School of Molecular and Life Sciences

The Serpent in the Garden of Weeden: A Comparison of Western Tiger Snake (*Notechis scutatus occidentalis*) Habitat Quality and Thermal Ecology in Native and Invasive Vegetation.

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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). The research as approved by the Curtin University Animal Ethics Committee (approvals ARE2019-24 and ARE2020-6) and was conducted under license from the Western Australian Department of Biodiversity Conservation and Attractions (FO25000294-2).

This project received additional funding from the Holsworth Wildlife Research Endowment.

Signature:

Date:

“Yous milkin’?”

- Old mate at Herdsman Lake

Acknowledgments

From the days when I could barely walk and used to catch frogs and lizards around the house in Gabon with my dad my lifelong ambition has been to work with wild animals, particularly reptiles, and even more specifically, snakes. Therefore, I feel like the most appropriate place to start with expressing my gratitude to all the people involved in making this research possible is with my parents, Koert Cornelis and Nicole Perdaen. Words cannot express the thanks I have for your continued love and unwavering support, not just during the process of accomplishing this body of work but, my entire life, even when I was undeserving of it. Thank you for inspiring me with the natural world and allowing me to become who I always wanted to be.

As for my supervisors, I would like to thank Bill Bateman for taking me on as a student and giving me the opportunity to work with one of the most venomous snakes in the world, and letting me run with the project how I saw fit. Christine Cooper, thank you for all your support with performing the surgeries on my snakes and helping me wrap my head around the intricate world of animal physiology. Alas I am but a mere ecologist who expects expensive equipment to work as it was designed to do. Brenton von Takach, thank you for your patience with all my questions regarding statistics, your inhuman understanding of modelling will forever remain a mystery to me. Finally, Damian Lettoof, although you were not officially a supervisor you had the most input into this project and always had my back (quite literally sitting behind me) whether it was in the field or in the office.

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Statement of Contribution by Others

During the extensive field component of this research and that on which I collaborated; I (along with my collaborators) was lucky enough to make some interesting observations of tiger snake behaviour and biology, most of which were published as natural history notes. These small publications did not warrant inclusion in the main text of my thesis, although I did reference some of them. However, these natural history notes deserve a place in the appendix, as a 'digestif' to the body of work I have presented here and by including them, this thesis is a more complete representation of the tiger snake research I have been a part of thus far. I have obtained permission from the copyright owners to use any third-party copyright material reproduced in this thesis, and to use any of my own published work in which the copyright is held by another party.

Appendix 1:

Cornelis, J., Lettoof, D. 2020. *Notechis scutatus occidentalis* (Western Tiger Snake). Defensive Behaviour. Herpetological Review 51 (3):623-624

Both authors, JC and DL, made the observation in the field and wrote the manuscript.

Appendix 2:

Lettoof, D., Cornelis, J., J. Harvey-Hall, and F. Aubret. 2020b. *Notechis scutatus occidentalis* (Western Tiger Snake). Diet. Herpetological Review 51:873.

DL, JC and JHH made the observation in the field. DL and FA wrote the manuscript and all authors contributed to the revisions of the manuscript.

Appendix 3:

Cornelis, J., and D. Lettoof. 2020. *Notechis scutatus occidentalis* (Western Tiger Snake). Reproduction/Unfertilized Ova Post-Parturition. Herpetological Review 51:873-874.

Both authors, JC and DL, made the observation in the field and wrote the manuscript.

Appendix 4:

Lettoof, D., A. Santoro, C. Swinstead, and Cornelis, J. 2021. First record of predation of a hatchling turtle by the Western tiger snake (*Notechis scutatus occidentalis*). Australian Zoologist.

DL and JC conducted the field work. DL and CS made the observation in the laboratory. DL and AS wrote the manuscript and all authors contributed to revisions of the manuscript

Appendix 5

Cornelis, J., Lettoof, D., Lam, L., Loughridge, S, and Aubret, F. 2021. Dystocia in a wild Western Tiger Snake (*Notechis scutatus occidentalis*). Australian Zoologist

JC and DL made the observation in the field. LL and SL contributed veterinary expertise. AF provided further historical, unpublished data from previous research. JC and DL wrote the manuscript and all authors contributed to revisions of the manuscript.

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Abbreviations

Abbreviation	Definition
BS	Black Swan Lake
db	Accuracy of thermoregulation, the absolute value of the deviation of T_b from T_{set}
de	Thermal quality of the habitat, the absolute value of the deviation of T_e from T_{set}. As I collected T_e's in two different microhabitat types I have two indices to represent them $de_{exposed}$ for T_e's collected in exposed microhabitats and $de_{shelter}$ for T_e's collected in sheltered microhabitats.
de_0	Deviation of environmental temperature is equal to zero (within T_{set})
$de_{exposed}$	Thermal quality of exposed habitats
$de_{shelter}$	Thermal quality of sheltered habitats
E	The effectiveness of thermoregulation calculated as the difference between the *de*-*db* which I did for both $de_{exposed}$ and $de_{shelter}$
$E_{exposed}$	The effectiveness of thermoregulation in exposed habitats
$E_{shelter}$	The effectiveness of thermoregulation in sheltered habitats
Ex	Exploitation of the thermal environment. Calculated as the time in which an animals *db* is zero concurrently with a *de* equal to zero divided by the total time *de* was equal to zero
$Ex_{exposed}$	Exploitation of the thermal environment in exposed habitats
$Ex_{shelter}$	Exploitation of the thermal environment in sheltered habitats
HL	Herdsman Lake
KL	Kogolup Lake
KO	Open kikuyu grass
KS	Sedge kikuyu grass
KW	Woodland kikuyu grass
NO	Open native vegetation
NS	Native sedge vegetation
NW	Native woodland vegetation
T_a	Ambient temperature
T_b	Body temperature
$T_{b,\ min}$	Minimum body temperature
$T_{b,active}$	Active body temperature
$T_{b,max}$	Maximum body temperature
T_e	Operative environmental temperature
T_{set}	Set-point range determined in a thermal gradient
Y	Yanchep National Park

Abstract

Expanding urban environments have a range of impacts on natural ecosystems. A major issue is the introduction and spread of invasive plant species. In south-western Australia, invasive plants have contributed to the degradation of many sensitive wetland areas, particularly within the urban footprint of the region's largest city, Perth. Kikuyu grass (*Pennisetum clandestinum*) is particularly pervasive in Perth's wetlands, outcompeting native vegetation and reducing habitat heterogeneity. However a top-order predator, the western tiger snake (*Notechis scutatus occidentalis*), persists in these heavily altered wetland environments. Here, I investigate the impacts of invasive kikuyu grass on the ecology and physiology of this elapid snake, with the aims of improving management of urban wetlands and increasing our understanding of the biology of this urban predator.

I quantified seven habitat characteristics at four wetlands, two with kikuyu grass as the dominant ground cover vegetation and two with predominately native vegetation. I found that, although kikuyu grass has reduced habitat heterogeneity and essentially converted a diverse plant community to a monoculture, structural habitat characteristics comparable to native plant communities have been retained. If habitat structure rather than vegetation composition are important for persistence of tiger snakes, tiger snakes in urban wetlands dominated by kikuyu grass may not have experienced a reduction in habitat suitability. I further explored this hypothesis by examining prey availability, predation risk and thermal biology of tiger snakes at wetlands dominated by kikuyu grass and those dominated by native vegetation.

Wetland degradation often adversely affects frog populations, which are the predominant food for tiger snakes in the Perth region. To investigate whether invasive kikuyu grass adversely impacts prey availability for tiger snakes, I conducted aural and visual frog surveys at the four wetlands. There was no evidence that overall frog abundance differed between kikuyu-dominated wetlands and wetlands with native vegetation. Indeed, motorbike frogs (*Litoria moorei*) were calling in greater abundance in kikuyu grass compared with native vegetation-dominated wetlands. I did not find any evidence from visual surveys that frog abundance differed between wetlands with either kikuyu grass or native vegetation. Overall, frog surveys suggest

that tiger snakes had equal foraging opportunities at all sites, with little influence of kikuyu grass on prey availability.

Predation risk for many snake species decreases with increasing body size, suggesting that smaller snakes have to balance avoidance of predators with taking opportunities to feed and thermoregulate. I found no difference in the predation risk for juvenile-sized tiger snakes between kikuyu grass and native vegetation. Overall predation risk for juvenile tiger snakes appears low, with a predation rate of 4.75% on artificial snake models. However, I did find predation risk increased in more open habitats and, interestingly, predation risk was higher in autumn, coinciding with the seasonal parturition of tiger snakes.

Tiger snakes are ectotherms which rely on environmental heat to maintain a suitable body temperature to perform vital physiological functions. I quantified the thermal properties of kikuyu grass and native vegetation for tiger snakes using operative temperature models, and found that thermoregulatory opportunities for tiger snakes were similar throughout the year for the two vegetation types. Winter was the most thermally challenging season for tiger snakes, with their shelter sites rarely reaching the lower bound of their preferred temperature range. During autumn, spring and summer the temperature within tiger snake shelter sites fell within the snakes' preferred temperature range for similar durations.

Body temperature and thermoregulatory efficiency of live tiger snakes implanted with temperature loggers during spring did not differ for snakes living in kikuyu grass compared with snakes living in native vegetation. Due to the similarity in thermal quality of tiger snake shelter sites within kikuyu grass and native vegetation the snakes' ability to thermoregulate within these environments remains unchanged by conversion of native vegetation to invasive grass. Tiger snakes are capable of exploiting temperatures in basking sites when these are optimal, but can still maintain their preferred body temperature within their shelter sites once basking site temperatures are so high the thermal environment is no longer favourable.

This thesis provides novel insights into the ecology and thermal biology of tiger snakes and their persistence in urban wetlands dominated by invasive plants. I found little evidence to suggest that tiger snakes are adversely impacted by the conversion of a diverse native plant community to an exotic monoculture. The similarities in prey availability, predation risk and physiological constraints of kikuyu-dominated wetlands compared to those retaining native vegetation permit the continued persistence of tiger snakes in these modified urban environments. Indeed, kikuyu grass provides for high-quality habitat, with abundant prey, low predation rates and favourable thermal conditions. In this context, there is no evidence that rehabilitation of urban wetlands by controlling kikuyu grass and replanting native vegetation will benefit tiger snakes.

Introduction

Urbanisation is a major driver of environmental change in Australia, with urban environments encroaching on surrounding natural ecosystems (Faulkner 2004, Coleman 2017, Cresswell and Murphy 2017). An increasingly urbanised environment alters ecological conditions by introducing invasive species, creating new biological interactions, changing disturbance regimes, and limiting space for plants and animals (McDonnell et al. 1993, Kinzig and Grove 2001, Hamer and McDonnell 2008, Štajerová et al. 2017). These changes can affect habitat structure which in turn influences prey abundance, predation pressure or the thermal quality of a habitat and therefore the suitability of the habitat for animals (Huey 1991, Webb et al. 2005, Lee et al. 2006). Species known as urban avoiders are incapable of adapting to such a drastic change in their environment (McKinney 2008) and decline in urban areas due to reduction of available habitat or homogenisation of habitat structure (Brooks et al. 2005). Other species, known as urban adapters, are capable of persisting in remnant fragmented habitats within urban areas or adapt to the modified habitat structure and composition (Bateman and Fleming 2012). Mammal and bird urban adapters are typically generalists; specialists tend to be urban avoiders (Bonier et al. 2007, Mazza et al. 2020). For reptiles, small species such as geckos typically do well on anthropogenic structures in urban areas (Zozaya et al. 2015) but even some large predatory species (e.g. pythons) do persist (French et al. 2018, Parkin et al. 2021). Tiger snakes (*Notechis scutatus*) could also be considered urban adapters as they continue to occur in urban remnant wetlands (Lettoof et al. 2020a).

Urban wetland vegetation is often degraded by weed invasions (Grella et al. 2018) causing compositional and structural changes as native species are displaced (Braithwaite et al. 1989, Reed et al. 2005). Invasive plant species are a threat to ecosystems worldwide; diverse plant communities promote ecosystem function (Schweiger et al. 2018) and environmental heterogeneity is fundamental for maintaining high levels of biodiversity (Stein et al. 2014). Habitat homogenisation has negative abiotic implications for microclimate (Saunders et al. 1991) and nutrient cycling (Vilà et al. 2011). Biotic aspects of the ecosystem are also affected, including species richness (Brooks et al. 2005), species interactions (Blair and Johnson 2008) and animal behaviour (Pyšek et al. 2012, Stewart et al. 2021). However, not all fauna is negatively affected by the invasion of exotic grass (Douglas et al. 2006). For some urban adapter reptiles, habitat structure is more important than species composition (Garden et al. 2007) and they may do well in altered habitats. Indeed cumulative impacts of invasive plants negatively affect specialist species that rely on environmental constancy (Devictor et al. 2008, Clavel et al. 2011) but may benefit generalist species which can expand their niche into disturbed environments (McKinney and Lockwood 1999, Nordberg and Schwarzkopf 2019c).

Tiger snakes are viviparous elapids found throughout southern and eastern Australia. Their behavioural and morphological plasticity have allowed them to persist in a diverse array of habitats, including offshore islands where they occupy habitats not occupied by mainland conspecifics (Shine 1987, Aubret and Shine 2010). Frogs are the primary prey of tiger snakes in the Perth region (Shine 1998, Lettoof et al. 2020c), although they will opportunistically take birds, mammals and reptiles (Lettoof et al. 2020b, Lettoof et al. 2020c, Lettoof et al. 2021b). Consequently, tiger snakes across their entire distribution are considered to be a generalist species (Greer 1997, Fearn 2011). However, most mainland populations exhibit a strong preference for wetland environments and frog prey (Aubret 2004, Aubret and Shine 2008, Mirtschin et al. 2017).

Wetlands are sensitive ecosystems globally, and are particularly susceptible to degradation by urbanisation (Faulkner 2004). Perth, a city of ~2 million people located in the south-west of Western Australia, has an increasing urban footprint. Consequently, ~70% of wetlands in the region have already been lost or degraded (Davis and Froend 1999, Kelobonye et al. 2019). Along with the loss of native plants, invasive plant species can further contribute to the degradation of wetlands (Campbell et al. 2002, Brooks et al. 2005). Tiger snakes are successful in urban wetlands (Butler et al. 2005b) and in Perth, western tiger snakes (*Notechis scutatus occidentalis*) are restricted to a small number of wetlands (Lettoof et al. 2021c) where they are bioindicators of wetland condition (Lettoof et al. 2021a) and are top predators in these environments (Lettoof et al. 2020a), including some wetlands dominated by kikuyu grass (*Pennisetum clandestinum*). Interestingly, these same wetlands are also some of the most contaminated by pollutants which tiger snakes bioaccumulate (Lettoof et al. 2020a) yet also harbour some of the largest effective population sizes (Lettoof et al. 2021c). As a top predator, tiger snake presence and abundance is sensitive to a healthy food web and adequate habitat (Sergio et al. 2008); hence their use as a bioindicator of wetland condition. Perhaps it is the quality of habitat provided by invasive vegetation that allows tiger snakes to persist in the degraded urban sites?

Kikuyu grass is recognised globally as an invasive species, particularly in wetlands (Bird et al. 2013, Boon and Tesfamichael 2017). In urban areas, including Perth, this grass has often spread from domestic lawns and established in surrounding bushland fragments causing a change in vegetation composition. Uncut kikuyu grass rapidly grows a dense matrix of stems which aids in it colonising new ground and outcompeting adjacent vegetation (Gonzalez 2009, Bradshaw et al. 2013). As wetlands in urban areas are often hotspots of biodiversity, such an invasion can have a profound effect on biodiversity, with interactions between native plants and animals often impacted by a reduction of habitat heterogeneity (McKinney 2008, Pillsbury and Miller 2008, Eagles-Smith et al. 2018, Mason et al. 2018).

Amphibians are key components to the function of wetland ecosystems, fulfilling both important predator and prey roles (Gibbons et al. 2006, Hamer and McDonnell 2008, Santos and Llorente 2009). Urban frog populations are often adversely affected by the urban degradation of wetlands (Scheffers and Paszkowski 2013, Sievers et al. 2019), especially via introduced contaminants (Ficken and Byrne 2013, Sievers et al. 2018), invasive vegetation (Maerz et al. 2005b) and invasive fish (Webb and Joss 1997). However, invasive grasses, such as kikuyu grass, may provide suitable habitat for frogs (Zavaleta et al. 2001, Maerz et al. 2005a). Prey availability influences growth rate, reproductive success, prey selection and space use by snakes (Madsen and Shine 1996, Hirai 2004, Brown et al. 2017). A critical step in understanding tiger snake habitat quality is first assessing frog abundance (Brown and Shine 2007) as snake persistence in degraded wetlands is likely to be driven by changes in prey availability (McCauley et al. 2006, Zipkin et al. 2020) and related factors such as time spent foraging (Battles et al. 2013).

When hunting/foraging, snakes are often required to forfeit the safety of their refugia, increasing the risk of predation especially for younger, smaller individuals (Lima and Dill 1990, Webb et al. 2005). However, sheltering from predators in refuges has associated costs such as foregoing foraging and thermoregulatory opportunities which may impact growth (Downes 2001, Webb et al. 2002, Amo et al. 2007, Webb et al. 2009). To mitigate these costs small snakes could use thermally favourable retreats where they do not need to trade off safety for thermoregulation (Webb and Whiting 2005, Andersson et al. 2010, Coombs 2016), or use structurally complex habitats to reduce predation rates that are often higher in more open environments (Anderson and Burgin 2008, Daly et al. 2008, Sato et al. 2014, Hansen et al. 2019). As invasive plants can alter habitat structure which could lead to increased predation risk, comparing predation risk between native vegetation and kikuyu grass is important for understanding if invasive kikuyu grass potentially influences tiger snake habitat use, and ultimately survival.

