

School of Molecular and Life Sciences

**Population Dynamics, Detectability and Behaviour of Tiger Snakes
(*Notechis Scutatus*) in Perth's Urban Wetlands**

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**This thesis is presented for the Degree of
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Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013). Chapters 2 and 3 received animal ethics approval from the Curtin University Animal Ethics Committee, Approval number ARE2021-21 and the Western Australian Department of Parks and Wildlife, Approval numbers FO25000370.

Signature:

Date: 29/06/23

“Nature is a never-ending learning process, every visit into the field teaches us something different. I think I could spend five lifetimes and still not know it all”.

– Subaraj Rajathurai

“An understanding of the natural world is a source of not only great curiosity, but great fulfilment. This is a story of our changing planet, and what we can do to help it thrive”.

– Sir David Attenborough

“What good is a fast car, a flash house, and a gold-plated dunny to me. Absolutely no good at all. I’ve been put on this planet to protect wildlife and wilderness areas, which in essence is going to help humanity”.

– Steve Irwin

Acknowledgement of Country

We acknowledge that Curtin University works across hundreds of traditional lands and custodial groups in Australia, and with First Nations people around the globe. We wish to pay our deepest respects to their ancestors and members of their communities, past, present, and to their emerging leaders. Our passion and commitment to work with all Australians and peoples from across the world, including our First Nations peoples are at the core of the work we do, reflective of our institutions' values and commitment to our role as leaders in the Reconciliation space in Australia.

I would specifically like to acknowledge and thank the Whadjuk, Yued and Gnaala Karla Booja people, the First Nations peoples whose land my research was conducted on.

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Statement of Contribution

During the course of this research on which I collaborated; I (along with my collaborators) were able to produce two chapters worthy of publication. The work we have put in greatly broadens our knowledge of tiger snake population dynamics and behaviour. I attained my co-authors permissions to use the two chapters for journal publication. See permissions below.

Chapter 2

Subaraj, S., von Takach, B., Phillips, B., Lettoof, D. C., Bateman, P. W. Surviving in the city: Investigating the population size, survival rates and detectability of a Western Tiger Snake (*Notechis scutatus occidentalis*) in urban wetlands. *In Preparation.*

Chapter 3

Subaraj, S., von Takach, B., Lettoof, D. C., Bateman, P. W. Urban snakes in a changing world: responses of western tiger snakes (*Notechis scutatus occidentalis*) to interactions with humans in urban wetlands. *In Preparation*

“Careful mate, they’ll chase ya”

- Old mate, Bibra Lake

General Abstract

Urbanisation and the rising growth of the human populations alters and transforms natural ecosystems. Wetland habitats can be affected by the changes brought about by urbanisation such as the alteration of wetland hydrology, the surround habitat structures and the introduction of anthropogenic contaminants. The health of wetlands can be reflected by top predators that inhabit these ecosystems, and western tiger snakes (*Notechis scutatus occidentalis*) in the southwest of Australia have been shown to be an ideal bioindicator. The continued persistence and survival of these top predator populations in these urban wetlands is impertinent towards a wetland ecosystems health. Understanding their population dynamics and behavioural ecology in response to anthropogenic activity is pivotal towards getting a snapshot into their continued persistence in urban wetlands and can induce better management and conservation of this top reptile predator.

In this thesis, I investigated the population size, survival rates and rates of capture of western tiger snakes in three different wetlands in Perth, Australia. The wetlands differed in their degrees of urbanisation, environmental contamination levels and habitat structures. I used a mark-recapture method to investigate their recapture rate and population sizes using Jolly-Seber models. I also investigated the behavioural response of tiger snakes in response to different human interactions and incorporated environmental, snake body condition and human presence variables in relation to their responses. I used generalised linear models to investigate the variables associated with a snake's response towards a human interaction.

I found that of the three chosen wetlands, the most contaminated and urban-impacted wetland contained the largest population size and survival rate, while the most natural wetland that was located outside the urban matrix had no recaptures and had to be excluded from the calculations. I found no association in two of the three human-snake interactions with the predictor variables and found that despite the larger human densities in the urban wetlands, the snakes had no behavioural variation amongst the three sites. The passive response to the interactions was the highest in the urban wetlands and across all three wetlands, the defensive response was the least recorded. Future investigation needs to be carried out on urban snakes and if their response rates differ to natural wetlands and if higher anthropogenic activity brings about increased plasticity in these urban populations.

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Glossary

Population: A group of individuals of the same species that live in the same geographic area and have the potential to interbreed.

Survival: The ability of an individual or a population to continue to persist in its environment over time, encompassing various aspects such as successful reproduction, overcoming threats and adapting to environmental changes.

Mark-recapture: A technique used, particularly on species that are difficult to directly observe and count, to estimate a population's size or other parameters such as survival rates.

Behavioural ecology: A scientific field that is focussed on animal behaviour and examines how animals interact with their environment, other individuals, resources, and how these behaviours enable their survival and reproduction.

Plasticity: The ability of individuals or a population to adjust and modify their behaviour, physiology and morphology in response to changes in their environment.

Interaction: The relationship and mutual influence between individuals, populations or species which affects their behaviour and ecology which ultimately affects their reproduction and survival.

Chapter 1. General Introduction



Western Tiger Snake (*Notechis scutatus occidentalis*)

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1.1 Introduction

The rising growth of the human population brings about the degradation of the natural environment from urbanisation (French et al., 2018; McKinney, 2008). Urbanisation alters the ecosystems of natural habitats through deforestation, introduction of invasive species, increasing human-wildlife interactions and pollution and a reduction in the diversity of species (Concepción et al., 2015; McKinney, 2002, 2008; Müller et al., 2020; Seto et al., 2012; Theodorou, 2022). This can create isolated natural pockets in an urban matrix (Bryant et al., 2017) and these natural habitats surrounded by a sea of urban infrastructure can serve as refuge zones for remnant populations of flora and fauna (Bryant et al., 2017; Fusco et al., 2021; Soanes & Lentini, 2019). Such habitat 'islands' are further impacted by the encroachment of human leisure activities or surrounding urban pollution.

However, not all species are able to adapt to the drastic change of urban encroachment and avoid the urban matrix completely (McKinney, 2002) which causes a decline or an extinction of populations in natural pockets of urbanisation zones (Bryant et al., 2017; McKinney, 2008). Native species' populations can also decline in urbanised areas through competition with invasive species brought in through human influence or imported infrastructure materials (McKinney, 2002). Additionally, monocultural vegetation growth greatly reduces the species-richness of areas through horticulture landscaping and suburban gardening (Marzluff and Ewing, 2001). However, more adaptable native species are able to persist in fragmented habitats or are able to adapt to live within urbanised areas (Bateman & Fleming, 2012), species that are unable to adapt to the urban matrix and fragmented areas tend to be specialists; species that require a certain habitat type or food source (Bonier et al., 2007; Mazza et al., 2020). Species that are able to adapt well to urbanisation are typically generalists; species that do not require a certain habitat type and have a wider more broad range of food sources (Nordberg & Schwarzkopf, 2019). Reptile diversity in urbanised areas is much lower than that of birds, but certain species such as geckos are more adaptable to human infrastructures (Zozaya et al., 2015), while larger reptilian predators like pythons and certain elapids are able to utilise human areas for easy food sources (French et al., 2018; Parkin et al., 2021). Tiger snakes (*Notechis scutatus*) appear to be more adaptable and

persist in remnant wetlands surrounded by urban and suburban areas (Lettoof et al., 2020).

Ecological indicator species are used as a simple way of understanding environment health or a novel stressor (Paoletti & Sommaggio, 1996; Burger et al., 2007). Wetlands are some of the most vital ecosystems in the globe, where their hydrological cycle is important both to of humans and a vast array of species diversity that rely on them (Xu et al., 2019). In the Southwest of Western Australia, the rapid growth of urbanisation has caused the devastation of a large portion of its wetland habitats and surrounding habitat and riparian vegetation are being overrun by invasive species (Brooks et al., 2005; Davis & Froend, 1999; Kelobonye et al., 2019; McKinney, 2008) Wetlands are a particularly sensitive ecosystem vulnerable to environmental degradation from forces such as urbanisation (Faulkner, 2004), and many aspects of wetland disturbance and integrity can be measured using indicator species (Burger et al., 2007; Sharma & Rawat, 2009). Tiger snakes have been shown to be an ideal indicator of wetland condition and stability (Lettoof et al., 2020). Recent research has shown that tiger snakes accumulate an array of contaminants from all wetland sites studied around Perth (Lettoof et al., 2020; Lettoof et al., 2020). Ongoing research indicates that tiger snakes suffer from worse health in the more contaminated wetlands (Lettoof et al., 2020; Lettoof et al., 2020).

The tiger snake (*Notechis scutatus*) is a large venomous Australian elapid found across Western Australia, South Australia, New South Wales, Victoria and Tasmania (Cogger, 2000; Wilson & Swan 2008). Its body coloration is variable throughout Australia, though in the western populations such as Perth, they are generally black with mild to distinct yellow banding (Bonnet et al., 2002). Mostly found on the mainland, there are isolated populations on a few Australian islands (Cogger 2000, Wilson and Swan 2008). They have been studied throughout their range with most of the research focussing on island populations and populations in natural wetlands (Aubret et al., 2007, 2011; Aubret & Shine, 2008; Bonnet et al., 2002; Butler et al., 2005b, 2005a; Shine, 1979).

Despite research into tiger snake health in Perth wetlands, little is known about how this translates into tiger snake population sizes in these wetlands and if these populations are stable, increasing or in decline. In Herdsman Lake for example, the snake population may be declining due to poor body condition and high contaminant

loads. However, urban populations may instead be increasing because of a lack of predators and competing species. Snake population research indicates that mark-recapture studies can be successful in estimating a population's size, density and abundance (Bartman & Kudla, 1981; Chim & Diong, 2013; Guimarães et al., 2014; Sun et al., 2001). By using the rate of recapture of individual snakes, I can first calculate the population size which will then enable us to calculate the density and abundance of tiger snake populations in these wetlands. With these data, I can then estimate the survivability of these populations using population viability analysis. A population viability analysis will help us understand the degree of persistence of tiger snake populations in these wetlands.

Most snake species are generally difficult to study, especially for population estimates. This is often because snakes are generally cryptic and shy due to their secretive behaviour (Durso et al., 2011). Studies have shown that behaviour of species can result in unequal catchability, e.g. aspic vipers (*Vipera aspis*): during visual encounter surveys reproductive females were caught more than were non-reproductive females (Willson et al., 2011). In my three Perth study sites, there are other elements that could affect the detectability of snakes such as poor health and body condition and human habituation and disturbance. Studies have shown that if constantly exposed to humans, certain species of reptile demonstrate bolder behaviour by becoming habituated to human presence (Avilés-rodríguez, 2019). This will presumably benefit the bolder individuals, and populations with selection for more bolder individuals may be better able to survive (Rodríguez-Prieto et al., 2010). In urban wetlands with high human traffic, I aim to determine if human habituation affects the detectability of tiger snakes. This research will help us understand the population dynamics of an urban-stressed snake population.

1.2 Aims

This thesis aims to assess how the population density and behavioural characteristics of Western tiger snakes (*Notechis scutatus occidentalis*) vary throughout wetlands spread around Perth's urban matrix, and how that affects their ability to persist in these wetlands. Using mark-recapture techniques along fixed and timed transects, I calculated their size and survival rates which allows for a more accurate population estimate in each wetland. I conducted behaviour studies on snake reactions when seen, handled and released to understand the snake-human interactions at these wetlands which will give rise to an understanding of their detectability and if human habituation is a factor for their survival in urbanised wetlands. Factoring variables such as environmental drivers and human disturbance enables a more in depth understanding of their behavioural responses.

The research aims of this study are to:

1. To determine and establish the population size, abundance and detection rate of tiger snakes in wetlands differing in urbanisation and environmental contamination, by conducting a systematic mark-recapture study.
2. To model the survivability of each wetland's population using Jolly Seber models
3. To determine if tiger snake behaviour differ between the survey sites and if it influences the detectability of the snakes.

