 females (blue polygons and dots) and 30 males (yellow polygons and dots) were included in activity area estimation. Polygons present activity areas; dots represent the locations of tuatara with activity area estimates as zero (i.e., repeated captures at exactly the same location). There were weakly significant smaller activity areas in females ($43.9 \pm 21.4 \text{ m}^2$) than in males ($70 \pm 13.7 \text{ m}^2$) (Kruskal-Wallis test; $P = 0.08$).

Table 3.4. Spearman rank correlation tests between overlap estimates and covariates of the focal male. Male-male overlap (male competition) and male-female overlap (female access) were explored based on activity areas (95% MCPs) derived from capture and recapture records in the latest three surveys (in 2016, 2018 and 2019).

Overlap type	Overlap estimates	Covariate of the focal male	Correlation coefficient (r_s)	Significance level (P)
Male-male $N=28$	Number of other males overlapped	SVL	0.02	0.92
		WT	-0.04	0.82
		BC	-0.04	0.83
	Cumulative overlap with other males	95% MCP	0.57	0.002**
		SVL	0.05	0.8
		WT	-0.004	0.98
		BC	0.007	0.97
		95% MCP	0.42	0.02*
		SVL	-0.03	0.88
		WT	-0.08	0.68
Male-female $N=28$	Number of females overlapped	BC	-0.08	0.68
		95% MCP	0.46	0.01**
		SVL	-0.05	0.8
	Cumulative overlap with females	WT	-0.1	0.62
		BC	-0.09	0.64
		95% MCP	0.42	0.03*
		95% MCP	0.42	0.03*

Table 3.5. Kruskal-Wallis test between overlapping and non-overlapping males on their covariates. Male-male overlap (male competition) and male-female overlap (female access) were explored based on activity areas (95% MCPs) derived from capture and recapture records in the latest three surveys (in 2016, 2018 and 2019).

Overlap type	Number of overlapping males	Number of non-overlapping males	Covariate of males	Non-overlapping males	Overlapping males	Significance level (<i>P</i>)
Male-male	15	13	SVL	200 ± 5.49	205 ± 3.93	0.386
			WT	281 ± 24.8	289 ± 17.5	0.804
			BC	1.06 ± 0.01	1.06 ± 0.008	0.803
			95% MCP	30.8 ± 6.92	113 ± 21.6	0.001***
Male-female	6	22	SVL	203 ± 3.89	203 ± 6.30	0.337
			WT	289 ± 17.5	272 ± 23.6	0.634
			BC	1.06 ± 0.008	1.05 ± 0.01	0.253
			95% MCP	55.7 ± 12.3	146 ± 38.2	0.016*

On average, each male overlapped 0.25 ± 0.098 females (range = 0-2). For each focal male, the average overlap size with a female was at $5.45 \pm 2.23 \text{ m}^2$ (range = 0-40.48), accounting for $6.06 \pm 2.93\%$ (range = 0-66.4%) of its activity area. On average, each male had the cumulative overlap with female(s) at $6.28 \pm \%$ (range = 0-66.4%) of its activity area. For each focal male, neither the number of females overlapped nor the cumulative overlap with females was significantly correlated with its SVL, WT or BC (Table 3.4). However, there was significant positive correlation between size of the activity area of the focal male and the number of females overlapped (Spearman rank correlation test; $r_s = 0.46$, $N = 28$, $P = 0.01$), and cumulative overlap with females (Spearman rank correlation test; $r_s = 0.42$, $N = 28$, $P = 0.03$) (Table 3.4). Twenty-two of 28 males did not overlap any females. There was no significant difference in WT, SVL and BC between overlapping males and non-overlapping males (Table 3.5). However, there was significant larger activity area in overlapping males than non-overlapping males (Kruskal-Wallis test; $P = 0.016$), with $146 \pm 38.2 \text{ m}^2$ and $55.7 \pm 12.3 \text{ m}^2$ respectively.

The nearest neighbour analysis provided an unreliable output due to the limited number of tuatara available for the analysis. Therefore, whether North Brother Island tuatara population is dispersed or randomly distributed is unclear. The mean distance between each male to its nearest five males is $15.80 \pm 4.63\text{m}$ (range = 8.60-22.99), without significant correlations with its SVL, WT and BC (Table 3.6). Likewise, the mean distance between each male to its nearest five females is $22.88 \pm 1.51\text{m}$ (range = 13.11-43.10), without significant correlations with its SVL, WT and BC (Table 3.6).

Translocated populations

On Matiu/Somes Island, there were 59 capture and recapture records of 24 individuals (mean captures = 2.46 ± 0.35 ; range = 1 - 7) in 2019, and 54 capture and recapture records of 31 individuals (mean captures = 1.74 ± 0.22 ; range = 1 - 6) in 2020. On average, the individual maximum travel distance was $21.45 \pm 5.88 \text{ m}$ ($N = 14$; range = 1.01 - 70.97) in 2019 and $44.16 \pm 15.55 \text{ m}$ ($N = 12$; range = 2.03 - 178.64) in 2020 (Figure 3.7). The average activity area was $177.38 \pm 113.04 \text{ m}^2$ ($N = 9$; range = 12.86 - 1070.97) in 2019 and $412.45 \pm 348.62 \text{ m}^2$ ($N = 6$; range = 1.66 - 2151.83) in 2020 (Figure 3.7). On Long Island, there were 27 capture and recapture records of 19 individuals in 2019 (mean captures = 1.42 ± 0.14 ; range = 1 - 3). The

individual maximum travel distance was 7.57 ± 1.46 m ($N = 7$; range = 1.66 - 11.93) (Figure 3.8).

There were insufficient capture records for activity area estimation.

Table 3.6. Spearman rank correlation tests between the focal male covariates and the distance to other five nearest males and to five nearest females. Male-male distance (male competition) and male-female distance (female access) were explored based on the centroids of activity areas derived from capture and recapture records in the latest three surveys (in 2016, 2018 and 2019).

Distance type	Covariate of the focal male	Correlation coefficient (r_s)	Significance level (P)
Male-male $N = 30$	SVL	0.25	0.19
	WT	0.28	0.13
	BC	0.25	0.18
Male-female $N = 30$	SVL	0.25	0.18
	WT	0.33	0.07
	BC	0.33	0.08



Figure 3.7. Tuataras maximum travel distances (left) and activity areas (right) on Matiu/ Somes Island in 2019 and 2020 surveys. Yellow dashed lines ($N = 14$) and polygons ($N = 9$) represent 2019 survey; blue dashed lines ($N = 12$) and polygons ($N = 6$) represent 2020 survey. Activity areas were estimated as 100% MCPs based on at least three capture and recapture records.



Figure 3.8. Tuatara maximum travel distances on Long Island in 2019 survey ($N = 7$).

Discussion

In the North Brother Island tuatara population, there were larger activity areas in males than females, but individual WT, SVL and BC did not predict the size of activity area in either sex. Individuals maintained larger activity areas when the population size became smaller. There was no evidence to support larger males maintaining exclusive activity areas (e.g., overlapping fewer other males, less percent of their activity area overlapped by other males, a larger distance to other males), or securing greater access to females (e.g., overlapping more females, larger percent of their activity area overlapped by females, a smaller distance to females). In North Brother Island tuatara population, individuals showed high site fidelity over years. By contrast, tuatara of translocated populations travelled large distances and showed large activity areas within a short survey.

Empirical studies on reptiles suggest a sufficient number of sightings for accurate estimates of activity areas (Rose, 1982; Stone & Baird, 2002). For example, a study showed the minimum sample sizes for collared lizards (*Crotaphytus collaris*) and lava lizards (*Microlophus albemarlensis*) were 45 and 84 sightings, respectively (Stone & Baird, 2002). In this study, the threshold of the minimum number of sightings for MCP estimation was five, which is lower than most of studies. I justified this lower number because tuatara show high site fidelity (Moore, Daugherty, & Nelson, 2009), therefore, even a small number of sightings can effectively reflect the spatial use of tuatara in a population proposed to be at or near carrying capacity (Hoare et al., 2006). Although the estimate of activity area increased with the number of locations for 95% MCP estimation in both sexes, the sex-specific difference in activity area size was confirmed in this population. There were consistent larger activity areas in males over survey data of 30 years, by decade, and over the surveys of 2016, 2018 and 2019. This male advantage in maintaining larger activity areas is in accordance with two previous studies in Takapourewa tuatara population (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009). Larger activity areas in males are prevalent in lizards, because by having large activity areas males can increase female access and reproductive success (Perry & Garland, 2002; Schoener & Schoener, 1982). Previous studies showed male tuatara are polygynous and defend females as a resource (Gillingham et al., 1995; Moore, Daugherty, Godfrey, et al., 2009), therefore, larger activity areas can improve male reproductive success by accessing more females. Also, tuatara are sexually dimorphic, where males have larger

body size and head size than females (Dawbin, 1982; Herrel et al., 2010), thus, males have dominance over females for resource availability such as food and space (Wörner, 2009; Chapter Four). Moreover, a consistent and strong male bias over 30 years in tuatara population on North Brother Island can only worsen the disadvantage of females in competition for space and food (Grayson et al., 2014; Nelson et al., 2002; Chapter Two). The body condition of adult female tuatara declined at a greater annual rate than that of males on North Brother Island with a long-term male bias (Hoare et al., 2006; Chapter Two).

The larger activity areas in the third decade than those in the first decade are closely related to the decreased population size. With the long-term male bias, the population size has decreased by 28% in the last 20 years in the North Brother Island tuatara population, which means a substantial decrease in population density (Chapter Two). The resources on North Brother Island are limited, thus the decreased population density can alleviate the intense resource competition and correspondingly reduce the costs on territorial defence. As a result, tuatara were supposed to enlarge their activity areas to access more resources to improve their fitness. This adjustment of activity areas in response to variations in territorial interactions, which is regulated by population density, is also observed in other vertebrates. For example, as the population density declined due to an outbreak of disease, surviving urban foxes (*Vulpes vulpes*) increased their activity areas because of less territorial interactions with conspecific competitors (Baker et al., 2000). Furthermore, survey data of translocated populations support the density-dependence in space use of tuatara. With the substantially less densities, individuals of translocated populations showed large distances and activity areas within one short survey (5 - 10 days), while tuatara on North Brother Island showed high site fidelity over many years of surveys.

The positive relationship between body size and activity area in vertebrates was not observed in this study. Neither SVL, WT nor BC predicted the size of activity area estimated over the 30-year survey data in both sexes of tuatara on North Brother Island. A previous study on Takapourewa showed SVL and BC of male tuatara had no influence on territory size, probably because high habitat diversity and food availability on the island can meet tuatara's all necessary requirements for resources within a relatively small space (Moore, Daugherty, & Nelson, 2009). However, resources are substantially limited on North Brother Island (Cree & Butler, 1993; Gibbs, 1999; Markwell, 1999), where tuatara are smaller and skinnier than

other populations (Cree et al., 1991; Thompson et al., 1992; Chapter Two). By contrast, individuals showed a rapid growth in SVL and WT after being translocated from North Brother Island to other islands (e.g. Titi Island, Nelson, Keall, Brown, et al., 2002). Therefore, the activity area on North Brother Island may not meet tuatara's necessary requirements for resources, and the lack of a relationship between body size and activity area size on the island could result from the following two reasons. First, instead of maintaining larger activity areas, larger individuals may use alternative tactics to gain advantage in resource competition. Behavioural observations of tuatara on Takapourewa and in captive facilities showed larger individuals have dominance in physical conflicts over resources competition (Moore, Daugherty, & Nelson, 2009; Wörner, 2009; Chapter Four). As such, larger tuatara on North Brother Island may have a physical advantage in securing resources. Second, various factors can influence activity area size, some of which were not included in the analyses of this study. For example, habitat type usually plays a key role on animal spatial distribution, because food abundance can vary between differing habitat types, which influences activity area size (Perry & Garland, 2002; Simon, 1975). On Takapourewa, tuatara in open habitats had larger territories than those in wooded habitats (Gillingham et al., 1995). Therefore, other factors such as the variable habitat characteristics on North Brother Island may mediate the relationship between body size and activity area.