Reptiles are dependent on heat gained from the environment for body temperature (T_b) regulation (Rafael et al. 2012), necessary to maintain vital physiological functions associated with metabolic rate (Lourdais et al. 2013), development (Autumn and De Nardo 1995), and reproduction (Lourdais et al. 2008). Thermal properties of the environment therefore influence snake behaviour, as selection of thermally optimal microhabitats (Hertz et al. 1994) often has to be traded-off with avoiding predation and acquiring food (Amo et al. 2007). Habitat structure will influence the micro-environment (Huey 1991) and even structurally similar grass types can offer slightly different thermal regimes (Bell et al. 2021). Quantifying the thermal environment within native and invasive vegetation, and examining how tiger snakes exploit these environments is, therefore, a key factor in understanding if and how invasive vegetation impacts tiger snake habitat quality.

Operative temperature (T_e) models have been widely used to measure the thermoregulatory opportunities available to ectotherms (Bakken et al. 1985, Dzialowski 2005). In addition, they provide more meaningful information concerning thermoregulatory opportunities and challenges rather than a simple measure of air temperature by integrating heat exchange over multiple pathways (Heath 1964, Shine and Kearney 2001). Often these models are made from copper pipe and are deployed in microhabitats to determine temperature availability and thermoregulatory opportunities (Bakken 1992, Lutterschmidt and Reinert 2012). Operative temperatures can then be related to T_b to investigate behavioural thermoregulation (Heath 1964, Bakken et al. 1985). The core principles are to compare the T_b selected by an animal in the field to the available T_e and set-point range ($T_{set;}$ determined in a controlled environment free of any costs associated with thermoregulation; Hertz et al. 1993, Christian and Weavers 1996). For example, black rat snakes (*Elaphe obsoleta*

obsoleta) achieved higher T_bs by investing less in thermoregulation while in edge habitats by exploiting high thermal quality sites compared to the lower T_bs achieved while investing more into thermoregulation by exploiting lower thermal quality sites in forest habitats (Blouin-Demers and Weatherhead 2002). Investigating tiger snake physiology and thermoregulatory behaviour on such a fine scale will allow comparison of the thermal quality of tiger snake shelter sites and therefore quantify the thermal impact of altering the plant community.

Considering tiger snakes are for the most part restricted to the wetlands they inhabit within the urban matrix (Lettoof et al. 2021c) the quality of their habitat is likely influencing their persistence in these environments. Here I assess the impact of invasive kikuyu grass on biotic and abiotic variables of tiger snake habitat in urban wetlands. I hypothesised that kikuyu grass offered an improved habitat quality over native vegetation which I investigated by examining habitat structure, prey availability (frog abundance), predation risk for juvenile tiger snakes, and the thermal quality of available microhabitats. Subsequently I hypothesised that a change in vegetation composition induced a behavioural shift in tiger snake body temperature regulation which I investigated by assessing daily patterns of tiger snake T_b, and the effectiveness of tiger snake thermoregulation. This study explores how the habitat modification through the proliferation of an invasive grass may provide a large elapid snake persisting in urban wetlands with a suitable alternative to native vegetation in terms of habitat quality and thermoregulatory opportunities.

Methods

Study sites

I examined western tiger snake ecology at four wetlands within 50km of the Perth CBD, in south-west Western Australia. At Herdsman Lake (HL; 31.92°S, 115.80°E) and Kogolup Lake (KL; -32.12°S, 115.83°E) kikuyu grass was the dominant ground cover vegetation, while at Loch McNess in Yanchep National Park (Y; -31.54°S, 115.68°E) and Black Swan Lake (BS; -32.47°S, 115.77°E) native vegetation predominated. Within these sites, I identified three broad habitat categories; open, sedge, and woodland. Kikuyu grass dominated at HL and KL where the open habitat (kikuyu open; KO) was a dense mat of kikuyu grass growing on its own without canopy cover, the sedge habitat (kikuyu sedge; KS) was categorised by a dense, tall (up to 2m) mass of kikuyu grass growing on a secondary structure provided by bulrush (*Typha* sp.) and the woodland habitat (kikuyu woodland; KW) had a dense mat of kikuyu grass growing in the shade of *Eucalyptus sp.* and *Melaleuca spp*., and additionally *Banksia spp.* at KL. At the sites dominated by native vegetation, BS and Y, the open habitat (native open; NO) was a mixed community with the dominant grass type *Schoenoplectus spp.* The sedge habitat (native sedge; NS) consisted of *Gahnia decomposita* and/or *Lepidosperma longitudinale* while the woodland habitat (native woodland; NW) had a mixed community understory growing in the shaded conditions provided by *Banksia*, *Melaleuca* and *Eucalyptus spp.*

To quantify the habitat structure for the selected habitat types I recorded vegetation features along two 100m transects in each habitat type at each of the four study sites. Every 10m along the transect I recorded: (1) canopy cover using a spherical densiometer (Forest Densiometers, Model A), (2) light availability with a digital lux meter (Dr.meter LX101BS) when the reading in ambient unshaded light was ca. 720000 lux, (3) number of trees (>150mm circumference) within a 2m radius, (4) number of woody plants (<150mm circumference) within a 2m radius, (5) the height of the tallest understorey plant, (6) approximate percent ground cover within a 2m radius, and (7) the vegetation density by inserting a 50 cm x 50 cm board inside the vegetation, taking a photograph, and then using ImageJ 1.x (Schneider et al. 2012) to calculate the surface area of the board not obscured by vegetation; if the vegetation was too dense to insert the board I recorded vegetation density as 100% (Fox et al. 1996, Colman et al. 2014, Colman et al. 2015).

Prey availability

I conducted aural frog surveys to estimate the abundance of calling males at the different lakes and visual surveys to measure abundance of frogs between different habitat types at the four sites. These surveys were conducted in October and November 2019 to coincide with peak tiger snake activity and peak calling activity for the expected dominant frog species: rattling froglet (*Crinia glauerti*), squelching froglet (*Crinia insignifera*), western banjo frog (*Limnodynastes dorsalis*), slender tree frog (*Litoria adelaidensis*), and motorbike frog (*Litoria moorei*; Hoskin et al. 2015). All surveys began after 19:00 on evenings when ambient temperature (T_a) at this time was >15°C and were completed before 22:30.

Aural frog surveys

The abundance of calling male frogs was estimated for each site, but not for specific habitat types within sites as it was impossible to deduce whether all the frogs heard were calling from within the specific habitat type being sampled. Calling males were identified to species and counted over a 20 min period while the observer remained static (de Solla et al. 2005). Frogs were only counted if their approximate location in the vicinity of the observer could be identified (Driscoll 1998) for example, frogs chorusing in the distance were not included as it was almost impossible to accurately estimate their numbers. The 20 minute call surveys were repeated at three different locations at each wetland every night and only a single wetland was surveyed per night to mitigate potential temporal effects caused by the time of night. Each site was surveyed six times, resulting in a total of 84 aural surveys.

Visual frog surveys

Standardised 10 minute active visual searches were conducted in the open, sedge and woodland habitat types at every wetland. I revisited the same area of the habitat type I was surveying on subsequent nights because some wetlands only contained one patch of suitable habitat that was comparable between wetlands. I commenced the search in the centre of each habitat type and walked a steady pace while counting individual frogs and identifying them to species by spotlighting individuals or their eye-shine for 10 minutes within a 50m radius of the starting point. Site rotation was as for aural surveys. Sites Y and BS were surveyed for five nights each, and KL and HL were surveyed on four nights each, for a total of 54 visual searches.

Predation risk

I constructed 120 soft clay models representing juvenile tiger snakes and 120 spherical control balls by hand from nontoxic Plastiplay^{TM} brown modelling clay (Figure 1). Total body length of the artificial snakes was ca. 25cm, width was 1cm and they were moulded into a sinusoidal shape. Control balls were 4cm in diameter and used to determine if predators discriminated foreign objects from artificial snakes (Nordberg and Schwarzkopf 2019b). The artificial snakes and balls were deployed in pairs at the four study sites in each of the three different habitat types; two wetlands were monitored simultaneously, one natural and one urban. In each habitat type ten artificial snakes were placed in exposed areas to simulate basking sites, and ten were hidden under vegetation to simulate refuge sites. Artificial snakes were separated by 5m with each model accompanied by a control ball lying 25cm away. All clay models were checked every day for a five day period and marks left by predators were counted, scored by intensity of attack, and the predators were identified as birds, rodents and, cats based on the shape of the marks left by the predators (Webb and Whiting 2005) or classified as unknown if the clay models were missing. Small marks, such as those left by house mice (*Mus musculus*) were scored as exploratory rather than predatory behaviour and were not considered to represent a realistic predatory attempt on a juvenile tiger snake; these were therefore omitted from analyses (Figure 2). Trials were conducted in autumn and repeated in spring for a total of 10 days of sampling at each site.

Figure 1 Artificial snake and control ball made from nontoxic Plastiplay^{TM} brown modelling clay and deployed in native woodland habitat at Yanchep National Park to quantify predation risk for juvenile western tiger snakes (*Notechis scutatus occidentalis*).

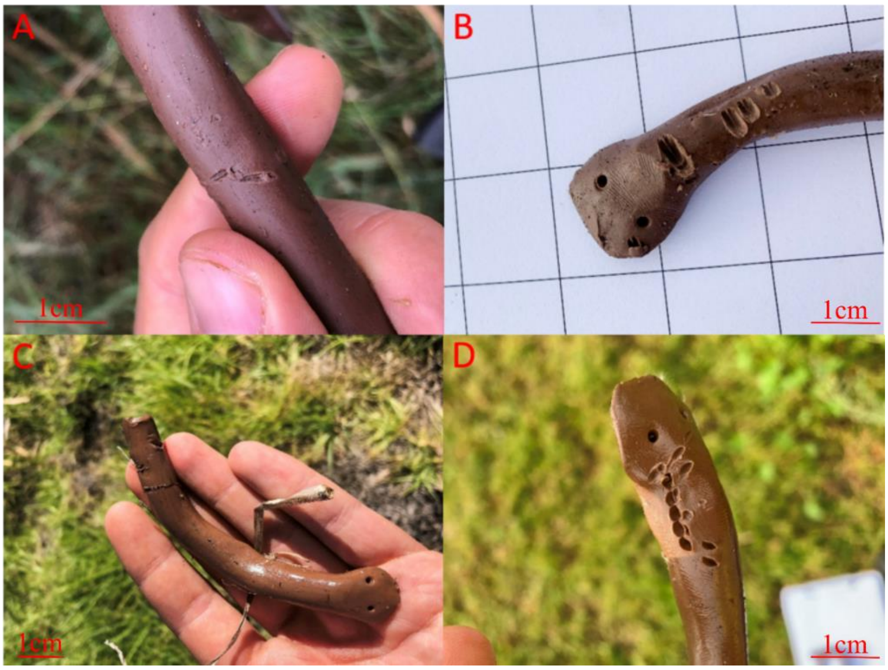

Figure 2 Examples of marks left by predators A) a small rodent and classed as exploratory behaviour, omitted from analysis, B) a rodent, C) a bird and D) a cat on artificial juvenile tiger (*Notechis scutatus occidentalis*) snakes deployed in different habitats at four wetlands in the Perth region.

Thermal ecology

Operative temperature model calibration

I constructed operative models using 30cm long sections of copper pipe (32mm diameter, wall 1mm thick) filled with water and painted to approximate the reflectivity of a tiger snake (Seebacher and Shine 2004, Lutterschmidt and Reinert 2012). The diameter of the pipe was similar to that of an adult tiger snake which allowed for a Thermochron iButton to be suspended in the centre of the pipe (achieved by inserting a wooden skewer into the centre of a rubber stopper at the end of the pipe and taping the iButton to the end of the skewer). The iButton was waterproofed with Plasti Dip and wrapped in plastic film. To determine the paint scheme for the copper models that most closely matched the reflectivity of tiger snakes I conducted several experiments with painted copper pipes with varying combinations of grey and white. These were fitted with iButtons and placed in direct sunlight for 24 hours alongside a tiger snake carcass also containing an iButton. The resulting temperature data were plotted and copper models were compared to the snake carcass by visually inspecting the graph. Once I determined the colour combination that resulted in the closest thermal match, I conducted a larger experiment with four pipes painted grey with two 5cm wide white bands and compared their thermal profile with that of four adult tiger snake carcasses placed outdoors in an exposed location for 48hrs. During this period air temperature ranged from 12.2°C to 27.2°C and the snakes and models were exposed to direct sunlight, cloud cover, rain (0.4mm) and variable wind speeds (max 54km/h). Temperature data were recorded at 10min intervals. I calculated thermal properties of the snake carcases and models (mean, minimum, and maximum temperatures, warming and cooling slopes) using a custom written VB program (Visual Basic V6; P.C. Withers)

Seasonal thermal quality of habitat

All of the microhabitats I studied at all of the lakes provided tiger snakes with the option to move into the sun to thermoregulate when sunlight was available, so I quantified the thermal quality of potential shelter sites in each of the different habitat types at the four lakes to determine if kikuyu grass or native vegetation differ in their thermal quality. I placed an operative temperature model in one shelter site in each of the three habitat types at each site, recording data at 10min intervals for seven days at each site every month for twelve months. I calculated the mean, maximum and minimum operative environmental temperature (T_e) of the sheltered microhabitats at ten minute intervals over 24hrs for each week at each site. The thermal quality (*de*) of tiger snake shelter sites was calculated as the absolute value of how much T_e in shelter sites deviated from the set-point range (T_{set}). So, I calculated the mean *de*, maximum *de* and the period *de* was equal to zero within T_{set}. This T_{set} was determined by Ladyman & Bradshaw (2003) as $24.0 \pm 0.9^{\circ}C – 30.9 \pm 0.3^{\circ}C$ for snakes from HL in a thermal gradient. I then grouped the resulting data into four seasons so that I could compare differences between kikuyu grass and native vegetation and the habitat types within plant communities. I assumed that tiger snake T_{set} does not change seasonally (Nordberg and Schwarzkopf 2019a) as the thermal gradient experiment was only conducted during one season (Ladyman and Bradshaw 2003)

Snake catching, housing, and morphometrics

Snakes were captured by hand in September and their capture location recorded with a Garmin 60 GPS. They were weighed using a 500g Pesola spring balance; snout-vent length and tail length were measured by gently stretching the snake along a ruler, and ventral scale clips were made for individual identification. Sex was determined by inserting a lubricated probe into the cloacal bursae to measure the depth of the hemipenal pocket (McDiarmid et al. 2012). Fourteen male tiger snakes with a body mass >200g were then transported to Curtin University campus where they were housed individually in plastic tubs (70×50×40cm) for up to a week prior to surgery to implant a radio-transmitter and temperature logger, and then 2-5 days post-surgery for post-surgical monitoring. Snakes from different localities were separated to maintain quarantine conditions. The snakes did not require feeding during the <2 weeks they were in captivity, although fresh water was provided *ad lib*. After this, snakes were returned to the capture site and radio-tracked for up to 2 months. Snakes were then recaptured and euthanised via an intracardiac injection of Lethabarb (pentobarbitone) and the transmitter and data loggers removed.

Implanting data loggers and transmitters

A small package consisting of a temperature data logger (Thermochron iButton) and a VHF transmitter (Holohil PD-2) with a combined mass of ~5g was surgically implanted into the intraperitoneal cavity of each of the 14 snakes under general anaesthesia. Temperature loggers were calibrated in a waterbath at $5^{\circ}C$ intervals from $25^{\circ}C$ to $50^{\circ}C$ prior to implantation and again post recovery of the data. The package was coated in biologically inert wax (Elvax) and then sterilised in hibitane for 24 hours prior to implantation. Anaesthesia was induced by an intramuscular injection of Alfaxalone (initial injection of 5mg kg^{-1}) and gaseous isoflurane in oxygen (3-4% for induction and ca. 1.5 to 2% for maintenance). Local anaesthetic (lignocaine 1mg kg^{-1}, 20mg/ml and bupivocaine 1mg ml^{-1}, 5mg ml^{-1}) was administered subcutaneously at the surgical site. The transmitter and iButton were inserted into the peritoneal cavity while the transmitter's whip antenna was inserted into a pocket under the skin. Analgesia was provided in the form of a subcutaneous injection of Meloxicam (5mg ml^{-1}; 0.2mg kg^{-1}).

Body temperature characteristics

The temperatures obtained from each iButton were corrected with that individual iButton's calibration curve. I used a custom written VB program (Visual Basic V6; P.C. Withers), adapted from studies of endotherms (Cooper and Withers 2004, Cooper et al. 2008), to calculate body temperature (T_b) characteristics (daily mean, minimum and maximum T_b) for each snake over the 6 to 8 weeks of T_b logging (Figure 3). Cooling and warming rates were calculated from the slope of the regression of T_b over time during passive morning warming and afternoon cooling periods. The T_b at which basking commenced and the rate of warming due to basking (basking was identified by an inflection in the rate of T_b increase; Figure 3) were also calculated.

The degree of heterothermy for each individual snake was quantified as the amplitude of the daily body temperature rhythm, determined by fitting a cosinor function (Nelson and Lee 1979) to the T_b data from the entire logging period (October-November). The 24h mesor of the T_b rhythm was obtained from the same analysis and the daily minimum was calculated as the mesor minus the amplitude and daily maximum as mesor plus the amplitude after Maloney et al. (2017). Cosinor analyses were carried out with a custom-written excel spreadsheet (P.C. Withers and S.K. Maloney).

