

**School of Science  
Department of Environment & Agriculture**

**The Ecology of Perth's Urban Reptiles Using a Snake and  
Skink as Models**

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**This thesis is presented for the Degree of  
Doctor of Philosophy  
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.

This project received additional funding from crowd-sourced funding via Kickstarter.com, and a Holsworth Wildlife Research Endowment.

The research presented and reported in this thesis was conducted in accordance with the National Health and Medical Research Council National Statement on Ethical Conduct in Human Research (2007, updated March 2014) and Australian Code for the Care and Use of Animals for Scientific Purposes 8<sup>th</sup> Edition (2013). The proposed research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Numbers AEC\_2014\_30 (Chapter 4 and Chapter 7). The study also received human ethics approval from the Curtin University Human Research Ethics Committee (EC00262), Approval Numbers #HRE2016-0030 and #HR91/2015 (Chapter 5), and #RDSE-09-15 (Chapter 6). Additional approvals were provided by the Western Australian Department of Biodiversity, Conservation and Attractions, Approval Numbers #SF010895 (Chapter 5), and #1-32-2 (Chapter 4 and Chapter 7), and Cockburn City Council (Chapter 5). Snakes were collected for Chapter 3 and Chapter 4 using Department of Biodiversity, Conservation and Attractions Reptile Removalist license #RR2020.

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Date: 30/11/2017



# Author Declaration

Chapters 2-7 have been prepared as manuscripts for peer-reviewed publication in scientific literature. These chapters are reproductions of the submitted/prepared manuscripts, with the exception of formatting consistent with the thesis.

The study presented in Chapter 2 was submitted for peer review by the Journal of Zoology on 28<sup>th</sup> September 2017:

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All authors contributed critically to the drafts and gave final approval for publication for the manuscripts presented in Chapters 2-7. The other authors of the manuscripts presented in this thesis accept and agree with the author contribution statements.

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*This thesis is dedicated to the charismatic snakes and lizards that sparked my imagination.*





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# General Abstract

Urbanisation presents unique challenges for wildlife and drives human-wildlife interactions, making it increasingly more important to understand the factors influencing the success, or otherwise, of animal taxa around cities. Urban greenspaces are important amenities for humans and animals alike, and humans using these spaces may incidentally encounter a free-living animal. Reptiles remain underrepresented in studies of urbanisation effects, despite their diversity of species and broad distribution across nearly every continent. Attitudes towards reptiles can also be highly polarising: a harmless lizard that is perceived as endearing may be approached in an entirely different manner to a venomous snake. Snakes are often perceived as nuisance or 'problem' animals near urban areas, even when they are useful pest controllers (e.g. for rodents) and are managed via translocation away from a private residence. Translocated snakes may experience modified behaviour, space use and survivorship, and few studies have investigated the impacts of translocation within a metropolitan area. In contrast, lizards may encounter a human within private residences and urban greenspaces, where interactions rarely result in translocations. In such encounters, being able to habituate through either tolerance or vigilance towards humans is necessary to persist within urban areas. Other interactions occur on roads, where reptiles bask, scavenge food, and cross between fragmented habitats but are exposed to the risk of death from traffic. Understanding perceptual biases towards reptile taxa may help determine management strategies as urban sprawl increases.

In this study, I first tested whether the degree of urban adaptation in reptiles was correlated with specific behavioural or life history traits across 440 reptile species (Chapter 2). Reptile groups had different degrees of urban adaptation: lizards were most likely described as urban adapters, snakes as periurban adapters, and turtles/tortoises as urban oblivious. Twelve factors fit the top models explaining degree of urban adaptation after phylogenetic correction. Reptile urban adapters were more likely to be intraspecifically combative/territorial, use a variety of diet items, be endemic and invasive to a variety of continents, large in body size with a relatively long tail, use a variety of habitats and habits, lay eggs, have sexual dimorphism, be diurnal, and lack sex specialisation. There are some similarities in the lifestyle requirements for urban adaptation in reptiles, but understanding the differences between reptiles and other taxa is likely to be important for successful urban conservation and management.

I then assessed the impacts of urbanisation on the behavioural ecology of two focal reptile species: the venomous dugite (*Pseudonaja affinis*, Elapidae) and harmless bobtail lizard (*Tiliqua r. rugosa*, Scincidae). I investigated how urbanisation affects the feeding ecology of dugites (Chapter 3): larger snakes had larger prey present, a greater number of prey items, and a greater diversity of prey, while urban dugites were relatively smaller (snout-vent length) than non-urban specimens, and females were relatively lighter than males; urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. I also observed the spatial ecology of dugites (Chapter 4): translocation influenced space use of dugites and detrimentally affected their survivorship; and compared to residents, translocated snakes had larger activity ranges, travelled greater distances, and suffered 100% mortality. Urban dugites,

which are considered one of the best-adapted urban reptile species in Perth, do not follow the typical diet pattern (i.e. exploiting increased food supplementation) of other urban-adapted carnivores, and were negatively impacted by translocation.

Next, I investigated the impacts of human attitudes towards urban reptiles. I assessed public attitudes towards reptiles on roads (Chapter 5): respondents to an online survey held high welfare values for animals on roads and felt that they were very likely to rescue animals, but motorists observed in the field generally ignored reptiles on a roadside, and modelling showed that crossing roads is risky for reptiles. I also tested the ability of the general public to correctly identify commonly-encountered reptile species (Chapter 6): overall surveyed respondents were able to identify live specimens on display, and adults were better at identifying venomous snakes than were children, but most reported snake-sightings across Western Australia lacked any identification attempt during actual interactions with free-living animals. Being able to correctly identify reptiles may influence the responses of motorists to reptiles on roads, affecting the likelihood of a reptile being killed when crossing roads. Accurate identification also benefits public health, potentially reducing dangerous encounters between humans and venomous snakes and allowing for correct treatment for snake bites.

Finally, I examined the behaviour of bobtails exposed to repeated encounters with humans (Chapter 7). Bobtails across a range of levels of habitat modification in urban spaces tended to attempt to flee from encounters with humans, and bobtails already moving when encountered were most likely to display this response. Urban bobtails were vigilant to human encounters, suggesting that coming across humans in urban areas is an additional source of stress and disturbance. Overall, living in an urban area is risky for reptiles, which are detrimentally affected by negative attitudes, persecution from the general public, and constant disturbances. The two focal species appear to lack the behavioural flexibility needed to persist within Perth, and rather mitigate disturbances by minimising interactions with humans. Current practices of translocation to manage reptiles and ongoing conflicts with reptiles on roads (usually as a result of negative human attitudes) negatively impact urban-adapted reptiles, and education of the general public will help to ensure these species are properly managed to allow their persistence within the urban sprawl.

# Table of Contents

<b>Chapter 1. General Introduction</b> .....	<b>1</b>
1.1 <i>Thesis overview</i> .....	2
<b>Chapter 2. What traits influence degree of urban adaptation? A global analysis of reptiles</b> .....	<b>5</b>
2.1 <i>Abstract</i> .....	6
2.2 <i>Introduction</i> .....	6
2.3 <i>Materials and methods</i> .....	7
2.3.1 <i>Dependent variable</i> .....	7
2.3.2 <i>Independent variables</i> .....	8
2.3.3 <i>Statistical analysis</i> .....	10
2.4 <i>Results</i> .....	11
2.5 <i>Discussion</i> .....	14
2.5.1 <i>Traits that were correlated with urban adaptation</i> .....	15
2.5.2 <i>Traits that were not correlated with urban adaptation</i> .....	19
2.5.3 <i>How can we help the success of urban reptiles?</i> .....	20
<b>Chapter 3. Does urbanisation influence the diet of a large snake?</b> .....	<b>23</b>
3.1 <i>Abstract</i> .....	24
3.2 <i>Introduction</i> .....	24
3.3 <i>Materials and methods</i> .....	25
3.3.1 <i>Study species</i> .....	25
3.3.2 <i>Dissections</i> .....	26
3.3.3 <i>Classification of urban and non-urban sites</i> .....	28
3.3.4 <i>Analyses</i> .....	28
3.4 <i>Results</i> .....	30
3.4.1 <i>Prediction 1: Urban dugites will more frequently contain prey than non-urban dugites, and have eaten larger meals</i> .....	30
3.4.2 <i>Prediction 2: Urban dugites will eat proportionally more introduced prey than non-urban dugites</i> .....	32
3.4.3 <i>Prediction 3: Urban dugites will eat a less-diverse range of prey species than non-urban dugites</i> .....	32
3.4.4 <i>Prediction 4: Urban dugites will be relatively larger than non-urban dugites</i> .....	32
3.5 <i>Discussion</i> .....	33
3.5.1 <i>Sampling bias</i> .....	34
3.5.2 <i>Application of urban ecology theory to snakes</i> .....	35

<b>Chapter 4. Impacts of translocation on a large urban-adapted venomous snake .....</b>	<b>37</b>
4.1 <i>Abstract</i> .....	38
4.2 <i>Introduction</i> .....	38
4.3 <i>Materials and methods</i> .....	40
4.3.1 Study species .....	40
4.3.2 Telemetry packages .....	40
4.3.3 GPS attachment .....	40
4.3.4 Radio-tracking .....	42
4.3.5 Analyses .....	43
4.4 <i>Discussion</i> .....	46
4.4.1 Comment on the efficacy of GPS tracking snakes .....	47
4.4.2 Conclusions .....	48
 <b>Chapter 5. Surveying attitudes towards reptiles on roads: questionnaire responses do not directly translate to behavioural action .....</b>	 <b>51</b>
5.1 <i>Abstract</i> .....	52
5.2 <i>Introduction</i> .....	52
5.3 <i>Materials and methods</i> .....	54
5.3.1 Online surveys – attitudes towards animals on roads .....	54
5.3.2 Field experiment – responses to reptiles on a roadside .....	55
5.3.3 Modelling – strike probability of reptiles crossing roads .....	56
5.4 <i>Results</i> .....	57
5.4.1 Online surveys – attitudes towards animals on roads .....	57
5.4.2 Field experiment – responses to reptiles on roads .....	57
5.4.3 Modelling – strike probability of reptiles crossing roads .....	60
5.5 <i>Discussion</i> .....	60
 <b>Chapter 6. What snake is that? Common Australian snake species are frequently misidentified or unidentified .....</b>	 <b>63</b>
6.1 <i>Abstract</i> .....	64
6.2 <i>Introduction</i> .....	64
6.3 <i>Materials and methods</i> .....	66
6.3.1 Snake identification survey .....	66
6.3.2 Calls to Wildcare Helpline .....	68
6.3.3 Statistical analysis .....	68
6.4 <i>Results</i> .....	68
6.4.1 Snake identification survey .....	68
6.4.2 Calls to Wildcare Helpline .....	69

6.5	<i>Discussion</i> .....	70
<b>Chapter 7. Responses of free-living urban-adapted lizards to escalating levels of human observation</b> .....		
<b>73</b>		
7.1	<i>Abstract</i> .....	74
7.2	<i>Introduction</i> .....	74
7.3	<i>Materials and methods</i> .....	76
7.3.1	Statistical analyses .....	77
7.4	<i>Results</i> .....	77
7.5	<i>Discussion</i> .....	78
<b>Chapter 8. General Discussion</b> .....		
<b>81</b>		
8.1	<i>Conclusion</i> .....	84
<b>Bibliography</b> .....		
<b>85</b>		





# List of Appendices

<b>Appendix 1. Dataset used for analysis comparing the degree of urban adaptation for turtles/tortoises, lizards and snakes (Chapter 2)</b> .....	<b>107</b>
<i>Appendix 1.1 References for Appendix 1.</i> ....	143
<b>Appendix 2. Phylogeny used for analysis comparing the degree of urban adaptation for turtles/tortoises, lizards and snakes (Chapter 2)</b> .....	<b>161</b>
<i>Appendix 2.1 References for Appendix 2.</i> ....	166
<b>Appendix 3. Additional methods descriptions</b> .....	<b>167</b>
<i>Appendix 3.1 Correlation analysis (Chapter 2)</i> .....	167
<i>Appendix 3.2 Additional accessed data (Chapter 3)</i> .....	168
<i>Appendix 3.3 Dugite GPS and VHF radiotelemetry (Chapter 4)</i> .....	171
<i>Appendix 3.4 Road field experiments (Chapter 5)</i> .....	173
<i>Appendix 3.5 Reptile identification survey (Chapter 6)</i> .....	177
<b>Appendix 4. Publications arising from this research</b> .....	<b>178</b>
<i>Appendix 4.1 Peer-reviewed papers arising from this research</i> .....	178
<i>Appendix 4.2 Conference presentations arising from this research</i> .....	178



# List of Figures

<b>Figure 2.1.</b> Levels of urban adaptation for reptile families (n species), sorted phylogenetically. Largest positive residuals ( $\chi^2$ test) indicate the level of urban adaptation that is most associated with each family: U = urban adapter; P = periurban adapter; O = urban oblivious; and A = urban avoider. *Largest positive residual for each urbanisation category. ....	12
<b>Figure 3.1.</b> Collection locations of dugite ( <i>Pseudonaja affinis</i> ) specimens used for this study: a) urban specimens (around the Perth metropolitan area where human population density exceeded 500 persons·km <sup>2</sup> at the time of the nearest Australian Bureau of Statistics census) are indicated by black dots, non-urban specimens are shown with grey squares; distribution of dugites containing prey in gut contents for a) urban and b) non-urban specimens. Legend: cross - non-native rodents; diamond - native rodents; plus – reptiles. ....	26
<b>Figure 3.2.</b> Comparison of urban and non-urban specimens collected over time. Only three snakes were collected prior to the 1950s: two urban snakes in the 1920s and one non-urban snake collected from the 1930s. Data represented as Decade (n). ....	31
<b>Figure 3.3.</b> Residual body mass (compared with SVL) for a) urban and non-urban dugites and b) specimens of each sex. Residuals were calculated using a linear regression of log-SVL against log-body mass. ....	32
<b>Figure 4.1.</b> Translocated dugites (black circles) used significantly larger areas of habitat (calculated as 95% and 50% kernel Brownian Bridge [KBB] home range), but did not travel greater distances than residents (open circles). Data corrected for the number of days tracked for each individual. ....	45
<b>Figure 5.1.</b> Mean scores for a) welfare, b) vehicle, c) safety, and d) rescue by respondents. Taxa had a significant effect for all factors. Separate letters for each factor indicate significant differences between taxa. ....	59
<b>Figure 5.2.</b> Probability of a reptile being struck by a motor vehicle while crossing a road at slow and fast velocities (see Methods for calculations). Legend: solid line = 1 m total length dugite, dashed line = 0.35 m total length bobtail, open circle = average road density calculated from our study, black circle = road density of our study road provided by City of Cockburn (2017). ....	60
<b>Figure 6.1.</b> Reptile species displayed for the snake identification survey: 1) dugite, 2) tiger snake, 3) south-west carpet python, 4) western blue-tongue lizard, 5) bobtail lizard. Photo credits: AK Wolfe (1, 5), Marcus Cosentino (2, 3), and Damian Lettoof (4). ....	67
<b>Figure 6.2.</b> Percentage of correct responses overall for 263 Western Australians identifying five reptiles. Legend: black = “what is it called?”, grey = “is it a snake?”, unfilled = “is it venomous?”. Different letters denote significant differences for each factor. ....	69
<b>Figure 6.3.</b> There was a significant effect of a) sex, b) age, and c) experience keeping reptiles as pets on percentage of correct responses for Western Australians identifying the common name of five reptiles. Overall, men (a) and respondents with experience keeping reptiles	

as pets (c) identified more species correctly. Adults (b) correctly identified dugites more than children. .... 70

**Figure A.3.3.1.** Attachment of telemetry package (heat-shrink sealed) onto a dugite tail: a) position of the silicone tubing threaded with fishing line; b) inserting the second silicone tube and anchoring the telemetry package; and c) anchored telemetry package, just prior to trimming the fishing line – the snake was then immediately taken to its release location. 172

**Figure A.3.3.2.** a) Released dugite (snake #2) following telemetry package attachment; b – d) shows the snake successfully traversing a metal fence unimpeded by the external package attached..... 172

# List of Tables

<b>Table 2.1.</b> Key traits identified to classify degree of urban adaptation for reptiles in this study (developed from Blair, 1996; Kark et al., 2007; Grant et al., 2011). *Some descriptions were identical for traits F (2 and 3) and G (1 and 2; 3 and 4); we used the more urban-adapted values where applicable. Each species was classified as belonging to the urban category with the highest tallied number (mode) of the seven traits; where calculating the mode did not determine a single category, we selected the more urban-adapted category. ....	9
<b>Table 2.2.</b> Factors used in multinomial logit-linked multiple regression for multimodel analysis of best models using AICc. ....	10
<b>Table 2.3.</b> Best models for factors correlated with degree of urbanisation. Mean standardised $\beta$ values adjusted for Akaike weight summed for top models ( $\bar{x}\beta \cdot w_i$ ) can be used to infer correlation between each factor and degree of urbanisation. Positive $\beta$ values trend towards urban adaptation, while negative $\beta$ values trend towards urban avoidance. Scores for each factor are explained in Table 2.2. For all models, $P < 0.0001$ . ....	13
<b>Table 3.1.</b> Diet of dugites collected from urban and non-urban locations. Urban snakes ate a similar diversity of prey. Collective number of species and groups identified to the finest possible scale are represented by n for each class and family. ....	27
<b>Table 3.2.</b> Length and body mass measurements for dugites by location and sex for dugite specimens with complete data. *Of the 229 specimens for which we were unable to determine sex, 226 were juveniles, SVL >40 cm. ....	29
<b>Table 3.3.</b> Summary of multiple regression analyses testing dependent factors addressing the four predictions of this study. Once the effects of body size and potential biases (sex, season, year of collection) were accounted for, urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. Beta ( $\beta$ ) values are provided for significant findings. $0 < \beta$ represents a trend towards: a) non-urban snakes for location, b) males for sex, and c) larger snakes for log-SVL. ....	31
<b>Table 4.1.</b> Capture information, times of monitoring, kernel Brownian bridge (KBB) estimation of spatial use, survival, and fates of six resident and four translocated dugites during the GPS tracking experiment. Overall means presented $\pm$ standard error. *Relocation distance was measured as straight-line distance between original capture and release locations. ....	41
<b>Table 4.2.</b> Habitat characters and approximate patch sizes for capture and release sites in the study. Legend: IM = inner metropolitan area; OM = outer metropolitan area. ....	44
<b>Table 5.1.</b> Summary of linear model analyses testing dependent factors for the online survey section of this study. Significant factors are in bold. ....	58
<b>Table 6.1</b> Identities of ‘problem’ snakes referred to the Western Australian Wildcare Helpline from 2007-2017 (inclusive). ....	71



# List of Abbreviations

+ve	Positive
-ve	Negative
AIC <sub>c</sub>	Akaike's Information Criterion with a correction for finite sample sizes
$\chi^2$	Chi square
$\chi^2_{MH}$	Cochran-Mantel-Haenzel chi square, test for 3-way chi square interactions
df	Degrees of freedom
DOP	Dilution of precision, location error for GPS data
FIC	Felsenstein's Independent Contrasts
GLMM	Generalised linear mixed model
GPS	Global positioning system
ID	Internal diameter
IRTtree	Item Response Tree, for analysing hierarchical behaviour data
KBB	Kernel Brownian Bridge, estimation for activity range
L Ratio	Likelihood ratio
log	Logarithmic transformation
MANOVA	Multivariate analysis of variance
max	Maximum
Mb	Wet body mass
min	Minimum
M <sub>prey</sub>	Wet body mass of prey items
n	Number of samples measured
PDAP	Phenotypic Diversity Analysis Programs, package for Mesquite
PERMANOVA	Non-parametric multivariate analysis of variance
SD	Standard deviation
SE	Standard error
Shannon H'	Diversity index
spp.	Species
SVL	Snout-vent length
TL	Total length
VHF	Very high frequency
WAM	Western Australian Museum
$w_i$	Akaike model weight, the AIC <sub>c</sub> value divided by the sum of all AIC <sub>c</sub> values
$\bar{x}$	Mean
$\bar{x}\beta \cdot w_i$	Mean standardised beta values adjusted for Akaike model weight
$\beta$	Beta
$\beta \cdot w_i$	Adjusted beta values for Akaike model weight
$\Delta AIC_c$	Delta AIC <sub>c</sub> , the difference between the mean AIC <sub>c</sub> value and of a model and the overall best fit model





# Chapter 1. General Introduction

Urbanisation presents unique challenges for wildlife through modification of habitats, species interactions, and human encounters. Land clearing for urban development destroys, degrades and fragments habitats (Dickman, 1987; Jellinek, Driscoll & Kirkpatrick, 2004; Garden, McAlpine & Possingham, 2010), while construction of buildings, roads, and fences segments the landscape (Andrews & Gibbons, 2005; Hibbitts *et al.*, 2017). Furthermore, chemicals (Coffin, 2007; Weir, Suski & Salice, 2010), light (Sol, Lapiedra & González-Lagos, 2013), and noise (Forman & Alexander, 1998) pollute the environment. Urban development therefore commonly leads to local extinctions for sensitive flora and fauna species (e.g. How & Dell, 1994; Williams *et al.*, 2005), while synanthropic (human-dependent) species, which are often invasive, proliferate and dominate (Blair, 1996; McKinney, 2008), increase resource competition (Williams, Pernetta & Horrocks, 2016) and alter predation dynamics (Loss, Will & Marra, 2013; Holderness-Roddam & McQuillan, 2014). For the relatively few native species that persist in urban areas, interactions with humans are nearly inevitable, either by incidental encounters in gardens and parks (Burger, 2003; Bell, 2010), or when animals attempt to cross the roads bisecting important habitats (Hels & Buchwald, 2001; Ciesiolkiewicz, Orłowski & Elzanowski, 2006; Steen *et al.*, 2006). As a result, urbanisation is a key force driving global native species decline (McKinney, 2006; Shochat *et al.*, 2006).

The challenges of urbanisation are not likely to decline in the foreseeable future. By 2030, two-thirds of the global population will become urbanised (United Nations, 2016). As urban expansion spreads, most habitat types will be affected by human activity, making urban areas increasingly important refugia sites for wildlife living alongside humans. Areas of intermediate disturbance, such as gardens, parks, and undeveloped tracts of land (e.g. habitats fringing roads, and empty suburban blocks; 'greenspaces') allow for maximal potential species diversity by providing regular sources of food and shelter, while minimising competitive exclusion through consistent, but periodic habitat change (Connell, 1978; Johst & Huth, 2005). Some species are able to make use of spaces with greater disturbance levels and fewer available resources, however, such as around and inside occupied human dwellings (e.g. Fearn *et al.*, 2001; Das, 2010; Mollov, 2011). It is these species with the greatest ability to persist within urban areas despite the challenges presented to them that are most likely to avoid extinction in the midst of global anthropogenic habitat changes.

Most studies of urban adaptation have focused on birds and mammals (see Chace & Walsh, 2006; Bateman & Fleming, 2012 for reviews), with very little known of the ability of reptiles to adapt to city-living. For decades, the adaptive flexibility of reptiles has been considered low (e.g. Bradshaw, 1988), and success outside of habitats to which they are adapted is reliant on having the largest brain relative to body size (Amiel, Tingley & Shine, 2011). However, urban adaptation is not a factor of brain size or behavioural flexibility, but a complex combination of life history traits (Kark *et al.*, 2007). Abundance in urban areas, the most-used measure to predict urban adaptation for other taxa (Blair, 1996; McKinney, 2008), is difficult to quantify for reptiles due to

their often cryptic natures (e.g. Whitaker & Shine, 1999a); this makes identifying the impacts of urbanisation a challenge.

Australia, home to the greatest global reptile diversity with over 900 described species (Chapman, 2009; Uetz, 2015), also has one of the world's recognised biodiversity hotspots in south-west Western Australia (Myers *et al.* 2000). The city of Perth, a uniquely-isolated metropolitan area sprawling 300 km along the coastline is located within this biodiversity hotspot and surrounded by conservation-significant habitats (e.g. banksia-eucalypt woodlands) (Threatened Species Scientific Committee, 2016). This vicinity of the city has been significantly cleared for housing development and agriculture, with only around 10% of native vegetation remaining (Myers *et al.*, 2000). Within the Perth metropolitan area, there are 77 described reptile species (Bush *et al.*, 2010) of varying abundance and habitat preferences. Of these species, two have been identified as iconic and abundant throughout Perth (How & Dell, 1993): the dugite (*Pseudonaja affinis*), a large venomous elapid snake, and the bobtail (*Tiliqua r. rugosa*), a large, relatively slow and well-armoured skink. Both species are diurnal, easily recognisable, and have ranges both within the city and in regional Western Australia (Cogger, 2014). They present a unique opportunity to study the impacts of urbanisation on the ecology of reptiles, and differences in human responses to these two species make an excellent contrast between conservation of an amicable and an inimical species.

## 1.1 Thesis overview

The main objective of the research in this thesis was to determine what, if any, benefits the urban-adapted reptiles of Perth, Western Australia, gain from urbanisation. In this study, I investigate both the biological life histories of these reptiles, as well as the social impacts of human interactions with reptiles. I compare and contrast specific ecological factors on urban individuals: diet, behavioural responses to human encounter, space use, human attitudes, and the impacts of roads. In this thesis I explore these five areas and the broader behavioural impacts of urbanisation on reptiles to add to the emerging area of urban adaptation using the following objectives:

- a) To determine what factors affect urban adaptation for reptiles and build a new reptile-centric framework for urban adaptation based on these factors;
- b) To determine if the diet of an obligate carnivore differs between urban and non-urban conspecifics;
- c) To determine if the activity ranges of urban dugites are affected by urban development and human disturbances;
- d) To investigate the likelihood of a reptile being struck on both the side of the road and during crossing, and to develop an understanding of the attitudes of the general public to reptiles on roads and their likelihood of rescuing them rather than running them over;

- e) To determine if the general public are able to correctly identify common reptile species in south-west Western Australia, if those species are venomous, and if they are snakes, and to determine the most commonly identified snake species encountered in Western Australian properties; and
- f) To investigate the responses of reptiles to human encounters across a gradient of urban modification.

The following chapters have been prepared as manuscripts for peer-reviewed publication in scientific literature.

To understand how dugites and bobtails might benefit from urbanisation, it was first necessary to review the current literature to define urban adaptation for reptiles. Chapter 2 presents a literature review and meta-analysis of the life history traits that may be associated with urban adaptation for reptiles. The review was conducted at a global scale for turtles/tortoises, lizards, and snakes, using independent factors describing diet, life history, habitat, habit, and continent(s) of endemism and invasiveness for each species. Investigating the similarities and differences in the lifestyle requirements for urban adaptation in reptiles, this is the first large-scale peer-reviewed literature review to consider urbanisation within the class Reptilia.

Chapter 2 reveals a significant effect of diet for urban-adapted reptiles: species with a greater variety of diet item types had a higher likelihood of being classified as urban adapters. In Chapter 3, I explore if variation of prey items in an obligate carnivore is significantly affected by urbanisation. I conduct a dietary analysis of dugites from museum and road-killed specimens to compare and contrast the prey items found in urban and non-urban individuals.

Another significant factor affecting urban adaptation in reptiles found in Chapter 2 is the tendency for urban adapters to be territorial. In Chapter 4, I investigate the spatial use of dugites within the Perth metropolitan area, and compare and contrast the activity ranges of established resident snakes and translocated individuals. This chapter also introduces my pioneered tracking method for snakes: using Global Positioning System (GPS) data-loggers, rather than manually collecting all data points with radio-telemetry.

Following the theme of reptile movements in urban landscapes in Chapter 5, I assess the impacts of a landform that was a major obstacle to snakes in Chapter 4: roads. I assess the impacts of roads on reptiles through two studies. Firstly, I investigate the conservation implications of attitudes of the general public towards vehicle-wildlife collisions via an online survey asking Western Australian motorists about their attitudes towards a wide range of animals commonly found on Perth roads. I then quantify behaviours of the general public to reptiles on roads through a field experiment, where I placed rubber model reptiles on an urban roadside and observed motorists' responses, either ignoring the models, attempting to run them over, or attempting to avoid them or to rescue them. I also use mathematical modelling to predict the likelihood of a reptile being struck on the road.

Human attitudes towards reptiles may differ when they are in a close-quarters situation, trying to manage a 'problem' snake on their property. The initial identification of a snake as venomous or harmless can affect a person's responses to 'problem' snakes. In Chapter 6 I test the ability of

the Western Australian public to correctly name and identify venomous and non-venomous reptiles common to the state's south-west. I also determine the most common snake species reported as 'problem' snakes in private residences, and the rate at which snakes are left unidentified by members of the public.

The behavioural responses of reptiles to humans can be observed to determine the behavioural flexibility, or tolerance towards human disturbance, of a species. In Chapter 7, I observe the behavioural responses of bobtails to human encounters of escalating disturbance, assessing the likelihood that urban bobtails can become habituated to anthropogenic disturbance through living near people.

Chapter 8 is a General Discussion, bringing the results of these studies together.

# Chapter 2. What traits influence degree of urban adaptation? A global analysis of reptiles

To understand how dugites and bobtails might benefit from urbanisation, I first assessed the current literature and defined urbanisation and urban adaptation for reptiles. I conducted a literature review and meta-analysis of the life history traits that may be associated with urban adaptation for reptiles. Research investigating urban impacts on wildlife has become increasingly popular since synthesis of the urban adaptation framework for birds in the mid-1990s. Further studies are generally limited to endothermic vertebrates (birds and mammals), which are biologically different to reptiles. As a result, reptiles may drift from established patterns of, and frameworks for, urban adaptation.

This chapter represents the main literature review component for the thesis, where I build a new reptile-centric framework for urban adaptation, and list the species that preliminarily represent urban adapters. However, many reptiles, including those found within urban areas, are understudied, and with greater understanding of the life histories of these cryptic and charismatic fauna, our interpretation of urban adaptation for reptiles will likely change in future.

The study presented in this chapter was submitted for peer review by the Journal of Zoology on 28<sup>th</sup> September 2017:

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2017) What traits influence degree of urban adaptation? A global analysis of reptiles. Journal of Zoology, *in review*.

All authors conceived the ideas and designed methodology; I collected the data; I analysed the data with guidance from PAF; I led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This chapter is a reproduction of the submitted manuscript, with the exception of formatting consistent with the thesis.

## 2.1 Abstract

With a rapidly urbanising world, it is becoming more important to understand the factors influencing the success, or otherwise, of animal taxa around cities. We tested whether the degree of urban adaptation in reptiles was correlated with specific traits. We conducted an analysis of the literature to compare the degree of urban adaptation for a total of 440 reptile species (turtles/tortoises, lizards and snakes) against 16 independent factors describing aspects of body size, life history, diet, habitat, habit, and continent(s) of endemism and invasion for each species. We used an information theoretic approach to generate a set of best-fit models that best explained degree of urban adaptation. Reptile groups had different degrees of urban adaptation: lizards were most likely described as urban adapters, snakes as periurban adapters, and turtles/tortoises as urban oblivious. Twelve factors fit the 15 top models explaining degree of urban adaptation after phylogenetic correction: reptile urban adapters were more likely to be intraspecifically combative/territorial, use a variety of diet items, be endemic and invasive to a variety of continents, large in body size with a relatively long tail, use a variety of habitats and habits, lay eggs, have sexual dimorphism, be diurnal, and lack sex specialisation. We have shown that there are some similarities in the lifestyle requirements for urban adaptation in reptiles, but understanding the differences between reptiles and other taxa is important for successful urban conservation and management.

## 2.2 Introduction

The majority of the world's human population resides in urbanised areas. By 2030, two-thirds of all people are expected to live in cities (United Nations, 2016). With expanding urbanisation across the world, natural landscapes face significant challenges (see McKinney, 2002 for review). Understanding the processes that influence the success, or otherwise, of animal taxa in the face of urbanisation is becoming more important, whether we want to conserve urban populations of such species or whether we want to control them.

Clearing for development and urban expansion destroys key habitat and fragments landscapes, while reduced permeability of urban landscapes due to physical barriers, e.g. roads and fences (Andrews & Gibbons, 2005; Hibbitts *et al.*, 2017), can cause extinction of urban populations of sensitive species (Kuchling & Dejose, 1989). Small patches of undisturbed land scattered through urban matrices, even if highly degraded, may support relictual populations of more robust taxa (Dickman, 1987; Jellinek *et al.*, 2004; Garden *et al.*, 2010). The most flexible species could actively move into anthropogenic landscapes, benefitting from increased food, water, shelter, and release from predation pressure (McKinney, 2008; Sol *et al.*, 2013), especially in suburban areas (Blair, 1996; Grant *et al.*, 2011). These urban-adapted, often invasive, species can further contribute to the decline of native species (McIntyre, 2000; Marzluff, 2001) and to biotic homogenisation (Blair, 1996). The sum of these responses often results in an increase in

abundance of a few common species, but usually a decline in total diversity for urban areas (Blair, 1996).

No international standardised method of defining city boundaries exists (United Nations, 2016), and many studies do not explicitly state parameters for what they consider to be an 'urban area'. Because suburban areas play an important role in maintaining biodiversity around cities, in this review, we define 'urban land' not only as cities, but also as the developed suburbs surrounding them. Highly developed city centres are so disturbed that often only human-dependent animals can survive successfully (McKinney, 2006). Suburban development allows for colonisation by pioneer, intermediate, and late successional stages over time, while minimising competitive exclusion through consistent, but periodic, habitat change, e.g. lawn-mowing (Johst & Huth, 2005). Species diversity may therefore be greatest in areas of moderate disturbance size and frequency, i.e. suburbia (as described by the intermediate disturbance hypothesis) (Connell, 1978).

Studies of urbanisation effects on vertebrates are skewed towards birds (see Chace & Walsh, 2006 for review) and mammals (see Bateman & Fleming, 2012 for review on carnivorous mammals). Of the terrestrial vertebrates, reptiles remain underrepresented in urban studies, despite their diversity of species and broad distribution across nearly every continent. Nearly one in five reptile species are also under risk of extinction, and human-induced habitat loss is a major threat to these species (Böhm *et al.*, 2013). Development of the concept of urban adaptation posits that there are particular traits that suit species for living in urban areas. For birds, five traits are identified: 1) diet generalists; 2) social; 3) sedentary; 4) nest in man-made structures; and 5) exhibit more novel resource innovations (Blair, 1996; Kark *et al.*, 2007). This classification system has also been applied to mammals (Randa & Yunker, 2006) and invertebrates (McIntyre, 2000). A single study to date, limited to eastern Australia, has investigated such traits for reptiles: 1) diet generalists; 2) either habitat generalists or preferences for moist environments; 3) highly fecund; and 4) small body size (Shea, 2010). The aim of this review is to explore whether these traits are correlated with the degree of urban-adaptation evident in reptiles (turtles/tortoises, lizards and snakes) worldwide.

## 2.3 Materials and methods

In this review, we compare the degree of urban adaptation in lizards, snakes, and turtles/tortoises with known life history traits. A total of 440 species with sufficient life history information were included in our analysis:  $n = 55$  turtles,  $n = 234$  lizards, and  $n = 151$  snakes. (Appendix 1) Many sources included comparisons between abundant and less common species in cities, and we included all taxa mentioned so long as we could obtain sufficient relevant life history information.

### 2.3.1 Dependent variable

Varying degrees of adaptation to urbanisation have been described for multiple taxa (e.g. Blair, 1996; McKinney, 2006; Grant *et al.*, 2011). Here we have adhered to four levels of urban

adaptation:

- 1) 'Urban avoiders' (*sensu* McKinney, 2006) were considered species that do not persist in human-modified landscapes, and are restricted to natural environments.
- 2) 'Urban oblivious' (*sensu* Grant *et al.*, 2011) describes the persistence of 'engulfed', relictual or cryptic populations of some species in urban areas. Many of these species, especially turtles, rely on small patches (e.g. temple ponds, botanical gardens, and small greenspaces surrounded by a built-up environment) and would likely disappear from metropolitan areas entirely if such refugia were removed.
- 3) 'Periurban adapters' tolerate a low degree of urbanisation on the outskirts of cities, but are most common in either natural environments or agricultural zones, towns, and other areas modified, but not dominated, by humans.
- 4) 'Urban adapters' (*sensu* McKinney, 2006) persist within areas of high perceived degree of urbanisation, i.e. metropolitan areas (including cities and suburbia). These species make use of the unique resources of metropolitan locations, such as living in or around human-modified structures and gardens, and eating anthropogenically-sourced foods.

The degree of urbanisation for each species was identified through a literature analysis. A search of the literature was conducted using Google Scholar in January 2016 for all papers including the following terms: urban\*; (city OR cities); suburb\*; reptile\*; snake\*; lizard\*; turtle\*; and tortoise\*. Quantifying population densities for many species can be difficult, due to their cryptic nature (e.g. Whitaker and Shine 1999), and we were thus unable to rely on abundance per se (the most-used measure to predict urban adaptation for other taxa) (Blair, 1996; McKinney, 2008) to classify the degree of urban adaptation for reptiles. Instead, we used descriptions provided by the original authors, sourced from other literature, or surmised. A species was classified as belonging to the urban category with the highest tallied number (mode) of seven urban adaptation-associated traits (Table 2.1, Appendix 1). Overall, there were more 'urban adapter' (n = 150) and 'urban avoider' (n = 130) species than 'urban oblivious' (n = 87) or 'periurban adapters' (n = 73).

### 2.3.2 Independent variables

A total of 16 independent factors were recorded within seven "urban categories" (body size, life history, diet, habitat, habit, and continent(s) of endemism and invasion) for each individual species (Table 2.2, Appendix 1). We collected life history information using the literature (especially Brandley, Huelsenbeck & Wiens, 2008; Meiri, 2010; Fleming, Valentine & Bateman, 2013; Mesquita *et al.*, 2015) and regional herpetology field guides. Categorical independent factors were scored either binomially (where there were two options, usually presence/absence) or on an increasing scale (e.g. for body size ranges). The traits of two urban categories (body size and life history) were considered separately. As the literature suggests that urban-adapted species are generalists (e.g. Blair, 1996; Kark *et al.*, 2007; Shea, 2010), we calculated the sum of factors within the remaining categories, and used those scores for statistical analysis (Table 2.2).



*A-priori* considerations for each of the traits were made using observations from the literature and our own practical assumptions (Table 2.2).

Table 2.1. Key traits identified to classify degree of urban adaptation for reptiles in this study (developed from Blair, 1996; Kark et al., 2007; Grant et al., 2011). \*Some descriptions were identical for traits F (2 and 3) and G (1 and 2; 3 and 4); we used the more urban-adapted values where applicable. Each species was classified as belonging to the urban category with the highest tallied number (mode) of the seven traits; where calculating the mode did not determine a single category, we selected the more urban-adapted category.

Trait	Level of urban adaptation			
	Less urban-adapted ←			→ More urban-adapted
	1. Urban avoider	2. Urban oblivious	3. Periurban adapter	4. Urban adapter
A. Spatial distribution and density	Nil or limited sightings in human-modified landscapes; reported as locally extinct or not present in urban areas.	Urban greenspaces; reported as uncommon in metropolitan areas, and restricted to greenspaces	Outer metropolitan areas/agricultural zones/small towns and villages; reported as uncommon in metropolitan areas, and abundant	Metropolitan areas, including city centres and suburbia; reported as abundant, common, or synanthropic
B. Sensitivity to humans and human-modified areas	High intolerance	Appear tolerant, able to limit interactions temporally and/or spatially	Limited tolerance where human densities are lower	Appear tolerant, able to either ignore people or limit interactions temporally
C. Patch sizes	Highly reliant on large, unfragmented patches	Restricted to small and/or isolated patches	Prefer large, continuous, patches	Can persist in patches of varied size, largely unaffected by fragmentation
D. Habit/habitat preferences	Specialists, often requiring niches that are not present in cities, e.g. tree hollows	Habitats that best allow for concealment from humans, e.g. in dense foliage, underground	Specialists	Generalists, including amongst rocks, shrubs, canopy and on the ground
E. Structural resource use	Natural environment	Natural environment or semi-natural sources, e.g. stone/wood walls, human-created ponds	May use anthropogenic sources with low disturbance, e.g. barns, building roofs	Found in close association with anthropogenic sources, e.g. lights, buildings, gardens
F. Vegetative resource use	Reliance on native species	Uses introduced species to a limited degree*	Uses introduced species to a limited degree*	Uses native and introduced species, including garden ornamentals and weeds
G. Anthropogenic food use	Nil*	Nil*	Reported diet to include human supplementation and/or synanthropic prey items, e.g. chickens, rats*	Reported diet to include human supplementation and/or synanthropic prey items, e.g. chickens, rats*

Table 2.2. Factors used in multinomial logit-linked multiple regression for multimodel analysis of best models using AICc.

Urban category	Factor	Occurs in <i>n</i> best models (%)	A-priori hypothesis; urban-adapted reptiles are more likely to:
<i>Categories with individually scored traits (score)</i>			
Size	Total length, cm (1 = [ $<10$ ], 2 = [10-20], 3 = [20-50], 4 = [50-100], 5 = [100-200], 6 = [ $>200$ ])	4 (27%)	Have a smaller body size (Shea, 2010), and a longer tail relative to snout-vent length.
	Snout-vent length (% of total length) (1 = [ $<33$ ], 2 = [33-50], 3 = [50-66], 4 = [66-75], 5 = [ $>75$ ])	10 (66%)	
Life history	Gregarious, e.g. communal basking/nesting (0 = no, 1 = yes)	-	Be social or gregarious and not display intraspecific combat/territoriality (Blair, 1996; Kark <i>et al.</i> , 2007).
	Intraspecific combat/territorial, e.g. mate competition (0 = no, 1 = yes)	15 (100%)	
	Sexual dimorphism, e.g. size, colour (0 = no, 1 = yes)	1 (7%)	Lack sexual dimorphism to allow all individuals to occupy a variety of habitats.
	Reproduction (0 = live-bearing, 1 = eggs)	1 (7%)	Be highly fecund (Shea, 2010), maximising reproductive output by allowing the mother to produce many offspring at minimal energetic cost.
	Sex specialisation, e.g. parthenogenesis, sperm storage (0 = no, 1 = yes)	2 (13%)	
	Circadian rhythm (0 = diurnal, 0.5 = mixed, 1 = nocturnal)	1 (7%)	Maximise active periods when humans are less likely to be present.
	Use of anthropogenic light (0 = no, 1 = yes)	-	Opportunistically use novel food sources.
	Venomous (0 = no, 1 = yes)	-	Be considered inoffensive to humans.
<i>Categories with tallied traits (n), sum of binomial scores (0 = no, 1 = yes) for each item.</i>			
Diet (4)	Vertebrates, invertebrates, vegetation, anthropogenic waste	15 (100%)	Use a variety of diet items (Blair, 1996; Kark <i>et al.</i> , 2007; Shea, 2010).
Habitat (7)	Coast, grasslands, lowlands, sandplains, scrub, slopes, woodlands	15 (100%)	Use a variety of habitats (Shea, 2010).
Habit (5)	Aquatic, cryptozoic, rupicolous, scansorial, terrestrial	4 (27%)	Use a variety of habits, due to lack of habitat specialisation.
Endemic continent/s (6)	Africa, Asia, Europe, North America, Oceania, South America	1 (7%)	Have wide distributions across multiple continents.
Invasive continent/s (6)	Africa, Asia, Europe, North America, Oceania, South America	1 (7%)	Have the demonstrated ability to expand to new areas.

### 2.3.3 Statistical analysis

To identify whether there was a taxonomic bias in which reptile families were more likely to be identified as urban adapted, we conducted a two-way  $\chi^2$  analysis with Yates correction using the factors of 'family' ( $n = 39$ ) and level of urban adaptation in RStudio 0.99.491 (RStudio Team, 2015). We then compared the residuals for the  $\chi^2$  test to identify which families were more associated with the four levels of urban adaptation than expected.

To identify factors with the highest degree of correlation with urbanisation ranking, we generated a phylogenetic tree for the species included in the analysis (Appendix 2) and used the PDAP package (Milford, Garland Jr & Maddison, 2002) in Mesquite 3.2 (Maddison & Maddison, 2017) to produce Felsenstein's Independent Contrasts (FICs) for each factor. To account for possible multicollinearity between factors, we generated a correlation matrix for the FICs of the independent variables in Microsoft Excel 2010; the greatest absolute correlation was between the factors SVL percentage and total length (0.22), and all other correlations were  $< \pm 0.21$  (Appendix 3.1).

We used a multinomial logit-linked multiple regression via an information theoretic approach to test competing hypotheses simultaneously on the FIC dataset with Akaike's information criterion (AIC) in STATISTICA 7.1 (Statsoft Inc., 2006). The model likelihood was corrected for the number of parameters in each model ( $AIC_c$ ) (Burnham & Anderson, 2002). The set of best-fit models was generated using all possible subsets of the global model. Models with a  $\Delta AIC_c \leq 2$  were considered to have support, and as multiple models had a  $\Delta AIC_c \leq 2$ , model averaging was carried out (Burnham & Anderson, 2002). The Akaike weight ( $w_i$ ) for each of these models was calculated (Burnham & Anderson, 2002) and the values were averaged across models (Grueber *et al.*, 2011). Standardised  $\beta$  values were calculated for each model to allow for direct comparison of their relative contribution in the prediction of urban ranking, and then adjusted for Akaike model weight ( $\beta \cdot w_i$ ).

## 2.4 Results

There were significant differences between reptile families for degree of urban adaptation ( $\chi^2_{114} = 180.05$ ;  $P < 0.001$ ). Overall, relatively more lizard species included in the analysis were considered urban adapters ( $n = 98$ , 42%), while the snakes were relatively more frequently periurban adapters ( $n = 34$ , 23%), and turtles/tortoises were more likely to be categorised as urban oblivious ( $n = 16$ , 29%) or urban avoiders ( $n = 28$ , 51%). Gekkonid lizards ( $n = 41$  spp.) had the largest positive residual for the urban adapter group, lamprophiid snakes ( $n = 15$  spp.) for the periurban adapter group, pygopodid lizards ( $n = 9$  spp.) for the urban oblivious group, and testudinid turtles ( $n = 9$  spp.) for the urban avoider group (Figure 2.1, Appendix 1).