In North Brother Island tuatara population, I did not observe an advantage of larger males in maintaining exclusive activity areas and securing greater access to females. By contrast, this advantage of large male tuatara was found in Takapourewa population (Moore, Daugherty, & Nelson, 2009). Compared with an even sex ratio in the Takapourewa tuatara population, there has been a strong and continuous male bias in the North Brother Island population, which can intensify male-male competition (Clutton-Brock et al., 1997; Holveck et al., 2015). Together with the limited resources, territorial defence on North Brother Island can be costly. As response to variations in sex ratios, males can change their mating tactics to maximize reproductive success (Jirotkul, 1999; Krupa & Sih, 1993; Wearing-Wilde, 1996). Behavioural observation on Takapourewa showed large male tuatara appear to tolerate the presence of smaller males, because large males always outcompete small ones in male-male conflicts and they can restrict small males from mating by interrupting courtship attempts (Moore, Daugherty, & Nelson, 2009). As such, on North Brother Island, there might be

alternative strategies in large males to acquire territorial dominance, which needs to be investigated by behavioural observations.

The tuatara population on North Brother Island provides a case study in activity area patterns in the context of a strong and continuous male bias. The intensified male-male competition driven by a long-term male bias could probably change ways of both intra- and intersexual interactions in a territorial population. However, some limitations may affect this study. First, the detectability of tuatara may influence the estimation of 95% MCP on North Brother Island. Tuatara are more likely to be spotted at open sites such as on the track, around houses or on open rocks rather than in the bushes, which could bias the 95% MCP estimates for animals in the bushier areas. The precision of 95% MCP estimates can be affected by using the centroid coordinates of grids on the map rather than the actual capture coordinates. Second, most individuals were not included in the analyses on overlap patterns, which may not reflect the full variation of spatial interactions of this tuatara population. It is challenging to capture every individual within a short survey, and most of the captured tuatara were excluded from 95% MCP estimation due to their limited number of captures and recaptures. For example, the population size of 2018 was estimated as 322 adults (Chapter Two), and 172 adults were captured in 2018 survey (Figure 3.5). However, there were only 42 adults included in the overlap pattern analyses based on capture and recapture records over 2016, 2018 and 2019 surveys. The excluded individuals certainly influence the behaviour and distribution of others (Moore et al., 2010). Therefore, future research on North Brother Island could focus on increasing the number of captures and recaptures especially in the area with low capture probabilities and recording actual coordinates of captures and recaptures using GPS to provide more detailed information for activity area patterns of this tuatara population. Third, the larger activity areas observed in the third decade compared to the first decade might be influenced by different units between the two grid maps. This potential confounding factor can be addressed by employing the earlier grid map for the capture and recapture records of the third decade.

Despite these limitations, long-term studies of reptile activity patterns are rare and this study provides several important implications for conservation management. First, resource limitation is an important factor driving the dynamics of relic populations at high density. Translocated populations ensure the future of this species in additional locations,

while also offering the opportunity to compare spatial structure and population dynamics under lower density. Second, management of populations should consider the current and future population sex ratio when considering habitat restoration or other restorations. Given the long-lived nature of this species, and many other reptiles, including detailed spatial information can be just as important as trends in population size and reproduction.

Chapter 4

Behavioural interactions between male and female tuatara using observations from captive populations

Introduction

In social animals, dominant individuals have increased access over other individuals to critical resources, such as food, shelter and mates, which in turn can increase fitness based on dominance status (Alberts, 1994; Kaufmann, 1983; Wagner & Gauthreaux, 1990). Individuals establish and maintain dominance through behaviours, such as mate guarding, eviction of competitors from territories, increasing their visibility, aggression and social stress. The development of dominant behaviours can be driven by multiple factors, such as physical condition, body size, age, personality, and population density (Chichinadze et al., 2014; Kaufmann, 1983; Ruby, 1984; Tibbetts et al., 2022). It is widely acknowledged that sexual selection, such as male-male competition and female choice, can influence individual fitness, and consequently, population viability (Candolin & Heuschele, 2008; Holman & Kokko, 2013; Kokko & Brooks, 2003; Lumley et al., 2015). Therefore, investigating dominant behaviours can provide implications for understanding how intra-specific interactions can be drivers of population viability.

Social dominance is often associated with sexual selection in reptiles, such as male-male competition and female mate choice (Mason & Parker, 2010). For example, in Iberian rock lizards (*Lacerta monticola*), males with larger heads exhibit dominance over males with smaller heads in male-male competition, as larger heads confer an advantage in male-male agonistic interactions (Lopez et al., 2002). Female Amazon lava lizards (*Tropidurus torquatus*) prefer males with dominant features, such as larger body size or head

dimensions, which can reflect the high quality of male territories (Calsbeek & Sinervo, 2002a, 2002b). Many empirical studies on reptiles showed social dominance and social behaviour can influence factors such as habitat use, resource acquisition and population size, which may ultimately have implications for population ecology and viability (Frost & Bergmann, 2012; Le Galliard et al., 2005; Pratt et al., 1992; Whiting & Miles, 2019). For example, juvenile zebra-tailed lizards (*Callisaurus draconoides*) reside in low-quality habitats as they are subordinate to adults in resource competition (Frost & Bergmann, 2012). An excess of male common lizards (*Zootoca vivipara*, formerly *Lacerta vivipara*) can result in male aggression to females, driving a decline in population size due to female emigration and a decline in female survival and fecundity (Le Galliard et al., 2005).

Observational studies play a crucial role in understanding the behaviour of animals. However, recording behaviour in natural populations is often challenging due to the difficulty in tracking individuals and obtaining multiple sightings of the same individual in complex environments, particularly for secretive species such as reptiles (Stamp Dawkins, 2008; Warwick, 1990). By contrast, studies of captive reptile populations allow for repeated behavioural data collection on the same individuals, with the understanding that captive individuals may show some behavioural differences from wild populations (Warwick, 1990).

Tuatara (*Sphenodon punctatus*) are long-lived reptiles endemic to New Zealand. They are sexually dimorphic in body size and head dimensions, with males being larger than females (Gillingham et al., 1995; Herrel et al., 2010). As social reptiles, male tuatara defend access to females within their territories using a set of behaviours, such as body inflation, positioning, crest erection, head-shaking, chasing and biting (Gillingham et al., 1995; Gillingham & Miller, 1991). Research on a well-studied tuatara population on Takapourewa (Stephens Island) showed males have larger territories than females (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009). Also, large males have dominance in male-male aggressive interactions, overlapping with more females in their territories, and excluding other males more effectively from their territories (Moore, Daugherty, & Nelson, 2009). As such, larger males are dominant in mating activity with higher mating success (Moore, Daugherty, Godfrey, et al., 2009). Additionally, in a study on captive juveniles which originated from Takapourewa, large individuals are more aggressive, and males outcompete

females for food and space (Wörner, 2009). Therefore, sex and size may play important roles in social dominance of tuatara on Takapourewa.

Tuatara are have a rare pattern of temperature-dependent sex determination (TSD), where males hatch from nests at higher temperatures (Cree et al., 1995; Mitchell et al., 2006). As such, tuatara populations are at risk of developing a male bias under a warming climate (Mitchell & Janzen, 2010). Since the late 1990s, there has been a consistent male bias in North Brother Island tuatara population, together with a continuous decline in body condition and survival with females having a steeper rate of decline, as well as a declining population size (Grayson et al., 2014; Hoare et al., 2006; Mitchell et al., 2010; Nelson, Keall, Pledger, et al., 2002). This long-term male bias poses a concern for population viability of tuatara on North Brother Island, because sex ratio can influence sexual selection (Clutton-Brock et al., 1984; Gwynne, 1990; Jirotkul, 1999), and ultimately have impacts on population viability (Dale, 2001; Heinsohn et al., 2019; Le Galliard et al., 2005). However, the impacts of a male bias on tuatara behaviour have not been investigated. Tuatara are extremely cryptic reptiles as they are nocturnal and inhabit underground burrows which leads to their low detectability in the wild (Ussher, 1999). As such, observations on the behaviours of captive tuatara can build understanding of how dominance is associated with intra-specific interactions, which in turn provides implications of a male bias for population viability.

In this study, I observed behaviours of captive tuatara to investigate the significance of dominance on individual interactions and space use. I tested the following hypotheses: (1) large males have an advantage in access to females; (2) males have larger activity areas than females; (3) males are seen out of the burrow more frequently (have higher visibility) than females; (4) females show low visibility when the nearest male is out of the burrow; (5) males and large tuatara have dominance in aggressive interactions.

Methods

Study sites

Behavioural observations of adult tuatara were performed in five facilities around New Zealand. These tuatara enclosures were located at Otorohanga Kiwi House (OKH), Zealandia Wildlife Sanctuary (ZWS), Auckland Zoo (AZ), Wellington Zoo (WZ) and Victoria University of

Wellington (VUW; Figure 4.1). All tuatara originated from Takapourewa genetic stock and each enclosure had adults of both sexes.

Three of the study sites were small enclosures supporting small numbers of tuatara: AZ (area = 14 m², *N* = 3, sex ratio = 1:2), VUW (area = 26 m², *N* = 3, sex ratio = 1:2) and WZ (area = 13 m², *N* = 2, sex ratio = 1:1). These facilities were comparable in size, density of animals, and feeding regimes (individuals are fed by keepers regularly). The whole enclosure area was visible in these small enclosures and all individuals were regularly observed (Figure 4.2 A – C). Two of the study sites, OKH and ZWS, were large enclosures supporting larger numbers of tuatara, and individuals seek food out themselves. OKH facility is an aviary dome enclosure, where observers can see the whole facility and all captive individuals while walking the main track through the enclosure (area = 1500 m², *N* = 16, sex ratio = 1:3; Figure 4.2 D). ZWS facility is a fenced research area within a fenced sanctuary, and observation was possible from a public track along the fence and up to six meters into the enclosure from the perimeter fence (Figure 4.2 E - F). Therefore, observations in ZWS were performed on adult individuals in this visible area (area = 1500 m², *N* = 18, sex ratio = 4:5), which is a subset of the total population in the larger tuatara research enclosure. ZWS is a mammal-free natural habitat with wild avian predators, while the other four facilities are enclosed from any potential predators. AZ and VUW enclosures had heat lamps running during the observation period. No manipulation of the composition of individuals in enclosures was attempted ensuring tuatara were well acclimated to their conditions.



Figure 4.5. Behavioural observations were performed in five captive tuatara facilities in New Zealand



Figure 4.2. Five tuatara facilities for behavioural observations. A. Auckland Zoo enclosure. B. Victoria University of Wellington enclosure. C. Wellington Zoo enclosure. D. Otorohanga Kiwi House Aviary Dome. E. Zealandia Wildlife Sanctuary tuatara research enclosure is a fenced research area (red line). F. Observed area (yellow grid) in Zealandia Wildlife Sanctuary tuatara research enclosure (red line).

Data collection

Behavioural observations were performed in late austral summer and early austral spring in 2020 and 2021. Observations were carried out during daylight hours on warm and sunny days (Table 4.1), as these conditions allow tuatara to effectively thermoregulate (Heath, 1964). During the study period, behavioural data were collected every 15 minutes at the AZ, WZ and VUW enclosures and every 30 minutes at the OKH and ZWS enclosures. This ensured that observers had enough time to traverse the research area and collect data on all present tuatara. I recorded the identity (by individual characteristics, such as colour beads on crest, crest shape, body size, body colour), sex (by secondary characteristics), specific location within the enclosure, and position (“out of the burrow” if more than half of their trunk was out of the burrow, otherwise “in the burrow”) of all observed animals. If known present individuals were not observed, I recorded them as “not observed”. There was plenty of time within each round of observation to record aggressive interactions between individuals. I recorded the identity and sex of the initiator (individual that initiated the aggressive interaction), the identity and sex of the receiver (individual that received the aggressive interaction), the behaviour of the initiator (advance or display), and the behaviour of the receiver (retreat, hold and advance). Individual snout-vent length (SVL) and weight (WT) were measured during the observation period for individuals in the AZ, WZ and VUW enclosures. Individual measurements were provided by Otorohanga Kiwi House from their latest record (in December 2019 or November 2020). Individual measurements were not available from ZWS enclosure as there is a larger population and these animals are not regularly captured. Finally, I recorded air temperatures for each observation time slot at all five facilities (Table 4.2).