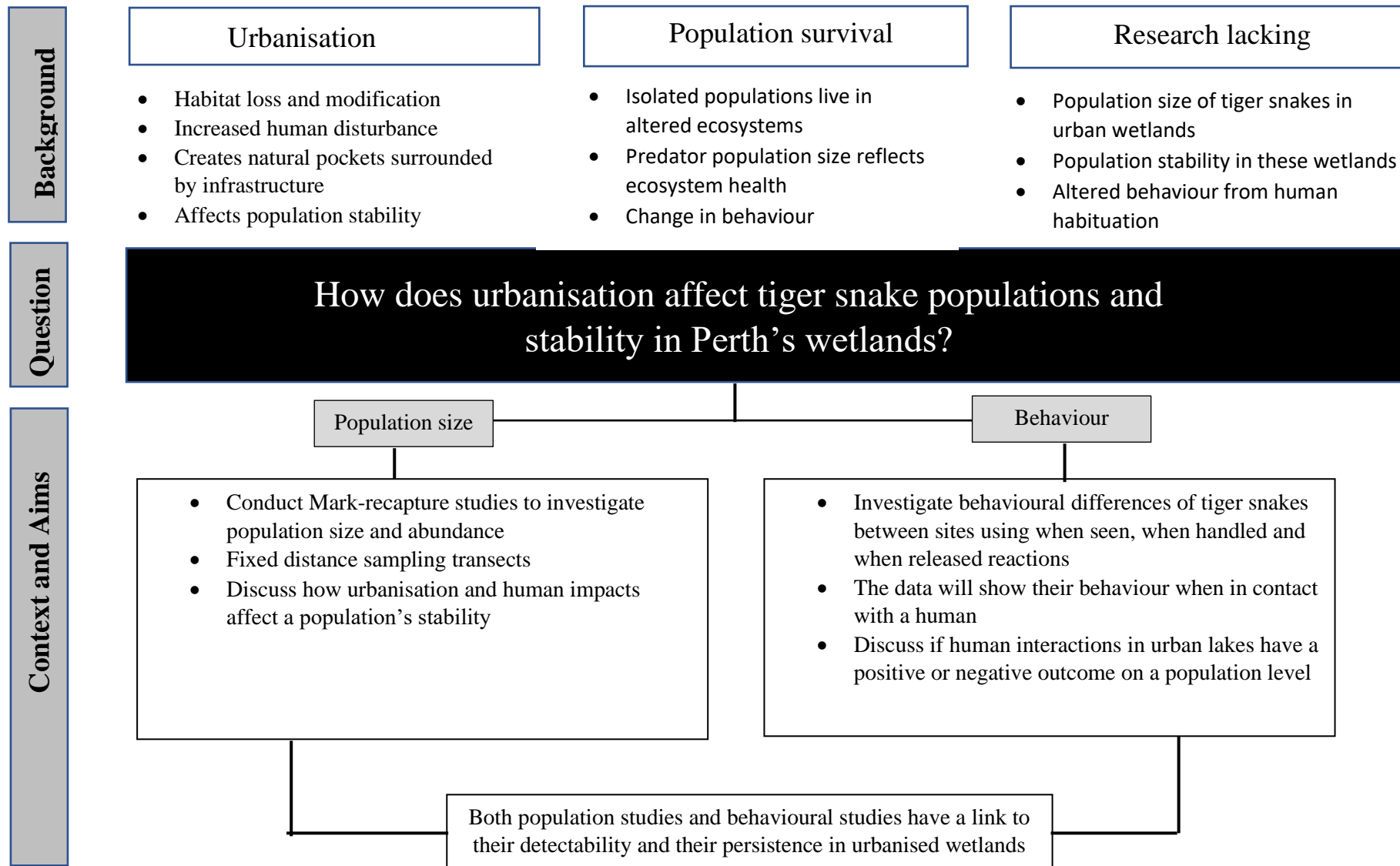


Fig. 1.1 Conceptual flow diagram of thesis research aims and direction

1.3 Study area

This study was conducted around Perth, Western Australia (31°56' S, 115°51' E). I focussed my research on three wetlands scattered within 50km of Perth City. The three research sites are Herdsman Lake (31.92°S, 115.80°E), Bibra Lake and Loch McNess (31.54°S, 115.68°E) which is situated within Yanchep National Park. Loch McNess is the northern most study site where it is 50km away from Perth City Central. Herdsman Lake is 42.25km South of Loch McNess and Bibra Lake is situated 17.5km south of Herdsman Lake.

The first site, Herdsman Lake, is the most polluted lake of the three lakes as it is surrounded by both urban and industrial estates. The landscape of this wetland has been changed heavily over the decades from landfills, drainage, massive gardening, reclamation and illegal dumping (Lettoof et al., 2020). The second site, Bibra Lake has a lower contamination factor and still retains both large woodland and riparian vegetation buffers even though it is in close proximity to suburban homes and roads (Lettoof et al., 2020). Loch McNess is the least modified of the three sites with minimal human disturbance given that it is the only survey site outside the urban matrix (Lettoof et al., 2020). Even though it is the least modified, it has a high contamination level from accumulated contaminated sediments caused by decreasing surface runoff and increasing disconnection to the groundwater system (Lettoof et al., 2020). The degree of urbanisation ranges from heavily modified (Herdsman), partially modified (Bibra), and minimally modified (Loch McNess).

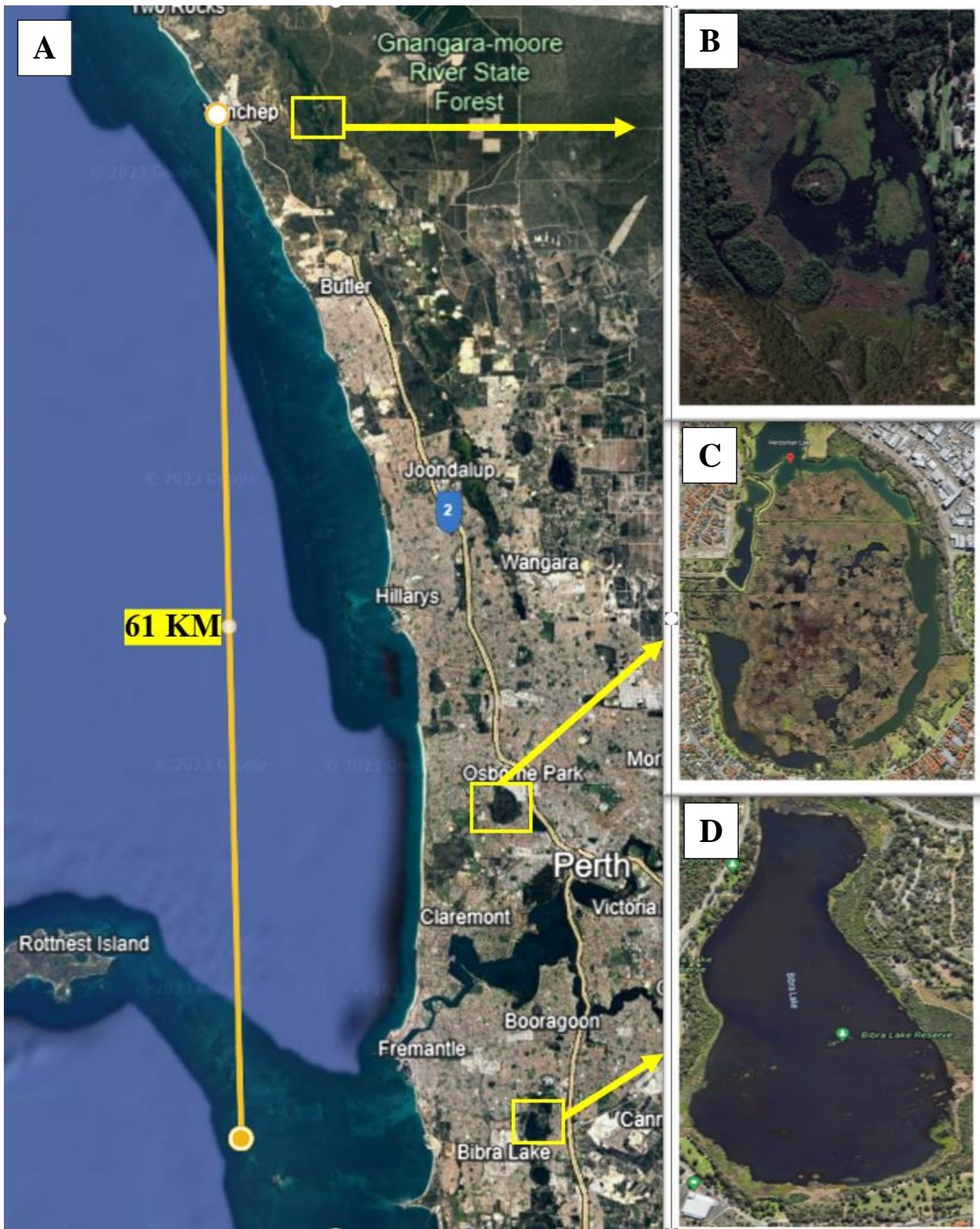


Figure. 1.2 Overview of study sites A) Aerial view of all three sites in Perth, B) Loch McNess in Yanchep National Park, C) Herdsman Lake and D) Bibra Lake (Images taken were from Google Earth Pro, 2019)

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Chapter 2. Surviving in the city: investigating population size, survival rates and capture frequency of a western tiger snakes (*Notechis scutatus occidentalis*) in urban wetlands

The study presented in Chapter 2 is in preparation for future submission to review for publication.

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2.1 Abstract

Population dynamics in urban wetland western tiger snakes (*Notechis scutatus occidentalis*) are understudied and could be subjected to the impacts of urbanisation. We investigated the population size, survivability and detectability of these urban wetland tiger snake populations. We surveyed three lakes in Perth, Western Australia and carried out mark-recapture studies to determine their persistence in urban wetlands. Jolly-Seber model was used to calculate a sample area's estimated population size and potential super population size. Cormack-Jolly-Seber model was used to calculate the survival rate and recapture rate at each wetland. We found for two of the wetlands, despite urbanisation, boasted large population sizes and significant survival rates. We also found that despite snakes having a cryptic nature their detection rates were higher than expected. The other wetland is our study yield disappointing results, not due to urbanisation but we theorised a natural disaster to be the cause. We suggest that urbanisation still impacts snakes, but their adaptability allows them to persist in urban areas.

2.2 Introduction

Increasing global urbanisation and the rising human population drives the degradation of natural habitats (French et al., 2018; McKinney, 2008). The effect of urbanisation on natural environments can be complex, involving deforestation, introduction of invasive species, increasing human-wildlife interactions and pollution and a reduction in the diversity of species (Concepción et al., 2015; McKinney, 2002, 2008; Müller et al., 2020; Seto et al., 2012; Theodorou, 2022). Urbanisation can however, also create novel habitats (Fleming & Bateman, 2018; Kowarik, 2011), or through increasing habitat heterogeneity, create refuges for biodiversity (Pautasso et al., 2011).

Species vary in their ability to adapt to urbanisation: those categorised as ‘urban avoiders’ are lost from the urban matrix completely, while ‘urban adapters’ are able to some extent to persist (McKinney, 2002), sometimes having elevated populations through loss of predators or competition, or through increased access to anthropogenic food (Bateman & Fleming, 2012). Bird and mammals urban adapters tend to be generalist species (Bateman & Fleming, 2012; Tryjanowski et al., 2001). Reptiles are less well-studied than other taxa in urban areas (Brum et al., 2023), although there is a growing body of recent research, particularly on snakes (Lettoof et al., 2023; Sullivan et al., 2017; Wolfe et al., 2018; Zappalorti & Mitchell, 2008).

Urbanisation creates isolated natural pockets in an urban matrix (Bryant et al., 2017) and these natural habitats surrounded by a sea of urban infrastructure can serve as refuge zones for remnant populations of flora and fauna (Bryant et al., 2017; Fusco et al., 2021; Soanes & Lentini, 2019). Some species are unable to adapt to the drastic change of urban encroachment and avoid the urban matrix completely which causes a decline or an extinction of populations in natural pockets of urbanisation zones (Bryant et al., 2017; McKinney, 2008). Native species’ populations can also decline in urbanised areas through competition with invasive species brought in through human influence or imported infrastructure materials (McKinney, 2002). Monocultural vegetation growth greatly reduces the species-richness of areas through horticulture landscaping and suburban gardening (Marzluff and Ewing, 2001). More adaptable native species are able to persist in fragmented habitats or are able to adapt to live within urbanised areas (Bateman & Fleming, 2012).

In the Southwest of Western Australia, the rapid growth of urbanisation has caused the devastation of a large portion of its wetland habitats and surrounding habitat (Brooks et al., 2005; Davis & Froend, 1999; Kelobonye et al., 2019). Wetland habitat loss and fragmentation

has a pernicious impact on wetland-dependent flora and fauna, altering species population abundance and overall diversity (Faulkner, 2004; McKinney, 2008). Encroaching urban areas introduce environmental contaminants, such as heavy metals, into wetland habitats through surface runoff, drainage and groundwater (Lettoof et al., 2020; Roy & Bickerton, 2012; Zhang et al., 2012). Perth's scattered wetlands have been impacted heavily throughout history by urbanisation, introducing contaminants from pest and weed management and surface run offs from the surrounding sea of urban areas encompassing these remnant wetlands (Clarke et al., 1990; Davis & Froend, 1999). Western tiger snake (*Notechis scutatus occidentalis*) populations still persist in some larger wetlands in Perth, remaining as an important top predator in these ecosystems (Aubret, 2005; Lettoof et al., 2021).