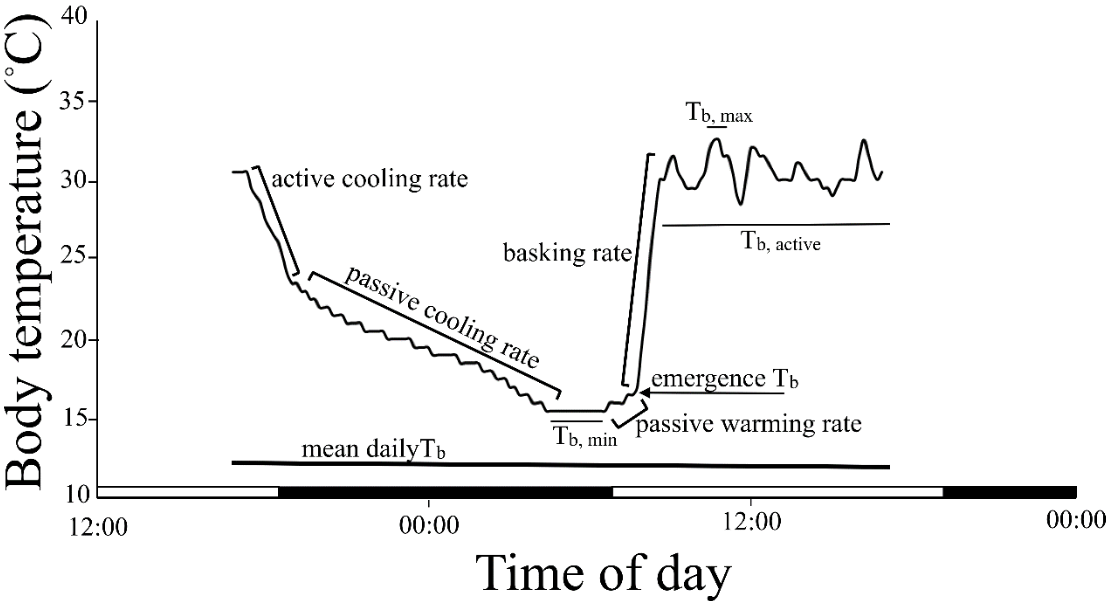

Figure 3 A typical 24h body temperature (T_b) profile of a western tiger snake (*Notechis scutatus occidentalis*) in an urban wetland, Perth, Western Australia, showing the periods used to calculate various T_b parameters. The dark bars indicate the period between sunset and sunrise.

Effectiveness of thermoregulation

Operative temperature models were deployed for 7-10 days each month during the period that T_b data were logged for live snakes (due to equipment failure T_e data were only collected in October at BS; Figure 4). This allowed comparison of indices of thermoregulation (see below) by relating T_b and T_e to the T_{set} the animal would try to achieve if the environment allowed. Six indices of thermoregulation were calculated for every 10min interval of each day. Thermoregulatory accuracy of snakes (*db*) was determined as the absolute mean of the deviations of T_b from T_{set} (Hertz et al. 1993, Jaramillo-Alba et al. 2020). Thermal quality of the habitat (*de*) was calculated as the mean of the deviations of T_e from T_{set}, but instead of calculating one absolute mean value (Hertz et al. 1993, Christian and Weavers 1996) I calculated a separate *de* for operative temperature models placed in exposed microhabitats where snakes were observed basking ($de_{exposed}$) and microhabitats used by snakes as shelter sites ($de_{shelter}$). To evaluate the effectiveness of thermoregulation I used the index proposed by Blouin-Demers and Weatherhead (2001) as the difference between *de* and *db* (*E*). Because I used two separate *de* values I calculated *E* in for both exposed ($E_{exposed}$) and sheltered ($E_{shelter}$) microhabitats.

Thermal exploitation

For each individual snake I calculated the proportion of time that *db*, $de_{exposed}$ and $de_{shelter}$ = 0 (i.e. were within the set-point range). I then calculated the proportion of time *db* = 0 during the time in which $de_{exposed}$ and $de_{shelter}$ = 0, to quantify how tiger snakes were exploiting optimal thermal conditions in both exposed and sheltered environments.

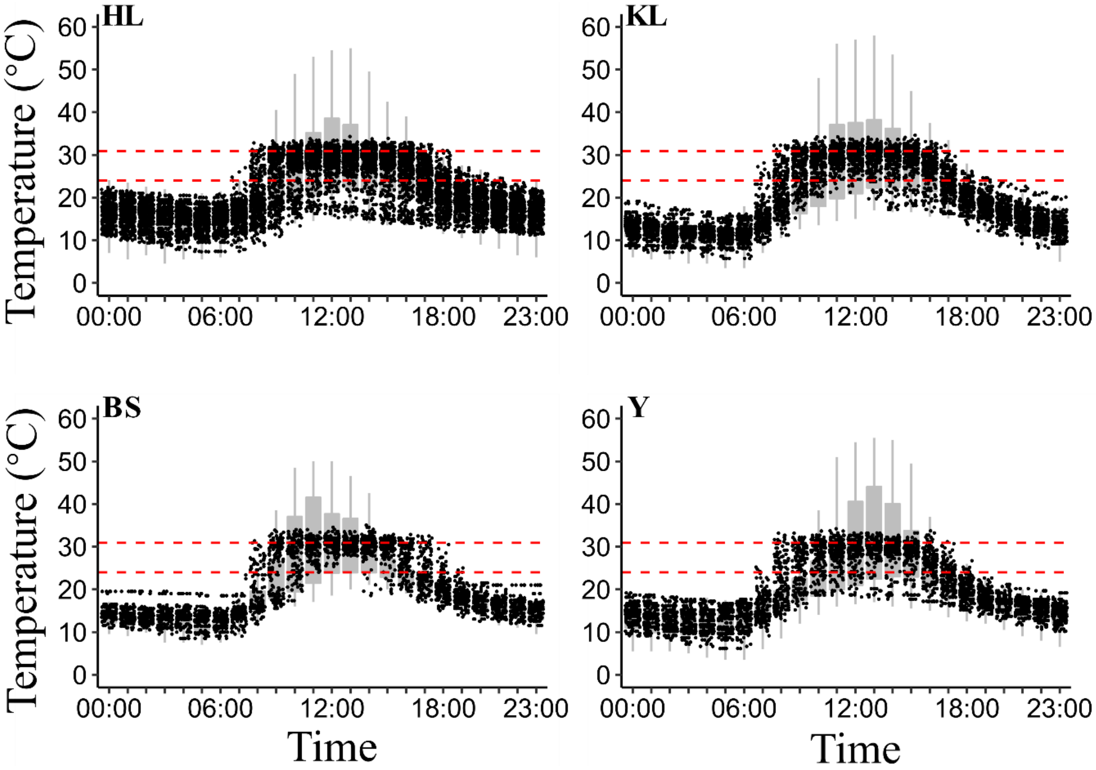

Figure 4 Distribution of environmental temperatures recorded in spring 2020 (grey bars indicate interquartile range of environmental temperatures and vertical grey lines indicate the minimum and maximum environmental temperatures) and snake body temperatures (points) for four wetlands in the Perth urban area, Western Australia (HL = Herdsman lake, KL = Kogolup Lake, BS = Black Swan Lake, Y= Yanchep National Park). Horizontal red lines indicates the set-point range. Number of individual snakes (N) = 3 at HL and KL, N = 4 at BS, N = 2 at Y. HL and KL are wetlands dominated by kikuyu grass while BS and Y are wetlands with native vegetation.

Statistical analyses

All analyses were conducted in R studio version 1.4.1103 (RStudio Team 2020). The lme4 package (Bates et al. 2014) was used for all linear mixed-effects models, for which the lsmeans package (Lenth 2018) was used to conduct post-hoc pairwise comparisons. Values are mean ± S.E. unless stated otherwise, with N = number of individuals and n = number of measurements.

Quantifying habitat structure

I used principal component analysis (PCA) to examine associations between the three habitat types dominated by kikuyu grass and their equivalent native habitat types based on measurements of the habitat characteristics. FactoMineR (Lê et al. 2008) and factoextra (Kassambara and Mundt 2020) packages were used to generate principal components (PCs) that designated each habitat variable with its importance to the PC. PCs with eigenvalues > 1 were considered useful for inference (Roznik and Reichling 2021). I then used an analysis of deviance to compare the PCs of the habitat types and to compare kikuyu grass with native vegetation, with post hoc pairwise comparisons to determine specific differences between habitat characteristics (Roznik and Reichling 2021).

Prey availability

I compared abundance of calling male frogs between lakes with kikuyu grass or native vegetation with linear mixed-mixed effects models. I used the frog count data as the dependent variable, plant community (kikuyu grass or native vegetation) as a fixed effect, and site and day as random factors.

For visual frog surveys I used generalised linear mixed-effects models with a negative binomial distribution to identify the best predictor variables of frog abundance. Predictor variables were first scaled and centred to improve model fitting, and correlated variables were removed to reduce multicollinearity (retaining variables with variance inflation factors < 5 and pairwise correlations < 0.7 using the usdm and psych packages (Naimi 2015, Revelle 2015, Lettoof et al. 2020c). For the total abundance of frogs the retained variables included plant community, habitat type, canopy cover, vegetation density, light availability, vegetation height, and woody vegetation as predictors. I then assessed the model fit with pseudo-R^2 values calculated with the glmmADMB package (Skaug et al. 2013). Model selection was then performed using the dredge function from the MuMIn package (Barton 2015) and all sub models were ranked according to Akaike's information criterion (AICc). All models with ΔAICc <2 were considered useful for inference. *Post-hoc* pairwise comparisons were used to examine differences in frogs visually observed between habitat types using the glht function from the multcomp package (Hothorn et al. 2016). I first ran these analyses with all frog species pooled to determine the habitat characteristics that best predicted the total abundance of frogs (e.g. total prey abundance) and then repeated the analysis for individual frog species separately. To improve model convergence I removed the least ecologically relevant predictors (Dormann et al. 2013). The final model for slender tree frogs included plant community, habitat type, canopy cover, light availability and vegetation density as predictor variables. The model for motorbike frogs included plant community, habitat type, canopy cover, vegetation density, vegetation height, ground cover, light availability, and woody vegetation as predictor variables. All models included site as a random effect.

Predation risk

I used a Student's t-test to investigate the difference in predation rate between snake models and control balls. As above, a model selection process using generalised linear mixed-effects models identified the most important predictor variables for predation risk on artificial snakes. However, this was run as a presence/absence binomial model of predator attacks. The model included plant community, habitat type, microhabitat, season, light availability and vegetation height as predictor variables and site as a random effect.

Thermal ecology

Operative model calibration

To ensure the copper operative temperature models accurately predicted tiger snake body temperature (T_b) I conducted a Pearson's correlation test on the T_b of tiger snake carcasses and the operative temperature (T_e) of the copper models. I then used linear mixed-effects models to compare the temperature characteristics of the snake carcasses and copper models using the various thermal characteristics as dependent variables, treatment (pipes or snake) as a fixed effect and ID (pipe number or carcass number) as a random factor to account for repeated measurements over time.

Seasonal thermal quality of habitat

Linear mixed-effects models were used to compare seasonal habitat temperature characteristics between vegetation types with the temperature characteristic as the dependent variable, vegetation type, habitat type and season as fixed effects, and site and day as random factors. Post-hoc pairwise comparisons were used to examine differences between habitat types

Daily patterns of Tb

The influence of plant community (kikuyu grass or native vegetation) on the T_b characteristics of tiger snakes was assessed using linear mixed-effects models. The various temperature characteristics were the dependent variable, plant community was a fixed effect and site, snake ID and day were random factors, to account for repeated measurements. Similar linear mixed-effects models were used to investigate the daily rhythm of tiger snake T_b between plant communities with the temperature characteristic as the dependent variable, but with site as the only random factor as there were no repeated individual snake or day data.

Effectiveness of thermoregulation

I compared the indices of thermoregulation for snakes inhabiting kikuyu grass and native vegetation with linear mixed-effects models, with the indices of thermoregulation as dependent variables, plant community and time of day (day or night; determined from sunrise and sunset using the NOAA ESRL Sunrise/Sunset Calculator web page https://gml.noaa.gov/grad/solcalc/sunrise.html) as fixed effects, and site, individual ID and day as random factors, followed by *post-hoc* pairwise comparisons. Similar linear mixed-effects models were used to compare thermal exploitation indices with vegetation type as a fixed effect and site as a random factor.

Results

Quantifying habitat structure

Three PCs were retained from the PCA analysis of habitat structure, collectively accounting for 73.7% of the total variance. PC1 explained 35.5% of the variance, with canopy cover and number of trees correlating positively and light availability correlating negatively with PC1. PC2 explained 23.8% of the variance with a negative correlation with canopy cover and positive correlations with ground cover and vegetation density. PC3 explained 14.4% of the variation, correlating positively with understory height (Table 1).

All three PCs differed significantly among habitat types ($F_{5,\ 234} \leq 149$, $P < 0.001$). For PC1, there was no significant difference between equivalent habitat types in native and introduced grass dominated communities (e.g. KO and NO; lsmeans *post-hoc* comparisons $P \geq 0.527$); while habitat types in the same plant community (e.g. KO vs KS) did differ (lsmeans *post-hoc* comparisons $P < 0.001$; Figure 5). For PC2 habitat types within kikuyu grass did not differ (lsmeans *post-hoc* comparisons $P \geq 0.918$) they did within native vegetation (lsmeans *post-hoc* comparisons $P \leq 0.007$) except for NO and NW (lsmeans *post-hoc* comparisons $P = 0.492$). All the habitats within kikuyu grass differed from those in native vegetation (lsmeans *post-hoc* comparisons $P < 0.001$). PC3 distinguished KS from all other habitat types (lsmeans *post-hoc* comparisons $P < 0.001$) and KW differed from all the native habitat types (lsmeans *post-hoc* comparisons $P \leq 0.018$; Figure 5). When comparing the overall structure between kikuyu grass and native vegetation in the second PCA, no structural differences were distinguished between kikuyu grass and native vegetation in PC1 and PC3 ($F_{1,\ 238} \leq 0.592$, $P \geq 0.442$). However, kikuyu grass differed significantly from native vegetation in PC2 ($F_{5,\ 238} = 495$, $P < 0.001$; Figure 5) with increased vegetation density and ground cover in kikuyu grass.

Table 1 Eigenvalues and loading values for the first three principal components (PC) (with eigenvalues >1) resulting fromprincipal components analysis of habitat characteristics in western tiger snake (*Notechis scutatus occidentalis*) habitats from four different wetlands, dominated by either invasive vegetation (Herdsman Lake and Kogolop Lake) or native vegetation (Black Swan Lake and Yanchep National Park) in the Perth region, Western Australia.

Eigenvalues and loading values			
	PC1	PC2	PC3
Eigenvalues	2.485	1.669	1.010
Variation explained (%)	35.503	23.843	14.429
Loading values			
Canopy cover (%)	0.893	-0.921	-0.164
Trees (#)	0.725	-0.061	-0.456
Woody vegetation (#)	0.577	-0.341	0.081
Ground cover (%)	0.110	0.865	0.004
Understory height (cm)	0.325	-0.295	0.830
Vegetation density (%)	0.185	0.811	0.243
Light availability (lux)	-0.821	-0.212	-0.140

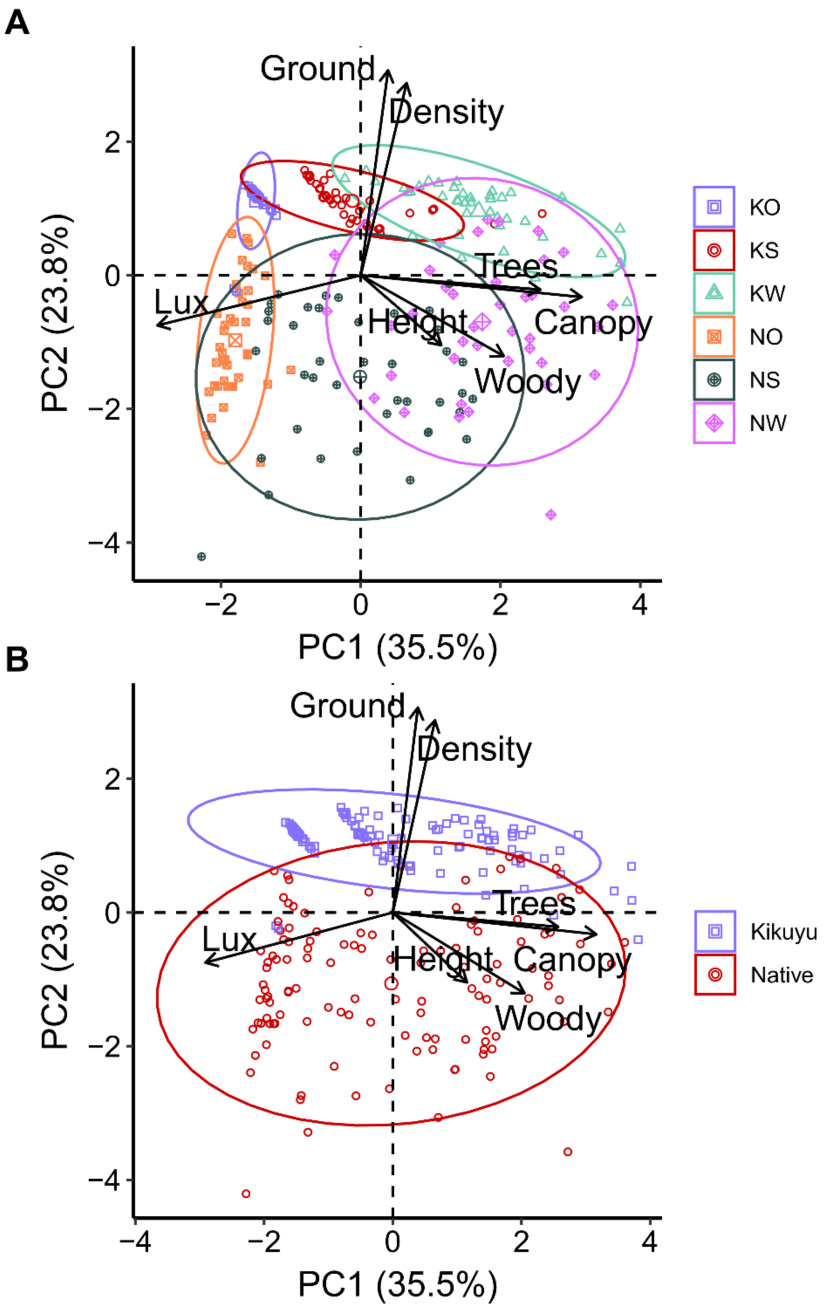

Figure 5 PCA ordination of habitat characteristics in western tiger snake (*Notechis scutatus occidentalis*) habitats from four different wetlands, dominated by either invasive vegetation (Herdsman Lake and Kogolop Lake) or native vegetation (Black Swan Lake and Yanchep National Park) in the Perth region, Western Australia. (A) ordination of the different habitat types within the wetlands KO, kikuyu open; KS, kikuyu sedge; KW, kikuyu woodland; NO, native open; NS, native sedge; NW native woodland and (B) the ordination of the habitat characteristics of the kikuyu grass and native vegetation plant communities. In both cased PC1 explains 35.5% and PC2 21% of the total variance. Arrows denote the influence of specified habitat characteristics and ellipses denote the groupings of the habitat types.