Table 4.2. Air temperatures in the captive facilities during behavioural observations

Temperatures (°C)	OKH	ZWS	AZ	WZ	VUW
Maximum	25.8	19.3	26.4	24.7	21.1
Minimum	17.4	11.5	19.9	15	13.9
Mean	20.8	15.3	23.4	19.7	18.6

Table 4.1. Demographic information of captive tuatara populations

Captivity facility	Location	Number observed*	Sex ratio (M:F)	Facility size (m ²)	Observation time	Observation days [#]	Observation duration [†]	Observation time slots	Density (individuals/m ²)
Auckland Zoo (AZ)	Auckland	3	1:2	14	11-20 February, 2020	8	9:30-17:00	244	0.21
Wellington Zoo (WZ)	Wellington	2	1:1	13	December 16, 2020 - January 16, 2021	15	9:30-16:30	187	0.15
Victoria University of Wellington (VUW)	Wellington	3	1:2	26	February 24, 2020 - March 14, 2021	13	9:30-17:00	248	0.12
Otorohanga Kiwi House (OKH)	Otorohanga	16	1:3	1500	February 2-14, 2021	12	10:00-16:00	58	0.01
Zealandia Wildlife Sanctuary (ZWS)	Wellington	18 [^]	4:5	1500	April 7 - May 5, 2021	13	10:30-16:00	56	0.01

*All enclosures only contained adult tuatara except for ZWS, where any subadults and juveniles were not included in this study.

[^]In ZWS, behavioural observation was performed in part of the whole research area, where tuatara were visible along the public track. Some adults observed rarely (ten observations or below) were considered as casual visitors, therefore, they were not included in the analysis.

[#]Observations were performed in warm and sunny days, which were appropriate to the activity period when tuatara might thermoregulate.

[†]Observation duration between facilities varied between enclosures because of differing open hours.

Data analyses

Animal observations

Tuatara were included in the analyses if an individual had more than ten sightings (seen out of the burrow or in the burrow). For tuatara in OKH and ZWS facilities, activity centre locations were extracted from the centroids of 95% Minimum Convex Polygons (MCPs) in QGIS (version 3.16.16). In AZ, WZ and VUW facilities, 95% MCPs were manually calculated because the small size of these enclosures prevented generating accurate estimates of 95% MCPs in QGIS. All other data analyses were performed in R (version 4.1.2).

Spatial distribution

Spatial distribution was investigated only in the OKH enclosure. The other four facilities were excluded for spatial distribution analysis due to the small population sizes at the AZ, WZ and VUW sites, and because only part of the ZWS enclosure was observed which may not reflect the actual spatial distributions. In the OKH enclosure, I created a distance matrix between tuatara activity centre locations. Based on this distance matrix, I used a linear regression of the mean distance of each male to the nearest five females against male's size (SVL) to examine the dominance of large males on access to females.

Activity areas

For tuatara in OKH and ZWS enclosures, activity areas were estimated using 95% MCPs in QGIS. For the three smaller enclosures (AZ, WZ and VUW), I manually estimated 95% MCPs of tuatara based on locations of observations on grid maps (Figure 4.3). The number of observations in each grid used by a tuatara was totalled. The 95% MCP was estimated based on the area of grids where each tuatara was observed after excluding grids with less than 5% of observations. Using the centroids of these grids, I calculated the size of activity areas by summing the area covered by the 95% MCP. Observations with areas that covered over half a grid were recorded as a full grid square, observations that covered a half grid were recorded as a 0.5 grid square, and observation areas that covered less than a half grid were excluded from the sum of area. Finally, I calculated each tuatara's activity area as a

percentage of the enclosure size and reported this by sex in the three smaller captive facilities.

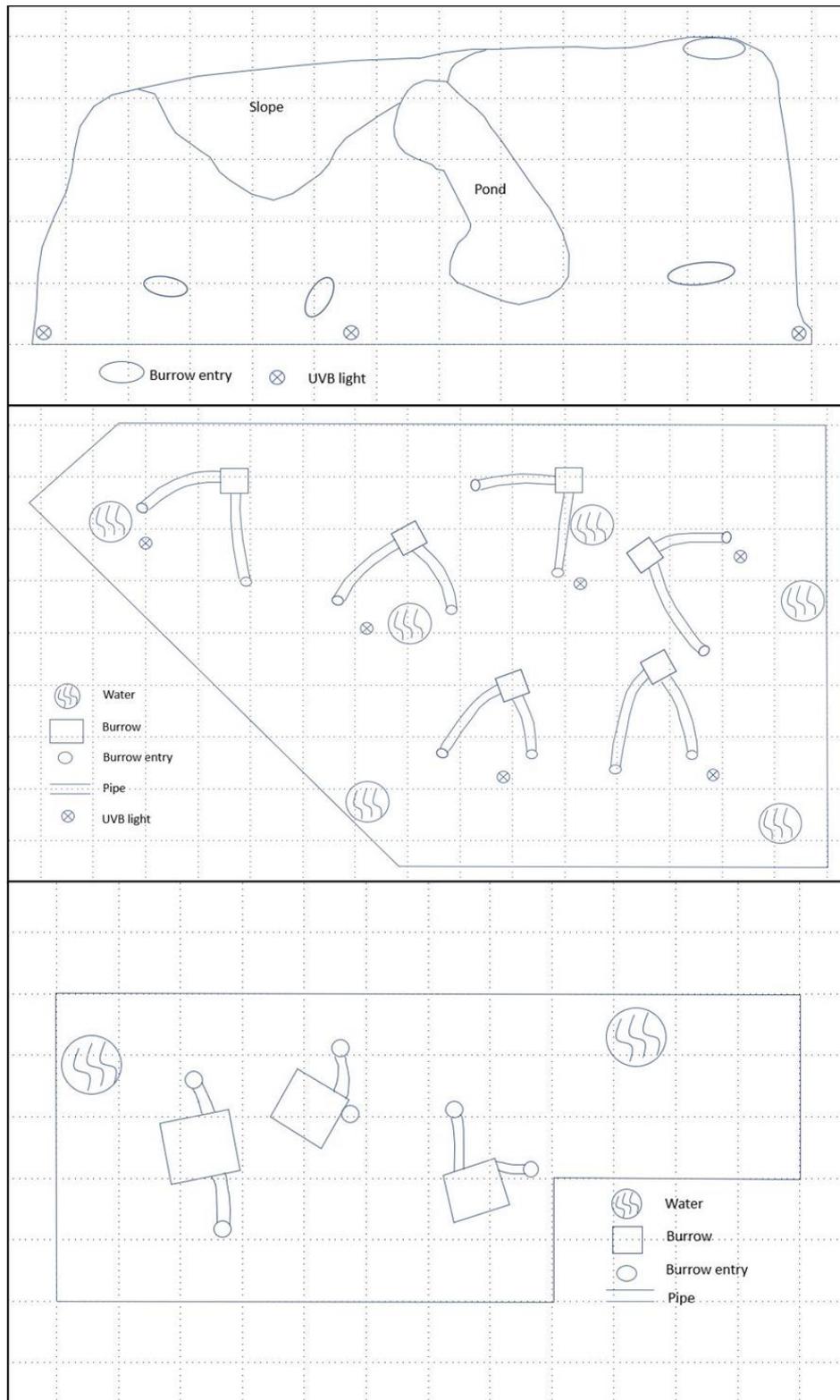


Figure 4.3. Grid maps of tuatara enclosures in Auckland Zoo (upper), Victoria University of Wellington (middle) and Wellington Zoo (lower). Size of each grid square: 50cm x 50 cm.

Dominance regarding position/visibility

I investigated tuatara dominance with regard to burrow position in all five facilities. Empirical studies on lizards demonstrated high visibility in dominant individuals to gain priority access to important resources (Ruby, 1981, 1984). Additionally, male territorial behaviour, including sitting in burrow entrances even in cold conditions, was observed in tuatara (Gillingham et al., 1995). Therefore, I designated dominance as “out of burrow” and sub-dominance as “in the burrow” or “not observed” in this study. Because environmental conditions varied among facilities, I performed analyses on the data sets from OHK and ZWS separately, and created a combined data set for the AZ, WZ and VUW enclosures to get an appropriate sample size. These enclosures had similar environmental conditions, methods of feeding the tuatara, and 2 – 3 individuals per enclosure. I performed generalized linear mixed models (GLMMs) to investigate the effects of fixed and random factors (described below for each dataset) on burrow position as a binomial dependent variable. Model selection was performed in each model set, comparing models including the null model based on delta Akaike’s information criterion (AIC) values.

The OHK model set included (1) null model, (2) sex, (3) SVL, (4) the distance to the nearest neighbour, (5) the mean distance to the nearest five neighbours, (6) the additive effect between sex and SVL, (7) the additive effect between sex and the distance to the nearest neighbour, and (8) the additive effect between sex and the mean distance to the nearest five neighbours as fixed factors. Models with interactions between sex and either SVL, the distance to the nearest neighbour, or the mean distance to the nearest five neighbours were not included due to high collinearity. Individuals and observation time slots were random factors for all models in the OHK model set.

The ZWS model set included (1) null model, (2) sex, (3) the distance to the nearest neighbour, (4) the additive effect between sex and the distance to the nearest neighbour, and (5) the additive effect and interaction between sex and the distance to the nearest neighbour as fixed factors. I did not estimate the mean distance to the nearest five neighbours because the observation was performed in part of the whole research area, where I might not see all neighbours for each individual. Individuals and observation time slots were random factors for all models in the ZWS model set.

The model set combining AZ, VUW and WZ facilities included (1) null model, (2) sex, (3) SVL, and (4) the additive effect between sex and SVL as fixed factors. The model of additive and interaction between sex and SVL was not included in the model set due to the high collinearity. I did not include the distance between individuals as a fixed factor due to the small population size in each facility. Individuals were the random factor for all models in the model set. Facilities and observation time slots were not included as random factors because the data set did not converge when including these factors.

Dominance of males over females regarding position/visibility

Sex was proposed as a factor with regard to dominance because previous studies showed males have social dominance over females (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009). Therefore, I performed GLMMs focused on focal female behaviour in data sets of OHK, ZWS, and combined data from the three smaller facilities (the reasons for combining data as explained above). The binary response variable was the focal female's position (in or out of the burrow as defined above). The categorical fixed factor was the position of that focal female's nearest male based on activity centres, and if available, either female SVL, male SVL or the SVL ratio of female to male was covariate. The distance between the focal female and the nearest male was not used as a covariate in this analysis (1) because in OHK and ZWS facilities some individuals switched between burrows, and when they were not seen I could not know which burrow they were in and thus the actual distance for each particular observation time slot, and (2) because in the combined data set of three facilities this distance was not comparable among facilities. I considered females, observation time slots and facilities (for the combined date set of three facilities) as random effects if applicable to the data set. Model selection was performed in each model set, comparing models including the null model based on delta AIC values.

The OHK and ZWS model sets included (1) null model and (2) the position of the focal female's nearest male as fixed factors, and females and observation time slots as random factors. In OHK model set, female SVL, male SVL and the SVL ratio of female to male were excluded from the model set due to high collinearity or uncertainty of collinearity (wide 95% confidence intervals).

The model set combining AZ, VUW and WZ facilities included (1) null model, (2) the position of the focal female's nearest male as fixed factors, and females as the random factor. Female SVL, male SVL and the SVL ratio of female to male were not included in the model set because SVLs were not comparable among facilities. I did not consider observation time slots or facilities as random factors because the data set did not converge, or the model did not meet assumptions of GLMMs when these factors were included.

Aggressive interactions

Based on the records of individual interactions, I investigated tuatara dominance with regard to sex and size (SVL). Both interactions regardless of individual sex and interactions within sex were used to test dominance regarding size. In each interaction, two animals were allocated as "large" and "small" by their SVLs. Although individual measurements were not available from ZWS, the apparent difference in SVL between two individuals in each interaction allowed me to group tuatara by size. Interactions between sexes were used to test the dominance regarding sex. The small number of observations of aggressive interactions prevented me performing GLMMs, therefore, each category of receivers' responses was calculated as a percentage of all interactions of the category.

