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Damian Lettoof[a,*], Brenton von Takach[b], P.W. Bateman[a], Marthe Monique Gagnon[c], Fabien Aubret[a,d]

[a] *Behavioural Ecology Lab., School of Molecular and Life Sciences, Curtin University, Brand Drive, Bentley, WA, 6102, USA*
[b] *Research Institute for the Environment & Livelihoods, Charles Darwin University, Darwin, NT, 0909, Australia*
[c] *School of Molecular and Life Sciences, Curtin University, Brand Drive, Bentley, WA, 6102, USA*
[d] *CNRS, Station d'Écologie Théorique et Expérimentale, UMR 5321 CNRS – Université Paul Sabatier, 09200, Moulis, France*

ABSTRACT

Tiger snakes (*Notechis scutatus*) in wetlands of South-West Western Australia (SW WA) are commonly parasitised by the nematode *Ophidascaris pyrrhus*. Host-parasite interactions are complex and can potentially be impacted by factors such as urbanisation or climate. We assessed whether urbanisation, distance to wetland sites, and climatic factors have influenced parasitism in tiger snakes from specimens collected over the last century. We dissected 91 museum specimens of tiger snakes across SW WA and counted gastrointestinal nematodes. Binomial generalised linear modelling, with presence/absence of nematodes as a response variable, was used to determine which factors were driving infection. Model selection using AIC_c values showed that proximity to wetlands, rainfall and topographic wetness were most strongly associated with the probability of infection of snakes by nematodes. We also found a slight positive correlation between nematode abundance and annual mean maximum temperature. We found no significant influence of distance to urban centre on nematode burdens; however, our results suggest that water-related variables are a key driver of nematode parasitism in tiger snakes in SW WA. We also suggest that urbanisation is still of interest as its role in wetland and climate modification may increase parasitism in wetland snakes.

1. Introduction

The modification and degradation of ecosystems through urbanisation has been well-documented for decades (Faulkner, 2004; Mcdonnell and Pickett, 1990; Santiago-Alarcon et al., 2018). Such modification has resulted in a plethora of impacts on wildlife; however, the first and most detectable change is often a reduction in species richness with some taxa unable to persist in urban areas, while others seem able to adapt or benefit (Bateman and Fleming, 2012; McKinney, 2008). Further research has included evaluation of the health of these taxa that persist in urban areas - urban utilizers/dwellers (Fischer et al., 2015) or urban adapters *sensu* McKinney (2008) - as a reflection, and thus indicator, of ecosystem health (Carignan and Villard, 2002; Siddig et al., 2016; van der Oost et al., 2003). One such measure of organism health is assessing the parasite abundance of target organisms, a typically sub-lethal impact that may have pernicious effects on individual fitness and thus long-term population persistence (Bower et al., 2019; Davis et al., 2012; Sanchez et al., 2018).

Urbanisation can either increase, decrease or have no detectable impact on host parasite infection (Ancillotto et al., 2018; Giraudeau et al., 2014). An increased level of parasite infection in urban areas has commonly been attributed to a reduced host immunocompetence from external stressors; for example, increased stress levels and/or host exposure to contaminants can result in a suppressed immune system in anurans (Linzey et al., 2003; Rohr et al., 2008) and reptiles (Day, 2003). The fragmentation of habitat through urbanisation can result in an increase of host density and in contact rates, thus facilitating horizontal transmission for parasites (Puttker et al., 2008); however, urban habitat fragmentation can also disrupt a complex parasite life cycle or transmission frequency between hosts resulting in decreased parasite abundance (Barbosa et al., 2005; Dugarov et al., 2018; Resasco et al., 2019; Santiago-Alarcon et al., 2018). Assessing the change of parasite abundance in top predators, such as larger snake species, can be an important indicator of the impact of urbanisation on ecosystems (Davis et al., 2012).

The tiger snake (*Notechis scutatus*) is a large (mean 1 m snout-vent-

length [SVL] on the mainland) polymorphic Australian elapid (Aubret, 2012; Shine, 1995). It occurs in disjunct populations across most of the southern parts of the country, and varies in both diet and habitat across its range (Aubret et al., 2004, 2006). In mainland South-West Western Australia (SW WA) it is abundant in wetlands and, despite the rapid expanse of urbanisation degrading and heavily modifying wetlands in SW WA (particularly Perth and its surrounds) (Davis and Froend, 1999), the tiger snake has remained an abundant top reptile predator in many urban wetlands (Aubret, 2005). In mainland SW WA, the tiger snake is primarily anurophagous (Aubret et al., 2006; Shine, 1987a), and like most other frog-eating snakes it has been recorded as having high abundance of parasitic worms (Fantham and Porter, 1954; Mayer et al., 2015; Yildirimhan et al., 2007).