Fifteen models received equal support ( $\Delta AIC_c \leq 2$ ) for being the best model to explain degree of urban adaptation across the 440 reptile species included in the dataset (Table 2.3). These 15 models included combinations of 12 factors. Reptile adaptation to urbanisation can therefore be described as:

$$0.691 \text{ (combat/territorial)} + 0.383 \text{ (diet)} + 0.121 \text{ (endemism)} + 0.111 \text{ (total length)} + 0.094 \text{ (habitat)} + 0.087 \text{ (reproduction)} + 0.084 \text{ (sexual dimorphism)} + 0.065 \text{ (habit)} + 0.034 \text{ (invasion)} - 0.085 \text{ (circadian rhythm)} - 0.116 \text{ (snout-vent length)} - 0.292 \text{ (sex specialisation)}.$$

None of the other four factors (Table 2.2) contributed to models with  $\Delta AIC_c \leq 2$ , and therefore did little to describe degree of reptile urban adaptation.

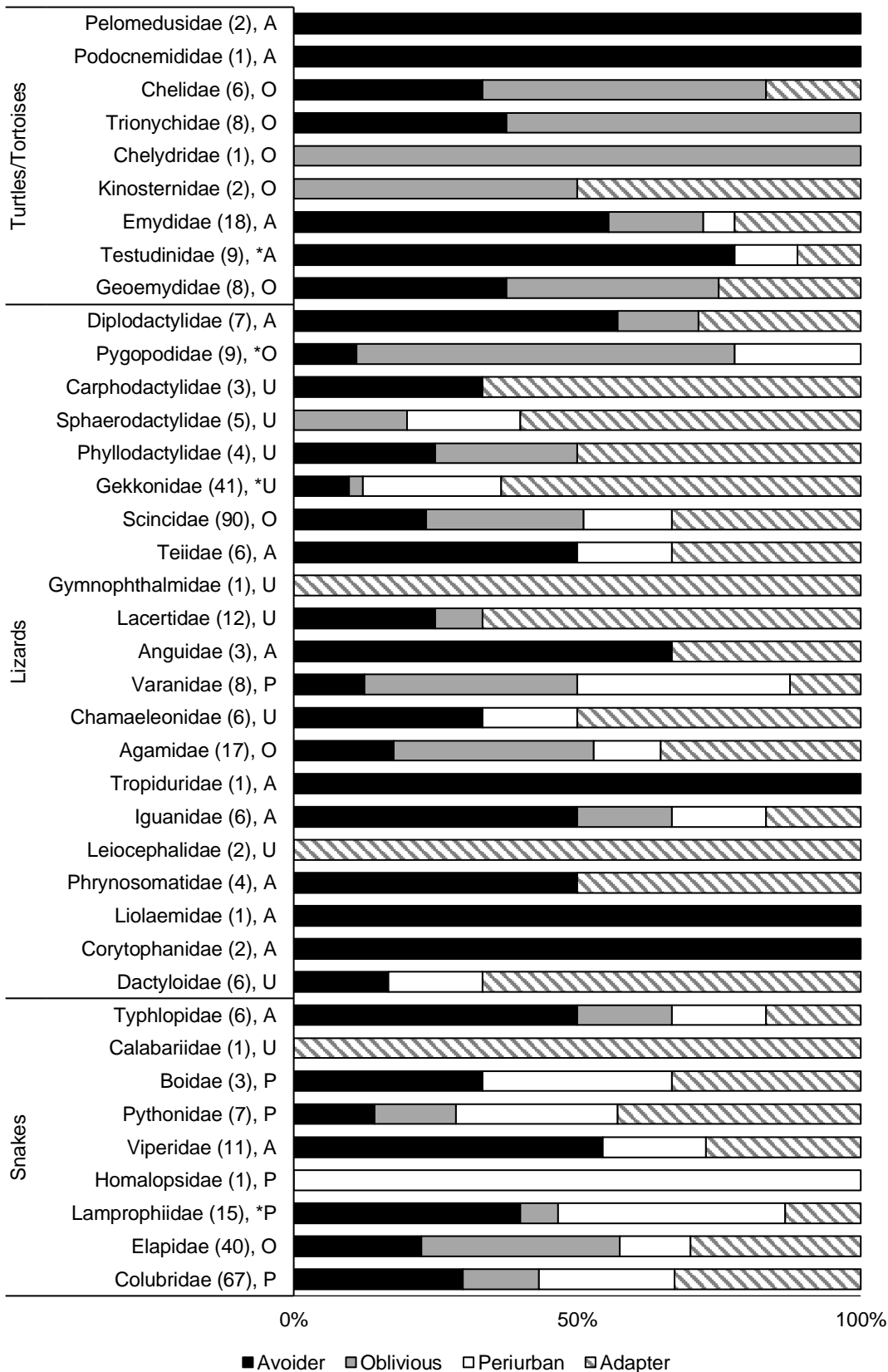


Figure 2.1. Levels of urban adaptation for reptile families (n species), sorted phylogenetically. Largest positive residuals ( $\chi^2$  test) indicate the level of urban adaptation that is most associated with each family: U = urban adapter; P = periurban adapter; O = urban oblivious; and A = urban avoider. \*Largest positive residual for each urbanisation category.

Table 2.3. Best models for factors correlated with degree of urbanisation. Mean standardised  $\beta$  values adjusted for Akaike weight summed for top models ( $\bar{x}\beta \cdot w_i$ ) can be used to infer correlation between each factor and degree of urbanisation. Positive  $\beta$  values trend towards urban adaptation, while negative  $\beta$  values trend towards urban avoidance. Scores for each factor are explained in Table 2.2. For all models,  $P < 0.0001$ .

Size		Life history		Diet		Distribution		Model-weighted standardised $\beta$ values, ordered by $\bar{x}\beta \cdot w_i$																								
Total length	Snout-vent length	Combat/territorial	Sexual dimorphism	Reproduction	Sex specialisation	Circadian rhythm	Diet	Habitat	Habit	Endemism	Invasion	df	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	L.Ratio ( $\chi^2$ )	$w_i$	Combat/territorial	Diet	Endemism	Total length	Habitat	Reproduction	Sexual dimorphism	Habit	Invasion	Circadian rhythm	Snout-vent length	Sex specialisation				
												4	1348.29	0	41.98	12.41	8.64	4.86			1.14											
												3	1348.77	0.48	39.46	9.77	7.02	3.77			0.98											
												4	1348.92	0.63	41.35	9.07	6.29	3.36		1.14	0.92											
												5	1349.23	0.94	43.08	7.75	5.27	2.99			0.66			0.5				-0.92				
												5	1349.26	0.97	43.06	7.66	5.21	2.9		0.74	0.72							-0.78				
												4	1349.58	1.29	40.69	6.52	4.57	2.48			0.6			0.44								
												5	1349.63	1.34	42.68	6.35	4.3	2.45			0.6							-0.75	-1.78			
												5	1349.83	1.54	42.49	5.75	3.9	2.1		0.7	0.54			0.38								
												4	1349.98	1.69	40.29	5.32	3.71	2.03			0.55								-1.62			
												5	1349.98	1.69	42.33	5.32	3.65	2.06			0.47			0.44				-0.63				
												5	1350.03	1.74	42.29	5.2	3.64	2.04	0.63		0.48							-0.63				
												5	1350.2	1.91	42.11	4.77	3.27	1.84			0.43					0.16		-0.59				
												5	1350.2	1.91	42.11	4.77	3.3	1.86			0.44						-0.41	-0.56				
												5	1350.23	1.94	42.08	4.7	3.26	1.85			0.43	0.41						-0.58				
												6	1350.26	1.97	44.11	4.64	3.09	1.73		0.44	0.41			0.29				-0.46				
																	$\bar{x}\beta \cdot w_i$	0.69	0.383	0.121	0.111	0.094	0.087	0.084	0.065	0.034	-0.085	-0.116	-0.29			

Intraspecific combat/territoriality, diet, and habitat occurred for all of the 15 top models and were among the strongest factors affecting degree of urban adaptation (Table 2.2, Table 2.3). The positive  $\beta$  coefficients indicate that urban-adapted reptiles were more likely to:

- Display intraspecific combat (usually during mate choice) or maintain territories in which they are sedentary, rather than live socially or have nomadic lifestyles;
- Use a range of diet items, rather than have specialist diet requirements;
- Have generalist habitat requirements, rather than be habitat specialists;
- Be endemic to a range of continents, and not restricted to one location;
- Be large in size (generally >50cm total length);
- Lay eggs, rather than give birth to live young;
- Have males and females with sexually dimorphic differences, e.g. with one sex being larger or differently coloured to the other sex;
- Use a range of habits, and not confined to a specialist habit type; and
- Have proliferated to a range of continents invasively with successfully established breeding populations outside of their endemic ranges.

The negative  $\beta$  coefficients indicate that urban-adapted reptiles were less likely to:

- Be nocturnal, with more successful species being diurnal;
- Have shorter tails relative to their body size, with more gracile species with longer tails more likely to be urban-adapted;
- Have sex specialisation (e.g. parthenogenesis, sperm storage), with most urban-adapters lacking this trait.

## 2.5 Discussion

Analysis of 16 traits for body size, life history, diet, habitat, habit, and continent(s) endemism and invasion for 440 reptile species worldwide revealed 12 factors influencing the degree of their urban adaptation. Lizards were better represented as 'urban adapters' than were the other taxa, snakes were more often considered 'periurban adapters', while turtles/tortoises were most likely to be categorised as 'urban oblivious' or 'urban avoiders'. The 12 traits in the top models explaining degree of urban adaptation across the dataset after phylogenetic correction were whether a species: 1) uses intraspecific combat and/or is territorial, 2) eats a variety of diet items, 3) is endemic to a variety of continents, 4) has a large body size, 5) uses a variety of habitats, 6) lays eggs, 7) has sexual dimorphism, 8) uses a variety of habits, 9) has proliferated to a range of continents invasively, 10) is diurnal, 11) has a longer tail relative to its SVL, and 12) lacks sex specialisation. Although other characteristics might be important for individual species, these 12 traits were those that best describe the degree of urban adaptation found across reptiles generally.

## 2.5.1 Traits that were correlated with urban adaptation

### 2.5.1.1 Intraspecific combat/territoriality

The trait most strongly correlated with urban adaptation in our reptile dataset was intraspecific combat/territoriality, with combative and territorial species more likely to become urban adapters. This is a commonly recorded life history trait amongst avian, mammalian and invertebrate urban adapters (Blair, 1996; McIntyre, 2000; Randa & Yunger, 2006; Kark *et al.*, 2007), as suitable habitat within cities is often limited, and maintaining territories can be vital for accessing resources. Reptiles that demonstrate some level of combat and territoriality are therefore more likely to successfully persist within urban areas. For example, the best urban-adapted reptile species are geckos (Gekkonidae), a family containing the highly synanthropic genus *Hemidactylus*, and the world's most invasive gecko, the Asian house gecko (*Hemidactylus frenatus*) (Hoskin, 2011; Cisterne *et al.*, 2014; Kraus, 2015). These species are highly competitive with other gecko species, and are among the most invasive reptiles in the world (Kraus, 2009). *Gekko* spp. (e.g. Tokay geckos *Gekko gecko*; Perry *et al.*, 2008; Das, 2010), *Gehyra* spp. (Fisher, 1997; Karunarathna *et al.*, 2008) and *Mediodactylus* spp. (Mollov, 2011) also live in close association with humans (Das, 2010) and exhibit strong inter- and intraspecific competition (Petren & Case, 1996; Hanley, Petren & Case, 1998; Williams *et al.*, 2016). Red-eared slider turtles (*Trachemys scripta*; Emydidae) are amongst the top 100 invasive species in the world (Lowe *et al.*, 2000), and are perhaps the best reptilian example of worldwide proliferation due to the pet trade (Ramsay *et al.*, 2007). In urban areas, these highly competitive generalists are at least partly responsible for the decline by exclusion of western pond turtles (*Emys marmorata*) in California, USA (Spinks *et al.*, 2003), European pond turtles (*Emys orbicularis*) in France (Cadi & Joly, 2003) and possibly painted turtles in Indiana, USA (Conner, Douthitt & Ryan, 2005).

### 2.5.1.2 Omnivorous diet

Diet was another important trait affecting urban adaptation for reptiles, with urban species often using a variety of diet items, eating vertebrates, invertebrates and vegetation. The potential food resources available within urban areas are plentiful for those species that can adapt to use them, such as invertebrates attracted to gardens and parks (McIntyre, 2000; Garden *et al.*, 2006; Lowe, Wilder & Hochuli, 2014) and lights (Perry *et al.*, 2008), and a range of native and introduced plant species (Garden *et al.*, 2007). Brown anoles (*Anolis sagrei*; Dactyloidae) – an invasive in USA, South America and Asia – appears to be most frequent in urban areas (Meshaka Jr, 2011), and is capable of not only out-competing other species for suitable niches (Salzburg, 1984), but also eating the competition (Stroud, Giery & Outerbridge, 2017). Many lacertids (Lacertidae) take a wide range of vertebrate, invertebrate and vegetative food items (Herrel, Vanhooydonck & Van Damme, 2004), which may help them to better exploit the urban food resources available. For larger carnivores, vertebrate prey such as synanthropic birds and bird eggs (Durner & Gates, 1993; Nande & Deshmukh, 2007; Sazima & D'Angelo, 2013), dogs (Luiselli, Angelici & Akani, 2001) and carrion (Kulabtong & Mahaprom, 2015) are also available in greater abundances in

urban areas than undisturbed environments. Monitor lizards (Varanidae) are highly carnivorous active hunters. They range in size and are widely regarded as inimical to humans (White & Burgin, 2004) but shelter either up trees or in underground burrows (Somaweera & Somaweera, 2009; Cogger, 2014) and so persist around urban areas, where they exploit anthropogenic resources, mostly food (Jessop *et al.*, 2012). For example, Asian water monitors (*Varanus salvator*) are found in the highly urbanised city of Bangkok, Thailand, and may opportunistically take rats, cats, dogs and food scraps in their diets (Kulabtong & Mahaprom, 2015). Many snakes also benefit from prey availability in urban areas. For example, dugites (*Pseudonaja affinis*; Elapidae) take advantage of invasive house mice (*Mus musculus*) (Wolfe, Bateman & Fleming, 2017). The flowerpot snake (*Indotyphlops braminus*; Typhlopidae) also thrives in all kinds of urban areas, and is an invasive across the world as a stowaway in potting mix via the flower trade (Kraus, 2009); these diet specialists may also suit suburban garden-living, as long as their preferred dietary ant species are abundant (Shea, 2010).

### 2.5.1.3 Endemic and invasive to a range of continents

Endemism, and, to a lesser degree, invasion to a range of continents also factored as significant traits associated with urban-adapted reptiles. Often, the most successful urban adapters are invasive species that can populate cities equally around the world (McKinney, 2006), and as hundreds of reptile species have been documented as having established successful invasive populations (Kraus, 2009), we suspected this generality may also apply for reptiles. However, upon closer inspection of species distributions across invasive territories, relatively few species have proliferated invasively to urban areas. For example, the hugely invasive Burmese python (*Python bivittatus*; Pythonidae) has caused significant damage to the Everglades region in southern USA, but is not often found near urban dwellings (Holbrook & Chesnes, 2011; Reed & Krysko, 2013; Pittman *et al.*, 2014). In comparison, the red-eared slider and Asian house gecko are successful invaders and thrive in urban wetlands and around houses respectively (Spinks *et al.*, 2003; Failey *et al.*, 2007; Hoskin, 2011; Price *et al.*, 2013; Williams *et al.*, 2016). Species able to natively inhabit a variety of continents may also have generalist habitat requirements and higher behavioural flexibility, allowing them to better cope with human-modified environments.

### 2.5.1.4 Body size: larger bodies, longer tails

Reptiles with larger body sizes (i.e. total length) and relatively longer tails (SVL as a percentage of total length) were more likely to be urban adapters. While this body size pattern may be similar as for urban-adapted mammals, where smaller-bodied species <1 kg are often specialised or sensitive to habitat fragmentation (Crooks, 2002; Gehring & Swihart, 2003; Bateman & Fleming, 2012), this may also reflect the lack of studies on urban reptiles. Large-bodied species which are inimical – e.g. varanid (Kulabtong & Mahaprom, 2015) and helodermatid (Sullivan, Kwiatkowski & Schuett, 2004) lizards and snakes (Shine & Koenig, 2001; Clemann, McGee & Odgers, 2004; Purkayastha, Das & Sengupta, 2011) – or charismatic – e.g. turtles (Spinks *et al.*, 2003; Stokeld *et al.*, 2014), garner more attention from the public than very small and relatively benign lizards.



Groups with the longest tails were nearly exclusively lizards, including urban-adapted geckos, dactylids, and chamaeleons. These taxa are all predominately scansorial, and being able to use a wide range of habitats – e.g. buildings and fences (Henderson & Powell, 2001) and vegetation strata (Germaine & Wakeling, 2001) – can lead to a more general and urban-tolerant lifestyle (Kark *et al.*, 2007).

### 2.5.1.5 Habitat and habit generalists

Globally, cities are often in areas of high biodiversity (Ives *et al.*, 2016), providing a diverse array of species to be potentially urban adapted. Reptile species that persist in these areas are therefore more likely to encounter urbanisation, and those species that are have suitable adaptations allowing them to occupy a diverse range of habitats and habits are therefore more likely able to persist in disturbed areas, while more sensitive species disappear (How & Dell, 1993). Alternatively this could be a result of observer bias, with the majority of urban-adapted species studied in the scientific literature potentially occurring near where researchers live or in areas with good access.

Aquatic/semi-aquatic species were more commonly identified as urban adapters by Shea (2010), but we found that species occupying a range of habits, which may include water bodies, were more commonly urban adapters. Humans are great modifiers of water use, especially within gardens. Lawn grass, ornamental plants and flowers in gardens provide diverse novel environments and often require regular watering; sprinkler systems ensure consistent watering without the presence of humans. Botanic gardens and urban created wetlands provide a range of micro-habitats to be used by adapters (Ward, Parker & Shackleton, 2010; Purkayastha *et al.*, 2011; Stokeld *et al.*, 2014), which are often buffered against drought (Rees, Roe & Georges, 2009). Perhaps one the greatest habitats for urban reptiles are golf courses, which offer varied shelter options and regular access to water, with regular intervals of limited human interaction (Hodgkison, Hero & Warnken, 2007; Burgin & Wotherspoon, 2009; Burgin *et al.*, 2011; Guzy, Price & Dorcas, 2013). The presence of regular water also provides suitable habitat for plants and other animals, which offer year-round shelter and food sources. However, water pollution is also identified as a leading factor for aquatic species decline (Czech, Krausman & Devers, 2000; Gibbons *et al.*, 2000), highlighting the potential risk for species that depend on water access, and a possible reason why water alone was not a significant factor.

### 2.5.1.6 Reproduction/sex specialisation

Although all turtles/tortoises are oviparous, reproductive methods (laying eggs versus live young) vary across the Squamata (lizards and snakes). Of the 419 squamates we included in our data set, oviparity was the dominant reproductive method (n = 339, 81%). Overall, oviparity was most common for all four urban categories, but was highest for periurban adapters (n = 63, 86%) and urban adapters (n = 126, 84%; avoiders n = 103, 79%; oblivious n = 68, 78%). While this trait was only significant in one model, laying eggs appears to be more advantageous for many

habitats and habits. Similarly, sex specialisation only appears to be of benefit for few species ( $n = 14$ , 3%).

Oviparity allows the parent to potentially produce larger clutch sizes or multiple clutches, which can lead to greater genetic diversity, and mortality of the parent does not necessarily result in mortality of the offspring (Tinkle & Gibbons, 1977). Disturbances associated with urbanisation – such as habitat fragmentation, light, sound and noise pollution, and human activities – can cause reptiles to limit their activities temporally or spatially, which can have significant negative physiological impacts (Longcore & Rich, 2004; Blumstein *et al.*, 2005; Rodríguez-Prieto, Martín & Fernández-Juricic, 2010; Kamrowski *et al.*, 2012). Where disturbances are more frequent and overall survival likelihood is low due to urbanisation, species with the ability to lay eggs can therefore reduce some of these costs to the parent by spending less time and fewer resources than would be required to produce live offspring. Having large clutch/litter sizes, or numerous clutches per year, may also increase the likelihood of the species successfully establishing or persisting in urban areas. For example, some urban-adapted nocturnal geckos lay only small clutches of one or two eggs, but do so frequently and communally where resources are readily available, e.g. around buildings with outdoor lights that attract insects (Hódar *et al.*, 2006; Perry *et al.*, 2008). Of the urban-adapted species we examined that did not lay eggs ( $n = 26$ ), many give birth to large litters. For example, rough-scaled sand boas (*Eryx conicus*, Boidae) can produce up to 17 young per litter (Lanza & Nistri, 2005), Jackson's chameleons (*Trioceos jacksonii*, Chamaeleonidae) around 20 young (Brain, 1962), blue-tongued lizards (*Tiliqua scincoides*, Scincidae) up to 25 young (Cogger, 2014), and tiger snakes (*Notechis scutatus*, Elapidae) up to 109 young (McPhee, 1959). Elsewise, the remaining urban-adapted species that have small litters of live young likely rely on other life history strategies to their benefit within urban areas.

Sex specialisation/s, such as parthenogenesis, sperm storage, and reproductive switching between oviparity and viviparity, tend to be advantageous for species that rapidly colonise areas. Two of the world's most invasive and urban-adapted reptiles have sex specialisations: the flowerpot snake is parthenogenetic (Nussbaum, 1980; Booth & Schuett, 2016), and the Asian house gecko uses sperm storage (Murphy-Walker & Haley, 1996; Yamamoto & Ota, 2006). However, few other species are quite so invasive, and as we suspect the majority of urban-adapted species were engulfed by urban development and sprawl, rather than colonised areas invasively, sex specialisation is an unnecessary trait for urban adaptation.

### 2.5.1.7 Sexual dimorphism

Highly modified urban environments have increased anthropogenic disturbances, and resource availability may be lower (e.g. Wolfe *et al.*, 2017), which appears to better suit species with generalist life history traits or homogeneity in sizes and colours between sexes due to disturbance (Conner *et al.*, 2005; Dodd & Dreslik, 2008). However, we found that sexual dimorphism was positively correlated with reptile urban adaptation. Sexual dimorphism may serve multiple purposes (for review, see Cox, Butler & John-Alder, 2007): testosterone drives body growth in

males, allowing them to attain large sizes for sexual competition (Stamps, 1977; Shine, 1989; Bonnet *et al.*, 1998; Cox, Stenquist & Calsbeek, 2009); larger males may have greater fitness to maintain territories (Trivers, 1976; Kratochvíl & Frynta, 2002; Cox, Skelly & John-Alder, 2003); larger females may have increased reproductive output (Carothers, 1984; Bonnet *et al.*, 2001; Aresco, 2005b); and more colourful males may attract more females for mating (Stuart-Fox & Ord, 2004), while dull colouration can allow better camouflage with the environments to improve the effectiveness of crypsis (Olsson, Stuart-Fox & Ballen, 2013). Males and females with different body sizes or colourations may occupy different niches and access different resources. This is particularly evident for snakes, for which the divergence of head sizes is most important with regards to feeding (Shine, 1991a). For example, male cottonmouths (*Agkistrodon piscivorus*, Viperidae) in the US have larger maximum gape sizes than females, allowing them to eat larger prey items (Vincent, Herrel & Irschick, 2004). In Australia, male carpet pythons (*Morelia spilota*, Pythonidae) are significantly smaller than females, and females can take substantially larger prey (Pearson, Shine & Williams, 2002; Pearson, Shine & How, 2006). Within our analyses, sexual dimorphism only occurred in one of the 15 best models, and although it is significant to consider for reptile urban adaptation, there are many species that are successful and lack this trait. This suggests that the trait may be advantageous for urban adapters, but it is not essential.

#### 2.5.1.8 Diurnal circadian rhythm

There was a significant effect of circadian rhythm on level of reptile urban adaptation, and surprisingly diurnal species were more likely to be urban-adapted. In the context of being obvious to people in urban areas, nocturnal geckos are the most prevalent. However, there are many species outside of the Gekkota that are successful in cities. Perhaps the best explanation for the success of diurnal species is from Koenig, Shine & Shea (2001) for blue-tongued lizards: they found the lizards were most active during the hours in which most humans leave home for work. For many generalist species, gardens form useful habitats with sources of food, shelter, and release from normal predators (albeit, with the potential increase of predation from synanthropic or novel species). For even a large-bodied reptile that may be perceived negatively by humans, such as a snake, these resources can be exploited without human intervention for most daylight hours in the week if the human is away from home. Perhaps our expectations for nocturnal species to be more successful is the result of few species that are extremely habituated to the passive presence of humans around lights – e.g. marbled gecko (*Christinus marmoratus*, Gekkonidae), Asian house gecko, mourning gecko (*Lepidodactylus lugubris*, Gekkonidae) (Petren & Case, 1998; How & Dell, 2000; Perry *et al.*, 2008; Kraus, 2009) – and there are many more species with very different life histories that are successful during the day that are not so often seen.

#### 2.5.2 Traits that were not correlated with urban adaptation

There were no significant effects of gregariousness or evidence for the use of anthropogenic light. The most significant factor of combat/territoriality seems to suggest that species that are less

social are more likely to persist within urban areas, despite the model for birds suggesting 'safety in numbers'. Additionally, as more urban-adapters were diurnal, having a propensity for anthropogenic light may make a reptile more obvious to humans, and negatively affect all but the most resilient species (e.g. some geckos). The final trait that was not significant was whether the reptile was venomous. Despite the fact that approximately 85% of all snake species are non-venomous (Gold, Dart & Barish, 2002), the general public holds an almost ubiquitous view that snakes in general are dangerous upon encounter (Whitaker & Shine, 2000; Pinheiro, Rodrigues & Borges-Nojosa, 2016). Licensed snake removalists are in high demand in many countries, including Australia and Brazil, to move unwanted snakes away from suburban homes upon incidental encounter (Clemann *et al.*, 2004; Teixeira *et al.*, 2015). Public perception of snakes as inimical extends to non-venomous species (Hunt & Fenton, 2007), including pythons (Pythonidae and Calabariidae) and boas (Boidae), which may explain why overall this trait did not influence degree of urban adaptation.

### 2.5.3 How can we help the success of urban reptiles?

Healthy ecosystems require heterogeneous representations of taxa (Standish, Hobbs & Miller, 2013). Despite the small potential for an encounter with a venomous snake in a local park or private garden, reptiles provide a benefit to urban communities. Reptiles fill a variety of trophic niches, such as digging for food or to create shelter, e.g. gopher tortoises (Catano & Stout, 2015), stirring up leaf litter and dispersing seeds (see Cortés-Gomez *et al.*, 2015 for review), and controlling pests (Kraus, 2009). For example, species that use the night light niche (mainly geckos) control insects around human habitations (Perry *et al.*, 2008), garden lizards often consume gardening pests such as snails and cockroaches (van Heezik & Ludwig, 2012), and snakes are important predators of rodents, especially in peri-urban and agricultural areas (Shine, 1989; Whitaker & Shine, 2000). Within suburbia, some species of snakes have adapted to become useful 'mousers' (Wolfe *et al.*, 2017), and those found on private residences may be an indicator of high densities of available prey. However, use of pesticides can lead to direct mortality (De Lathouder, Jones & Balcombe, 2009) and diminished prey for insectivores (Hódar, Pleguezuelos & Poveda, 2000). Many species are aesthetically pleasing, and in some cases religious icons, such as turtles for Hindu temples (Bonin, Devaux & Dupre, 2006). For those who appreciate them, these reptiles provide a 'cultural ecosystem service' (Dickinson & Hobbs, 2017).

Successful conservation programs in urban areas use community engagement to foster support (Gramza *et al.*, 2016; Hogberg *et al.*, 2016; Liordos *et al.*, 2017). Promoting a greater understanding of the importance of maintaining urban wildlife and necessary habitat within local communities should have flow-on effects to policy makers, both within urban planning and ecological research. Understanding that urban areas offer a diverse array of microhabitats that are possibly exploitable by some species is also important (Mollov, 2011). The taxa we studied – turtles/tortoises, lizards, and snakes – are all different in their ecological requirements, and understanding the differences, both intra- and inter-taxonomically with other vertebrates, is important for urban conservation and management. Furthermore, we have shown that the

lifestyle requirements for urban adaptation in reptiles differs greatly from other taxa previously studied. Urban reptiles do not appear to use as many anthropogenically provided resources as mammals and birds, and increased disturbances such as clearing urban green spaces for urban development will negatively impact most remaining urban species (Gibbons *et al.*, 2000; Böhm *et al.*, 2013). Current models and traits describing urban adapters will likely have a significant bias against many cryptic or understudied reptile species and may potentially misdiagnose conservation actions. However, by considering reptiles in conjunction with mammals and birds as significant urban vertebrate fauna, projects to conserve urban wildlife may use a more balanced approach to better represent healthy urban ecosystems.



## Chapter 3. Does urbanisation influence the diet of a large snake?

As diet is a significant factor affecting the likelihood of a reptile being classified as an urban adapter, it is a useful first step to investigate if dugites and bobtails benefit from urbanisation via use of novel food items. This chapter was originally designed to incorporate diet data for both dugites and bobtails to compare and contrast the diets of road-killed and museum specimens collected from both urban and non-urban areas. As dugites are obligate carnivores and have simple digestive systems, diet items were relatively easy to remove and identify from the stomach, regardless of whether they were collected fresh (roadkill) or fixed in formalin (museum specimens).

During the three-year collection period (2014-2016), I had difficulty finding road-killed bobtails with intact bodies, as their smaller size and more complex digestive systems than dugites meant prey items were often rotten or contaminated by road debris. Relatively few bobtail specimens were available from the museum, and, although additional samples were obtained from wildlife rehabilitation centres, there was not enough time to dissect and identify the stomach contents of a large enough sample size of bobtails for analysis. The bobtail dataset will be completed and published as a separate paper to the thesis in future.

The study presented in this chapter has been published in the peer-reviewed journal *Current Zoology* on 27<sup>th</sup> June 2017:

**Wolfe, Ashleigh K.**, Philip W. Bateman, and Patricia A. Fleming. (2017) Does urbanization influence the diet of a large snake? *Current Zoology*, 1-8, *advance access*. doi: 10.1093/cz/zox039.

All authors conceived the ideas and designed methodology; I collected the data; I analysed the data with guidance from PAF; I led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This chapter is a reproduction of the submitted manuscript, with the exception of formatting consistent with the thesis. Additional methods descriptions are available in Appendix 3.1. A copy of the published article has been supplied in Appendix 4.

## 3.1 Abstract

Urbanisation facilitates synanthropic species such as rodents, which benefit the diets of many predators in cities. We investigated how urbanisation affects the feeding ecology of dugites (*Pseudonaja affinis*), a prolific elapid snake in south-west Western Australia. We predicted that urban snakes: 1) more frequently contain prey and eat larger meals, 2) eat proportionally more non-native prey, 3) eat a lower diversity of prey species, and 4) are relatively heavier, than non-urban dugites. We analysed the diet of 453 specimens obtained from the Western Australian Museum and opportunistic road-kill collections. Correcting for size, sex, season, and temporal biases, we tested whether location influenced diet for our four predictions. Body size was a strong predictor of diet (larger snakes had larger prey present, a greater number of prey items, and a greater diversity of prey). We identified potential collection biases: urban dugites were relatively smaller (snout-vent length) than non-urban specimens, and females were relatively lighter than males. Accounting for these effects, urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. Other urban-adapted carnivores appear to benefit from urbanisation through increased food supplementation, but we found the opposite of this: urban dugites were less likely to contain a meal, and their meals were smaller, indicating they did not make greater use of synanthropic species than was evident for non-urban snakes. In contrast to other carnivores, snakes do not appear to fit a consistent directional pattern for size differences between urban and non-urban populations.

## 3.2 Introduction

Urbanisation is generally perceived as a negative influence on biodiversity (McKinney, 2006). Urbanisation can be a strong driver of landscape change, and the disturbance associated with cities may cause local flora and fauna extinctions, where isolation of refugia and discrete habitat boundaries lead to mortality of sensitive species (e.g. Fahrig, 2001; Williams *et al.*, 2005; Cushman, 2006; Garden *et al.*, 2007). A decline of sensitive native species in urban areas can therefore lead to biotic homogenisation and the dominance of few usually invasive species, such as synanthropic rodents and birds (Blair, 1996; McKinney, 2008). Coupled with anthropogenic food sources and domestic animals, these invasive species can increase prey availability for predators. Many predators, native or introduced, therefore appear to thrive in and around cities (Roth & Lima, 2003; Chace & Walsh, 2006; Bateman & Fleming, 2012).

Many snake species have persisted in or invaded urban areas. For example black-necked spitting cobras (*Naja nigricollis*) in Africa (Luiselli & Angelici, 2000; Akani *et al.*, 2002), eastern carpet pythons (*Morelia spilota mcdowelli*) (Fearn *et al.* 2001) and tiger snakes (*Notechis scutatus*) (Butler, Malone & Clemann, 2005a; Hamer, 2011) in Australia, as well as rock pythons (*Python sebae*) (Reed & Krysko, 2013), corn snakes (*Elaphe guttata*) and DeKay's snakes (*Storeria dekayi wrightorum*) in the USA (Neill, 1950). Despite their prevalence, there have been few descriptions of urban snake behaviour and feeding ecology.



Differences in prey diversity and food availability can influence snake body size in urban areas. For example, invasive brown tree snakes (*Boiga irregularis*) on Guam feed on different prey in urban and non-urban areas, with urban snakes growing larger due to a greater range of available prey compared with non-urban sites, where there have been local prey extinctions recorded as a result of predation pressure (Savidge, 1988). By contrast, *P. sebae* in suburban areas in Nigeria supplement their diet with synanthropic rats and domesticated poultry, but are significantly smaller than conspecifics from non-urban environments: the authors did not suggest any reason for this difference (Luiselli *et al.* 2001). In the present study, we investigate the effect of urbanisation on the feeding ecology of the dugite (*Pseudonaja affinis*, Elapidae; Gunther 1872). This species is one of the most common snakes of south-west Western Australia, thriving in woodlands, heaths, and urban environments (Chapman & Dell, 1985), possibly *via* supplementation from the spread of the invasive house mouse (*Mus musculus*) (Shine, 1989). Although the house mouse is a small species, it is larger than the majority of urban lizards in Western Australia (How & Dell, 2000), and its communal nesting and prolific breeding (e.g. Gomez *et al.*, 2008; Vadell, Cavia & Suarez, 2010) appears to provide dugites with frequent opportunities to eat multiple individuals (and therefore larger meals). Dugites are regarded as one of the best urban-adapted large-bodied reptiles in Australia (How & Dell, 1993), which makes them ideal model animals for urban/non-urban comparisons. Assuming dugites benefit from the presence of synanthropic rodents, then we make the following predictions for comparisons between urban and non-urban dugite specimens:

- 1) urban dugites will more frequently contain prey than non-urban dugites, and have eaten larger meals;
- 2) urban dugites will eat proportionally more introduced prey than non-urban dugites;
- 3) urban dugites will eat a less-diverse range of prey species than non-urban dugites; and
- 4) urban dugites will be relatively larger than non-urban dugites.

## 3.3 Materials and methods

### 3.3.1 Study species

The dugite is a highly venomous elapid distributed across the southern part of Western Australia and parts of South Australia (Figure 3.1a). Dugites are diurnal, active-foraging predators that grow up to 2 metres in total length and can travel at least 1.5 km per day (AKW unpubl. data). The diet of dugites was explored and compared with congeners by Shine (1989) who examined 179 museum specimens, although he did not consider differences across space or time. Unfortunately, the specimens attributed to that study were since disposed of and we were unable to revisit that dataset.



Figure 3.1. Collection locations of dugite (*Pseudonaja affinis*) specimens used for this study: a) urban specimens (around the Perth metropolitan area where human population density exceeded 500 persons·km<sup>2</sup> at the time of the nearest Australian Bureau of Statistics census) are indicated by black dots, non-urban specimens are shown with grey squares; distribution of dugites containing prey in gut contents for a) urban and b) non-urban specimens. Legend: cross - non-native rodents; diamond - native rodents; plus – reptiles.

### 3.3.2 Dissections

We dissected 568 dugites, of which 548 were from the Western Australian Museum (WAM) (specimens collected between 1910 and 2015 from across the entire known Western Australian range of the species) and 20 were opportunistically collected as road-kill (collected 2014–2015). Of the 568 dissected dugites, we were able to obtain complete data (location, snout-vent length [SVL], wet mass of the preserved snake after draining excess preservative liquid ( $M_b$ ), and collection date) for 453 specimens, of which 112 dugites contained prey. The numbers of individuals included in each analysis therefore varies accordingly.

Prior to dissections, we recorded SVL,  $M_b$ , and sex (for all specimens >40 cm SVL; juveniles, n = 226, could not be sexed with confidence even upon dissection). Each specimen was opened via a ventral incision at the subcaudal third, the stomach located and removed. Whole stomachs (from the end of the oesophagus to the beginning of the small intestine) were extracted, weighed complete, cut open lengthwise and examined for any prey contents, and then re-weighed empty. Prey items were classified to the lowest possible taxonomic group; prey items were identifiable to species (66%), genus (6%) and family (28%), which were used for statistical analyses. We identified 20 native prey species (129 prey items) and 3 introduced

Table 3.1. Diet of dugites collected from urban and non-urban locations. Urban snakes ate a similar diversity of prey. Collective number of species and groups identified to the finest possible scale are represented by *n* for each class and family.

Taxon	Native (N) or Introduced (I)	Urban	Non-urban
Mammals, Rodents (n = 4 taxa)			
<i>Mus musculus</i>	I	9	71
<i>Notomys mitchelli</i>	N	–	2
<i>Rattus norvegicus</i>	I	1	1
<i>Rattus rattus</i>	I	2	–
Reptiles (n = 28)			
Geckos (n = 6 taxa)			
<i>Christinus marmoratus</i>	N	3	13
<i>Diplodactylus granariensis</i>	N	–	2
<i>Diplodactylus pulcher</i>	N	–	1
<i>Strophurus assimilis</i>	N	–	2
<i>Strophurus spinigerus</i>	N	1	–
Unidentified	N	–	4
Pygopods (n = 2 taxa)			
<i>Lialis burtonis</i>	N	–	1
<i>Pygopus lepidopodus</i>	N	–	1
Agamids (n = 3 taxa)			
<i>Ctenophorus</i> sp.	N	–	1
<i>Pogona minor</i>	N	2	1
Unidentified	N	–	2
Skinks (n = 10 taxa)			
<i>Acritoscincus trilineatus</i>	N	3	7
<i>Ctenotus catenifer</i>	N	–	1
<i>Ctenotus fallens</i>	N	–	1
<i>Ctenotus labillardieri</i>	N	–	9
<i>Ctenotus</i> sp.	N	1	10
<i>Hemiergis peronii</i>	N	–	1
<i>Hemiergis quadrilineata</i>	N	10	–
<i>Lerista distinguenda</i>	N	–	2
<i>Tiliqua rugosa</i>	N	1	3
Unidentified	N	15	37
Snakes (n = 2 taxa)			
<i>Pseudonaja affinis</i>	N	–	2
Unidentified	N	–	1
Number of prey items		48	176
Number of taxa		11	24
Evenness		0.63	0.33
Simpson dominance		0.81	0.78
Shannon H'		1.94	2.08

species (82 prey items) (see Table 3.1 for classification). As many of the prey items were partially digested, we counted the total number of prey items and recorded total wet mass of all preserved prey items (after draining excess preservative) ( $M_{\text{prey}}$ ) contained within each stomach. Items such as sand, rocks, and leaves were considered incidental gut contents and excluded from prey mass calculations.

### 3.3.3 Classification of urban and non-urban sites

Collection dates and GPS coordinates for each snake were available for all road-killed specimens, and 89% of museum specimens ( $n = 509$ ) (Figure 3.1a). To account for urban growth over time, we categorised these GPS coordinates as either 'urban' or 'non-urban' sites using data for the closest census date (Australian Bureau of Statistics census dates: 1911; 1933; 1947; 1955; 1962; 1969; 1974; 1982; 1988; 1993; 1997; 2001; & 2011, Appendix 3.1) to calculate the number of people per square kilometre, classed by local government areas. All locations that had  $>500$  persons·km<sup>-2</sup> were considered urban (only sites within the Perth metropolitan region reached this population density), and all other coordinates were considered non-urban (Figure 3.1a). To determine if there was a skew in collection dates between urban and non-urban sites, we performed a two-way chi squared analysis comparing collection locations across each decade ( $n = 10$ ) for all specimens with complete records ( $n = 453$ ).

### 3.3.4 Analyses

Over half of the museum specimens we dissected had information about the collector (338 unique collectors: general public = 37 specimens, scientist = 205 specimens, undetermined = 211 specimens). To test for collection bias in the specimens included in this analysis ( $n = 453$  specimens with complete data records), we used a multiple regression to compare body size (log-SVL) as the dependent variable with location (urban = 0, non-urban = 1) and collector (general public = 0, undetermined = 0.5, scientist = 1). Relatively larger (SVL) snakes were collected from non-urban areas ( $F_{2,450} = 23.25$ ;  $P < 0.001$ ) (Table 3.2), and by scientists ( $t_{450} = 5.51$ ;  $P < 0.001$ ). As it is not possible to distinguish between differences in population demographics or collection bias, we were unable to determine if there were any real differences in body size between locations. Because body size is known to influence diet in snakes (e.g. Shine 1989; King 2002; Bryant *et al.* 2012; Miranda *et al.* 2016), body size was therefore accounted for by including log-SVL as a covariate in all analyses. There were also sex differences in body size (of 453 specimens with complete data: female = 119, male = 105, undetermined sex = 229) (Table 3.2), with females being smaller than males ( $M_b$ :  $F_{1,492} = 106.5$ ;  $P < 0.001$ ; SVL:  $F_{1,492} = 107.4$ ;  $P < 0.001$ ). Therefore, the sex of specimens (female = 0, undetermined = 0.5, male = 1) included in analyses to account for this sex bias that could influence diet. We predicted that animals would be more active and therefore have a greater mass of food in their stomachs for warmer months; therefore season (winter = 0, autumn/spring = 0.5, summer = 1) was included as an independent factor in analyses. Furthermore, we predicted there would be a decrease in prey diversity or

availability over time due to homogenisation of the landscape due to anthropogenic influences, and therefore included collection date (year) as an independent factor in analyses.

Table 3.2. Length and body mass measurements for dugites by location and sex for dugite specimens with complete data. \*Of the 229 specimens for which we were unable to determine sex, 226 were juveniles, SVL >40 cm.

Sex (n Urban, Non-urban)	Urban	Non-urban
	Mean SVL $\pm$ SE (range), cm	
Females (44, 75)	90.8 $\pm$ 28.0 (42.4 - 132.0)	98.0 $\pm$ 25.5 (41.5 - 156.0)
Males (35, 70)	93.0 $\pm$ 28.7 (44.3 - 167.8)	104.3 $\pm$ 24.5 (40.0 - 168.5)
Undetermined sex* (116, 113)	27.4 $\pm$ 4.7 (19.6 - 61.0)	28.1 $\pm$ 11.3 (16.1 - 136.0)
	Mean body mass $\pm$ SE (range), g	
Females (44, 75)	252.2 $\pm$ 191.0 (16.6 - 604.9)	287.7 $\pm$ 200.9 (19.6 - 1170.0)
Males (35, 70)	296.1 $\pm$ 335.6 (16.1 - 1940.0)	336.1 $\pm$ 312.3 (18.0 - 1800.0)
Undetermined sex* (116, 113)	7.3 $\pm$ 8.0 (2.9 - 89.0)	15.1 $\pm$ 75.1 (2.3 - 800.0)

### 3.3.4.1 Prediction 1: Urban dugites will more frequently contain prey than non-urban dugites, and have eaten larger meals

To determine if there was an effect of urbanisation on the proportion of specimens ( $n = 453$ ) containing prey items, we performed a logistical multiple regression with stomach contents (empty = 0, containing prey = 1) as the dependent variable, and location, sex, body size (log-SVL), season, and collection date as independent variables.

To determine if there was an effect of urbanisation on the total mass of prey eaten ( $n = 112$  dugites containing prey), we performed a multiple regression with  $\log-M_{\text{prey}}$  as the dependent variable, and location, sex, body size, season and collection date as independent variables.

### 3.3.4.2 Prediction 2: Urban dugites will eat proportionally more introduced prey than non-urban dugites

To determine whether there was an effect of location on diet composition for  $n = 112$  dugites containing prey, we performed a two-way non-parametric MANOVA (PERMANOVA) using a Euclidean similarity index and 9,999 permutations, with  $\log-(M_{\text{prey}}+1)$  as dependent factors (mass calculated separately for all agamids, geckos, pygopodids, rodents, skinks, and snakes), location and sex as independent grouping factors, and body size, season, and collection date as covariates. We then repeated this PERMANOVA analysis using the total  $\log-(M_{\text{prey}}+1)$  for all native or all introduced prey species.

### 3.3.4.3 Prediction 3: Urban dugites will eat a less-diverse range of prey species than non-urban dugites

To determine if there was an effect of location on the number of prey items for  $n = 112$  dugites containing prey, we performed a multiple regression with the total number of prey items per individual as dependent variable, and location, sex, body size, season, and collection date as independent variables. We carried out a similar analysis with prey species richness as the dependent variable. The effect of location on prey diversity was tested by comparing a Shannon diversity index between locations via a diversity  $t$ -test.

### 3.3.4.4 Prediction 4: Urban dugites will be relatively larger than non-urban dugites

To determine if there was an effect of urbanisation on snake body condition (i.e. mass relative to body size), we performed a multiple logistic regression for  $n = 453$  specimens with  $\log\text{-}M_b$  as the dependent variable, and location, sex, body size, season, and collection date as independent variables.

Values are presented as  $\bar{x} \pm 1$  SD, range: min–max. Parametric analyses were conducted using STATISTICA 7.1 (StatSoft Inc. 2006). Non-parametric and diversity analyses (predictions 2 and 3) were conducted using PAST 3.1 (Hammer *et al.* 2001).

## 3.4 Results

A total of 195 (43%) of the 453 specimens with complete data were collected in urban areas. The majority of collections occurred in 1960–1989 (Figure 3.2). There was a significant difference in location of collection over time ( $\chi^2_8 = 22.9$ ;  $P = 0.003$ ), with a relatively greater proportion of urban animals collected over more recent decades (Figure 3.2). We found prey items in the stomach for 112 (24.7%) of the 453 specimens with complete data; 44 specimens contained more than one prey item, and 21 specimens contained more than one prey species. In total we identified 224 prey items of at least 23 species. Overall observed dugite diet was made up of 38.4% mammals and 61.6% reptiles (Figure 3.1b and c). A total of 55 (24.6%) prey items were autotomised lizard tails (i.e. no evidence of the lizard bodies), which we classified as belonging to geckos and skinks.