Results

Animal observations

I spent 8 - 15 days at each of the captive facilities to perform behavioural observations, with 56 - 244 observation time slots per enclosure (Table 4.1). Thermal conditions during observation period varied among captive facilities, with highest temperatures in AZ enclosure and lowest temperatures in ZWS enclosure (Table 4.2). In the OHK facility, 16 tuatara (four males and 12 females) were observed (activity center locations, Figure 4.4). The number of sightings per individual was 37.75 ± 2.42 times (range = 24 - 55) on average. Male individuals were seen 40.2 ± 4.85 (range = 28 - 49) times and female individuals were seen 36.9 ± 2.87 (range = 24 - 55) times on average. In the ZWS facility, as tuatara were observed along a strip of habitat contiguous with a larger area, only tuatara with more than ten sightings were considered as residents of the observation area and thus included in the analyses. As a result, there were 18 residents (10 females and 8 males) were included in the analyses (activity center locations, Figure 4.4). Of these residents, on average, male

individuals were seen 31.8 ± 4.09 times (range = 11 – 46) and female individuals were seen 26.3 ± 3.04 times (range = 14 – 44). There were three adults (one male and two females) in the AZ facility, with 244 sightings for each individual. There were three adults (one male and two females) in the VUW facility, with 225 sightings for the male, and 239 and 234 sightings respectively for two females. There were two adults (one male and one female) in the WZ facility, with 130 and 149 sightings respectively.

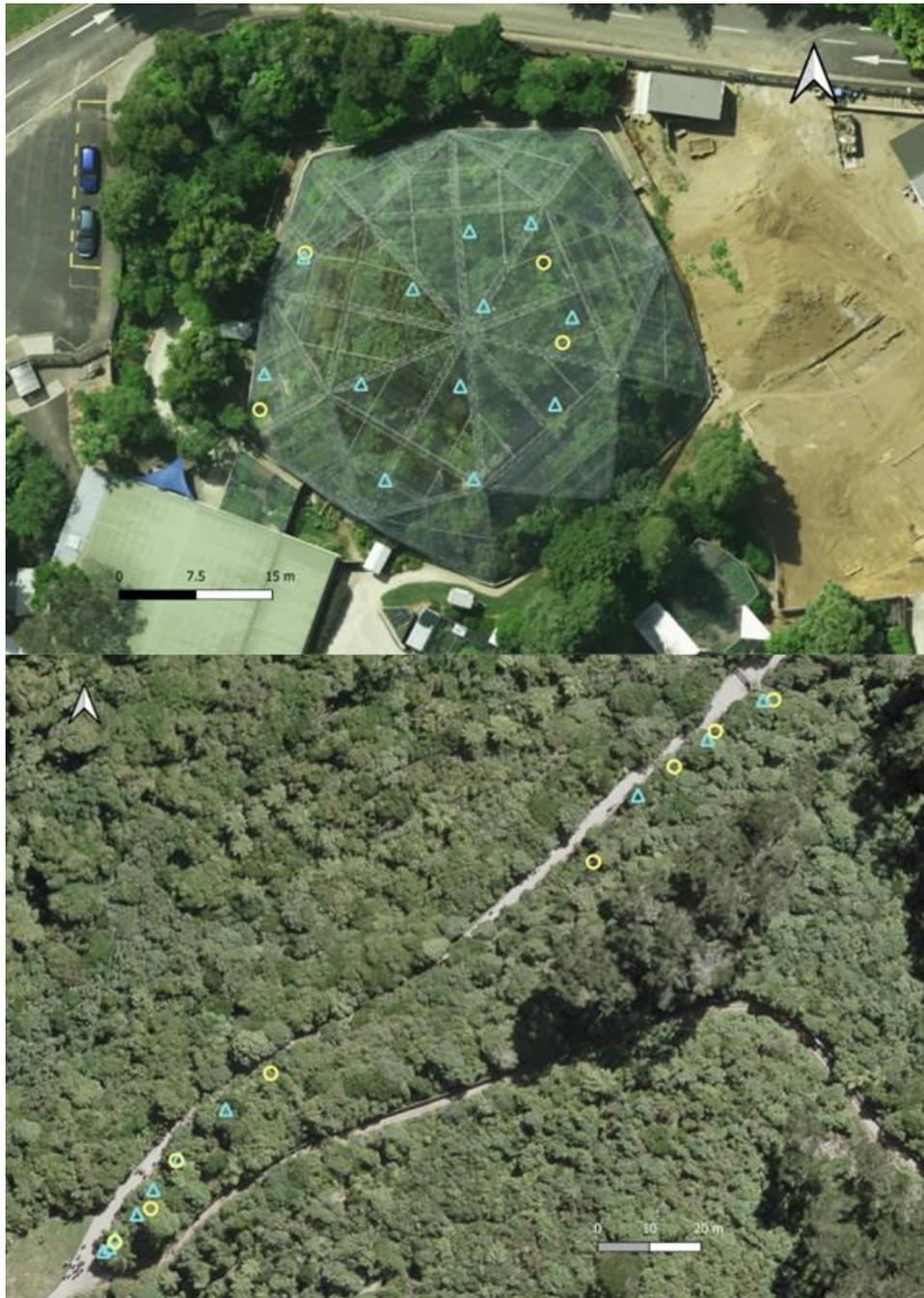


Figure 4.6. Activity centres of tuatara in Otorohanga Kiwi House aviary dome (upper) and Zealandia tuatara research area (lower). Yellow circles for males and blue triangles for females.

Spatial distribution

For males in the OKH enclosure, there was a significant negative relationship between the mean distance to the nearest five females (range = 7.65 - 12.52m) and male SVL ($F_{(1,2)} = 29.61, P = 0.03$), meaning larger males were closer to females.

Activity areas

Activity area was estimated as 0 for 13 of 16 individuals in the OKH enclosure and 16 of 18 individuals in the ZWS enclosure because they were observed at the exact same one or two locations. Only three individuals in the OKH enclosure (0.25 m², 11.9 m² and 13.6 m² respectively) and two individuals in the ZWS enclosure (4.5 m² and 4.9 m² respectively) had activity areas other than 0. Therefore, OKH and ZWS enclosures were excluded from space use analyses.

In the AZ and VUW enclosures males showed an advantage in space use over females. The male used 45.1% of the enclosure at AZ and 22.5% of the enclosure at VUW. By contrast, females used 12.4% and 7.1% of the enclosure at AZ, and 21.1% and 7.6% of the enclosure at VUW. In the WZ facility, the female used 14.4% of the enclosure, while I could not estimate the male's activity area because the male was always sighted in the exact same location which prevented me estimating the percentage of its activity area of the observed area.

Dominance regarding position/visibility

In the OHK model set, the null model was selected as the best model because of the lowest AIC value (Table 4.3). Therefore, neither sex, SVL, the mean distance to nearest five neighbours or the distance to the nearest neighbour had a significant effect on individual's position in OKH population.

Table 4.3. Model selection on dominance of in or out of the burrow based on data sets from Otorohanga Kiwi House enclosure, Zealandia Wildlife Sanctuary enclosure separately, and the combined data set for the Auckland Zoo, Wellington Zoo and Victoria University of Wellington enclosures

Response variable	Data set	Fixed effect(s)	Random effects	Number of parameters	AIC values	Delta AIC	Weight
In or out of the burrow	Otorohanga Kiwi House*	null		3	1100.2	0	0.297
		distance to the nearest neighbour		4	1101.1	0.9	0.189
		mean distance to the nearest five neighbours		4	1102	1.8	0.121
		sex	(1 individuals) + (1 observation time slots)	4	1102.1	1.9	0.115
		SVL		4	1102.1	1.9	0.115
		sex + distance to the nearest neighbour		5	1103	2.8	0.073
	Zealandia Wildlife Sanctuary	sex + mean distance to the nearest five neighbours		5	1103.8	3.6	0.049
		sex + SVL		5	1104.1	3.9	0.042
		sex + distance to the nearest individual		5	1241.9	0	0.442
		sex x distance to the nearest individual		6	1242.1	0.2	0.4
		distance to the nearest individual	(1 individuals) + (1 observation slots)	4	1245	3.1	0.094
		sex		4	1247.1	5.2	0.033
Combination of AZ, WZ and VUW ^a	null		3	1247.2	5.3	0.031	
	sex		2	1445	0	0.406	
	sex + SVL	(1 individuals)	3	1446	1	0.246	
	SVL		4	1446.6	1.6	0.182	
			3	1446.8	1.8	0.165	
			3				

* In data set of Otorohanga Kiwi House, all models including interaction items between sex and any covariate were removed due to high collinearity.

^a In the combined data set of AZ, WZ and VUW enclosures, the model including interaction between sex and SVL was not included due to high collinearity.

The number of observations for each site corresponds to the observation time slots shown in Table 4.1.

In the ZWS model set, the model with additive effect between sex and the distance to the nearest neighbour showed the lowest AIC value and was therefore selected as the best model (Table 4.3). There was a significantly negative relationship between the position and the distance to the nearest neighbour ($P = 0.003$), however, the effect size of the distance to the nearest neighbour was small, with a Cohen's d of -0.37 . When the distance to nearest individual was controlled for, males were significantly more likely to be out of the burrow than females (GLMM, $\beta = 0.90$, $SE = 0.37$, $P = 0.016$).

For the combined data set of AZ, VUW and WZ facilities, the null model was selected as the best model based on the lowest AIC value, indicating sex and SVL had no effect on individual position in three smaller captive populations (Table 4.3).

Dominance of males over females regarding position/visibility

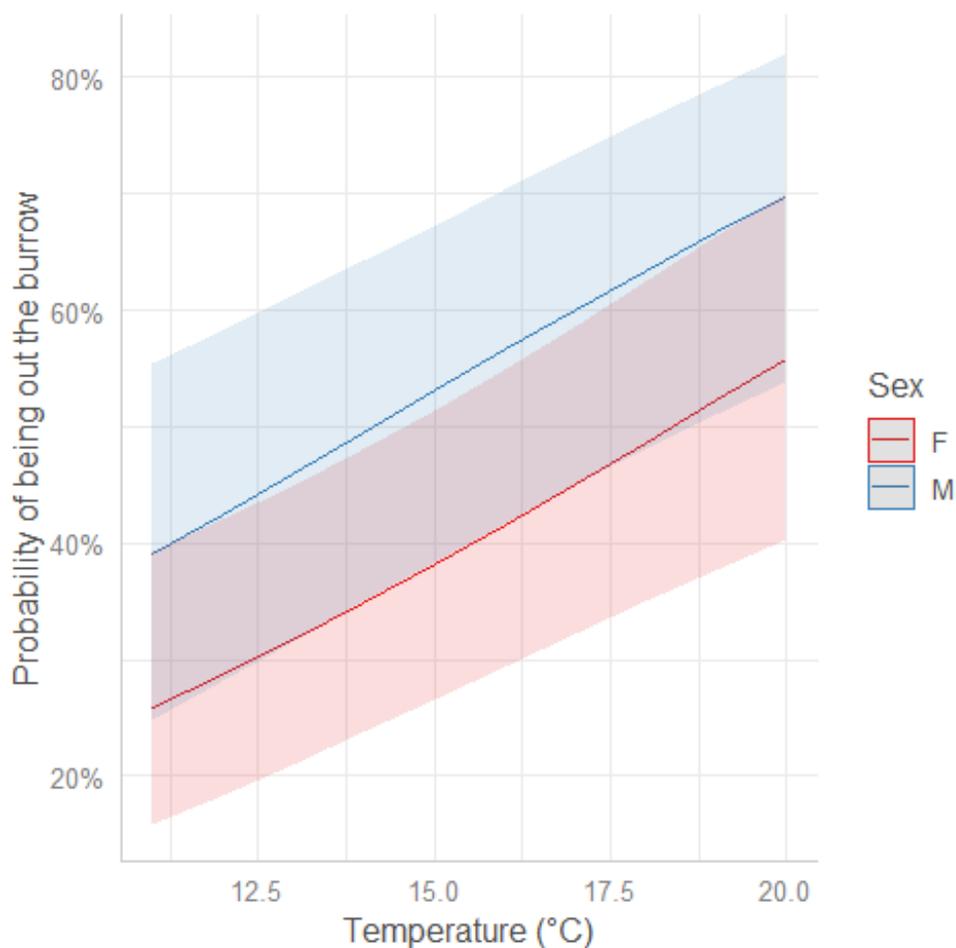


Figure 4.7. Predicted probabilities of being out of the burrow for female and male tuatara at differing air temperatures.