The western tiger snake (*N. s. occidentalis*) is a large venomous Australian elapid found across Western Australia, South Australia, New South Wales, Victoria and Tasmania (Cogger, 2000; Wilson & Swan 2008). It occurs in disjunct populations across a variety of habitat types, preying on an array of vertebrates, though it is mostly anurophagous (Aubret et al., 2006; Aubret et al., 2004; Lettoof, 2021). In South-West Western Australia (SW WA), this species is found in abundance in wetland habitats ranging from little to heavy urbanisation (Davis & Froend, 1999; Lettoof, 2021). Despite urbanisation heavily modifying wetlands—especially in and around Perth—tiger snakes still persist in abundance as a top reptilian predator (Aubret, 2005; Lettoof et al., 2020). Tiger snakes have been studied in much of their range with most of the research focussing on island populations, tiger snake health and natural history (Aubret et al., 2007, 2011; Aubret & Shine, 2008; Bonnet et al., 2002; Butler et al., 2005b, 2005a; Lettoof, 2021; Shine, 1979).

The study of animal populations in urban refuge patches is a rapidly growing field of research (Brum et al., 2023), with mark-recapture studies being widely used to investigate population size, survival rates, detection rates and other key parameters (Gould & Nichols, 1998; Otis et al., 1978). This methodology is time consuming and challenging but remains has the most effective field technique for population studies on many vertebrate taxon groups (Chim & Diong, 2013; Roff, 1973; Wanger et al., 2009). Around the world, population ecological studies have a substantial taxon bias, with herpetofauna being understudied when compared with other vertebrate groups (Bonnet et al., 2002). Snake populations, in particular, suffer misrepresentation from capture-recapture studies as snake capture methodology involves hand-capture and active searching, ineffective passive trapping on snakes and their cryptic and elusive nature (Stevenson et al., 2009). Snakes occupy the upper trophic levels in ecological

food webs as a predator with a heavy influence on a diverse number of prey population sizes (Bonnet et al., 2002; Lind et al., 2005; Weatherhead & Blouin-demers, 2004). Snake populations impact the overall health and function of ecosystems as top predators (Lind et al., 2005; Shine & Bonnet, 2000), especially in wetland habitats where studies have shown them to be bioindicators of a wetland health (Lettoof et al., 2022).

In recent years, several research projects have been carried out on the health and impacts of urbanisation on tiger snakes in wetlands around Perth (Cornelis, 2021; Lettoof, 2021). The introduction of anthropogenic pollutants into Perth's urban wetlands revealed tiger snakes accumulate a suite of contaminants, associated with lower population body condition and warrant their use as an indicator of wetland health (Lettoof, Bateman, et al., 2020; Lettoof, Lohr, et al., 2020; Lettoof & Orton, 2020; Lettoof et al., 2021). Invasive flora and the impacts on tiger snake mobility, habitat and prey have shown another extension of urbanisation impacts on a wetland trophic predator (Cornelis et al., 2022, 2023). The introduction of contaminants, habitat degradation and stressors associated with urbanisation on these persisting populations invites the following questions 1) what is the population sizes of these urban wetlands, 2) the capture frequency of snakes within heavy human traffic areas and 3) the survivability of these populations and is there cause for concern for this top wetland predator. I achieved this by conducting mark-recapture sampling at all three wetlands to obtain a recapture frequency which is then tested against body condition data of the snakes to calculate a survival rate.

2.3 Methods

2.3.1 Study sites

Tiger snakes were caught at three wetlands around Perth, Western Australia (Fig. 2.1): Herdsman Lake (31°55'12"S, 115°48'19"E), Bibra Lake (32°05'30"S, 115°49'27"E) and Loch McNess in Yanchep National Park (31°32'44"S, 115°40'50"E). Both Herdsman Lake and Bibra Lake are wetlands located within Perth's urban matrix while Yanchep is located towards the northern outskirts of the Perth region away from heavy suburban areas. These sites were selected based off their varying degrees of anthropogenic disturbance and knowledge created by several tiger snake researchers (Bonnet et al., 2005; Cornelis, 2021; Lettoof, 2021). The degree of urbanisation ranges from heavily modified (Herdsman Lake), partially modified (Bibra Lake), and minimally modified (Loch McNess) (Lettoof et al., 2020). While both Bibra Lake and Herdsman Lake are wetlands surrounded by urbanisation, their vegetation structure differs with Bibra having larger riparian and woodland buffers due to its connectivity with the main Beeliiar Regional Park, whereas Herdsman is completely isolated with minimal woodland buffers. Loch McNess is a small natural wetland, within Yanchep National Park with thick surrounding woodland buffers and connectivity to other larger inaccessible wetlands to the North and Northwest sections of the park.

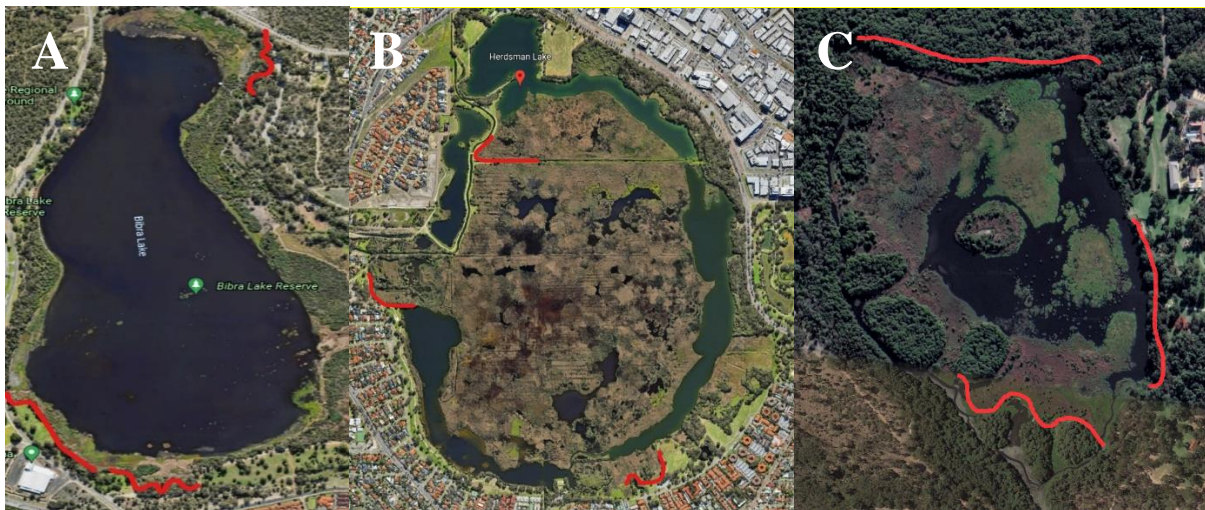


Figure 2.1 The three wetlands where mark-recapture surveys were carried out on tiger snake populations inhabiting the lakes (A = BL, B = HL and C = YC, red lines represent the fixed 300m transects where snakes were surveyed) Satellite images were obtained from Google Earth Pro in 2021.

2.3.2 *Mark-recapture*

We conducted systematic fixed-transect surveys in each wetland during spring 2021 and autumn and spring 2022. Two survey cycles were carried out a per season (Spring: September, October and November; Autumn: April and May) with the exception of spring 2022 where three survey cycles were carried out, where each cycle consisted of five survey days in a row. There were three transects at each wetland which were sampled by three researchers walking slowly for 30 minutes along a fixed 300 metres transect. The transects were strategically placed in multiple broad habitat types within each lake, varying riparian and canopy cover ranging from low to full coverage, based on known use by past tiger snake researchers (Damian Lettoof, pers. comm). Surveys were conducted between 0730 – 1100 hours each day to coincide with optimum basking times (Cornelis, 2021). Each day that any snakes were caught, were placed in calico bags, processed after all three transects were surveyed and returned to each capture location. Each captured snake was marked with a unique number using a standard ventral scale clipping (Plummer & Ferner, 2012, Brown & Parker, 1976).

2.3.3 *Measurements*

Additional data was taken to have a more in depth look at morphological variation of tiger snake populations. The following data was recorded:

1. Snout-vent length (SVL; measured (cm) from the tip of the snout to the cloacal scale).
2. Sex by probing, probes were lubed and inserted into the snake cloaca towards the tail. If the probe went past the third subcaudal scale it was a male due to their deep hemipenes pockets, while in females the probe does not go past the second subcaudal scale.
3. Presence and absence of prey by massaging the belly.
4. Snake mass (grams). Snakes were placed in calico bags and the weight was measured manually using a handheld micro-lined spring scale. Once the snake was removed from the bag, the bag weight was measured and subtracted from the total.
5. Bodily injuries, tail damage, emaciated and gravid conditions were also collected.

SVL was used as a primary gauge of measurement due to a large number of snakes having tail damage (97 individuals), thus unable to attain an accurate total snake length. Gravid females were excluded from SVL measurement, to reduce the stress on those snakes.

2.3.4 *Environmental variables*

Environmental conditions are the main driving factors for snake detection (Brown et al., 2002; Eskew & Todd, 2017; Lettoof et al., 2020; Sun et al., 2001). Two main environmental variables, temperature and wind, were taken at the start and end of each transect as well as at the point of each snake capture. Throughout each transect total human presence (humans counted present along the parallel walking path to each transect <10m) was also recorded to understand anthropogenic presence impacts on snake detection and captures.

2.3.5 *Statistical analyses*

Mark recapture data collected was analysed in R studio version 4.1.3 (R Core Team, 2023), using the program MARK (White & Burnham, 1999). The data was first organised into capture history tables and each season was turned into one cycle. To estimate population size we used a Jolly-Seber model (JS) which fitted in assumptions for the capture probability and survival rate for the fitted capture history table (Schwarz & Arnason, 2021). We then used the top model for the population and super population estimate. To estimate survival and capture rate we used a Cormack-Jolly-Seber model (CJS) which is an extension of the Jolly-Seber model and utilised the same capture history table and take the recapture frequency to predict the survival and capture rates (White & Burnham, 1999). The model is fitted, and the results are plotted as sub-models on a logit scale which we converted back into a more easily interpreted value using the inverse logit function, generating useful survival and capture rate estimates. This estimation is particularly useful when studying cryptic species such as snakes.

2.4 Results

A total of 127 adult tiger snake individuals (Table 2.1) were captured across all three sites during surveys, excluding 6 juvenile snakes and 21 snakes that were seen but not able to be captured. Juvenile snakes were also excluded from the population mean SVL and mass. On a whole, snakes at Bibra and Herdsman had similar SVLs, with the Bibra snakes having larger mass measurements. Bibra had a recapture rate of 40% and 29.2% from Autumn 2022 and Spring 2022. Herdsman had a recapture rate of 33.3% and 35% from Autumn 2022 and Spring 2022 (Table 2.2). Yanchep had no recaptures between seasons and had to be excluded from the JS and CJS models. Though we caught multiple snakes within each season, the snakes being caught were often the same individuals, particularly the larger males. One particular male was caught on nine of the fifteen days surveyed in Spring 2022. Several males were caught multiple times within the same general area every season.

Table 2.1: Total number of adult tiger snakes at three wetlands in Perth, Australia, with mean values of length and body mass measurements.

Site	Sex (n)	mean SVL (cm)	SE	mean mass (g)	SE
Bibra	Male (32)	78.09	1.32	249.0	11.49
	Female (8)	70.63	2.32	192.19	16.30
Herdsman	Male (34)	80.23	0.94	235.0	8.69
	Female (37)	70.89	1.50	190.41	7.95
Yanchep	Male (9)	79.72	3.98	221.94	24.57
	Female (7)	66.62	3.48	157.86	13.97

Table 2.2: Total number of captured and recaptured tiger snakes between three sampling seasons across three survey sites in Perth, Australia (Recap = Recaptured snakes).

Site	Bibra		Herdsman		Yanchep	
Season	Capture	Recap	Capture	Recap	Capture	Recap
Spring 2021	21	0	37	0	10	0
Autumn 2022	10	4	15	5	1	0
Spring 2022	24	7	40	14	6	0

The Jolly-Seber model gave a mean population size estimate (N) of 26.5 and 73.7 snakes at the Bibra lake and Herdsman Lake sampling areas respectively (Table 2.3). These estimates are mean values of the three sampling occasions (occ). They represent the population size of the three transect survey areas combined within each wetland. The Jolly-Seber model estimated potential population size of 46.6 and 104.4 snakes for Bibra and Herdsman respectively (Table 2.3). The Nsuper value represents the population size taking into account both the captured individuals and individuals that were not captured.

Table 2.3: Population size of tiger snakes within each survey site per sampling cycle/season (N= Estimated population size, Nsuper= Potential estimated super population size).

Site	Occ	N	Nsuper
Bibra	1	23.17	46.61
	2	24.41	46.61
	3	31.86	46.61
Herdsman	1	85.24	104.42
	2	67.19	104.42
	3	68.58	104.42

The Cormack-Jolly-Seber model gave a higher probability of survival of 0.68 between surveyed seasons to Herdsman Lake in comparison to Bibra lake which was 0.55 (Fig. 2.2). The probability of capture represents the recapture probability of an observed individual snake. Bibra had a higher probability of capture of 0.35 while Herdsman was 0.2 (Fig. 2.2).