The tiger snake is commonly infected with the ascaridoid nematode *Ophidascaris pyrrhus*, the life history of which is unknown (Jones, 1980; Watharow, 1997). Other species of *Ophidascaris* and ascaridoid nematodes often develop indirectly in reptiles, amphibians or mammals (Ash and Beaver, 1962; Sprent, 1970). Larvae of the first and third stage infect intermediate host's (reptile, amphibian or mammal) via egg consumption and encyst the lungs, muscles and liver. If this host is then consumed by a snake the adult nematodes parasitise the posterior stomach wall (Sprent, 1955). Adult female nematodes lay eggs in the digestive tract of the snake from where they pass into the environment with faeces. Eggs are then consumed by an invertebrate or vertebrate host (Anderson, 1988; Sprent, 1954). As nematode infection is common in tiger snakes (Jones, 1980), and frogs are known to host a variety of nematode species larvae (Kelehear and Jones, 2010; Lettoof et al., 2013; Mayer et al., 2015), it is likely that *O. pyrrhus* uses frogs as an intermediate host (Jones, 1980). Adult *Ophidascaris* feed on the host's digested prey (Elbihari and Hussein, 1973; Jones, 1980; Sprent, 1988). Most individual nematodes thread the middle of their bodies into the stomach wall creating deep lesions of calcified material and necrotic debris (DL pers. obs.). Although the impact of these lesions on the host snake's health is unknown, the intensity of nematode infection is more concerning. A large burden of gastric nematodes can cause malnutrition from substantial loss of nutrients to the parasites (Hlaing et al., 1991), or intestinal blockages (de Silva et al., 1997). Observations of wild tiger snakes in poor body condition frequently identify a high intensity of *O. pyrrhus* infection (DL and FA pers. obs.).

Most natural wetlands of SW WA are ephemeral, with water levels peaking in spring (October) and at their lowest in autumn (April) (Davis and Froend, 1999). However, the seasonal filling of wetlands is under pressure from regional climate shift and urbanisation. Since the 1960s, remnant wetlands have received less water as mean annual rainfall has decreased by 100–150 mm and mean annual temperature has increased by about 1 °C (Bureau of Meteorology, 2019). Even so, water levels in several urban wetlands have risen due to increased surface run off, storm water drainage networks and elevated groundwater levels (Clarke et al., 1990; Lund, 1992). Urban altered wetlands that are now isolated and permanent may influence nematode abundance in several ways: (a) nematode eggs persist longer in water and thus increase in prevalence, abundance and transmission year round (Marcogliese, 2008); (b) reduced and isolated habitat for both frogs and snakes increases host densities and thus parasite exposure and transmission frequency (Mugabo et al., 2015); and (c) host frogs and snakes are potentially immunocompromised by contaminants in urban wetlands (Linzey et al., 2003; Martin et al., 2010).

By inspecting the stomach contents of tiger snake museum specimens collected across SW WA we aimed to investigate the impact of urbanisation on nematode burdens over 100 years of collection and across the entire range of SW WA tiger snakes. Specifically, we aimed to identify what factors might influence parasitism in tiger snakes including proximity to urban centres and wetlands, and climatic variables. Considering the influence urbanisation can have on parasitism we predicted that parasite prevalence and abundance in tiger snakes would be higher closer to urban centres and wetlands, and in areas with

a wetter, warmer climate. The results of this study provide insight into the influence of urbanisation and climate on host-parasite interactions of snakes, and highlight the importance of museum specimens in assessing spatial and temporal changes in urban ecology.

2. Methods

2.1. Snake morphology, diet and nematode parasitism

We examined the tiger snake records from the Western Australian Museum (WAM) to determine when and where specimens were collected across SW WA (specimens were collected between 1917 and 2018). From this we excluded specimens collected from offshore islands as the island ecology and diet of these tiger snakes differs from mainland wetland conspecifics (Aubret et al., 2006). Where possible, we attempted to examine similar numbers of specimens from urban and non-urbanised locations, as well as across collection dates. If multiple snakes were collected from the same location on similar dates (indicating a collection survey), two were randomly selected for examination.