### 3.4.1 Prediction 1: Urban dugites will more frequently contain prey than non-urban dugites, and have eaten larger meals

Fewer urban snakes contained prey items than non-urban snakes (Logistic multiple regression testing whether snakes had prey in their stomachs or not:  $t_{447} = 2.8$ ;  $\beta = 0.1$ ;  $P = 0.0046$ ; Table

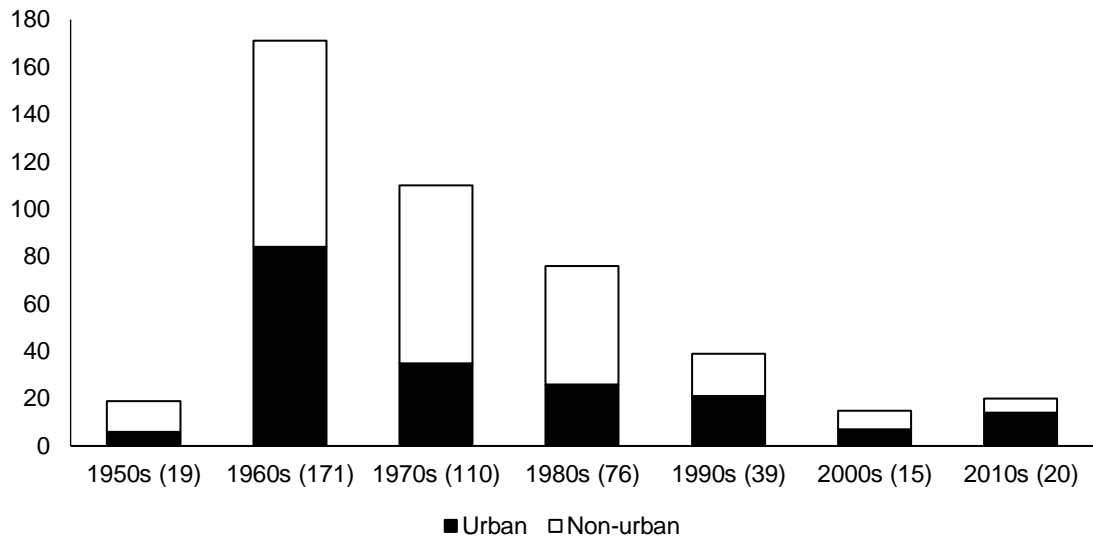


Figure 3.2. Comparison of urban and non-urban specimens collected over time. Only three snakes were collected prior to the 1950s: two urban snakes in the 1920s and one non-urban snake collected from the 1930s. Data represented as Decade (n).

3.3). There was also an effect of snake body size, with larger snakes (log-SVL) more likely to have prey present (Table 3.3). There was no significant effect of sex, season, or year of collection on the presence of prey. Urban snakes contained a similar total mass of prey ( $\bar{x} = 3.6 \pm 7.2$ , 0.001–27.7 g) as non-urban snakes ( $\bar{x} = 6.0 \pm 10.1$ , 0.001–54.5 g) ( $t_{106} = -1.0$ ;  $P = 0.31$ ; Table 3.3). Larger snakes (log-SVL) had a greater mass of prey present, but there was no significant effect of sex, season, or year of collection on prey mass (Table 3.3).

Table 3.3. Summary of multiple regression analyses testing dependent factors addressing the four predictions of this study. Once the effects of body size and potential biases (sex, season, year of collection) were accounted for, urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. Beta ( $\beta$ ) values are provided for significant findings.  $0 < \beta$  represents a trend towards: a) non-urban snakes for location, b) males for sex, and c) larger snakes for log-SVL.

Prediction	Dependent factors		Independent factors				
			Location	Sex	Body size (log-SVL)	Season	Year
1a	Prey present (y/n)	$t_{447} =$	<b>2.8; <math>\beta=0.12</math>; <math>P=0.0046</math></b>	0.33; $P=0.74$	<b>4.6; <math>\beta=0.32</math>; <math>P&lt;0.0001</math></b>	0.61; $P=0.54$	1.0; $P=0.30$
1b	Mass of prey (g)	$t_{106} =$	-1.0; $P=0.31$	0.39; $P=0.69$	<b>8.9; <math>\beta=3.1</math>; <math>P&lt;0.0001</math></b>	-1.8; $P=0.062$	0.31; $P=0.75$
3a	Number of prey items (count)	$t_{106} =$	-0.061; $P=0.95$	0.32; $P=0.75$	<b>3.2; <math>\beta=2.5</math>; <math>P=0.0016</math></b>	0.022; $P=0.98$	-0.55; $P=0.59$
3b	Number of prey species (count)	$t_{106} =$	0.93; $P=0.35$	0.72; $P=0.47$	<b>2.3; <math>\beta=0.53</math>; <math>P=0.024</math></b>	0.097; $P=0.92$	0.38; $P=0.71$
4	Dugite body mass	$t_{447} =$	<b>2.1; <math>\beta=0.023</math>; <math>P=0.034</math></b>	<b>2.1; <math>\beta=0.032</math>; <math>P=0.035</math></b>	<b>151.3; <math>\beta=2.8</math>; <math>P&lt;0.0001</math></b>	1.1; $P=0.27$	-1.9; $P=0.059$

### 3.4.2 Prediction 2: Urban dugites will eat proportionally more introduced prey than non-urban dugites

There was no significant effect of location on diet composition (Two-way PERMANOVA:  $F_{1,106} = 2.6$ ;  $P = 0.062$ ) or effect of sex ( $F_{2,106} = 1.7$ ;  $P = 0.091$ ). Similarly, there was no location effect on diet composition in terms of whether prey was native or introduced (urban introduced  $M_{\text{prey}}$ :  $\bar{x} = 2.1 \pm 6.7$ , 0–27.1 g, native:  $\bar{x} = 1.2 \pm 2.4$ , 0–11.7 g; non-urban introduced  $\bar{x} = 4.2 \pm 9.4$ , 0–52.5 g, native  $\bar{x} = 2.3 \pm 5.0$ , 0–25.7 g) ( $F_{1,106} = 2.6$ ;  $P = 0.062$ ). There was also no sex effect on diet composition in terms of whether prey was native or introduced ( $F_{2,106} = 1.7$ ;  $P = 0.093$ ).

### 3.4.3 Prediction 3: Urban dugites will eat a less-diverse range of prey species than non-urban dugites

Urban dugites ate a similar number of prey items as non-urban dugites ( $t_{106} = -0.06$ ;  $P = 0.95$ ; Table 3.3). Larger snakes (log-SVL) had more prey items, but there was no effect of sex, season, or year of collection on number of prey items (Table 3.3). Similarly, larger snakes ate a greater diversity of prey (number of species), but there was no effect of location, sex, season, or year of collection (Table 3.3). This analysis was supported by a diversity  $t$ -test, which indicated that urban dugites had a similar diversity of prey present as non-urban dugites (Shannon  $t_{111.94} = -0.86$ ;  $P = 0.39$ ; Table 3.1).

### 3.4.4 Prediction 4: Urban dugites will be relatively larger than non-urban dugites

Urban dugites were relatively lighter than non-urban dugites ( $t_{447} = 2.1$ ;  $\beta = 0.023$ ;  $P = 0.034$ ; Figure 3.3a; Table 3.3) once correlation with body length (log-SVL) was accounted for. Females were relatively lighter than all other specimens (Figure 3.3b), but there was no significant effect of year or season of collection on relative body mass (Table 3.3).

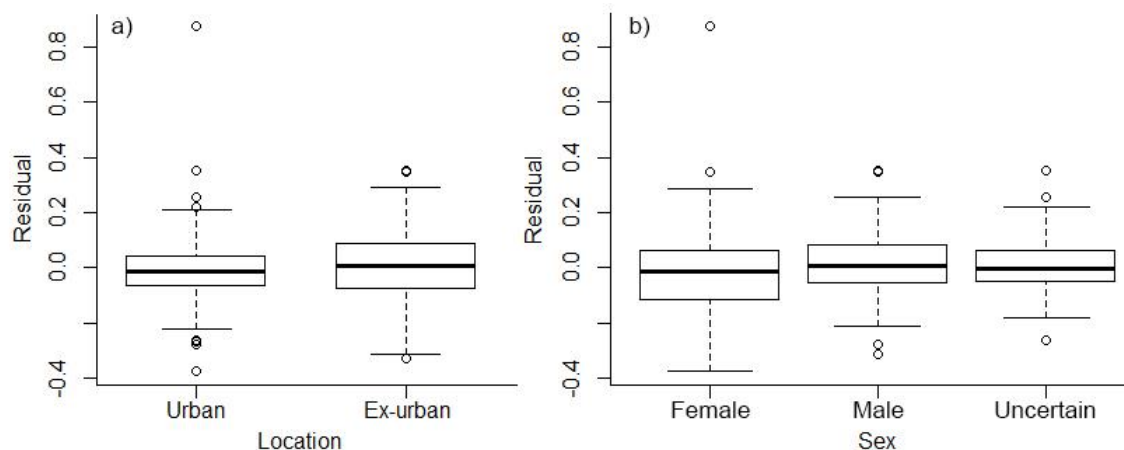


Figure 3.3. Residual body mass (compared with SVL) for a) urban and non-urban dugites and b) specimens of each sex. Residuals were calculated using a linear regression of log-SVL against log-body mass.



### 3.5 Discussion

Many mammalian urban adapters have access to increased food supplementation, providing larger and/or more frequent meals (see Bateman & Fleming, 2012). This is also indicated in reptiles for *B. irregularis* (Savidge, 1988) and *P. sebae* (Luiselli *et al.*, 2001), which take larger prey in urban areas, possibly due to prey availability. We had therefore predicted that the presence of synanthropic prey in urban areas would provide greater opportunity for dugites. However, our predictions were not supported by this dataset of 453 dugite specimens. Once the effects of body size and potential biases (sex, season, year of collection) were accounted for, urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. Location did not affect the number of prey items, the diversity of prey, or the relative proportions of native or non-native prey.

As has been reported across many snake diet studies (e.g. Shine, 1989; King, 2002; Bryant *et al.*, 2012; Miranda *et al.*, 2016), body size (log-SVL) was a strong predictor of dugite diet. Larger snakes more frequently contained meals, and those meals were of a greater mass. Larger snakes also contained a greater number and greater diversity of prey items than smaller snakes. Body size was also significantly different between the sexes. Despite dugites, along with other Australian brown snakes, being considered to not have marked sexual size dimorphism (Shine, 1989), we found that females were relatively lighter than males.

Although we predicted urban snakes would be relatively heavier than non-urban snakes, our finding to the contrary is not unsurprising, as living in high-disturbance areas may better suit smaller snake individuals (i.e. younger snakes) and smaller-bodied species. For example, road mortality from vehicle-wildlife collisions is biased towards larger-bodied species or individuals (e.g. Shine & Koenig, 2001; Gibbs & Shriver, 2002; Steen *et al.*, 2006). Smaller snakes may also be better able to find cover in high-disturbance areas. Smaller garter snakes (*Thamnophis ordinoides*) flee to cover quicker than larger conspecifics (Bell, 2010), and smaller grass snakes (*Natrix natrix*) are more likely to be found under cover than in the open than were larger individuals (Gregory, 2016).

Our observed dugite diet of mostly mammals (38.4%) and reptiles (61.6%) did not vary between urban and non-urban snakes. This diet composition is similar to that recorded by Shine (1989), who also used WAM specimens (n = 179), but found different proportions of prey representation to us; his specimens contained birds and more mammals (grouped together, 51%) than reptiles (47%) as prey, and also included frogs (2%). These differences are likely due to different snake size ranges of the specimens dissected between the two studies (SVL =  $108.8 \pm 2.6$  cm for females and  $108.5 \pm 2.7$  cm for males, n.s., Shine 1989; SVL =  $90.8 \pm 2.8$  cm for females and  $104.3 \pm 4.5$  cm for males, with significant effects of sex and location, this study). Dugites tend to eat more endothermic prey with increasing SVL (Shine 1989), which may explain why we found more reptiles and fewer mammals in our, on average, smaller specimens.

There was no difference in the relative proportions of native or non-native prey for urban or non-urban dugites, which reflects that urban snakes make extensive use of native species, despite living in the urban matrix. All reptiles identified were native (Cogger, 2014), and many reptile prey

species identified are considered common in urban bush remnants across Perth (How & Dell, 2000; Davis & Doherty, 2015). The most common prey species found exclusively in urban areas was a native reptile, the two-toed earless skink (*Hermiergus quadrilineata*). This skink species occurs within some of the dugite's non-urban range along the south-western coastline, but it is recognised as one of the most abundant lizards within the Perth metropolitan area (Davis & Doherty, 2015), and is most commonly found near urban environments (Cogger, 2014). Another prolific urban species, Buchanan's snake-eyed skink (*Cryptoblepharus buchananii*) (Bush *et al.* 2010), was not identified as a prey item for any snake; however, of the 56 autotomised tails found present in dugite stomachs, we expect that some of these may have belonged to the snake-eyed skinks, as dugites have been observed eating these in the wild (AKW pers. obs.). Therefore dugites do not face a lack of native reptile prey in urban areas.

The only introduced mammalian prey were rodents: *M. musculus*, *Rattus norvegicus* (brown rat), and *Rattus rattus* (black rat); all are synanthropic species. Urban dugites did not appear to make greater use of synanthropic species than was evident for non-urban specimens. While both specimens of *R. rattus* were found in urban snakes, *M. musculus* and *R. norvegicus* were found in the stomachs of both urban and non-urban dugites. The prevalence of rodents in landscapes associated with grain farmland is not a particularly surprising result, and Western Australia's farming 'wheatbelt' comprises of 154,862 km<sup>2</sup>, or approximately 30% of the distribution range of dugites in Western Australia (Wheatbelt Development Commission, 2015). Many non-urban specimens found containing rodents were outside of the wheatbelt region; the spread of rodents across the southern half of the dugite range may be exacerbated by the scattering of towns across southern WA. The extensive spread of introduced rodents across southern Western Australia appears to supplement all dugites, not just those in urban areas, as we had originally predicted.

### 3.5.1 Sampling bias

There was a significant sampling bias of collection location on body size: relatively larger snakes were collected from non-urban areas. Snakes in particular are stigmatised for their potential to have a venomous bite (whether they are venomous or not), and large individuals are often relocated away from urban areas for safety concerns (Shine & Koenig, 2001; Department of Parks and Wildlife, 2013), possibly reducing the average size of animals persisting in urban sites. Additionally, although killing any wildlife, including snakes, is illegal in Western Australia, we have observed dugites dead in backyards and on roads in ways that could only be deliberate (AKW pers. obs.). Human predation on snakes therefore must also play a role in shaping the demographics of urban snake populations. Urban development encroachment, introduced predators (e.g. cats, dogs, foxes) and pressures (e.g. modified land use), or low behavioural plasticity and adaptation to change may also potentially contribute to the observed size differences between urban and non-urban locations. Alternatively, urban snakes may exhibit increased secretive behaviours to minimise interactions with people, inevitably reducing foraging activity and feeding opportunities.

We found that relatively larger dugites were also collected more frequently by scientists (as identified by collectors' names). This presents an interesting point for future studies of museum specimens, as significant biases may result due to the method of capture of specimens. For example, members of the public most likely donated dugites to the museum that were found dead or were killed on their property for fear of a venomous bite, while scientists embark on trapping exercises or encounter specimens of high quality and donate those exceptional specimens to the museum. We found no evidence of similar studies accounting for such biases, but we recommend incorporating this information into future comparative analyses, wherever possible.

Although size difference comparisons between urban and non-urban snakes in the literature are limited, a consistent directional pattern does not currently appear to exist: *B. irregularis* are larger in urban areas (Savidge, 1988), while urban individuals of *P. sebae* are relatively smaller (Luiselli *et al.* 2001). In human-disturbed sites in New Hampshire, USA, snakes found within smaller patches were relatively larger than those found in larger patches (Kjoss & Litvaitis, 2001). In Japan, mamushi snakes (*Gloydius blomhoffii*) were relatively smaller in areas where they are hunted than conspecifics in non-hunting grounds, an example of rapid evolutionary responses to predation pressure (Sasaki, Fox & Duvall, 2008). By contrast, the size of massasauga rattlesnakes (*Sistrurus catenatus catenatus*) in Canada, was unaffected by disturbance from humans.

### 3.5.2 Application of urban ecology theory to snakes

Degrees of adaptation to urbanisation have been described as three levels: avoidance, adaptation, and exploitation (Blair, 1996; McKinney, 2006). Due to sensitivity to anthropogenic changes, 'urban avoiders' remain in their highest densities in unmodified natural environments. 'Urban adapters' prefer areas of intermediate disturbance (i.e. suburbia) due to an ability to use novel resources such as garden plants. Finally, 'urban exploiters' appear to show preference for highly modified areas (i.e. inner metropolitan areas) due to an ability to exploit the availability of anthropogenic resources such as buildings (shelter) and refuse (food). This classification method has been useful for describing responses to urbanisation for birds (Blair, 1996), mammals (Randa & Yunker, 2006), and insects (McIntyre, 2000). Building on this, a set of five rules for urban exploiters was developed by Kark *et al.*, (2007) using birds as a model; urban exploiters most commonly are:

- 1) omnivorous or diet generalists (with some specialisation seen in urban adapters);
- 2) social;
- 3) sedentary and maintain territories;
- 4) nest in man-made structures (though adapters use vegetation); and
- 5) have relatively larger brains, greater behavioural flexibility, and use novel food items.

For mammalian carnivores, body size is also likely to influence the ability of mammals to exploit the urban landscape, with medium-sized (1–20 kg) generalist predator species identified as the best urban adapters: larger species are more likely to attract human attention and smaller species more likely to be sensitive to habitat fragmentation (Crooks, 2002; Gehring & Swihart, 2003; Bateman & Fleming, 2012).

Applying the descriptions of urban adaptation developed by Blair (1996) and Kark *et al.*, (2007), based on persistence in urban areas, we consider dugites as urban adapters ('suburban adaptable'). The apparent lack of feeding innovations for urban dugites and complete diet overlap between urban and non-urban dugites suggests that dugites living within the Perth metropolitan area are not using any available extra dietary resources, or using dietary resources differently. Perhaps urban dugites lack feeding innovations because native food is abundant for urban dugites, while there is also an abundance of synanthropic species associated with farming in non-urban locations. Some Australian reptile species such as the blue-tongue lizard (*Tiliqua scincoides*) (Koenig *et al.* 2001) and the common skink (*Oligosoma nigriplantare polychroma*) (van Heezik & Ludwig, 2012) use household gardens for food, water, and avoidance of predators, and most of the urban dugite prey species we identified are both common in gardens/urban remnants and less urbanised parts of Western Australia. Perhaps the definitions of urban adaptation are not suited for ectothermic vertebrates, or dugites fit into another category: 'urban oblivious', usually a term used for cryptic generalists, usually ignored by humans (Grant *et al.* 2011).

Unlike other taxa that experience food supplementation by urban areas, dugites do not appear to derive any particular dietary benefit from living in cities. However, there is more to urban adaptation than diet alone, and the other factors, such as increased temperatures (Brazel *et al.*, 2000; Ackley *et al.*, 2015), and available cover (e.g. tin sheeting, brick piles, garden beds) (Brown & Sleeman, 2002; Purkayastha *et al.*, 2011) may provide an anthropogenic niche for these snakes that is worth exploiting despite increased predation from domestic pets (Shine & Koenig, 2001) and restricted movement due to habitat fragmentation (How & Dell, 2000). Finally, a major setback for snakes in urban areas, especially for venomous species, is their direct conflict with humans (Whitaker & Shine, 2000; Clemann *et al.*, 2004). Snakes play an important role in controlling rodents and stabilising food webs, and the persistence of these important predators therefore requires that we know more about their habitat and diet requirements. Despite all of the potential challenges for snakes in urban areas, dugites, which do not appear to conform to standard urban-adaptation conventions, remain one of the best urban-adapted vertebrates in Perth.

# Chapter 4. Impacts of translocation on a large urban-adapted venomous snake

Another trait commonly used by urban-adapted reptiles is intraspecific combat/territoriality. While the combative behaviours of both dugites and bobtails are understood to be present when fighting over mates, their home/activity ranges, and whether they establish territories within urban areas are not well known.

This study aimed to determine if the activity ranges of dugites and bobtails are affected by urban development by comparing and contrasting the spatial use of urban and non-urban conspecifics. The project aimed to track 20 free-living dugites and bobtails each, as well as 20 'problem' dugites post-translocation. However, the project had several limitations.

During the first tracking season in November 2014, I trialled SirTrack PinPoint 50 GPS trackers on four bobtails and one dugite, but the trial was considered unsuccessful after some trackers fell off of the animals (including the dugite), and others provided <10 of 70 data points each over a 14-day period (<15% successful data captures). In the following tracking season in 2015, I used a different GPS device, Telemetry Solutions FLR V GPS data-loggers (used in the study), which provided more (approximately 25%) successful data captures. As external attachment of GPS trackers has not before been attempted for snakes, it was inevitable that this study would encounter such limitations, and Chapter 4.5.1 mentions some of these in detail.

Another limitation of the study was the difficulty obtaining adequate sample sizes of animals to track. Despite spending two seasons trapping for snakes, I was only able to catch two free-living non-'problem' dugites and eight 'problem' snakes, all captured by hand. I had greater success capturing bobtails, and I tracked 12 individuals. However, half of these individuals showed symptoms of upper respiratory tract infections ('bobtail flu') and required at least 28 days of rehabilitation at local wildlife rehabilitation centres following the animal welfare ethics protocols for the experiment. Following rehabilitation, all bobtails shed their skins, and the trackers along with them, within 1 week of release, and there was insufficient data for analysis.

The study presented in this chapter has been accepted by the peer-reviewed journal *Wildlife Research* on 30<sup>th</sup> March 2018:

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2018) Impacts of translocation on a large urban-adapted venomous snake. *Wildlife Research*, *in press*.

All authors conceived the ideas and designed methodology; I collected the data; I analysed the data with guidance from PAF; I led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This chapter is a reproduction of the submitted manuscript, with the exception of formatting consistent with the thesis. Additional methods descriptions are available in Appendix 3.2.

## 4.1 Abstract

**Context.** Translocation as a tool for management of nuisance or ‘problem’ snakes near urban areas is currently used worldwide with limited success. Translocated snakes experience modified behaviours, spatial use, and survivorship, and few studies have investigated the impacts of translocation within a metropolitan area.

**Aims.** In this study we investigated the impacts of translocation on the most commonly encountered snake in Perth Western Australia, the dugite (*Pseudonaja affinis*, Elapidae), by comparing the space use of resident and translocated snakes.

**Methods.** We captured 10 dugites and attached telemetry packages, composed of a radiotelemetry transmitter and global positioning system (GPS) data-logger, externally to their tails. Snakes were either released within 200 m of their initial capture sites (residents, n = 6) or moved to new unconnected habitat at least 3 km away (translocated, n = 4). Spatial use data was analysed using general linear models to identify differences between resident and translocated dugites.

**Key results.** Translocation influenced space use of dugites and detrimentally affected their survivorship. Compared to residents, translocated snakes had larger activity ranges and there was a trend towards travelling greater distances over time. Mortality for all snakes was high: 100% for translocated snakes, and 50% for residents.

**Conclusions.** Urban dugites face many threats, and snakes were negatively impacted by translocation. The GPS technology we used did not improve the quality of the data over traditional radiotelemetry methods, due to the cryptic nature of the snakes that spent much of their time under cover or underground.

## 4.2 Introduction

Translocation, or the intentional release of individuals of a species into a site different from their origin (Griffith *et al.*, 1989), is used for the conservation and management of wildlife. While potential benefits exist, and activities such as repatriation may help to bolster vulnerable populations and prevent species extinctions (e.g. Burton & Rivera-Milán, 2014; Lepeigneul *et al.*, 2014; Attum & Rabia, 2016), translocations can be fraught with unintended consequences. Behaviourally, animals can experience reproductive dysfunctions (Reinert, 1991) or demonstrate predator naivety (Moseby, Carthey & Schroeder, 2015) and spatial ignorance, e.g. inability to locate suitable food or shelter (Reinert & Rupert, 1999).

Snakes are often translocated for non-conservation reasons, namely the management of individuals near urban areas that are regarded as a nuisance or potentially dangerous (hereafter ‘problem’ snakes) (e.g. Shine & Koenig, 2001; Butler, Malone & Clemann, 2005b; Vyas, 2013; Devan-Song *et al.*, 2016; Pinheiro *et al.*, 2016). However, moving snakes from their capture location appears to be only a short-term solution (Clemann *et al.*, 2004; Pittman *et al.*, 2014), and

few studies report translocation success (Dodd & Seigel, 1991; Plummer & Mills, 2000). Although studies assessing impacts of translocation for snakes are limited, the overall patterns in behavioural change affecting spatial use and survival appear to be consistent. Compared to residents with established home ranges, translocated snakes tend to:

- 1) Move greater distances (Nowak, Hare & McNally, 1999; Brown, Bishop & Brooks, 2009; DeGregorio *et al.*, 2017);
- 2) Show greater variability in daily distance travelled (Reinert & Rupert, 1999; Plummer & Mills, 2000);
- 3) Be more likely to make extensive unidirectional trips (Reinert & Rupert, 1999; Plummer & Mills, 2000; Pittman *et al.*, 2014; Devan-Song *et al.*, 2016);
- 4) Make forays outside of suitable habitats (Butler *et al.*, 2005b);
- 5) Occupy larger activity ranges (Nowak *et al.*, 1999; Butler *et al.*, 2005a, 2005b; Roe *et al.*, 2010; Holding *et al.*, 2014; DeGregorio *et al.*, 2017); and
- 6) Experience lower survivorship (Roe *et al.*, 2010; Devan-Song *et al.*, 2016).

For example, translocated timber rattlesnakes (*Crotalus horridus*, Viperidae) in non-urban Pennsylvania USA occupied areas up to 10 times larger than residents, moving nearly three times farther in total distance, and were ultimately half as likely to survive (Reinert & Rupert, 1999). Butler *et al.*, (2005b) presented similar findings for tiger snakes (*Notechis scutatus*, Elapidae) in urban Melbourne, Australia: translocated individuals occupied activity areas up to 10.4 times larger, and moved more than 3 times farther than residents, but survival rates were similar at 75% (residents) and 88% (translocated).

Translocated snakes most likely increase their movement and activity ranges due to attempts to relocate their original home ranges (being 'lost'), and individuals may return to their capture site if the translocation site is close enough. For example, invasive Burmese pythons (*Python molurus bivittatus*, Pythonidae) in Florida USA that were translocated up to 36 km away from their capture points moved faster and moved greater distances than did residents to return to their established home ranges (Pittman *et al.*, 2014). On a smaller scale, 12 of 14 western rattlesnakes (*Crotalus oreganus*, Viperidae) translocated 500 m returned to their original capture areas after less than a month (Brown *et al.*, 2009). For individuals unable to return, use of scent-trails from residents may help to identify resources and ultimately reduce activity ranges after successive active seasons (Reinert & Rupert, 1999). In South Carolina USA, translocated free-living ratsnakes (*Pantherophis obsoletus*, Colubridae) initially moved more frequently and used more space post-translocation than did residents, but after 1 month, the snakes were observed behaving similarly to residents (DeGregorio *et al.*, 2017); although the authors did not attempt to explain the mechanisms of this behavioural change, the presence of residents and established scent trails may have assisted individuals of this non-territorial and communal species.

In Western Australia, private citizens with relevant experience can obtain a government-approved license allowing them to remove 'problem' snakes to nearby suitable habitats (usually urban bushland). Within the Perth metropolitan region, dugites (*Pseudonaja affinis*, Elapidae) are the

most commonly encountered snakes, making up nearly 90% of all calls for snake relocators (AKW unpubl. data; Chapter 6). Dugites are highly venomous, diurnal, active-foraging predators, and perhaps one of the best urban-adapted reptiles in the area (How & Dell, 1993). In this study we investigated the impacts of translocation on urban dugites by comparing the space use of resident and translocated snakes.

## 4.3 Materials and methods

### 4.3.1 Study species

Dugites were captured opportunistically in the Perth metropolitan area, Western Australia, either as free-living animals ( $n = 2$ ) or as 'problem' snakes found on private properties that were intended to be translocated to nearby suitable habitat ( $n = 8$ ) (Table 4.1). We only used healthy non-sloughing adults (SVL > 100 cm) during their active season (September–December) for this study.

### 4.3.2 Telemetry packages

Telemetry packages were composed of a global positioning system (GPS) data-logger (FLR V ultra-lightweight GPS, Telemetry Solutions) attached lengthwise to a very high frequency (VHF) transmitter with resin (either PD-2, 40 ppm, Holohil Systems Ltd. or R1680, 30 ppm, Advanced Telemetry Systems Australia) or two-part epoxy glue and heat-shrink tubing (19 mm internal diameter, 4 times shrink rate). The FLR V data-loggers had two 4 mm internal diameter tubes attached to the ends. Together with the VHF transmitters, the telemetry packages measured 70 x 14 x 12 mm (length x width x height) and weighed 14 g. A 2 x 3 mm connection point on the GPS data-logger, which allowed us to recharge the devices, directly upload fix schedules, and download data, was filled with silicone sealant and allowed to dry prior to attachment, ensuring the entire device was waterproof.

The telemetry packages were set to attempt a GPS fix once every 2 h from 8:00 am to 4:00 pm (inclusive) within a 60 second window, totalling five potential fixes per day for 2 months. Successful GPS fixes were obtained when the GPS data-loggers were facing the sky with little or no physical obstructions (i.e. tree canopy cover, leaf litter). The best fixes were obtained when snakes were stationary and in the open (i.e. basking), and GPS fixes could not be recorded when the snakes were underground. Bluetooth remote data download allowed GPS data to be downloaded without physically interacting with the snakes during the tracking period.

### 4.3.3 GPS attachment

Snakes are traditionally radio-tracked through implantation of very high frequency (VHF) radio-telemetry transmitters (e.g. Bryant *et al.*, 2010) due to difficulties in attaching trackers externally.



Table 4.1. Capture information, times of monitoring, kernel Brownian bridge (KBB) estimation of spatial use, survival, and fates of six resident and four translocated dugites during the GPS tracking experiment. Overall means presented  $\pm$  standard error. \*Relocation distance was measured as straight-line distance between original capture and release locations.

No.	Sex	SVL (cm)	Body mass (g)	Capture situation	Relocation distance* (km)	Dates monitored (DD/MM/YY)	No. fixes	Space used (KBB 95%, m <sup>2</sup> /day)	Home range (KBB 50%, m <sup>2</sup> /day)	Mean distance between fixes (m) $\pm$ SD	Minimum distance travelled (m/day)	Survival (d)	Fate
Residents													
1	F	124	520	Problem	0.04	18/11/15 - 20/11/15	2				10.3	2	Struck by motor vehicle
2	M	146	455	Problem	0.20	28/11/15 - 10/12/15	3	0.3	0.06	47.1 $\pm$ 66.6	7.9	12	Predated by <i>Varanus gouldii</i>
3	F	136	405	Free-living	0.00	11/10/16 - 25/10/16	12	0.6	0.1	16.9 $\pm$ 13.5	3.4	14	Shed tracker, survived
4	F	123	486	Problem	0.03	14/10/16 - 19/10/16	18	2.1	0.3	35.5 $\pm$ 34.7	25.5	5	Predated by <i>Felis catus</i>
5	F	128	427	Free-living	0.00	19/10/16 - 23/10/16	15	0.8	0.2	21.2 $\pm$ 18.3	15.3	4	Shed tracker, survived
6	F	150	402	Problem	0.05	30/12/16 - 29/01/17	5	0.04	0.01	28.0 $\pm$ 32.4	2.0	30	Shed tracker, survived
	$\bar{x}$ =	134 $\pm$ 4.67	449 $\pm$ 19.2				9.17 $\pm$ 2.75	0.77 $\pm$ 0.79	0.13 $\pm$ 0.12	29.7 $\pm$ 5.37	10.83 $\pm$ 9.72	11.2 $\pm$ 4.23	
Translocated													
7	M	118	510	Problem	8.28	05/10/15 - 11/10/15	10	1.4	0.3	98.6 $\pm$ 141	66.6	6	Predated by <i>Vulpes vulpes</i>
8	F	127	657	Problem	52.5	05/10/15 - 26/10/15	15	18.7	3.0	216 $\pm$ 262	41.6	21	Predated by unknown bird of prey
9	F	120	417	Problem	3.53	23/10/15 - 10/12/15	15	7.5	1.2	75.2 $\pm$ 57.7	3.2	49	Predated by <i>Varanus gouldii</i>
10	M	165	1100	Problem	64.7	13/11/15 - 14/12/15	15	17.4	4.0	287 $\pm$ 362	33.5	31	Struck by motor vehicle
	$\bar{x}$ =	133 $\pm$ 11.0	671 $\pm$ 151.3				13.8 $\pm$ 1.25	11.3 $\pm$ 8.26	2.14 $\pm$ 1.69	169 $\pm$ 50.0	31.0 $\pm$ 25.5	26.8 $\pm$ 9.02	

However, GPS transmitters require direct access to the sky to communicate with satellites, making internal implantation impossible for this method. External attachment methods for tracking snakes were initially tested on green whip snakes (*Hierophis viridiflavus*, Colubridae) by Ciofi & Chelazzi (1991) and recently re-evaluated on eastern massasaugas (*Sistrurus catenatus*, Viperidae) and corn snakes (*Pantherophis guttatus*, Colubridae) by Riley *et al.* (2017). Both studies tested placement of tracking devices on the tail (i.e. posterior to the cloaca), attached via subdermal incision, where a thread was run under the subcaudal scales. This process allowed for minimal operative and post-operative times, reliable anchoring of the tracker to the snake, and limited restrictions to overall movement of the snake and tail. In the present study, we used a modified method to attach our GPS data-logger/VHF transmitter telemetry packages.

Immediately following capture, snakes were transported to Curtin University for telemetry package attachment. Snakes were cooled to 15°C in a refrigerator for up to 30 min and 3% lidocaine gel was topically applied to desensitise the incision area prior to attachment; we determined that the snakes were adequately anaesthetised when there was a lack of pinch response (Mader, 2006). We restrained snakes by placing their heads and as much of the body as possible in a 1 m length of clear vinyl tubing of varying diameter to suit each snake's girth.

We attached the telemetry package as low on the tail as possible to prevent any damage to internal organs (e.g. for males, piercing a hemipenis) and to ensure the width of the telemetry system was smaller than the girth of the snake at its widest point. We inserted two pieces of 0.5 x 1.3 mm (internal diameter x wall thickness) silicone tubing threaded with 0.4 mm thick 15 kg strength monofilament nylon fishing line through the tubes attached to the telemetry packages. Two subcutaneous incisions were made to the 18<sup>th</sup> and 35<sup>th</sup> subcaudal scales with a size 1 half-curved reverse cutting needle, threaded with the fishing line. As the needle was passed under the subcaudal scales and through to the other side of the tail, the fishing line pulled the silicone tubing through. Snakes were then provided non-steroidal anti-inflammatory relief (Metacam; 5mg/ml injection at the incision site). The telemetry system was anchored dorsally by tying the fishing line with an anchor hitch knot. The entire process, from restraining the snakes in vinyl tubing to tying the knots, took less than 10 min per snake. As captivity appears to negatively affect translocation success in snakes (Roe *et al.*, 2010; DeGregorio *et al.*, 2017), all individuals were immediately released into suitable natural habitats within the Perth metropolitan area (Table 4.2) following surgical procedures.

At the conclusion of radio-tracking, live snakes were recaptured, cooled/restrained, and freed of the telemetry systems by cutting the fishing line, removing the line and tubing from the tail, and cleaning the incision sites with water and alcohol, allowing for immediate release back into the wild.

#### 4.3.4 Radio-tracking

A total of 10 snakes had telemetry packages attached. Resident snakes: n = 2 free-living snakes were released back at the initial encounter site, and n = 4 'problem' snakes from private properties with nearby suitable bushland present (no more than 200 m from initial encounter site) were

released in that bushland. Translocated snakes:  $n = 4$  'problem' snakes without nearby suitable bushland present were translocated to a new bushland site, at least 3 km away from and not connected by bushland corridors to the initial encounter site. Descriptions of release sites are provided in Table 4.2. Although dugites are found in a variety of habitats, including highly urbanised areas with limited vegetation (Bush *et al.*, 2010), we attempted to release all animals into sites with native ground and canopy cover, visible coarse woody debris, and few weeds. All animals captured in private residences were released in sites at least 130 times greater area than the capture site (Table 4.2).

We aimed to track snakes for up to 2 months to allow for the establishment of an entire home range (Lelievre *et al.*, 2012). We checked animals at least once per week to download GPS data and take a manual GPS fix to add to the dataset. We also used this time to observe the snakes and ensure that they were moving unimpeded by the trackers. On five occasions we were concerned that a snake had lost its tracker under the ground/pavement, and we carefully excavated the ground to confirm this suspicion. One individual (snake #9) was found alive underground; 1 snake was found cached half-eaten in a fox den, and 3 had shed their trackers. Fortunately, all snakes that shed their trackers were resident snakes that stayed near to their capture sites, and we were able to positively identify them on later opportunistic recaptures (see Results).

### 4.3.5 Analyses

As GPS location fixes were unable to be recorded at regular intervals due to the semi-fossorial and cryptic nature of the snakes, there were highly variable differences between fix times. To account for this, we plotted trajectories for each animal ('as.ltraj' function in the adehabitatLT package) for estimation of Kernel Brownian Bridge Home-Range ('kernelbb' function in the adehabitatHR package) in RStudio 1.0.153 (RStudio Team, 2015). The Brownian Bridge Kernel method considers the times and paths between points to predict the maximum likelihood of space use, providing a more accurate prediction of home ranges (activity ranges for this study) regardless of sample size (Horne *et al.*, 2007). We calculated maximum activity range (95%), core activity range (50%), and minimum total recorded distance travelled (straight-line trajectories) for each snake, first removing all GPS points that were unreliable due to high location error (dilution of precision  $>10$ ) (Bjørneraas *et al.*, 2010). As there were large differences in number of days tracking each snake, we then standardised activity ranges and travel distances by dividing them by the total number of tracking days for each snake. To determine the effects of translocation, relocation distance (calculated as a straight-line distance), SVL, and sex on time-standardised spatial use, we generated general linear models (lme4 package) for analyses of variance ('Anova' function). Averages are presented  $\bar{x} \pm SD$ .

Table 4.2. Habitat characters and approximate patch sizes for capture and release sites in the study. Legend: IM = inner metropolitan area; OM = outer metropolitan area.

Location	Animal no. (Continuous patch size, m <sup>2</sup> )	Habitat characters
<i>Capture sites</i>		
Private residence, IM	1 (170), 2 (195), 7 (90)	Paved yard, low non-native vegetative cover.
Private residence, OM	8 (3,300), 10 (36,500)	Open, mowed lawn, sparse eucalypt overstorey.
Bibra Lake Reserve, urban park/bushland, IM	3, 5 (1,550,000)	Banksia-eucalypt (30%) and melaleuca (35%) woodland, open grass and sand (35%), surrounding 1,000,000 m <sup>2</sup> wetland.
Native Animal Rescue, urban bushland, IM	4, 6 (145,000)	Banksia-eucalypt woodland, surrounding 25,000 m <sup>2</sup> wetland.
Kwinana Alumina Refinery, tailings runoff storage pond, IM	9 (3,800,000)	Banksia-eucalypt woodland, surrounding 4,500,000 m <sup>2</sup> tailings runoff storage pond.
<i>Release sites</i>		
Freshwater Reserve, urban park/bushland, IM	1 (46,000)	Melaleuca woodland (80%), open grass (20%).
Bandicoot Reserve, urban bushland, IM	2 (57,500)	Banksia-eucalypt woodland.
Bibra Lake Reserve, urban park/bushland, IM	3, 5 (1,550,000)	Banksia-eucalypt (30%) and melaleuca (35%) woodland, open grass/sand (35%), surrounding 1,000,000 m <sup>2</sup> wetland.
Native Animal Rescue, urban bushland, IM	4, 6 (145,000)	Banksia-eucalypt woodland, surrounding 25,000 m <sup>2</sup> wetland.
Banksia Eucalypt Woodland, urban bushland, IM	7 (431,000)	Banksia-eucalypt woodland.
Yanchep National Park, semi-rural bushland, OM	8, 10 (>5,000,000)	Banksia-eucalypt woodland, surrounding 200,000 m <sup>2</sup> wetland.
Thomsons Lake, urban bushland, IM	9 (2,650,000)	Banksia-eucalypt woodland, surrounding 2,500,000 m <sup>2</sup> wetland.

number of days that snakes were tracked, nor did it affect survival. All deaths of snakes during this study were the result of predation events ( $n = 5$ ) or motor vehicle strike ( $n = 2$ ); only three female resident snakes were found alive at the end of the intended 2-month tracking period, and all shed their trackers before 2 months had elapsed (Table 4.1). Trackers were shed on two occasions when the VHF device separated from the GPS data-logger (residents #3 and #5), presumably during underground forays, and we were unable to locate the animals for up to 2 weeks. The third tracker was shed when snake #6 found refuge underground in a buried motor vehicle engine and the fishing line became abraded. Seven snakes were observed in-situ either under human constructions (#2 under a house, #3 and #5 under paving stones) or in burrows (#6, #8, #9, #10). Snake #9 was recorded underground in the same burrow multiple times within a 33 day period, but we also observed tracks in the sand indicating the snake was basking next to the burrow and made forays around the burrow multiple times post-translocation; however, no other translocated snake was observed using the same burrow more than once. The 2 free-living resident snakes (#3 and #5) that we tracked showed a preference for basking at one specific site each. All snakes (dead or alive; predators did not consume the tails or trackers) were eventually reclaimed and their identities confirmed by inspection for the incision sites on their tails. Although we found minor abrasions on the snakes' tails where the telemetry packages were anchored, we found no evidence of infection or major damage as a result of external telemetry package attachment.

Translocated snakes had significantly larger time-standardised activity ranges, both for 95% ( $F_{1,7} = 8.27$ ;  $P = 0.024$ ; translocated:  $\bar{x} = 11.3 \pm 8.26$  m<sup>2</sup> per day, resident:  $\bar{x} = 0.77 \pm 0.80$  m<sup>2</sup> per day) and 50% ( $F_{1,7} = 7.30$ ;  $P = 0.031$ ; translocated:  $\bar{x} = 2.14 \pm 1.69$  m<sup>2</sup> per day, resident:  $\bar{x} = 0.13 \pm 0.12$  m<sup>2</sup> per day) Kernel Brownian Bridge (KBB) ranges, than resident snakes (Figure 4.1). As straight-line relocation distances from original capture points increased, time-standardised spatial use also increased for both 95% ( $F_{1,7} = 60.0$ ;  $P < 0.001$ ;  $R^2 = 0.88$ ) and 50% ( $F_{1,7} = 122.6$ ;  $P < 0.001$ ;  $R^2 = 0.95$ ) ranges.

When corrected for the number of days tracked, translocated snakes did not travel significantly greater total distances ( $F_{1,8} = 5.14$ ;  $P = 0.053$ ; translocated  $\bar{x} = 31.0 \pm 25.5$  m per day, resident  $\bar{x} = 10.8 \pm 9.72$  m per day) than did resident snakes. There was no significant relationship between relocation distance and total distance travelled ( $F_{1,8} = 2.40$ ;  $P = 0.160$ ;  $R^2 = 0.16$ ) (Figure 4.1).

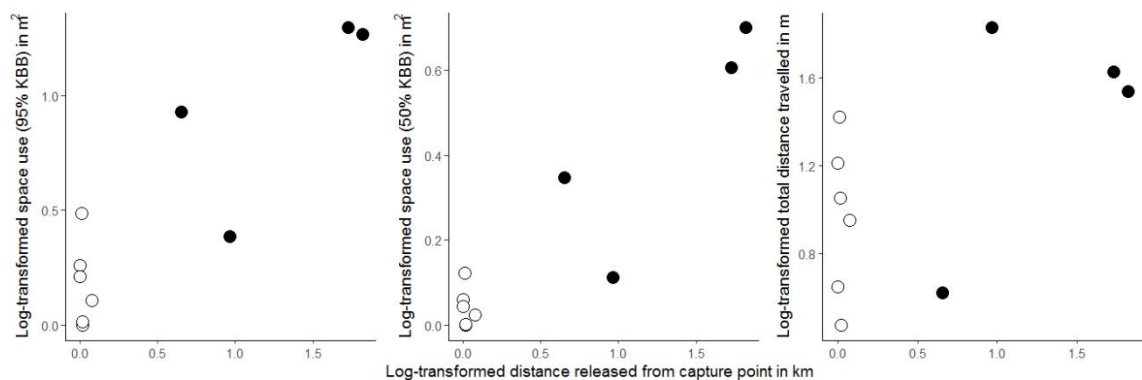


Figure 4.1. Translocated *dugites* (black circles) used significantly larger areas of habitat (calculated as 95% and 50% kernel Brownian Bridge [KBB] home range), but did not travel greater distances than residents (open circles). Data corrected for the number of days tracked for each individual.

## 4.4 Discussion

Despite having a low sample size, we found a significant relationship between translocation and space use of urban dugites, and that translocation detrimentally affected their survivorship. Translocated snakes had significantly larger activity ranges (95% and 50% Kernel Brownian Bridge estimation), but did not travel significantly greater distances between points, than did resident snakes. Relocation distance was significantly positively correlated with spatial use, and all snakes translocated >200 m from their original capture location showed increased activity ranges. Mortality was 100% for the four translocated snakes, and seven of the eight 'problem' snakes died due to predation or motor vehicle strike. These results suggest two findings: 1) urban dugites live in near-constant high-risk environments, and 2), translocation negatively affects dugites, where regardless of the distance they are moved, their likelihood of surviving is small.

Space use analysis of the eastern brown snake, *Pseudonaja textilis* in agricultural areas, shows that these snakes have high site fidelity for mouse and lizard burrows, which they use as a central base for foraging (Whitaker & Shine, 2003). As dugites have a similar diet to eastern brown snakes (Shine, 1989; Wolfe *et al.*, 2017) we suspect that their habitat use might be similar. The dugites that we tracked for the longest period (>30 days; resident #6, translocated #9, #10) were all observed to use burrows. Only 1 translocated snake (#9) was observed to use the same burrow regularly. Although we were unable to track them for as long, the resident snakes all showed high site fidelity. Both free-living resident snakes (#3 and #5) shed their trackers, and we were only able to recapture them opportunistically to assess their condition and ensure complete removal of the trackers because of their reliability in returning to bask at the same sites.