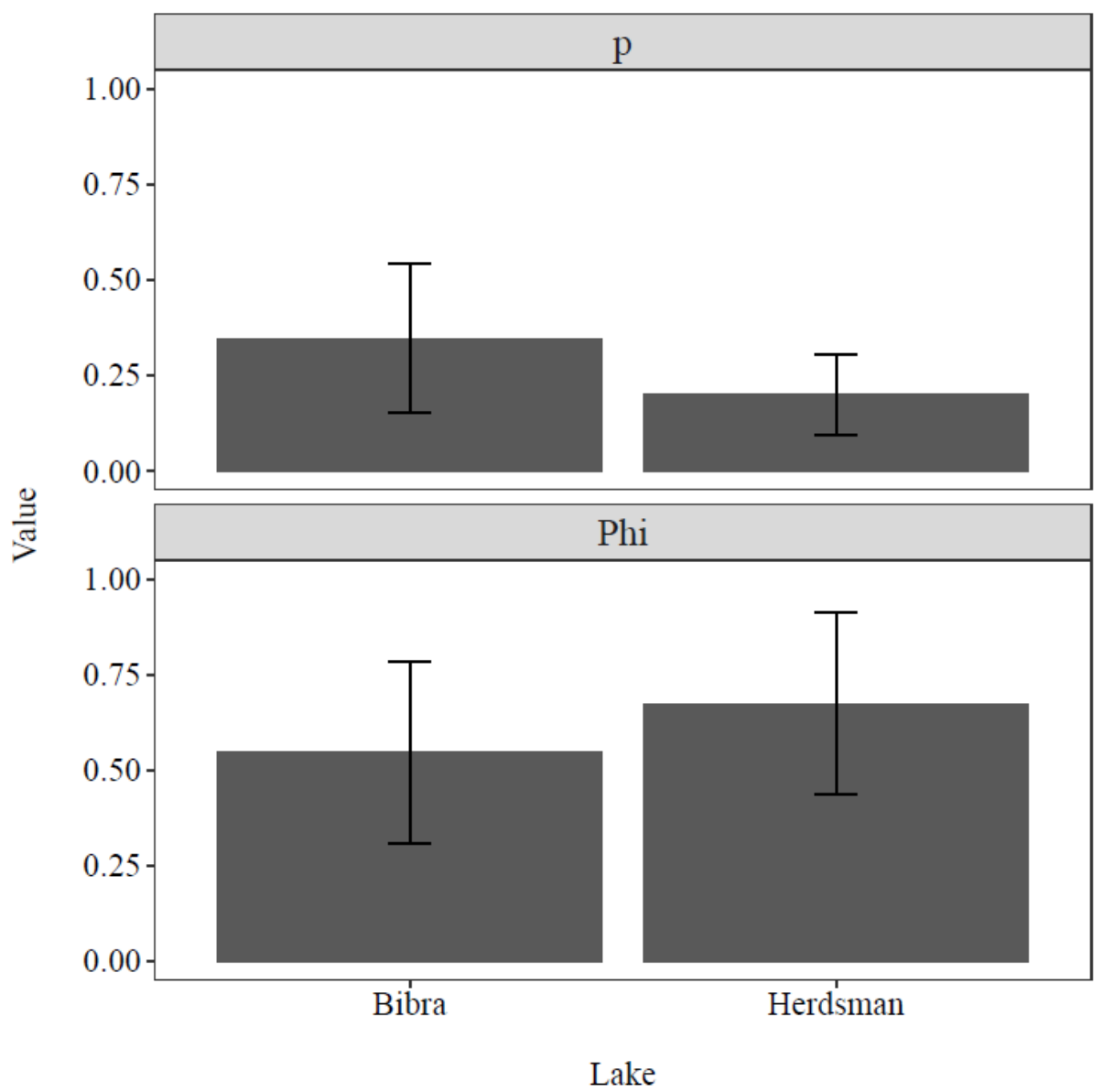


Fig. 2.2 Survival rate (Phi) and probability of capture (p) of tiger snakes within the sampling area of each survey site, error bars represent the standard error.

2.5 Discussion

We found that despite being isolated islands in a sea of urbanisation, Bibra Lake and Herdsman Lake both appear to have large populations of tiger snakes. Our data indicates both a high population size and a high survival rate for tiger snakes within the sampled areas at Bibra and Herdsman Lake, which is likely to translate to the rest of the habitat around each wetland.

We used a mark recapture approach to estimate the population size, survival rate and detection rate of a large Australian elapid snake in two of Perth's urban wetlands. The mark-recaptured analysis we used indicated that Herdsman Lake has the largest population of tiger snakes in the surveyed area, and that Bibra Lake has the highest probability of recapture. The Cormack-Jolly-Seber model suggested that the Herdsman Lake population has a higher probability of survival than those at Bibra Lake. Loch McNess in Yanchep had to be excluded from the analyses due to a lack of recaptured snakes between cycles and a relatively low number of snakes captured over the three cycles despite the efforts of the research team.

Bibra Lake, while considered an urbanised wetland, retains a large portion of its riparian zone and surrounding native bushland (Chambers et al., 2017). The lake itself has heavy anthropogenic presence with an array of urban structures and leisure activities carried out there. The tiger snakes at Bibra have an overall better body condition in comparison to the other survey sites (Lettoof et al., 2022), where we too recorded larger numbers of longer and heavier males. The population size estimate showed it to be approximately 27 individuals within the area surveyed with the Nsuper population having approximately 47 snakes with respect of turnover rates and difficulties in detecting a cryptic species (Table 2.3). We propose that more work to be done to investigate the potential of large dominant male tiger snakes having a territorial range. Another noticeable observation on the tiger snakes at Bibra Lake, was the somewhat lack of females caught during the surveys, eight adults in total (Table 2.1). We speculated that two reasons may be plausible, given that we surveyed three transects each being 300m in length and only four individuals escaped capture, it's possible that females tend to emigrate more around the lake, which could result in lower abundance of females within the fixed transects. The other possibility is that the transect areas at Bibra lake may have a more male dominant population caused from sex biased dispersal where the males are philopatric, which has been documented in other Australian snakes (Dubey et al., 2008; Keogh et al., 2007). Further investigation into Bibra lake's disproportionate tiger snake sex ratio needs to be done to understand if this a survey bias or if the females are more dispersed around the wetland.

Herdsman lake is a wetland, like many others in the South-west of Western Australia, that has gone through heavy modification. Most of the habitat has non-native grasses, frequently mown lawns, and remanent bushland (Cornelis, 2021). However, it still maintains a riparian zone around some parts of the lake with thick grass clumps that can be more than a metre in height. There are also a large number of small, vegetated islands scattered throughout the lake with a high density of tall rush. It is because of the thick vegetation, islands and remanent bushland that allow for a population of tiger snakes to persist in the wetland despite of its decades of human impact. The population of tiger snakes there is larger than that of Bibra Lake and, though Yanchep's population size was unquantifiable, it could potentially be larger than Yanchep's tiger snake population (Table 2.3). Within the 900 metres of survey area, an estimated population of 74 snakes and an estimated super population of 104 snakes. However, from past research done, we knew Herdsman could produce those numbers, what was not predicted was the high survival rate of these snakes. With Herdsman's past human impact and the proximity of the urban areas to the wetland, the water is riddled with heavy metals and rodenticides (Lettoof et al., 2020; Lettoof et al., 2022). Despite this, Herdsman Lake boasts a large population size and the highest survival rate. We postulate that the adaptability of large elapids to urban degraded areas is often overlooked, if suitable environmental habitats are retained and a bountiful diverse selection of prey items available, tiger snakes can continue to persist in urban wetlands.

Loch McNess in Yanchep National Park tells a different story to the other two survey sites. Having no recaptures between seasons and an overall low number of individuals caught, we suggest that the tiger snake population is under threat and a cause for concern for their persistence in that wetland. Loch McNess is a small wetland located in the greater Yanchep National Park wetland complex, this natural wetland is surrounded by native vegetation and large sections of native bushlands. The wetland is also minimally modified and retains most of its natural vegetation. Past research has shown a population of tiger snakes living in that wetland (Cornelis, 2021; Lettoof, 2021), though the numbers caught there is not the same as the other two wetlands, we hypothesised that the turnover rate (snakes dying off or snakes replaced through migration or dispersal) was high, and the thick vegetation made for a lower detectability rate. The vegetation and riparian zone around Loch McNess are larger than the other two sites because it is not an urban bushland, most human footpaths are not close to the water's edge, which makes the vegetation along the transects more dense. However, in the three seasons surveyed, only 16 individuals were captured with no recaptures between season

and only a handful of captures within the two springs 2021 and 2022. Another note is that this study continued marking snakes in populations utilised by prior researchers (Lettoof et al., 2022). In Bibra and Herdsman we encountered many individuals marked by past researchers, yet during the Yanchep surveys we only encountered one snake that was marked previously on the eastern side of the wetland. Loch McNess's groundwater table has been drained and the wetland has receded since the 1990s, exposing sediments which caused the encroachment of weeds and the release of metal pollutants (Lettoof et al., 2022; Lettoof et al., 2021). Our primary theory is that this disaster coupled with the devastating forest fires that occurred in 2019/2020 summer is the suspected cause a lack of snakes caught at the wetland. The fires set ablaze a large portion of the surrounding bushland and wetland around the Northern, Western and Southern portion of the wetland (Fontaine, 2022). We postulate that either a large portion of the snakes perished in the fires or migrated further into the inaccessible parts of the Yanchep wetland complex. The fires also altered the landscape, creating thick layers of deadfall on the ground enabling further encroachment of invasive weeds that took over large sections of the Northern and Southern transects. The observational difference was noticeable to personnel who conducted tiger snake research before the fires. Studies done on the tiger snake population at Loch McNess showed the lowest genetic diversity which reduced adaptation, thus this population is likely less equipped to deal with change (Lettoof et al., 2021). More studies need to be done to on tiger snakes in the wetland and access needed for the other areas in the wetland complex to look for marked snakes.

The effect of urbanisation has detrimental effects on native ecosystems and the species that inhabit them (Brum et al., 2022; Cornelis et al., 2021; Theodorou, 2022). Habitat fragmentation, pollution and the introduction of invasive species causes a ripple effect of stress and pressure of native flora and fauna (Cornelis et al., 2022; Faulkner, 2004; Müller et al., 2020). Tiger snakes, as a top predator reflect the health of a wetland ecosystem (Lettoof et al., 2020), which carries forth our aim of understanding their population dynamics amidst the rising rate of urbanisation.

Urbanisation impacts on an ecosystem and the flora and fauna diversity and populations within is complicated but comprehensible after decades of research. Investigating the impacts on a single species' population and its survivability in a habitat is complex, much less a cryptic species like tiger snakes. These urban wetlands have undergone much human impacts, yet this top predator continues to persist despite anthropogenic pressure. We suggest that these urban wetlands still retain suitable habitable riparian and wooded zones for the snakes to persist, and

for their prey to inhabit. As long these zones are maintained to serve as buffers, tiger snake populations should continue to inhabit these wetlands. While these urban wetlands still retain suitable tiger snake habitat, the same is not reflected in most of Perth's urban wetlands. It is important to note that while we can draw this consensus for tiger snakes, the same cannot be assumed for other species of herpetofauna and other taxon groups. We suggest that this study has shed some light on an urban elapid's population dynamics amidst urban areas. This study 1) demonstrates the capability to understand a snake's population within a two-year sample period, 2) our capacity to estimate capture probabilities despite a snake's cryptic nature, 3) showcases prior wetland perturbation coupled with natural unforeseeable disasters can have a detrimental effect on a snake's population in a short period of time and 4) emphasises the adaptive capabilities of a large Australian elapid living in wetland islands within a bustling and ever-growing city.

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Chapter 3: Urban snakes in a changing world: responses of western tiger snakes (*Notechis scutatus occidentalis*) to interactions with humans in urban wetlands.

The study presented in Chapter 2 is in preparation for future submission to review for publication.

Subaraj, S., von Takach, B., Lettoof, D. C., Bateman, P. W. Urban snakes in a changing world: responses of western tiger snakes (*Notechis scutatus occidentalis*) to interactions with humans in urban wetlands. *In Preparation*

3.1 Abstract

Behavioural ecology of urban reptiles is understudied worldwide, species such as tiger snakes are facing constant anthropogenic pressure and impacts. We investigated the behavioural responses of tiger snakes to human activity patterns, taking into account environmental variables, snake morphometric data, and snake body condition. We used Generalised Linear Models and Multi-Model Inference Packages to gauge correlations between behavioural responses and the predictor variables. We found that abiotic factors and body condition of snakes were the main predictor variables to influence behavioural responses. We found that most snakes across all wetlands had high flee responses and avoided confrontational defensive displays. In high human traffic areas, snakes adopted a more passive or freeze response, likely due to habituation and learned behaviour. We suggest that human habituation is a key factor in behavioural plasticity of a tiger snake in urban wetlands.