Specimens were partially dissected to allow inspection of the stomach. Since sampling involved destructive modification of the specimens, we were limited by museum policy in the number of specimens we could sample (n = 91). Of the 91 dissected tiger snakes, we obtained the SVL, wet mass (after draining of excess preservative liquid), location and year of collection. A number of specimens (n = 27) had no year of collection attached, so we estimated year of collection based on the registration identification number relative to other registered reptile specimens. Upon dissection all nematodes and prey items (identified to lowest possible taxonomic level) were carefully removed, counted and stored in separate collection jars. Nematodes were identified as *O. pyrrhus* (Sprent, 1988). Thirty five tiger snake specimens (including 11 juveniles) could not be sexed with confidence. Four specimens consisted solely of viscera and the original body could not be located; however, these could still be dissected for nematode counts and prey identification.

2.2. Classifying urbanisation

Classifying 'urbanisation' is ambiguous and is often based on human densities (Madsen et al., 2010). Our research is based on the hypothesis that environmental degradation from urbanisation would be driving parasite prevalence and abundance, hence our measure of urbanisation is calculated from degree of urban infrastructure. We could not accurately classify the historical outlines of the urban centres, as detailed records and aerial photographs are not available for all locations prior to the 1960s. We also decided not to classify areas based on government census human density data, as Local Government Areas (LGAs) in SW WA have historically been quite large and the urban settlements occupied a small portion of each LGA. Thus, human densities calculated over this large area do not accurately represent if the snake was collected from an 'urban' area. We therefore calculated a distance to urban centre (DUC) for each specimen.

2.3. Spatial analysis and climate data

The location of each specimen was determined using the GPS coordinates provided by WAM records, and plotted using QGIS (QGIS, 2018). Each specimen was colour-coded to indicate nematode abundance (total number of nematodes; Fig. 1). DUC was calculated by measuring the distance between the specimen and the closest urban centre, which we consider to be a good proxy measure of urbanisation across the spatial and temporal scales of the study. The point of urban centre was the middle of the CBD of the five largest cities in SW WA. These cities were selected by inspecting census data of 1911 (ABS, 1911) for human population confirming they have been the largest
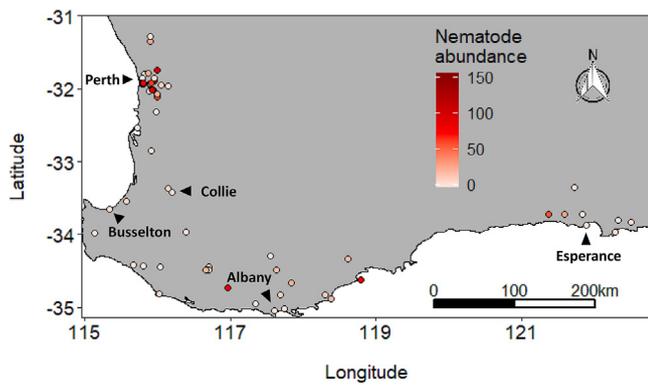
Fig. 1. The abundance of nematode infection for each tiger snake specimen in South-West Western Australia. Arrows indicate major cities used as urban centres. Colour indicates the number of worms (intensity) found in the stomach of each specimen. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

since specimen collection began. These centre points are located in the City of Perth, City of Busselton, City of Collie, City of Albany, and City of Esperance.

As nematodes are probably acquired through predation on frogs we also compared distance to wetlands for each specimen, as well as basic climatic factors that may influence the parasite's lifecycle. To determine distance to wetlands we used regional surface water hydrology GIS shape files (representing major natural and man-made features including lakes, reservoirs and farm dams) generated in from Geoscience Australia (Geoscience Australia, 2019) and measured the distance of each specimen from the closest water body. While contemporary mapping is not appropriate for calculating urbanisation categories in this study, we suggest that the number of wetlands and the boundaries of those wetlands are typically more stable components of the environment and are thus less likely to have experienced major differences over the past century. It is possible that a small number of wetlands have been lost or created over this time, however we believe that these are unlikely to have a substantial impact on the results of the study. The location (coordinates in decimal degrees) of all 80 adult snakes were uploaded into the Atlas of Living Australia's (ALA) Spatial Portal (https://spatial.ala.org.au/#), and five environmental variables at each point were extracted: mean annual precipitation (RAIN), topographic wetness index (TWI), mean annual maximum temperature (MAXTEMP), mean annual temperature (MEANTEMP) and mean annual minimum temperature (MINTEMP) (von Takach Dukai et al., 2019). Variables extracted from the ALA have been derived from various sources, and are based on an average of 50 years of climate data centred on 1990 (Williams et al., 2010; Xu and Hutchinson, 2013).