In the OHK population, the null model was selected as the best model due to the smaller AIC value than the model including the nearest male's position (delta AIC = 0.92). Therefore, the dominance of males on females for positions was not detected in OHK tuatara. In the ZWS population, the model including the nearest male's position was the best model due to a smaller AIC value than the null model (delta AIC = 2.86). Based on the best model, females were significantly more likely to be out of the burrow when males were out of the burrow (GLMM, $\beta = 0.51$, $SE = 0.23$, $P = 0.026$), indicating there was no dominance of males on females for positions. As for the data set of the combination of three small sites, the model including the nearest male's position as the best model due to the smaller AIC values (delta AIC = 19.6). Based on the best model, females were significantly more likely to be out of the burrow when males were out of the burrow (GLMM, $\beta = 1.27$, $SE = 0.27$, $P < 0.001$), indicating there was no dominance of males on females for positions. Therefore, the visibility of females was not affected by the appearance of the nearest male in all captive facilities in this study. To understand the reason for this result, the probability of being out of the burrow for both sexes at differing air temperatures was estimated, showing the visibility of both sexes increased with increasing air temperatures (take ZWS facility as example, Figure 4.5).

Aggressive interactions

In total, I observed 37 interactions regardless of individual sex (among six females and eight males) in four of the enclosures (none observed at WZ facility). Twenty-five interactions were observed between sexes (among three males and four females at AZ, VUW and ZWS facilities). Twelve interactions were observed between two males when competing for access to a female (at OKH facility). I did not observe interactions between females in all captive facilities. As such, I was able to explore the effect of size on dominance based on 37 interactions regardless of individual sex and based on 12 interactions between males, and explore the effect of sex on dominance based on 25 interactions between sexes (Table 4.4). In interactions regardless of sex and interactions between sexes, large individuals (73%) and males (92%) started most interactions. In interactions between two males at OKH facility, the small male started most interactions (67%). In response to interactions, small individuals in interactions regardless of sex (85% of interactions), the small male in interactions between males (100% of interactions) and females in interactions between sexes (83% of

interactions) retreated more frequently and did not advance. By contrast, large individuals in interactions regardless of sex, the large male in interactions between males and males in interactions between sexes either held their position or advanced but did not retreat. Besides aggressive interactions, tuatara postures which reflected the social dominance were observed. For example, in the OKH facility, the large male showed a dominant posture (limb-erect and head-up, Figure 4.6A) and the small male showed a submissive posture (lying flat on the ground, Figure 4.6B) when competing for female access. By contrast, the small male showed a dominant posture in the absence of the large male (Figure 4.6C). The female showed a submissive posture in the presence of both males (Figure 4.6D).

Table 4.4. Aggressive interactions between tuatara in captive facilities

Grouping variable	Group	Initiator	Receiver		
			Retreat	Hold	Advance
size (regardless of sex)	small	27% (10)	85% (23)	15% (4)	0% (0)
	large	73% (27)	0% (0)	90% (9)	10% (1)
size (between males)	small	67% (8)	100% (4)	0% (0)	0% (0)
	large	33% (4)	0% (0)	100% (8)	0% (0)
sex	female	8% (2)	83% (19)	17% (4)	0% (0)
	male	92% (23)	0% (0)	50% (1)	50% (1)

Initiator stands for the tuatara starting the interaction, receiver stands for the other individual receiving the interaction. Numbers in brackets stand for the number of individuals. In each interaction testing the effect of size, two animals were allocated as “large” and “small” by their SVLs.



Figure 4.6. Dominant and submissive postures of tuatara in OKH facility. The large male was in dominant posture (A) and the small male was in submissive posture (Figure B) during the display for female access (female, D). The small male was in dominant posture (C) in the absence of the large male. The female (D) was in submissive posture in the presence of both males.

Discussion

The behavioural observations of captive tuatara showed (1) larger males had an advantage in accessing females by keeping a smaller distance to females, (2) males had dominance over females in space use by maintaining larger activity areas than females, (3) males tended to come out of the burrow more frequently than females in the ZWS facility, while this aspect of male dominance was not detected in other facilities, (4) females did not tend to be in the burrow when the nearest male was out of the burrow, and (5) males and large individuals had dominance in winning aggressive interactions. Despite differing biotic and abiotic factors between facilities, these results were largely consistent over the five captive facilities. In general, this study showed the social dominance of male and large tuatara in captive facilities.

Male dominance in space use over females in this study is in accordance with observations of wild tuatara. On Takapourewa, males maintained significantly larger territories than females (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009). Likewise, there were significantly larger activity areas for males of North Brother Island tuatara based on 30 years survey data (Chapter 3). In captivity, juvenile males outcompete juvenile females for resource availability such as food and space (Wörner, 2009). Furthermore, in this study, male tuatara showed an absolute advantage over females in winning aggressive interactions, and there was higher visibility of males than females in the ZWS facility. Dominant individuals have priority access to important resources, while subordinates avoid dominant individuals to reduce collisions and attacks, resulting in the difference in individual visibility (Šárová et al., 2010; Shimmura et al., 2007). Male dominance in space use over females is prevalent in reptiles, which is related to the social structure (Perry & Garland, 2002), and ultimately increases the access to females and improves male reproductive success (Stamps, 2014).

Tuatara are sexually dimorphic, where males have larger body size and head size than females (Dawbin, 1982; Herrel et al., 2010). As such, the male dominance may be related to the advantage of male large size. For example, larger male tuatara were observed to win 100% male-male contests on Takapourewa by evicting smaller males with aggressive behaviour, such as, chasing, biting, or interrupting in the middle of courtship (Moore,

Daugherty, & Nelson, 2009). Similarly, at the OKH enclosure in this study, the larger male outcompeted the smaller male in all observed aggressive interactions by holding the position instead of retreating or presenting a submissive posture when competing for access to a female. While most individuals in the OKH population were extremely static during observation period, larger males were found in closer proximity to females than smaller males, consistent with a dominance through a size advantage. Large male advantage for access to females was also observed in a previous study in a wild tuatara population. On Takapourewa, larger male tuatara were found to have territories that overlapped with more females than small male tuatara, providing an advantage for mating opportunities (Moore et al., 2009). Large male advantage was also observed in many reptile species. For example, large male western whiptails (*Cnemidophorus tigris*) won male aggressive interactions and thereof obtained access to more females and higher reproductive success (Anderson & Vitt, 1990). Similarly, female red-black salamanders (*Plethodon cinereus*) were observed to be significantly nearer to larger males and to leave smaller males (Mathis, 1991). In addition, the dominance of male tuatara through a size advantage in resource competition may contribute to the lower visibility of females than males in the ZWS facility to avoid confrontation with larger tuatara. Size-related social dominance is a main driver for individual visibility in reptiles (Ruby, 1981, 1984), because large individuals are more effective in winning aggressive encounters and accordingly increasing access to important resources (Cox et al., 2003). For example, larger male green anoles (*Anolis carolinensis*) showed higher visibility and more mating records than smaller males because a large body size is probably a predictor for a successful aggressive interaction (Ruby, 1984). An outstanding question for tuatara is whether female preference for large males can also contribute to large male advantage for access to females. Further studies should investigate female mate preferences in tuatara.

Local population sex ratio may also drive behavioural patterns. Empirical studies showed an increasing percentage of males can intensify male harassment and aggressiveness towards females (Johanos et al., 2010; Le Galliard et al., 2005), which can incur costs on females such as a reduction in lifespan, survival and reproductive success (Le Galliard et al., 2008; Ojanguren & Magurran, 2007; Sakurai & Kasuya, 2008). As a result, females may use avoidance as a strategy to reduce costs from male harassment, which is

common in reptiles (Cooper & Greenberg, 1992; Wikelski et al., 1996). A significant difference in visibility between sexes was not detected in OKH enclosure, where there was a female-biased sex ratio (25% males). By contrast, with an approximately balanced sex ratio in ZWS enclosure (there was a balanced sex ratio when this research area was established), females showed significantly lower visibility than males. In this study, males at ZWS enclosure were observed approaching females, forcing females to hide in the bush, retreat to the burrow, or switch into other burrows.

Population density can shift social dominance where an increasing population density can intensify resource competition and aggressive interactions (Kaufmann, 1983; Manenti et al., 2015). The OKH enclosure and the observed area of the ZWS enclosure were comparable in density of tuatara that were included in the analyses (Table 4.1). However, in the ZWS facility, 13 tuatara were excluded from the analyses because they were either juveniles or adults with low sightings, while all individuals in OKH facility were included in the analyses. This means the actual population density was lower in OKH facility (93.8 m² per individual) than in ZWS facility (48.5 m² per individual). Less intense resource competition in OKH captive population may explain a non-significant difference in visibility between sexes due to the likely fewer aggressive interactions. By contrast, more intense resource competition in the ZWS enclosure due to a larger density may increase female tuatara's disadvantage in social interactions, contributing to lower visibility of females than males. Notably, when the population density is high, which can occur in captive facilities, subordinates cannot avoid dominant individuals through dispersal or avoidance as effectively as individuals in the wild (Creel, 2001; Warwick, 2023). In this study, the most severe physical interactions occurred in the AZ and VUW facilities where males chased off females by biting, while in ZWS and OKH facilities tuatara only displayed to each other or approached without physical conflicts. The territory size of tuatara was on average 13.9 m² for females and 30.6 m² for males in the wild population on Takapourewa (Moore, Daugherty, & Nelson, 2009). By contrast, tuatara in AZ, WZ and VUW facilities had extremely limited space (4.7 m² - 8.7 m² per individual), meaning female tuatara at these sites might have to be out of the burrow for critical resources for life such as foraging and basking due to the absolute area they have access to and despite the risk of male aggressiveness. As

such, the high population density in the AZ, WZ and VUW facilities likely contributed to the non-significant differences in visibility between sexes at these sites.

The response to abiotic factors driving reptile behaviour is an additional overlay on the biotic factors discussed above. Various abiotic factors can influence daily activity of reptiles, such as, spatial heterogeneity, photoperiod, and environmental temperatures, and the effects of some of these factors might be mediated by others (Avery & Bond, 1987; Rismiller & Heldmaier, 1988; Ruby, 1984; Winne & Keck, 2004). Since reptiles are ectothermic species, environmental temperatures can substantially influence activity patterns through thermoregulation (Adolph & Porter, 1993). Previous studies showed tuatara are able to adjust their thermoregulatory behaviour and thereby visibility as a response to changes in environmental thermal conditions (Besson & Cree, 2010; Vermunt et al., 2014). For example, in the ZWS enclosure, the visibility of both sexes increased with increasing air temperatures (Figure 4.5), indicating thermal conditions may play a key role in mediating individual visibility of tuatara and other social interactions. However, male dominance in visibility over females was not confounded by thermoregulation because males had higher visibility than females throughout the thermal range (Figure 4.5).

The contributions to understanding individual tuatara behaviour provide implications for captive management of tuatara populations, particularly with regard to sex composition, social dominance and enclosure size. More importantly, behavioural interactions between male and female tuatara in captive facilities indicate that male dominance over females is a major driver for intra-specific interactions, whether by the nature of sex differences or size, which may in turn have impacts on tuatara population parameters and viability. A male-biased sex ratio may worsen the subordinate status of females, negatively affecting resource acquisition and intensifying male harassment to females, incurring extra costs on female fitness. As a result, male dominance by individual behaviour and sex ratio may be the mechanisms for the pattern of decline in female body condition and fecundity, ultimately driving a substantial decline in the population size of tuatara on North Brother Island. Whether this effect is maintained at lower population densities or we risk population extinction remains to be resolved.

Chapter 5

What are implications of a sustained male-biased sex ratio for the population viability of North Brother Island tuatara?

Introduction

Sex ratio is a major driver of population dynamics because it can influence sexual selection and individual behaviour (Clutton-Brock et al., 1984; Gwynne, 1990; Jirotkul, 1999), and ultimately have impacts on population viability (Dale, 2001; Heinsohn et al., 2019; Le Galliard et al., 2005). Most vertebrates have an approximately balanced sex ratio of offspring due to genetic sex determination (GSD), where offspring sex is determined by sex chromosomes (Bull, 1980, 1983). By contrast, some vertebrates (particularly many reptiles) exhibit temperature-dependent sex determination (TSD), where incubation temperature influences sexual differentiation during a specific duration of embryonic development (Bókony et al., 2019; Bull, 1980; Janzen & Paukstis, 1991). Therefore, a warming climate poses an increasing concern for species with TSD because increasing temperatures can cause overproduction of one sex, which is detrimental to population viability (Janzen, 1994; Mitchell & Janzen, 2010; Valenzuela et al., 2019).