3.2 Introduction

Urbanisation is rapidly expanding across many previously unaltered landscapes (French et al., 2018; McKinney, 2008). Urbanisation alters the ecosystems of natural habitats through deforestation, introduction of invasive species, increasing human-wildlife interactions and pollution and a reduction in the diversity of species (Concepción et al., 2015; McKinney, 2002, 2008; Müller et al., 2020; Seto et al., 2012; Theodorou, 2022). Urbanisation can create isolated natural pockets in an urban matrix (Bryant et al., 2017) and these natural habitats surrounded by a sea of urban infrastructure can serve as refuge zones for remnant populations of flora and fauna (Bryant et al., 2017; Fusco et al., 2021; Soanes & Lentini, 2019).

Successful mammal ‘urban adapters’ (McKinney, 2006) are usually habitat or trophic generalists that exploit novel niches (Bateman & Fleming, 2012; Lowry et al., 2013), or, in the case of birds, are also more gregarious or sedentary (Kark et al., 2007) or have large breeding ranges, high fecundity, dispersal and survival (Møller, 2008). Less is known about what makes a successful reptile urban adapter; however, behavioural flexibility and adaptive adjustments are likely to be universal traits of successful urban taxa (Evans et al., 2010; Lowry et al., 2013; Patricelli & Blickley, 2006; Slabbekoorn & Peet, 2003; Sol et al., 2013).

Studies have shown that behavioural traits in urban-dwelling animals can differ from those in non-urbanised areas (Donaldson et al., 2007; Kitchen et al., 2010). These behavioural differences in urban areas may be driven by novel selection pressures modifying allele frequencies, or plastic responses arising during development or in different contextual settings (Lowry et al., 2013; Nordberg & Schwarzkopf, 2019). One aspect of behavioural flexibility in such animals is how they modify their antipredator behaviour towards humans (Beale & Monaghan, 2004). Species persisting in urban areas, under constant anthropogenic stress and impacts, showcase phenotypic plasticity which leads to successful establishment in urban habitats (Bouchard et al., 2007; Levey et al., 2009; Slabbekoorn & Boer-visser, 2006). Broadly, urban adapters can either be pre-adapted to withstanding disturbance, can become habituated, or be the result of selection for more disturbance-tolerant individuals. While behavioural ecology of urban-adaptor species have been researched worldwide (Murgui & Hedblom, 2017; Sol et al., 2013), taxonomic bias has led to heavy emphasis on birds and mammals (Collins et al., 2021; Magle et al., 2012), with few studies on reptile taxa (Brum et al., 2022; Winter et al., 2016).

Reptiles play pivotal roles in ecosystems as essential agents for nutrient transport, trophic interactions (both as prey and predators), and ecosystem engineering (Burgos-Rodríguez et al., 2016; Miranda, 2017). Recent studies conducted in the past decade have presented compelling evidence highlighting the vulnerability of reptiles to landscape modification (Böhm et al., 2013; Powers & Jetz, 2019). Among reptiles and other terrestrial vertebrates, snakes are one of the most challenging groups to research and study due to their cryptic nature (Willson & Winne, 2016). Large adult snakes occupy the upper trophic levels in ecological food webs as both predator and prey (Bonnet et al., 2002; Lind et al., 2005; Weatherhead & Blouin-demers, 2004). Despite the important role snakes play in an ecosystem, little research has been done on their behavioural ecology in urban-modified landscapes (Brum et al., 2022).

Past research on tiger snakes focussed on island populations and populations in natural wetlands (Aubret et al., 2007, 2011; Aubret & Shine, 2008; Bonnet et al., 2002; Butler et al., 2005b, 2005a; Shine, 1979), with more recent research expanding upon their role as a bioindicator of wetland health (Lettoof, 2021).

In the last five years, extensive research has been done on tiger snakes around Perth's urban wetlands (Cornelis, 2021; Lettoof, 2021). These studies have shed the impacts of anthropogenic presence around wetlands and the role of tiger snakes as a bioindicator of wetland health (Lettoof, Bateman, et al., 2020; Lettoof, Lohr, et al., 2020; Lettoof & Orton, 2020; Lettoof et al., 2021). Invasive flora such as kikuyu grass have impacted tiger snake mobility, habitat and prey preferences in the Perth region, resulting in lower diversity of prey species and smaller home ranges (Cornelis et al., 2022, 2023). The western tiger snake (*Notechis scutatus occidentalis*) is a large polymorphic venomous Australian elapid found across several southern states in Australia (Cogger, 2000; Wilson & Swan 2008). Tiger snake populations occur across a variety of habitat types, though it is mostly anurophagous, this species predated on an array of vertebrates (Aubret et al., 2006; Aubret et al., 2004; Lettoof, 2021). In South-West Western Australia (SW WA), this species is found in abundance in wetland habitats ranging from little to heavy urbanisation (Davis & Froend, 1999; Lettoof, 2021). Tiger snake populations have continued to persist in Perth's urban wetlands. These wetlands are, to a greater or lesser extent, urbanised and accessible to large numbers of people who use it for recreation. As such, the persistence of a large, venomous snake presents us with an opportunity to explore how this species reacts to human disturbance.

Here, we explore the role of adaptive behaviours as a contributor to the persistence of tiger snakes in urban wetlands. Specifically, we look at the variability of snake behavioural responses to interactions with humans in relation to variation in human activity across urban sites. We predict that snakes in wetlands with higher levels of human activity will show adaptation to this disturbance by demonstrating more passive responses and minimal defensive responses to interactions with researchers, while those in wetlands with lower levels of human activity or wetlands will demonstrate higher flee responses to interactions with researchers.

3.3 Methods

3.3.1 Study Sites

Three wetlands spread across Perth, Western Australia were chosen for this behaviour study on Tiger snakes: Herdsman Lake (31°55'12"S, 115°48'19"E), Bibra Lake (32°05'30"S, 115°49'27"E) and Loch McNess (31°32'44"S, 115°40'50"E) at Yanchep National Park. Both Herdsman Lake and Bibra Lake are wetlands located within Perth's urban matrix while Loch McNess in Yanchep is located towards the northern outskirts of the Perth region away from heavy suburban areas. These sites were selected based off general knowledge from past snake researchers (Bonnet et al., 2005; Cornelis, 2021; Lettoof, 2021), and varying degrees of urbanisation ranging from heavily modified (Herdsman Lake), partially modified (Bibra Lake) and minimally modified (Yanchep) (Lettoof et al., 2020). Both Bibra Lake and Herdsman Lake are surrounded by urban areas, though Bibra Lake still retains a larger riparian zone and woodland buffer with existing connectivity to the main Beeliar Regional Park and the wetlands within. Herdsman Lake however is completely isolated and retain very little woodland areas around the wetland. It also comprises of heavily manicured lawns and its riparian zones consist mostly of Kikuyu grass (Cornelis et al., 2022). Loch McNess is a smaller wetland in Yanchep National Park, which has a large series of wetland complexes to the North and Northwest of Loch McNess. Most of the wetland is encompassed by large woodland buffers and native riparian zones, with only the eastern side containing human modification and manicured lawns.

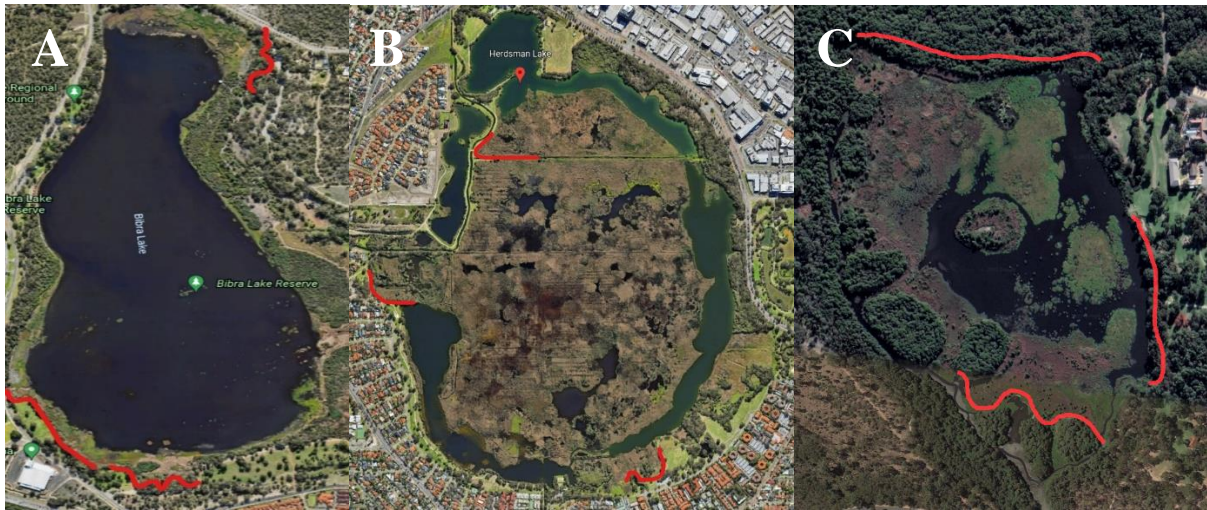


Figure 3.1 The three wetlands where behavioural analysis was carried out on tiger snake populations inhabiting the lakes (A = BL, B = HL and C = YC, red lines represent the fixed 300m transects where snakes were surveyed) Satellite images were obtained from Google Earth Pro in 2021.

3.3.2 *Field procedure and data collection*

Sampling sessions were carried out in Spring 2021, Autumn 2022 and Spring 2022. We conducted fixed transect surveys across the three sites, with three transects per site. Each transect was 300 metres and was surveyed for thirty minutes between 0730-1130 hours. The transects were strategically placed along areas of varying riparian and canopy cover ranging from low to full coverage. Snakes were caught by hand or by a pinner (modified pole with a soft Y-shaped end to gently press down on snakes) within the fixed parameters of the time and transect area. We recorded Snout-vent length (SVL), body mass and sex of the snake, each snake was uniquely marked with a unique number using a standard ventral scale clipping (Plummer & Ferner, 2012, Brown & Parker, 1976). We recorded the ambient temperature and wind speed at each specific snake capture point. During each survey, humans were also counted to record the density of human presence at each transect during the survey's timeframe.

3.3.3 Behaviour responses

We analysed the behavioural responses of three primary interactions between the snake and the researcher. The three interactions were when the snake was seen/approached, when the snake was captured and handled and, when the snake was released. The three interaction points were used as a direct assessment of a snake's basic response to a human, playing upon the fight or flight response in any animal. The fight or flight response was categorised as Defensive or Flee. The Passive response was added to investigate if tiger snakes adopt a placid reaction to a direct interaction. These responses are the three most basic behaviours shown when an animal encounters a human.

Table 3.1 Behavioural interactions of a tiger snake in response to a direct interaction with a human

Category	Reaction	Description
Seen/approached behaviour	Passive	Remains still and calm
	Defensive	Neck flare and strikes
	Flee	Starts slithering off when seen
Handled behaviour	Passive	Remains calm, no biting attempts and no attempts and trying to flee
	Defensive	Attempting to bite and flaring
Released behaviour	Passive	Remains still and calm
	Defensive	Neck flare and strikes
	Flee	Starts slithering off when released

3.3.4 Statistical analyses

All analyses were carried out in R studio version 4.1.3 (R Core Team, 2023). We investigated the correlations between the behavioural responses of tiger snakes against various variables such as environmental conditions, anthropogenic factors and body condition. Incomplete data and repeatedly surveyed individuals were removed, retaining a total of 119 unique snakes for analysis. We checked for multicollinearity among continuous predictor variables (using the VIF function of the `usdm` package), ensuring that none had a VIF value > 5 and correlations using the `pairs.panels` function of the `psych` package (Imdadullah et al., 2016; Revelle, 2015). A global model was constructed for each of the behavioural response variables (seen, handled and released), against the predictor variables (temperature, wind, human presence, body condition, site and sex). Due to multiple responses for each variable, we used the multinomial log-linear function `multinom` of the package `nnet`. We checked global model fits, using the `Anova` function of the `car` package, as well as checked `qqplots` and histograms of the residuals (for normality). We then used the `dredge` function of the Multi-Model Inference (MuMIn) package to fit all possible combinations of predictor variables (submodels) of the global model, and ranked submodels by AICc (Aikakes information criterion standardised for sample size). All submodels with a ΔAICc of ≤ 2 were considered useful for inference (Burnham et al., 2011; Burnham & Anderson, 2004). We extracted model effects for all predictor variables considered important (retained in multiple top submodels and showing significant p-values in the `Anova` function) and plotted model predictions. To achieve a better model fit, scaled predictor variables were incorporated to reduce multicollinearity variance factors to < 5 by removing correlated variables.. We ran the `glm`, checked the model fit and used a `dredge` function for all sub models to look for ΔAICc value ≤ 2 . Results were visualised and the graphs were plotted using `ggplot2` package.