Prey availability

Aural surveys

Five frog species were recorded during the frog call surveys: rattling froglets (n = 354), squelching froglets (n = 2), banjo frogs (n = 73), slender tree frogs (n = 791), and motorbike frogs (n = 333). Only two individual squelching froglets were heard at KL so this species was excluded from the analysis.

Plant community (kikuyu grass or native vegetation) did not have a significant effect on the abundance of calling male slender tree frogs, banjo frogs, and rattling froglets, or on the collective abundance of all frogs combined ($F_{1,2} \leq 3.3$, $P \geq 0.209$), but it did significantly influence the abundance of calling motorbike frogs ($F_{1,2} = 36.8$, $P = 0.026$), with a greater abundance of motorbike frogs in kikuyu dominated sites (Figure 6). With the exception of motorbike frogs ($LRT_1 = 0.002$, $P = 0.959$) site significantly influenced the abundance of calling male frogs ($LRT_1 \leq 42.6$, $P < 0.001$) while day influenced the density of all frogs combined and slender tree frogs specifically ($LRT_1 \leq 7.23$, $P \leq 0.028$).

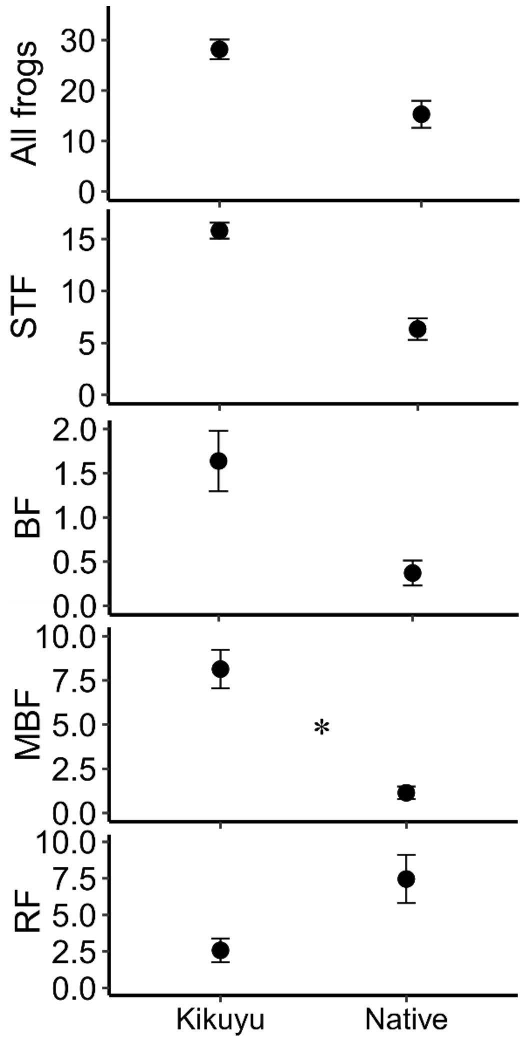

Figure 6 Calling male frog abundance in four wetlands in the Perth region, Western Australia dominated by kikuyu grass (Herdsman Lake and Kogolup Lake) or native vegetation (Black Swan Lake and Yanchep National Park) for all frog species combined, slender tree frogs (*Litoria adelaidensis;* STF), banjo frogs (*Limnodynastes dorsalis;* BF), motorbike frogs (*Litoria moorei;* MBF) and rattling froglets (*Crinia glauerti;* RF). * denotes a significant difference between vegetation types. Values are mean ± S.E.

Visual surveys

Four species were observed during visual surveys: rattling froglets (n = 2), slender tree frogs (n = 330), motorbike frogs (n = 343), and moaning frog (*Heleioporus eyrie*; n = 22). Only two individual rattling froglets were found at Y so rattling froglets were excluded from this analysis. Moaning frogs were included in the pooled analysis but there were insufficient individuals to evaluate their habitat preferences separately from the other species.

A single top model was produced for total frog abundance that identified the variables canopy cover, habitat type, vegetation height and light availability (lux) as significant contributors. Frogs were more abundant in areas with low canopy cover, higher understorey vegetation and increased lux (Table 2). Habitat type significantly influenced frog abundance with sedge and woodland habitats having greater frog abundance than open habitats. Plant community (kikuyu grass or native vegetation) was not a significant determinate of frog abundance.

Vegetation density, lux and habitat type were identified as important predictors for slender tree frogs, occurring in all of the top models. There was a greater abundance of slender tree frogs in habitats with increased vegetation density and light availability, while sedge and woodland habitats had a greater abundance of slender tree frogs than open habitats (Table 3). For motorbike frogs, vegetation density, canopy cover, vegetation height, and ground cover were identified as the most important predictors of abundance as they occurred in most of the top models. Motorbike frog abundance increased in habitats with greater canopy cover, ground cover and vegetation height, while motorbike frog abundance decreased in habitats with increased vegetation density (Table 4).

Table 2 Results of generalised linear mixed-effects models comparing the best predictor variables for one top model and the null model, identifying the strongest predictor variables of total frog abundance based on ΔAICc and weight in four wetlands in the Perth region, Western Australia. The estimate and standard error (estimate) and P-value are reported for each predictor variable. The variance of the random effect (R. E. Var), degrees of freedom (df), log-likelihood (logLik), Akaike's Information Criterion (AICc), difference in AICc between models (ΔAICc), and weight are reported for each model. *Post-hoc*/response indicate Tukey *post-hoc* tests for each categorical variable and whether frog abundance had a positive (+) or negative (-) response to the habitat characteristics. Significant p-values are in bold.

Terms		estimate	P-value	*Post-hoc*/ Response	R. E. Var	df	logLik	AICc	ΔAICc	weight
Global model: Frogs observed ~ Plant Community + Habitat + Canopy + Density + Lux + Height + Woody + (1|Site)										
Sub-model 1										
Canopy cover		-1.11 (0.39)	**0.006**	(-)	0.006	8	-174.7	368.6	0	0.12
Habitat	Sedge	2.92 (0.81)	**< 0.001**	Sedge < Open; Woodland < Open						
	Woodland	6.29 (1.66)								
Height		0.39 (0.09)	**< 0.001**	(+)						
Lux		1.81 (0.4)	**< 0.001**	(+)						
Null model										
NA		NA	NA	NA	NA	3	-182.4	371.3	2.69	0.03

Table 3 Results from generalised linear mixed-effects model indicating the best predictor variables for four top models and the null model identifying the strongest predictor variables of slender tree frog (STF; *Litoria adelaidensis*) abundance based on ΔAICc and weight in four wetlands in the Perth region, Western Australia. The estimate and standard error (estimate) and P-value are reported for each predictor variable. The variance of the random effect (R. E. Var), degrees of freedom (df), log-likelihood (logLik), Akaike's Information Criterion (AICc), difference in AICc between models (ΔAICc), and weight are reported for each model. *Post-hoc*/Response indicate Tukey *post-hoc* tests for each categorical variable and whether frog abundance had a positive (+) or negative (-) response to the habitat characteristics. Significant p-values are in bold.

Terms		estimate	P-value	*Post-hoc*/Response	R. E. Var	df	logLik	AICc	ΔAICc	weight
Global model: STF ~ Plant Community + Habitat + Canopy + Density + Lux + (1|Site)										
Sub-model 1										
Habitat	Sedge	4.67 (1.44)	**< 0.001**	Sedge < Open;	0.333	7	-132.3	281.18	0	0.27
	Woodland	6.22 (2.16)		Woodland < Open						
Density		0.91 (0.37)	**0.010**	(+)						
Lux		3.37 (0.96)	**0.001**	(+)						
Sub-model 2										
Plant community		1.1 (0.9)	0.232	NS	0.272	8	-131.6	282.4	1.22	0.14
Habitat	Sedge	4.03 (1.46)	**0.001**	Sedge < Open;						
	Woodland	5.29 (2.17)		Woodland < Open						
Density		1.06 (0.35)	**0.003**	(+)						
Lux		2.95 (0.97)	**0.004**	(+)						

Table 3 Continued

Terms		estimate	P-value	*Post-hoc*/Response	R. E. Var	df	logLik	AICc	ΔAICc	weight
Sub-model 3										
Plant community		1.61 (0.94)	0.094	NS	0.266	9	-130.1	282.4	1.29	0.14
Habitat	Sedge	6.51 (2.03)	< **0.001**	Sedge < Open;						
	Woodland	10.79 (3.85)		Woodland < Open						
Canopy		-1.33 (0.77)	0.090	NS						
Density		1.44 (0.41)	**0.001**	(+)						
Lux		4.1 (1.16)	**< 0.001**	(+)						
Sub-model 4										
Habitat	Sedge	6.5 (2.08)	< **0**	Sedge < Open;	0.407	8	-131.6	282.5	1.34	0.13
	Woodland	10.26 (3.97)	**.001**	Woodland < Open						
Canopy		-0.97 (0.8)	0.233	NS						
Density		1.21 (0.46)	**0.012**	(+)						
Lux		4.21 (1.19)	< **0.001**	(+)						
Null Model										
N/A		N/A	N/A	N/A	N/A	3	-141.8	290.0	8.91	0.00

Table 4 Results from generalised linear mixed-effects model indicating the best predictor variables for four top models and the null model identifying the strongest predictor variables of motorbike frog (MBF; *Litoria moorei*) abundance based on ΔAICc and weight in four wetlands in the Perth region, Western Australia. The estimate and standard error (estimate) and P-value are reported for each predictor variable. The variance of the random effect (R. E. Var), degrees of freedom (df), log-likelihood (logLik), Akaike's Information Criterion (AICc), difference in AICc between models (ΔAICc), and weight are reported for each model. *Post-hoc*/Response indicate Tukey *post-hoc* tests for each categorical variable and whether frog abundance had a positive (+) or negative (-) response to the habitat characteristics. Significant p-values are in bold.

Terms	estimate	P-value	*Post-hoc*/ Response	R. E. Var	df	logLik	AICc	ΔAICc	weight
Global model: MBF ~ Plant Community + Habitat + Canopy + Density + Height + Ground + Lux + Woody + (1|Site)									
Sub-model 1									
Canopy	0.3 (0.09)	**0.003**	(+)	0.281	7	-145.7	307.9	0	0.10
Density	-0.91 (0.2)	< **0.001**	(-)						
Ground	0.83 (0.24)	**0.001**	(+)						
Height	0.34 (0.12)	**0.009**	(+)						
Sub-model 2									
Canopy	0.43 (0.15)	**0.006**	(+)	0.323	8	-145.1	309.5	1.53	0.04
Density	-0.98 (0.2)	< **0.001**	(-)						
Ground	0.9 (0.26)	**0.001**	(+)						
Height	0.45 (0.15)	**0.006**	(+)						
Woody	-0.2 (0.18)	0.268	NS						
Sub-model 3									
Density	-0.67 (0.17)	< **0.001**	(-)	0.208	6	-147.8	309.5	1.59	0.04
Ground	0.44 (0.23)	0.070	NS						
Lux	-0.4 (0.11)	**0.001**	(-)						

Table 4 Continued

Terms	estimate	P-value	*Post-hoc*/ Response	R. E. Var	df	logLik	AICc	ΔAICc	weight
Sub-model 4									
Plant Community	-2.13 (0.74)	**0.006**	Kikuyu < Native	0.308	7	-146.7	309.9	1.92	0.03
Canopy	0.38 (0.1)	**< 0.001**	(+)						
Density	-1.19 (0.25)	**< 0.001**	(-)						
Height	0.44 (0.14)	**0.003**	(+)						
Null Model									
N/A	N/A	N/A	N/A	N/A	3	-157.2	320.9	13.0	0.00

Predation risk

Of 1200 artificial snakes and control balls respectively, 57 predation attempts were recorded for artificial snakes, while only 17 were recorded for control balls. Hence, artificial snakes were significantly more likely to be predated than control balls (t_{958} = 3.98, P <0.001). The top models identified habitat type, season, and light availability as the best predictors of predation for artificial snakes. Predation risk was higher in sedge habitats (n = 29) than woodland habitats (n = 9), more attacks occurred in autumn (n = 42) than in spring (n = 15), and predation risk increased with increasing light availability (Table 5).

Table 5 Results from generalised linear mixed-effects model indicating the best predictor variables for five top models and the null model identifying the strongest predictor variables of predation risk on artificial snakes based on ΔAICc and weight in four wetlands in the Perth region, Western Australia,. The estimate and standard error (estimate) and P-value are reported for each predictor variable. The variance of the random effect (R. E. Var), degrees of freedom (df), log-likelihood (logLik), Akaike's Information Criterion (AICc), difference in AICc between models (ΔAICc), and weight are reported for each model. Post-hoc/Response indicate Tukey post-hoc tests for each categorical variable and whether frog abundance had a positive (+) or negative (-) response to the habitat characteristics. Significant p-values are in bold

Terms		estimate	P-value	Post-hoc/Response	R. E. Var	df	logLik	AICc	ΔAICc	weight
Global model: Attacks ~ Plant community + Habitat type + Microhabitat + Season + Light availability + Vegetation Height + (1|Site)										
Sub-model 1										
Habitat	Sedge	0.61 (0.39)	**0.037**	Sedge < Woodland	0.064	6	-140.5	293.2	0	0.15
	Woodland	-0.42 (0.5)								
Lux		0.36 (0.17)	**0.039**	(+)						
Season		-1.1 (0.34)	**0.001**	Autumn < Spring						
Sub-model 2										
Plant community		-0.69 (0.51)	0.180	NS	0.035	7	-139.7	293.7	0.55	0.11
Habitat	Sedge	0.64 (0.39)	**0.036**	Sedge < Woodland						
	Woodland	-0.4 (0.51)								
Lux		0.38 (0.17)	**0.032**	(+)						
Season		-0.98 (0.29)	**0.001**	Autumn < Spring						
Sub-model 3										
Habitat	Sedge	0.8 (0.46)	**0.031**	Sedge < Woodland	0.071	7	-140.2	294.6	1.45	0.07
	Woodland	-0.17 (0.6)								
Lux		0.59 (0.35)	0.090	NS						
Microhabitat		0.5 (0.64)	0.437	NS						
Season		-1.1 (0.34)	**0.001**	Autumn < Spring						
Sub-model 4										
Habitat	Sedge	0.74 (0.44)	**0.034**	Sedge < Woodland	0.061	7	-140.3	294.8	1.65	0.06

Table 5 Continued

Terms		estimate	P-value	Post-hoc/Response	R. E. Var	df	logLik	AICc	ΔAICc	weight
Sub-model 3										
Habitat	Sedge	0.8 (0.46)	**0.031**	Sedge < Woodland	0.071	7	-140.2	294.6	1.45	0.07
	Woodland	-0.17 (0.6)								
Lux		0.59 (0.35)	0.090	NS						
Microhabitat		0.5 (0.64)	0.437	NS						
Season		-1.1 (0.34)	**0.001**	Autumn < Spring						
Sub-model 4										
Habitat	Sedge	0.74 (0.44)	**0.034**	Sedge < Woodland	0.061	7	-140.3	294.8	1.65	0.06
	Woodland	-0.37 (0.51)								
Lux		0.35 (0.17)	**0.042**	(+)						
Season		-1.1 (0.34)	**0.001**	Autumn < Spring						
Vegetation height		-0.12 (0.19)	0.526	NS						
Sub-model 5										
Plant Community		-0.78 (0.53)	0.169	NS	0.038	8	-139.3	294.9	1.74	0.06
Habitat	Sedge	0.87 (0.47)	**0.034**	Sedge < Woodland						
	Woodland	-0.09 (0.6)								
Lux		0.67 (0.35)	0.066	NS						
Microhabitat		0.61 (0.65)	0.361	NS						
Season		-1.1 (0.34)	**0.001**	Autumn < Spring						
Null model										
N/A		N/A	N/A	N/A		2	-152.1	308.3	15.1	0.00

Thermal ecology

Operative model calibration

Carcass temperatures were highly correlated with that of the copper models (Pearson's correlation: t_{1149} = 88.2, P < 0.001, slope = 0.90, R^2=0.93). Further, the mean, minimum, and maximum temperatures, and the warming and cooling slopes were not significantly different between operative models and snake carcasses ($F_{1,6} \leq$ 1.309, P ≥ 0.296; Figure 7).