*Pseudonaja* species reach maturity quickly and produce large litters with no parental care (Shine, 1989), often every year (Shine, 1979). Offspring must quickly find sufficient refuge, and although offspring mortality rates have not been studied, few young are likely to survive to reproduce. Similarly, urban displacement of adult snakes as part of translocation requires that individuals quickly find suitable new habitat. When standardised for time spent tracking, translocated dugites experienced an increase of nearly 15 times total activity range (95% KBB), 17 times core activity range (50% KBB), and 3 times total distance travelled between fix points. The only translocated snake that broke the trend of increasing spatial use over time was snake #9, which located a refuge site within 6 days; it did, however, make large forays. Displaced snakes must locate new resources, such as refuge sites, to survive. The likelihood of a translocated adult snake finding suitable refugia in continuous woodland is highly variable (e.g. 25-100% for viperid and colubrid species) (Reinert & Rupert, 1999; Devan-Song *et al.*, 2016; DeGregorio *et al.*, 2017). Natural habitats within urban areas are fragmented, patchy, and often highly degraded (Dickman, 1987; Jellinek *et al.*, 2004; Garden *et al.*, 2010). As suitable refuge sites in natural environments are scarce, snakes must use the next-best option: anthropogenic refuges such as litter, debris, and crevices near and inside houses (Shine, 1979; Fearn *et al.*, 2001; Whitaker & Shine, 2003; Vyas, 2013).

Even in urban areas, snake species appear to prefer native patches and surrounding neighbourhoods with natural gardens (Dickman, 1987; How & Dell, 2000; Kjos & Litvaitis, 2001;

Barrett & Guyer, 2008; McKinney, 2008; Garden *et al.*, 2010). As areas become disturbed by humans, snakes move towards less-disturbed habitats (Whitaker & Shine, 1999a), which may, for a time (e.g. when the residents are at work), be a quiet suburban garden. Unfortunately, removing snakes from familiar habitats can negatively affect survival (Roe *et al.*, 2010; Devan-Song *et al.*, 2016), and increase stress (Heiken *et al.*, 2016). Within urban areas, fences and roads form barriers to movement (e.g. Shine *et al.*, 2004), and introduced predators such as cats, dogs, and foxes are more likely to impose pressures on snakes searching for new refuges (e.g. Shine & Koenig, 2001). We identified two predators as non-native (domesticated cat, *Felis catus*, and red fox, *Vulpes vulpes*) and two native species (Gould's monitor, *Varanus gouldii*, and unknown bird of prey). Two snakes were killed by motor vehicles. For a snake to succeed within an urban environment facing a range of novel and natural threats, establishing and maintaining a home range as quickly as possible is essential.

#### 4.4.1 Comment on the efficacy of GPS tracking snakes

This study may be the first to radio-track snakes using GPS technology. We trialled this technology in the hope that we could minimise the number of encounters with snakes as part of data collection, as human interaction can affect the behaviour and movements of free-living reptiles (e.g. Parent & Weatherhead, 2000; Kerr *et al.*, 2004). While we do not believe that any snakes died as a result of the external attachment, we recommend caution for future studies using this technology at its current level of development (e.g. size/mass constraints). Snakes make use of confined spaces that can often contain acute angles or jutting debris (e.g. rocks, tree roots, and in our study, a buried motor vehicle engine). While previous studies have suggested external attachment of small VHF trackers as successful (Ciofi & Chelazzi, 1991; Riley *et al.*, 2017), the addition of another larger GPS device may increase risk of entanglement. The data collected by the GPS trackers was also limited and often unreliable due to the snakes being near-constantly under cover or underground, and some fixes were immediately discarded due to high location error (as determined by horizontal dilution of precision). GPS tracking is attractive because it promises reduction in overall costs (i.e. labour and transport); however, for our snakes this was not the case, with very few fixes obtained for the cost of the technology. For example, snake #9 was tracked for 49 days, but we obtained only 15 fixes, 7 of which were from the GPS tracker and 8 through manually locating the animal through its VHF signal. The GPS devices (costing \$2,000 USD each) delivered for a total of \$285.71 per location, while the VHF tracker (\$220) was much more efficient (\$27.50 per location). Although using VHF trackers increases interactions with snakes, had we relied on the VHF trackers rather than on GPS data (we had to wait to retrieve the GPS unit to know how successful it had been), we may have collected more locational data.

Another limitation for relying on GPS devices was that we could only afford to study a relatively small number of animals. Although other studies using VHF telemetry to compare spatial use of resident and translocated snakes use similar sample sizes ( $n = 15$ , Reinert & Rupert 1999;  $n = 11$ , Plummer & Mills 2000;  $n = 6$  Butler *et al.* 2005b), their comparisons were all within the same geographical area and represent the populations within the study location. As we were only able

to capture dugites opportunistically, and required problem snakes from private residences, we were limited in where we could release snakes. This resulted in our 10 study animals being distributed across the urban matrix, and we would have benefitted from a larger sample size (Börger *et al.*, 2006; Lindberg & Walker, 2007). However, as mortality was high, we feel that increasing the sample size would pose ethical issues. Future studies with a greater survival rate should consider a larger sample size, supported through use of VHF trackers rather than GPS (Hebblewhite & Haydon, 2010).

## 4.4.2 Conclusions

Urban dugites face many threats, and translocation of 'problem' snakes increases their risk due to inability locate suitable refuges, increased risk of predation, and greater vulnerability to road strike due to their increased movements. Australian snake relocators typically move up to 100 snakes in a season (Clemann *et al.*, 2004), and none are able to follow those snakes over time to determine translocation success or failure. Simply assuming that a translocation is successful because the snake does not return back to the original private residence is inadequate. The ill-informed advocacy for translocations as a humane method of animal management has been refuted in USA (Nowak *et al.*, 1999), China (Devan-Song *et al.*, 2016), and now Australia. We agree with the sentiments of Dodd & Seigel (1991), that translocating a reptile appears to change the question from *if* it dies to *when* it dies.

Instead of advocating the movement of snakes from private properties, we should be focusing on educating the general public. Due to a general fear or hate towards snakes (Whitaker & Shine, 2000), the average Australian may be difficult to convince that protecting snakes from unnecessary harm is a worthy activity. In Western Australia, all fauna, including snakes, are protected (Biodiversity Conservation Act 2016 (WA) s. 151), although elapids may be legally killed if they are considered an immediate danger to humans or to pets/livestock (Wildlife Conservation Act 1950 (WA); Government of Western Australia 1984). Snakes rarely instigate conflicts with humans (Pope, 1937), and cryptic species such as brown snakes will not encounter a human unless in an extenuating circumstance, such as being provoked by the human, a pet, or gardening equipment (Whitaker & Shine, 1999a; Shine & Koenig, 2001).

Members of the public should consider the positive of promoting urban biodiversity, which includes snakes. Urban areas can provide important refuges for snakes, which can then control pests, e.g. rodents (Luiselli *et al.*, 2001; Wolfe *et al.*, 2017), and also provide 'cultural ecosystem services' for snake enthusiasts (Dickinson & Hobbs, 2017). Removing a snake from an area does not necessarily prevent it from returning (Butler *et al.*, 2005a), even at long distances for larger species (Pittman *et al.*, 2014). Alternatively, removing a snake from a suitable urban niche may open up the space for another individual to occupy. Understandably, not all human-snake conflicts are avoidable, but it is important to take all possible steps to reduce the risk. Snake avoidance training for dogs is available (Livingston, 2017; Manning, 2017), and educating the public about snakes and ethical management practices helps to reduce fear and, ultimately, conflict (Bonnet *et al.*, 2016; Pinheiro *et al.*, 2016). Interactive activities, allowing people to touch



and observe animals wherever possible (although dangerous animals should only ever be observed) are effective to help overcome fears and promote positive attitudes (e.g. Gottfried, 1980; Ballouard *et al.*, 2012, 2013), and would be beneficial to incorporate into school programs to educate children and their parents.



# Chapter 5. Surveying attitudes towards reptiles on roads: questionnaire responses do not directly translate to behavioural action

Roads are major landmarks that I found to negatively affect the spatial use of dugites via causing direct mortality in Chapter 4. As road spaces are shared between wildlife and motorists, it is important to consider both the ecological and social aspects of vehicle-wildlife collisions. This study aimed to investigate the likelihood of a reptile being struck on both the side of a road and during crossing, and develop an understanding the attitudes of the general public to reptiles, in comparison to other animals, on roads and their likelihood of rescuing them, rather than running them over.

The biggest limitation of this study was that I could only secure permission to conduct field experiments on one road in the City of Cockburn. I had initially aimed to study at least four roads across different levels of urban development of a similar size, structure, and posted speed limit. Unfortunately, this was not possible, as the potential safety implications of a motorist causing a traffic accident in response to a rubber snake on the side of the road was considered an extreme risk by all other city councils I approached. However, this appears to be a similar issue for the few other successfully-published species across the world that conducted equivalent experiments. Regardless, this study forms the first of its kind in an urban context.

The study presented in this chapter was submitted for peer review by Anthrozoös on 13<sup>th</sup> March 2018:

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2018) Surveying attitudes towards reptiles on roads: questionnaire responses do not directly translate to behavioural action. *Anthrozoös*, *in review*.

All authors conceived the ideas and designed methodology; I collected the data; I analysed the data with guidance from PAF; I led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. This chapter is a reproduction of the submitted manuscript, with the exception of formatting consistent with the thesis. Additional methods descriptions are available in Appendix 3.4.

## 5.1 Abstract

Roads pose significant threats to reptiles, who use them for basking, scavenging food, and crossing. Within urban areas, roads bisect important refuges such as wetlands. Human attitudes may vary across reptile taxa, and understanding motorists' perceptual biases may help determine management strategies as urban sprawl increases. We conducted an online survey asking Western Australian motorists about their attitudes towards animals, including snakes and lizards, on roads. Motorists ranked their degree of concern for animal welfare, damage to their vehicle, and their personal safety when involved in a vehicle collision with 10 different animal taxa. Respondents also ranked their rescue likelihood for these taxa. We then conducted a field experiment to observe motorist responses to snakes and lizards, where we placed model snakes, bobtails, and controls on the shoulder of an urban road next to a wetland in Perth, Western Australia. We also modelled the probability of a reptile being struck while crossing our study road at two different road vehicle densities. The respondents to our online survey had a high mean degree of concern for the welfare of animals on roads ( $\bar{x} = 8.02 \pm 2.73$  SD out of 10) and low concern for vehicle damage ( $\bar{x} = 2.87 \pm 2.75$ ) and personal safety ( $\bar{x} = 2.91 \pm 2.88$ ). Respondents also claimed a high mean rescue likelihood ( $\bar{x} = 7.06 \pm 3.40$ ). In contrast, motorists observed in the field experiment generally ignored objects, including reptiles, on the roadside (79% of  $n = 1,500$ ). We did not observe any intentional strikes on reptiles, and only one motorist made a rescue attempt (bobtail); all other responses were to slow down or move away from the treatment. Estimates of strike probability for a reptile crossing our study road at a low road vehicle density (2.23 vehicles·min<sup>-1</sup>) was >75% for both slow-moving (1 m·min<sup>-1</sup>) bobtails and dugites, but reduced to ≤16% if reptiles were moving quickly (60 m·min<sup>-1</sup>). Although motorists did not intentionally strike model reptiles, surveyed attitudes did not directly translate to behavioural action, and crossing a road is risky for an urban reptile.

## 5.2 Introduction

Roads of all sizes and construction impose important ecological impacts on fauna, including reduced gene flow, modification of population dynamics, degradation of surrounding habitat, and direct mortality (Hels & Buchwald, 2001; Andrews & Gibbons, 2005; Andrews, Gibbons & Jochimsen, 2008). Reptiles are at particular risk on roads: many species move slowly on roads (e.g. Aresco, 2005b) and remain stationary while scavenging for food or basking (Smith & Dodd, 2003; Rytwinski & Fahrig, 2012). Although reptiles are infrequently detected in road-kill counts (Taylor & Goldingay, 2010; Santos *et al.*, 2016), they are common victims on urban roadways (Ciesiolkiewicz *et al.*, 2006; Lumney, Munn & Meikle, 2008). As urban greenspaces such as reserves, wetlands, golf courses, and backyards are becoming increasingly important refuges for urban wildlife (Koenig *et al.*, 2001; Garden *et al.*, 2007; Burgin *et al.*, 2011; Stokeld *et al.*, 2014), it is important to understand the impacts of humans and their driving behaviour on fauna, especially around such refuges.

Human attitudes towards reptiles vary between taxa, with a generalisation of fear, hatred, or negativity for snakes and large lizards (Whitaker & Shine, 2000; Sullivan *et al.*, 2004; Ghimire, Phuyal & Shah, 2014; Crawford & Andrews, 2016; Pinheiro *et al.*, 2016), versus endearment for turtles and small lizards (Koenig *et al.*, 2001; Hoskin, 2011; Crawford, Poudyal & Maerz, 2015; Crawford & Andrews, 2016). Affective reactions (e.g. feelings of like or dislike) can influence judgement, even without provision of prior cognitive information (Zajonc, 1980), and people who are inherently phobic of a taxon group are more likely to have a negative attitude towards them (Knight, 2008). These perceptual biases may play a role in motorists' responses to reptiles on roads, a place that is difficult to study due to potential safety implications, but which is vital to understand to determine management strategies as urban sprawl increases. For example, model snakes on a rural highway bordering woodland in the USA were observed in a field experiment as being struck by motorists at a greater than random frequency (Rothman, 1987). This observation was similarly made for model snakes on highways bordering native prairie in the USA (Langley, Lipps & Theis, 1989) and at a national park in Brazil (Secco *et al.*, 2014), as well as for model snakes and turtles on a paved causeway bordering a wetland reserve in Canada (Ashley, Kosloski & Petrie, 2007). By contrast, Beckmann and Shine (2012) reported that model amphibians and snakes were largely ignored by motorists on a regional Australian road. A considerable study design difference for this study could explain the differing conclusions – models were observed 1.5 h after dusk by Beckmann & Shine (2012), while all other studies were conducted during the day – or perhaps Australian motorists have different perceptions towards wildlife compared to North and South American motorists.

Assessing motorists' attitudes towards wildlife through use of written or verbal surveys can be a less risky way for researchers to understand motorists' behaviour. For example, patrons of the nature-based tourist destination, Jekyll Island (Georgia USA), who completed a written survey, were less concerned with striking a snake on a road than with other taxa (Crawford & Andrews, 2016); but this survey was not followed-up with field experiments on roads. To date, two studies have compared survey results with field experiments. Of local students in Georgia, USA, surveyed by Langley *et al.* (1989), 20% claimed to intentionally strike animals on roads, with snakes targeted more frequently than other taxa, and field experiments indicated that nearly all snake models were intentionally struck on the road. In contrast, Beckmann & Shine (2012) found that locals claimed to selectively strike invasive cane toads (*Rhinella marina*, Bufonidae) over snakes and frogs, but intentional strikes were not observed for any model. More evidence is required to assess if surveyed motorists' attitudes towards wildlife translate to, and can be used as a proxy for, behavioural action.

No studies to date have investigated the attitudes of motorists towards reptiles within urban areas. Dugites (*Pseudonaja affinis*, Elapidae) and bobtail lizards (*Tiliqua r. rugosa*, Scincidae) are reptiles commonly observed basking on or crossing urban roads in south-west Western Australia, and these large-bodied reptiles are frequently the victims of motor vehicle collisions (e.g. Wolfe *et al.*, 2017). *Pseudonaja* species such as dugites are highly venomous and regarded as dangerous to humans (Whitaker & Shine, 2000), while bobtails are well-liked by the general public. We conducted an online survey asking Western Australian motorists about their attitudes

towards 10 animal taxa, including snakes and lizards, on roads. We assumed that respondents who scored their concern highly held more positive values towards the object being valued (welfare, vehicle, or safety) (Crawford & Andrews, 2016). We then observed motorist responses to snakes and lizards via a field experiment where we placed model snakes, bobtails, and controls on the shoulder of a metropolitan road bisecting urban nature reserves. As motorist responses to reptiles may vary according to placement (i.e. road side or centre of the lane) (Secco *et al.*, 2014), we then modelled the probability of a reptile being struck by a motor vehicle while crossing our study road at two traffic densities.

## 5.3 Materials and methods

### 5.3.1 Online surveys – attitudes towards animals on roads

The online survey was conducted in accordance to Curtin University's Human Research Ethics license HRE2016-0030. We conducted an online survey with Qualtrics (Qualtrics, 2017), which we advertised through Twitter, Facebook, and an email list to contacts working in local government, environment-based community groups, wildlife researchers, and wildlife rehabilitation volunteers. All respondents held (or have held in the past) a valid Western Australian drivers' license. The survey asked people about their sociodemographics (sex, age, and whether they reside in an urban or non-urban area, determined by post code), and whether they work/volunteer in animal care or wildlife relocation (hereafter referred to as 'animal carers'). The survey then asked respondents about their attitudes towards animals on roads (10 taxa: cat, dog, fox, rabbit, kangaroo, 'other small native animal such as a bandicoot or possum' [small mammal], bird, turtle, bobtail lizard, and snake), whether they have previously rescued an animal from the roadside, and how often they see animals in association with or on roads (every day, at least once per week, at least once per month, at least once per year, or never). A copy of the survey is available in Appendix 3.4.1.

To evaluate respondents' attitudes towards animals on roads we used a 10 point scale (1–10) and asked respondents to rank their degree of concern towards wildlife on roads and their level of concern (1 = least concern, 10 = most concern), in the hypothetical event of a collision, for: 1) the animal's welfare ('welfare'); 2) damage to the respondent's vehicle ('vehicle'); and 3) the respondent's personal safety ('safety'). We also asked respondents to rank 4) their likelihood of stopping to rescue the animal (1 = least likely, 10 = most likely; 'rescue') (developed from Crawford & Andrews, 2016).

We used a stepwise method to generate multiple linear models with the 'lmer' function (lme4 package) in RStudio (RStudio Team, 2015) using the four respondent opinions (welfare, vehicle, safety, and rescue) as separate dependent factors, and respondent sociodemographic factors (sex, age, and urban/non-urban) and whether they are an animal carer as independent factors. For rescue likelihood, we also included whether the respondent has rescued that animal before, and how frequently they see those taxa on roads as independent factors. Of the models with a

$\Delta AICc \leq 2$  (Burnham & Anderson, 2002), the simplest was selected for further analysis as equivalent models with more factors did not alter the significance of our findings and were considered uninformative (*sensu* Arnold, 2010). Multiple means comparisons were performed using Tukey tests where differences between taxa were detected.

### 5.3.2 Field experiment – responses to reptiles on a roadside

The field experiment was conducted in accordance to Curtin University's Human Research Ethics license HR91/2015. We conducted the field experiment on a road in the residential suburb of Bibra Lake in the Perth Metropolitan area, Western Australia. Hope Road (-32.084478, 115.827786) is a two-lane road of total 7 m wide between the white solid border lines, with 1 m wide gravel shoulders bordered by grass. The posted speed limit is 70 km·h<sup>-1</sup>. The road bisects Bibra Lake Reserve, a state-managed Bush Forever site (State Government of Western Australia, 2000), with the Bibra Lake wetland situated to the south and fenced woodland to the north. Significant fauna for Bibra Lake include waterbirds and quenda (*Isodoon obesulus*, Peramelidae) (State Government of Western Australia, 2000), as well as large populations of tiger snakes (*Notechis scutatus*, Elapidae), dugites, bobtails, and south-western long-necked turtles (*Chelodina colliei*, Chelidae) (Dooley *et al.*, 2006).

To assess motorist responses, we used three lifelike reptile models:

- 1) rubber 'bobtail', 0.35 m long, created by casting a bobtail carcass in a plaster mould and filling with silicone, painted brown with white dorsal stripes to mimic a bobtail;
- 2) 'long snake': 0.37 m long toy rubber snake, with a sinuous shape painted brown to mimic a dugite; and
- 3) 'coiled snake': 0.37 m long toy rubber snake in a 0.13 m diameter coil painted brown to mimic a dugite.

We compared these with motorists' responses to an inanimate object on roads:

- 4) brown disposable paper coffee 'cup', 0.15 m long, which was stuck to the road with adhesive putty to prevent it from blowing away; and
- 5) 'null' treatment (observation without any model on the road) to record motorist behaviour on the road without the presence of an animal or other object.

We conducted the study during October 2015 at one location on Hope Road during non-peak traffic hours (10 am – 1 pm) during sunny days with good visibility on the road. We predicted that cars traveling closely were less likely to respond to objects on roads due to decreased visibility and the increased likelihood of causing an accident with other vehicles nearby. To account for this and the possibility of second party bias, we only included vehicles that were traveling alone (>100 m from another vehicle). The observers were obscured from motorists behind trees, with good visibility of the models, which were 20 m away on the grassed verge. Treatment order was randomised for each day, continuing observations until 300 vehicles drove past each treatment. We placed treatments at the road shoulder, resting at the outside edge of the solid white line

bordering the shoulder and road, appearing as though the treatment was facing towards the road (bobtail and long snake), or sitting on the edge of the road (coiled snake and cup).

We recorded vehicle size, motorist sex, presence/absence of passengers. We defined vehicle size classes as follows: motor/bicycles had only 2 wheels (hereafter referred to as 'cyclists'); small cars were compact class, usually two-door two-wheel-drive; medium cars were standard sedans, hatchbacks, and wagons; large cars were sports utility vehicles, four-wheel-drives, vans, service vehicles (e.g. ambulances), or vehicles with utility trays; and trucks were heavy utility vehicles, often with >2 axels. During the study, we observed some motorists who were distracted and obviously not paying attention to the road, e.g. looking at themselves in the rear-view mirror, eating/drinking, using a cell phone and interacting with objects in the passenger seat or rear of the vehicle; these motorists were recorded as being 'distracted', as the observers could clearly tell that they were not looking at the road when they passed the treatments.

We assessed responses from motorists to treatments on roads categorically as either 'ignore' or 'respond'. A response to a treatment was categorised as either: approaching the solid white line to strike the treatment; stopping the vehicle to rescue; slowing down the vehicle (as noted by the brake lights); moving to the far side of the lane away from the treatment; or any combination of the aforementioned. As we were interested in determining if motorists reliably stayed within the lane when no reptile was present on the roadside, we counted all motorists approaching the solid white line or moving to the far side of the lane during the null observation treatment as 'respond'. Of the motorists that did respond to a treatment (n = 315), only two drove onto the solid white boundary line (once each for the cup and null), and one was observed attempting to rescue a model (bobtail). We were therefore unable to test for differences between response types due to low sample sizes.

To determine factors associated with motorists' responses, we conducted separate Cochran-Mantel-Haenzel (3-way interaction)  $\chi^2$  tests ( $\chi^2_{MH}$ ) with continuity correction: we included motorist response frequencies (ignore/respond) and treatment (bobtail, coiled snake, long snake, cup, null) with vehicle size, motorist sex, presence/absence of passengers, and motorist distraction as separate independent factors. Where the  $\chi^2_{MH}$  tests were significant, we then carried out separate 2-way  $\chi^2$  tests to examine within-group effects of the factors.

### 5.3.3 Modelling – strike probability of reptiles crossing roads

The likelihood of a model being struck by a motor vehicle while crossing roads may differ depending on whether it is on the side or middle of a road (Secco *et al.*, 2014), but our field experiments only observed models on the side of the road. To determine the probability of a reptile being struck by a motor vehicle when crossing our study road in the shortest route possible (i.e. perpendicular to the road, which has been observed for multiple snake species) (Shine *et al.*, 2004; Andrews & Gibbons, 2005; Ciesiolkiewicz *et al.*, 2006), we modelled a calculation simplified from Hels & Buchwald (2001):

$$\text{Strike probability} = 1 - e^{-Na/v},$$



where  $N$  = the density of vehicles travelling on the road (vehicles·min<sup>-1</sup>, 'road density'),  $a$  = the strike zone (twice the animal's total length plus twice the width of a vehicle's tyre), and  $v$  = the animal's crossing velocity (m·min<sup>-1</sup>). We plotted two linear functions for  $N$  using the 'ggplot' function (ggplot2 package) in RStudio (RStudio Team, 2015) to compare strike probability at different road densities. As the calculation relies on differing animal sizes, we used the values 0.35 m total length (TL) to represent an adult bobtail, 1 m TL for an adult dugite (Wolfe *et al.*, 2017), and 0.25 m for the width of an average vehicle tyre. We compared the average number of vehicles we observed travelling on the road during the field experiments (2.23 vehicles·min<sup>-1</sup>) with the road density count assessed by the relevant City Council (4.27 vehicles·min<sup>-1</sup>) (City of Cockburn, 2017). Values are presented as  $\bar{x} \pm 1$  SD.

## 5.4 Results

### 5.4.1 Online surveys – attitudes towards animals on roads

Survey respondents ranged from 19–94 years of age ( $\bar{x} = 41.48 \pm 13.76$ ,  $n = 362$ ), and were more likely to be a female from an urban suburb without experience as an animal carer. Of the four dependent factors tested, respondents expressed the greatest concern for animal welfare ( $\bar{x} = 8.02 \pm 2.73$  out of 10), followed by personal safety ( $\bar{x} = 2.91 \pm 2.88$ ) and then damage to their vehicle ( $\bar{x} = 2.87 \pm 2.75$ ), and claimed to be very likely to rescue animals on roads ( $\bar{x} = 7.06 \pm 3.40$ ). A summary of the test statistics for all effects is provided in Table 5.1.

Sex of the respondent and whether they lived in urban or non-urban areas influenced welfare concern scoring. Respondents held the least concern for the welfare of foxes and rabbits, and the greatest concern for the welfare of turtles, small mammals, dogs, and kangaroos (Figure 5.1a). Women ( $n = 272$ ) expressed greater concern for welfare ( $\bar{x} = 8.33 \pm 2.52$ ) than men ( $n = 90$ ;  $\bar{x} = 7.08 \pm 3.10$ ) and women were relatively more concerned for the welfare of rabbits, foxes, and cats than were men. Urban residents ( $n = 304$ ) also scored more concern for rabbits, foxes, and cats than did non-urban respondents ( $n = 58$ ). Concern for vehicle damage was highest for kangaroos and lowest for bobtails, snakes, rabbits, and turtles (Figure 5.1b). Concern for personal safety was highest for kangaroos, and lowest for bobtails, turtles, rabbits, birds, and small mammals (Figure 5.1c). Rescue likelihood was greatest for dogs and turtles, and least for snakes and foxes (Figure 5.1d). Women were overall more likely to rescue animals on roads ( $\bar{x} = 7.38 \pm 3.30$ ) than men ( $\bar{x} = 6.08 \pm 3.50$ ), and respondents who had rescued animals were more likely to do so again.

### 5.4.2 Field experiment – responses to reptiles on roads

Of 1,500 observations, 21% of motorists responded to an object on the road. Motorists were significantly more likely to respond to the coiled snake (35%), bobtail (30%), and cup (26%) than to the long snake (1%) and null (12%;  $\chi^2_4 = 136.81$ ;  $P < 0.001$ ). There was no significant effect

Table 5.1. Summary of linear model analyses testing dependent factors for the online survey section of this study. Significant factors are in bold.

Independent factors		Dependent factors			
		Welfare	Vehicle	Safety	Rescue
Taxa	$F_{9,3222} =$	<b>95.42; <math>P &lt; 0.001</math></b>	<b>177.49; <math>P &lt; 0.001</math></b>	<b>168.07; <math>P &lt; 0.001</math></b>	<b>17.03; <math>P &lt; 0.001</math></b>
Gender	$F_{1,358} =$	<b>20.19; <math>P &lt; 0.001</math></b>	1.78; $P = 0.183$	1.74; $P = 0.188$	<b>14.46; <math>P &lt; 0.001</math></b>
Location	$F_{1,358} =$	0.461; $P = 0.498$	-	-	-
Carer	$F_{1,358} =$	-	2.12; $P = 0.147$	3.06; $P = 0.081$	-
Previously rescued	$F_{1,358} =$	-	-	-	<b>147.12; <math>P &lt; 0.001</math></b>
Taxa *Gender	$F_{9,3222} =$	<b>10.09; <math>P &lt; 0.001</math></b>	1.06; $P = 0.393$	<b>2.68; <math>P = 0.004</math></b>	<b>2.06; <math>P = 0.030</math></b>
Taxa *Location	$F_{9,3222} =$	<b>6.20; <math>P &lt; 0.001</math></b>	-	-	-
Taxa *Carer	$F_{1,358} =$	-	<b>6.53; <math>P &lt; 0.001</math></b>	<b>3.40; <math>P &lt; 0.001</math></b>	-
Taxa *Previously rescued	$F_{1,358} =$	-	-	-	<b>7.28; <math>P &lt; 0.001</math></b>
Gender *Location	$F_{9,358} =$	0.011; $P = 0.918$	-	-	-
Gender *Carer	$F_{1,358} =$	-	0.18; $P = 0.673$	0.002; $P = 0.968$	-
Gender *Previously rescued	$F_{1,358} =$	-	-	-	<b>5.96; <math>P = 0.015</math></b>
Taxa *Gender *Location	$F_{9,3222} =$	1.18; $P = 0.301$	-	-	-
Taxa *Gender *Carer	$F_{1,358} =$	-	0.673; $P = 0.734$	0.55; $P = 0.842$	-
Taxa *Gender *Previously rescued	$F_{1,358} =$	-	-	-	0.61; $P = 0.752$

of motorist sex or presence/absence of passengers on whether motorists responded to treatments. We found significant 3-way effects of vehicle size ( $\chi^2_{MH,4} = 136.66$ ;  $P < 0.001$ ) and whether the motorist was distracted ( $\chi^2_{MH,4} = 136.72$ ;  $P < 0.001$ ). Compared to other vehicles, motorcyclists were most likely to respond to the long snake (50% of  $n = 4$ ), small cars to the coiled snake (22% of  $n = 104$ ), medium cars to the cup (35% of  $n = 77$ ), large cars to the null (65% of  $n = 37$ ), and trucks to the bobtail (10% of  $n = 90$ ;  $\chi^2_{16} = 93.69$ ;  $P < 0.001$ ). Undistracted motorists responded to all models significantly more than the null ( $\chi^2_4 = 28.22$ ;  $P < 0.001$ ); this trend was opposite for distracted motorists.

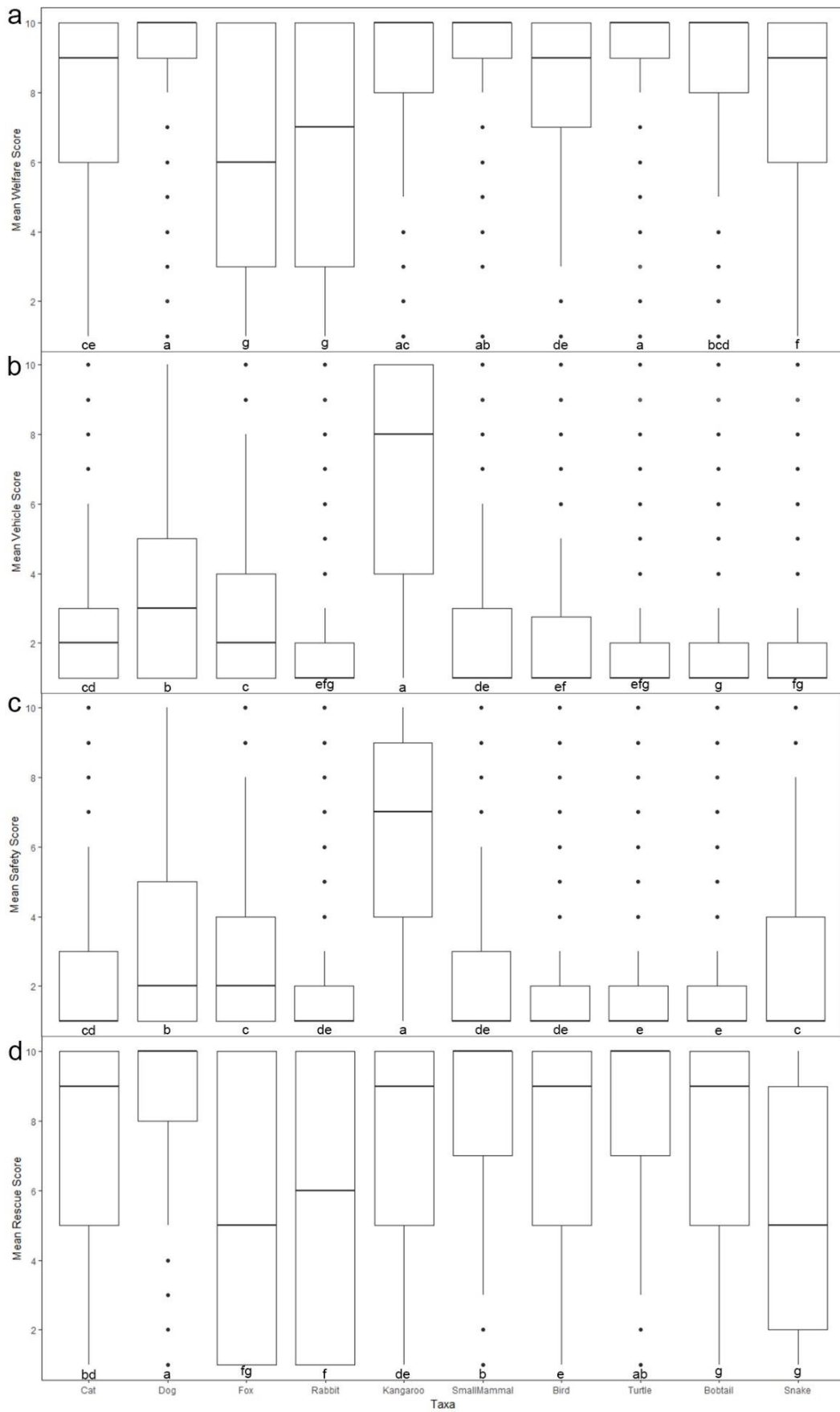


Figure 5.1. Mean scores for a) welfare, b) vehicle, c) safety, and d) rescue by respondents. Taxa had a significant effect for all factors. Separate letters for each factor indicate significant differences between taxa.

### 5.4.3 Modelling – strike probability of reptiles crossing roads

The probability of a reptile being struck by a motor vehicle is presented in Figure 5.2. Strike probability was highest for the slow ( $1 \text{ m}\cdot\text{min}^{-1}$ ) velocity, and approached 1 for both the observed and actual road densities. For the faster ( $60 \text{ m}\cdot\text{min}^{-1}$ ) velocity, strike probability was highest (0.16) for the dugite at the higher road density (4.27 vehicles $\cdot\text{min}^{-1}$ ).

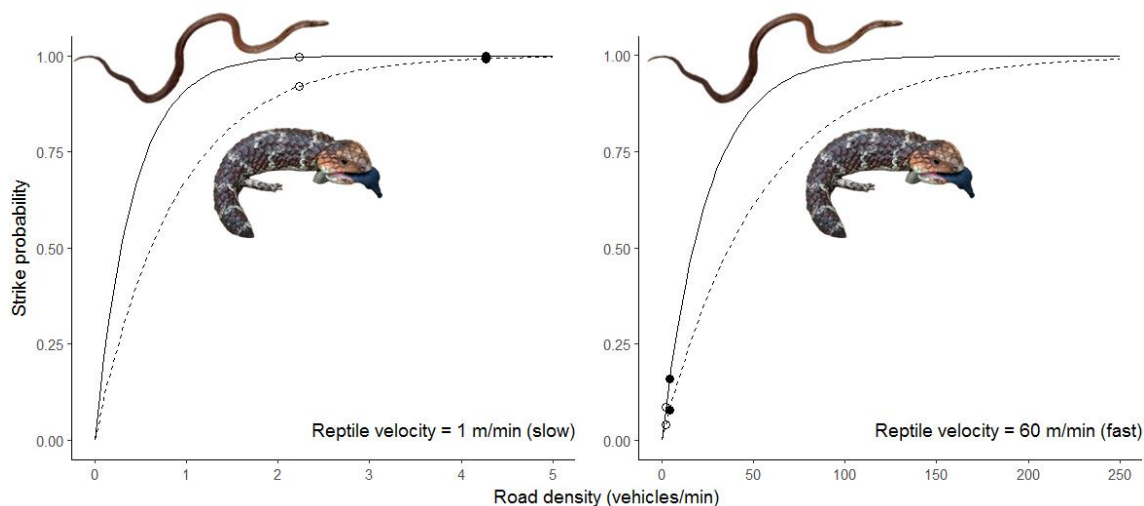


Figure 5.2. Probability of a reptile being struck by a motor vehicle while crossing a road at slow and fast velocities (see Methods for calculations). Legend: solid line = 1 m total length dugite, dashed line = 0.35 m total length bobtail, open circle = average road density calculated from our study, black circle = road density of our study road provided by City of Cockburn (2017).

## 5.5 Discussion

The respondents to our online survey had a high degree of concern for the welfare of animals on roads, and no motorists in our field experiment were observed intentionally striking reptile models. Online survey respondents also claimed to be highly likely to rescue animals on roads, but we only observed one motorist out of a possible 900 stop to rescue a reptile. Even though we did not observe any negative responses to reptiles on the road in the field, we found that claims on an online survey did not directly translate to behavioural action; motorists were most likely to ignore reptiles on the side of the road. Despite the lack of intentional strikes, crossing a road is very risky for a slow-moving reptile, and crossing more quickly does not eliminate all risk.

Our study found that Western Australian motorists were more concerned for the welfare of all native taxa than for foxes and rabbits, which are introduced pests responsible for habitat degradation and threats to native species (Cowan & Tyndale-Biscoe, 1997). Even snakes, which are often venomous (How & Dell, 1993) and were ranked similarly to dogs and foxes for personal safety concern (Figure 5.1) were ranked higher for welfare than the two non-synanthropic pest species. Inimical species, such as snakes, are often considered as a significantly lower welfare or conservation concern than more aesthetically endearing animals (Knight, 2008; Crawford & Andrews, 2016; Fleming & Bateman, 2016) but do not usually compare native species to introduced pests. However, Australia has a uniquely isolated landscape, and the general public's

attitudes appear to reflect an understanding of the consequences of invasive species (e.g. Beckmann & Shine, 2012).

Even though the current body of evidence for significant incidences intentional motor vehicle strikes on reptiles is limited, we were surprised to observe no strikes on reptile models. Strike rates appear to be lower for the road edge as compared to the centre of the road between the painted dashed lines (Secco *et al.*, 2014), most likely because reptiles on the roadside are easier to miss than an animal moving on the roadway, and the motorists would likely increase their reactions (as either an attempt to strike and kill or avoid the reptile) towards a more obvious target. However, the relationship between road edges and centres has only been explored previously in one study. For example, for the models that were struck at both locations on the road, Secco *et al.* (2014) recorded intentional strikes (but at a similar rate to the controls), and by not reporting the total number of observations, future comparisons to their study are not possible. Regardless, our field experiment was the first to observe no intentional strikes by motorists, and the second in Australia (after Beckmann & Shine, 2012) to find motorists generally ignored reptiles on roads.

While Western Australian motorists generally had positive responses to reptiles on roads, the risk of reptiles being struck is still high. For a slow-moving reptile crossing a road, even at the relatively low road density we observed ( $2.23 \text{ vehicles} \cdot \text{min}^{-1}$ ) (which is considered semi-permeable for wildlife; Luell *et al.*, 2003), the probability of being struck by a vehicle was >75% (Figure 5.2). This value may be even greater where behaviour of the reptiles increases the amount of time spent on roads, such as by becoming immobilised on roads when passed by a motor vehicle (Andrews & Gibbons, 2005), and crossing roads multiple times (Hels & Buchwald, 2001), or for roads with multiple lanes (e.g. turtles crossing a 4-lane highway in USA had <1% chance of survival; Aresco, 2005b). Even in the absence of intentional strikes, it is unlikely that reptiles crossing our study road would always survive; all previous studies found models struck in the centre of the road, whether they were intentional or not (Langley *et al.*, 1989; Ashley *et al.*, 2007; Beckmann & Shine, 2012; Secco *et al.*, 2014). While some vehicle strikes are not immediately fatal, few reptiles found injured on roads survive, e.g. in New South Wales, Australia, mortality for reptiles involved in motor vehicle collisions and admitted for rehabilitation was >75% (Shine & Koenig, 2001).

The nature of urban road infrastructure poses a significant threat to wildlife. For example, Western Australia has over 57,000 km of sealed roads servicing nearly 2,200,000 registered vehicles (Main Roads Western Australia, 2016). Wetlands are important hotspots for reptiles, and urban wetlands, such as at the one our study site, are often surrounded or bisected by roads (e.g. Dooley *et al.*, 2006). Many reptile species cross roads during the breeding season in search of mates or to lay eggs (e.g. Bonnet, Naulleau & Shine, 1999; MacKinnon, Moore & Brooks, 2005; Steen *et al.*, 2006). The resulting high mortality rates around wetlands negatively affect populations by causing unbalanced and unsustainable age and sex ratios (Marchand & Litvaitis, 2004; Aresco, 2005b; Gibbs & Steen, 2005), and mitigation measures are needed to reduce these effects.

Management methods to limit reptiles crossing roads currently employ use of alternative crossing areas such as culverts and underpasses (Ng *et al.*, 2004; Mata *et al.*, 2005; Taylor & Goldingay, 2010; Chambers & Bencini, 2015). Drift fences, which create a barrier to the road and guide

animals to crossing structures can also substantially decrease risk for species that follow them. For example, Aresco (2005b) found drift fences decreased the mortality likelihood for turtles crossing roads from >99% to <2%. However, fences can be damaged and must be constantly maintained to ensure their success (Baxter-Gilbert *et al.*, 2015), and, together with walls, only work for the species that are unable to climb over (Iuell *et al.*, 2003; Dodd, Barichivich & Smith, 2004). Alternatively, peak dispersal times for reptiles are predictable, and temporarily closing roads or reducing speed limits during the breeding season can be a useful way to prevent road strikes (Bonnet *et al.*, 1999).

Western Australians appear to have generally positive attitudes towards reptiles on roads, including snakes, and survey respondents who had previously rescued animals on roads were likely to perform rescues again in future. Educating the local public about reptiles can help foster stewardship and reduce negative attitudes (Bonnet *et al.*, 2016; Pinheiro *et al.*, 2016), and may also help to reduce the number of road mortalities.

# Chapter 6. What snake is that? Common Australian snake species are frequently misidentified or unidentified

In Chapter 5 I identified that Western Australian motorists are compassionate towards the welfare of most animals on roads, including a range of reptile taxa. However, reptiles are anecdotally regarded with fear and anger more than empathy when encountered on foot. The Western Australian Wildcare Helpline connects members of the public with local reptile removalists, while also recording information about the kinds of snakes people interact with. The single largest limitation of these records is that the Helpline relies on the identification of the general public, and not the licensed removalist.

The taboo for snakes does not generally discriminate between species, and although the common names of the most abundant snake species in the Perth region are well known, it is possible that a harmless species may be labelled with a venomous name. This misidentification can further exacerbate human perceptions of snakes.

The aims of this study was to determine if the general public are able to correctly identify some of the most common large-bodied reptile species in south-west Western Australia, differentiate between venomous and non-venomous snake species, and distinguish the differences between a snake and a lizard. I then analysed Wildcare Helpline records to identify the most commonly identified snake species encountered in Western Australian properties.

The study presented in this chapter has been formatted as a manuscript for submission for peer review:

**Wolfe, Ashleigh K.**, Philip W. Bateman, and Patricia A. Fleming. (2018) What snake is that? Common Australian snake species are frequently misidentified or unidentified, *in prep.*

All authors conceived the ideas and designed methodology; I collected and analysed the data; I led the writing of the manuscript. All authors contributed critically to the drafts. This chapter is presented as a standalone manuscript, with the exception of formatting consistent with the thesis.

## 6.1 Abstract

Snakes are commonly found in urban areas around the globe, and the ability for the general public to correctly discern dangerous species affects the treatment provided by health care professionals. An inability to identify reptile species may cause people to be unaware of potential risk or to act aggressively towards the reptile, whether it is actually dangerous or not. Western Australia is an ideal location to study the public's ability to correctly identify potentially dangerous species, as it has a huge diversity of reptiles, including a high abundance of venomous snakes within urban areas. In the interest of public health and the general understanding of the Western Australian public, we organised displays of five live reptile species commonly found around Australia, and particularly in south-west Western Australia, and asked participants "what is it called?", "is it a snake?" and "is it venomous?". We used: the venomous elapids - dugite (*Pseudonaja affinis*) and tiger snake (*Notechis scutatus*); the non-venomous south-west carpet python (*Morelia spilota imbricata*); and the non-venomous skinks – bobtail lizard (*Tiliqua r. rugosa*) and western blue-tongue lizard (*Tiliqua occipitalis*). We also obtained data for 9,627 calls to the Western Australian Parks and Wildlife Service's Wildcare Helpline, where 'problem' snakes are reported so that they can be removed from private properties, and identified differences between the types of snakes sighted by location (urban/non-urban). Survey respondents could tell a snake apart from a lizard, but were less able to positively identify which species were venomous, or provide a common name, and 79% snakes reported to the Wildcare Helpline were unidentified. Adults surveyed were better at identifying dugites (south-west Western Australia's most common snake, 82% correct), than were children (48% correct), but there were no other effects of sex, age, or location. As dugites and tiger snakes made up 89% of identified sightings, we recommend education on how to identify these species and to understand the potential danger of interacting with venomous snakes to help increase knowledge and reduce human-wildlife conflicts.

## 6.2 Introduction

Snakes are found across the globe and frequently encountered by humans in urban settings. As some snake species are venomous, these encounters are often associated with negative responses from humans. Although only 15% of snake species are venomous (Gold *et al.*, 2002), misidentification can be a fatal mistake. Firstly, inappropriately handling any snake can lead to a bite, and, once bitten by a venomous snake first thought to be non-venomous, incorrect identification of the snake can cause complications or death by failure to administer anti-venom (Silva, Gamlaksha & Waidyaratne, 2013) or administration of incorrect anti-venom (Looareesuwan, Viravan & Warrell, 1988; Sutherland & Leonard, 1995). Incorrectly identifying a harmless species as venomous can unnecessarily use hospital resources, either as staff time (Joseph *et al.*, 2007), or anti-venom (Ariaratnam *et al.*, 2009). Many snake bite cases are left unidentified (Pathmeswaran *et al.*, 2006), and as doctors are not snake identification experts, mistakes in identifying appropriate treatment are not uncommon (Looareesuwan *et al.*, 1988; de



Silva *et al.*, 2011). As anti-venoms may cause allergic reactions such as anaphylaxis (Gold *et al.*, 2002; de Silva *et al.*, 2011) and even death (Shine, 1991b), such inappropriate administration should be minimised wherever possible. Understanding the ability for the general public to correctly identify common local snake species is therefore an important task for the benefit of public health worldwide.