3.4 Results

A total of 43 individuals from Bibra Lake, 61 individuals from Herdsman Lake and 15 individuals from Yanchep were captured. During the handled interaction, Bibra lake had the highest passive response at 58% while Yanchep Lake had the highest flee response at 74% (Fig 3.2). During the release interaction, flee behaviour was the most prominent behavioural response with Bibra Lake, Herdsman Lake and Yanchep tiger snakes at 61%, 64% and 87% respectively (Fig 3.2). During the seen interaction, the passive response was the major response for the Bibra Lake and Herdsman Lake snake at 67% and 69% respectively, while the Yanchep population had a preference for flight at 53% (Fig 3.2). Amongst the three interactions, only the handled interaction had positive association with the top models ($\Delta AICc \leq 2$), where the predictor variables had significance with the interaction ($p < 0.05$) (Table 3.2).

We obtained the human density present during each transect survey period between the three wetlands surveyed which showed that the most urban wetlands, Bibra Lake and Herdsman Lake had the higher human densities at an average of 17 people per day for both wetlands (Fig 3.3). Yanchep had the lowest human density of 7 people per day (Fig 3.3).

Table 3.2 Mixed effects models for the handled behavioural interaction of tiger snakes in Perth, Australia. All models that differed ($\Delta AICc$) from the top model by ≤ 2 are shown, as well as the intercept-only (null) model. (T = Temperature, SMI = Body condition, and SI = Site).

	Best model	log(l)	AICc	delta	weight
M1	SMI+T	-111.52	235.78	0	0.27
M2	SI+SMI+T	-107.48	237.01	1.23	0.15
M3	T	-114.47	237.29	1.51	0.13
M4	SI+T	-110.03	237.38	1.59	0.12
Null	-	-124.16	252.41	16.63	6.60

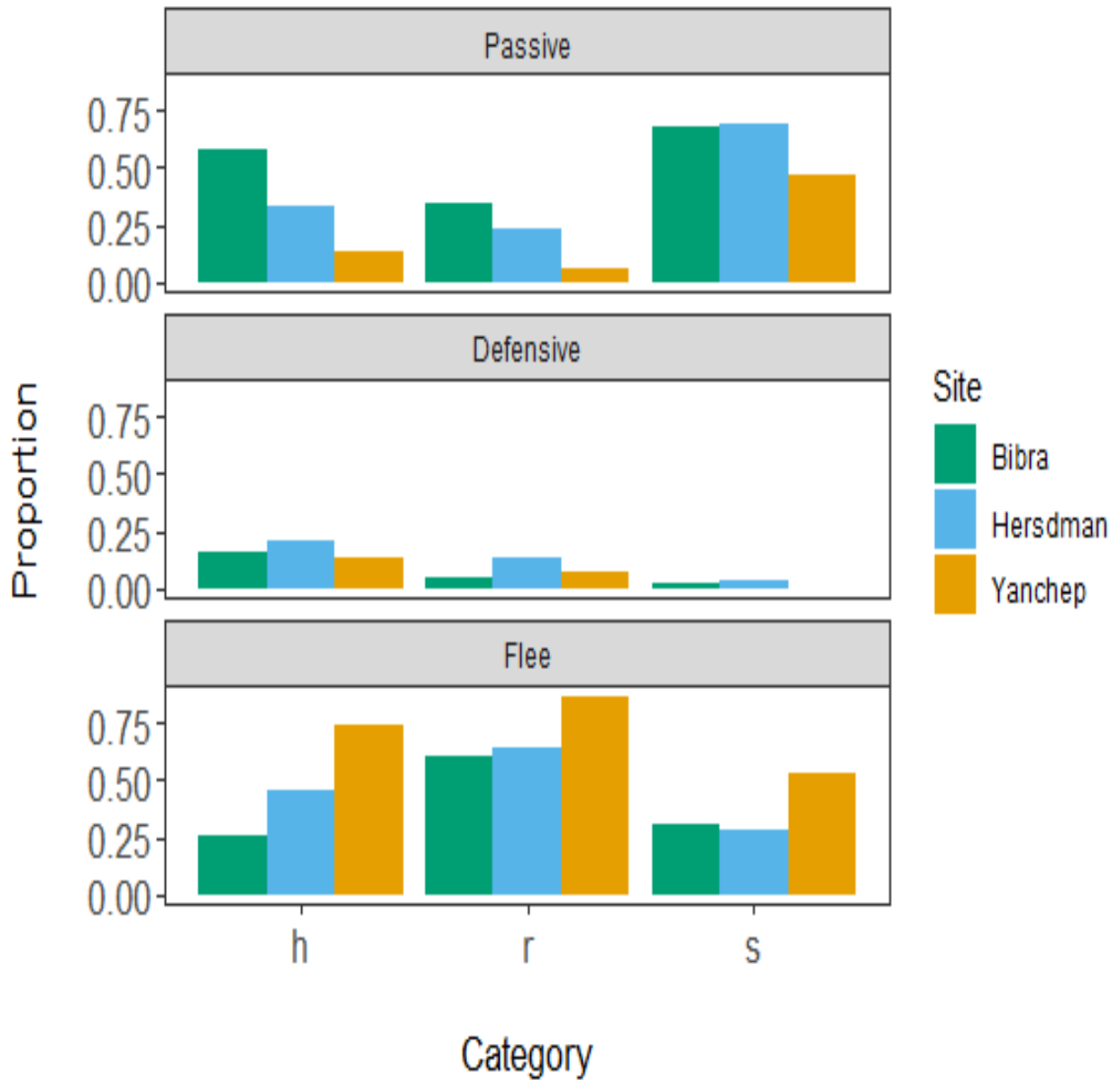


Figure 3.2 Proportion of snakes that displayed per site that displayed passive, defensive and flee response to the three human-snake interactions (h = handled; r = release; s = seen).

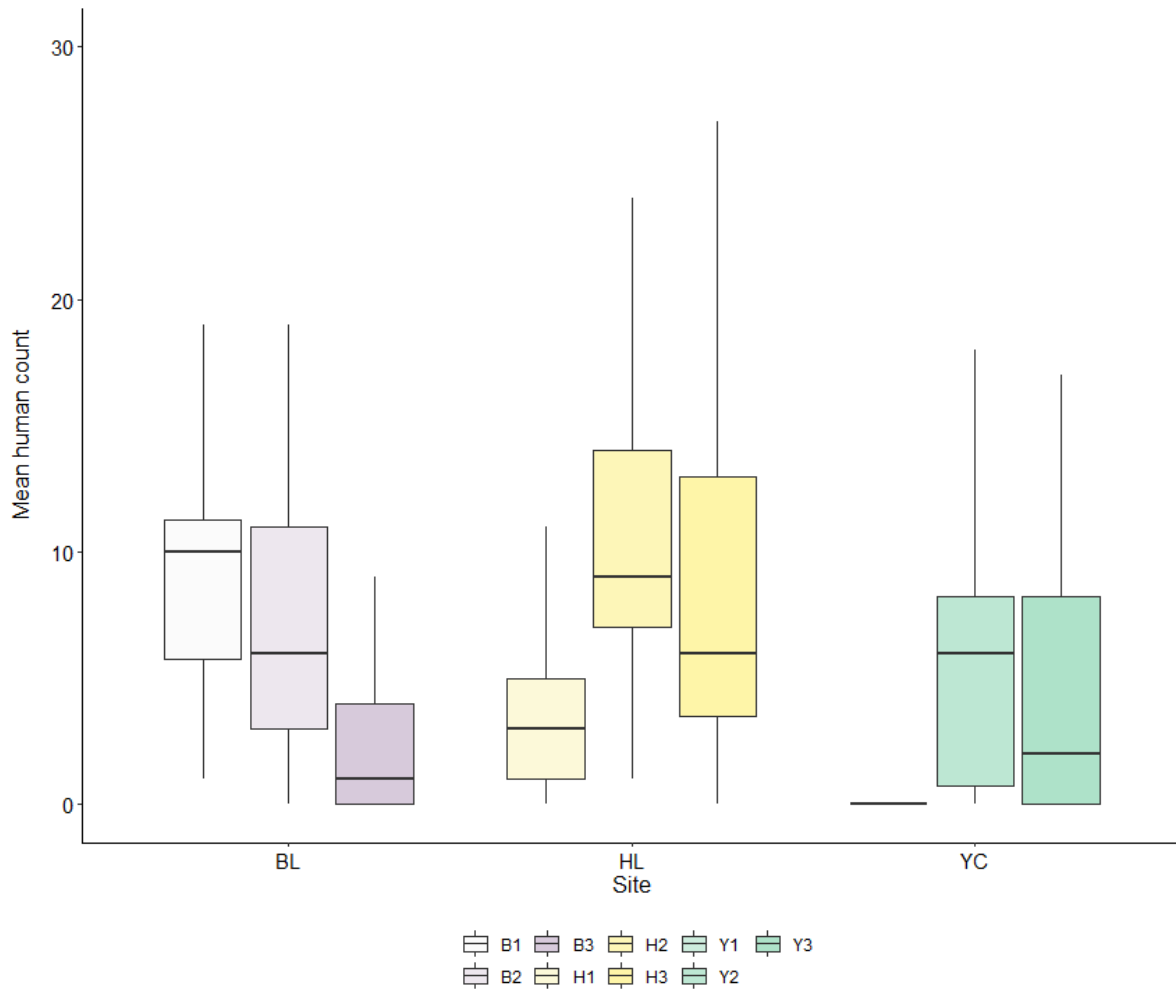


Figure 3.3 Mean human density at each of the three transects between all three survey sites. (BL = Bibra Lake, HL = Herdsman Lake and YC = Loch McNess in Yanchep).

There was no site level correlation ($p > 0.05$) observed between the behavioural interaction and the variables measured. The flee response to this interaction was removed from further analysis due to defensive behaviours displayed which negates a pure flee reaction. All three wetlands had the same two predictor variables that were present in most of the top models ($\Delta AIC \leq 2$), with temperature being significant ($p < 0.05$) and body condition being close to significance ($p = 0.097$). Higher body condition levels saw an increased passive response while higher temperature levels saw an increase in defensive responses. (Fig. 3.4 & 3.5).

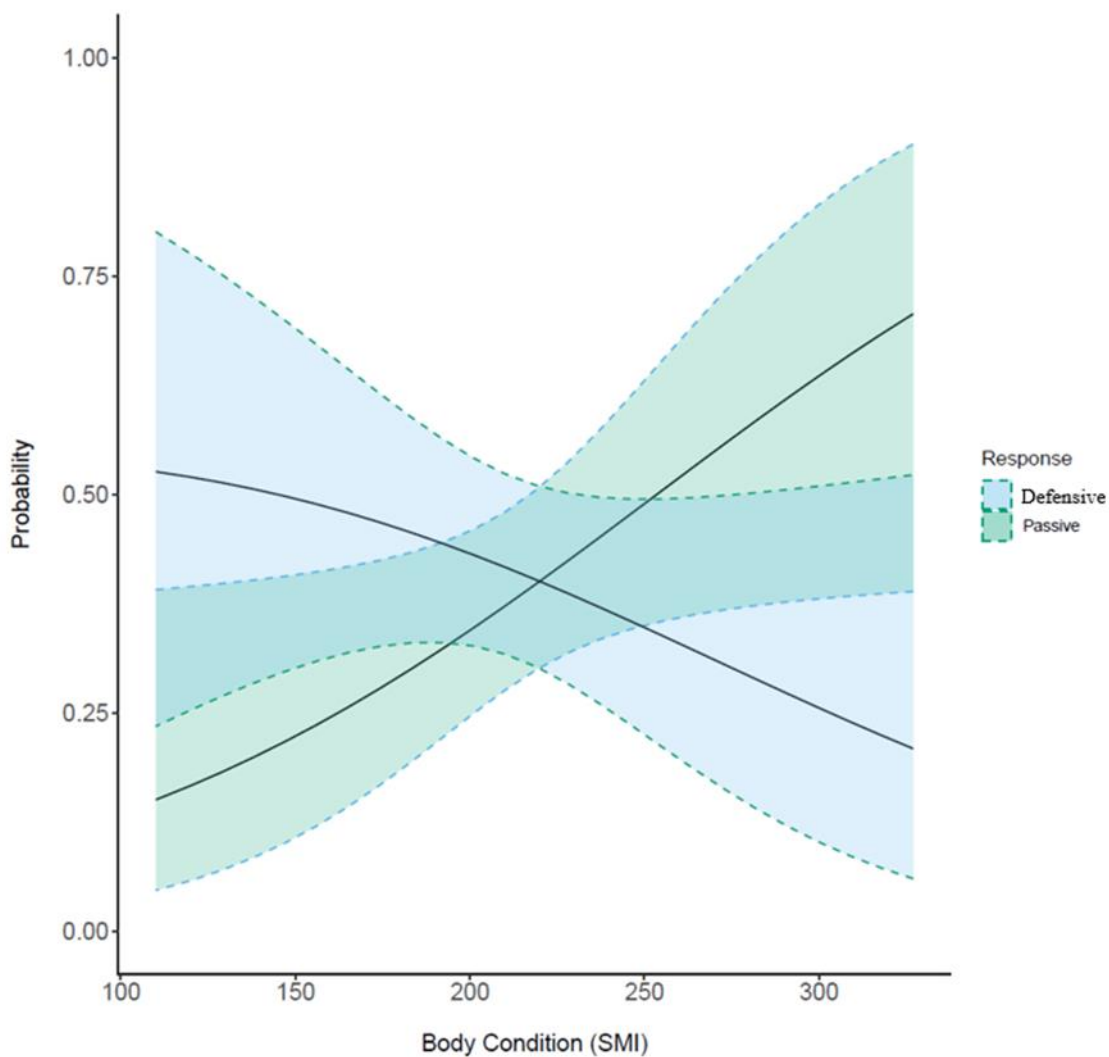


Fig. 3.4 Probability of a defensive or passive response rate against body condition incorporating tiger snakes from all three sites. Coloured areas represent the upper and lower confidence levels.