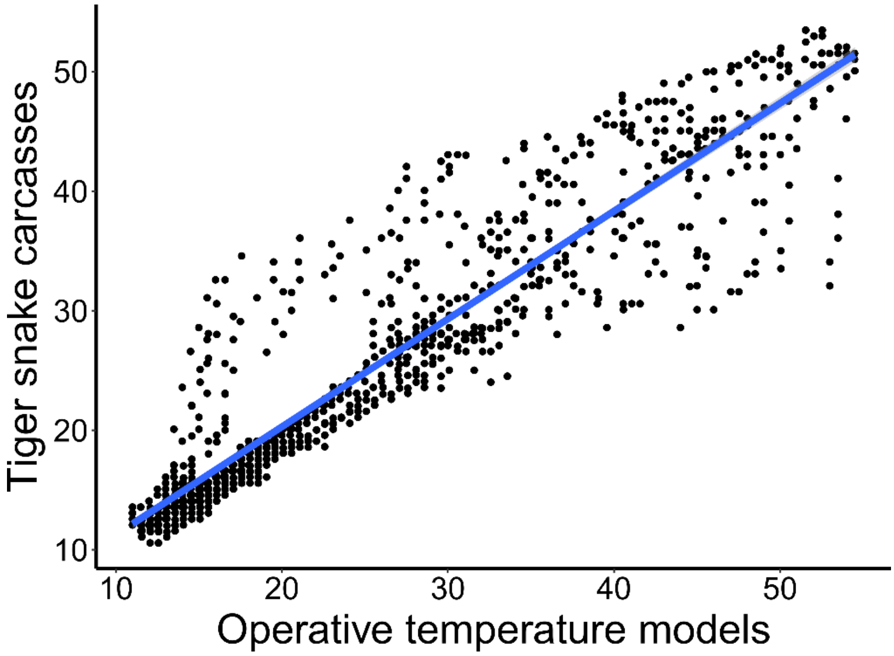

Figure 7 correlation of temperatures between tiger snake (*Notechis scutatus occidentalis*) carcasses and copper pipe operative temperature models. Pearson's correlation: t_{1149} = 88.2, P < 0.001, slope = 0.90, R^2=0.93.

Seasonal thermal quality of habitat

The maximum deviation (*de*) of operative temperatures (T_e) from the set-point range (T_{set}) was highly correlated with all variables ($R \geq 0.90$) except $T_{e,max}$ ($R = 0.68$) and de_0 ($R = 0.43$). However due to a lack of variance causing model convergence issues in $T_{e,max}$ and as it was approaching the correlation threshold ($R = 0.70$) only de_{max}, and de_0 were investigated individually. Plant community did not significantly influence de_{max}, or de_0 ($F_{1,\,2} \leq 0.05$, $P \geq 0.837$). Habitat type significantly influenced de_{max} ($F_{2,\,990} = 31.9$, $P < 0.001$) but not de_0 ($F_{2,\,990} = 1.69$, $P = 0.184$); de_{max} differed significantly between all habitats (lsmeans *post-hoc* comparisons $P \leq 0.002$) with the highest de_{max} in the open habitats and the lowest de_{max} in woodland habitats. Season significantly influenced de_{max} and de_0 ($F_{3,\,992} \leq 258$, $P < 0.001$). Autumn and spring did not differ significantly with respect to both variables (lsmeans *post-hoc* comparisons $P \geq 0.083$) but the remaining comparisons between seasons were all significant (lsmeans *post-hoc* comparisons $P \leq 0.033$), with greater de_0 and lower de_{max} in summer and the highest de_{max} in winter where the lower bound of T_{set} was rarely attained (Table 6). There was a significant interaction effect between plant community and habitat type for de_{max} and de_0 ($F_{2,\,990} \leq 5.28$, $P \leq 0.007$).The lsmeans *post-hoc* tests indicated that open habitats had higher de_{max} than woodland habitats, but there were no differences between the same habitat types in different plant communities (Figure 8A). There was also a significant interaction for de_0 between plant community, habitat, and season ($F_{6,\,990} \leq 3.04$, $P \leq 0.038$). The highest de_0 occurred in KW in summer while de_0 was quite similar in the remaining habitats year round except for winter where de_0 was never attained in any of the habitat types (Figure 8B). Site significantly influenced de_{max}, and de_0 ($LST_1 \geq 10.2$, $P \leq 0.001$) but day did not influence either variable ($LST_1 \geq 0.008$, $P \geq 0.248$).

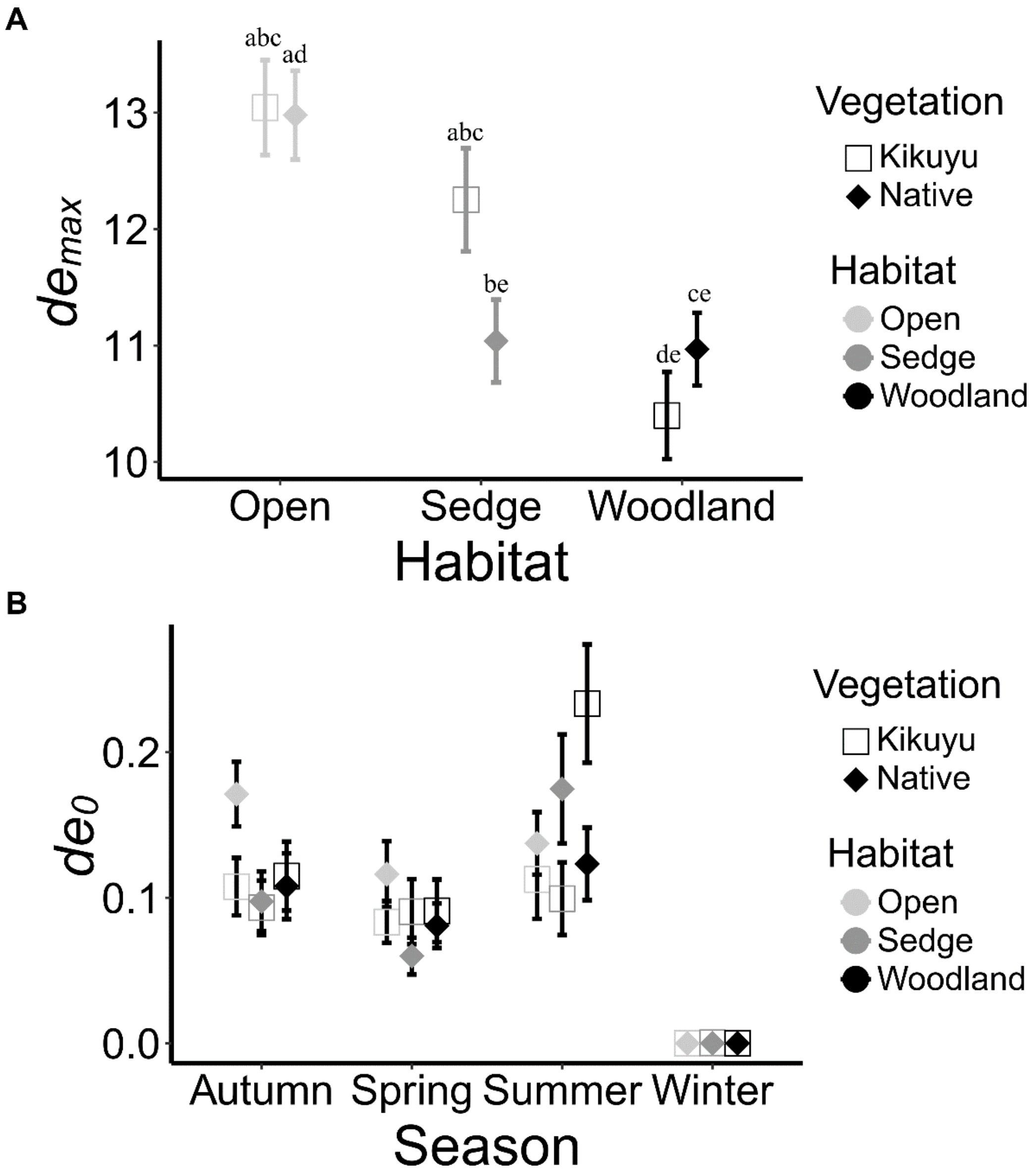

Figure 8 (A) mean (± SE) maximum deviation of environmental temperature (de_{max}) in sheltered microhabitats in three habitat types at sites dominated by kikuyu grass and native vegetation; different letters indicate significant differences (B), proportion of time the environmental temperature in sheltered microhabitats fell within the body temperature set-point range (de_0) for western tiger snakes (*Notechis scutatus occidentalis*) in three habitat types at sites dominated by kikuyu grass or native vegetation over four seasons.

Table 6 Mean ± SE maximum and minimum operative temperatures (T_e) for western tiger snakes (*Notechis scutatus occidentalis*) in each habitat type at sites dominated by kikuyu grass (Herdsman Lake and Kogolup Lake) or native vegetation (Black Swan Lake and Yanchep National Park) over four seasons in the Perth region, Western Australia. Mean ± SE, maximum and the proportion of time the operative temperatures did not deviate from the set-point range (*de* = 0) of tiger snakes in each habitat type in both kikuyu grass and native plant communities (Plant. Com) across four seasons.

Season	Plant. Com	Habitat	T_e			*de*		
			mean	max	min	mean	max	%=0
Spring								
	Kikuyu	Open	16.2 ± 0.36	33.8	4.0	7.9 ± 0.53	20.0	8.3
		Sedge	17.0 ± 0.41	29.0	6.0	7.1 ± 0.66	17.9	9.0
		Woodland	18.1 ± 0.42	32.0	8.5	6.1 ± 0.75	15.4	9.1
	Native	Open	16.8 ± 0.37	34.0	6.0	7.5 ± 0.73	17.9	11.6
		Sedge	17.2 ± 0.31	32.0	4.5	6.8 ± 0.55	19.4	5.9
		Woodland	17.1 ± 0.39	36.8	8.5	7.1 ± 0.88	15.4	8.0
Summer								
	Kikuyu	Open	23.6 ± 0.51	38.5	10.3	3.2 ± 0.84	13.6	11.2
		Sedge	23.3 ± 0.48	37.5	7.5	3.2 ± 0.71	16.4	9.9
		Woodland	22.8 ± 0.48	38.0	11.5	2.7 ± 0.7	12.4	23.3
	Native	Open	23.0 ± 0.42	42.0	7.4	3.2 ± 0.79	16.5	13.7
		Sedge	21.8 ± 0.34	35.2	6.7	2.6 ± 0.62	14.7	17.4
		Woodland	22.5 ± 0.44	38.5	8.5	3 ± 0.75	14.4	12.3
Autumn								
	Kikuyu	Open	16.9 ± 0.71	34.5	0.0	7.2 ± 0.78	25.9	10.7
		Sedge	16.6 ± 0.79	33.5	0.5	7.5 ± 0.89	25.4	9.3
		Woodland	18.4 ± 0.81	36.8	1.3	6.3 ± 0.96	22.6	11.4
	Native	Open	17.3 ± 0.67	34.0	1.0	7.1 ± 0.71	22.9	17.1
		Sedge	17.3 ± 0.66	32.5	4.0	6.9 ± 0.85	19.9	9.7
		Woodland	18.2 ± 0.74	38.4	5.0	6.4 ± 1.07	18.9	10.7
Winter								
	Kikuyu	Open	11.0 ± 0.37	22.0	0.0	12.9 ± 0.33	24.0	0.0
		Sedge	11.4 ± 0.37	24.5	0.0	12.5 ± 0.4	23.9	0.0
		Woodland	12.7 ± 0.35	23.0	3.0	11.2 ± 0.41	20.9	0.0
	Native	Open	12.1 ± 0.34	23.5	1.5	11.8 ± 0.5	22.4	0.0
		Sedge	12.6 ± 0.31	22.0	3.0	11.3 ± 0.42	20.9	0.0
		Woodland	12.4 ± 0.32	19.0	3.5	11.5 ± 0.28	20.4	0.0

Patterns of body temperature

The plant community in which tiger snakes resided had no significant effect on their mean daily T_b parameters ($F_{1,\ 1.6\text{-}1.9} \leq 10.3$, $P \geq 0.111$; Table 7). Plant community also did not significantly influence mean passive or active warming or cooling rates of tiger snakes ($F_{1,\ 1.6\text{-}1.9} \leq 2.50$, $P \geq 0.281$; Table 7). With the exception of $T_{b,min}$ and the passive cooling rate ($LRT_1 \geq 5.27$, $P \leq 0.021$) which ranged from 10.2 ± 0.19°C at KL to 14.0 ± 0.17°C at HL and 0.67 ± 0.09°C h^{-1} at HL to 1.28 ± 0.06°C h^{-1} at KL, respectively; site did not significantly influence mean daily T_b parameters ($LST_1 \geq 0.92$, $P \geq 0.338$); while the random effect of snake ID influenced all T_b parameters ($LRT_1 \geq 5.06$, $P \leq 0.024$) except $T_{b,max}$ and passive cooling rate ($LRT_1 \geq 0.38$, $P \geq 0.162$). Day also influenced all T_b parameters ($LRT_1 \geq 4.07$, $P \leq 0.043$) besides active cooling rate and passive warming rate ($LRT_1 \geq 0.37$, $P \geq 0.537$). Plant community had no effect on any of the variables (amplitude, acrophase, mesor, r^2, daily minimum or maximum) describing the the daily cycle of tiger snake T_b ($F_{1,\ 1.6\text{-}1.9} \leq 2.31$, $P \geq 0.279$; Table 7), although site did significantly influence amplitude, daily minimum and maximum of the daily T_b rhythm ($LRT_1 \geq 4.66$, $P \leq 0.036$).

Table 7 Mean ± SE maximum and minimum of the daily patterns of body temperature and daily body temperature rhythm for twelve free-living western tiger snakes (*Notechis scutatus occidentalis*) from four wetlands dominated by either kikuyu grass (Herdsman Lake and Kogolup Lake) or native vegetation (Black Swan Lake and Yanchep National Park) in the Perth region, Western Australia.

	Kikuyu grass	Native vegetation
Daily patterns		
$T_{b,active}$ (˚C)	28.9 ± 0.11 (n = 282)	29.3 ± 0.08 (n = 282)
$T_{b,emergence}$ (˚C)	16.2 ± 0.18 (n = 255)	16.2 ± 0.16 (n = 241)
$T_{b,max}$ (˚C)	31.8 ± 0.17 (n = 310)	32.3 ± 0.15 (n = 307)
Highest $T_{b,max}$ (˚C)	35.7	36.2
$T_{b, min}$ (˚C)	12.2 ± 0.16 (n = 310)	13.1 ± 0.13 (n = 307)
Lowest $T_{b,min}$ (˚C)	2.6	6.1
Mean daily T_b (˚C)	20.1 ± 0.12 (n = 310)	20.6 ± 0.10 (n = 307)
Active cooling rate (˚C h^{-1})	6.3 ± 0.24 (n = 208)	6.9 ± 0.24 (n = 191)
Basking rate (˚C h^{-1})	12.7 ± 0.36 (n = 256)	14.1 ± 0.36 (n = 243)
Passive cooling rate (˚C h^{-1})	0.9 ± 0.05 (n = 265)	0.8 ± 0.02 (n = 270)
Passive warming rate (˚C h^{-1})	1.7 ± 0.06 (n = 244)	1.9 ± 0.08 (n = 218)
Daily rhythm	(N = 6)	(N = 6)
Amplitude (˚C)	16.6 ± 0.83	15.6 ± 0.50
Acrophase	13:48:29	13:47:03
Mesor (˚C)	19.9 ± 0.47	20.6 ± 0.43
Maximum (˚C)	36.1 ± 0.62	36.3 ± 0.20
Minimum (˚C)	3.8 ± 1.20	4.9 ± 0.92
r^2	0.9 ± 0.00	0.9 ± 0.00

Effectiveness of thermoregulation and exploitation

Plant community did not influence the amount of time tiger snake T_b was within T_{set} (db_0), the amount of time $de_{exposed}$ and $de_{shelter}$ were within T_{set} (equal to zero), or the amount of time tiger snakes exploited the available T_{set} in $de_{exposed}$ ($EX_{exposed}$) and $de_{shelter}$ ($EX_{shelter}$: $F_{1,\ 0.3} \leq 6.025$, $P \geq 0.494$; Table 8). Site did not influence any of the exploitation indices ($P \geq 0.618$). Plant community did not significantly influence db, $de_{exposed}$, $de_{shelter}$, $E_{exposed}$, or $E_{shelter}$ ($\chi^2_1 \geq 0.002$, $P \geq 0.098$) but these same variables were significantly influenced by night and day ($\chi^2_1 \geq 311$ $P < 0.001$). The interaction between plant community and time of day was significant for db, $de_{exposed}$, $de_{shelter}$ and $E_{shelter}$ ($\chi^2_1 \geq 19.1$, $P < 0.001$) but not $E_{exposed}$ ($\chi^2_1 = 0.130$, $P=0.718$). Tiger snake db was lower during the day (db_{day}) when $de_{exposed}$ and $de_{shelter}$ provided more favourable thermal environments (Table 8). This was reflected by tiger snakes thermoregulating more effectively during the day, with higher E values during the day ($E_{exposed.day}$; $E_{shelter.day}$) compared to at night (lsmeans *post-hoc* comparisons $P < 0.001$; Table 8). Site significantly influenced $de_{exposed}$ *and* $de_{shelter}$ ($LRT_1 \geq 16.8$, $P < 0.001$) ranging from 6.6 ± 0.04 at HL to 8.3 ± 0.08 at Y and from 5.5 ± 0.03 at HL to 7.1 ± 0.05 at KL, respectively. Snake ID significantly influenced db, $de_{shelter}$, $E_{exposed}$, and $E_{shelter}$ ($LRT_1 \geq 12.8$, $P < 0.001$).

Table 8 Proportion of time spent within set-point range for body temperature (db_0), operative environmental temperature in exposed microhabitats ($de_{exposed,\ 0}$) and sheltered microhabitats ($de_{shelter,\ 0}$) and the snake's thermal exploitation of exposed ($EX_{exposed}$) and sheltered microhabitats ($EX_{shelter}$) i.e. both *db* and *de* were within the set-point range at the same time for western tiger snakes (*Notechis scutatus occidentalis*), along with accuracy of body temperature (*db*), thermal quality of exposed ($de_{exposed}$) and sheltered microhabitats ($de_{shelter}$), and the effectiveness of tiger snake thermoregulation (*E*) in these microhabitats during the day and night. Values are mean ± S.E.