2.4. Correlations and logistic regression

All analyses were conducted in R Studio version 3.5.2 (R Core Team, 2018). We conducted a preliminary investigation into correlations between the specimen nematode abundance and various spatial and climatic factors, using Spearman's rank correlation coefficient. Any samples without complete data were removed. We then used a binomial generalised linear model (GLM) to assess the influence of time, distance to nearest urban centre, distance to nearest wetland, and climatic variables on nematode prevalence. To account for increasing urbanisation through time we included an interaction between DUC and year. We first scaled and centred all predictor variables to improve model fitting, and then removed correlated variables to reduce multicollinearity (retaining variables with variance inflation factors < 5 and pairwise correlations < 0.7). We then ran a binomial GLM (using the *glm* function), and checked the model fit of the global model using pseudo-R-squared values calculated in the glmmADMB package

Table 1
Length and body mass measurements for 88 complete tiger snake specimens held at the Western Australian Museum.

Sex (n)	mean SVL ± SE (range), cm	Mean wet mass ± SE (range), g
Male (33)	78.6 ± 28.6 (49.9–113)	364.4 ± 36.6 (50–900)
Female (21)	79.3 ± 25.8 (60.2–100)	316.0 ± 22.1 (100–600)
Undetermined sex (23)	68.5 ± 24.2 (50.1–90.0)	22.6 ± 23.9 (100–450)
Juvenile (11)	36.1 ± 17.2 (27–45.6)	45.5 ± 6.7 (25–100)

(Fournier et al., 2012). Model selection was performed using the *dredge* function and all sub-models were ranked according to AICc values (i.e. corrected for small sample sizes). All models with ΔAICc < 2 were considered useful for inference. We checked for signatures of spatial autocorrelation using a variogram of the model residuals, created using the geoR package (Ribeiro and Diggle, 2018), and found no strong evidence of spatial autocorrelation. Results were visualised and the results were plotted using the ggplot2 package (Wickham, 2016).

3. Results

3.1. Snake morphology and diet

A total of 88 tiger snakes with complete carcasses were dissected (Table 1), with three additional viscera-only samples. The majority of snakes were collected between 1930 and 1989 (n = 46). A body condition index could not be calculated due to the varying degree of damage and drainage capabilities of the specimens. However, based on absence of body fat and muscle mass only five (5.6%) of the 88 specimens appeared to be in very poor body condition (more in section 3.2). Prey items were found in the stomach of 38 (41.8%) of the 91 specimens (whole snakes plus viscera specimens) and 11 specimens contained more than one prey item. The majority of tiger snake prey items were frogs (86.8%; Table 2).

3.2. Abundance and intensity of nematode infection

Nematodes were found in the stomachs of 74% of the adult specimens, with the mean intensity of infected adult snakes being 31 nematodes (range = 1 to 152, SE = 4.87). The five snakes considered to be in poor body condition had a nematode intensity of 72–152 individuals. Only four other snakes had intensities within that range (79–136) and were considered in normal body condition. Nematodes were detected in three (27%) of the 11 juvenile specimens, with the smallest infected specimen measuring 31.9 cm (SVL). Five (5.7%) of 88

Table 2
Prey items observed in the digestive tracts of 91 tiger snake specimens and viscera from the Western Australian Museum.