There are three patterns of TSD based on the shift in offspring sex ratio as incubation temperature increases (Valenzuela & Lance, 2004). Relative to the MF pattern (males hatch at lower temperatures and females hatch at higher temperatures) and the FMF pattern (lower and higher temperatures produce females and intermediate temperatures produce males), the FM pattern (females are produced at lower temperatures and males are produced at higher temperatures) is more problematic under climate change. This is because increases in nest temperature can produce excess males, which can intensify male-male competition and male aggressiveness to females, and ultimately, reduce individual

fitness and threaten population viability (Holveck et al., 2015; Le Galliard et al., 2005; Smith, 2007).

To date, tuatara are the only known species with TSD pattern of FM (Cree et al., 1995; Mitchell et al., 2006). A male bias in the North Brother Island tuatara population was first observed in the late 1990s (Nelson et al., 2002). In the following 20 years under a consistent male bias, there was a continuous decline in body condition and survival, posing an increasing concern for the population viability of tuatara on the island (Grayson et al., 2014; Hoare et al., 2006). Tuatara have survived climate shifts over the last 100,000 years (Cree, 2014; Miller et al., 2012), although how historical and current climates affect their sex ratios and other population parameters is still unclear. Moreover, recent research on another tuatara population hypothesised that behavioural variation in nesting phenology may offset the male bias even if the environmental temperature increases by up to 2°C (Nelson et al., 2018). Thus, there is a need to investigate the sex ratio pattern of the North Brother Island tuatara population over a longer term, and its subsequent effects on other population parameters and population viability.

Overview of study

I collected and updated an additional decade of tuatara population survey data from North Brother Island, extending the total duration of the mark-recapture dataset to 30 years. In Chapter Two, I estimated the current sex ratio and updated other important demographic parameters, such as survival and population size. I used long-term records of capture location to investigate individual activity area patterns in Chapter Three. In Chapter Four, I investigated the behaviour of tuatara in captivity to help interpret the implications of sex ratio on behaviour. Here I compile the findings from these data chapters to discuss the combined implications for the population viability of North Brother Island tuatara.

Summary of results

Using the updated survey data, I found a consistent male bias over 30 years in the North Brother Island tuatara population. After a slight male-bias (1.17 by 1988) was found in the late 1990s (Nelson, Keall, Pledger, et al., 2002), the estimated adult population sex ratio became further skewed towards males during the following two decades of surveys

(Grayson et al., 2014; Mitchell et al., 2010). In my work, I estimated the sex ratio as 1.66 males per female by 2018. Previous studies found a continuous decline in body condition and survival, with a steeper rate of decline in females (Grayson et al., 2014; Hoare et al., 2006). By 2018, I estimated the survival had slightly increased and was more even at 95.28% for males and 95.26% for females. However, the population size decreased 28% from 445 adult individuals in 1996 to 322 in 2018, and females showed a further prolonged breeding cycle from every 9 years between 1989 and 2001 to every 14.4 years between 2011 and 2019. I also estimated the sex ratio for new cohorts recruiting into the adult population and found the male-bias for these individuals has become less skewed. These individuals entering the adult population may have contributed to a stabilising or lessening of the male-biased sex ratio after 2005. Meanwhile, there was also an increase in male body condition and survival for both sexes in the new cohorts. From 2008 to 2018, the survival of new cohorts increased from 95.95% to 97.29% for males, and from 95.73% to 96.28% for females.

In Chapter Three, I found that there were larger activity areas in male tuatara than females on North Brother Island. Also, individuals used larger activity areas when the population size became smaller. Relative to males, females had more male neighbours, and relative to females, males had more female neighbours, reflective of the territorial behaviour of this species (Moore, Daugherty, & Nelson, 2009). However, there was no relationship between male body size (SVL) and activity area. Large males did not maintain exclusive activity areas (e.g., overlapping fewer other males, less percent of their activity areas overlapped by other males or a larger distance to other males) or secure greater access to females (e.g., overlapping more females, larger percent of their activity areas overlapped by females or a smaller distance to females). I found larger activity areas during short surveys of individuals in translocated populations (Matiu/Somes Island population, Long Island population) compared to the activity areas of individuals on North Brother Island over 30 years.

In Chapter Four, the observations of captive tuatara indicated the social dominance of male and large tuatara despite differing biotic and abiotic factors among captive facilities. Males and large individuals were dominant in aggressive interactions. Males had larger activity areas than females, and large males maintained smaller distances to females than

small males. In two large captive populations, there was no significant difference in the frequency of being out of burrow between two sexes in the female biased and less dense population, while males came out of the burrow more frequently than females in the denser population with a larger percentage of males. However, females did not tend to be in the burrow when the nearest male was out of the burrow in all captive populations.

Effects of sex ratio bias on other population parameters of tuatara

Tuatara are territorial reptiles where males defend their activity areas for female access (Moore, Daugherty, & Nelson, 2009). Studies have found that a male bias can intensify male-male competition and male aggressiveness to females (Holveck et al., 2015; Le Galliard et al., 2005). My results suggest that a strongly skewed and long-term male bias in the North Brother Island tuatara population has impacted body condition and survival, which in turn has led to a smaller population size over time.

Male tuatara showed larger activity areas than females on the North Brother Island population and captive populations. This male advantage in space occupancy was also observed in the Takapourewa population (Gillingham et al., 1995; Moore, Daugherty, & Nelson, 2009). Behavioural observations in captive populations showed that males were more aggressive than females and always outcompeted females in aggressive interactions. Therefore, the dominance of male tuatara over females in resource competition is likely a contributing factor on North Brother Island as well. Together with the limited food resources on North Brother Island (Hoare et al., 2006), the strongly skewed male bias over 30 years could exacerbate a female disadvantage in resource acquisition, driving the decline in body condition and survival. A continuously declining body condition of females may be driving the observed low incidence of gravidity in females. In addition, female fecundity is correlated with size (smaller females have lower clutch sizes), and female tuatara on North Brother Island are small compared to those in other populations (Cree et al., 1991); size is also resource-dependent (Nelson, Keall, Brown, et al., 2002) and thus females on North Brother Island likely have lower access to resources compared to other populations. Together these patterns support that a male bias and male dominance in this population as a contributing mechanism for the observed declines in population size.

As the population size has declined recently, the density of tuatara on the island has become lower, which may contribute to lessening resource competition and reduced costs on territorial defence over time. This would explain the larger individual activity areas found in the latest ten years compared to the first ten years during the study period. The density-dependence of activity areas is supported by the activity area patterns found in translocated tuatara populations on Matiu/Somes Island and Long Island. These islands are larger than North Brother Island, supporting much smaller tuatara populations with substantially denser vegetation and greater variety of habitat. As predicted, individuals from these translocated populations were found to have substantially larger activity areas than tuatara on North Brother Island.

Additionally, the sex ratio of new cohorts has become less skewed over time compared to the adult population, which could reduce male-male competition and male aggressiveness to females. The improved body condition and survival of the new cohorts is consistent with a response to the declining population size and less intense competition for resources.

The effects of changes in sex ratio for population viability of North Brother Island tuatara

TSD is hypothesised to have adaptive significance in that incubation temperatures producing one sex result in higher fitness for individuals of that sex (Valenzuela, 2021; Warner & Shine, 2008). However, anthropogenic climate warming poses an increasing concern for species with TSD because the relatively fast rising temperatures may lead to strongly skewed sex ratios or even populations with single sex (Janzen, 1994; Mitchell & Janzen, 2010; Valenzuela et al., 2019). Empirical studies have shown that a skewed sex ratio can be a major threat to population viability (Heinsohn et al., 2019; Le Galliard et al., 2005). Thus, population viability in a warming climate has been investigated in many species with TSD.

As most species of reptiles with TSD have the MF or FMF patterns, climate warming may be more likely to result in female-biased populations because more females are hatched at nests in warmer temperatures. For example, the climate warming has contributed to female-biased sex ratios in some sea turtle populations, and some studies have predicted extreme female-biased hatchlings or even 100% female hatchlings at

warmer beaches (Hanson et al., 1998; Jensen et al., 2018; Laloë et al., 2016; Mrosovsky & Provancha, 1992). However, despite the concern for population viability due to female biases, recent studies showed the projection of sea turtle populations in a warming climate is not as pessimistic as previous studies suspected (Hays et al., 2010; Laloë et al., 2014). Male sea turtles breed more frequently than females, thus, the increasing female-biased sex ratio means larger numbers of breeding females, which can increase population growth (Hays et al., 2010, 2017, 2022). For example, in a study on loggerhead turtles (*Caretta caretta*), the strong female skew in hatchlings (70% females) was translated into a balanced operational sex ratio (50% females), because males visited the breeding site 2.6 times more frequently than females (Hays et al., 2010). Therefore, rather than a threat to population viability, a strong female bias could boost population growth of sea turtles due to increased reproduction, unless extreme warming scenarios result in all-female hatchlings or high embryo mortality (Hays et al., 2017).

By contrast, tuatara are reptiles with TSD where males hatch at higher temperatures (Cree et al., 1995; Mitchell et al., 2006). In a warming climate, the sex ratio of tuatara populations will likely become skewed to a male bias due to the overproduction of males from nests (Carter et al., 2018; Mitchell et al., 2008). This poses a threat to the population viability of tuatara populations because a male bias can be an important driver of population decline (Gownaris & Boersma, 2019; Le Galliard et al., 2005; Morrison et al., 2016).

A previous study on Takapourewa showed hatchling sex ratios were correlated with incubation temperatures, but a balanced hatchling sex ratio was predicted in a warmer year based on the incubation temperatures recorded in nests (Nelson et al., 2004a). This is proposed to be due to the large population size of tuatara and the variety of nesting habitat on Takapourewa that may offer this tuatara population resilience to the effects of a warming climate in the short term (Nelson et al., 2004a). This resilience may contribute to a balanced sex ratio also found on Takapourewa from survey data in 2002 (Moore, Daugherty, & Nelson, 2009). Relative to Takapourewa, North Brother Island supports a substantially smaller tuatara population, and has less habitat variety and shallower soil for nesting. In addition, tuatara on North Brother Island inhabit and nest on the northern face, which increases the sun exposure of nesting sites. As such, the nests on North Brother Island are

more likely to produce male-biased tuatara hatchlings (Mitchell et al., 2008; Nelson et al., 2004a). Furthermore, three earlier studies detected an increasing male-bias in the adult tuatara population, indicating the effects of a male-biased hatchling sex ratio has impacted the population on the island (Grayson et al., 2014; Mitchell et al., 2010; Nelson et al., 2002).

Driven by the concern about the viability of North Brother Island tuatara population due to an increasing male bias, Mitchell et al. (2010) and Grayson et al. (2014) performed population viability analyses on this tuatara population based on the population parameters at the time. Using program VORTEX (version 9.99b), both studies examined the viability of 500 simulated populations over 2000 years. These two studies tested the effect of an increasing male hatchling sex ratio on population decline in North Brother Island tuatara population. In models with adult survival set at 95%, the simulated populations resulted in probabilities of extinction within 2000 years once the hatchling sex ratio was up to 75% males, and reached 100% of simulated populations becoming extinct if hatchling sex ratio exceeded 85% males (Grayson et al., 2014; Mitchell et al., 2010). Survival was also detected as a major driver for population viability. The population was found at risk of extinction when survival fell below 91%, and the extinction probability was 100% when survival dropped to 88%, even with a simulated balanced hatchling sex ratio (50% males)(Grayson et al., 2014). Grayson et al. (2014) also used additional survey data and found a slightly lower female survival than in males (1-2% difference in survival between two sexes). When simulated, this difference could drive the population to extinction more rapidly. Furthermore, when inbreeding depression was considered, simulated populations also declined more rapidly, with a steeper rate of decline at a higher level of inbreeding depression (Mitchell et al., 2010).

Based on the predicted hatchling sex ratio (56%, from the soil temperature model developed by Mitchell et al. (2008)) and the estimated survival of both sexes (91% for females and 92% for males) by 2011, Grayson et al. (2014) predicted the extinction probability of this tuatara population at 12% within 2000 years, with an average time to extinction of 1183 years over 500 simulations. Based on the updated population parameters in Chapter Two, I reanalysed the viability of North Brother Island tuatara population using the same general model and version of Vortex (9.99b) to further this discussion.