	Kikuyu grass	Native vegetation
Exploitation		
db_0	0.4 ± 0.01 (n=3780)	0.4 ± 0.02 (n = 1726)
$de_{exposed,\ 0}$	0.2 ± 0.01 (n=1996)	0.2 ± 0.01 (n = 812)
$de_{shelter,\ 0}$	0.2 ± 0.02 (n=1688)	0.2 ± 0.02 (n = 832)
$EX_{exposed}$	0.5 ± 0.02 (n=1190)	0.6 ± 0.03 (n = 559)
$EX_{shelter}$	0.3 ± 0.03 (n=1205)	0.4 ± 0.05 (n = 588)
Thermoregulation	(n = 8649)	(n = 3358)
db_{day}	3.2 ± 0.04	3.1 ± 0.06
db_{night}	8.3 ± 0.04	9.0 ± 0.04
$de_{exposed.day}$	5.2 ± 0.05	5.9 ± 0.08
$de_{exposed.night}$	9.5 ± 0.04	10.8 ± 0.05
$de_{shelter.day}$	4.6 ± 0.04	4.3 ± 0.06
$de_{shelter.night}$	8.0 ± 0.04	8.6 ± 0.04
$E_{exposed.day}$	2.0 ± 0.05	2.7 ± 0.07
$E_{exposed.night}$	1.2 ± 0.02	1.8 ± 0.03
$E_{shelter.day}$	1.4 ± 0.02	1.1 ± 0.03
$E_{shelter.night}$	-0.3 ± 0.01	-0.3 ± 0.02

Discussion

I investigated a suite of habitat quality factors to determine whether an invasive species, kikuyu grass, provides tiger snakes with suitable habitat as an alternative to native vegetation that has been outcompeted in urban wetlands. My results indicate that the quality of available tiger snake habitat appears equivalent in the wetlands studied irrespective of the dominant vegetation type. Even though, habitat compositional heterogeneity at sites with kikuyu grass has been reduced with a reduction in bare ground and increase in vegetation density; the transition from native vegetation to invasive grass has had little effect on prey availability, predation risk for juvenile snakes, thermal properties of the vegetation or thermoregulatory efficiency and daily T_b patterns of tiger snakes. Thus, my hypotheses that kikuyu grass offers tiger snakes with an improved habitat quality and that therefore tiger snakes have modified how they thermoregulate in these environments were not supported. However, it is still possible that the high quality of habitat provided by kikuyu grass aids the persistence of tiger snakes restricted to degraded and contaminated urban wetlands.

Habitat structure

Kikuyu grass grows in a dense matrix of stems which facilitates its colonisation of ground cover and often results in native plant communities transformed into a monoculture (Gonzalez 2009, Bradshaw et al. 2013). Consequently, increased vegetation density and ground cover were the two habitat structural features that most differentiated between sites with kikuyu grass and native vegetation. Interplant distance is often much lower for exotic grasses compared to native grasses, which reduces the amount of bare ground and plant diversity, resulting in reduced environmental heterogeneity (Litt and Steidl 2011, Lindsay and Cunningham 2012, Abom et al. 2015). Species richness and abundance of small reptiles is negatively affected by invasive vegetation (Valentine et al. 2007, Hacking et al. 2014) but the Eastern brown snake (*Pseudonaja textilis*), another large elapid, was more abundant in the dense habitat structure provided by grader grass (*Themeda quadrivalvis*) than in native vegetation (Abom et al. 2015). Abom et al. (2015) also reported that the thermal quality of the shelter sites within grader grass did not differ from shelter sites within the native vegetation, similar to my findings for kikuyu grass (see below). Therefore, despite a reduction in compositional heterogeneity that has occurred in Perth wetlands where kikuyu grass has outcompeted native plants, many structural and thermal components remain comparable between wetlands with kikuyu grass and native vegetation.

Prey availability

I found almost no difference in overall frog abundance between wetlands dominated by kikuyu grass or native vegetation, despite different species of frogs favouring different habitat characteristics. Frog populations can be influenced by changes in wetland vegetation (Scheffers and Paszkowski 2013) with some species being negatively affected by invasive plants (Maerz et al. 2005b) while others adapt to living in the complex habitat structure they provide (Bower et al. 2006). The tree frogs (slender tree frogs and motorbike frogs; Hylidae) are arboreal and more reliant on emergent vegetation than the other ground-dwelling frog species recorded (Limnodynastidae; Bush et al. 2010, Cogger 2014). The abundance of these ground-dwelling frogs could be more dependent on factors other than the vegetation composition in the specific habitats I sampled. Since frog abundance was unaffected by the proliferation of kikuyu grass in the urban sites it is unlikely that tiger snakes, whose diet is dominated by frogs (Lettoof et al. 2020c), have experienced a reduction in prey availability associated with a spread of kikuyu grass.

Calling male motorbike frogs were more abundant in wetlands where kikuyu grass was the dominant vegetation but visual surveys at the same study sites found no difference in the abundance of this species. It is therefore possible that this species was equally abundant at all wetlands but the proportion of calling males differed. Even during a large chorus, non-calling satellite male frogs are often present (Driscoll 1998, Goldingay et al. 1999). Alternatively, it is possible that due to the complex, dense structure created by kikuyu grass there was a detectability issue and I was unable to observe all frogs sheltering within the vegetation (Heard et al. 2008, Vences et al. 2008). This is one reason why it is important to use more than one survey technique to monitor frog populations (Crouch and Paton 2002, Kendell 2002, Brown et al. 2007).

Slender tree frogs and motorbike frogs accounted for the majority of frogs I observed during visual searches. Both of these species are associated with permanent water bodies and emergent vegetation (Bush et al. 2010, Cogger 2014) and, because they perch on the vegetation within the habitat types surveyed, they were easiest to detect. Meanwhile, rattling froglets were infrequently observed during the visual searches because they are small (20-24mm) and mainly inhabit saturated vegetation on the water's edge (Cogger 2014, Hoskin et al. 2015). Similarly banjo frogs, although much larger than rattling froglets, were restricted to the water's edge because they deposit their egg masses on floating vegetation (Hoskin et al. 2015) which is why I never detected them during the visual surveys. Finally, I only observed moaning frogs at some of my sites and could not determine their preferred habitat characteristics based on the habitat types sampled. I suspect this is due to the breeding behaviour of moaning frogs which, unlike the other, lacustrine breeding frogs (Reynolds 2009), deposit their eggs in sandy burrows in the vicinity of swamps (Cogger 2014).

I could determine which habitat characteristics most influenced frog abundance overall, which were a high degree of light availability and vegetation height, corresponding to the sedge habitats. Slender tree frogs and motorbike frogs make the most use of emergent vegetation and are likely to be most affected by changes in wetland vegetation (Webb and Joss 1997; Scheffers and Paszkowski 2013). These species had opposing preferences for vegetation density, with slender tree frog abundance increasing with increased vegetation density while motorbike frog abundance decreased in these habitats. Slender tree frogs and motorbike frogs were the most frequently observed species perching on the vegetation where tiger snakes were most often observed (pers. obs) so it is no surprise that these two species, especially motorbike frogs, make up the majority of tiger snake diet in this region (Lettoof, unpublished data).

Predation risk

Changes to habitat structure can influence the predation risk for reptiles by altering the quality of refuge sites or structural features predators use to hunt (Hawlena et al. 2010, Martin and Murray 2011, Steidl et al. 2013). There was no evidence of differences in predation risk for juvenile tiger snakes in wetlands dominated by kikuyu grass compared with those in native vegetation indicating a change in vegetation composition and habitat structure has not made juvenile snakes more vulnerable to predators. However, I did find a seasonal effect on predation risk and that artificial snakes placed in woodland habitats were predated on the least.

While only 4.75% of 1200 artificial snakes were predated this is comparable to the predation rates (7.44%) observed for artificial juvenile broad headed snakes (*Hoplocephalus bungaroides*; Webb and Whiting 2006) and uropeltid snakes (5%; Cyriac and Kodandaramaiah 2019) with similar sample sizes. The low number of predation events could be due to methodological limitations such as using static brown models instead of brightly-coloured (Worthington-Hill and Gill 2019, Herr et al. 2020) or dynamic models (Cain and Cross 2019). In any case, the depredated artificial snakes showed obvious signs that the predators treated them as live snakes with strikes aimed primarily at the head and tail (Webb and Whiting 2006) and on several occasions I found models that had been grabbed by the tail by an avian predator and flipped over with peck marks on the ventral surface. Nevertheless, predation of juvenile tiger snakes might be a rare occurrence and the predation rate observed could be an overestimate as static artificial snakes do not retreat into vegetation when approached by a predator and live juvenile snakes spend limited time basking (Webb and Whiting 2005).

Despite the difference in vegetation density and bare ground between sites with kikuyu grass or native vegetation my results suggest that this change in habitat structure has not influenced the predation risk for juvenile tiger snakes (Ferreira and Faria 2021). This is contrary to the findings of similar studies where invasive vegetation either increased predation risk, e.g. liolaemid sand lizards (*Liolaemus wiegmannii* and *L. multimaculatus*; Stellatelli et al. 2015) or decreased predation risk, e.g. rainbow skinks (*Carlia schmeltzii*; Hacking et al. 2014), although in the latter example it was suggested that the structural and thermal characteristics of grader grass caused the skinks to avoid these habitats. My results suggest that predation risk was more dependent on the openness of habitat structure rather than whether the vegetation comprised kikuyu grass or native vegetation. Artificial snakes placed in woodland habitats had the lowest predation rates while predation risk was greater in habitats with increased light availability i.e. more open environments. The artificial snakes are probably more conspicuous to visual predators in habitats that have reduced structural complexity (Daly et al. 2008, Sato et al. 2014). This is consistent with other studies that found predator diversity was greater along habitat edges (Anderson and Burgin 2008). Birds for example use elevated perches along habitat edges to forage in open environments (Hansen et al. 2019) or in otherwise homogenous habitats (Hawlena et al. 2010).

I also recorded a higher predation risk for artificial snakes in autumn than in spring. This coincides with the seasonal parturition of tiger snakes at the end of summer and in autumn (Shine 1977, Cornelis and Lettoof 2020). A common hypothesis for why Australian snakes reproduce seasonally is that the emergence of more neonates dilutes the predation risk for individual snakes even if predators converge on habitats with increased availability of juvenile snakes (predator-swamping; Arnold and Wassersug 1978, Delm 1990, Spencer et al. 2001) but has not previously found much support (Brown and Shine 2006). Furthermore, Nordberg and Schwarzkopf (2019b) found that predation rates on lizards decreased with an increase in the availability of alternative prey rather than abundance of predators. However, as I did not survey for the abundance of juvenile tiger snakes, alternative prey or predators (Nordberg and Schwarzkopf 2019b, Bell et al. 2021) I cannot draw any robust conclusion as to why I observed a higher predation risk for artificial snakes in autumn but a seasonal increased abundance of juvenile tiger snakes may support the predator-swamping hypothesis (Brown and Shine 2006).

Thermal ecology

I found no evidence that a change in vegetation composition from native vegetation to kikuyu grass – reduced bare ground and increased vegetation density – has affected the thermal quality of shelter sites for tiger snakes. As the thermal environments within these plant communities are so similar, the daily patterns of tiger snake T_b and the snakes' ability to exploit optimal temperatures and thermoregulate in these environments have remained unaffected despite a change in habitat composition. Few studies have investigated the daily T_b of wild snakes on this fine a scale (recording T_b every 10min), and there is a particular paucity of these data for Australian elapids. By providing tiger snakes with high thermal quality refugia the prospect of continued habitat alteration by invasive vegetation may not have negative outcomes for tiger snakes, and the data presented herein could serve as a baseline for future monitoring.

As ectotherms, many aspects of tiger snake behaviour and physiology are related to T_b regulation (Brattstrom 1965) which is largely determined by the thermal quality of their environment (Blouin-Demers and Weatherhead 2002). Throughout the year, I found that tiger snake shelter sites were similar in thermal quality regardless of whether the vegetation was kikuyu grass or native vegetation. Open habitats provided the greatest thermal heterogeneity with the highest de_{max} stemming from both high and low T_es while woodland habitats provided more stable thermal environments with the lowest de_{max} and less extreme temperature fluctuations (Table 6; Blouin-Demers and Weatherhead 2002).

Seasonally there were very little differences in thermal quality of tiger snakes shelter sites, especially between spring and autumn, a finding also recorded by Row and Blouin-Demers (2006) for milk snakes (*Lampropeltis triangulum*), where spring and autumn were very similar in thermal quality and summer offered the most optimal thermal environment. Although summer can be quite challenging for tiger snakes as T_es in shelter sites exceeded the voluntary thermal maxima of 35.5°C (Lillywhite 1980), on average *de* was lowest in summer and shelter sites had the highest proportion of time when *de* was equal to zero. Summer is also when the thermal qualities between habitat types varied the most with kikuyu woodland (KW) offering the most stable environment with the highest proportion of time within T_{set} while the majority of habitat types were quite similar throughout the year. Winter was the exception where at all sites it was the most thermally challenging season for tiger snakes with T_es barely exceeding the lower bound of T_{set} (Table 6); unsurprisingly winter also corresponds with a period of inactivity for tiger snakes.

In spring, when I recorded tiger snake T_bs and T_e in both exposed and sheltered microhabitats the thermal quality of microhabitat types varied between day and night and the accuracy of tiger snakes' T_b compared to their T_{set} mirrored these fluctuations. Although most of the individual tiger snakes did not make use of all of the studied habitat types, these habitat types were all available to each snake, as for milk snakes in Row and Blouin-Demers' (2006) study. The novel approach of combining the temperatures from operative models in the different exposed and sheltered microhabitats respectively, rather than combining all the T_es into a single index, allowed me to gain a more complete representation of the daily thermal regime that tiger snakes experience.

Throughout the day, shelter sites were an important resource for tiger snakes as they offered a relatively consistent thermal quality. Typically, there were only two windows of opportunity for tiger snakes to move out of their shelter sites and bask - early morning and late afternoon (Figure 9). In between these times, during the day, snakes had to avoid potentially lethal T_es (Vickers and Schwarzkopf 2016). It seems that tiger snakes are very capable of exploiting the optimal temperatures available, with an $Ex_{exposed}$ of 60% and $Ex_{shelter}$ of 37%, by transitioning between the exposed and sheltered microhabitats to exploit thermoregulatory opportunities at different times of day (Figure 9). This ability to exploit thermal opportunities is greater than observed for most snakes (Webb and Shine 1998, Brown and Weatherhead 2000, Weatherhead et al. 2012) presumably due to the broad T_{set} range for tiger snakes of 24.0°C – 30.9°C (Ladyman and Bradshaw 2003). Having a T_{set} spanning 6.9°C allows tiger snakes to achieve a longer period within T_{set} compared to snakes which have a narrow T_{set} range and therefore experience greater deviations from their preferred T_b. For example, water snakes have a broader T_{set} (24.7°C – 29.8°C; Brown and Weatherhead 2000) than do black rat snakes (26.5°C – 29.8°C; Blouin-Demers and Weatherhead 2001) and thus water snakes experienced a greater amount of time with their T_b within T_{set} (Blouin-Demers et al. 2003). The species most similar to tiger snakes in their ability to exploit thermal opportunities in wetland environments are cottonmouths (*Agkistrodon piscivorus*), but they have a narrow T_{set} (24.9°C – 27.9°C) with an average *Ex* around 55% (Mueller and Gienger 2019). Presumably they would have to put more effort into thermoregulation than do tiger snakes (Blouin-Demers and Weatherhead 2002).

There are various studies describing the behavioural thermoregulation of tiger snakes (Shine 1979, Lillywhite 1980, Schwaner 1989, Ladyman and Bradshaw 2003) however, the accuracy with which tiger snakes manage their T_b in the field has not been previously determined. Usually, T_b of snakes in the field is measured using either temperature sensitive radio-transmitters (Blouin-Demers and Weatherhead 2002, Whitaker and Shine 2002) or by inserting a temperature probe into the cloaca (Rohr and Malone 2001, Rafael et al. 2012). The results of these methods are heavily dependent on the sampling regime, and without recording temperatures at frequent intervals it can be difficult to gain a complete record of the daily thermal patterns. Despite the increasing use of small temperature data loggers, such as iButtons, to record T_b data at frequent intervals (Lelièvre et al. 2010, Nordberg and Cobb 2016, Mueller and Gienger 2019) few have used this method to investigate heating and cooling rates of snakes, or reptiles in general. Heating and cooling rates of reptiles have generally been determined in controlled, captive environments (Lillywhite and Seymour 1978, Grigg et al. 1979, Shine et al. 2000, Rice et al. 2006) while field studies on rates of T_b change in reptiles have only been conducted on wild freshwater crocodiles (*Crocodylus johnstoni*; Seebacher 1999), bearded dragons (*Pogona barbata*) and lace monitors (*Varanus varius*) in natural outdoor enclosures (Seebacher 2000).