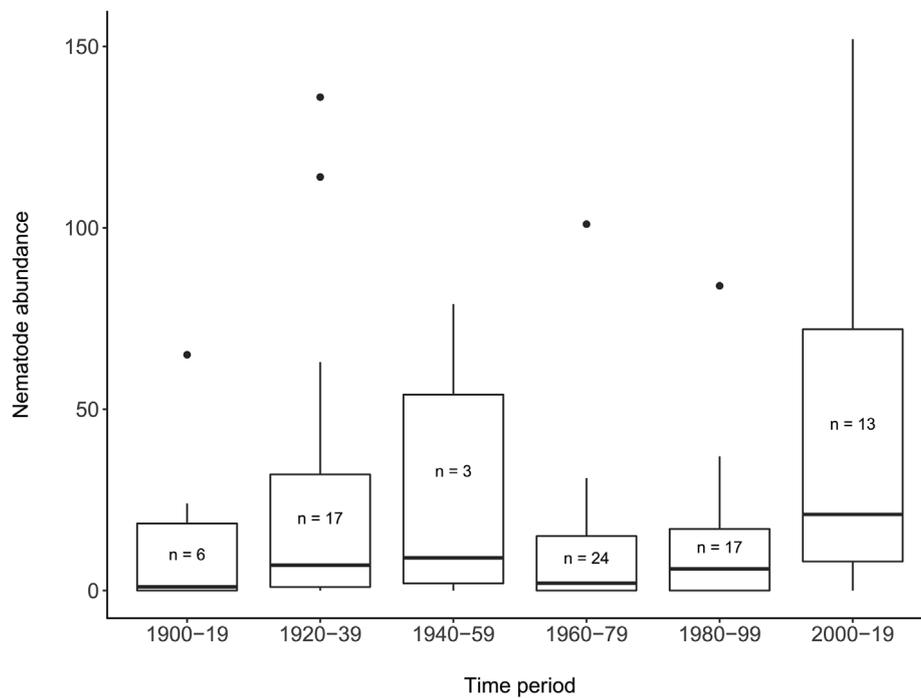| Taxon	No. of individuals	Percentage of prey
Frogs		86.8%
Limnodynastes dorsalis	11	
Litoria sp.	9	
Pseudophryne sp.	3	
Heleioporus sp.	3	
Unidentified	20	
Mammals		5.7%
Mus musculus	1	
Unidentified rodent	2	
Reptiles		1.8%
Actritoscincus trilineatus	1	
Birds		5.7%
Unidentified	3	
Fish		1.8%
Unidentified	1	

Fig. 2. Abundance (mean number nematodes per snake) of stomach nematodes in adult SW WA tiger snakes based on specimen collection time period. Bars represent standard errors and dots represent outliers, n = sample size for each period.

whole body specimens contained infections of 40 + individuals of unidentified helminths encysted throughout the muscle wall. Nematode abundance varied greatly both spatially (Fig. 1) and temporally (Fig. 2). We found no significant correlations between nematode abundance and distance to urban centre, year of collection, distance to wetland or any climatic variables except for mean maximum temperature ($r = 0.257$, $p = 0.002$).

3.3. Probability of nematode infection

MAXTEMP and MINTEMP highly correlated with MEANTEMP ($r = 0.825$, $p < 0.001$ and $r = 0.903$, $p < 0.001$ respectively), and were excluded from the global model. The global model included the variables: DUC, distance to wetland, year (of collection), DUC with year as an interaction (D*Y), MEANTEMP, RAIN, TWI and SVL. Seven top models (ΔAICc < 2) were produced, which frequently identified the variables distance to wetland, mean annual precipitation and TWI (Tables 3 and 4). DUC, D*Y and MEANTEMP were not present in any of the top models. The three water-related variables (distance to wetland, RAIN and TWI) were the strongest predictors of nematode infection, as they occurred in many of the top models whereas year and SVL were only in one or two top sub-models. We found an inverse relationship between probability of nematode infection and the three water-based variables (Fig. 3). The probability of nematode infection decreased

(from over 0.8 to below 0.3) for snakes collected away from wetlands; however, nematode infection increases in areas with lower rainfall (infection probability of 0.9 in areas with mean annual precipitation around 400 mm dropping to 0.3 when precipitation is over 1100 mm), and TWI (infection probability dropping from 0.9 to 0.3 with increasing TWI).

4. Discussion

We used natural history collections to investigate the spatial and temporal influence that multiple climatic, environmental and urbanisation variables have on the prevalence and abundance of parasitic nematodes in a large Australian elapid snake. We found that the probability of tiger snake infection with nematodes increased with proximity to wetland sites but declined with increasing rainfall and topographic wetness. Thus, our prediction that tiger snake nematode prevalence and abundance would be higher closer to wetlands was supported. Interestingly, we did not detect any influence of distance to urban centres on the probability of infection.