Western Australia has 593 species of reptiles and growing, of which 14% are venomous snakes (Doughty, Ellis & Bray, 2017). Snake bites in Australia have been reported to average 1,000 to 3,000 cases per year (White 1998), with 49 related deaths in the last 35 years (12 in Western Australia) (Bush, 2016). These numbers are only a fraction of those reported for regional areas in developing countries (Mohapatra *et al.*, 2011), but even the potential for a snake to have a venomous bite can drive negativistic human attitudes towards an entire taxa (Tomažič, 2011; Alves *et al.*, 2012).

Despite the increasing abundance of venomous snakes within urban areas in Western Australia (How & Dell, 1993; Wolfe *et al.*, 2017), the current level of knowledge to manage snakebite correctly is lacking. Recent snakebite deaths in Western Australia are due to misuse of correct first aid when bitten, and the belief (particularly in rural areas) that most bites are 'dry' and no medical aid is needed at all (White, 2000; Isbister, 2006). This is compounded by Western Australian elapids having small fangs and bites that are usually asymptomatic, reducing realisation of being bitten (White, 1991; Allen *et al.*, 2012; Isbister *et al.*, 2012). A further contributing factor is that negativistic attitudes drive people to be aggressive towards snakes, increasing the likelihood of being bitten (Sutherland, 1992; Isbister & Brown, 2012). For example, members of the public in eastern Australia, were 20 times more likely to approach a snake, and 100 times more likely to attack a snake than vice versa (Whitaker & Shine, 2000).

Correctly identifying the type of snake responsible for a bite can reduce the time taken to administer correct anti-venom (White, 2000). Although Australian venomous snake bites can be treated using polyvalent anti-venoms, doctors prefer to use monovalent anti-venoms to reduce the risk of side effects from large antibody volumes (O'Leary & Isbister, 2009). Species that produce a relatively higher volume of venom (such as black snakes and taipans) also require more anti-venom to neutralise effects, and incorrectly administering high dosages of anti-venom containing foreign proteins increases the risk of systemic hypersensitivity reactions (Isbister & Brown, 2012). Snake venom detection kits ('sVDKs') are also available in Australia to identify which anti-venom to use, but they are not always correct (Isbister & Brown, 2012).

Studies that have explored the ability of people to identify snakes and other herpetofauna show mixed results. In California USA, 81% of people were able to distinguish the two venomous species of local snake from the four non-venomous species. Men were more accurate than women and adults were more accurate than children (Corbett *et al.*, 2005). In Australia, residents of rural areas were more likely to correctly identify venomous species than were urban dwellers (Morrison *et al.*, 1983). However, overall, Morrison *et al.* (1983) found only 19% of people could identify a snake to species, and only 4% of urban dwellers could identify a non-venomous python. A related study that tested the ability of Australians to distinguish non-native, invasive cane toads (*Rhinella marina*, Bufonidae) from native frogs showed that while accuracy of identification was

higher for people living in areas where the toads occur, the error rates were still up to 43% (Somaweera, Somaweera & Shine, 2010).

Western Australia's capital city of Perth has significant snake populations, notably dugites (*Pseudonaja affinis*, Elapidae) and tiger snakes (*Notechis scutatus*, Elapidae), which are both highly venomous elapids (How & Dell, 2000; Bush *et al.*, 2010; Wolfe *et al.*, 2017), and congeners (*Pseudonaja* spp.) and conspecifics (tiger snakes) are also commonly found across most of Australia. Consequently, the Western Australian Parks and Wildlife Service has over 2,000 registered reptile removalists who, for either a voluntary or paid effort, actively remove unwanted or 'problem' snakes from private residences following calls to the Wildcare Helpline. While elapids are the only group of potentially dangerous reptiles in these urban areas, each year hundreds of call-outs are for harmless lizards, which many people appear not to be able to distinguish from snakes (pers. obs.). Each year there are also anecdotal reports of sightings for dangerous snake species that are not present in Western Australia (e.g. red-bellied black snakes, *Pseudechis porphyriacus*, Elapidae); these misidentifications are often from Australians who have spent some time living in eastern Australia where those species are extant (pers. obs.).

An inability to identify reptile species may have one of two unwanted consequences:

- 1) people are not aware of the potential risk from a snake; or
- 2) people react aggressively to the reptile, resulting in an increased chance of being bitten (Whitaker & Shine, 2000), or they kill a harmless species (referred to as 'friendly fire' by Somaweera *et al.*, 2010).

In the interest of public health and the general understanding of the Western Australian public, we ran a series of surveys to test the public's ability to correctly name and identify venomous and non-venomous reptiles. We also examined eight years of calls to the Wildcare Helpline for 'problem' snakes to assess the species most commonly encountered by Western Australians.

## 6.3 Materials and methods

### 6.3.1 Snake identification survey

We conducted surveys at four separate public events in south-west Western Australia:

- 1) West Australian Herpetological Society's Reptile Expo, intended for members of the public with an interest in reptiles;
- 2) Curtin University Open Day, open to members of the public interested in pursuing tertiary education;
- 3) 'Meet a Scientist' day at Scitech Discovery Centre, an interactive public science venue aimed towards educating children in primary school (to approximately 12 years old) and their parents; and

- 4) Boyanup Farmer's Market, a monthly regional market open to the public and attended by locals living outside of the Perth metropolitan area.

We displayed five different reptile species, commonly found across Australia as well as Western Australia, in separate glass enclosures for the public (Figure 6.1):

- 1) Dugite (venomous);
- 2) Tiger snake (venomous);
- 3) South-west carpet python (*Morelia spilota imbricata*, Pythonidae) (non-venomous);
- 4) Western blue-tongue lizard (*Tiliqua occipitalis*, Scincidae) (non-venomous); and
- 5) Bobtail lizard (*Tiliqua r. rugosa*, Scincidae) (non-venomous).

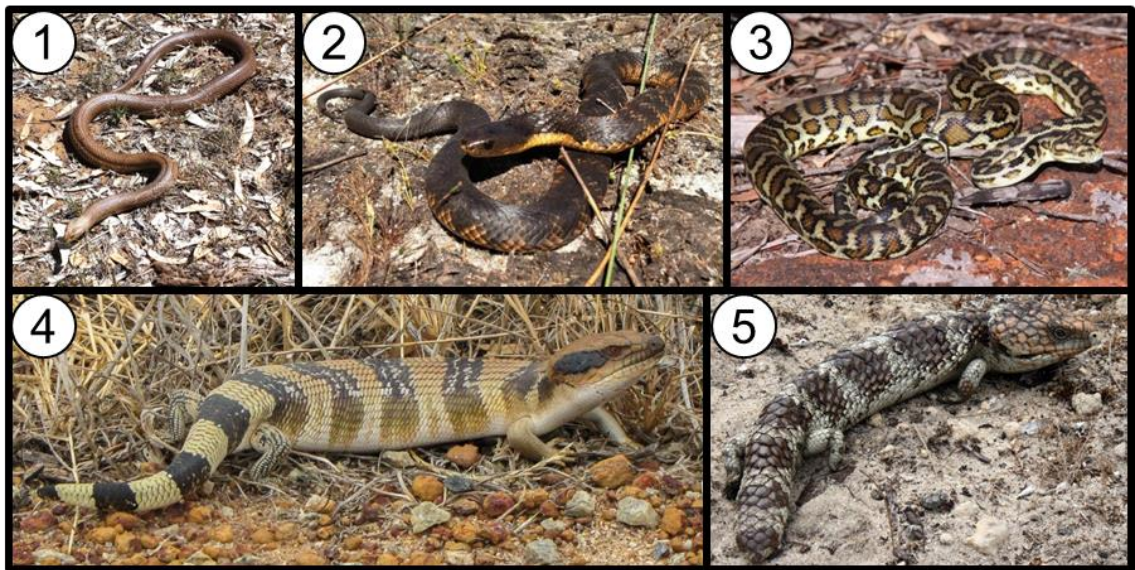


Figure 6.1. Reptile species displayed for the snake identification survey: 1) dugite, 2) tiger snake, 3) south-west carpet python, 4) western blue-tongue lizard, 5) bobtail lizard. Photo credits: AK Wolfe (1, 5), Marcus Cosentino (2, 3), and Damian Lettoof (4).

Lizards were presented in enclosures measuring 0.45 m high x 0.45 m wide x 0.45 m deep (0.09 m<sup>3</sup>), and snakes were in enclosures measuring 0.60 m high x 0.45 m wide x 0.45 m deep (0.12m<sup>3</sup>). The enclosures were placed in a random order on tables so survey participants could safely view each animal from a distance of 1 m. Participants were each provided with a survey form, which asked them to respond to three questions to determine if they could accurately:

- 1) provide a common name, “*what is it called?*”;
- 2) discern the difference between the snakes and lizards, “*is it a snake?*”; and
- 3) identify which species were venomous, “*is it venomous?*”.

Participants (n = 263) also provided their age, sex, suburb/area of residence, and whether they have experience keeping reptiles as pets. Consent was acknowledged as participants placing their completed surveys into a sealed ballot box, and underage children completed their surveys with supervision of a guardian. A copy of the survey is provided in Appendix 3.5.

## 6.3.2 Calls to Wildcare Helpline

To assess the number of snakes reported to the Western Australian Parks and Wildlife Service, we obtained information for all snakes reported from 2007-2014 (inclusive) to the Wildcare Helpline. Of a total of 9,627 calls, telephone operators noted the caller suburb and date ( $n = 9019$ ), and attempted to identify the snake species, by either the caller's identification or a description of the animal ( $n = 1,960$  all other entries considered an unknown snake species,  $n = 7,667$ ).

## 6.3.3 Statistical analysis

To determine if the accuracy of responses was related to sociodemographic factors, we created a series of binomial probit-linked models using the 'glmer' function (lme4 package) in RStudio 1.0.153 (RStudio Team, 2015). We used the number of correct responses for each of the three questions as separate dependent factors, as species, age (as 'adult' or 'child', where all respondents under the age of 18 were considered children), sex (male, female, unknown), residence location (as 'urban' or 'non-urban', determined by post code), and experience with reptiles as pets as independent fixed factors. We included each survey respondent as a random factor. Non-significant factors were considered uninformative and removed from the final models (Engqvist, 2005). Post-hoc Tukey tests were conducted for significant factors, and we used pairwise comparisons with a Bonferroni adjustment ('lsmeans' function) for significant interaction effects.

To determine the effect of time (year of call), location (urban/non-urban), and species on calls for 'problem' snakes to the Wildcare Helpline from 2007-2014, we included these as independent factors, and frequency data as the dependent factor, in separate two-way  $\chi^2$  analyses in RStudio 0.99.491 (RStudio Team, 2015). For snake species, we only included entries where an attempt at identification was made ( $n = 1960$ ).

# 6.4 Results

## 6.4.1 Snake identification survey

Of 263 respondents who attempted to identify reptiles, identification for each species was correct more often for tiger snakes (74% correct), bobtails (72% correct), and dugites (59% correct;  $\chi^2_4 = 76.9$ ;  $P < 0.001$ ; Figure 6.2). Significantly fewer correct responses were for blue-tongue lizards (56% correct) and south-west carpet pythons (42% correct). Respondents correctly discerned between snakes and lizards ( $n = 261$ ;  $\geq 95.0\%$  correct for all species;  $\chi^2_4 = 6.65$ ;  $P = 0.156$ ), but were consistently less able to tell venomous and non-venomous species apart (77-90% correct;  $\chi^2_4 = 25.0$ ;  $P < 0.001$ , Figure 6.2). Respondents most frequently correctly identified tiger snakes as venomous, and least frequently identified south-west carpet pythons as non-venomous.

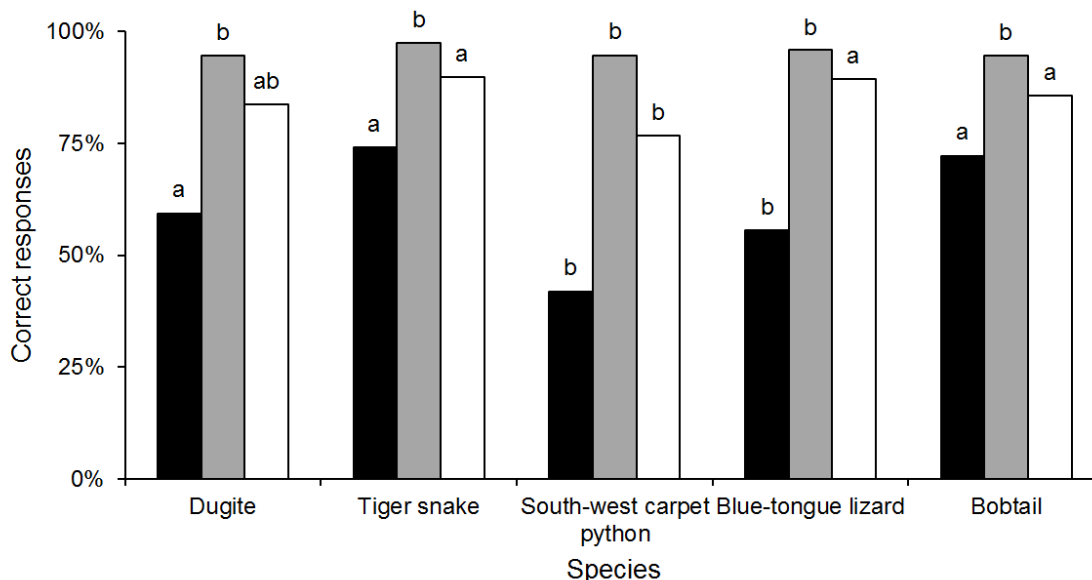


Figure 6.2. Percentage of correct responses overall for 263 Western Australians identifying five reptiles. Legend: black = “what is it called?”, grey = “is it a snake?”, unfilled = “is it venomous?”. Different letters denote significant differences for each factor.

We found a significant effect of sex for ability to identify reptile names ( $\chi^2_2 = 6.85$ ;  $P = 0.033$ ; Figure 6.3a). Males ( $n = 125$ ; 64% correct) identified more reptiles than females ( $n = 108$ ; 55% correct;  $z = 2.66$ ;  $P = 0.021$ ). The 30 respondents who did not identify their sex had similar scores to men (69% correct;  $z = 1.06$ ;  $P = 0.530$ ). There was also a significant interaction effect of age ( $\chi^2_{10} = 53.5$ ;  $P < 0.001$ ) and experience with reptiles as pets ( $\chi^2_5 = 19.8$ ;  $P = 0.001$ ) on ability to identify reptile names (Figure 6.3). Adults ( $n = 111$ ) more frequently correctly identified dugites (77% correct) than children ( $n = 152$ ; 47% correct;  $z = 5.16$ ;  $P < 0.001$ ), and respondents who kept reptiles as pets ( $n = 35$ ; 21 males and 14 females) correctly identified carpet pythons more frequently (74% correct) than did those without such experience ( $n = 228$ ; 37% correct;  $z = 4.18$ ;  $P = 0.001$ ). There were no significant effects of any sociodemographic factors on ability to identify whether animals were snakes. For discerning between venomous species, there was a significant effect of experience with reptiles as pets ( $\chi^2_1 = 5.72$ ;  $P = 0.017$ ). Reptile keepers could tell the difference between venomous and non-venomous species (92% correct) more often than non-keepers (84% correct). No differences in urban/non-urban locations were detected for any factor when creating the models.

## 6.4.2 Calls to Wildcare Helpline

Of the 1,960 calls to Wildcare Helpline where an attempt at snake identification was made, most calls stated ‘brown snakes’ (*Pseudonaja* spp.,  $n = 1,330$ ) and ‘tiger snakes’ ( $n = 418$ ;  $\chi^2_4 = 3047$ ;  $P < 0.001$ ). Two other snake types were identified >10 times: ‘python’ (Pythonidae,  $n = 83$ ), and ‘king brown’ (*Pseudechis australis*, Elapidae,  $n = 19$ ). All other descriptions were for colours only (e.g. ‘dark’, ‘green’, ‘grey/silver’), or for species not found in Western Australia (red-bellied black snake,  $n = 4$ ), or occurred <10 times (e.g. ‘sea snake’,  $n = 10$ ) - these descriptions were grouped together as ‘other’ ( $n = 220$ , Table 6.1). Most calls were from urban residents ( $n = 1,771$ ).

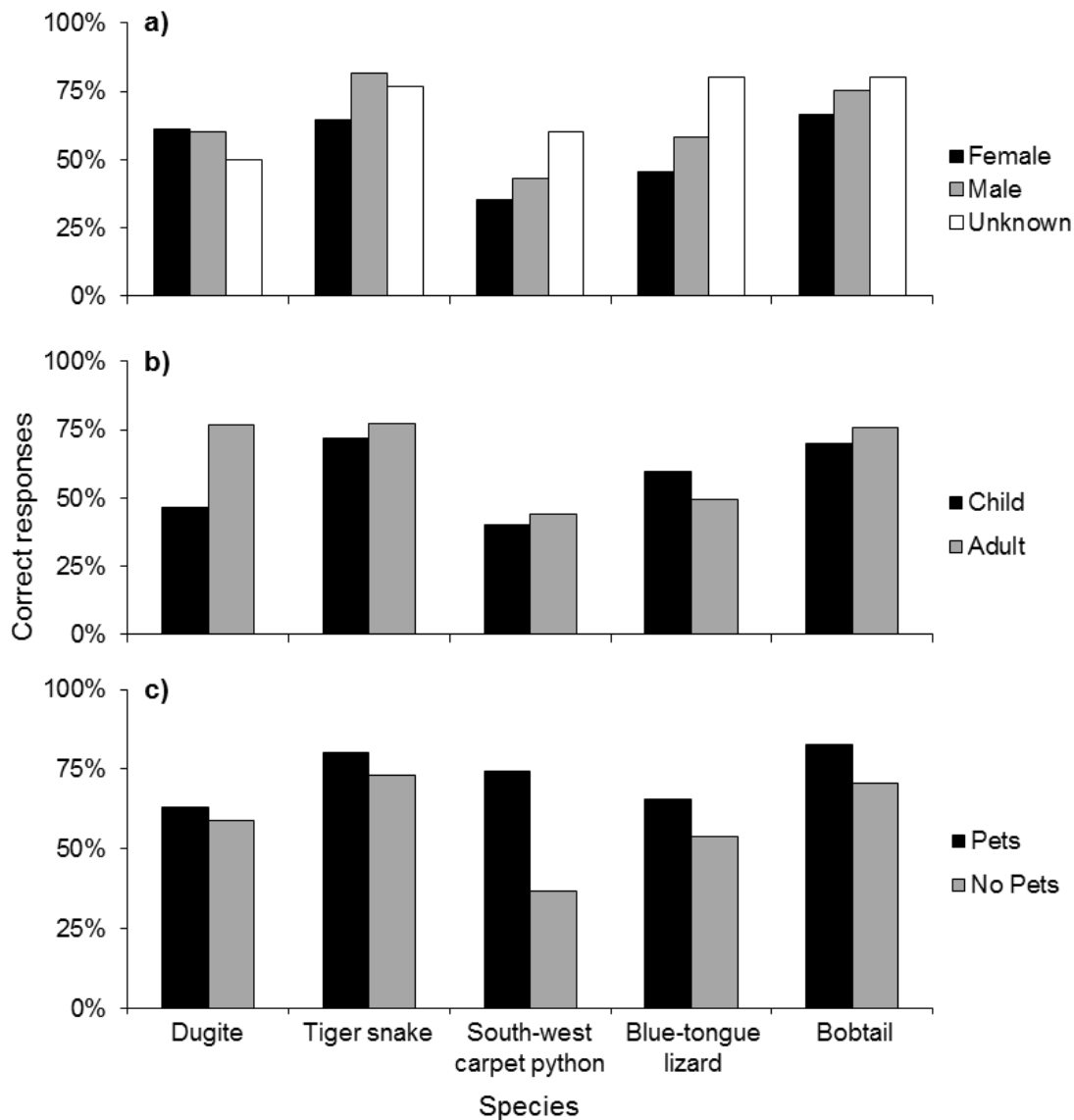


Figure 6.3. There was a significant effect of a) sex, b) age, and c) experience keeping reptiles as pets on percentage of correct responses for Western Australians identifying the common name of five reptiles. Overall, men (a) and respondents with experience keeping reptiles as pets (c) identified more species correctly. Adults (b) correctly identified dugites more than children.

Compared to urban residents, although non-urban dwellers called less, they made proportionately more calls for all species except dugites ( $\chi^2_4 = 62.2$ ;  $P < 0.001$ ; non-urban dugite reports = 46%, urban dugite reports = 70%). There was also an effect of location on the number of annual calls for snakes ( $\chi^2_7 = 82.4$ ;  $P < 0.001$ ): the number of calls from non-urban residents has been steadily increasing, from 52 in 2007 to 161 in 2014.

## 6.5 Discussion

We found that respondents were much better at telling if a reptile is a snake or if it is venomous than they were at identifying the species by their common names. Similarly to Corbett *et al.* (2005) in California USA, we found that adults were better at identifying venomous snakes (south-west Western Australia's most common venomous species, the dugite) than children.

Table 6.1 Identities of 'problem' snakes referred to the Western Australian Wildcare Helpline from 2007-2017 (inclusive).

Species	n urban calls	n non-urban calls
Commonly identified species (n = 1850)		
Brown snake ( <i>Pseudonaja</i> spp.)	1243	87
Tiger snake ( <i>Notechis scutatus</i> )	355	63
Python	61	22
King brown ( <i>Pseudechis australis</i> )	14	5
'Other' (n = 220)		
Colour description (n = 90)		
Dark	34	4
Green	15	2
Grey/silver	11	-
Banded	8	1
Black and white	3	-
Black and brown	3	-
Yellow	3	-
Cream	4	1
Blue	1	-
Type description (n = 20)		
Sea snake	9	1
Red-bellied black snake ( <i>Pseudechis australis</i> )	3	1
Death adder ( <i>Acanthophis antarcticus</i> )	3	-
Bardick ( <i>Echiopsis curta</i> )	-	1
Western shovelnose snake ( <i>Chionactis occipitalis</i> )	-	1
Blind snake ( <i>Anilius</i> spp.)	1	-
Unknown (n = 7,667)	7031	636
Total	8802	825

Like Morrison *et al.* (1983), we also found an effect of sex (but not location; urban or non-urban) on the ability of people to identify snake species. Our respondents identified all species with accuracies ranging 42% - 74%, which is between the 81% accuracy in Americans recorded by Corbett *et al.* (2005), and the 19% average for Australians recorded by Morrison *et al.* (1983). However, most people calling for help with a 'problem' snake do not attempt to identify the snake.

Although most of our survey respondents were able to tell the difference between the five species presented, we believe that this is an overestimation of the public's ability for particular reasons. Several hundred patrons visited the Reptile Expo, Scitech Discovery Centre, and the farmer's market, and several thousand patrons attended the Curtin University Open Day, but many who passed by our display either refused to come near due to a fear of reptiles, or insisted that they would not even attempt to guess the species names because they did not know. This is reflected by the Wildcare Helpline data: 80% of 'problem' snakes were not identified. We must therefore consider the self-selection bias inherent in our survey. Western Australia has a diverse range of cultures, with 24% of residents who were born in a country other than Australia (Australian Bureau

of Statistics, 2016), and an absence of education on indigenous reptiles for migrants may affect their attitudes (Teixeira *et al.*, 2015; Pinheiro *et al.*, 2016).

In Australia, a continent with a diverse array of venomous snakes, it is perhaps safer to assume that any snake is venomous, which may explain why so many carpet pythons were considered venomous by the respondents; however, we were surprised by the number of people who misidentified venomous snakes as harmless. We suggest, based on brief conversations with some respondents, that many people without any experience with reptiles use inaccurate, non-Australian, conventions to identify snakes, i.e. snakes with 'round eyes' are harmless, and a 'broadly triangular head' is seen as indicating a dangerous, venomous species. Such cues for differentiating venomous from non-venomous snakes are nowhere universal, and for our study species, dugites and tiger snakes have round eyes and non-triangulated heads, and carpet pythons have elliptical eyes and triangular heads. Although Australian elapids can flatten their necks to appear triangular when threatened, and there is some evidence that a 'triangulated' head shape on models of snakes can reduce predatory attacks (Valkonen, Nokelainen & Mappes, 2011), the trend is inconsistent and should not be relied upon. These misconceptions may explain why 21% of children and 9% of adults thought that dugites were harmless.

Unfortunately, there are no hard and fast rules that Australians can use to tell venomous species from harmless ones, and understanding the species present in an area is necessary to ensure correct identification. Dugites and tiger snakes made up 89% of identified sightings for the Wildcare Helpline data, and most were identified in urban areas (i.e. Perth metropolitan centre, where both species are extant). The number of species sighted increases in non-urban areas, but they are rarely reported. For the majority of people living in the urban centre, we recommend education about how to identify dugites, tiger snakes, and common lizard species, as well as understanding the potential danger of interacting with venomous snakes, to help increase knowledge of these species and reduce human-wildlife conflicts and 'friendly fire' killing of harmless taxa (Somaweera *et al.*, 2010). Similar studies would be of interest in other cities worldwide where snakes are common to help better understand the likelihood of the public to misidentify potentially harmful species.



# Chapter 7. Responses of free-living urban-adapted lizards to escalating levels of human observation

Urban-adapted species can cope with living alongside humans in two ways: 1) becoming habituated and either ignoring or taking advantage of human presence, or 2) becoming increasing sensitised and minimising interactions. This chapter aimed to investigate the responses of urban and non-urban bobtails and dugites to human encounters to assess which of these strategies they may use. Dugite interactions were limited to <20 sightings, and those that were not captured for GPS tracking in Chapter 4 quickly fled from observation, making it difficult to collect morphometric and life stage information. In contrast, bobtails were ideal animals to study responses to humans, due to being relatively slow-moving, abundant in urban parklands, and having a deimatic threat display. Although I was unable to observe bobtails from sites outside of the Perth metropolitan area, I was able to instead compare responses according to the different levels of habitat modification in which the bobtails were found.

The study presented in this chapter has been formatted as a manuscript for submission for peer review:

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All authors conceived the ideas and designed methodology; I collected and analysed the data; I led the writing of the manuscript. All authors contributed critically to the drafts. This chapter is presented as a standalone manuscript, with the exception of formatting consistent with the thesis.

## 7.1 Abstract

Urbanisation presents unique challenges for wildlife and drives human-wildlife interactions. Urban greenspaces are important amenities for humans and animals alike, and humans using these spaces may incidentally encounter a free-living animal. Humans can represent 'predation-free' predators where they encounter wildlife, and habituation through tolerance and modifying vigilance behaviour towards humans is a key attribute of urban-adapted species. We observed the anti-predator responses of bobtail skinks (*Tiliqua r. rugosa*,  $n = 63$ ) in the Perth metropolitan area to human observation using an escalating stepwise method: 1) initial encounter at distance ( $10 \pm 5$  m from the focal animal); 2) moving to 1 m of the bobtail and observing, standing, for 30 s; and 3) tapping the bobtail on the head. Interactions occurred in environments of three levels of modification: 'high', properties with garden beds and urban reserves with  $<0.5$  km<sup>2</sup> of natural habitat; 'intermediate', urban reserves 0.5-5 km<sup>2</sup> natural habitat; and 'low', large reserves  $>5$  km<sup>2</sup> natural habitat. Multiple interactions were recorded for 13 individuals to determine the effect of repeated observations on bobtail anti-predator responses to human encounter. A generalised linear mixed model determined bobtails were most likely to attempt to flee from human encounters, rather than ignoring humans or using a deimatic threat display, especially when the bobtails were already moving when first encountered. Repeated encounters had no significant effect on bobtail behavioural responses. The tendency for urban bobtails to have constant vigilance to humans suggests that these urban adapters do not habituate to human encounter at any habitat modification level.

## 7.2 Introduction

Increasing urban encroachment presents unique challenges for wildlife. In addition to direct physical impacts, such as habitat destruction and fragmentation (Jellinek *et al.*, 2004), pollution (McKinney, 2008), and the introduction of non-native predators (Woods *et al.*, 2003; White *et al.*, 2006; Loss *et al.*, 2013; Holderness-Roddam & McQuillan, 2014), urbanisation tends to drive increased interactions between people and wildlife. Urban greenspaces, which provide essential habitat for many species still persisting within cities (González-García *et al.*, 2009; Garden *et al.*, 2010; Pellitteri-Rosa *et al.*, 2017), are also becoming increasingly important amenities for people living within metropolitan areas (Dickinson & Hobbs, 2017). Humans using these spaces recreationally, e.g. by playing sport, fishing or walking, may incidentally encounter a free-living animal (e.g. Burger, 2003; Bell, 2010).

Human-wildlife interactions, however benign, can have physiological and behavioural consequences on the animal concerned in response to disturbance (e.g. Bateman & Fleming, 2017). In urban areas, where individuals of some species may face constant or repeated exposure to humans or human-related disturbance, humans can represent predators, regardless of whether they actually interact with wildlife (Beale & Monaghan, 2004). Animals may theoretically become either highly sensitised to human encounters and respond increasingly

negatively in subsequent encounters (Breuer, Hemsworth & Coleman, 2003), or become desensitised (habituated) to human encounters, decreasing their anti-predatory responses over time (following the threat-sensitivity hypothesis, avoiding potential predators according to the actual risk they pose, e.g. Bateman & Fleming, 2014; Worrell *et al.*, 2017). However, only a fraction of encounters with humans actually result in death of the focal animal(s) (Frid & Dill, 2002; Beale & Monaghan, 2004). Habituation, through tolerance and modified vigilance behaviour towards humans within urban areas, is the hallmark of urban adapters: species that make use of anthropogenically-modified environments, especially in metropolitan areas (Blair, 1996; McKinney, 2006). This tolerance to humans is necessary to facilitate successful lifestyles that make use of food and shelter associated with human settlements (Wolfe *et al. in review* [Chapter 3]).

Animals have primary and secondary defences against predation (Edmunds, 1974): primary defences exist even in the absence of the predator (e.g. camouflage and armour), and secondary defences are those that the animal uses when it is aware of the predator. Most animals have multiple secondary defences that they employ progressively as risk increases (e.g. Bateman & Fleming, 2009), such as crypsis, flight, and deimatic displays (Cloudsley-Thompson, 1995; Olofsson *et al.*, 2012). Secondary defences are likely to be costly to an animal either because it has to expend energy or because it has to suspend its normal activities (Ydenberg & Dill, 1986). Habituation to human disturbance by urban adapters can reduce costs to foraging, stress physiology, and reproduction, but it is important to note that habituation does not necessarily mean that anti-predation or anti-disturbance behaviour is lost entirely. For example, while Geffroy *et al.* (2015) claimed that species habituated to humans are bolder and therefore might become more susceptible to predation, Bateman & Fleming (2014) indicated that even in the most urbanised settings, and with constant exposure to human presence, urban-adapters can remain appropriately sensitive to potential risk cues.

Although it has been claimed that lizards are generally not very reactive to human observers (Fox, McCoy & Baird, 2003), they have proved to be an excellent model taxon for understanding anti-predator escape behaviour and associated tactics where humans pose the disturbance (e.g. Whitaker, Ellis & Shine, 2000; Gibbons & Dorcas, 2002; Bauder *et al.*, 2015; Cooper, 2015). For example, Australian sleepy lizards (*Tiliqua rugosa*, Scincidae) respond to observation and handling through an increase in average stride frequency for up to an hour post-handling, regardless of the handling intensity (observation only, <1 min, or up to 45 min) (Kerr *et al.*, 2004).

In south-west Western Australia, the local subspecies of sleepy lizards (*Tiliqua r. rugosa*) are known as 'bobtails'. Bobtails are iconic reptiles in the Perth metropolitan area, and are considered one of the most significantly urban-adapted species present in the region (How & Dell, 1993). These large-bodied reptiles reach up to 31 cm snout-vent length (SVL) and 700g body mass (Haight, 2007), are found in urban greenspaces such as fragmented reserves, parks, golf courses, and suburban backyards (Fergusson & Algar, 1986; How & Dell, 2000; Bush *et al.*, 2010; Harris, Mills & Bencini, 2010; Chambers & Bencini, 2015). They make an ideal species to study the behavioural impacts of human encounters within urban areas. Bobtails have a primary defence of cryptic colouration and can be hard to see if they are not moving; secondarily they will often

attempt to flee under dense, spinose vegetation (Fergusson & Algar, 1986; AKW, pers. obs.). If unable to do this, they can resort to a dramatic deimatic display by opening their mouth and repeatedly protruding their distinctive blue tongues, orienting towards the disturbance to allow them to bite if necessary. Although bobtails have a powerful bite, they are generally regarded as inoffensive by the general public and are well-liked by Perth residents (AKW & PWB, unpubl. data).

We hypothesised that bobtails living in urban areas, where they are exposed to direct human encounters, would become habituated to human disturbance by reducing their anti-predator behaviours. We predicted that, while urban bobtails will still show defence responses towards human approach, individuals approached repeatedly in a set way will show increased habituation to these encounters by moderating their responses over time.

## 7.3 Materials and methods

Bobtail response to human encounter was recorded via opportunistic observations ( $n = 63$ ) from 2014–2016 in the Perth metropolitan area, Western Australia. Bobtails were observed in environments with different levels of habitat modification, classified by the amount of continuous undeveloped surrounding habitat:

- 1) 'high modification': Curtin University campus grounds and suburban yards with maintained garden beds adjacent to buildings, and small urban reserves ( $<0.5 \text{ km}^2$  natural habitat) ( $n = 19$  bobtails);
- 2) 'intermediate modification': medium urban reserves ( $0.5\text{--}5 \text{ km}^2$  natural habitat) ( $n = 22$  bobtails); and
- 3) 'low modification': large urban and peri-urban reserves located on the periphery of the metropolitan area ( $>5 \text{ km}^2$  natural habitat) ( $n = 22$  bobtails).

A total of 50 bobtails were observed once only, while 13 bobtails (included in a separate radio-tracking project) were observed multiple times ( $\bar{x} = 4.69 \pm 3.07$ , range = 2–11 times each), for a total of 112 observations. Upon encounter, we observed antipredator behaviour (responses included fleeing from the observer or deimatic gape display) using an escalating stepwise method, stopping at the first behavioural response to observation or until we exhausted all steps:

- 1) Response at distance (initial observation of the animal, at  $10 \pm 5 \text{ m}$  from the focal animal) ( $n = 112$ ) (scored as '3' if the animal responded);
- 2) If there was no response, then we approached the focal animal and recorded its response when the observer stood 1 m away, observing for 30 s ( $n = 104$ ) (scored as '2' if the animal responded); and
- 3) If there was still no response, the bobtail was tapped lightly once on the top of the head with a hand ( $n = 60$ ) (scored as '1' if the animal responded; '0' if no response was recorded).

Following observations, we then captured each bobtail and measured its size (SVL), age (juveniles and subadults <32 cm, and adults >32 cm SVL) (Haight & Jackson, 2016), sex (via inspection for hemipenis bulges in sub-adults and adults), and external body temperature (via laser thermometer [TIF7610, Amprobe, Miramar], pointed on a dark brown dorsal scale). Handling lasted for less than 5 min on all occasions. We also measured ambient temperature, the temperature of the substrate upon which the bobtail was situated at initial encounter, season encountered, location observed (high, intermediate, or low habitat modification), and whether the bobtail was moving at initial approach ('motion'). We included each of these measures, as well as the encounter number for the 13 bobtails with multiple interactions, to test for an effect on behavioural response to human encounter.

### 7.3.1 Statistical analyses

To determine if the responses of bobtails to human observation was related to degree of habitat modification, we generated multiple GLMMs using the 'lmer' function (lme4 package) in RStudio (RStudio Team, 2015). We included size (SVL), age, sex, temperature, season, location, and motion as fixed effects. We included interaction day (1 for initial interaction, and incrementally increasing for subsequent repeated interactions for  $n = 13$  individuals) as a fixed factor, and individual bobtail identification as a random effect to account for pseudoreplication. Factors that were not significant were removed from the final models (Engqvist, 2005). Post-hoc Tukey tests were conducted for significant factors. To determine the difference in behavioural responses (flee, gape, nil) of bobtails to human observation, we conducted a one-way  $\chi^2$  analysis with Yates correction on the overall dataset. Values are presented as  $\bar{x} \pm SD$ .

## 7.4 Results

The majority of encounters occurred during the spring months ( $n = 56$ ), followed by summer ( $n = 44$ ), autumn ( $n = 11$ ), and winter ( $n = 1$ ). More bobtail encounters were with adults ( $n = 85$ ) than sub-adults/juveniles ( $n = 27$ ). Overall, we found no significant effects of size, sex, temperature, season, or degree of habitat modification on the behavioural responses of bobtails to human interactions.

Of the  $n = 112$  observations, only 8 individuals responded at distance ( $n = 8$  observations), 31 individuals responded when the observer was within 1 m ( $n = 44$  observations), 14 individuals responded to being tapped on the head ( $n = 28$  observations), and 10 individuals did not respond to any of these provocations ( $n = 32$  observations).

The best model to describe the responsiveness of bobtails to approach, where a larger score indicates a more responsive bobtail, included motion ( $\chi^2_1 = 21.14$ ;  $P < 0.001$ ; moving  $\bar{x} = 3.00 \pm 0.60$ , still  $\bar{x} = 2.06 \pm 0.93$ ) and interaction day (greater responsiveness for initial approach compared with repeated approaches) as fixed effects, and individual bobtails as a random effect.

Overall, bobtails were more likely to attempt to flee from the observer than use a deimatic display or not respond at all ( $\chi^2_2 = 27.07$ ;  $P < 0.001$ ). On their first encounter, bobtails in motion were significantly more likely to attempt to flee than use another response ( $\chi^2_2 = 9.60$ ;  $P = 0.008$ ). All repeated-measures bobtails ( $n = 13$ ), and all bobtails that scored a 0 or 1 (observation escalated to a head tap,  $n = 24$ ) were those that were initially stationary.

## 7.5 Discussion

We found urban bobtails were most likely to attempt to flee from encounters with human observers, rather than ignoring them or using a deimatic threat display. This was especially evident for bobtails already in motion, which were more likely to attempt to flee from observers than those that were still at encounter. This suggests that urban bobtails, regardless of level of habitat modification, did not habituate to human encounters.

Many publications exploring the response of reptiles to human disturbance as proxies for predators mention possible habituation effects, e.g. lizards: *Agama planiceps* (Carter, Goldizen & Heinsohn, 2012), *Callisaurus draconoides* (Cooper & Sherbrooke, 2013), *Cnemidophorus murinus* (Cooper *et al.*, 2004), *Anolis grahami* and *A. lineatopus* (Cooper, 2010); snake: *Agkistrodon piscivorus* (Glaudas, 2004); and tortoise: *Gopherus polyphemus* (Bateman *et al.*, 2014). Such habituation may come with adaptive benefits, e.g. individuals of *Podarcis hispanica* that habituated fastest to the stimulus of a human's presence increased their body condition more than did the individuals that habituated less readily (Rodríguez-Prieto *et al.*, 2010). However, we did not find this habituation effect for bobtails.

Skinks of the genus *Tiliqua* use their bright blue tongues, which make a stark contrast against the pink mucous membranes in the mouth, for diemantic displays (Carpenter & Murphy, 1978). This gaping tongue display also reveals large jaw muscles, which may display to potential predators the capability of strong bite force (Lappin *et al.*, 2006). However, we found bobtails were much more likely to flee from the escalated observations or ignore them than gape. The dominant defensive behaviours against humans for bobtails are therefore attempting to flee to shelter (high perceived risk) and use of crypsis (low perceived predation risk). The conspicuous blue tongues, which are important socially with conspecifics, likely function secondarily as anti-predatory devices, and mostly for avian predators (Abramjan *et al.*, 2015).

The presence of cryptic colouration and 'body armour' in the form of tough dorsal scales appear to play a secondary role in the responses of bobtails to observers. Use of crypsis employs the strategy that a prey animal will not be engaged by a nearby predator, and effectively decreases risk perception of prey (Stankowich & Blumstein, 2005). Cryptic behaviour is most effective when the animal is already still, e.g. eastern brown snakes (*Pseudonaja textilis*) encountered by people tended to rely on crypsis when they were at rest upon encounter and otherwise fled (Whitaker & Shine, 1999b). In our experience, we are most successful at locating individual bobtails visually when they are in the open and when they are making noises by moving in vegetation, and it is therefore likely that during this study we were unaware of other nearby bobtails because they

remained still. For bobtails in particular, having body armour is likely most useful during interactions with actual predators: if the bobtail is discovered and needs to escape, it is unlikely that a predator will cause enough damage to the dorsal surface to be lethal before the bobtail reaches cover.

Overall, bobtails' tendency to attempt to flee from encounters with humans suggests that they are highly aware of, and negatively affected by, the presence of people within urban areas. Despite the public's general positive attitudes towards endearment of this native pet species, the behaviour of bobtails in Perth does not appear to lend itself well to urban adaptation. Their urban success must, therefore, be a factor of other life history traits, such as their prolific longevity (Whiting & While, 2017), and generalist habitat and diet requirements (Dubas & Bull, 1991). This may also be true for other cryptic reptile species common to urban areas, and a detailed understanding of the mechanisms affecting urban adaptation in reptiles is needed to ensure future management will aid their persistence.





# Chapter 8. General Discussion

In this thesis I have determined the traits influencing degree of urban adaptation for reptiles, and observed, for two reptile species commonly found in the Perth metropolitan area, how a selection of these traits impact reptile behavioural ecology.

In Chapter 2 I identified that reptiles do not use the same model for urban-adaptation as for birds and mammals. While all three taxa groups benefit from being diet generalists and using a range of refuges, including man-made structures, urban-adapted reptiles are not generally social, and sedentariness and novel resource innovations are not well described for this group. Rather, urban-adapted reptiles have a much more complex relationship with humans and urbanisation. Additional important traits include intraspecific combat/territoriality (as opposed to sociality), endemism and invasiveness to a variety of continents, large body size with a relatively long tail, habitat and habit generalism, egg-laying reproduction, sexual dimorphism, diurnal lifestyle, and lack of sex specialisation. It is likely that other traits are important for urban-adapted reptiles, which should become evident once this understudied class becomes better known by researchers in future. These findings are the first to consider a global model for reptiles within an urban context, and should form the foundation for further studies to aid reptile management as urban development expands worldwide.

The two study species for this thesis, dugites and bobtails, are both abundant within the Perth metropolitan area, and they should be considered urban adapters. However, their life histories do not completely fit the global model for urban-adapted reptiles. While both bobtails and dugites fight conspecifics for a mate (Bonnet *et al.*, 1998; Murray & Bull, 2004), have relatively large bodies (Chapter 3; Chapter 7), use a variety of habitats (including urban and peri-urban areas) (Chapter 3; Chapter 7), and use a variety of diet items – bobtails are omnivorous (Cooper, 2000; Shea, 2006), and although dugites are obligate carnivores, they eat a range of prey species (Chapter 3) – there are some evident differences. Only dugites lay eggs (Shine, 1989; Bull, Cooper & Baghurst, 2015), and neither species have marked sexual dimorphism (Chapter 2; Chapter 3; Chapter 7). Both species are also largely terrestrial (Chapter 3; Chapter 7), have relatively short tails, and naturalised populations are confined to the Australian continent. Despite not conforming to all the trends that contribute to the best model determining reptile adaptation, bobtails and dugites are extremely successful in Perth. It is likely that such success, as for other species that may not completely fit within the boundaries of the analysis in Chapter 2, are due to having highly flexible habitat and diet requirements, and the ability to mitigate the impacts of human disturbances (usually by avoiding them). In the chapters following Chapter 2, I explored how some of the most significantly-associated traits from the urban model may contribute towards the continued persistence of these species within Perth.

In Chapter 3 I investigated whether carnivorous dugites might modify their diets within urban areas. Instead, I found that dugites from both urban and non-urban distributions ate a diverse range of prey items, with larger snakes eating larger prey, a greater number of prey items, and a greater diversity of prey. Urban dugites, which were relatively shorter and lighter than non-urban snakes, were less likely to have prey present in their stomachs than were non-urban snakes. In

contrast to mammalian carnivores up to 20 kg body mass, which benefit from diet supplementation of synanthropic species such as rodents (Contesse *et al.*, 2004; White *et al.*, 2006; Bateman & Fleming, 2012), urban dugites did not make greater use of such synanthropic species than was evident for non-urban snakes. I did encounter a significant sampling bias of collection location on body size, and it is possible that larger individuals, which may be more difficult to come across in urban areas, do make greater use of rodents than smaller species. Alternatively, as dugites are diet generalists in the wild, the individuals that are able to tolerate the additional environmental stresses of city life may simply benefit from this innate trait of the species. As most other reptile species still persisting in Perth are also diet generalists (How & Dell, 1993), this seems to be the more likely case, and dugites presumably possess multiple traits that allow them to survive in the city.

One possible trait affecting their survival in the city may be increased territoriality and the ability for dugites to quickly establish small home ranges. In Chapter 4 I followed the movements of 10 adult urban dugites to investigate whether individuals that ventured near private properties in suburbia had similar activity ranges as those that were relatively isolated in urban bush patches. I also analysed the effects of translocation on their space use. Although this study was conducted with a limited number of snakes, it was the first of its kind to use GPS data loggers to track the movements of snakes. Using GPS technology, I determined that translocation caused snakes to use larger activity ranges and travel greater distances, and also detrimentally affected their survivorship. All translocated snakes died to predators and being struck by motor vehicles while crossing roads, and resident snakes also suffered similar fates (but only those individuals that were found near private properties). Urban spaces have many threats for snakes, and translocation of 'problem' snakes increases their risk due to inability to locate suitable refuges, increased predation risk, and greater vulnerability to road strikes due to their increased movements. I also found that resident snakes living within patches of urban bush were highly sedentary, where they likely have an established source of food and refuges, and if quickly establishing and maintaining a territory is important for urban snakes, populations are likely negatively affected by ongoing urban development and sprawl. Once a snake is displaced, either as an intentional translocation as a 'problem' snake, or due to habitat destruction, it must locate new resources to survive.