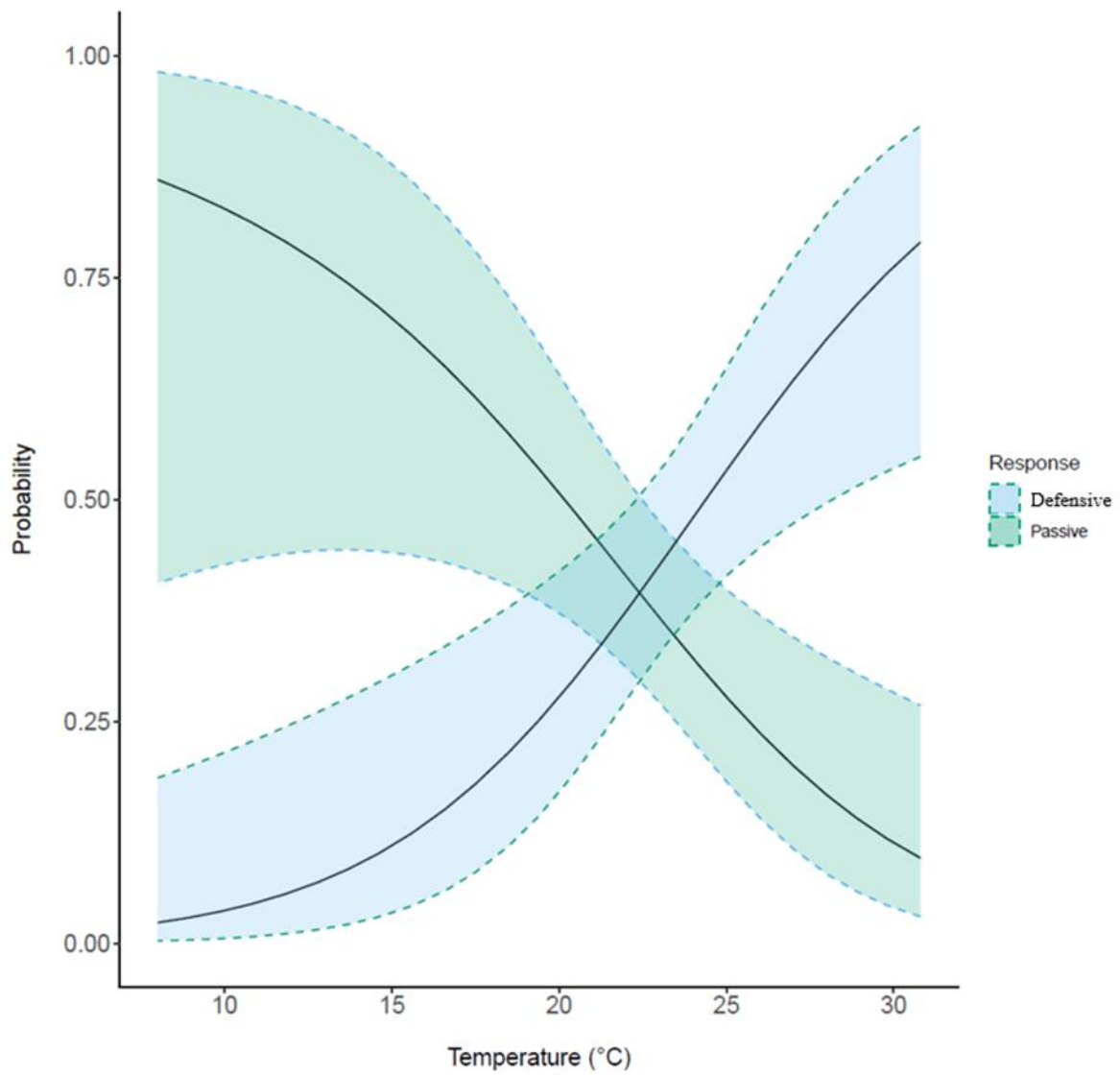


Fig. 3.5 Probability of a defensive or passive response rate against temperature incorporating tiger snakes from all three sites. Coloured areas represent the upper and lower confidence levels.

3.5 Discussion

We investigated the behavioural responses to humans of tiger snakes across three wetlands around Perth, Western Australia that varied in level of urbanisation and degree of human use. We found that each wetland population varied in their behavioural response to handling by site, but certain behavioural responses were the same across sites. We found that environmental factors and snake body condition appeared to be most important in influencing behavioural responses across all the sites. However, site level variability in the response types also points to other factors, such as human presence and wetland terrain. Our results have also shown that one of the most venomous snakes on the planet will actively attempted to flee from a human being and only resort to defensive behaviour as a last resort.

Limited research on behavioural ecology has been carried out on snakes, though they inhabit the upper trophic levels in a food web and have a direct impact on an ecosystem. Their cryptic nature and inconsistent activity times make sampling them a challenge. Tiger snakes are abundant in some of Perth's urban wetland areas and despite an ever-growing urban matrix, this species appears able to adapt and thrive in remanent fragmented green spaces with a constant human presence, as has been suggested for other taxa (Lowry et al., 2013; Wolfe et al., 2018).

Behavioural responses by snakes to human interactions when seen, handled and released showed little variation across sites. However, snakes with a higher body condition (presumably healthier) demonstrated a higher flee response. Amongst the three behavioural interactions, only the handled interaction was positively associated with the variables of temperature and body condition. Increased temperature and snake with higher body condition was therefore significantly linked to defensive behaviours when handled. While most snakes preferred to flee, when handled the snakes resort to their defensive displays of flaring and biting which past research has shown to be the case when cornering or aggravating a snake (Fabien Aubret, 2005; Whitaker et al., 2000).

The behaviour of tiger snakes when released indicated a higher defensive response was linked with higher temperatures. This is perhaps intuitive with an ectothermic animal which can be more active in warmer ambient temperatures (Shine & Koenig, 2001). The release interactions yielded the only site level variability of the different snake. Flight was the highest behavioural response for the release interaction and the defensive response was least likely. Snakes from Bibra Lake and Herdsman Lake had a higher passive response rate than those from Yanchep,

with Bibra having the highest passive response. Our models suggest that snakes from Bibra Lake and Herdsman Lake had a 30% and 24% probability of displaying a passive response upon release. This compares to only a 6.25% probability of a passive response at Yanchep. We suggest that this is due to Bibra and Herdsman being urban wetlands, whereas Yanchep is a natural wetland with little human modification. With a greater human presence at Bibra and Herdsman, snakes in those wetlands would have more experience and interactions with humans. Humans in these, wetlands generally do not notice a snake unless it is directly beside the path or if a snake is actively moving which catches a person's attention (Subaraj S., pers. obs.).

Snakes often choose the flee response as their primary method of evading potential threats or predators (Dixon, 1998; Whitaker & Shine, 1999). Snakes display a great reluctance to engage in a confrontational responses towards humans, something which is familiar to herpetologists (Bonnet et al., 2005; Prior & Weatherhead, 1994) but probably contradicts what the general public believe (even with constant outreach and awareness). Species like eastern brown snakes (*Pseudonaja textilis*), another Australian elapid found in urban areas, show substantial toleration to aggravation before launching a defensive display or strikes (Whitaker et al., 2000). Tiger snakes boast an impressive and intimidating defensive flare response, with some individuals seen flaring and mock charging (Subaraj. S. pers. obs.). When we stood to one side the snakes quickly dropped their defensive displays and quickly slithered towards the nearest bush. They re-adopted their flare response when we proceeded to block their path towards the nearest shelter. The misconception that the general populace have about snakes, tiger snakes in particular, being aggressive and chasing people, comes from misguided and misinformed observations of their behaviour. Unless cornered or stepped on, snakes choose the flight over fight response, unfortunately sometimes that flight is towards the nearest shelter which a human might be standing between. Studies have shown that animals have the capacity to distinguish between predators and non-predators through learned behaviours and habituation (Chivers et al., 2014; Coleman et al., 2008). We suggest that tiger snakes view humans as non-threatening predators, that we are no different to a kangaroo in their habitat, a large mammalian animal that the snake must flee from in order to avoid being stepped on.

We recorded human density present during each transect across the survey periods where they had no association with any of the top models of the three interactions. The increased human densities in the urban wetlands, Bibra Lake and Herdsman Lake, had no impact on the behaviours of the tiger snake populations in these wetlands. In areas of increased human

activity, animals either have a heightened fight or flight response (Ford & Reeves, 2008; Maritz, 2012), or become desensitised and habituated (Avilés-rodríguez, 2019; Coleman et al., 2008). Habituation has not only been proven in lizards (Rodríguez-Prieto et al., 2010; Rodríguez-Prieto et al., 2011) but has been shown to improve the body condition of a lizard, where individuals that were quicker to adapt to the low risk predator had an advantage over those that did not (Rodríguez-Prieto et al., 2010). Animals that flee from any predator, either low or high risk, result in greater energy expansion and inhibits foraging and hunting success (Amo et al., 2006; Martín & López, 1999). We find that when looking at the behavioural plasticity of urban tiger snakes, habituation could be a potential factor to their continued persistence in urban wetlands. We suggest that further investigation into the adaptability and habituation of snakes on an urban plain will benefit fragmented habitats in an urban matrix. This study 1) demonstrates the ability to conduct behavioural studies on a cryptic species, 2) confirms to an extent that habituation is possible in snakes, 3) shows a snake's reluctance to show aggression towards humans and 4) stresses the importance for further behavioural studies on urban reptiles.

3.6 References

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Chapter 4: General discussion

4.1 Summary of findings

In this thesis, I have demonstrated how urban wetland tiger snake populations are impacted and influenced by anthropogenic presence and environmental factors. In addition, I show the interactions between behavioural traits in urban snake populations and humans, which sheds light on the adaptive behavioural plasticity of snakes in an urban area. As snake populations and behavioural ecology are greatly understudied worldwide, the findings in this thesis highlight the significance of studies on these upper trophic predators and their influence on the ecosystems they are in. This thesis also aims to correct the general populace's misconceptions of snake behaviour in response to humans. In the following discussion, I outline the broad findings of this thesis, indicate its limitations and improvements and propose my personal considerations on important future research directions for snake populations and their behavioural ecology.

Snakes occupy the upper trophic levels in ecological food webs as both predator and prey, and often have an influence on a diverse number of prey population sizes (Bonnet et al., 2002; Lind et al., 2005; Weatherhead & Blouin-demers, 2004). Snake populations impact the overall health and function of ecosystems as top predators (Lind et al., 2005; Shine & Bonnet, 2000), especially in wetland habitats where studies have shown them to be bioindicators of a wetland health (Lettoof et al., 2022). In Chapter 2, I conducted a Mark-recapture study three wetland tiger snake populations in Perth, Western Australia to investigate their population dynamics. Using a Jolly-Seber model, I was able to successfully calculate the population sizes of the combined surveyed areas within Bibra Lake and Herdsman Lake. Applying a Cormack-Jolly-Seber model, I successfully calculated the survival rate and the recapture rate of the tiger snakes in both the Bibra Lake and Herdsman Lake populations. From these results, I suggest that despite being heavily impacted by urbanisation and anthropogenic stress both Bibra Lake and Herdsman Lake tiger snake wetlands populations are persisting in these. The steady rate of recaptures from both these sites coupled with finding a large proportion of snakes marked by researchers since 2018 (Lettoof, 2021), indicates that these populations should still continue to persist.