Urbanisation results in a suite of novel selection pressures for native fauna (French et al., 2018; McKinney, 2008), influencing the health, fitness, and parasite abundance of many taxa (Bradley and Altizer, 2007; French et al., 2008; Giraudeau et al., 2014; Winchell et al., 2019). Here, we found that water availability was more strongly associated

Table 3

Seven top models and the null model identifying the strongest predictor variables of nematode infection based on ΔAICc and weight (Dis.W = Distance to wetland, D*Y = interaction between DUC and year and M.Temp = mean annual temperature).

	DUC	Dis.W	D*Y	M.Temp	RAIN	SVL	TWI	Year	logLik	AICc	Δ	weight
Mod1	–	◆	–	–	◆	–	◆	–	−40.38	89.31	0	0.057
Mod2	–	◆	–	–	◆	–	–	–	−41.94	90.21	0.90	0.036
Mod3	–	◆	–	–	◆	–	◆	◆	−39.85	90.54	1.23	0.031
Mod4	–	–	–	–	◆	–	–	–	−43.31	90.79	1.48	0.027
Mod5	–	◆	–	–	◆	◆	◆	–	−40.03	90.90	1.59	0.026
Mod6	–	–	–	–	◆	–	◆	–	−42.44	91.21	1.90	0.022
Mod7	–	◆	–	–	◆	◆	–	–	−41.37	91.29	1.98	0.021
Null	–	–	–	–	–	–	–	–	−45.12	92.29	2.98	0.013

Table 4
Standard errors for the strongest predictor variables for the top seven models. Reported as estimate (standard error).

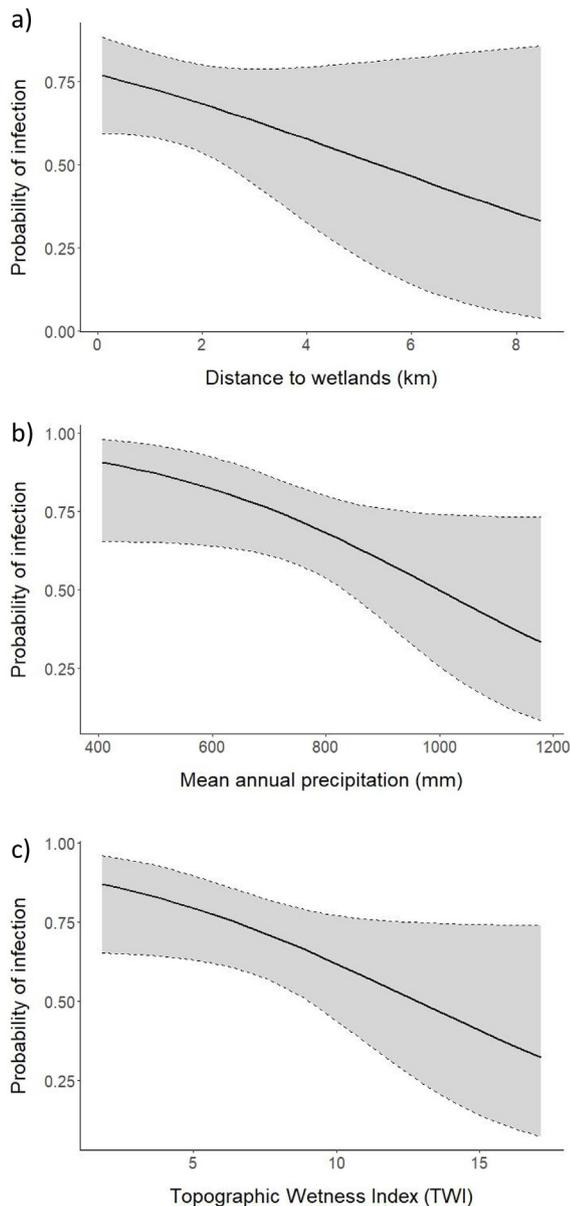|	Intercept	Dis.W	RAIN	SVL	TWI	Year
Mod1	1.12 (0.29)	−0.56 (0.27)	−0.61 (0.29)	–	−0.47 (0.27)	–
Mod2	1.07 (0.27)	−0.43 (0.26)	−0.60 (0.28)	–	–	–
Mod3	1.13 (0.29)	−0.61 (0.28)	−0.62 (0.28)	–	−0.57 (0.29)	−0.31 (0.30)
Mod4	1.03 (0.27)	–	−0.49 (0.27)	–	–	–
Mod5	1.13 (0.29)	−0.54 (0.27)	−0.64 (0.29)	0.22 (0.27)	−0.44 (0.27)	–
Mod6	1.06 (0.27)	–	−0.47 (0.27)	–	−0.34 (0.25)	–
Mod7	1.09 (0.28)	−0.43 (0.26)	−0.64 (0.29)	−0.29 (0.27)	–	–