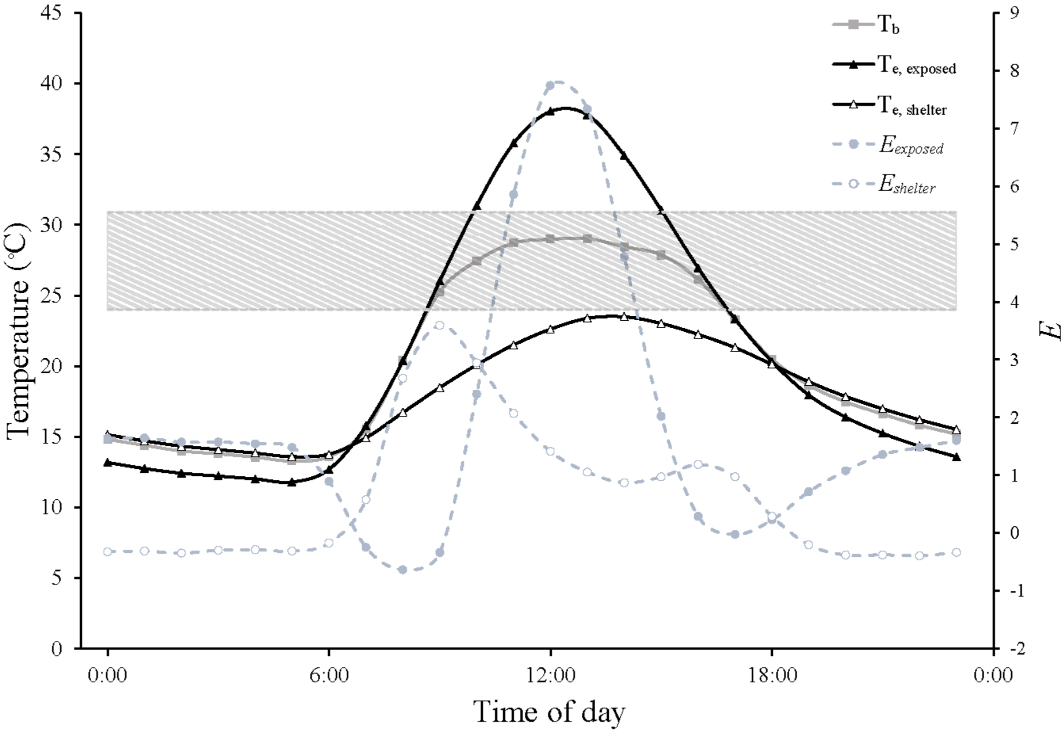

Figure 9 Daily variation in hourly measures of effectiveness of thermoregulation (*E*) of western tiger snakes (*Notechis scutatus occidentalis*). Positive values represent effective thermoregulation, values close to zero represent avoidance of thermally optimal environments. Grand mean tiger snake body temperatures (T_b), operative temperatures in both exposed ($T_{e,\text{ exposed}}$) and sheltered ($T_{e,\text{ shelter}}$) environments, and the effectiveness of thermoregulation in both exposed ($E_{exposed}$) and sheltered ($E_{shelter}$) environments. The grey area represents the body temperature set-point range.

In the early morning, as the sun rises so do the T_es in snake basking sites and shelter sites, which cause the tiger snake's T_b to warm at a rate of 1.8°C h^{-1} while they remain in their shelter sites. This passive warming rate is much slower than the rate at which endotherms rewarm when coming out of torpor (Geiser and Baudinette 1990, McKechnie and Wolf 2004, Cooper et al. 2008). I found tiger snakes would consistently emerge from their shelter sites to bask when their T_b reached around 16°C.

Therefore, tiger snake T_b and behavioural thermoregulation is ultimately dependant on the thermal quality of their shelter site. This is similar to how the pre-emergence T_b of Eastern brown snakes is dependent on the temperature of the soil in which they shelter (Whitaker and Shine 2002).

Once emerged, tiger snake T_b changed at a rate of around 13.5°C h^{-1} while basking, resembling wild garter snakes (*Thamnophis elegans vagrans*; Peterson 1987) outperforming birds (McKechnie and Wolf 2004, Cooper et al. 2008) and monitor lizards (Seebacher 2000, Zaar et al. 2004) but, not quite achieving the average rewarming rate for mammals (Geiser and Baudinette 1990) or the basking rate of bearded dragons in the field (Seebacher 2000). However, the highest rate of temperature change that I recorded in basking tiger snakes was just over 43°C h^{-1}, which was the same rate of change for Eastern tiger snakes in a laboratory experiment (*N. s. scutatus*; Lillywhite and Seymour 1978) but far greater than for mammals of similar body mass (Geiser and Baudinette 1990) or even other reptiles besides iguanas (*Iguana iguana*; Pough and McFarland 1976). Therefore, by behaviourally thermoregulating tiger snakes can achieve a greater warming rate than endotherms can metabolically. Achieving such high warming rates greatly reduces the trade-off between thermoregulation, predator avoidance and food acquisition (Amo et al. 2007).

Within a few hours of emerging T_e in basking sites begins to exceed the critical thermal maxima for tiger snakes (38.0°C; Spellerberg 1972) and sometimes reached over 50°C (Figure 4) but, by this time the sheltered microhabitats had also warmed up to the point where these sites offered the greatest thermal quality (Figure 9). Therefore, snakes could thermoregulate more effectively by retreating into the shelter sites by the late morning than by remaining in the open (Huey et al. 1989). Sometimes the thermal quality in the shelter sites was such that it fell within T_{set}.

The favourable thermal environment of tiger snake shelter sites is what allows them to maintain a daily active T_b of 29.1 ± 0.07°C and an average maximum T_b of 32.0 ± 0.11°C, similar to those reported for tiger snakes from HL in a thermal gradient in the laboratory (Ladyman and Bradshaw 2003), and for Franklin Island tiger snakes (*N. s. niger*; Schwaner 1989), Australian copperheads (*Austrelaps ramsayi* and *A. superbus*; (Rohr and Malone 2001) and those of several other temperate climate snakes (Lillywhite 1980, Peterson 1987, Forsman 1995, Brown and Weatherhead 2000).

However, the highest maximum T_b that I recorded of 36.2°C slightly exceeds the voluntary thermal maxima of tiger snakes (*N. s. scutatus*; 35.5°C) but still resembles the voluntary maxima of large elapids sympatric with tiger snakes in eastern Australian (Lillywhite 1980).

When tiger snakes are actively cooling their T_b by seeking out a shelter site for the night, their T_b changed at an average rate of 6.9°C h^{-1}, which was slower than the average reported cooling rate of other reptiles in captivity while the highest cooling rate of 34.9°C h^{-1} exceeded the reported cooling rates in these species (Pough and McFarland 1976, Seebacher 2000). I suspect the high cooling rate is due to the tiger snake getting wet, as the cooling rate in water would exceed the cooling rate in air (Grigg et al. 1979). Following retreat-site selection, snake T_b, and rates of change thereof, is dependent on the quality of refuge the snakes had chosen (Huey et al. 1989). At night the rate at which tiger snakes cooled down passively was on average 0.9 ± 0.03°C h^{-1} resembling the cooling rates of endothermic birds and mammals in the field (e.g. kookaburras and numbats; Cooper and Withers 2004, Cooper et al. 2008). The mean minimum T_b experienced by these snakes (12.6 ± 0.10°C) resembled those reported for Franklin Island tiger snakes (11.9°C; Schwaner 1989). The lowest minimum T_b I observed (2.6°C) was approaching the critical thermal minima for tiger snakes (2.0°C; Lillywhite 1980) and much lower than expected considering these temperatures were recorded in spring, their main active season (Butler et al. 2005a). Investigating tiger snake physiology in winter could be an interesting direction for future research to determine how cold these animals can get in the wild and how frequently they emerge to thermoregulate midwinter (Nordberg and Cobb 2016).

Introduced kikuyu grass was, no different to native vegetation in its effect on T_b variables or the daily circadian heterothermy of western tiger snakes. This is presumably because regardless of vegetation type tiger snakes have similar opportunities to bask in the sun and the thermal quality of their shelter sites does not differ. However, in sheltered microhabitats, tiger snakes in kikuyu grass were better at approaching preferred T_b. This could be due to different thermal properties of the vegetation itself but results on the thermal quality of habitat indicate otherwise. Therefore, I suspect this difference is caused by me selecting thermally more favourable shelter sites than did the tiger snakes themselves in the wetlands with native vegetation (Figure 8; Blouin-Demers and Nadeau 2005). In a study on Australian house geckos (*Gehyra dubia*), the geckos found more favourable microclimates than were sampled by the authors (Nordberg and Schwarzkopf 2019a). No matter how accurately one tries to sample environmental temperatures with operative models, there is always the potential that the study species differ in their ability to occupy favourable thermal microclimates.

Conclusion

Invasive kikuyu grass creates a more homogenous habitat than native vegetation in urban wetlands; however, there are still many similarities in the thermal properties and habitat quality for tiger snakes between the plant communities. In my study sites, tiger snakes have an abundance of food despite wetlands differing in dominant vegetation, and the predation rate for juveniles is similar. Furthermore, daily T_b patterns of tiger snakes and their ability to thermoregulate and exploit available thermoregulatory opportunities were not influenced by the dominant vegetation community at the wetlands. I did find the structurally complex – woodland and sedge – habitats within the kikuyu grass and native plant communities provided the greatest abundance of prey, lowest predation risk, and most stable thermal regime compared to the open habitats.

In conjunction with the low juvenile predation risk, the fact that the vegetation in which tiger snakes shelter is also occupied by their main prey, the high thermal quality of these shelter sites, and the snakes' ability to exploit basking opportunities, there are likely to be limited costs associated with having to trade off thermoregulation for other activities such as foraging and antipredator behaviour (Peterson 1987, Webb and Whiting 2005, Webb et al. 2009, Tetzlaff et al. 2017). This could explain how tiger snakes are capable of successfully exploiting optimal temperatures in exposed habitats and why tiger snakes were rarely observed doing anything besides basking (pers. obs). Moreover, their generalist nature and adaptive plasticity could be aiding their persistence in these wetlands as this species has adapted to far more extreme environments than a change in vegetation composition (Aubret et al. 2007, Aubret and Shine 2007, 2010).

Considering tiger snakes are one of the few native top order predators persisting in Perth's urban environments, it is reassuring that the tiger snake habitat quality of my study sites is not negatively impacted by the invasion of kikuyu grass.

Invasive plants are a threat to many animal species, as they impact on animal behaviour (Stewart et al. 2021), reduce habitat heterogeneity (Law and Dickman 1998) and therefore reduce habitat suitability (Abom et al. 2015). However, consistent with the findings of Garden et al. (2007) habitat structure appears more important to the persistence of the snakes than vegetation composition, and consequently urban reptile species can be positively associated with weedy plant species if they provide a favourable habitat structure. In light of this, my findings can be interpreted in two ways: 1) tiger snakes likely require riparian vegetation of a certain quality to persist in urban wetlands which, in my study system, is provided by kikuyu grass; 2) regenerating these wetlands to a more natural vegetation composition will maintain habitat quality for tiger snakes *and* potentially benefit additional species. Bower et al. (2014) have shown that restoring a wetland through the management of invasive grass may decrease the relative abundance of common and abundant herpetofauna but increase the habitat suitability for a diversity of other native species. Although I did not measure tiger snake abundance it is possible that restoration could result in a decline in the relative abundance of tiger snakes, which could be facilitated by a factor of the vegetation not investigated herein, but this is unlikely. Despite a significant difference between natural vegetation and kikuyu-dominated habitat structure, prey availability, predation risk and the thermal environment were not statistically different. Therefore, the available tiger snake habitat quality appears equivalent in wetlands dominated by either native or invasive kikuyu grass.

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Appendix 1: *Notechis scutatus occidentalis* (Western Tiger Snake). Defensive Behaviour

Notechis scutatus occidentalis is a large, polymorphic elapid found across a variety of habitats across southwestern Australia, but it is particularly abundant in wetlands (Mirtschin et al. 2017) due to its preference for feeding on frogs (Aubret et al. 2006, Lettoof et al. 2020). Although *N. s. occidentalis* is mainly terrestrial, individuals are known to occasionally forage in the aquatic environment (Aubret and Shine 2008). Across their range *N. scutatus* have also been observed fleeing into the water (Mirtschin and Bailey 1990) and swimming underwater has been recognised as a behaviour to escape predation (Aubret 2004). Aubret (2004) reported that under laboratory conditions, *N. s. occidentalis* from the urban wetland Herdsman Lake, WA, Australia, can hold their breath for over 20 min and suggested this could be advantageous to escape predation.

At 1249 h on 23 September 2019, at Herdsman Lake (-31.920225°S 115.804478°E, WGS 84), we released a small (SVL = 72.3 cm) adult *N. s. occidentalis* after recording morphometric data, and observed it fleeing into the water. We have released hundreds of *N. s. occidentalis* and the usual response is to hide in vegetation, but occasionally some will choose the water and swim away. This individual swam straight down to the bottom of the water (ca. 50 cm deep) and proceeded to hide under debris. We remained quiet and motionless while recording the time the snake spent under the debris. After a total of 18 min 36 sec the snake surfaced and took its first breath of air (Fig. 10). This is not incorporating an approximate 2 min delay before we initiated the recording. This is not the longest apnoea record for the species (Aubret 2004), but to our knowledge it is the first known *in situ* record of apnoea, as well as the first record of a wild *N. s. occidentalis* selecting to hide beneath submerged debris for an extended period of time as opposed to swimming away and resurfacing, as an antipredator behaviour.

Figure 10 *Notechis scutatus occidentalis* surfacing to breathe with the rest of the body still hidden under debris.

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Appendix 2: *Notechis scutatus occidentalis* (Western Tiger Snake) Diet

Notechis scutatus is a large, polymorphic elapid generally found in wetlands across Southern Australia, yet some populations exist on offshore islands in habitats not typically occupied by mainland conspecifics (Shine 1987). The successful colonisation of these islands is a result of their behavioural and morphological plasticity (Aubret and Shine 2009). Mainland *N. scutatus occidentalis* primarily feed on frogs (Lettoof et al. 2020. IJP:PAW. 11:32-39); however, they will occasionally take lizards, and small mammals and birds (Shine 1987; Aubret 2004).

On the 30th of September 2019, an adult male (SVL = 81.6 cm) *N. s. occidentalis* was observed and captured by hand at Bibra Lake (-32.090009, 115.824388, WGS 84). We collected morphological data under permits DBCA: FO25000149 and ARE2018-23 as part of a population health monitoring project. We partially palpate any snakes found with prey items until enough of the item is visible to determine what taxa it belongs to, and then the item is returned to the snakes' stomach. This snake had a particularly large prey item and when palpated to the point of seeing the back legs they were of a young quenda *(Isoodon fusciventer*; Fig. 11). As far as we are aware this is the first record of a tiger snake consuming an *Isoodon sp*.

While some tiger snakes populations consisting of large individuals have been recorded possums (Oliver et al. 2010), mainland tiger snakes found in the vicinity of Perth are particularly small (Aubret et al. 2006) and feed on relatively small prey (mice, frogs and small skinks; Aubret 2004). Carnac island counterparts reach larger sizes however, and feed on larger prey items (nesting sea-birds chicks; Bonnet et al. 2002). Following their recent introduction on Island Carnac (Ladyman et al. 2020), tiger snakes have seemingly successfully adapted to the island environment, notably via the expression of high levels of adaptive plasticity in response to prey size, allowing them to exploit large and abundant prey items, and thrive (Bonnet et al. 2002). While plasticity levels were shown to be minimal in mainland WA populations of tiger snakes (Aubret et al. 2004, 2009), they were not nil. We suggest that occasional feeding opportunity of large prey items such as young quendas or possums may foster the maintenance of minimal levels of adaptive plasticity in swallowing performances in mainland Tiger snakes. Island colonisation, or introduction, may then generate bottlenecks and increase plasticity levels to significant levels, as was previously described in several tiger snakes populations across Australia (Aubret et al. 2004, 2009; Aubret 2015).

Figure 11 *Notechis scutatus occidentalis* regurgitating a young quenda (*Isoodon fusciventer*) characterised by its feet.

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Appendix 3: *Notechis scutatus occidentalis* (Western Tiger Snake). Reproduction / Unfertilised Ova Post-Parturition

At 1122 h on 8 May 2020, at Yanchep National Park, WA, Australia (-31.547272°S, 115.681819°E, WGS 84), we encountered an adult female *Notechis scutatus occidentalis* in a basking position and beginning to shed. An unfertilised ova lay beside the snake's tail presumably passed post-parturition (Fig.12). The snake was identified as an individual being monitored in an ongoing study that was normally in very good body condition; the snake had been released in April 2019 after spending 6 months in captivity and had not been recaptured since (D. Lettoof. Unpublished data). However, at the time of encounter the snake appeared relatively emaciated, suggesting the snake has recently given birth (Naulleau and Bonnet 1996). *Notechis scutatus* have been recorded breeding throughout the year (Shine 1977a), although spring and early summer (October-December) tends to be the main breeding season for live-bearing Australian elapids, and parturition occurs at the end of summer (February-April; Shine 1977b). In captivity, snakes depositing unfertilised ova during parturition is a common observation (Aldridge et al. 2008); however, we believe this is the first time this phenomenon has been observed in a wild *N. scutatus* and potentially the first record for a snake in the wild.

Figure 12 *Notechis scutatus occidentalis* unfertilised ova

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Appendix 4: First record of predation of a hatchling turtle by the Western tiger snake (*Notechis scutatus occidentalis*).

Abstract

Snake-Turtle interactions have been rarely documented. We recorded a hatchling *Chelodina oblonga* within the stomach contents of a Western tiger snake (*Notechis scutatus occidentalis*). This is the first recorded observation of an interaction between snakes and hatchling freshwater turtles in Western Australia. Field based palpitation failed to detect the hatchling, suggesting that without dissection, turtle hatchling predation by snakes more generally could be higher than commonly reported. Snake predation of hatchlings could be placing additional pressure on threatened populations of freshwater turtles in Australia, warranting further investigation.