Recent studies conducted in the past decade have presented compelling evidence highlighting the heightened vulnerability of reptiles to human-induced alterations in landscapes (Böhm et al., 2013; Powers & Jetz, 2019). Among reptiles and other terrestrial vertebrates, snakes are

one of the most challenging groups to research and study due to their cryptic nature (Willson & Winne, 2016). In Chapter 3, I conducted a behavioural study to investigate the behavioural responses of snakes towards a human encounter across 2 urban wetlands and one natural 1 wetland. I found that that temperature and a snake's body condition play a critical role in their response to a human, with higher ambient temperatures and snakes with a better body condition have a preference to flee rather than remain passive. Despite the variation in habitat types between the sites, there was little behavioural variability between the sites, with only the released snakes showing site varied behavioural response. Despite tiger snakes being a large venomous elapid, defensive responses were minimal during the when seen and when released interactions. However, defensive responses did increase when the snakes were handled where at higher temperatures and better body conditions.

The population dynamics and behavioural ecology of herpetofauna, particularly snakes, is greatly understudied and misrepresented (Brum et al., 2023) in comparison to other vertebrate taxon groups (Bonnet et al., 2002; Collins et al., 2021; Magle et al., 2012), to which this thesis aims to amend. In this thesis I demonstrated that (a) urbanisation and human presence plays a significant role in the population dynamics and behavioural ecology of a top wetland predator; (b) the importance of population studies on an upper trophic animal and how they can benefit our understanding of an ecosystem's health; (c) how behavioural studies done on the interactions between humans and snakes stem from their plasticity and an ecosystem's health; (d) that humans are viewed as non-threatening predators with their reluctance to showcase defensive displays.

4.2 Limitations

The overall challenge to this thesis is the cryptic nature of snakes. Snakes are poorly misrepresented in population studies due to their low capture rates and their sensitivity to environmental drivers such as temperature (Brum et al., 2023). Tiger snakes are no exception with their peak activity period constrained to Spring. This meant that sampling periods were only effective for 2 months of the year. Another aspect is urban wetland sampling. In these urban wetlands, the encroachment of weeds made the understory dense which made it increasingly difficult to detect snakes. Snake population papers are few, as a result most of this study relied on innovative methodologies put forth by this research or past tiger snake researchers. For Chapter 3 in particular, behavioural studies carried out on snakes are very rare, as such most behavioural responses and methods used relied greatly on researcher experience and experimental methodologies.

I was unsuccessful in quantifying any results from Loch McNess in Yanchep National Park, due to a potential decline in the tiger snake population at the wetland resulting from gradual anthropogenic impacts (Lettoof et al., 2021; Lettoof et al., 2022) and an added catalyst of a severe forest fire in 2019/2020 (Fontaine, 2022).

The results from this thesis would have been complemented by obtaining body temperature readings of snakes and ground temperature readings. However, such data was unable to be obtained due to limited funding. I have shown that population and behavioural research is in need of further exploration, and I shall now discuss areas in which I consider important for our future understanding of reptile populations and behavioural plasticity.

4.3 Conclusions and future direction

Natural habitats are increasingly degraded with the increase in urbanisation and the ever-growing human population (Concepción et al., 2015; Lettoof et al., 2021; Theodorou, 2022). With urbanisation continuing to rise in natural habitats such as Australia's wetlands, the population dynamics and behavioural traits of tiger snakes continue to be impacted and the specie's survival and persistence has become increasingly reliant on its adaptability (Lowry et al., 2013). As I demonstrated in Chapter 2, wetland tiger snake populations continue to persist and survive in urban wetlands, as indicated by recaptures. Such recaptures helped to quantify the estimated population sizes and survival rates of the populations in the surveyed areas. This study also demonstrated that the tiger snake population outside the urban matrix in Yanchep is in potential peril. However, to my best knowledge, little research has been conducted on the population dynamics of large snakes to aid in modelling its recovery or direction. Additionally, if this research and prior research conducted on Yanchep had not investigated upon the tiger snake population there, we would not have been able to see the population decline, highlighting the importance of researching such top order predators, particularly given their potential roles in ecosystem functioning and health. It is imperative that further investigation on this population be carried to enforce and encourage better management and protection of this top predator.

My thesis has shown the importance of using a top predator snake as an indication of an ecosystem's health and the impacts of anthropogenic presence in their habitats through an understanding of their populations and their behaviour. Urbanisation is constantly encroaching on our natural spaces and populations and habitats continue to get fragmented and isolated. By investigating other tiger snake populations in wetlands similar to the wetlands that I have surveyed, understanding of the factors influencing their continued persistence in those wetlands could be made. Additionally, this thesis can also be adapted and translated to other upper trophic snakes that could be potentially impacted by urbanisation such as red-bellied black snakes (*Pseudechis porphyriacus*). Even mid trophic species such as the western crowned snake (*Elapognathus coronatus*), a fellow wetland specialist in the southwest like tiger snakes, can benefit from future investigations into their populations.

Research has shown that behavioural plasticity of animals in response to changing natural habitats are crucial to their persistence and survival (Bonier et al., 2007; Brum et al., 2023; Gabor et al., 2022). As a result, behavioural studies to investigate top predators such as snakes

and their response to human interactions can instigate better management practices to avoid conflicts, which is often detrimental to snakes (Onyishi et al., 2021). My thesis demonstrates the possibility of conducting behavioural studies on a cryptic species like tiger snakes within a two-year timeframe. However, a further analysis to incorporate more predictor variables like body temperature and ground temperature could be crucial to better investigate their response to humans. In addition, more detailed analysis on the effects of direct human-snake interactions needs to be undertaken to further investigate habituation and the benefits or effects it plays on a snake population. In the long run, with the underrepresentation of snakes in both behavioural studies and population dynamics, further studies on snakes can shed light upon their role as a top trophic predator and their effects on an ecosystem's health.

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Appendix 1: Aberrant colouration of a Western tiger snake (*Notechis scutatus occidentalis*)

This observation presented in Appendix 1 is in preparation for future submission to review for publication.

Subaraj, S., Cable, I., Lam, G. H. S. Aberrant colouration of a Western tiger snake (*Notechis scutatus occidentalis*). *In Preparation*

Notechis scutatus occidentalis is a large polymorphic elapid that inhabits most habitat types across Southwestern Australia (Lettoof et al., 2020). Tiger snakes have a diet that consists of smaller vertebrates but, with a preference for frogs, they are more abundant around wetland habitats across their range (Aubret & Shine, 2008; Lettoof et al., 2020; Shine, 1979). Colorations in snakes serve important purposes like to aid in thermoregulation or mimicry but, in rare cases individuals may lack pigmentation causing anomalies such as hypomelanism (Borteiro et al., 2021; Whitford et al., 2017). Western Tiger Snakes are typically dark brown to black with transverse dorsal yellow to orange banding (Bonnet et al., 2002). Some individuals have non distinct to no banding, making them a pattern less uniform colour.

This encounter was during a mark-recapture for a population study on tiger snakes under permits DBCA: FO25000370 and ARE2021-21. At 0915hrs on 28 October 2021, at Herdsman Lake (-31.919391°S, 115.805195°E, WGS 84) we encountered an unusual looking snake basking on the riparian vegetation beside a small channel. Initially, from a distance, the snake was mis-identified as a Dugite (*Pseudonaja affinis*) based on its coloration. Upon approaching it, its trademark flaring of the neck gave it away as a Western Tiger Snake. The snake was captured by hand to collect morphometric data and to be numbered via ventral scale clipping. This mid-sized male (SVL= 79.3 cm) had some form of hypomelanism or amelanism where there is less than normal amount of melanin pigmentation. It lacked any banding, partial dark spots along the sides and, was brown in coloration on its dorsal side that got paler as it got closer to the ventral side. Its ventral coloration was light cream with small partial brown

blotches. The most unusual feature of the snake was its tongue which was pink unlike the usual black tongues that normal tiger snakes have.



Figure 1 (A) an aberrant morph of a Western Tiger Snake (*Notechis scutatus occidentalis*) with a pink tongue, (B) cream ventrals with spotting along the lateral side and, (C) defensive display with its chocolate brown dorsal side.

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Appendix 2: Tiger Snake (*Notechis scutatus occidentalis*) predation on a Dusky Moorhen (*Gallinula tenebrosa*)

This observation presented in Appendix 2 is in preparation for future submission to review for publication.

Subaraj, S., Cable, I., Lam, G. H. S. Tiger Snake (*Notechis scutatus occidentalis*) predation on a Dusky Moorhen (*Gallinula tenebrosa*). *In Preparation*

The Western Tiger Snake (*Notechis scutatus occidentalis*) is a large Australian elapid that occurs across most of the southern and eastern parts of the continent (Aubret et al., 2006; Lettoof, 2021). Tiger snakes are mostly found in habitat types around freshwater bodies, with disjunct island populations (Bonnet et al., 2005; Bonnet et al., 2002). Tiger snakes are primarily anurophagous, though larger individuals opportunistically predate on small avian, mammalian and, reptilian fauna (Aubret et al., 2004; Hall & Fearn, 2017; Lettoof et al., 2020).

This encounter was during a mark-recapture population study on tiger snakes under permits DBCA: FO25000370 and ARE2021-21. At 1002hrs on 1 October 2022, at Herdsman Lake (-31.919391°S, 115.805195°E, WGS 84), we encountered a tiger snake with an unusually large, elongated food bulge in its stomach. The snake was bagged to be scale clipped and measured. During the taking of the morphometric measurement, the snake began to regurgitate its meal where we observed that the snake had predated upon a waterbird chick. Upon closer inspection, the elongated toe digits, lack of prominent webbing and the coloration of the bird suggested the identification of the waterbird species as a Dusky Moorhen (*Gallinula tenebrosa*). This was one of three encounters in this study where wetland birds were found in the stomach of a large tiger snake.

Carnac Island tiger snakes, which were recently introduced, are generally larger and predate primarily on sea-bird chicks (Bonnet et al., 2002), unlike their mainland counterparts in Perth which are generally smaller in comparison and are primarily anurophagous (Aubret et al., 2004; Lettoof et al., 2020). This island population displayed high levels of adaptive plasticity towards prey sizes and successfully thrived upon large prey items (Bonnet et al., 2002). Plasticity levels found in mainland south-western populations showed minimal levels (Aubret & Shine, 2009). This would suggest that opportunistic feeding of larger prey items like water bird chicks maintains the minimal levels of adaptive plasticity. Opportunistic feeding by larger snakes

could also coincide with breeding season of small mammals and water birds, where juveniles are abundant and readily available. Introducing or natural colonization of these mainland populations into areas where smaller prey items are absent, like islands, would cause the a significant increase in the plasticity levels (Aubret, 2015; Aubret & Shine, 2009).

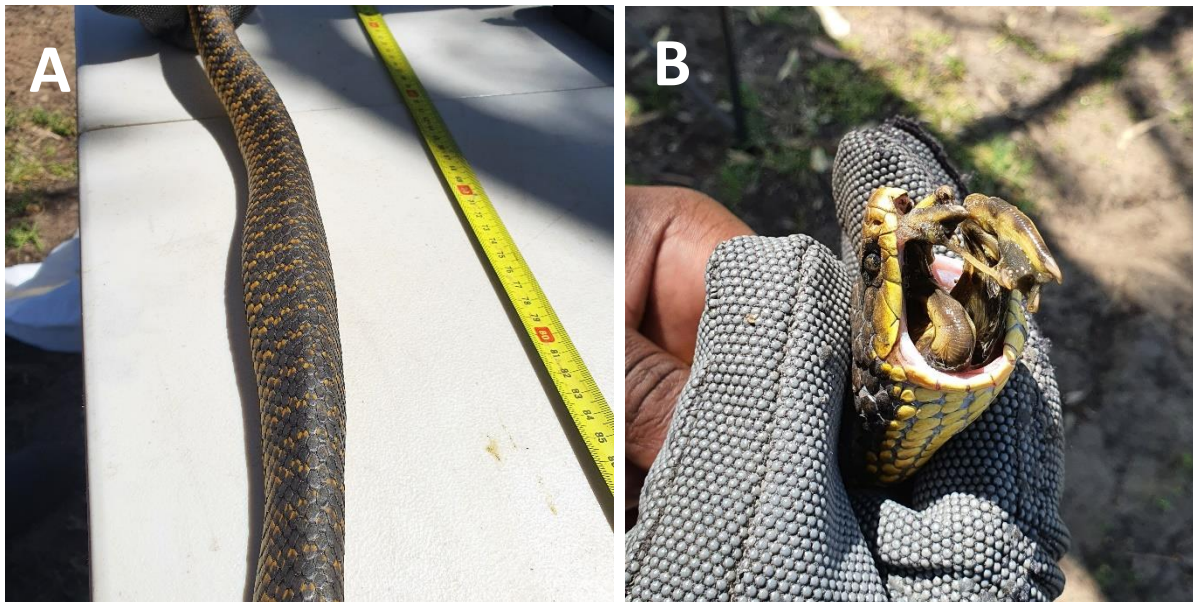


Figure 1: (A) Elongated food bulge of a large Tiger Snake, (B) Moorhen chick palpated to the entrance of the mouth for identification.

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