Fig. 3. Probability of tiger snake stomach nematode infection in relation to a) distance to wetlands, b) mean annual precipitation and c) topographic wetness index (TWI). Shaded areas represents 95% confidence intervals.

with infection than was our metric of urbanisation, suggesting that urbanisation is perhaps less important than biotic environmental variables in determining the relationship between nematode infection and tiger snakes in this region. Importantly, our data suggests that wetlands in drier climate areas are strongly related to nematode parasitism in this species of snake.

Our hypothesis that the relationship between tiger snakes and the complex life cycle of the nematode *O. pyrrhus* would be sensitive to urbanisation (at least for our urbanisation metric: distance to urban centres) was not supported. Tiger snakes that were collected closer to urban centres were not found to have higher infection rates or abundance of infection from nematodes relative to snakes collected in non-urbanised areas; and although the sample size is small we did not detected a change in parasitism over 100 years. Urban wetlands in SW WA have been fragmented, polluted and subjected to modification of structure and hydrology (Davis and Froend, 1999; Kobryn, 2001; Lund, 1992). These wetlands (especially those associated with the Swan Coastal Plain) are naturally ephemeral and seasonal drying may remove (via desiccation) a large proportion of nematode eggs before consumption by a host (Perry, 1989; Wharton, 1980). Dredging activities have, however, led to some urban wetlands becoming permanently inundated with water, allowing nematodes and their hosts to persist year-round. Permanent water and urban run-off also allows a suite of contaminants to persist which snakes potentially bioaccumulate, putting stress on their immune system, as has been recorded in other taxa (Martin et al., 2010; Patz et al., 2000; Riley et al., 2007). Our findings with respect to urbanisation may be due to a number of factors. The cities of SW WA used in this study are relatively small compared to other cities in Australia. The degree of urbanisation may not have been strong enough to influence parasitism in tiger snakes, and the lack of samples from recent decades following the increase of Perth's metropolitan area by 45% since 1990 (MacLachlan et al., 2017) may not be adequate to identify more recent changes. Alternatively, it is possible that intensity of parasite infection is more relevant to host health than is the presence/absence of nematodes, as the five snakes we found in poor body condition had some of the highest intensities of infection (72–152 individuals). While the restrictions on samples sizes meant that we were unable to determine if nematode intensity had changed over time, it is possible that larger sample sizes and a well-designed sampling/collection methodology would allow for a more detailed analysis into whether nematode intensity varies with urbanisation and other environmental variables, and how this impacts snake health.

As frogs are probably the main intermediate host, we also hypothesised that nematode prevalence and infection would be greater if the snakes were collected within or close to wetlands. Our results found higher probability of infection close to wetlands, which suggest a higher frequency of exposure to frogs as an infected food source. The diet and parasite infection of other snakes supports this hypothesis: *O. pyrrhus* has been detected in Western brown snakes (*Pseudonaja mengdeni*), mulga snakes (*Pseudechis australis*) and bardick (*Echiopsis curta*) (Jones, 1978, 1980), although most infections have been detected in tiger snakes. All these species are known to predate on frogs (Madsen and Shine, 1994; Shine, 1987b). Dugites (*Pseudonaja affinis*) are the only other large snake parapatric with tiger snakes and *O. pyrrhus* has not been recorded in them (Ashleigh Wolfe, pers. comm.; Jones, 1978, 1980). Mainland tiger snakes feed heavily on frogs (Aubret et al., 2006; Shine, 1987a and Table 2) whereas dugites prefer reptiles and mammals (Shine, 1989; Wolfe et al., 2018) and thus are not exposed to infection. Additionally, tiger snakes introduced from WA mainland to Carnac Island, WA, a desert island without frogs, are exempt of

nematodes (Aubret, 2005). Thus, diet offers a convincing explanation as the source of nematodes.