Mitchell et al. (2010) listed and justified the parameter settings for viability analyses of the North Brother Island tuatara population (Table S5.1). Using this model, I updated three parameters: starting population size, survival, and carrying capacity. The previous two studies set the starting population size at 550 based on the actual number of captures in 2000 and 2001 surveys (Grayson et al., 2014; Mitchell et al., 2010). Chapter Two of this study showed a rapid decline in population size over time, and by 2018 the estimated adult population size was 322 (PLI 292 – 368). In my simulations, I set the starting population size as 400 based on the upper bound of PLI of adult population size estimate and the low capture probability of juveniles (Dawbin, 1982; Nelson, Keall, Pledger, et al., 2002). Also, I updated the survival estimates as 95.26% for females and 95.28% for males based on the estimates by 2018 (Chapter Two). Additionally, I set three levels of carrying capacity in the simulations, which is also used to model density-dependent reproductive rates. First, I used 500 as carrying capacity which was used in previous two studied (Grayson et al., 2014; Mitchell et al., 2010). Second, I calculated the current carrying capacity of North Brother Island at 337 based on the starting population size that returns the updated female breeding rate at (7%, Chapter Two). Third, I set 250 as carrying capacity, which is a threshold for the conservation status of a species to be determined critically endangered (IUCN, 2021). For each level of carrying capacity, I set the standard deviation as 10% of carrying capacity (Mitchell et al., 2010).

Using the updated population size, survival and carrying capacities, I tested the population viability with differing male hatchling sex ratios. I performed simulations using the hatchling sex ratio of 56% males (based on Grayson et al., 2014 and Mitchell et al., 2008), and at hatchling sex ratios between 60% and 80% males by intervals of 2.5% (Table S5.2). At the carrying capacity of 500, there were probabilities of extinction in 2000 years when the male hatchling sex ratio increased to 75%, similar to the threshold found by Mitchell et al. (2010) and (Grayson et al., 2014). When the carrying capacity decreased to 337 or 250, there were probabilities of extinction once the male hatchling sex ratio increased to 72.5% (Table 5.1). Although the current hatchling sex ratio is unknown, I estimate the adult sex ratio could largely reflect the hatching sex ratio because adult survivals of both sexes were very close in this tuatara population (Chapter Two). The current adult male sex ratio was 62.5% (1:1.66 by 2018, Chapter Two). With the hatchling sex ratio

of 62.5% males, all simulated populations with the three different carrying capacities survived in simulations that were run for 2000 years, but at a lower population size (Table 5.1). For example, at the current carrying capacity of 337, the population size was expected to decline to 255.5 over 2000 years, which is close to the threshold for the conservation status of critically endangered (250, IUCN, 2021). Additionally, I performed simulations over 4000 years at hatchling sex ratios of 62.5% and 65% males for each carrying capacity, which showed the same results as simulations run for 2000 years (exactly the same estimates of population growth rate and probability of extinction, and very close estimates of population size, Table S5.2). With the updated population parameters, the tuatara population on North Brother Island is predicted to have higher viability than the simulations of Grayson et al. (2014). This is mainly due to the higher adult survival, and the similar survival estimates for both sexes.

Modelling population viability includes several facets that are not well covered using the current methodology. The maximum lifespan of tuatara was set as 100 years in the simulations (and is a hard limit for the software), but a recent study showed tuatara's lifespan can be as long as 137 years (modelled using North Brother Island data; Reinke et al., 2022), indicating that individuals in this tuatara population might be able to reproduce for longer than the Vortex simulations could model. Senescence in captive tuatara has been observed (pers. comm. Nicola Nelson), but the ages of those individuals or differences in the decline in reproductive capacity between males and females are unknown. Although not incorporated in these updated analyses, inbreeding depression should not be neglected as a driver of population decline. Based on the updated annual female gravidity rate of 7% and an estimated tuatara population estimate of 118 females on North Brother Island (Chapter Two), we expect that only around eight females will be gravid on average each year in this population. Together with the average clutch size and mortalities of eggs, hatchlings, and juveniles (Cree et al., 1991; Mitchell et al., 2010), we estimate only about six tuatara maturing into the adult population each year. Given the low numbers of individuals, inbreeding depression and/or genetic drift present real issues for population viability. These very low numbers also present the additional risk of random events affecting demographic parameters and having higher importance for this population (Lacy, 2000).

Table 5.1 The results of population viability analyses in North Brother Island tuatara population at the hatchling sex ratios when simulations start to show probabilities of extinction and at current hatchling sex ratio

		Carrying capacities		
		500	337	250
Hatchling sex ratio when simulations start to show probabilities of extinction	Hatchling sex ratio (% males)	75	72.5	72.5
	Probability of extinction	0.008	0.002	0.018
	Population size \pm SD	272.62 \pm 64.26	206.36 \pm 43.09	145.20 \pm 38.39
Current hatchling sex ratio	Hatchling sex ratio (% males)	62.5	62.5	62.5
	Probability of extinction	0	0	0
	Population size \pm SD	381.63 \pm 37.07	255.51 \pm 26.44	189.36 \pm 22.65

The population viability analyses in this table were performed with 500 iterations within 2000 years at three levels of carrying capacities.

Settings of population parameters were justified in Table S5.1. Full output of population viability analyses was detailed in Table S5.2.

Moreover, the rate of global warming is unprecedented (Osman et al., 2021), which may further skew the sex ratio of the North Brother Island tuatara population by producing more male-biased hatchlings from nests. Although population simulations showed this population is still viable at the male hatchling sex ratio of 70% under the current carrying capacity (337), the population size experiences a rapid decline once the male hatching sex ratio is up to 65%. Based on thermal conditions at nest in 2011, Grayson et al. (2014) estimated the hatchling sex ratio of this population at 56%. Over the past 100 years, four of five New Zealand's warmest years occurred after 2011 (Mullan et al., 2010). This indicates North Brother Island tuatara population is likely experiencing a faster escalation of the hatchling sex ratio, and a 72.5% male hatchling sex ratio may occur in a short term, where simulated populations become at risk of extinction.

Like sea turtles, the tuatara lineage has survived historical climates including cold periods (ice ages) and warm periods (interglacials), therefore, they might have some capacity for adaptation over time (Cree, 2014; Miller et al., 2012; Poloczanska et al., 2009). However, it is challenging for tuatara populations to adapt to the rapid climate change due to their longevity, late maturity, and restricted range on islands and in protected areas. Together with a small number of tuatara, as well as north-facing habitat with less variety and shallower soil for nesting (Nelson et al., 2004a), the resilience of North Brother Island tuatara population to climate warming by variation in nesting behaviour may be limited.

To sum up, a strongly skewed male bias has been documented in the North Brother Island tuatara population over 30 years, together with a consistent decline in body condition, population size, and slight reductions in survival. The male-biased adult sex ratio can intensify the dominance of males over females, leading to declining female fecundity and a continued threat to population viability. Moreover, the warming climate may exacerbate the projection of this tuatara population by further skewing the male-biased hatchlings from nests. Although this population currently seems numerically viable for the long-term based on the current population parameters, population simulations indicated low female fecundity and further skewed male hatchling sex ratios could drive this population to extinction at a rapid rate if demographic parameters shift.

Tuatara hatchling sex ratio in a year is influenced by the air temperatures during the incubation period, but this hatchling sex ratio is unlikely detected until hatchlings reach

maturity and become regularly detectable in population surveys. The new cohorts showed a less skewed sex ratio and improved survival over time, which may contribute to a less male-biased sex ratio of the population after 2005 (Chapter Two). As more new cohorts occur into this population, the effects of the new cohorts on population demography will become apparent. Therefore, longer-term monitoring on the North Brother Island tuatara population is needed to investigate the lagged impact of environmental temperatures on sex ratio and other population parameters as well as population viability. Furthermore, this longer-term monitoring can reveal the patterns of sex ratio fluctuation: whether the male bias becomes more evident under climate warming, or the sex ratio generally fluctuates around 1:1 despite irregular fluctuations based on the climate-mediated sex determination (Figure 5.1) and behaviour of nesting females.

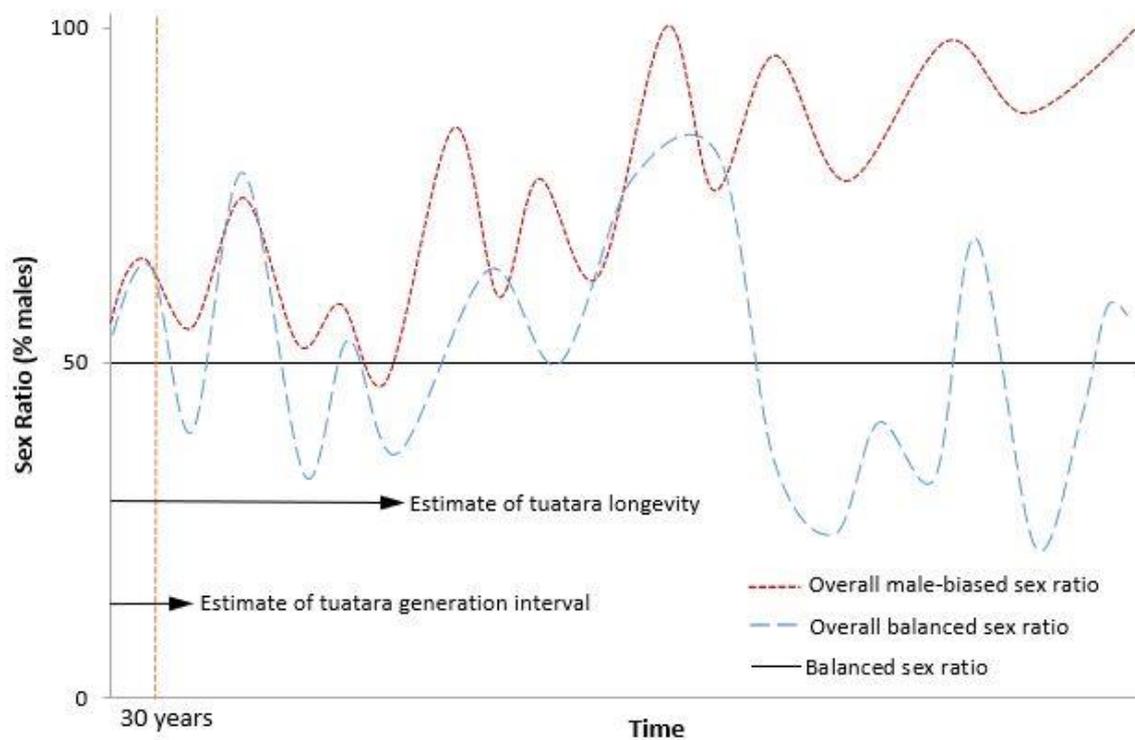


Figure 5.1 Two possibilities of the temporal trend of sex ratio in North Brother Island tuatara population in a warming climate. Red dashed line shows the sex ratio will become more evident. Blue dashed line shows there will be an overall balanced sex ratio despite of irregular fluctuations. Orange dashed line stands for where the current sex ratio is at based on the 30-year survey data. The mean generation interval of tuatara is between 32 and 44 years (Mitchell et al., 2010). The estimate of tuatara longevity is 137 years (Reinke et al., 2022).

Limitations of this study

Tuatara are long-lived species, and the generation interval of the Northern Brother Island population was estimated at around 40 years (Mitchell et al., 2010). In this study, population parameters were estimated based on 30 years' survey data, which is relatively short to investigate the sex ratio fluctuation over time in a warming climate. Instead, a longer-term monitoring spanning multiple generations may better reflect the temporal pattern of tuatara sex ratio on this island.

During tuatara population surveys on North Brother Island, locations of captures and recaptures were recorded on a grid map. When estimating the activity areas, captures and recaptures that occurred in the same grid cell were recorded as the geographical coordinates of the centroid, which reduced the accuracy of activity area estimates. Also, researchers caught tuatara at night when visibility of landmarks is obscured, therefore, there were likely small levels of imprecision in the location records. For example, of 2851 records of capture locations over 30 years, five errors were found and corrected. In addition, two versions of grid maps were used through the 30 years' surveys, with one used by 2000 and the other used from 2001. Two grid maps are different in the smallest unit of grid cell, which is another factor influencing the accuracy of activity area. Furthermore, tuatara population surveys were performed every few years and usually for five nights within each survey, resulting in limited captures and recaptures for most of individuals to estimate activity areas. Therefore, only a small portion of individuals were included to explore the activity areas and spatial interactions, which may not effectively reflect the more complex situation of this population. This might be the reason that large males were not detected to have larger activity areas, maintain exclusive activity areas, or secure greater access to females.