Introduction

Freshwater turtles are imperilled globally (Stanford et al. 2020) being among the most endangered vertebrate groups, with approximately 61% of species at risk of extinction or already extinct (Lovich et al. 2018). Australian freshwater turtles are in a similar position with approximately half of the 25 extant species currently listed as vulnerable, endangered, or critically endangered, with declines documented in multiple species in recent decades (Spencer et al. 2018, Van Dyke et al. 2019, Santoro et al. 2020). Causes of decline include mortality of nesting females through predation (Thompson 1983, Spencer 2002) and wildlife-vehicle incidents (Spencer 2002, Santori et al. 2018), destruction of nests through predation (Thompson 1983, Spencer 2002, Giles et al. 2008), habitat decline (Santoro et al. 2020) and novel diseases (Spencer et al. 2018).

Freshwater turtles rely on both the aquatic and terrestrial habitats of wetlands to complete their life cycles (Burke et al. 2000). While many species are either apex predators or high in the food chain in the aquatic environment, once in the terrestrial environment, turtles are highly vulnerable to predation (Tucker and Janzen 1999, Spencer and Thompson 2003, Segura et al. 2020). Freshwater turtle life histories are characterised by long generation times, high adult survivorship, late age maturation, low annual reproductive effort, as well as low and variable recruitment (Iverson 1991, Congdon et al. 1993, Spencer 2018). Therefore, the survival of adults is more influential on population persistence than any other stage (Heppell 1998); however, given the increased predation pressure placed on both adults and nests by invasive species in Australia (e.g. red foxes *Vulpes vulpes* (Giles et al. 2008; Spencer, 2002; Thompson, 1983)), understanding the threats to the survival and recruitment of hatchlings into populations is more critical than ever.

On the Swan Coastal Plain in south-west Western Australia, the Oblong turtle (*Chelodina oblonga*) persists in a number of urban wetlands (Santoro et al. 2020); however, relative abundances in most wetlands are alarmingly low. In addition, the latter study revealed that adults made up ~90% of captures and juveniles were absent from captures at ~40% of wetlands. Known predators of *C. oblonga* include foxes (*V. vulpes*) (Dawson *et al.* 2016), the Australian raven (*Corvus coronoides*;AS pers obvs.), Australian white ibis (*Threskiornis molucca*; JC pers obs.) cormorants (*Phalacrocoracidae*) and White-necked herons (*Ardea pacifica*; (Cann and Sadlier 2017). A top predator of wetlands, Western tiger snakes (*Notechis scutatus occidentalis*), are abundant in at least seven of the wetlands surveyed by Santoro, Chambers *et al.* (2020; DL and AS pers. obs.), yet the predation pressure by snakes is not understood in Australia, nor globally.

Across their Southern and Eastern Australian range, tiger snakes collectively show a generalist diet with a high degree of plasticity based on the population. For example, mainland tiger snakes found around wetlands dominantly eat frogs, and occasionally small birds, mammals and lizards (Shine 1987, Lettoof et al. 2020), island populations can specialise in only bird chicks or lizards (Schwaner 1991, Aubret et al. 2004), and Tasmanian tiger snakes have a large proportion of mammals in their diet (Fearn et al. 2012). Interestingly, Western tiger snake hatchlings from an island with only bird and lizards available have been shown to still preference the scent of frogs and mice (Aubret et al. 2006). A summary of all known tiger snake diet records in Greer (2020) indicates that the most commonly detected dietary taxa is frogs. Snake-turtle predation events are seemingly rare globally, and within Australia; here we present the first known record of an Oblong turtle hatchling predation by a snake.

Observation

On 17/09/20 an adult female Western tiger snake was hand caught from fringing vegetation at Bibra Lake, Perth, Western Australia (Fig. 14; 32° 5′ 32 S, 115° 49′ 27 E) by DL and JC, and euthanised as part of an ongoing research project (Western Australia's Department of Biodiversity, Conservation and Attractions Permit No. FO25000149; Curtin University Animal Research Ethics Committee Approval No. ARE2020-15). Prior to euthanasia the snake was measured (Snout-vent length: 667 mm, body mass: 147.5 g), assessed for external condition and ectoparasites, and gently palpated for food items. Palpation of the stomach revealed the feet of a motorbike frog (*Litoria moorei*), and a large stomach burden of *Ophidascaris pyrrhus* nematodes. The snake was dissected on 27/10/2020 by DL and CS to assess endoparasite abundance and diet. Dissecting the stomach revealed the back legs and half-digested body of the motorbike frog, entangled and being fed on by nematodes. Beyond the nematode colony, at the posterior end of the stomach, was a hatchling long-necked turtle (Fig. 14). The turtle was 55 mm total length, 25 mm carapace length, and 2.8 g body weight, and there was no evidence of feeding from the nematodes.

Figure 13 (A) a Western tiger snake (*Notechis scutatus occidentalis*) from Bibra Lake, and (B) an example of a bank at Bibra Lake where Oblong turtles nest and tiger snakes shelter in fringing vegetation

Figure 14 The hatchling oblong turtle (*Chelodina oblonga*) found inside the Western tiger snake's (*Notechis scutatus occidentalis*) stomach.

Discussion

Predation of freshwater turtle hatchlings by snakes has rarely been recorded in Australia. We could only find a single record of such an occurrence, which was the observation of a *Emydura krefftii* turtle hatchling being predated by a Mulga snake (*Pseudechis australis*) (Cann 1978). There has been a further observation of a dugite (*Pseudonaja affinis affinis)* attempting to a swallow an adult *C. oblonga* but could not get past the carapace (Maryan and Gaikhorst 2005). In the United States Eastern Diamondback rattlesnakes (*Crotalus adamanteus*), indigo snakes (*Drymarchon corais*) and Eastern coachwhips (*Masticophis flagellum*) are known to predate on young gopher tortoises (Butler and Sowell 1996, Perez-Heydrich et al. 2012), and larger African snakes have been found predating on small hingeback tortoises (*Kinixys spekii*) (Coulson and Hailey 2001). Nevertheless, snakes do not seem to be a common predator of turtles, as many Australian snakes do not forage in the water and the carapace is too large for a snake to swallow.

The turtle hatchling may have been scavenged, as hatchling turtles can die from desiccation while migrating (Janzen et al. 2000; Kolbe and Janzen, 2002; Paterson *et al.* 2013), and tiger snakes are known to eat carrion (Fearn 1993; Aubret et al. 2005). However, Oblong turtle nest are usually within 500m of the water's edge (Clay, 1981), and a large portion the Bibra Lake population nests among fringing vegetation (Fig. 13). We find it unlikely that a hatchling would have died due to desiccation with such close proximity to the lake.

Due to their small size, research on the aquatic movements and behaviour of freshwater turtle hatchlings is scarce. Rosenberg and Swift (2013) reported that hatchling western pond turtles (*Actinemys marmorata*) were always located in areas with woody debris and dense submerged vegetation, were within 1 m of the shore, and moved up to 38 m between observations (~1-3 days). When AS has observed hatchling *C. oblonga* in aquatic environments, they show similar behavioural traits, and can swim relatively quickly. We suggest a hatchling within the aquatic environment would be relatively difficult for a foraging snake to capture. There is significant overlap between peak movement periods of hatchling oblong turtle and Western tiger snakes. Oblong turtle hatchlings are recorded as emerging from their nests and migrating to the nearest waterbody between May and August (Burbidge 1967, Clay 1981), however AS has observed hatchlings emerging in late September in 2019 and 2020. Western tiger snakes in Perth show peak abundance in between August and September (DL and JC pers obs, surveying from August through to April) as they begin mating season. Therefore, we suspect the hatchling *C. oblonga* must have been predated on land or the shallow waters edge and was only swallowed because of its small size.

Chelodina oblonga populations are believed to be declining through a lack of recruitment (Santoro et al. 2020). Further research into *C. oblonga* populations currently occurring at wetlands within the Beeliar Regional Park by AS has revealed that *C. oblonga* populations face significant threats from terrestrial predation of nesting females and eggs by introduced species (such as red foxes (*Vulpes vulpes*)) and domestic dogs (*Canis familiaris*). Anecdotal reports have also identified the laughing kookaburra (*Dacelo novaeguineae*) as a predator of hatchling turtles (pers. obvs. AS and DL). Native species such as the Australian Raven (*Corvus coronoides*) have been identified as significant predators and observed attacking and killing nesting females, and both ravens and quenda (*Isoodon fusciventer*) have been observed destroying nests. Currently, aspects of the early life history of the oblong turtle such as survivorship rates of hatchlings and the relative impact of known predators remains unknown. However, observations from tracking hatchlings with UV powders during migration to waterbodies after emergence from nests allude to high rates of suspected avian predation (AS pers. obs.). The finding of a hatchling oblong turtle within the stomach contents of a Western tiger snake suggests that they could be another native predator that is reducing the recruitment of juveniles to the population.

Traditionally, snake diet is assessed by manual palpation of prey items on live animals, or dissection of carcasses (Dorcas and Willson 2009). Both methods have limitations, for example: easily digestible soft-bodied prey such as amphibians can be underrepresented in museum snake specimens (Glaudas et al. 2017), and small prey items may be more difficult to detect by palpation (Dorcas and Willson 2009). The turtle hatchling was not detected during palpitation in the field, rather by dissection of the stomach. Although small prey items may be difficult to detect via palpation we regularly palpate metamorph frogs (DL and JC, pers. obs.), and rather dietary unknowns are usually a result of Western tiger snakes' common infection with gastric nematodes. Nematode colonies are attached to the stomach wall (Lettoof et al. 2020) and often entangle prey items when feeding; thus, prey can often be felt through palpation but cannot be removed. Specifically, near 500 tiger snakes have been palpated in the field by DL and JC, and in 43% of snakes with prey items cannot have them removed. We propose predation of hatchling turtles may be higher than detectable without dissection, especially in species with gastric nematodes, and may warrant further investigation.

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Appendix 5: Dystocia in a wild Western Tiger Snake (*Notechis scutatus occidentalis*)

Abstract

Dystocia in reptiles is the retention of ova or foetuses within the female due to the failure of the female to complete parturition, oviposition or resorption. This disorder is commonly observed in captive reptiles, but has rarely been reported in wild reptiles. We observed a large internal obstruction in an adult female Tiger Snake captured as part of an ongoing population study. We failed to palpate out the object in the field, so we took the snake to a veterinary practice for professional assistance. All non-lethal methods of extracting the object were unsuccessful so we euthanised the specimen and post-mortem dissection revealed five mummified stillborn young lodged in a sealed reproductive tract. Reproductive abnormalities are frequent in Tiger Snakes and large proportions of litters can be comprised of unfertilised eggs, fertilised aborted eggs and stillborn young, yet none of these observations ever resulted in dystocia. It is interesting that this observation occurred in a snake from Herdsman Lake, Western Australia, where the Tiger Snake population is subjected to many anthropogenic stressors. We cannot determine what caused this case of dystocia but suspect it may have been caused by some sort of negative effect onset by the quality of the environment.

Introduction

Dystocia is diagnosed in reptiles as the retention of ova or foetuses within the female due to the failure of the female to complete parturition, oviposition or resorption (DeNardo 2006). Dystocia is a disorder commonly observed in captive reptiles, especially snakes (Bel et al. 2015; Rowland 2016). Despite decades of field research and dissections of wild reptiles dystocia has rarely been reported in wild reptiles, and even less in viviparous species (DeNardo 2006).

Western Tiger Snakes (Notechis scutatus occidentalis) are ~1m viviparous elapids that are commonly found around wetlands of South-West Western Australia. In Perth, Western Australia, tiger snakes persist in several wetlands surrounded by varying degrees of urban modification (Lettoof et al. 2020a). Although tiger snakes are one of the most studied species of snake in Australia, observations of in situ reproductive and parturition events have rarely been reported. Nevertheless, studies involving the capture of wild, pregnant tiger snakes to monitor their birthing in captivity (Aubret 2005; Aubret 2012) have shown that stillborn neonates, and unfertilised ova (Cornelis & Lettoof 2020), are a common occurrence. These anomalies can be birthed over the course of many days following the successful parturition of live young, which are generally born on the same day (Aubret unpublished data).

Observation

On 10 September 2020, we captured an adult female tiger snake (SVL 792 mm and 230g) at Herdsman Lake in Perth (-31.9 S, 115.8 E) as part of an ongoing population study (DBCA Permit No. 08-002624-1 and Curtin University AEC Approval No. ARE2018-23); and during the measuring we observed a large internal obstruction in close proximity to the rectum. Our initial suspicion was the snake had consumed a foreign object that could not be passed through the digestive tract, as a deceased snake at Herdsman Lake had been found with a plastic bottle cap stuck in a similar region (Lettoof & Orton, 2020). After a failed attempt to softly palpate out the object in the field, we took the snake to a veterinary practice for professional assistance.

We first conducted an ultrasound examination, and observed some mass of similar consistency to bone in the coelomic cavity. It is very unusual to find bones so far down the digestive track, as bones are usually totally digested (Daltry et al. 1998). An endoscopy was performed from the cloaca to inspect the lower gastrointestinal tract. Alfaxalone was administered intravenously as sedation prior the procedure. Lubrication and saline were inserted into the cloaca in attempt to gently palpate the obstruction out, however the mass could not be aborally advanced.

We advanced the endoscope to the level where the coelomic swellings were, a small amount of dried, brown faecal matter was seen and removed, however was not the cause of the swelling. The intestinal wall was intact and empty, with normal appearance of the serosa lining. A bulging was seen adjacent to the intestinal wall when the coeliac wall was pressed and the endoscope was next to the first and second most distal swelling. With these findings, it was suspected that the masses were more likely from the oviduct or within the coelomic cavity. The opening of the oviduct could not be located during endoscopy.

Attempts to remove the masses by endoscopy were not successful. Due to voluntary services, time restrictions and lack of facilities for post-treatment recovery of a wild venomous snake, it was decided that euthanasia was the most humane option. Post-mortem dissection revealed five mummified stillborn young lodged in a sealed reproductive tract (Figure 15). The amiotic sacks of the stillborn young were firmly adhered to the oviduct, which explained why manipulation towards the cloaca was not possible during the endoscopy. Digital manipulation directly over the oviduct during post mortem was also unsuccessful, causing the rupture of the oviductal wall. Although not performed, it is anticipated that embryos would be detected on radiographs. Underlying metabolic bone disease, pelvic stenosis, coelomic masses, or calculi can also be detected to assist with findings the underlying cause of the dystocia with this method.

The retained young were peeled away from the oviductal wall after a longitudinal incision was made. Severe adhesions have formed between the retained eggs and the oviduct. There was no abnormal coelomic mass, or any cystic or cloacal calculi found within the coelom. A few firm faeces were found in the intestinal tract, however the size was not expected to have caused a complete obstruction, unless other factors such as severe dehydration complicated the condition.

Figure 15 Four mummified foetuses removed from a blocked reproductive tract

Discussion

Reproductive abnormalities can be frequent in tiger snakes. Specifically, between 2002 and 2003, between 15-56% of the litters from Herdsman Lake and 47-66% of the litters from Carnac Island were comprised of unfertilised eggs, fertilised aborted eggs and stillborn young (Aubret 2005). In 2006, several pregnant females collected from Reevesby Island, South Australia, gave birth to a high number of stillborns (between 8 and 19) over a period of 40 days (Aubret unpublished data). The longer these stillborns were retained the more mummified they were when they were eventually birthed (Aubret Pers. Obs.). Despite the frequency of litter defects, none of these observations ever resulted in dystocia, although, on some occasions hard masses were noticed inside the tiger snake bodies but did not warrant enough concern to justify euthanasia (Aubret Pers. Obs).

Over the last two decades, the authors FA, DL and JC have measured and inspected roughly 2000 wild tiger snakes, including over 80 wild-collected females that gave birth to more than 1100 live neonates (Aubret 2012); and yet this is the only confirmed case of dystocia. The pathogenesis of dystocia (and post-ovulatory egg stasis) in reptiles includes but is not limited to: salpingitis, oviductal rupture, over-size or malformation of the eggs/embryos, in addition to other concurrent diseases such as gastrointestinal tract obstruction, pelvic stenosis, nutritional or metabolic imbalances such as hypocalcaemia and hypovitaminosis A (Doneley et al. 2018). In viviparous snakes, embryonic death due to uterine infections or suboptimal temperatures is also a known cause (Donnelly 2003), and females breeding for the first time or with a history of egg/embryo retention have increased risk of dystocia (DeNardo 2006). Minor symptoms of dystocia include straining, nesting behaviour, lethargy and coelomic distension, whereas prolonged dystocia can result in cloacal prolapse, posterior paresis, anorexia, loss of body condition and ultimately death (Doneley et al. 2018).

We cannot determine what caused this observed case of dystocia; however, it is interesting that this observation occurred in a snake from Herdsman Lake. Of the studied populations, snakes at Herdsman Lake are subjected to the most anthropogenic stressors such as human interference, frequent mechanic modification of vegetation, and pollution (authors, Pers. Obs); where they accumulate the highest concentrations of antimony, arsenic, barium, cobalt, manganese, molybdenum, silver, strontium, thorium and uranium as well as high concentrations of copper, mercury, selenium and brodifacoum (an anticoagulant rodenticide; Lettoof et al. 2020a; Lettoof et al. 2020b; Lettoof et al. 2021). Knowledge on the toxicological effects of contaminants in snakes is extremely limited; however, perhaps chronic contamination could influence the nutritional or metabolic imbalances that can cause dystocia. Recent research has also identified mothers can transfer some of these accumulated metals into developing offspring (Lettoof et al. 2020c), which could also influence reproductive abnormalities. Although there was no variation in the percentage of stillborn or malformed neonates, or aborted eggs between litters of snakes from Herdsman Lake or Carnac Island (Aubret 2005); and presumably Carnac island is considerably less polluted than Herdsman Lake; the retention of the stillborn young may have been caused by some sort of negative effect onset by the quality of the environment.

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Appendix 6: Peer reviewed paper not included in this thesis

Cornelis, J., Parkin, T., Bateman, P. W. (2021). Killing them softly: a review on snake translocation and an Australian case study. Herpetological Journal, 31(3), 118-131. https://doi.org/10.33256/31.3.118131