Dugites are not the only reptile species that risks direct mortality from crossing roads. As urbanisation causes increased fragmentation of greenspaces, often bisecting important habitats such as wetlands, I discovered in Chapter 5 that both dugites and bobtails are at risk of motor vehicle strike when crossing roads. When surveyed, Western Australian motorists expressed high levels of concern for the welfare of these reptiles on roads and claimed to be very likely to rescue a bobtail (and to a lesser degree, a snake). Despite this positive attitude, when I observed 1,500 motor vehicles on a road bisecting an urban wetland reserve, only one person stopped to rescue a model (bobtail). Motorists generally ignored objects, including reptiles, on the roadside (79%), rather than attempting to rescue or move them, and I did not observe any intentional strikes on any reptile models. Those motorists who did respond did so by slowing down or moving away from the model. When crossing a road, I modelled a >75% strike probability for both a bobtail

and dugite at the low road vehicle density I observed (2.23 vehicles/min) if they were moving slowly ( $1 \text{ m}\cdot\text{min}^{-1}$ ). Even when the modelled reptile was moving quickly (60 m/min), the strike risk was not nullified ( $\leq 16\%$ ). Although motorists did not intentionally strike model reptiles, the attitudes reflected in the online survey were not directly translated to behavioural action on the roads (i.e. people claimed to be very likely to rescue a reptile, but only 1 did), and crossing a road is risky for an urban reptile.

The impacts of attitudes of the general public towards reptiles are important beyond interactions on roads. People commonly encounter reptiles within urban areas, and their responses during these interactions are at least partially affected by their ability to correctly identify reptile species and judge the risk associated with encounters. In Chapter 6 I found that Western Australians were able to discern the difference between a snake and a lizard, but were less able to tell if a reptile was venomous, or accurately provide a common name. I also found that most calls reporting 'problem' snakes do not attempt to identify the species. Of the identified species, the majority of reports were for dugites, and as most reports were in urban areas, this is unsurprising. However, knowing a species' name does not guarantee a member of the public understands the risk associated with interacting with the animal: 21% of children and 9% of adults surveyed thought dugites were harmless. Considering the abundance of dugites in Perth, the inability of some residents to recognise these snakes has two potential consequences:

- 1) people may interact with a dugite not knowing the risk, have a negative interaction (possibly requiring medical treatment), and distrust other snakes after the interaction; or
- 2) people may be unnecessarily afraid of a dugite and interact with it (putting themselves at risk) or request it to be moved, even if it is not a direct threat (e.g. a snake passing through the garden).

As translocation is a commonly-employed, but apparently ineffective management tool that negatively impacts the ecology and survival of urban dugites (Chapter 4), a lack of education and misidentification of reptiles ultimately drives human-wildlife conflicts. This problem is not localised to Western Australia, but studies are limited to only few surveys (Morrison *et al.*, 1983; Corbett *et al.*, 2005). To better understand the risks of the general public mistakenly identifying potentially harmful species, surveys should be conducted wherever venomous snakes are common, and the results used to inform education and healthcare practices.

While humans are often unable to discern the risk of interaction with a reptile, bobtails are highly vigilant to human encounter. In Chapter 7 I found that urban bobtails were most likely to attempt to flee from encounters with humans rather than ignore or use a deimatic threat display. Bobtails that were already moving when initially encountered were more likely to flee from observers than those that were still. Where flight is not effective, bobtails secondarily use their cryptic colouration and armoured bodies, and lastly implement a deimatic gape display and attempt to bite the observer. Bobtails did not become habituated to areas with frequent human traffic, even when human-bobtail interactions remained solely visual encounters rather than physical ones. Their lack of behavioural flexibility around human observers shows that they are constantly vigilant to humans, and the presence of humans is an additional stress to their life in urban areas.

## 8.1 Conclusion

My study quantitatively explored the traits that are best associated with urban adaptation, and investigated the relationships between some of these traits, and the impacts of urbanisation for two reptiles in Perth. Overall, dugites are considered an inimical species as they are highly venomous and responsible for deaths in Western Australia, while bobtails are capable of administering a painfully strong bite, but are otherwise harmless. Very few people, most of whom are skilled professionals, keep dugites as pets or for venomous snake relocation training, while bobtails are common household pets of those with herpetile-keeping licenses. Despite these differences, these snakes and skinks share many natural history traits, owing to their persistence within urban areas in the face of so many challenges associated with living near humans. Neither species fit the model for urban-adapted reptiles perfectly, but they should still be considered urban adapters.

Despite being obligate carnivores, dugite diets are varied regardless of whether they are within an urban or natural area, but smaller-bodied individuals appear to be less flexible in their diets, restricted to eating smaller, usually native, prey items. Dugites that stay within established home ranges can grow to large sizes and access suitable resources within a much smaller area than if they are translocated as 'problem' snakes. It is likely that disturbances such as land clearing cause a snake to disperse, encounter a human, and be considered a 'problem' animal. Once a dugite is translocated, its likelihood of surviving to establish a new home range and access resources diminishes. A significant factor of urban areas that negatively affects the survival of dugites is road mortality, and, although I did not observe any motorists intentionally striking model snakes on the side of a road, most members of the general public are fearful of snakes and unable or unwilling to correctly identify native species as harmful or harmless. These findings suggest that, if given the opportunity to thrive within less-disturbed greenspaces within the urban matrix free from persecution of humans, the diet flexibility of dugites lends them an advantage over other snakes in their ability to persist within the metropolitan area.

Similarly to dugites, bobtails are a secretive taxon with a high likelihood of succumbing to direct mortality when crossing roads, even with the public considering them less offensive and being more likely to rescue them. Although bobtails are commonly found on footpath edges and in garden beds, they are highly responsive to human interaction and appear to prefer limited disturbances.

With a rapidly urbanising world, it is becoming more important to understand the factors affecting the ecology of urban animals. This thesis has found that, even with conservation strategies to help urban reptiles, they are still, to a great extent, dependent on the attitude and mercy of their human neighbours. As reptiles have a wide range of life history strategies, and both potentially harmful and harmless species equally inhabit cities, targeted education programs are likely to be most effective in helping to inform the public about the benefits of having reptiles part of urban biodiversity.

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*Every reasonable effort has been made to acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.*

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## Appendix 1. Dataset used for analysis comparing the degree of urban adaptation for turtles/tortoises, lizards and snakes (Chapter 2)

The following appendix for Chapter 2 presents the entire dataset used in the meta-analysis. References for the data are separate from the thesis, and are presented in Appendix 1.1.

Species	Urban category <sup>a</sup>				Total length <sup>b</sup> SVL % <sup>c</sup>	Life history							Diet				Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference																
	Avoiders <sup>a</sup> traits	Oblivious <sup>a</sup> traits	Perurbans <sup>a</sup> traits	Adapters <sup>a</sup> traits		Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>		North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)						
Turtles																																																					
Pleurodira																																																					
Pelomedusidae																																																					
<i>Pelusios castaneus</i>	1	6 ABC DEF	1 G	0	0	3	5	0	0	0	1	0	0.5	0	0	0	1	1	1	0	3	0	0	1	1	0	0	0	2	1	0	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	1	1,2	
<i>Pelusios subniger</i>	1	6 ABC DEF	1 G	0	0	3	4	0	0	1	1	0	0.5	0	0	1	1	1	0	3	0	0	1	0	0	0	0	1	1	0	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1,2,3,4,5
Podocnemididae																																																					
<i>Podocnemis expansa</i>	1	6 ABC DEF	1 G	0	0	4	5	1	0	1	1	0	0.5	0	0	0	0	1	0	1	1	0	0	1	0	0	2	1	0	0	0	1	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1,2	
Chelidae																																																					
<i>Pseudemydura umbrina</i>	1	5 ABC EF	1 G	1 D	0	3	4	0	0	1	1	0	0.5	0	0	1	1	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1,6,7		
<i>Chelodina colliciei</i>	2	0 ABC EG	5 DF	2	0	4	3	0	0	0	1	0	0.5	0	0	1	1	1	0	3	1	0	0	0	1	0	0	2	1	0	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1,6,7,8	
<i>Chelodina expansa</i>	2	0 ABC EG	5 DF	2	0	4	3	0	0	0	1	0	0	0	0	1	1	0	0	2	1	0	0	0	1	0	0	2	1	0	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1,7,8,9,10		
<i>Chelodina longicollis</i>	2	1 D	5 ABC EG	1 F	0	3	3	0	0	1	1	0	0.5	0	0	1	1	0	0	2	1	0	0	0	0	0	1	1	0	0	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1,2,7,8,9,10,11,12,13,14,15				
<i>Emydura macquarii</i>	4	1 D	1 G	1 E	4 ABC F	3	3	0	0	1	1	0	0.5	0	0	1	1	1	0	3	0	0	1	0	0	0	0	1	1	0	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1,2,7,8,9,13			
<i>Myuchelys latisternum</i>	1	6 ABC DEF	1 G	0	0	3	4	0	0	0	1	0	0.5	0	0	1	1	1	0	3	1	0	0	0	0	0	1	1	0	0	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1,2,7				
Cryptodira																																																					
Trionychidae																																																					
<i>Lissemys punctata</i>	2	1 D	5 ABC EG	1 F	0	3	4	0	0	1	1	0	0.5	0	0	1	1	1	0	3	0	1	0	1	0	0	0	2	1	0	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1,2,16,17			



Species	Urban category <sup>a</sup>				Size	Life history							Diet			Habitat						Habit					Endemic continent/s					Invasive continent/s					Reference														
	Avoiders <sup>a</sup> traits	Oblivious <sup>a</sup> traits	Perurbans <sup>a</sup> traits	Adapters <sup>a</sup> traits		Total length <sup>b</sup>	SVL <sup>c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)		
<i>Glyptemys muhlenbergii</i>	1 ABC DEF	6 G	1 0	0 0	2 3	3	0	0	0	1	0	0	0	0	1	1	1	0	3	0	0	0	1	0	0	1	2	1	0	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	25
<i>Emys orbicularis</i>	1 ABC DEF	6 G	1 0	0 0	3 3	3	1	0	0	1	0	0.5	0	0	1	1	1	0	3	0	0	0	0	1	0	1	2	1	0	1	1	1	4	0	1	0	1	0	0	2	1	0	0	0	0	0	0	0	1	1, 2, 27	
<i>Clemmys guttata</i>	1 ABC EF	5 G	1 D	1 0	2 3	3	0	0	0	1	0	0.5	0	0	1	1	1	0	3	0	0	1	0	1	0	0	2	1	0	1	0	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1, 18, 25	
<i>Terrapene carolina</i>	4 EG	2 D	1 ABC F	4 0	3 4	4	0	0	0	1	0	0.5	0	0	1	1	1	0	3	0	0	0	0	1	0	0	1	1	0	1	0	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1, 2, 18, 25, 26
<i>Deirochelys reticularia</i>	1 ABC DEF	6 G	1 0	0 0	3 3	3	0	0	0	1	0	0	0	0	1	1	0	0	2	0	0	0	1	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1, 18, 25		
<i>Chrysemys picta</i>	2 DEF ABC G	3 4	4 0	0 0	3 3	3	0	0	0	1	0	0	0	0	1	1	1	0	3	0	1	0	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	1	0	0	1	1, 2, 18, 19, 25, 28			
<i>Pseudemys concinna</i>	2 D ABC EG	1 5 F	1 0	0 0	3 4	4	0	0	1	1	0	0.5	0	0	1	0	1	0	2	0	0	0	1	0	0	0	1	1	0	0	1	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1, 2, 18, 19	
<i>Pseudemys nelsoni</i>	4 D EG F ABC	1 2 3	1 0	3 0	3 3	3	0	0	0	1	0	0	0	0	1	0	1	0	2	0	0	0	1	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1, 2, 18	
<i>Pseudemys rubiventris</i>	2 D ABC EG	1 5 F	1 0	0 0	3 3	3	0	0	1	1	0	0	0	0	1	1	1	0	3	0	0	1	1	0	0	0	2	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1, 18, 25		
<i>Trachemys decussata</i>	1 ABC EF	5 G	1 D	1 0	4 3	3	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	2	1	0	1	0	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1, 2		
<i>Trachemys terrapen</i>	3 D EG F ABC	1 2 4	4 0	0 0	3 4	4	0	0	0	1	0	0.5	0	0	1	1	1	0	3	0	0	0	1	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1, 2		
<i>Trachemys stejnegeri</i>	4 D EG F ABC	1 2 3	1 0	3 0	3 3	3	0	0	0	1	0	0.5	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1, 2		
<i>Trachemys scripta</i>	4 EG ABC DF	0 2 5	0 0	5 0	3 3	3	1	1	1	1	0	0	0	0	1	1	1	0	3	1	1	1	1	1	1	7	1	0	1	1	1	4	0	0	0	0	1	0	1	1	1	1	1	0	1	5	1, 2, 4, 8, 14, 16, 18, 19, 25, 27, 29, 30				
<i>Malaclemys terrapin</i>	1 ABC DEF	6 G	1 0	0 0	3 3	3	0	0	1	1	0	0	0	0	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1, 18, 25		

Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size		Life history						Diet			Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference												
		Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>§</sup> traits	Adapters <sup>§</sup> traits	Total length <sup>b</sup>	SVL <sup>b,c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)
<i>Graptemys pseudogeographica</i>	1	6 ABC DEF	1 G	0	0	3	4	1	0	1	1	0	0	0	1	1	1	0	3	0	0	0	1	1	0	0	2	1	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1, 25, 31
<i>Graptemys geographica</i>	1	6 ABC DEF	1 G	0	0	3	3	0	0	1	1	0	0	0	1	1	1	0	3	0	0	0	1	0	0	1	1	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1, 2, 18	
<i>Testudo hermanni</i>	1	6 ABC DEF	1 G	0	0	3	5	0	0	0	1	0	0.5	0	0	1	1	1	0	3	0	1	1	1	1	0	1	5	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1, 2, 27		
<i>Testudo kleinmanni</i>	1	5 ABC EF	1 G	1	0	3	4	0	0	0	1	0	0.5	0	0	1	1	1	0	3	1	1	0	1	0	0	0	3	0	0	1	1	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	1, 2	
<i>Testudo graeca</i>	1	6 ABC DEF	1 G	0	0	3	5	0	0	1	1	0	0.5	0	0	0	0	1	0	1	0	1	1	1	0	1	5	0	0	0	1	2	0	1	0	1	0	0	2	1	0	0	0	0	0	1	1, 2, 27		
<i>Testudo marginata</i>	1	5 ABC EF	1 G	1	0	3	5	0	0	0	1	0	0.5	0	0	1	1	1	0	3	0	0	0	1	0	0	1	2	0	0	1	1	3	0	0	0	1	0	0	0	1	0	0	0	0	0	1, 2, 27		
<i>Stigmochelys pardalis</i>	1	6 ABC DEF	1 G	0	0	4	5	0	0	1	1	0	0	0	0	1	1	0	2	0	0	1	1	0	0	1	3	1	0	1	1	4	0	1	0	0	0	0	1	0	0	0	0	0	0	1, 2, 30, 32			
<i>Astrochelys radiata</i>	1	5 ABC EF	2 DG	0	0	4	5	0	0	1	1	0	0.5	0	0	1	0	1	0	2	0	0	0	1	0	0	1	0	0	1	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	1, 2, 3			
<i>Chersina angulata</i>	4	0 G	1 DEF	3 ABC	3	3	5	0	0	1	1	0	0	0	0	1	1	1	0	3	1	1	0	1	0	0	0	3	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	1, 2, 4		
<i>Chelonoidis denticulata</i>	1	5 ABC EF	2 DG	0	0	4	5	0	0	0	1	0	0.5	0	0	1	0	1	0	2	0	0	0	0	1	0	0	1	0	0	1	0	2	0	0	0	0	1	1	2	0	0	0	0	0	0	1, 2		
<i>Kinixys belliana</i>	3	0 G	1 ABC	6 DEF	0	3	5	0	0	1	1	0	0.5	0	0	1	1	1	0	3	1	1	1	0	1	0	1	5	0	0	1	1	3	0	1	0	0	0	0	1	0	0	0	0	0	1, 2, 3, 4, 5			
<i>Pangshura sylhetensis</i>	2	0 ABC EG	5 DF	2	0	3	4	1	0	0	1	0	0.5	0	0	1	1	1	0	3	0	0	0	0	1	0	1	2	1	0	1	0	1	3	1	0	0	0	0	0	1	0	0	0	0	0	1, 17, 21, 23, 33		





Species	Urban category <sup>a</sup>				Size	Life history							Diet				Habitat					Habit			Endemic continent/s					Invasive continent/s					Reference															
	Avoiders <sup>a</sup> traits	Oblivious <sup>a</sup> traits	Perurbans <sup>a</sup> traits	Adapters <sup>a</sup> traits		Total length <sup>b</sup>	SVL <sup>b</sup> %	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)		Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)	
<i>Crenadactylus ocellatus</i>	1 ABC EF	5 1 G	1 D	0	1	3	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	7	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39
Pygopodidae																																																		
<i>Pygopus lepidopodus</i>	3 EF	2 DG	3 ABC	0	3	3	0	0	0	1	0	0.5	0	0	1	0	0	0	1	1	0	1	1	1	0	0	4	0	0	1	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6, 7, 8, 9, 10, 11, 13, 39
<i>Aprasia pulchella</i>	2 EF	2 ABC	4 D	0	2	3	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	2	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 38, 39	
<i>Aprasia repens</i>	2 EF	2 ABC	4 D	0	2	5	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	2	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 37, 38, 39	
<i>Pletholax gracilis</i>	2 DEF	3 ABC	4 G	0	3	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	5	0	1	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 38, 39		
<i>Lialis burtonis</i>	2 ABC DEG	0 6 F	1 D	0	3	4	0	0	0	1	0	0.5	0	0	0	1	0	0	1	1	1	1	1	1	1	7	0	0	1	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 11, 13, 37, 39, 40		
<i>Delma concinna</i>	1 ABC DEF	6 1 G	0	0	3	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	5	0	1	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 39		
<i>Delma grayii</i>	2 DF	2 ABC	5 EG	0	3	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0	0	4	0	1	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 39	
<i>Delma fraseri</i>	2 F	1 ABC	5 D	0	3	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 38, 39	
<i>Delma impar</i>	3 EG	0 2 EG	5 ABC	0	3	2	0	0	0	1	0	0.5	0	0	1	0	0	0	1	0	0	1	1	1	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	7, 8, 9, 10, 37, 38, 39		
Carphodactylidae																																																		
<i>Underwoodisaurus milii</i>	1 ABC EF	5 1 G	0 D	1	2	3	1	0	0	1	0	1	0	0	1	1	0	0	2	1	1	0	1	1	0	0	4	0	1	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	6, 7, 8, 13, 37		
<i>Phyllurus platurus</i>	4 DEG	0 3 DEG	0 ABC	4 F	2	3	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	1	0	0	2	0	1	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	7, 8, 13, 39		
<i>Saltuarius swaini</i>	4 EG	0 2 EG	1 F	4 ABC D	3	3	0	0	0	1	0	0.5	0	0	1	0	0	0	1	1	0	0	1	1	0	1	4	0	1	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	7, 8, 11	



Species	Urban category <sup>a</sup>				Size	Life history							Diet				Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference																			
	Avoiders <sup>a</sup> traits	Oblivious <sup>a</sup> traits	Perurbans <sup>a</sup> traits	Adapters <sup>a</sup> traits		Total length <sup>b</sup>	SVL <sup>c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozooic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)							
<i>Phelsuma laticauda</i>	4	0	1	1	5	2	2	0	0	1	1	0	0.5	1	0	1	0	0	0	1	1	0	1	1	1	0	0	4	0	1	0	0	1	2	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	2	2, 3, 14, 37, 39, 42
<i>Phelsuma cepedian</i>	3	0	2	4	1	2	2	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	2	0	1	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	2, 3, 37, 39		
<i>Phelsuma guimbeui</i>	4	0	2	2	3	2	2	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	3	0	1	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	2	14			
<i>Phelsuma dubia</i>	3	0	1	4	2	2	2	0	0	0	1	0	0	0	1	0	1	0	2	1	0	1	0	0	0	0	2	1	1	0	0	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	2, 3, 5				
<i>Phelsuma madagascariensis</i>	4	0	1	1	5	3	2	0	0	0	1	0	0.5	1	0	1	0	0	0	1	0	0	1	1	0	0	2	0	1	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	2	2, 3, 37, 39, 42			
<i>Afrogecko porphyreus</i>	3	0	1	4	2	1	3	1	0	0	1	0	1	1	0	1	0	0	0	1	1	0	0	1	1	0	1	4	0	1	1	1	1	4	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	4, 30, 37, 42			
<i>Christinus marmoratus</i>	4	0	1	0	6	2	3	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	3	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	6	6, 7, 8, 9, 10, 37, 39				
<i>Ebenavia inunguis</i>	1	6	1	0	0	1	3	0	0	0	1	0	0.5	0	0	1	0	0	0	1	0	0	1	0	0	0	2	0	1	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	2, 4, 5				
<i>Afroedura pondolia</i>	3	2	1	3	1	1	3	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	4, 30				
<i>Homopholis walbergii</i>	4	0	1	0	6	2	3	0	0	0	1	0	0.5	1	0	1	0	0	0	1	1	0	1	0	0	0	3	1	1	1	1	1	5	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	4, 42				
<i>Chondrodactylus turneri</i>	1	5	2	0	0	2	3	0	0	0	1	0	0.5	1	0	1	0	0	0	1	0	0	1	0	0	0	1	2	0	1	0	1	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	4, 5, 42				
<i>Chondrodactylus bibronii</i>	4	0	1	0	6	2	4	1	0	0	1	0	1	1	0	1	1	0	0	2	0	0	1	0	0	0	1	0	1	0	1	1	3	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	2	2, 4, 30, 37, 39, 42						
<i>Nactus pelagicus</i>	3	0	1	4	2	2	2	0	0	0	1	1	1	1	0	1	0	0	0	1	1	1	1	1	1	1	7	0	1	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7	7, 8, 14, 37, 39, 42, 43				
<i>Heteronotia binoei</i>	1	5	2	0	0	1	3	0	0	0	1	1	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6	6, 7, 8, 37, 39, 43					

Species	Urban category <sup>a</sup>				Size	Life history							Diet					Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference															
	Avoiders <sup>a</sup> traits	Oblivious <sup>a</sup> traits	Perurban <sup>a</sup> traits	Adaptier <sup>a</sup> traits		Total length <sup>b</sup>	SVL <sup>c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>		Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)				
<i>Lepidodactylus lugubris</i>	4	0	1	0	6	1	3	1	0	0	1	1	1	1	0	1	0	1	0	2	1	0	0	0	1	1	0	3	1	1	0	1	1	4	1	0	1	0	0	0	0	2	0	0	0	0	1	1	2	2, 7, 8, 14, 37, 39, 42, 43, 50, 51, 52			
<i>Gekko gecko</i>	3	0	1	5	1	3	3	1	1	0	1	0	1	1	0	1	1	0	0	2	0	0	0	0	1	0	0	1	0	1	0	1	1	3	1	0	0	0	0	0	1	0	1	0	0	1	0	2	2, 14, 16, 17, 18, 21, 37, 39, 42, 50, 51, 53, 54				
<i>Gekko chinensis</i>	3	0	1	4	2	2	3	0	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0	2	0	1	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	16, 42, 55				
<i>Gekko japonicus</i>	4	0	1	1	5	2	3	0	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	2	0	1	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	16			
<i>Hemiphyllodactylus typus</i>	4	0	1	0	6	1	3	0	0	0	1	1	1	1	0	1	1	0	0	1	1	0	1	1	1	1	6	1	1	1	0	1	4	1	0	1	0	0	0	2	0	1	0	0	1	0	2	2, 16, 17, 42, 50, 52, 53, 54					
<i>Gehyra mutilata</i>	4	0	1	0	6	2	5	0	1	0	1	0	1	1	0	1	1	0	2	0	0	0	0	1	0	0	1	0	1	0	1	1	3	1	0	0	0	0	0	1	0	1	1	0	1	1	4	2, 3, 7, 16, 17, 37, 39, 42, 43, 50, 51, 52, 53, 54					
<i>Gehyra oceanica</i>	3	0	1	4	2	2	3	1	0	1	1	0	1	1	0	0	1	1	0	2	0	0	0	0	1	0	0	1	0	1	0	1	3	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	14, 37, 39, 42, 43				
<i>Gehyra variegata</i>	3	0	3	4	0	1	3	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	1	0	2	0	1	1	1	1	4	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 43				
<i>Mediodactylus kotschy</i>	4	0	2	0	5	1	2	0	0	1	1	0	0.5	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	3	0	1	1	1	1	4	1	0	0	1	0	0	2	0	0	0	0	0	0	2, 27, 56
<i>Cyrtopodion scabrum</i>	4	0	1	1	5	1	3	0	0	0	1	0	0.5	1	0	1	0	0	0	1	1	1	1	0	0	0	3	0	0	0	1	1	2	1	1	0	0	0	0	2	0	0	0	0	1	0	1	2, 18, 37, 39, 42, 56, 57					
<i>Bunopus tuberculatus</i>	1	5	1	0	1	1	2	0	0	1	1	0	1	1	0	1	0	0	0	1	0	1	1	0	1	1	5	1	1	1	1	1	5	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	37, 39, 42, 50, 56, 58				
<i>Cyrtodactylus khasiensis</i>	3	0	1	6	0	2	2	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	1	1	0	1	4	0	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	16, 21, 50				
<i>Hemidactylus maculatus</i>	4	0	2	0	5	3	2	1	0	0	1	0	1	0	0	1	1	0	0	2	0	0	0	0	1	1	0	2	0	1	1	1	1	4	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	17, 50, 52, 59, 60			



Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size	Life history							Diet				Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference															
		Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurban <sup>§</sup> traits	Adapted <sup>§</sup> traits		Total length <sup>b</sup>	SVL <sup>%c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)			
<i>Ctenotus fallens</i>	2	1 F	5 ABC EG	1 D	0	3	1	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	4	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 65, 66	
<i>Ctenotus robustus</i>	2	1 F	5 ABC EG	1 D	0	3	2	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	7	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 11, 38, 39, 40, 65
<i>Ctenotus labillardieri</i>	1	5 ABC EF	1 G	1 D	0	2	2	0	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	1	0	1	5	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 65		
<i>Ctenotus delli</i>	1	5 ABC EF	1 G	1 D	0	2	2	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1	0	1	5	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 39, 65, 66		
<i>Ctenotus gemmula</i>	1	5 ABC EF	2 DG	0	0	2	2	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0	5	0	0	1	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 65, 66			
<i>Ctenotus impar</i>	1	5 ABC EF	2 DG	0	0	2	2	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0	5	0	0	1	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 39, 65, 66			
<i>Ctenotus arcanus</i>	1	6 ABC DEF	1 G	0	0	2	2	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0	5	1	0	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 40, 65				
<i>Lerista bougainvillii</i>	2	0 ABC EG	5 DF	2	0	2	2	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 37, 39			
<i>Lerista lineopunctulata</i>	2	0 ABC EG	5 DF	2	0	2	3	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	4	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39				
<i>Lerista praepedita</i>	2	0 ABC EG	5 DF	2	0	1	3	0	0	0	1	0	0	0	1	0	0	0	1	1	1	0	1	1	0	0	4	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 39				
<i>Lerista lineata</i>	2	0 ABC EG	5 DF	2	0	1	3	0	0	0	1	0	0	0	1	0	0	0	1	1	1	0	1	0	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 39				
<i>Lerista christinae</i>	3	0 G	1 ABC DEF	6 D	0	1	2	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	0	6	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6, 7, 8, 66				
<i>Lerista elegans</i>	1	5 ABC EF	1 G	1 D	0	1	2	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0	5	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 66					

Species	A-priori traits <sup>†</sup>				Size Total length <sup>b</sup> SVL <sup>b</sup> %	Life history					Diet					Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference												
	Urban category <sup>a</sup>	Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>§</sup> traits		Adapters <sup>§</sup> traits	Gregarious <sup>‡</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)
<i>Lerista distinguenda</i>	2	0	5 ABC EG	2 DF	0	1	2	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	7	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 39, 66
<i>Hemiergis decresiensis</i>	2	0	4 ABC G	1 D	2 EF	2	2	0	0	0	0	0.5	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	7, 8, 11, 37, 39
<i>Hemiergis quadrilineata</i>	4	0	1 G	1 D	5 ABC EF	3	1	0	0	0	0	0.5	0	0	1	0	0	0	1	1	1	0	1	0	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	6, 7, 8, 66	
<i>Hemiergis initialis</i>	1	5 ABC EF	1 G	1 D	0	1	3	1	0	0	0	0.5	0	0	1	0	0	0	1	1	0	0	1	1	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	6, 7, 8, 37, 39, 66	
<i>Anepischetosia maccoyi</i>	3	1 D	1 G	5 ABC EF	0	2	2	0	0	0	1	0	0.5	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	7, 8, 9, 10		
<i>Saiphos equalis</i>	2	0	5 ABC EG	2 DF	0	2	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	7, 8, 13, 38		
<i>Coeranoscincus reticulatus</i>	1	5 ABC EF	2 DG	0	0	3	2	0	0	0	1	0	0.5	0	0	1	0	0	0	1	1	1	0	1	1	5	0	0	1	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	7, 8, 38, 40			
<i>Ophioscincus truncatus</i>	2	0	5 ABC EG	2 DF	0	2	2	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0	4	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	7, 8, 40, 67		
<i>Eulamprus tympanum</i>	2	0	4 ABC E	1 F	2 DG	2	2	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0	1	1	1	1	4	1	1	1	1	5	0	0	1	0	0	0	1	0	0	0	0	0	7, 8, 9, 10, 37, 39			
<i>Eulamprus quoyii</i>	4	0	2 EG	0	5 ABC DF	3	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	1	4	1	1	1	1	5	0	0	1	0	0	0	1	0	0	0	0	0	7, 8, 11, 13, 37, 38, 39, 40			
<i>Concinnia tenuis</i>	1	5 ABC EF	2 DG	0	0	2	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	7, 11, 13, 40			
<i>Concinnia martini</i>	3	0	3 DEG	4 ABC	0 F	2	2	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	2	0	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	7, 40			
<i>Calyptotis scutirostrum</i>	2	2 EF	4 ABC G	1 D	0	2	2	0	0	0	1	0	0.5	0	0	1	0	0	0	1	1	0	0	1	0	1	3	0	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	7, 8, 38, 40			





Species	A-priori traits <sup>†</sup>				Size	Life history							Diet					Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference														
	Urban category <sup>a</sup>	Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>§</sup> traits		Adapters <sup>‡</sup> traits	Total length <sup>b</sup>	SVL <sup>%,c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)		
<i>Cryptoblepharus buchananii</i>	4	0	1	0	6	2	2	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	2	0	1	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	7, 8, 66
<i>Cryptoblepharus plagiocephalus</i>	4	0	2	2	3	1	2	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2, 6, 7, 8, 37, 39
<i>Cryptoblepharus virgatus</i>	4	0	1	0	6	1	2	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	3	0	1	0	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 37, 39, 40, 69
<i>Cryptoblepharus poecilopleurus</i>	1	5	1	0	1	1	2	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	2	1	1	0	1	1	4	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	2, 14, 42		
<i>Niveoscincus coventryi</i>	1	5	1	1	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	2	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 10, 37, 39	
<i>Niveoscincus metallicus</i>	4	0	1	1	5	2	2	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0	0	4	0	0	0	1	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 37, 39, 70
<i>Saproscincus mustelinus</i>	4	0	2	0	5	2	2	1	0	0	1	0	0.5	0	0	1	0	0	0	1	1	0	0	1	1	0	0	3	0	0	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 11, 13	
<i>Saproscincus spectabilis</i>	4	0	2	0	5	2	2	1	0	0	1	0	0.5	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 11, 13	
<i>Bassiana duperreyi</i>	2	0	5	2	0	2	2	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 70
<i>Bassiana platynota</i>	1	5	1	1	0	2	2	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	3	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 13
<i>Acritoscincus trilineatus</i>	2	2	5	0	0	2	2	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	1	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 39, 66	
<i>Morethia lineoocellata</i>	1	5	1	1	0	2	2	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	7	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 37	
<i>Morethia obscura</i>	2	1	5	1	0	1	2	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	1	1	1	0	0	4	0	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39	
<i>Menetia greyii</i>	2	1	6	0	0	1	3	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	1	1	0	0	4	0	0	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 43	



Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size	Life history							Diet				Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference														
		Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>§</sup> traits	Adapters <sup>‡</sup> traits		Total length <sup>b</sup>	SVL <sup>‡</sup> % <sup>c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)		
<i>Egernia cunninghami</i>	2	0	6	1	0	3	3	1	0	0	0	0	0	0	1	1	1	0	3	0	0	0	0	0	0	1	1	0	1	1	0	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 13, 37, 39
<i>Egernia saxatilis</i>	1	5	1	1	0	3	2	1	0	0	0	0	0	0	1	0	1	0	2	0	0	0	0	0	0	1	1	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 11
<i>Liopholis whitii</i>	3	0	2	5	0	3	2	1	0	0	0	0	0	0	1	0	1	0	2	1	0	1	1	1	0	1	5	0	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	7, 8, 9, 13, 37, 39, 43, 70	
<i>Lissolepis luctuosa</i>	2	0	5	2	0	3	2	0	0	0	0	0.5	0	0	1	0	1	0	2	1	0	0	0	0	0	0	1	1	0	1	0	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 39		
<i>Lissolepis coventryi</i>	2	0	5	2	0	3	2	0	0	0	0	0.5	0	0	1	0	1	0	2	1	0	0	0	1	1	0	3	1	0	1	0	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7, 8, 9		
<i>Eutropis carinata</i>	4	0	1	1	5	3	2	1	0	0	0	0	0	0	1	1	0	0	2	1	0	1	1	1	0	0	4	0	0	1	1	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	17, 34, 37, 39, 52, 62	
<i>Eutropis multifasciata</i>	2	2	4	0	1	3	2	0	0	0	0	0	0	0	1	1	0	0	2	0	0	1	0	1	1	1	4	1	1	1	1	5	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	2	2, 16, 21, 37, 39, 50, 51, 53, 54			
<i>Pseudemoia entrecasteauxii</i>	3	0	2	5	0	2	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	4	0	0	1	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 37, 39, 70		
<i>Pseudemoia pagenstecheri</i>	4	1	2	0	4	2	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	4	1	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 37, 39		
<i>Pseudemoia rawlinsoni</i>	3	1	1	5	0	2	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	7, 8, 9, 10			
<i>Pseudemoia spenceri</i>	3	0	1	5	1	2	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	2	0	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 9, 10			
<i>Emoia impar</i>	3	0	2	5	0	2	2	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	2	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	2, 14			
<i>Emoia cyanura</i>	4	0	3	1	3	2	2	1	0	1	1	0	0	0	1	0	0	0	1	1	0	1	1	1	0	0	4	0	0	1	0	2	1	0	1	0	0	0	2	0	0	0	0	1	1	2	2, 14, 16, 37, 39, 43					
<i>Trachylepis quinquetaeniata</i>	3	0	1	6	0	3	2	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	2	0	0	0	1	2	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	2, 43, 289				

Species	Urban category <sup>a</sup>				Size	Life history							Diet					Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference															
	Avoiders <sup>a</sup> traits	Oblivious <sup>a</sup> traits	Perurbans <sup>a</sup> traits	Adapters <sup>a</sup> traits		Total length <sup>b</sup>	SVL <sup>c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>		Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)				
<i>Heremites auratus</i>	4	0	2	2	3	3	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	2	1	1	0	0	1	3	1	0	0	1	0	0	0	2	0	1	0	0	0	0	1	2, 27, 50, 56	
<i>Plestiodon fasciatus</i>	1	6	1	0	0	3	2	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	25, 37, 38, 39, 43		
<i>Plestiodon laticeps</i>	4	0	2	0	5	3	3	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	0	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	18, 26, 37, 38, 39			
<i>Chalcides chalcides</i>	4	0	1	1	5	3	2	0	0	1	0	0	0.5	0	0	1	0	0	0	1	1	1	1	0	0	1	5	1	0	1	0	1	3	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	27, 37, 38, 39, 45			
<i>Chalcides ocellatus</i>	4	0	2	1	4	3	3	0	0	0	0	0.5	0	0	1	1	0	0	2	1	1	0	1	1	1	0	5	1	0	1	1	1	4	0	0	0	1	0	0	1	1	1	0	0	0	0	0	2	2, 5, 27, 37, 38, 39, 50, 52, 56, 74				
<i>Chalcides viridanus</i>	4	0	2	0	5	2	3	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	7	0	1	1	1	1	4	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	2, 27				
<i>Chalcides sexlineatus</i>	4	0	2	1	4	2	2	0	0	0	0	0.5	0	0	1	0	0	0	1	0	1	1	0	1	1	1	5	1	0	1	1	1	4	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2, 27, 37, 39			
Teiidae																																																					
<i>Salvator merianae</i>	1	6	1	0	0	4	2	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	37, 39, 75, 76			
<i>Tupinambis teguixin</i>	1	6	1	0	0	5	2	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2, 37, 39		
<i>Aspidoscelis sexlineata</i>	1	6	1	0	0	2	2	0	0	0	1	1	0.5	0	0	1	0	0	0	1	0	1	1	1	0	0	4	1	0	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	18, 25, 43			
<i>Aspidoscelis neomexicana</i>	4	0	1	1	5	3	1	0	0	0	1	1	0.5	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2, 18, 43			
<i>Ameiva ameiva</i>	4	1	1	0	5	4	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	2	1	0	0	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	1	1	2, 18, 37, 38, 39, 43						
<i>Cnemidophorus lemniscatus</i>	3	1	1	3	2	3	1	0	0	0	1	0	0	0	0	1	0	1	0	2	1	0	0	0	1	0	2	0	1	1	0	1	3	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	2, 18, 37, 39, 43		
Gymnophthalmidae																																																					



Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size	Life history							Diet				Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference													
		Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>§</sup> traits	Adapters <sup>‡</sup> traits		Total length <sup>b</sup>	SVL <sup>c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)	
<i>Anguis fragilis</i>	1	5 ABC EF	1 G	1 D	0	3	2	1	0	0	0	0	0	0	1	1	0	0	2	0	0	0	1	1	0	1	3	0	0	1	1	1	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	2, 27, 37, 38, 39, 43, 45		
<i>Ophisaurus ventralis</i>	4	0	2 DG	0	5 ABC EF	4	2	0	0	1	0	0	0	1	1	0	0	2	0	0	1	0	1	0	0	2	0	0	1	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	18, 26, 37, 38, 39
<i>Elgaria multicarinata</i>	1	5 ABC EF	2 DG	0	0	3	2	0	0	0	1	0	0.5	0	0	1	0	0	1	1	0	1	0	1	0	0	3	0	0	1	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2, 37, 38, 43		
<i>Varanidae</i>																																																			
<i>Varanus niloticus</i>	4	0	1 G	0	6 ABC DEF	6	2	1	0	0	1	0	0	0	1	1	0	0	2	1	0	0	1	0	1	0	3	1	1	1	1	1	5	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	2, 4, 5, 29, 37, 39		
<i>Varanus bengalensis</i>	3	0	1 G	5 ABC EF	1 D	5	2	0	1	1	1	0	0	0	1	1	1	0	3	1	1	1	1	1	0	1	6	1	1	1	1	1	5	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	8, 16, 17, 34, 37, 39, 50, 52, 53, 56, 59, 80
<i>Varanus indicus</i>	1	6 ABC DEF	1 G	0	0	5	2	0	0	1	1	0	0	0	1	1	0	0	2	1	0	0	0	1	0	0	2	1	1	0	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2, 7, 8, 14, 37, 39	
<i>Varanus salvator</i>	3	0	1 G	6 ABC DEF	0	6	2	1	0	0	1	0	0	0	1	1	0	0	2	1	0	0	0	1	0	1	3	1	1	0	0	1	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	16, 17, 34, 37, 39, 50, 51, 52, 53, 54, 81
<i>Varanus varius</i>	3	0	1 G	6 ABC DEF	0	5	1	0	0	0	1	0	0	0	1	1	0	0	2	1	0	1	0	1	0	1	4	0	1	0	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 11, 13, 37, 39, 40	
<i>Varanus gouldii</i>	2	0	5 ABC DG	2 EF	0	5	2	0	0	0	1	0	0	0	1	1	0	0	2	1	1	0	0	1	0	0	3	0	0	1	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 43	
<i>Varanus rosenbergi</i>	2	0	5 ABC EG	2 DF	0	5	1	0	0	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	0	5	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39		
<i>Varanus tristis</i>	2	0	5 ABC DG	2 EF	0	4	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	2	0	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 43		
<i>Chamaeleonidae</i>																																																			
<i>Bradypodion pumilum</i>	1	6 ABC DEF	1 G	0	0	2	2	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	2	1	1	0	0	1	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2, 4, 37, 39, 43		
<i>Bradypodion ventrale</i>	1	6 ABC DEF	1 G	0	0	2	3	1	0	0	0	0.5	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	4, 30		

Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size	Life history							Diet					Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference												
		Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>§</sup> traits	Adapters <sup>‡</sup> traits		Total length <sup>b</sup>	SVL <sup>c</sup> %	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>		Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)	
<i>Chamaeleo chamaeleon</i>	4	0	1	2	4	3	2	0	0	1	1	0	0.5	0	0	1	1	0	0	2	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2, 27, 37	
<i>Chamaeleo africanus</i>	4	0	1	2	4	3	2	0	0	0	1	0	0.5	0	0	1	0	0	0	1	1	1	1	0	0	0	4	1	1	0	0	1	3	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	2	2, 27, 82	
<i>Chamaeleo calyptratus</i>	3	1	1	5	0	3	2	0	0	1	1	0	0	0	0	1	1	1	0	3	0	0	0	1	1	1	4	0	1	1	0	1	3	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	2, 14, 37, 39
<i>Trioceros jacksonii</i>	4	0	1	1	5	2	2	0	0	0	0	0.5	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	2, 14			
Agamidae																																																			
<i>Leiolepis belliana</i>	3	0	2	5	0	3	2	0	1	1	1	0	0	0	0	1	0	1	0	2	0	1	1	1	1	1	5	0	0	1	0	1	2	1	0	0	0	0	0	1	0	0	0	1	0	1	2, 16, 37, 38, 39, 50, 53, 54				
<i>Agama agama</i>	4	0	1	0	6	3	2	1	1	1	1	0	0.5	1	0	1	0	1	0	2	1	0	1	0	1	0	3	0	1	0	1	1	3	0	1	0	0	0	0	1	0	0	0	1	0	1	2, 5, 29, 37, 39, 42, 43				
<i>Stellagama stellio</i>	4	0	3	0	4	3	2	0	0	0	1	0	0	0	0	1	1	1	0	3	0	0	0	0	0	1	1	0	1	1	1	4	0	0	0	1	0	0	1	1	1	0	0	0	2	2, 27, 37, 39					
<i>Calotes mystaceus</i>	4	0	1	1	5	3	2	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	4	0	1	0	0	1	2	1	0	0	0	0	0	1	0	0	0	1	0	1	2, 16, 50, 53, 54					
<i>Calotes versicolor</i>	4	0	1	0	6	3	1	0	1	1	1	0	0	0	0	1	1	1	1	4	0	0	1	1	1	0	4	1	1	1	0	1	4	1	0	0	0	0	0	1	0	1	0	1	0	2	2, 16, 17, 21, 34, 37, 38, 43, 50, 52, 53, 54, 56, 59, 62				
<i>Calotes calotes</i>	2	3	4	0	0	4	1	0	0	0	1	0	0	0	0	1	0	1	0	2	0	0	1	1	0	1	4	0	1	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	17, 34, 37, 50, 52				
<i>Psammophilus dorsalis</i>	2	0	5	1	1	3	2	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	1	1	5	0	1	0	1	1	3	1	0	0	0	0	0	1	0	0	0	0	0	0	17, 39, 50, 83, 84				
<i>Pogona barbata</i>	3	1	1	5	0	4	2	0	0	0	1	0	0.5	0	0	1	1	1	0	3	0	0	0	1	0	0	1	0	1	1	0	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	7, 8, 9, 10, 11, 13, 37, 40				
<i>Pogona minor</i>	2	2	5	0	0	3	2	0	0	0	1	0	0	0	0	1	1	1	0	3	1	1	0	1	1	0	4	0	1	0	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0	6, 7, 8, 37, 39, 43				

Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size Total length <sup>b</sup> SVL % <sup>c</sup>	Life history					Diet					Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference															
		Avoiders <sup>‡</sup> traits	Oblivious <sup>‡</sup> traits	Perurbans <sup>‡</sup> traits	Adapters <sup>‡</sup> traits		Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>		Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)				
<i>Tympanocryptis pinguicollis</i>	1	5 ABC EF	1 G	1 D	0	2	2	0	0	0	1	0	0	0	0	0.5	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	1	1	3	0	0	1	0	0	0	0	0	0	0	0	0	0	7, 8, 9
<i>Diporiphora australis</i>	1	5 ABC EF	2 DG	0	0	3	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	4	1	1	1	0	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7, 8, 39, 40		
<i>Rankinia diemensis</i>	2	2 EF	4 ABC G	1 D	0	3	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	0	0	4	0	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 10, 37, 39				
<i>Ctenophorus adelaidensis</i>	2	1 F	5 ABC EG	1 D	0	2	2	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	7	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39				
<i>Ctenophorus ornatus</i>	2	1 F	5 ABC EG	0 D	1	3	2	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	3	0	1	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 37, 39, 43					
<i>Amphibolurus muricatus</i>	4	0	1 G	0	6 ABC DEF	3	2	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	4	1	1	1	1	5	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 9, 10, 11, 39, 40, 85					
<i>Chlamydosaurus kingii</i>	1	6 ABC DEF	1 G	0	0	4	2	0	0	0	1	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	2, 7, 8, 37, 39						
<i>Intellagama lesueurii</i>	4	0	1 G	0	6 ABC DEF	4	1	0	0	0	1	0	0.5	0	0	0	0	1	1	1	0	3	1	0	0	0	0	0	0	1	1	1	0	1	1	4	0	0	1	0	0	0	1	0	0	0	0	7, 8, 10, 11, 12, 13, 40				
Tropiduridae																																																				
<i>Plica plica</i>	1	6 ABC DEF	1 G	0	0	3	2	0	0	1	1	0	0.5	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	2	0	0	0	0	0	1	1	0	1	0	2	2, 37, 39, 42, 43				
Iguanidae																																																				
<i>Brachylophus fasciatus</i>	1	5 ABC EF	2 DG	0	0	4	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	1	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	2	14, 37, 39, 86				
<i>Conolophus subcristatus</i>	1	5 ABC EF	2 DG	0	0	5	2	1	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	14, 37, 39					
<i>Ctenosaura pectinata</i>	4	0	2 DG	0	5 ABC EF	5	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	3	0	1	1	0	0	0	2	0	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	2	18, 37, 39					
<i>Ctenosaura similis</i>	3	0	1 G	6 ABC DEF	0	5	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	2	1	0	0	0	1	0	2	0	0	0	1	1	2	0	0	0	0	0	1	1	0	0	0	1	0	1	2, 37, 39, 43, 75			



Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size	Life history							Diet				Habitat					Habit					Endemic continent/s					Invasive continent/s					Reference											
		Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>§</sup> traits	Adapters <sup>‡</sup> traits		Total length <sup>b</sup>	SVL <sup>c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>
<i>Iguana iguana</i>	1	5 ABC EF	1 G	0 D	1	5	1	0	0	1	1	0	0	0	1	1	1	0	3	1	0	1	1	1	0	0	4	1	1	1	1	1	5	0	0	0	0	1	1	2	0	1	1	0	0	0	0	2	2, 14, 18, 37, 39
<i>Sauromalus hispidus</i>	1	5 ABC EF	2 DG	0	0	3	3	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	37, 39, 87
<i>Leiocephalus schreibersi</i>	4	0	1 G	1 D	5 ABC EF	3	2	0	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	18
<i>Leiocephalus carinatus</i>	4	0	1 G	0	6 ABC DEF	3	2	0	0	0	1	0	0.5	1	0	1	0	0	0	1	1	1	0	1	1	0	4	0	1	0	1	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	18, 37, 38, 39, 42, 43
<i>Phrynosoma cornutum</i>	1	5 ABC EF	1 G	1 D	0	1	3	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	3	0	0	1	1	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	18, 37, 39, 43
<i>Uta stansburiana</i>	1	5 ABC EF	2 DG	0	0	2	2	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	3	0	1	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	18, 37, 39, 43
<i>Sceloporus occidentalis</i>	4	0	2 EG	0	5 ABC DF	2	2	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	4	0	1	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	37, 39, 88
<i>Sceloporus undulatus</i>	4	0	2 EG	0	5 ABC DF	2	3	0	0	0	1	0	0	0	0	1	1	0	0	2	1	1	1	1	0	1	6	0	1	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	18, 25, 37, 39, 43
<i>Liolaemus wiegmanni</i>	1	6 ABC DEF	1 G	0	0	2	2	0	0	0	1	0	0.5	0	0	1	0	1	0	2	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	2, 43	
<i>Basiliscus basiliscus</i>	1	6 ABC DEF	1 G	0	0	4	1	0	0	0	1	0	0.5	1	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	37, 38, 39, 42, 43		
<i>Basiliscus vittatus</i>	1	6 ABC DEF	1 G	0	0	3	1	0	0	1	1	0	0	0	0	1	1	0	0	2	0	0	1	0	0	0	1	1	0	0	0	1	2	0	0	0	0	1	1	2	0	0	0	0	0	0	0	2	18, 37, 39
Dactyloidae																																																	













Species	A-priori traits <sup>†</sup>				Size Total length <sup>b</sup> SVL % <sup>c</sup>	Life history							Diet				Habitat					Habit			Endemic continent/s					Invasive continent/s					Reference															
	Urban category <sup>a</sup> Avoider <sup>‡</sup> traits Oblivious <sup>§</sup> traits Perurban <sup>§</sup> traits Adaptier <sup>§</sup> traits					Gregarious <sup>‡</sup>	Combat/territorial <sup>‡</sup>	Dimorphism <sup>‡</sup>	Reproduction <sup>‡</sup>	Sex specialisation <sup>‡</sup>	Circadian rhythm <sup>‡</sup>	Use urban light <sup>‡</sup>	Venomous <sup>‡</sup>	Invertebrates <sup>‡</sup>	Vertebrates <sup>‡</sup>	Plants/fungi <sup>‡</sup>	Anthro. Waste <sup>‡</sup>	Sum (Diet)	Coastal <sup>‡</sup>	Sandplains <sup>‡</sup>	Grassland <sup>‡</sup>	Scrub <sup>‡</sup>	Woodland <sup>‡</sup>	Lowland <sup>‡</sup>	Slopes <sup>‡</sup>	Sum (Habitat)	Aquatic <sup>‡</sup>	Scansorial <sup>‡</sup>	Cryptozoiic <sup>‡</sup>	Rupicolous <sup>‡</sup>	Terrestrial <sup>‡</sup>	Sum (Habit)	Asia <sup>d</sup>	Africa <sup>d</sup>		Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)			
<i>Parasuta nigriceps</i>	1	5 ABC EF	1 G	1 D	0	4	4	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 90, 191
<i>Parasuta gouldii</i>	2	0	5 ABC EG	2 DF	0	3	4	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0	1	4	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6, 7, 8, 90, 192
<i>Vermicella annulata</i>	2	2 EF	4 ABC G	1 D	0	4	4	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	7	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7, 8, 13, 90, 193	
<i>Vermicella calonotus</i>	2	2 EF	4 ABC G	1 D	0	3	5	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	5	0	0	1	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	6, 7, 8, 90, 194		
<i>Hemiaspis signata</i>	2	0	5 ABC EG	1 F D	1	4	3	0	1	0	0	0	0.5	0	1	0	1	0	1	1	1	1	1	1	7	1	0	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	7, 8, 11, 13, 90, 119, 174, 195		
<i>Echiopsis curta</i>	2	2 EF	4 ABC G	1 D	0	4	3	0	0	0	0	0	0.5	0	1	1	1	0	0	2	1	1	1	1	0	5	0	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 90, 196			
<i>Drysdalia coronoides</i>	2	1 D	5 ABC EG	1 F	0	3	5	0	1	0	0	0	0.5	0	1	0	1	0	0	1	0	0	1	1	4	1	0	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	7, 9, 10, 90, 119, 175, 197			
<i>Drysdalia mastersii</i>	1	5 ABC EF	1 G	1 D	0	3	4	0	1	0	0	0	0.5	0	1	0	1	0	0	1	1	1	1	1	0	5	0	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	7, 8, 11, 90, 198			
<i>Austrelaps superbus</i>	4	0	1 G	3 DEF	3 ABC	5	2	1	1	0	0	0	0.5	0	1	0	1	0	0	1	0	0	1	1	5	1	0	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	7, 8, 9, 10, 90, 175, 199, 200			
<i>Notechis scutatatus</i>	4	0	2 EG	0	5 ABC DF	5	3	0	1	0	0	0	0.5	0	1	0	1	0	0	1	1	1	1	1	7	1	0	1	1	1	4	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	6, 7, 8, 10, 11, 13, 90, 119, 174, 175, 201, 202, 203			
<i>Hoplocephalus bungaroides</i>	1	5 ABC EF	1 G	0 D	1	5	5	0	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	1	3	0	1	0	1	1	3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	7, 8, 11, 90, 119, 204			
<i>Pseudohaje goldii</i>	4	0	2 EG	2 DF	3 ABC	5	5	0	0	0	1	0	0	0	1	0	1	0	0	1	0	0	0	1	2	1	1	0	0	1	3	0	1	0	0	0	1	0	0	0	0	0	0	0	0	5, 97, 119, 205				
Colubridae																																																		
<i>Grayia Smythii</i>	2	1 D	4 ABC G	2 EF	0	5	2	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	3	1	0	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	5, 96, 97, 98, 136, 206				
<i>Ahaetulla nasuta</i>	3	0	1 G	6 ABC DEF	0	5	2	0	0	1	0	0	0	0	1	1	1	0	0	2	0	0	1	1	5	1	1	0	0	1	3	1	0	0	0	0	1	0	0	0	0	0	0	0	0	16, 17, 21, 34, 53, 54, 62, 91, 92, 113, 207				







Species	Urban category <sup>a</sup>	A-priori traits <sup>†</sup>				Size	Life history							Diet				Habitat					Habit				Endemic continent/s					Invasive continent/s					Reference																	
		Avoiders <sup>‡</sup> traits	Oblivious <sup>§</sup> traits	Perurbans <sup>¶</sup> traits	Adapters <sup>  </sup> traits		Total length <sup>b</sup>	SVL <sup>%,c</sup>	Gregarious <sup>d</sup>	Combat/territorial <sup>d</sup>	Dimorphism <sup>d</sup>	Reproduction <sup>e</sup>	Sex specialisation <sup>d</sup>	Circadian rhythm <sup>f</sup>	Use urban light <sup>d</sup>	Venomous <sup>d</sup>	Invertebrates <sup>d</sup>	Vertebrates <sup>d</sup>	Plants/fungi <sup>d</sup>	Anthro. Waste <sup>d</sup>	Sum (Diet)	Coastal <sup>d</sup>	Sandplains <sup>d</sup>	Grassland <sup>d</sup>	Scrub <sup>d</sup>	Woodland <sup>d</sup>	Lowland <sup>d</sup>	Slopes <sup>d</sup>	Sum (Habitat)	Aquatic <sup>d</sup>	Scansorial <sup>d</sup>	Cryptozoiic <sup>d</sup>	Rupicolous <sup>d</sup>	Terrestrial <sup>d</sup>	Sum (Habit)	Asia <sup>d</sup>		Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Endemic)	Asia <sup>d</sup>	Africa <sup>d</sup>	Oceania <sup>d</sup>	Europe <sup>d</sup>	North America <sup>d</sup>	South America <sup>d</sup>	Sum (Invasive)				
<i>Boiga forsteni</i>	1	5 ABC EF	1 G	0 D	1 D	5	4	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	1	1	1	1	0	4	0	1	1	1	1	1	4	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	92, 243, 244
<i>Elaphe climacophora</i>	3	0	1 G	5 ABC DEF	0	5	5	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	2	0	1	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	2, 90, 136, 245		
<i>Coronella brachyura</i>	2	0	4 ABC G	2 EF	1 D	4	5	0	0	0	1	0	0	0	0	1	1	0	0	2	0	0	1	1	1	0	1	4	0	1	0	1	1	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	92, 136, 246, 247			
<i>Pantherophis obsoletus</i>	4	0	1 G	2 EF	4 ABC D	5	3	1	1	1	1	0	0.5	0	0	0	1	0	0	1	1	1	1	1	1	1	1	7	1	1	0	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	18, 25, 26, 90, 104, 248, 249			
<i>Pantherophis guttatus</i>	4	0	2 DG	2 EF	3 ABC	5	5	0	1	0	1	0	0.5	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	2	0	1	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	18, 25, 26, 90, 100, 104, 133, 250		
<i>Cemophora coccinea</i>	3	0	2 DG	5 ABC EF	0	4	5	0	0	0	1	0	0.5	0	0	0	1	0	0	1	0	1	1	0	1	0	0	3	0	0	1	0	1	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	18, 26, 136, 251			
<i>Lampropeltis calligaster</i>	1	5 ABC EF	1 G	1 D	0	5	3	0	1	1	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	3	0	0	1	1	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	18, 25, 90, 133, 252				
<i>Lampropeltis triangulum</i>	3	0	1 G	5 ABC EF	1 D	5	2	0	1	0	1	0	0.5	0	0	0	1	0	0	1	1	1	1	1	1	1	1	7	1	0	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	18, 25, 90, 100, 133, 253			
<i>Lampropeltis getula</i>	4	0	2 EG	2 DF	3 ABC	5	3	0	1	1	1	0	0.5	0	0	0	1	0	0	1	1	0	1	1	1	1	5	1	0	1	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	18, 25, 90, 100, 133, 254				
<i>Ptyas mucosa</i>	4	0	1 G	1 D	5 ABC EF	6	2	0	1	1	1	0	0.5	0	0	0	1	0	0	1	1	1	1	1	1	1	7	1	1	0	0	1	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	16, 17, 21, 34, 53, 54, 62, 90, 91, 92, 101, 133, 255				
<i>Opheodrys aestivus</i>	1	6 ABC DEF	1 G	0	0	4	2	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	3	1	1	0	0	1	3	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	18, 25, 26, 90, 133, 256				
<i>Coluber constrictor</i>	4	0	1 G	2 EF	4 ABC D	5	3	0	1	1	1	0	0	0	0	1	1	0	0	2	0	0	1	1	1	0	1	4	1	1	0	1	1	4	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	18, 25, 90, 133, 257				
<i>Elachistodon westermanni</i>	1	6 ABC DEF	1 G	0	0	4	5	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	2	0	1	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	17, 92, 119, 258, 259					
<i>Amphiesma stolatum</i>	3	0	1 G	6 ABC DEF	0	4	4	0	0	1	1	0	0	0	0	1	1	0	0	2	1	0	1	0	1	1	5	1	0	1	0	1	3	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	16, 17, 21, 34, 54, 59, 91, 92, 94, 95, 133, 260				







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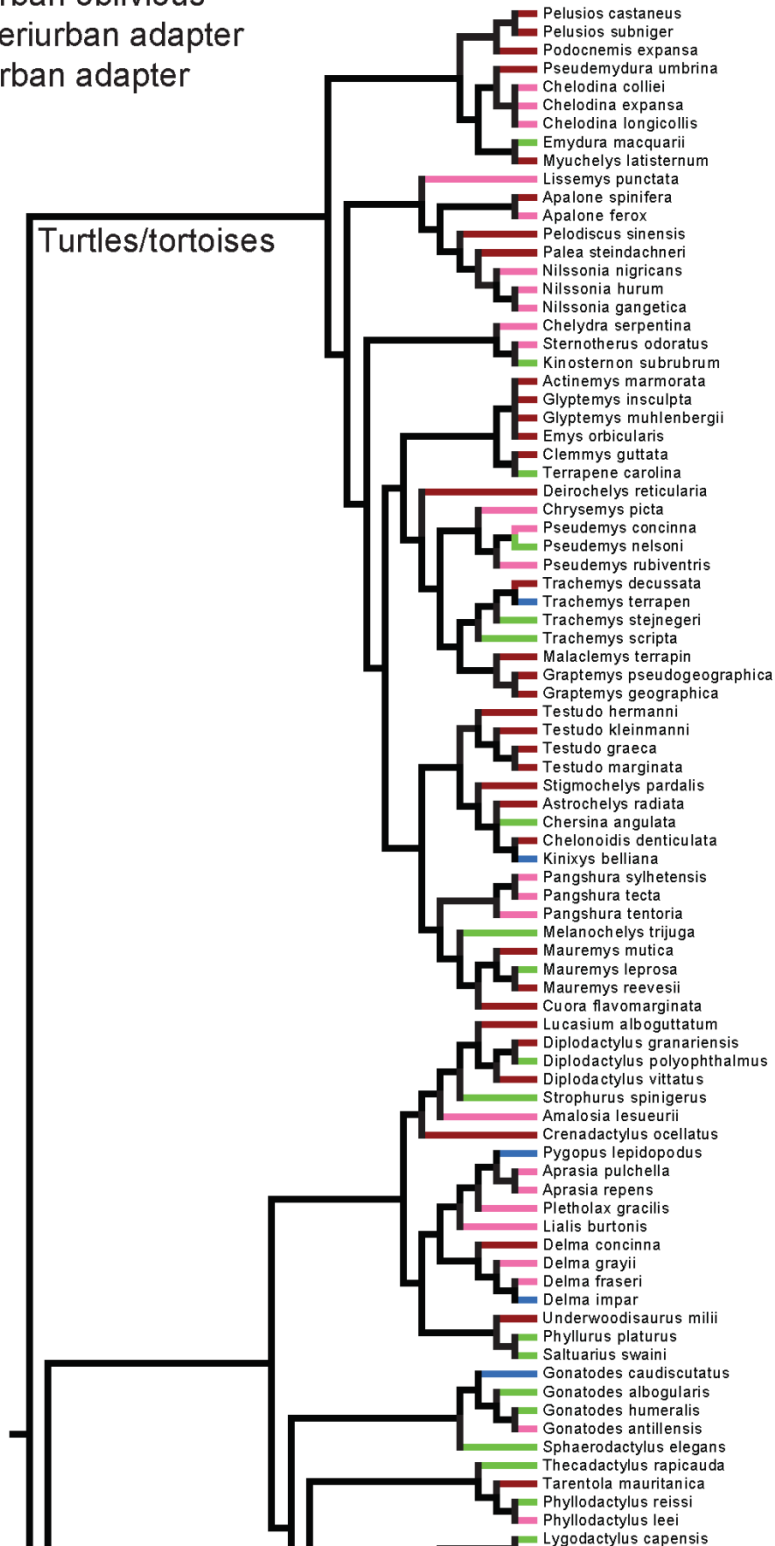


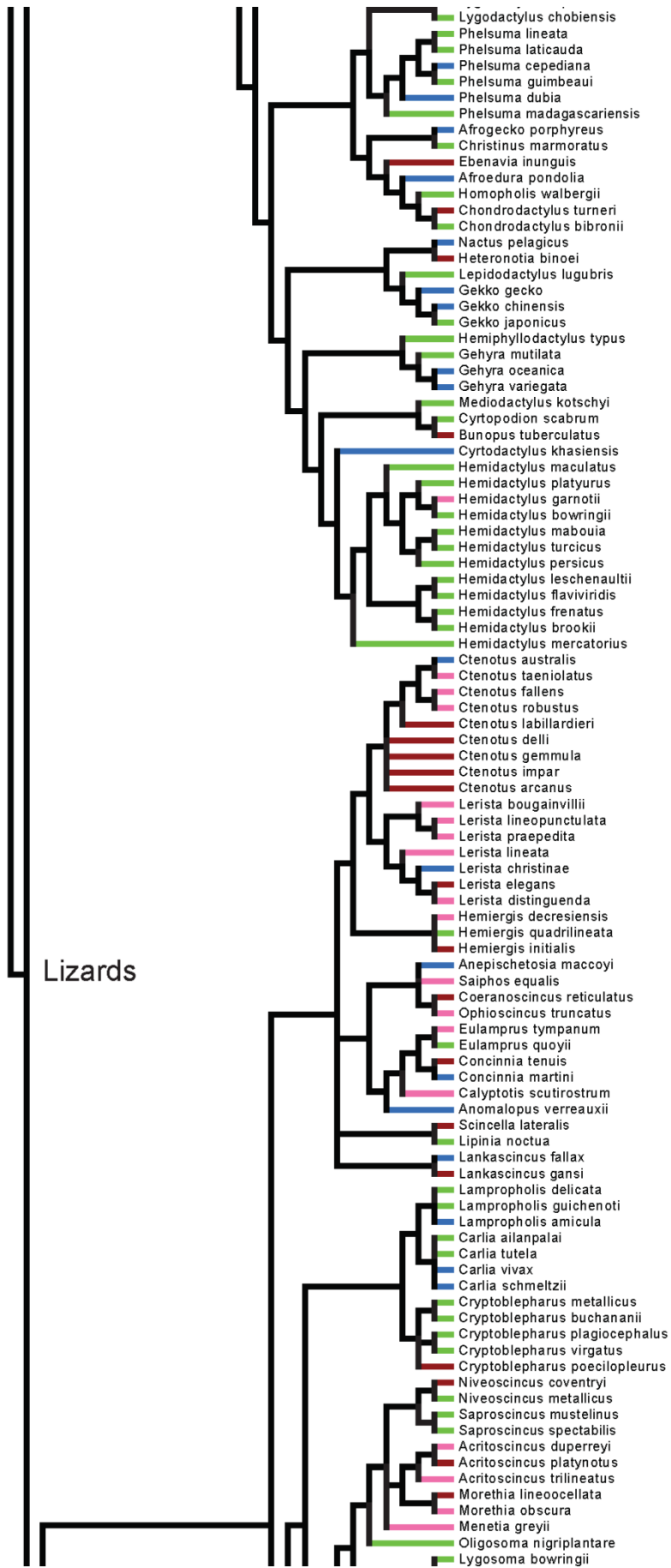
Appendix 2. Phylogeny used for analysis comparing the degree of urban adaptation for turtles/tortoises, lizards and snakes (Chapter 2)

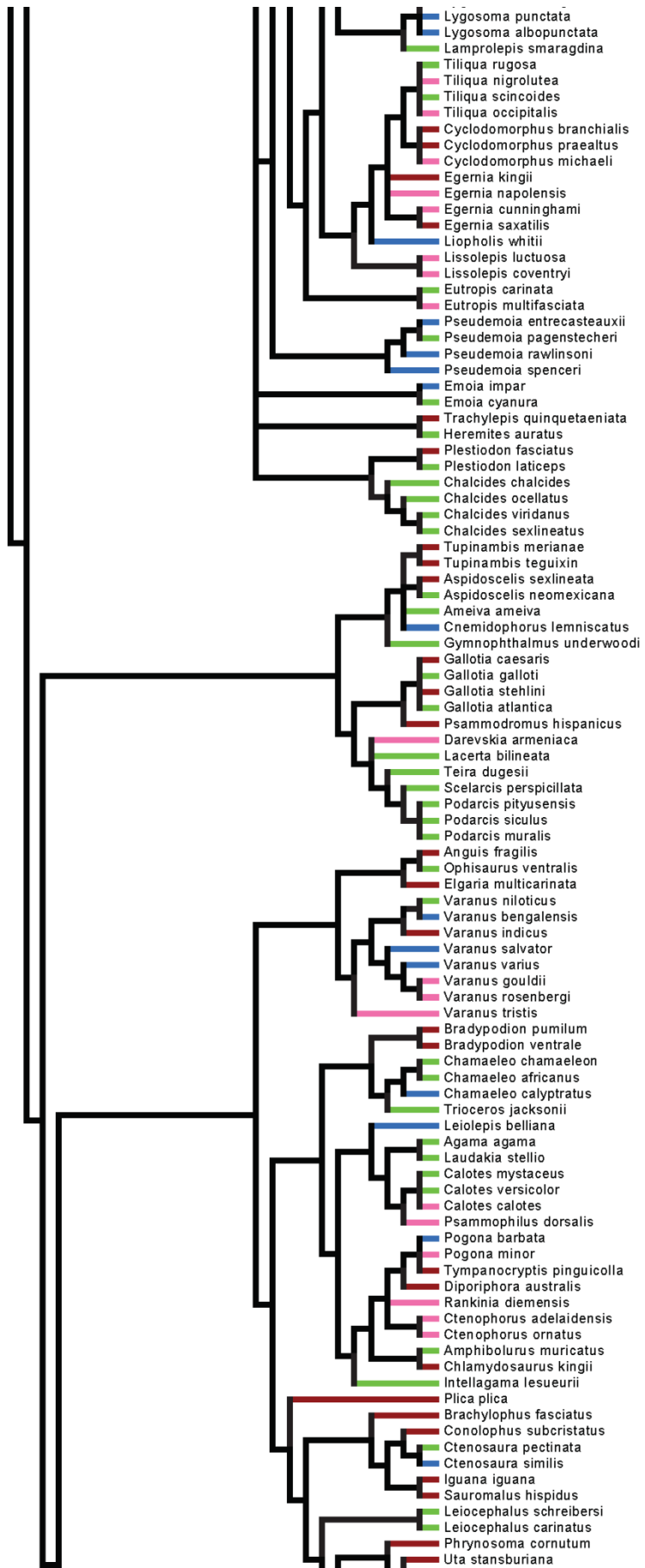
References for this appendix are separate from the thesis, and are presented in 0.

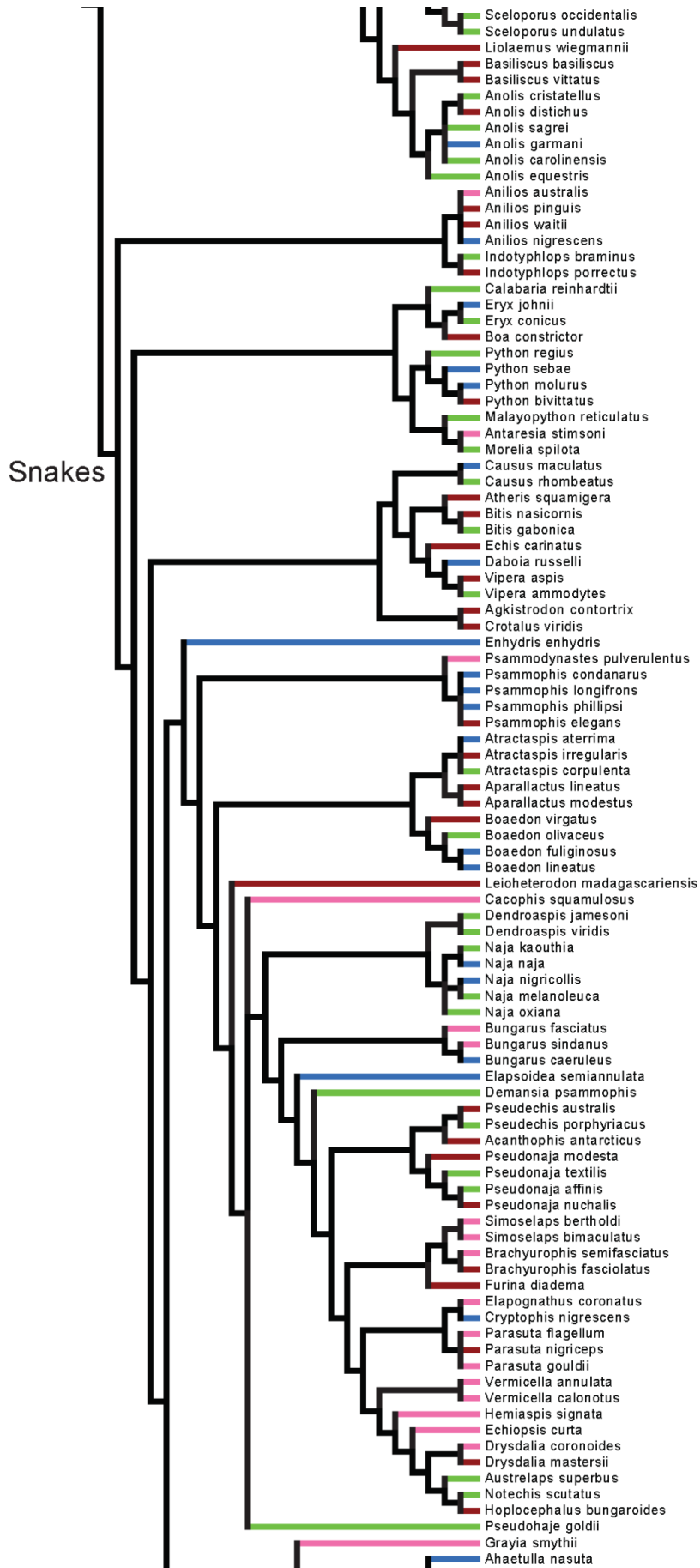
Key

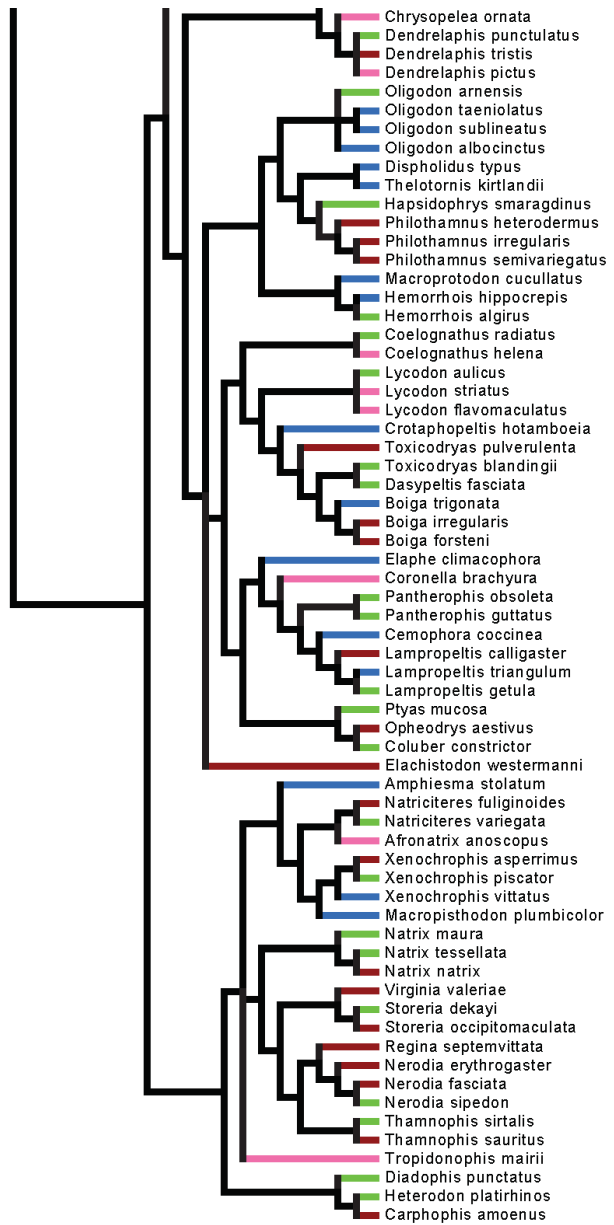
- Urban avoider
- Urban oblivious
- Periurban adapter
- Urban adapter











## Appendix 2.1      References for Appendix 2.

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### Appendix 3. Additional methods descriptions

As the chapters in this thesis are presented as standalone manuscripts, some of the methods have been omitted. Here, I present the additional methods that were unable to be included in the manuscripts.

#### Appendix 3.1 Correlation analysis (Chapter 2)

To test for multicollinearity between independent variables within the dataset, I conducted a correlation matrix in STATISTICA 7.1 (Statsoft Inc., 2006) for the standardised FICs following phylogenetic correction (Table A.3.1.1).

Table A.3.1.1. Correlation matrix ( $r$ ) for FICs of independent variables in Chapter 2. Significant values ( $p < 0.05$ ) are indicated in bold.

Independent variable	Circadian rhythm	Combat/territorial	Sum (Diet)	Dimorphism	Sum (Endemic)	Gregarious	Sum (Habitat)	Sum (Habit)	Sum (Invasive)	Reproduction	Sex specialisation	SVL%	Total length	Use urban light	Venomous
Combat/territorial	0.08	1.00													
Sum (Diet)	-0.04	-0.05	1.00												
Dimorphism	-0.03	<b>0.12</b>	-0.07	1.00											
Sum (Endemic)	-0.02	0.02	-0.01	-0.02	1.00										
Gregarious	0.08	<b>-0.17</b>	0.07	<b>-0.18</b>	0.09	1.00									
Sum (Habitat)	-0.04	<b>-0.16</b>	0.03	<b>-0.19</b>	0.01	<b>0.11</b>	1.00								
Sum (Habit)	-0.01	<b>-0.11</b>	0.06	-0.07	0.08	<b>0.21</b>	<b>0.21</b>	1.00							
Sum (Invasive)	-0.03	<b>-0.16</b>	<b>0.15</b>	<b>-0.16</b>	0.09	<b>0.17</b>	<b>0.12</b>	0.09	1.00						
Reproduction	-0.02	-0.02	-0.04	0.03	-0.04	-0.03	-0.01	-0.04	-0.01	1.00					
Sex specialisation	0.09	<b>0.10</b>	-0.06	0.05	<b>0.15</b>	0.02	0.07	0.01	<b>0.18</b>	0.00	1.00				
SVL%	<b>-0.11</b>	-0.09	-0.03	-0.09	0.02	0.00	<b>0.15</b>	0.07	-0.04	-0.08	-0.04	1.00			
Total length	<b>0.10</b>	0.09	<b>-0.12</b>	0.02	-0.04	-0.05	0.01	-0.04	-0.02	-0.06	<b>0.12</b>	<b>-0.22</b>	1.00		
Use urban light	<b>0.13</b>	<b>-0.12</b>	-0.04	-0.04	0.03	<b>0.17</b>	0.08	0.01	<b>0.21</b>	0.03	0.03	-0.03	-0.06	1.00	
Venomous	0.00	0.03	-0.04	<b>0.15</b>	-0.04	-0.01	<b>-0.13</b>	-0.04	0.01	0.09	0.05	-0.07	0.01	-0.09	1.00

## Appendix 3.2 Additional accessed data (Chapter 3)

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### Appendix 3.3 Dugite GPS and VHF radiotelemetry (Chapter 4)

In Chapter 4 I investigated the spatial use of dugites in Perth to assess if these successful urban adapters are negatively affected by urban fragmentation and translocation. I attached telemetry packages to a total of 10 snakes, either hand captured by myself ( $n = 2$ ) or by licensed reptile removers ( $n = 8$ ) with permission by the Western Australian Parks and Wildlife Service for me to use the animals in this study.

I restrained snakes by placing their heads and as much of the body as possible in a 1 m length of clear vinyl tubing of varying diameter to suit each snake's girth. A laboratory assistant then held the snake in the tube to minimise movement, while I made two subcutaneous incisions to the 18<sup>th</sup> and 35<sup>th</sup> subcaudal scales with a size 1 half-curved reverse cutting needle. This allowed for the telemetry package to be placed as low on the tail as possible to prevent damaging internal reproductive organs and to ensure the width of the telemetry package was smaller than the girth of the snake at its widest point. Needles were sterilised prior to use with 70% ethanol, and a new needle was used for each snake. For each incision, the needle was pre-threaded with a piece of 0.5 x 1.3 mm (ID x wall thickness) silicone tubing threaded with 0.4 mm thick 15 kg strength monofilament nylon fishing line through the tubes attached to the telemetry packages. As the needle was passed under the subcaudal scales and through to the other side of the tail, the fishing line pulled the silicone tubing through. The fishing line was then tied with an anchor hitch knot, and the snakes were provided non-steroidal anti-inflammatory relief (Metacam; 5mg/ml injection at the incision site). The entire process, from restraining the snakes in vinyl tubing to tying the knots, took less than 10 min per snake. A series of photographs of the procedure is presented in Figure A.3.3.1.

Resident snakes ( $n = 2$ ) were free-living individuals, captured in urban bushland and released back at the initial encounter site. 'Problem' snakes ( $n = 8$ ) were captured on private properties; four 'problem' snakes were within 200 m of suitable bushland, where they were released; another four 'problem' snakes did not have suitable bushland within 200 m, and were translocated at least 3 km away to a new patch of bushland that was unconnected by any natural corridors to the initial encounter site (Table A.3.3.1).

I checked each snake within 2 days of telemetry package attachment to ensure the procedure was successful, and then at least one per week after the first check. During checks, I verified each animal's location by remotely downloading the GPS data via Bluetooth, which had a 5 – 20 m range depending on whether the snake was above or under the ground. I then took a manual GPS fix with a handheld GPS device to add to the dataset. I also used this time to observe the snakes, whenever possible, and ensure they were moving unimpeded by the trackers (e.g. Figure A.3.3.2).

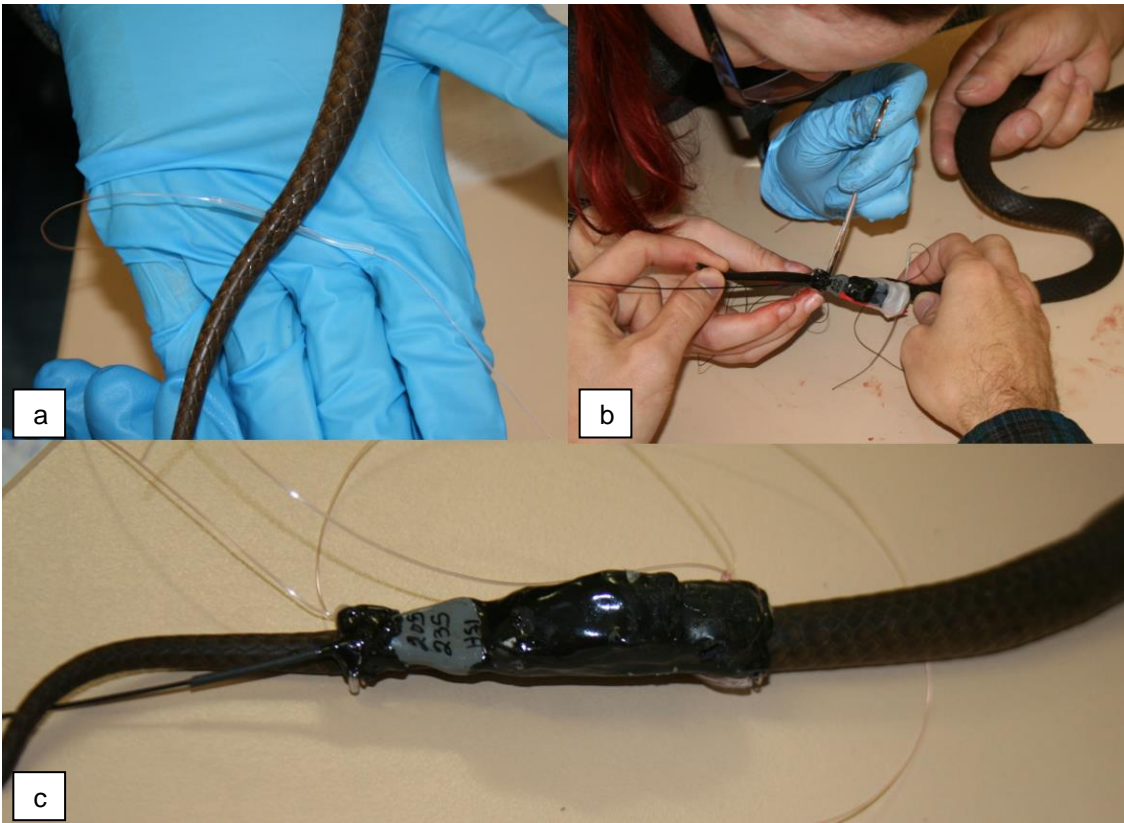


Figure A.3.3.1. Attachment of telemetry package (heat-shrink sealed) onto a dugite tail: a) position of the silicone tubing threaded with fishing line; b) inserting the second silicone tube and anchoring the telemetry package; and c) anchored telemetry package, just prior to trimming the fishing line – the snake was then immediately taken to its release location.



Figure A.3.3.2. a) Released dugite (snake #2) following telemetry package attachment; b – d) shows the snake successfully traversing a metal fence unimpeded by the external package attached.

## Appendix 3.4 Road field experiments (Chapter 5)

In Chapter 5 I used online surveys, field experiments, and mathematical modelling to predict the likelihood that a Western Australian motorist would: a) rescue; b) intentionally strike; and c) accidentally strike reptiles on roads. I conducted the field experiment on Hope Road (-32.084478, 115.827786) in the residential suburb of Bibra Lake, 6163.

To assess motorist responses, I used three lifelike reptile models (Figure A.3.4.1):

- 1) rubber 'bobtail', 0.35 m long, created by casting a bobtail carcass in a plaster mould and filling with silicone, painted brown with white dorsal stripes to mimic a bobtail;
- 2) 'long snake': 0.37 m long toy rubber snake, with a sinuous shape painted brown to mimic a dugite; and
- 3) 'coiled snake': 0.37 m long toy rubber snake in a 0.13 m diameter coil painted brown to mimic a dugite.



*Figure A.3.4.1. Rubber/plastic models used in the road field experiment: a) from top: bobtail, long snake and coiled snake; b) example of model placement on the study road, Hope Road, Bibra Lake 6153.*

All models were tested for road safety by placing them in a parking lot and consecutively running them over 10 times with a Hyundai i30. As the models all retained their shape and did not do any damage to the vehicle, they were considered suitable for the field experiment.

I conducted the study during October 2015 at one location on Hope Road during non-peak traffic hours (10 am – 1 pm) during sunny days with good visibility on the road. I sat 20 m away from the models on the grassed verge, obscured from motorists behind a tree. A field assistant sat 150 m up the road, also obscured by a tree, and used an ultra-high frequency citizens band wireless handheld radio to notify me when a vehicle was travelling alone and could be included in the dataset.

## Appendix 3.4.1 Online survey

- 1) Do you hold (or have you held in the past) a valid Australian driver's license? This includes P-plates.

Response options - check box (pick one): Yes; No.

- 2) Do you have P-plates?<sup>1</sup>

Response options - check box (pick one): Yes, Red Ps; Yes, Green Ps; No, I have a full license.

- 3) What is your gender?

Response options - check box (pick one): Male; Female; Other/prefer not to say.

- 4) What is your age?

Response options - text box, respondent to enter their response.

- 5) Are you an animal carer/relocater?

Response options - check box (pick one): Yes; No.

- 6) On a scale from 1-10, where 1 is not concerned at all, and 10 is very upset, how concerned would you be for the welfare of the following animals if you were involved in a collision with: Cat; Dog; Rabbit; Fox; Bird; Bobtail/shingleback lizard; Turtle; Snake; Kangaroo; Other small native mammal, such as a bandicoot or possum.

Response options - respondent to select a number between 1-10 for each animal.

- 7) On a scale from 1-10, where 1 is not concerned at all, and 10 is very upset, how concerned would you be for potential damage to your vehicle if you were involved in a collision with: Cat; Dog; Rabbit; Fox; Bird; Bobtail/shingleback lizard; Turtle; Snake; Kangaroo; Other small native mammal, such as a bandicoot or possum.

Response options - respondent to select a number between 1-10 for each animal.

- 8) On a scale from 1-10, where 1 is not concerned at all, and 10 is very upset, how concerned would you be for your own safety if you were involved in a collision with: Cat; Dog; Rabbit; Fox; Bird; Bobtail/shingleback lizard; Turtle; Snake; Kangaroo; Other small native mammal, such as a bandicoot or possum.

Response options - respondent to select a number between 1-10 for each animal.

- 9) On a scale from 1-10, where 1 is not at all likely, and 10 is very likely, what is the likelihood that you would stop and rescue on the road/roadside: Cat; Dog; Rabbit; Fox; Bird; Bobtail/shingleback lizard; Turtle; Snake; Kangaroo; Other small native mammal, such as a bandicoot or possum.

Response options - respondent to select a number between 1-10 for each animal.

- 10) Have you ever rescued an animal from the road/roadside?

Response options - check box (pick one): Yes; No.

11) What kinds of animals have you rescued from the road/roadside? (if response to 10 = Yes)

Response options - check box (select all that apply): Cat; Dog; Rabbit; Fox; Bird; Bobtail/shingleback lizard; Turtle; Snake; Kangaroo; Bandicoot; Possum; Other (please state).

12) Where did you take the animal/s you rescued? Select all that apply. You may also list the names of centres, suburbs, or your affiliations if you wish.

Response options - check box (select all that apply): Vet; Cat Haven; Ranger/council pound; Cared for it yourself; Relocated away from the road in nearby land; Wildlife rehabilitation centre; Other (please state).

13) How often do you see the following animals (dead or alive) on roads? Cat; Dog; Rabbit; Fox; Bird; Bobtail/shingleback lizard; Turtle; Snake; Kangaroo; Other small native mammal, such as a bandicoot or possum.

Response options - respondent to select one for each animal: Never; At least once per year; At least once per month; At least once per week; Every day.

<sup>1</sup>P-plates refers to an Australian provisional driving license, for motorists with <2 years' experience driving. In Western Australia, Red P-plates are given to motorists with <6 months' experience driving; they then graduate to green P-plates until they have had their license for 2 years.





## Appendix 3.5 Reptile identification survey (Chapter 6)

Have a good look at the reptiles in the display cases numbered 1-5. When you are confident of your answer, please fill out the following for each reptile:

	1	2	3	4	5
What is its name?					
Is it a snake?					
Is it venomous?					

What is your gender?  Male  
 Female  
 Other/Prefer not to say

What is your age?  Under 18  40-50  
 18 – 25  50-60  
 25-30  60-70  
 30-40  Over 70

What suburb (or region if outside of Perth) do you live in?  Perth Suburb \_\_\_\_\_  
 Outside of Perth \_\_\_\_\_  
 Outside of Western Australia \_\_\_\_\_

Do you currently keep reptiles as pets?  Yes  
 No, but I used to  
 No, never

Thank you for completing our survey! Once you are finished please fold your survey and place it in the ballot box.

## Appendix 4. Publications arising from this research

### Appendix 4.1 Peer-reviewed papers arising from this research

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2018) Impacts of translocation on a large urban-adapted venomous snake. *Wildlife Research*, *in press*.

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2018) What traits influence degree of urban adaptation? A global analysis of reptiles. *Journal of Zoology*, *in review*.

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2018) Surveying attitudes towards reptiles on roads: questionnaire responses do not directly translate to behavioural action. *Frontiers of Ecology and Evolution*, *in review*.

**Wolfe, Ashleigh K.**, Philip W. Bateman, and Patricia A. Fleming. (2017) Does urbanization influence the diet of a large snake? *Current Zoology*, 1-8, *advance access*. doi: 10.1093/cz/zox039.

Bateman, Philip W., Patricia A. Fleming, and **Ashleigh K. Wolfe**. (2016) A different kind of ecological modelling: the use of clay model organisms to explore predator-prey interactions in vertebrates. *Journal of Zoology* 301, 251-262. doi: 10.1111/jzo.12415.

Published papers have been attached.

### Appendix 4.2 Conference presentations arising from this research

**Wolfe, Ashleigh K.**, and Philip W. Bateman. (2017) Can the average Western Australian differentiate between harmless and venomous endemic reptiles? Australian Society of Herpetologists, Fairbridge, Australia.

**Wolfe, Ashleigh K.**, and Philip W. Bateman. (2017) Management of reptile predators using models at proxies. WA Wetland Management Conference, Bibra Lake, Australia.

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2016) A review of factors affecting reptile successes in urban areas. Ecological Society of Australia, Fremantle, Australia.

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2016) GPS tracking dugites (*Pseudonaja affinis*) in Perth via external tail attachment: an effective alternative to implants? Australian Society of Herpetologists, Launceston, Australia.

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2016) Ontogenetic diet shifts in dugites (*Pseudonaja affinis*) across time and space. Australian Society of Herpetologists, Launceston, Australia.

**Wolfe, Ashleigh K.**, Patricia A. Fleming, and Philip W. Bateman. (2015) Assessing intentional motor vehicle strikes of reptiles. Australian Wildlife Management Society, Perth, Australia.

- Wolfe, Ashleigh K.** (2015) Reptile rehabilitation admissions in a city, using volunteer records from wildlife centres. Australian Wildlife Management Society, Perth, Australia.
- Wolfe, Ashleigh K.** (2015) Causes of reptile death in a city using volunteer records from wildlife rehabilitation centres. International Ethological Congress – Behaviour 2015, Cairns, Australia.
- Wolfe, Ashleigh K.,** Philip W. Bateman, and Patricia A. Fleming. (2015) The ecology of Perth's urban reptiles using a snake and skink as models. Australian Society of Herpetologists, Eildon, Australia.
- Wolfe, Ashleigh K.,** Philip W. Bateman, and Patricia A. Fleming. (2014) Perth's urban reptile ecology: does living in the city affect reptile diet? Royal Society of Western Australia Centenary Postgraduate Symposium, Perth, Australia.