Tuatara behavioural observations were performed in artificial environments instead of in the natural populations. Tuatara behaviour might be influenced by many anthropogenic factors, such as limited space, artificial feeding, and visitor disturbance. Also, tuatara are nocturnal and more active at night even in captive facilities (Wörner, 2009). Captive tuatara were observed during the day, which may not effectively reflect all interactions between individuals.

The current hatching sex ratio produced from nests was not examined in recent surveys. Instead, I used the current adult sex ratio as an approximate estimate of the hatchling sex ratio, which may influence the accuracy of the population viability output.

Recommendations

Future research on the North Brother tuatara population could (1) continue to perform population surveys to investigate the sex ratio fluctuation patterns in a warming climate, and observe nesting behaviour to understand the potential for tuatara to offset the male bias; (2) record locations of captures and recaptures using GPS to improve accuracy of activity area estimates; (3) perform population surveys more frequently, with more searching nights within each survey to increase captures and recaptures, thus, more individuals can be included to acquire more information in activity area patterns (e.g., large males' advantage in spatial interactions with others); (4) if possible, tuatara behaviour should be observed on the island during night to reflect the actual behaviour and interactions in the natural environment; (5) estimates of the current hatchling sex ratio by examining thermal conditions in nests would be informative, and enable reanalysis of population viability for improved population projections. Meanwhile, the sex ratio pattern and the ensuing consequence on population viability should be investigated in other tuatara populations, particularly the Takapourewa population, but also populations within the wider latitudinal range, to understand whether the male bias and population decline is unique to the North Brother Island population or is common to all tuatara populations. Such research could contribute to understanding the pattern of sex ratio fluctuations and its consequence on the viability of tuatara populations in a warming climate, particularly since most tuatara populations are further north and experiencing warmer temperatures. This understanding can provide implications for specific interventions on tuatara populations, such as artificial egg incubation for female hatchlings, translocations to more southern (cooler) or forested sites, or habitat modifications. Furthermore, the adult sex ratio pattern of tuatara can be used as an early warning signal for population consequences of a sex ratio bias in other species with TSD.

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Supplemental Material

Table S2.1. The candidate model set for each open model analysis.

No.	Survival	Capture	No.	Survival	Capture
1*	time	time	21	T	time
2	time	sex	22	T	sex
3*	time	time+sex	23	T	time+sex
4*	time	time*sex	24	T	time*sex
5	time	.	25	T	.
6	sex	time	26	T+sex	time
7	sex	sex	27	T+sex	sex
8	sex	time+sex	28	T+sex	time+sex
9	sex	time*sex	29	T+sex	time*sex
10	sex	.	30	T+sex	.
11*	time+sex	time	31	T*sex	time
12	time+sex	sex	32	T*sex	sex
13*	time+sex	time+sex	33	T*sex	time+sex
14*	time+sex	time*sex	34	T*sex	time*sex
15	time+sex	.	35	T*sex	.
16*	time*sex	time	36	.	time
17	time*sex	sex	37	.	sex
18*	time*sex	time+sex	38	.	time+sex
19*	time*sex	time*sex	39	.	time*sex
20	time*sex	.	40	.	.

An open model analysis models survival and capture probability simultaneously. Survival was modelled (1) as combinations of time and sex, including time only (time), sex only (sex), additive effects (time+sex), and additive and interactive effects (time*sex), (2) as combinations of a temporal linear trend (T) and sex, including a linear trend only (T), additive effects (T+sex), and additive and interactive effects (T*sex), or (3) as a constant (.). Capture probability was modelled either as combinations of time and sex, including time only (time), sex only (sex), additive effects (time+sex), and additive and interactive effects (time*sex), or as a constant (.).

* As the final survival and capture probability are confounded in a fully time-dependent model (i.e., survival and capture probability simultaneously vary among surveys; Lebreton et al., 1992), I imposed the constraint on these models that the capture probabilities of last two surveys were equal.

Table S2.2. Relative importance of variables in the open model analyses.

Open model analysis of the population				Open model analysis of the new cohort			
Survival Rate		Capture Probability		Survival Rate		Capture Probability	
Variables	Sum of Weights	Variables	Sum of Weights	Variables	Sum of Weights	Variables	Sum of Weights
.	0.33684	time+sex	0.92502	.	0.39301	time	0.38349
T	0.28251	time*sex	0.075	T	0.21265	.	0.31394
sex	0.12308			sex	0.18279	sex	0.15564
T+sex	0.10268			T+sex	0.08993	time+sex	0.14362
T*sex	0.05371			T*sex	0.05996	time*sex	0.00327
time	0.0734			time	0.04299		
time+sex	0.0278			time+sex	0.0181		
				time*sex	0.00053		

Sum of weights of each variable was calculated over all models within the model set for model averaging including this variable. Variables with high weights were considered as important variables explaining variations in survival rate and capture probability.

Table S2.3. The candidate model set for each closed model analysis and descriptions of the model structure.

Models	Model structure descriptions
M(0)	No variation in capture probability.
M(t)	Capture probability varies among differing survey nights.
M(b)	Capture probability varies between first capture and recapture.
M(h)	Capture probability varies among differing mixtures of heterogeneity*.
M(RE)	Capture probability varies based on a continuous mixture of heterogeneity.
M(tb)	Capture probability is modelled as the additive effect of (t) and (b).
M(th)	Capture probability is modelled as the additive effect of (t) and (h).
M(tRE)	Capture probability is modelled as the additive effect of (t) and (RE).
M(bh)	Capture probability is modelled as the additive effect of (b) and (h).
M(bRE)	Capture probability is modelled as the additive effect of (b) and (RE).
M(tbh)	Capture probability is modelled as additive effect of (t), (b) and (h).
M(tbRE)	Capture probability is modelled as the additive effect of (t), (b) and (RE).

Model M(tbh) was the most general model in the model set and was tested for the overdispersion with Fletcher \hat{c} for each closed model analysis.

* Two-mixture heterogeneity was selected where finite mixtures were considered as the source of heterogeneity, because two mixtures are generally supported by most data sets (Cooch & White, 2019).

Table S2.4. Estimates of population size from closed model analyses.

Survey	Males and females					Males					Females					Sum* N
	N	SE	LPLI	UPLI		N	SE	LPLI	UPLI		N	SE	LPLI	UPLI		
Mar-96	445	35	389	528		293	26	253	356		155	24	122	221		448
Dec-97	406	42	340	509		259	32	211	342		149	30	110	236		408
Mar-05	363	35	308	449		268	32	220	348		94	17	74	145		362
Nov-10	279	25	240	340		200	25	164	266		78	17	59	132		278
Nov-11	353	25	312	409		224	24	188	287		131	21	102	189		354
Nov-16	303	18	275	348		207	15	185	244		96	11	82	125		303
Nov-18	322	19	292	368		204	15	183	242		118	12	101	151		322
Mar-05	121	80	48	423		75	51	32	275		NA	NA	NA	NA		NA
Nov-10	105	36	64	218		89	41	47	230		21	11	13	69		111
Nov-11	146	51	85	305		121	63	58	342		35	12	22	77		157
Nov-16	131	24	99	198		85	16	65	132		49	18	30	109		134
Nov-18	139	19	114	191		89	13	71	127		50	11	38	87		139

The female population size in 2005 survey was inestimable due to low capture numbers. LPLI and UPLI stand for lower and upper 95% profile likelihood confidence intervals, respectively.

*This column is the sum of the estimates of closed model analyses for males and females separately on each survey.

Table S5.1 Parameter settings for population viability analyses in North Brother Island tuatara population

Parameters	Settings
Number of iterations	500
Number of years	2000; 4000*
Age normally begin breeding	females: 15; males: 20
Maximum age (cessation of breeding)	100
Breeding system	Polygynous
(% males in breeding pool)	25%
Density dependent reproduction?	Yes
Maximum % females breeding (M)	50
% breeding at carrying capacity (C)	15
Exponential steepness (B)	1.2
Allee parameter (A)	0
Environmental variation in % females breeding	2.8
Maximum clutch size	10
Clutch size distribution:	
0-2	0
3	3.7
4	11.11
5	25.93
6	20.37
7	22.22
8	12.96
9	1.85
10	1.86
Annual mortalities % (SD):	
0-1 (eggs)	50.0 (13.6)
1-2 (hatchlings)	27.8 (7.6)
2-3	21.7 (5.9)
3-6	14.4 (3.9)
6-9	7.0 (1.9)
9-12	6.0 (1.6)
12-adult	males: 4.72* (1.4); females: 4.74* (1.4)
Carrying capacities (K)	500 (50)
(SD:10% of carry capacities)	337* (34)
	250* (25)
Starting population size (N)	400*
Hatchling sex ratio (% males)	56^; between 60-80 by intervals of 2.5

Parameters that were updated in this study. ^Parameter that was updated and justified by Grayson et al. (2014). Other parameters were set and justified by Mitchell et al. (2010). At all male hatchling sex ratios, the simulations were performed within 2000 years. Besides, the simulations were performed within 4000 years at the hatchling sex ratios of 62.5% and 65% males. Mortalities of both sexes were set at 4.74% for females and 4.72% for males based on survival estimates by 2018. Starting population size (N) was set at 400 based on the upper bound of PLI of adult population size estimate (368) by 2018 and juveniles' low capture probability (Dawbin, 1982; Nelson, Keall, Pledger, et al., 2002). Carrying capacity (K) was set for three levels. Two previous studies used carrying capacity at 500 (Grayson et al., 2014; Mitchell et al., 2010). The current estimate of carrying capacity (337) was calculated based on the equation of 'Female Breeding Rate' in Vortex (9.99b): % female breeding = $M - ((M - C) * ((N / K)^B)) * (N / (A + N))$. In this equation, the female breeding rate was 7% which was estimated in Chapter Two. The third level of carrying capacity was set at 250, which is the threshold of conservation status as critically endangered (IUCN, 2021)

Table S5.2 Population viability analyses in North Brother Island tuatara population

Hatchling SR (male %)	Carrying capacity = 500						Carrying capacity = 337						Carrying capacity					
	r (population growth rate)	SD(r)	PE (Probability of extinction)	N (Population size)	SD (N)	TE (Time to extinction)	SE(TE)	r (population growth rate)	SD(r)	PE (Probability of extinction)	N (Population size)	SD (N)	TE (Time to extinction)	SE(TE)	r (population growth rate)	SD(r)	PE (Probability of extinction)	N (Population size)
56	0.007	0.067	0	399.79	34.54	0		0.007	0.071	0	270.08	24.18	0		0.007	0.076	0	196.86
60	0.005	0.066	0	389.51	36.86	0		0.005	0.071	0	259.31	24.61	0		0.005	0.076	0	193.52
62.5	0.004	0.065	0	381.63	37.07	0		0.004	0.07	0	255.51	26.44	0		0.004	0.075	0	189.36
62.5*	0.004	0.065	0	382.04	37.58	0		0.004	0.07	0	254.77	27.9	0		0.004	0.075	0	187.33
65	0.003	0.065	0	370.68	38.64	0		0.003	0.07	0	249.4	26.86	0		0.003	0.075	0	182.38
65*	0.003	0.065	0	370.82	39.9	0		0.003	0.07	0	247.62	29.36	0		0.003	0.075	0	181.66
67.5	0.002	0.065	0	358.08	45.16	0		0.002	0.07	0	237.42	31.93	0		0.002	0.075	0	174.87
70	0.001	0.065	0	342.41	47.03	0		0.001	0.071	0	223.26	35.7	0		0.001	0.076	0	164.13
72.5	0	0.066	0	311.72	51.34	0		0	0.072	0.002	206.36	43.09	1070	0		0.078	0.018	145.2
75	0	0.068	0.008	272.62	64.26	1268	282.43	0	0.074	0.03	173.64	53.66	1087.9	135.11	0	0.081	0.114	117.38
77.5	0	0.071	0.044	216.11	81.76	1130	120.54	-0.001	0.08	0.218	111.94	76.17	1041.3	46.27	-0.001	0.087	0.458	59.44
80	-0.001	0.078	0.354	107.49	98.07	1073.7	38.11	-0.002	0.087	0.668	35.31	57.76	957.31	26.46	0.003	0.094	0.886	9.22

Hatchling sex ratios with asterisk stand for simulations with 500 populations within 4000 years, otherwise, 500 populations within 2000 years. Settings of population parameters were justified in Table S5.1.