Somewhat counter to our initial predictions, our results also indicate that the probability of nematode infection increases in areas with less rainfall and lower topographic wetness. This suggests that wetlands, particularly more permanent ones in drier areas, are important drivers of infection in tiger snakes. While we can only speculate, one possibility is that tiger snakes may be more likely to disperse from wetlands in areas of higher rainfall. Heavy urbanisation can decrease precipitation and moisture availability in the landscape by replacing vegetated land with infrastructure (Zhang et al., 2014), as well as funnelling the remaining water into permanent wetlands. Tiger snakes occupying the more northern limit of their range, such as Perth, are at risk from a range of environmental modifications that may increase parasitism such as restriction to isolated wetlands, reduced rainfall and overall drier conditions (McFarlane et al., 2012; Rotstayn et al., 2010).

In addition, we found a slight positive correlation between mean annual maximum temperature and nematode abundance. Due to the limited sample size we interpret this result as a potential trend, and discuss the possible outcomes a changing environment could have on temperature influenced parasitism. Temperature drives activity in both nematodes as poikilotherms and their snake hosts as ectotherms. Exposure to higher maximum temperatures may have an impact on nematode abundance in a number of ways. Regions with higher maximum temperatures allow snakes to reach their preferred body temperature quickly (Schwaner, 1989; Shine, 1979; Wang et al., 2002). Attaining preferred body temperature earlier in the day gives snakes a longer window of activity each day, including foraging time. Consequently this increases the feeding rate and period of activity for parasitic nematodes (assuming adult *O. pyrrhus* is a snake-specific parasite and has a very similar preferred body temperature). Nematodes operating at their optimum temperature maximise reproductive output (Morgan and van Dijk, 2012), and warmer conditions can increase parasite developmental rates in eggs and intermediate life stages (Griffin, 1993; Kutz et al., 2001, 2004; van Dijk et al., 2008).

Urbanisation through infrastructure and deforestation causes an increase in temperature through the urban heat island (UHI) effect (Arnfield, 2003), and some parasites and diseases have been shown to be positively influenced as a result (Buczek et al., 2014; Trajer et al., 2014). If the UHI effect were a significant driver of nematode parasitism we would expect to see abundance and intensity increase in specimens collected closer to urban centres, and in more recent years. However, our urban sample size with its lack of recent specimens was too small to accurately detect potential changes. Perth is the largest city of SW WA and yet is still relatively small in comparison to other major cities of the world (Newman, 2016), subsequently it still has a low UHI effect (Camilloni and Barros, 1997; Earl et al., 2016). Future studies using a more robust dataset of temperatures, with higher sample sizes and urbanisation scores may be able to accurately detect influences of temperature and the UHI effect on parasitism.

Some limitations in our study should be noted. We were restricted by the number of specimens we were allowed to destructively sample, by juveniles not being used in the statistical analyses, and gaps in the spatial and temporal scale of the natural history collection. The three specimens collected post-2003 were all collected from heavily urbanised wetlands and were all in poor body condition containing a high intensity of nematodes (> 79/snake). While this is a small sample size these snakes potentially indicate an increase in the infection rates in urban areas over the last two decades. It is also possible that these specimens were collected as opportunistically found carcasses suffering from poor body condition. This would bias the sample and not be an accurate representation of the nematode intensity of the entire urban snake population. Such limitations are common when using natural history collections for ecological studies (Lister and Climate Change Research Group, 2011).

The impact of urbanisation on habitats, climate, organisms and their life cycles is complex and difficult to elucidate fully. While we found a strong influence of water availability on the probability of infection with nematodes, we did not observe any significant influence from our particular urbanisation metric. We suggest that modifications to urban wetland structure and hydrology, and water availability in the landscape is driving parasitic nematode prevalence in tiger snakes, with further study required to examine fine-scale processes. As it is likely that prey items such as frogs are the key infection source for tiger snakes, the effects of urbanisation on frog abundance is also likely to be relevant. This study 1) demonstrates that proximity to wetlands and climatic factors are influencing nematode prevalence, 2) nematode abundance is potentially influenced by warmer temperatures, 3) highlights how these influencing variables are sensitive to a changing environment, specifically urbanisation, and 4) emphasises the importance (as well as limitations) of museums and the systematic collection of specimens for detecting spatial and temporal changes in ecology.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Acknowledgements

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