## Article

# Does urbanization influence the diet of a large snake?

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## Abstract

Urbanization facilitates synanthropic species such as rodents, which benefit the diets of many predators in cities. We investigated how urbanization affects the feeding ecology of dugites *Pseudonaja affinis*, a common elapid snake in south-west Western Australia. We predicted that urban snakes: 1) more frequently contain prey and eat larger meals, 2) eat proportionally more non-native prey, 3) eat a lower diversity of prey species, and 4) are relatively heavier, than non-urban dugites. We analyzed the diet of 453 specimens obtained from the Western Australian Museum and opportunistic road-kill collections. Correcting for size, sex, season, and temporal biases, we tested whether location influenced diet for our 4 predictions. Body size was a strong predictor of diet (larger snakes had larger prey present, a greater number of prey items, and a greater diversity of prey). We identified potential collection biases: urban dugites were relatively smaller (snout-vent length) than non-urban specimens, and females were relatively lighter than males. Accounting for these effects, urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. Other urban-adapted carnivores appear to benefit from urbanization through increased food supplementation, but we found the opposite of this: urban dugites were less likely to contain a meal, and their meals were smaller, indicating they did not make greater use of synanthropic species than was evident for non-urban snakes. In contrast to other carnivores, snakes do not appear to fit a consistent directional pattern for size differences between urban and non-urban populations.

**Key words:** adaptation, dissection, feeding ecology, reptile.

Urbanization is generally perceived as a negative influence on biodiversity (McKinney 2006). Urbanization can be a strong driver of landscape change, and the disturbance associated with cities may cause local flora and fauna extinctions, where isolation of refugia and discrete habitat boundaries lead to mortality of sensitive species (e.g., Fahrig 2001; Williams et al. 2005; Cushman 2006; Garden et al. 2007). A decline of sensitive native species in urban areas can, therefore, lead to biotic homogenization and the dominance of few usually invasive species, such as synanthropic rodents and birds (Blair 1996; McKinney 2008). Coupled with anthropogenic food sources and domestic animals, these invasive species can increase prey availability for predators. Many predators, native or introduced, therefore appear to thrive in and around cities (Roth and Lima 2003; Chace and Walsh 2006; Bateman and Fleming 2012).

Many snake species have persisted in or invaded urban areas. For example black-necked spitting cobras *Naja nigricollis* in Africa (Luiselli and Angelici 2000; Akani et al. 2002), carpet pythons *Morelia spilota mcdowelli* (Fearn et al. 2001) and tiger snakes *Notechis scutatus* (Butler et al. 2005; Hamer 2011) in Australia, as well as rock pythons *Python sebae* (Reed and Krysko 2013), corn snakes *Elaphe guttata* and DeKay's snakes *Storeria dekayi wrightorum* in the USA (Neill 1950). Despite their prevalence, there have been few descriptions of urban snake behavior and feeding ecology.

Differences in prey diversity and food availability can influence snake body size in urban areas. For example, invasive brown tree snakes *Boiga irregularis* on Guam feed on different prey in urban and non-urban areas, with urban snakes growing larger due to a greater range of available prey compared with non-urban sites,



**Figure 1.** Collection locations of dugite *P. affinis* specimens used for this study: a) urban specimens (around the Perth metropolitan area where human population density exceeded 500 persons·km<sup>2</sup> at the time of the nearest Australian Bureau of Statistics census) are indicated by black dots, non-urban specimens are shown with grey squares; distribution of dugites containing prey in gut contents for b) urban and c) non-urban specimens. Legend: cross—non-native rodents; diamond—native rodents; plus—reptiles. Study location with reference to the wider Australian continent is shown in center right.

where there have been local prey extinctions recorded as a result of predation pressure (Savidge 1988). By contrast, *P. sebae* in suburban areas in Nigeria supplement their diet with synanthropic rats and domesticated poultry, but are significantly smaller than conspecifics from non-urban environments: the authors did not suggest any reason for this difference (Luiselli et al. 2001). In the present study, we investigate the effect of urbanization on the feeding ecology of the dugite *Pseudonaja affinis*, Elapidae (Günther 1872). This species is one of the most common snakes of south-west Western Australia, thriving in woodlands, heaths, and urban environments (Chapman and Dell 1985), possibly *via* supplementation from the spread of the invasive house mouse *Mus musculus* (Shine 1989). Although the house mouse is a small species, it is larger than the majority of urban lizards in Western Australia (How and Dell 2000), and its communal nesting and prolific breeding (e.g., Gomez et al. 2008; Vadell et al. 2010) appears to provide dugites with frequent opportunities to eat multiple individuals (and therefore larger meals). Dugites are regarded as one of the best urban-adapted large-bodied reptiles in Australia (How and Dell 1993), which makes them ideal model animals for urban/non-urban comparisons. Assuming dugites benefit from the presence of synanthropic rodents, then we make the

following predictions for comparisons between urban and non-urban dugite specimens:

1. Urban dugites will more frequently contain prey than non-urban dugites, and have eaten larger meals.
2. Urban dugites will eat proportionally more introduced prey than non-urban dugites.
3. Urban dugites will eat a less diverse range of prey species than non-urban dugites.
4. Urban dugites will be relatively larger than non-urban dugites.

## Materials and Methods

### Study species

The dugite is a highly venomous elapid distributed across the southern part of Western Australia and parts of South Australia (Figure 1a). Dugites are diurnal, active-foraging predators that grow up to 2 m in total length and can travel at least 1.5 km/day (A.K.W., unpublished data). The diet of dugites was explored and compared with congeners by Shine (1989) who examined 179 museum specimens, although he did not consider differences across space or time.

**Table 1.** Length and body mass measurements for dugites by location and sex for dugite specimens with complete data

Sex ( <i>n</i> urban, non-urban)	urban		non-urban	
	mean SVL ± SE (range), cm		mean body mass ± SE (range), g	
Females (44, 75)	90.8 ± 28.0 (42.4–132.0)	98.0 ± 25.5 (41.5–156.0)	252.2 ± 191.0 (16.6–604.9)	287.7 ± 200.9 (19.6–1170.0)
Males (35, 70)	93.0 ± 28.7 (44.3–167.8)	104.3 ± 24.5 (40.0–168.5)	296.1 ± 335.6 (16.1–1940.0)	336.1 ± 312.3 (18.0–1800.0)
Undetermined sex* (116, 113)	27.4 ± 4.7 (19.6–61.0)	28.1 ± 11.3 (16.1–136.0)	7.3 ± 8.0 (2.9–89.0)	15.1 ± 75.1 (2.3–800.0)

\*Of the 229 specimens for which we were unable to determine sex, 226 were juveniles, SVL <40cm.

Unfortunately, because the specimens attributed to that study were disposed of we were unable to revisit that dataset.

### Dissections

We dissected 568 dugites, of which 548 were from the Western Australian Museum (WAM) (specimens collected between 1910 and 2015 from across the entire known Western Australian range of the species) and 20 were opportunistically collected as road-kill (collected 2014–2015). Of the 568 dissected dugites, we were able to obtain complete data (location, snout-vent length [SVL], wet mass of the preserved snake after draining excess preservative liquid [ $M_b$ ], and collection date) for 453 specimens, of which 112 dugites contained prey. The number of individuals included in each analysis therefore varies accordingly.

Prior to dissections, we recorded SVL,  $M_b$ , and sex (for all specimens >40 cm SVL; juveniles,  $n = 226$ , could not be sexed with confidence even upon dissection) (Table 1). Each specimen was opened via a ventral incision at the subcaudal third, the stomach located and removed. Whole stomachs (from the end of the esophagus to the beginning of the small intestine) were extracted, weighed complete, cut open lengthwise, and examined for any prey contents, and then reweighed empty. Prey items were classified to the lowest possible taxonomic group; prey items were identifiable to species (66%), genus (6%), and family (28%), which were used for statistical analyses. We identified 20 native prey species (129 prey items) and 3 introduced species (82 prey items) (see Table 2 for classification). As many of the prey items were partially digested, we counted the total number of prey items and recorded total wet mass of all preserved prey items (after draining excess preservative) ( $M_{prey}$ ) contained within each stomach. Items such as sand, rocks, and leaves were considered incidental gut contents and excluded from prey mass calculations. The raw data for this study is provided in Supplementary Appendix 1.

### Classification of urban and non-urban sites

Collection dates and GPS coordinates for each snake were available for all road-killed specimens and 89% of museum specimens ( $n = 509$ ) (Figure 1a). To account for urban growth over time, we categorized these GPS coordinates as either “urban” or “non-urban” sites using data for the closest census date (Australian Bureau of Statistics census dates: 1911; 1933; 1947; 1955; 1962; 1969; 1974; 1982; 1988; 1993; 1997; 2001; and 2011) (see Supplementary Appendix 2 for references) to calculate the number of people per square kilometer, classed by local government areas. All locations that had >500 persons·km<sup>-2</sup> were considered urban (only sites within the Perth metropolitan region reached this population density), and all other coordinates were considered non-urban (Figure 1a). To determine if there was a skew in collection dates between urban and non-urban sites, we performed a 2-way chi-squared analysis comparing collection locations across each decade ( $n = 10$ ) for all specimens with complete records ( $n = 453$ ).

### Analyses

Over half of the museum specimens we dissected had information about the collector (338 unique collectors: general public = 37 specimens, scientist = 205 specimens, undetermined = 211 specimens). To test for collection bias in the specimens included in this analysis ( $n = 453$  specimens with complete data records), we used a multiple regression to compare body size (log-SVL) as the dependent variable with location (urban = 0, non-urban = 1) and collector (general public = 0, undetermined = 0.5, scientist = 1). Relatively larger (SVL) snakes were collected from non-urban areas ( $F_{2,450} = 23.25$ ;  $P < 0.001$ ) (Table 1), and by scientists ( $t_{450} = 5.51$ ;  $P < 0.001$ ). As it is not possible to distinguish between differences in population demographics or collection bias, we were unable to determine if there were any real differences in body size between locations. Because body size is known to influence diet in snakes (e.g., Shine 1989; King 2002; Bryant et al. 2012; Miranda et al. 2017), body size was, therefore, accounted for by including log-SVL as a covariate in all analyses. There were also sex differences in body size (of 453 specimens with complete data: female = 119, male = 105, undetermined sex = 229) (Table 1), with females being smaller than males ( $M_b$ :  $F_{1,492} = 106.5$ ;  $P < 0.001$ ; SVL:  $F_{1,492} = 107.4$ ;  $P < 0.001$ ). Therefore, the sex of specimens (female = 0, undetermined = 0.5, male = 1) was included in analyses to account for this sex bias that could influence diet. We predicted that animals would be more active and therefore have a greater mass of food in their stomachs for warmer months; therefore season (winter = 0, autumn/spring = 0.5, summer = 1) was included as an independent factor in analyses. Furthermore, we predicted there would be a decrease in prey diversity or availability over time due to homogenization of the landscape due to anthropogenic influences, and therefore included collection date (year) as an independent factor in analyses.

### Prediction 1: Urban dugites will more frequently contain prey than non-urban dugites, and have eaten larger meals.

To determine if there was an effect of urbanization on the proportion of specimens ( $n = 453$ ) containing prey items, we performed a logistical multiple regression with stomach contents (empty = 0, containing prey = 1) as dependent variable, and location, sex, body size (log-SVL), season, and collection date as independent variables.

To determine if there was an effect of urbanization on the total mass of prey eaten ( $n = 112$  dugites containing prey), we performed a multiple regression with log- $M_{prey}$  as the dependent variable, and location, sex, body size, season, and collection date as independent variables.

### Prediction 2: Urban dugites will eat proportionally more introduced prey than non-urban dugites.

To determine whether there was an effect of location on diet composition for  $n = 112$  dugites containing prey, we performed a 2-way

**Table 2.** Diet of dugites collected from urban and non-urban locations

Taxon	Native (N) or introduced (I)	Urban	Non-urban
Mammals, Rodents ( $n = 4$ taxa)			
<i>Mus musculus</i>	I	9	71
<i>Notomys mitchelli</i>	N	–	2
<i>Rattus norvegicus</i>	I	1	1
<i>Rattus rattus</i>	I	2	–
Reptiles ( $n = 28$ )			
Geckos ( $n = 6$ taxa)			
<i>Christinus marmoratus</i>	N	3	13
<i>Diplodactylus granariensis</i>	N	–	2
<i>Diplodactylus pulcher</i>	N	–	1
<i>Strophurus assimilis</i>	N	–	2
<i>Strophurus spinigerus</i>	N	1	–
Unidentified	N	–	4
Pygopods ( $n = 2$ taxa)			
<i>Lialis burtonis</i>	N	–	1
<i>Pygopus lepidopodus</i>	N	–	1
Agamids ( $n = 3$ taxa)			
<i>Ctenophorus</i> sp.	N	–	1
<i>Pogona minor</i>	N	2	1
Unidentified	N	–	2
Skinks ( $n = 10$ taxa)			
<i>Acritoscincus trilineatus</i>	N	3	7
<i>Ctenotus catenifer</i>	N	–	1
<i>Ctenotus fallens</i>	N	–	1
<i>Ctenotus labillardieri</i>	N	–	9
<i>Ctenotus</i> sp.	N	1	10
<i>Hemiergis peronii</i>	N	–	1
<i>Hemiergis quadrilineata</i>	N	10	–
<i>Lerista distinguenda</i>	N	–	2
<i>Tiliqua rugosa</i>	N	1	3
Unidentified	N	15	37
Snakes ( $n = 2$ taxa)			
<i>Pseudonaja affinis</i>	N	–	2
Unidentified	N	–	1
Number of prey items		48	176
Number of taxa		11	24
Evenness		0.63	0.33
Simpson dominance		0.81	0.78
Shannon H'		1.94	2.08

Urban snakes ate a similar diversity of prey. Collective number of species and groups identified to the finest possible scale are represented by  $n$  for each class and family.

non-parametric MANOVA (PERMANOVA) using a Euclidean similarity index and 9,999 permutations, with  $\log(M_{\text{prey}}+1)$  as dependent factors (mass calculated separately for all agamids, geckos, pygopods, rodents, skinks, and snakes), location and sex as independent grouping factors, and body size, season, and collection date as covariates. We then repeated this PERMANOVA analysis using the total  $\log(M_{\text{prey}}+1)$  for all native or all introduced prey species.

### Prediction 3: Urban dugites will eat a less diverse range of prey species than non-urban dugites.

To determine if there was an effect of location on the number of prey items for  $n = 112$  dugites containing prey, we performed a multiple regression with the total number of prey items per individual as dependent variable, and location, sex, body size, season, and collection date as independent variables. We carried out a similar analysis

with prey species richness as the dependent variable. The effect of location on prey diversity was tested by comparing a Shannon diversity index between locations via a diversity  $t$ -test.

### Prediction 4: Urban dugites will be relatively larger than non-urban dugites.

To determine if there was an effect of urbanization on snake body condition (i.e., mass relative to body size), we performed a multiple logistic regression for  $n = 453$  specimens with  $\log-M_b$  as the dependent variable, and location, sex, body size, season, and collection date as independent variables.

Values are presented as  $x \pm 1$  Standard Deviation, range: min-max. Parametric analyses were conducted using STATISTICA 7.1 (StatSoft Inc. 2006). Non-parametric and diversity analyses (predictions 2 and 3) were conducted using PAST 3.1 (Hammer et al. 2001).

## Results

A total of 195 (43%) of the 453 specimens with complete data were collected in urban areas. The majority of collections occurred in 1960–1989 (Figure 2). There was a significant difference in location of collection over time ( $\chi^2_8 = 22.9$ ;  $P = 0.003$ ), with a relatively greater proportion of urban animals collected over more recent decades (Figure 2). We found prey items in the stomach for 112 (24.7%) of the 453 specimens with complete data; 44 specimens contained more than 1 prey item, and 21 specimens contained more than 1 prey species. In total we identified 224 prey items of at least 23 species. Overall observed dugite diet was made up of 38.4% mammals and 61.6% reptiles (Figure 1b, c). A total of 55 (24.6%) prey items were autotomized lizard tails (i.e., no evidence of the lizard bodies), which we classified as belonging to geckos and skinks.

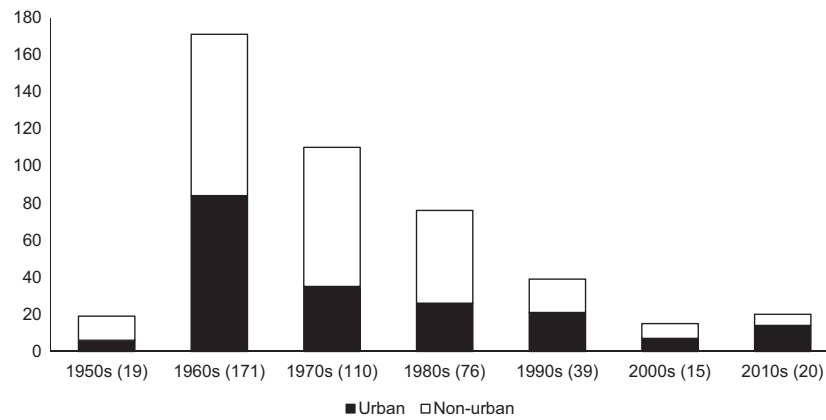
### Prediction 1: Urban dugites will more frequently contain prey than non-urban dugites, and have eaten larger meals.

Fewer urban snakes contained prey items than non-urban snakes (Logistic multiple regression testing whether snakes had prey in their stomachs or not:  $t_{447} = 2.8$ ;  $\beta = 0.1$ ;  $P = 0.0046$ ; Table 3). There was also an effect of snake body size, with larger snakes ( $\log\text{-SVL}$ ) more likely to have prey present (Table 3). There was no significant effect of sex, season, or year of collection on the presence of prey.

Urban snakes contained a similar total mass of prey ( $x = 3.6 \pm 7.2$ , 0.001–27.7 g) as non-urban snakes ( $x = 6.0 \pm 10.1$ , 0.001–54.5 g) ( $t_{106} = -1.0$ ;  $P = 0.31$ ; Table 3). Larger snakes ( $\log\text{-SVL}$ ) had a greater mass of prey present, but there was no significant effect of sex, season, or year of collection on prey mass (Table 3).

### Prediction 2: Urban dugites will eat proportionally more introduced prey than non-urban dugites.

There was no significant effect of location on diet composition (2-way PERMANOVA:  $F_{1,106} = 2.6$ ;  $P = 0.062$ ) or effect of sex ( $F_{2,106} = 1.7$ ;  $P = 0.091$ ). Similarly, there was no location effect on diet composition in terms of whether prey was native or introduced (urban introduced  $M_{\text{prey}}$ :  $x = 2.1 \pm 6.7$ , 0–27.1 g, native:  $x = 1.2 \pm 2.4$ , 0–11.7 g; non-urban introduced  $x = 4.2 \pm 9.4$ , 0–52.5 g, native  $x = 2.3 \pm 5.0$ , 0–25.7 g) ( $F_{1,106} = 2.6$ ;  $P = 0.062$ ). There was also no sex effect on diet composition in terms of whether prey was native or introduced ( $F_{2,106} = 1.7$ ;  $P = 0.093$ ).



**Figure 2.** Comparison of urban and non-urban specimens collected over time. Only 3 snakes were collected prior to the 1950s: 2 urban snakes in the 1920s and 1 non-urban snake collected from the 1930s. Data represented as Decade (n).

**Table 3.** Summary of multiple regression analyses testing dependent factors addressing the 4 predictions of this study

Prediction	Dependent factors	Independent factors				
		Location	Sex	Body size (log-SVL)	Season	Year
1a	Prey present (yes/no) $t_{447} =$	2.8; $\beta = 0.12$ ; $P = 0.0046$	0.33; $P = 0.74$	4.6; $\beta = 0.32$ ; $P < 0.0001$	0.61; $P = 0.54$	1.0; $P = 0.30$
1b	Mass of prey (g) $t_{106} =$	-1.0; $P = 0.31$	0.39; $P = 0.69$	8.9; $\beta = 3.1$ ; $P < 0.0001$	-1.8; $P = 0.062$	0.31; $P = 0.75$
3a	Number of prey items (count) $t_{106} =$	-0.061; $P = 0.95$	0.32; $P = 0.75$	3.2; $\beta = 2.5$ ; $P = 0.0016$	0.022; $P = 0.98$	-0.55; $P = 0.59$
3b	Number of prey species (count) $t_{106} =$	0.93; $P = 0.35$	0.72; $P = 0.47$	2.3; $\beta = 0.53$ ; $P = 0.024$	0.097; $P = 0.92$	0.38; $P = 0.71$
4	Dugite body mass $t_{447} =$	2.1; $\beta = 0.023$ ; $P = 0.034$	2.1; $\beta = 0.032$ ; $P = 0.035$	151.3; $\beta = 2.8$ ; $P < 0.0001$	1.1; $P = 0.27$	-1.9; $P = 0.059$

Once the effects of body size and potential biases (sex, season, year of collection) were accounted for, urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. Beta ( $\beta$ ) values are provided for significant findings.  $0 < \beta$  represents a trend toward: 1) non-urban snakes for location, 2) males for sex, and 3) larger snakes for log-SVL.

### Prediction 3: Urban dugites will eat a less diverse range of prey species than non-urban dugites.

Urban dugites ate a similar number of prey items as non-urban dugites ( $t_{106} = -0.06$ ;  $P = 0.95$ ; Table 3). Larger snakes (log-SVL) had more prey items, but there was no effect of sex, season, or year of collection on number of prey items (Table 3). Similarly, larger snakes ate a greater diversity of prey (number of species), but there was no effect of location, sex, season, or year of collection (Table 3). This analysis was supported by a diversity  $t$ -test, which indicated that urban dugites had a similar diversity of prey present as non-urban dugites (Shannon  $t_{111.94} = -0.86$ ;  $P = 0.39$ ; Table 2).

### Prediction 4: Urban dugites will be relatively larger than non-urban dugites.

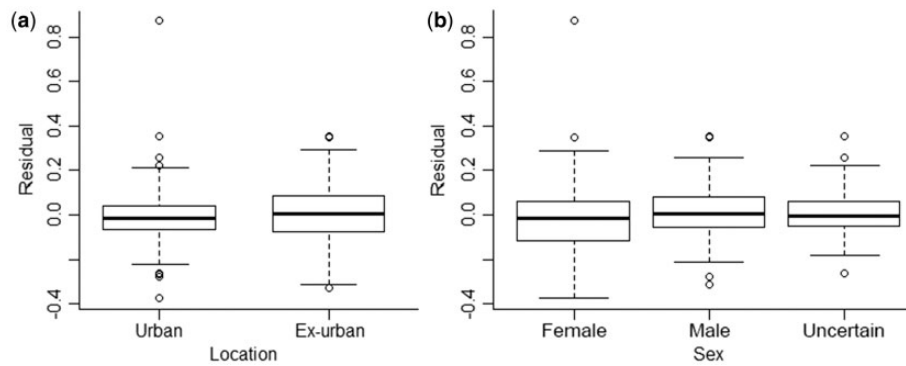
Urban dugites were relatively lighter than non-urban dugites ( $t_{447} = 2.1$ ;  $\beta = 0.023$ ;  $P = 0.034$ ; Figure 3a; Table 3) once correlation with body length (log-SVL) was accounted for. Females were relatively lighter than all other specimens (Figure 3b), but there was no significant effect of year or season of collection on relative body mass (Table 3).

## Discussion

Many mammalian urban adapters have access to increased food supplementation, providing larger and/or more frequent meals (see Bateman and Fleming 2012). This is also indicated in reptiles for *B. irregularis* (Savidge 1988) and *P. sebae* (Luiselli et al. 2001), which take larger prey in urban areas, possibly due to prey availability. We had, therefore, predicted that the presence of synanthropic prey in urban areas would provide greater opportunity for dugites. However, our predictions were not supported by this dataset of 453 dugite specimens. Once the effects of body size and potential biases (sex, season, year of collection) were accounted for, urban snakes were less likely to have prey present in their stomachs and were relatively lighter than non-urban snakes. Location did not affect the number of prey items, the diversity of prey, or the relative proportions of native or non-native prey.

As has been reported across many snake diet studies (e.g., Shine 1989; King 2002; Bryant et al. 2012; Miranda et al. 2017), body size (log-SVL) was a strong predictor of dugite diet. Larger snakes more frequently contained meals, and those meals were of a greater mass. Larger snakes also contained a greater number and greater diversity of prey items than smaller snakes. Body size was also





**Figure 3.** Residual body mass (compared with SVL) for a) urban and non-urban dugites and b) specimens of each sex. Residuals were calculated using a linear regression of log-SVL against log-body mass.

significantly different between the sexes. Despite dugites, along with other Australian brown snakes, being considered to not have marked sexual size dimorphism (Shine 1989), we found that females were relatively lighter than males.

Although we predicted urban snakes would be relatively heavier than non-urban snakes, our finding to the contrary is not unsurprising, as living in high-disturbance areas may better suit smaller snake individuals (i.e., younger snakes) and smaller-bodied species. For example, road mortality from vehicle–wildlife collisions is biased towards larger-bodied species or individuals (e.g., Shine and Koenig 2001; Gibbs and Shriver 2002; Steen et al. 2006). Smaller snakes may also be better able to find cover in high-disturbance areas. Smaller garter snakes *Thamnophis ordinoides* flee to cover quicker than larger conspecifics (Bell 2010), and smaller grass snakes *Natrix natrix* are more likely to be found under cover than in the open than larger individuals (Gregory 2016).

Our observed dugite diet of mostly mammals (38.4%) and reptiles (61.6%) did not vary between urban and non-urban snakes. This diet composition is similar to that recorded by Shine (1989), who also used WAM specimens ( $n = 179$ ), but found different proportions of prey representation to us; his specimens contained birds and more mammals (grouped together, 51%) than reptiles (47%) as prey, and also included frogs (2%). These differences are likely due to different snake size ranges of the specimens dissected between the two studies (SVL =  $108.8 \pm 2.6$  cm for females and  $108.5 \pm 2.7$  cm for males, no significant difference (n.s.), Shine 1989; SVL =  $90.8 \pm 2.8$  cm for females and  $104.3 \pm 4.5$  cm for males, with significant effects of sex and location, this study). Dugites tend to eat more endothermic prey with increasing SVL (Shine 1989), which may explain why we found more reptiles and fewer mammals in our, on average, smaller specimens.

There was no difference in the relative proportions of native or non-native prey for urban or non-urban dugites, which reflects that urban snakes make extensive use of native species, despite living in the urban matrix. All reptiles identified were native (Cogger 2014), and many reptile prey species identified are considered common in urban bush remnants across Perth (How and Dell 2000; Davis and Doherty 2015). The most common prey species found exclusively in urban areas was a native reptile, the 2-toed earless skink *Hermiergis quadrilineata*. This skink species occurs within some of the dugite's non-urban range along the south-western coastline, but it is recognized as one of the most abundant lizards within the Perth metropolitan area (Davis and Doherty 2015), and is most commonly found near urban environments (Cogger 2014). Another prolific

urban species, Buchanan's snake-eyed skink *Cryptoblepharus buchananii* (Bush et al. 2010), was not identified as a prey item for any snake; however, of the 56 autotomized tails found present in dugite stomachs, we expect that some of these may have belonged to the snake-eyed skinks, as dugites have been observed eating these in the wild (A.K.W., personal observations). Therefore, dugites do not face a lack of native reptile prey in urban areas.

The only introduced mammalian prey were rodents: *M. musculus*, *Rattus norvegicus* (brown rat), and *Rattus rattus* (black rat); all are synanthropic species. Urban dugites did not appear to make greater use of synanthropic species than was evident for non-urban specimens. While both specimens of *R. rattus* were found in urban snakes, *M. musculus* and *R. norvegicus* were found in the stomachs of both urban and non-urban dugites. The prevalence of rodents in landscapes associated with grain farmland is not a particularly surprising result, and Western Australia's farming 'wheatbelt' comprises 154,862 km<sup>2</sup>, or approximately 30% of the distribution range of dugites in Western Australia (Wheatbelt Development Commission 2015). Many non-urban specimens found containing rodents were outside of the wheatbelt region; the spread of rodents across the southern half of the dugite range may be exacerbated by the scattering of towns across southern Western Australia. The extensive spread of introduced rodents across southern Western Australia appears to supplement all dugites, not just those in urban areas, as we had originally predicted.

### Sampling bias

There was a significant sampling bias of collection location on body size: relatively larger snakes were collected from non-urban areas. Snakes, in particular, are stigmatized for their potential to have a venomous bite (whether they are venomous or not), and large individuals are often relocated away from urban areas for safety concerns (Shine and Koenig 2001; Department of Parks and Wildlife 2013), possibly reducing the average size of animals persisting in urban sites. Additionally, although killing any wildlife, including snakes, is illegal in Western Australia, we have observed dugites dead in backyards and on roads in ways that could only be deliberate (A.K.W., personal observations). Human predation on snakes, therefore, must also play a role in shaping the demographics of urban snake populations. Urban development encroachment, introduced predators (e.g., cats, dogs, foxes) and pressures (e.g., modified land use), or low behavioral plasticity and adaptation to change may also potentially contribute to the observed size differences

between urban and non-urban locations. Alternatively, urban snakes may exhibit increased secretive behaviors to minimize interactions with people, inevitably reducing foraging activity and feeding opportunities.

We found that relatively larger dugites were also collected more frequently by scientists (as identified by collectors' names). This presents an interesting point for future studies of museum specimens, as significant biases may result due to the method of capture of specimens. For example, members of the public most likely donated dugites to the museum that were found dead or were killed on their property for fear of a venomous bite, while scientists embark on trapping exercises or encounter specimens of high quality and donate those exceptional specimens to the museum. We found no evidence of similar studies accounting for such biases, but we recommend incorporating this information into future comparative analyses, wherever possible.

Although size difference comparisons between urban and non-urban snakes in the literature are limited, a consistent directional pattern does not currently appear to exist: *B. irregularis* are larger in urban areas (Savidge 1988), while urban individuals of *P. sebae* are relatively smaller (Luiselli et al. 2001). In human-disturbed sites in New Hampshire, USA, snakes found within smaller patches were relatively larger than those found in larger patches (Kjoss and Litvaitis 2001). In Japan, mamushi snakes *Gloydius blomhoffii* were relatively smaller in areas where they are hunted than conspecifics in non-hunting grounds, an example of rapid evolutionary responses to predation pressure (Sasaki et al. 2008). By contrast, the size of massasauga rattlesnakes *Sistrurus catenatus catenatus* in Canada, was unaffected by disturbance from humans (Parent and Weatherhead 2000).

### Application of urban ecology theory to snakes

Degrees of adaptation to urbanization have been described as 3 levels: avoidance, adaptation, and exploitation (Blair 1996; McKinney 2006). Due to sensitivity to anthropogenic changes, “urban avoiders” remain in their highest densities in unmodified natural environments. “Urban adapters” prefer areas of intermediate disturbance (i.e., suburbia) due to an ability to use novel resources such as garden plants. Finally, “urban exploiters” appear to show preference for highly modified areas (i.e., inner metropolitan areas) due to an ability to exploit the availability of anthropogenic resources such as buildings (shelter) and refuse (food). This classification method has been useful for describing responses to urbanization for birds (Blair 1996), mammals (Randa and Yunker 2006), and insects (McIntyre 2000). Building on this, a set of 5 rules for urban exploiters was developed by Kark et al. (2007) using birds as a model; urban exploiters most commonly are: 1) omnivorous or diet generalists (with some specialization seen in urban adapters); 2) social; 3) sedentary and maintain territories; 4) nest in man-made structures (though adapters use vegetation); and 5) have relatively larger brains, greater behavioral flexibility, and use novel food items. For mammalian carnivores, body size is also likely to influence the ability of mammals to exploit the urban landscape, with medium-sized (1–20 kg) generalist predator species identified as the best urban adapters: larger species are more likely to attract human attention and smaller species more likely to be sensitive to habitat fragmentation (see Bateman and Fleming 2012).

Applying the descriptions of urban adaptation developed by Blair (1996) and Kark et al. (2007), based on persistence in urban areas, we consider dugites as urban adapters (“suburban adaptable”). The apparent lack of feeding innovations for urban dugites and complete diet overlap between urban and non-urban dugites

suggests that dugites living within the Perth metropolitan area are not using any available extra dietary resources, or using dietary resources differently. Perhaps urban dugites lack feeding innovations because native food is abundant for urban dugites, while there is also an abundance of synanthropic species associated with farming in non-urban locations. Some Australasian reptile species such as the blue-tongue lizard *Tiliqua scincoides* (Koenig et al. 2001) and the common skink *Oligosoma nigriplantare polychroma* (van Heezik and Ludwig 2012) use household gardens for food, water, and avoidance of predators, and most of the urban dugite prey species we identified are both common in gardens/urban remnants and less urbanized parts of Western Australia. Perhaps the definitions of urban adaptation are not suited for ectothermic vertebrates, or dugites fit into another category: “urban oblivious”, usually a term used for cryptic generalists, usually ignored by humans (Grant et al. 2011).

Unlike other taxa that experience food supplementation by urban areas, dugites do not appear to derive any particular dietary benefit from living in cities. However, there is more to urban adaptation than diet alone, and the other factors, such as increased temperatures (Brazel et al. 2000; Ackley et al. 2015), and available cover (e.g., tin sheeting, brick piles, garden beds) (Brown and Sleeman 2002; Purkayastha et al. 2011) may provide an anthropogenic niche for these snakes that is worth exploiting despite increased predation from domestic pets (Shine and Koenig 2001) and restricted movement due to habitat fragmentation (How and Dell 2000). Finally, a major setback for snakes in urban areas, especially for venomous species, is their direct conflict with humans (Whitaker and Shine 2000; Clemann et al. 2004). Snakes play an important role in controlling rodents and stabilizing food webs, and the persistence of these important predators, therefore, requires that we know more about their habitat and diet requirements. Despite all of the potential challenges for snakes in urban areas, dugites, which do not appear to conform to standard urban-adaptation conventions, remain one of the best urban-adapted vertebrates in Perth.

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### Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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## REVIEW

# A different kind of ecological modelling: the use of clay model organisms to explore predator–prey interactions in vertebrates

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plasticine; predation; colour morph; habitat; morphology; predator behaviour; clay models; nest predation.

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**Abstract**

We review the use of clay models to explore questions about predation rates on small vertebrate taxa that are typically difficult to observe directly. The use of models has a relatively long history and we examine the range of taxa studied, which includes squamate reptiles, amphibians, mammals and birds. Within this review, we have also included studies of model eggs, which are used in nest predation studies. We review the questions that have been asked and the interpretations arising from the data. The use of clay model animals has provided us with insights into how differences in prey morphology, size, and colour influence the rate at which they are attacked by predators. This allows us insights into the ecological, behavioural and evolutionary selective pressures of different predators on small vertebrate prey, including analysis of what characteristics predators target and how predators approach their prey (e.g. which part of the body is attacked). Further available interpretations include how regional and habitat variation influences predation events on models. We also briefly discuss the potential for clay models to study interspecific sociality and competition. Finally, we review the problems and limitations with the method and make some suggestions for further studies and amendments to help standardize this creative tool for ecological research.

**Introduction**

The study of predator–prey interactions is fundamental to ecology, and the associated physiological, anatomical and behavioural adaptations of both predators and prey are fertile areas of research in evolutionary and behavioural ecology (e.g. Ruxton, Sherratt & Speed, 2004; Caro, 2005; Cooper & Blumstein, 2015). Predation interactions can be studied by direct observation in the field, laboratory manipulation, gut or faecal analysis, field manipulations, or any number of sub-disciplines (Zanette & Sih, 2015). However, much of these data rely on inference, and there are many difficulties in studying predation events in the wild, particularly for small and cryptic predators and prey, including the actual observations of predation events and obtaining quantifiable data on how predators find and handle the prey based on variation in the prey's appearance or habitat use.

One technique that has been used with some success to study predation interactions is the use of clay models of prey organisms that are left in the field for predators to find and attack (Irschick & Reznick 2009). Marks left in the clay by the predator are considered indicative of a potential predation event and can provide information on the predator species

through imprints of teeth, beaks or claws. Here, we review the range of vertebrate taxa and questions to which this simple but effective technique has been applied, identifying the influence of morphological and colour differences in prey ('Do prey trait differences influence, attack rate?'), effects of predator diversity and behaviour ('Predator variation and behaviour') and differential habitats ('Does habitat variation influence 'attack' rate?'). We also review the use of models to test intraspecific interactions ('Social interactions'). We discuss interpretation and problems with the method, and conclude with suggested applications for future research. We searched for papers through Google Scholar using the search terms 'plasticine' or 'clay' + 'model' and a variety of taxon terms such as 'amphibian', 'reptile', 'snake', 'lizard', etc., both with and without the term 'predation' or similar iterations. We used the reference lists of the retrieved publications to find other publications and thus reduce bias in our primary search (Haddaway *et al.*, 2015).

**The method**

The method of using clay models is, at heart, extremely simple. Soft, non-toxic modelling clay is used to create models of

particular 'prey'. These models are placed in the field under different conditions (i.e. cover, height, microhabitat, etc.) for a period of time to record predatory 'attacks'. Where potential predators attack the models, they leave quantifiable evidence as beak, claw or teeth marks (e.g. Webb & Whiting, 2006; Dell'Aglio *et al.*, 2012; Santos *et al.*, 2013; Fresnillo, Belliure & Cuervo, 2015), or if the models are removed entirely, they can leave predator tracks nearby.

Models tend to be easy to produce and deploy in large numbers (Yeager, Wooten & Summers, 2011) and it is relatively easy to make reasonably accurate models for most taxa (but see 'Accuracy of models – does accuracy of the models' appearance, smell and 'behaviour' matter?') that capture the body size, basic morphology/shape or colour of the prey species under consideration. Models have been constructed of various materials. 'Plasticine' is often named as the modelling material, but this often seems to be used as a synonym of 'modelling clay' rather than as a brand name, for example, 'plasticine' (Caran D'Ache, Modela Noir) (Valkonen *et al.*, 2011a), 'plasticine' (Rainbow modelling clay) (Webb & Whiting, 2006), 'modelling plasticine' (no brand) (Diego-Rasilla, 2003; Dell'Aglio *et al.*, 2012). Others named are Sculpey III modelling clay (Brodie, 1993; Bittner, 2003; Husak *et al.*, 2006) and Plastalina (Bateman, Fleming & Rolek, 2014). Other materials used are paraffin wax, plaster, and clay-covered plastic models (e.g. Stuart-Fox *et al.*, 2003; Husak *et al.*, 2006; Rojas, Rautiala & Mappes, 2014). Throughout this paper, we use the term modelling clay except where we specify the type of material used.

Models certainly vary in accuracy (i.e. accurate model of a species, general body shape of a taxon or only a particular shape) according to the method of construction. Models created by hand can vary in shape to some degree, but tend to be the only reasonable method for making small and elongated shapes. Some modelling clays can be heated and poured into moulds made of the target species, although moulds tend to work best only for basic (rounded) body shapes and larger sizes. Most importantly, this method allows us to experimentally manipulate trait(s) on models that do not differ from each other in any other way. We can also consider variables that we would not be able to manipulate with live animals, such as colour and shape variables that are not naturally found in the target species, we can put out models of target species in sites in which they would not naturally occur and, perhaps most fundamentally, such a method is welfare positive as it does not involve live prey animals and the impact on the predators is minimal. Using clay model eggs can even reduce predation on real nests, as predators may learn to associate nests with unrewarding prey (e.g. Price & Banks, 2012).

## The cast: model 'prey' and their potential predators

The first uses of clay model vertebrates in the field were with snakes (Madsen, 1987; Brodie, 1993). Since then, use of models has expanded to include many lizards, snakes, and frogs as prey. Model birds, mammals, and salamanders have been less commonly investigated, while a large body of papers uses

model eggs to record nest predation (Fig. 1a). Models of invertebrates – usually representing caterpillars – have also been used extensively in foraging studies (e.g. Loiselle & Farji-Brener, 2002; Gonzalez-Gomez, Estades & Simonetti, 2006; Poch & Simonetti, 2013), but is beyond the remit of this review. We noted very few studies on mammal prey, possibly because most mammals, and therefore their predators, are nocturnal; perhaps nocturnal predators hunting by smell are less likely to be motivated to take a bite out of a clay model than a diurnal animal hunting largely by sight. Regular checking of models might reveal whether predator attacks are largely during daylight or in the dark.

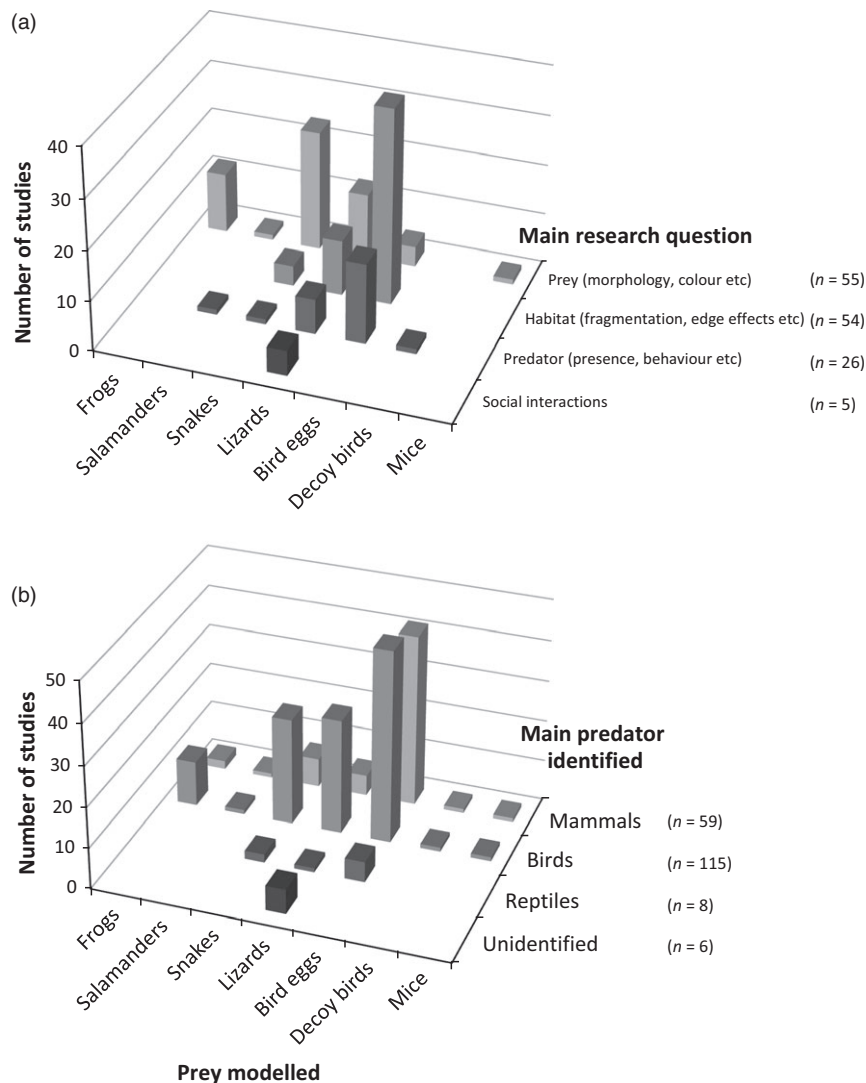
Prey animal size is also constrained in clay model experiments: most taxa modelled are small, although model snakes can be long, which may limit the use of this technique in mammals beyond the size of mice. The target predators are also assumed to be relatively small, which is usually associated with cryptic habits and difficulty of observation by other techniques.

For many research questions using clay models, it is not necessary to identify the predators to species level, and most studies consequently only record predators broadly as 'birds', 'mammals', etc. The principle predators identified with the use of clay models are birds and mammals; reptile (snakes and lizards) and arthropod predators have also been recognized and Fig. 1a shows their distribution across published studies by prey species. Birds and mammals are commonly identified as the predators in studies on bird eggs, and birds are the dominant predator identified for studies on snakes and lizards and also for frogs and for caterpillars.

Predator species can be identified where the marks left can be confidently assigned to a particular species, especially where there is a limited diversity of predator species (e.g. on islands; Velo-Antón & Cordero-Rivera, 2011; Castilla & Labra, 1998). The marks made on models can be particularly distinctive (e.g. Brodie, 1993; Webb & Blumstein, 2005), and some researchers go to the effort of identifying predator species through comparison of these marks with beak sizes from museum specimens of birds or teeth marks left by mammals (e.g. Boulton & Cassey, 2006; Matthews, Dickman & Major, 1999; Valkonen *et al.*, 2011a; Webb & Blumstein, 2005). Another option to identify predator species is to set up cameras to monitor predatory attacks on models (e.g. Pietz & Granfors, 2000) or carry out surveys to assess what potential predators are present (e.g. Diego-Rasilla, 2003; Sato *et al.*, 2014).

## The questions

Clay models can demonstrate differential rates of 'attacks' and therefore reveal vulnerability of the modelled species to predation. This approach has therefore been used to investigate differences in traits of the prey species, their social interactions, predator numbers or behaviour, or differences in habitat that affect vulnerability to predation. The most frequent study organisms have been bird eggs and snakes, followed by lizards and frogs, concentrating on questions to do with predator type, habitat variation and prey morphology (Fig. 1b). None of these questions are necessarily mutually exclusive and there is often overlap for particular studies as they all converge on gaining



**Figure 1** Summary of  $n = 143$  studies in terms of (a) the ‘prey’ modelled and the potential predators identified and (b) in terms of the ‘prey’ modelled and the research question. Where multiple predators were identified (a) or research questions were addressed (b), these studies have been represented multiple times.

information on differential rates of attack (Fig. 2); for example, it is common to investigate the relative influence of different prey traits under different habitats.

**Do prey trait differences influence ‘attack’ rate?**

A number of studies have explored whether differences in traits of the prey animals, such as morphology, size, and colour of the models, influence rates of attack.

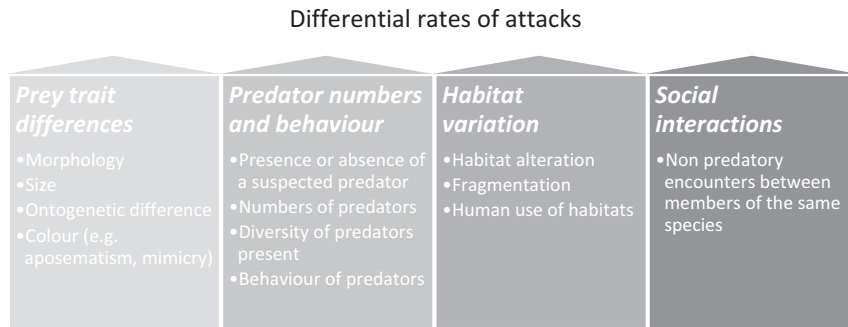
**Morphology**

One of the benefits of using clay models is that it is possible to alter the shape of the models to manipulate their appearance to would-be predators. Many non-venomous colubrids commonly triangulate their heads when disturbed, making them

look superficially like viperids (Valkonen, Nokelainen & Mappes, 2011b). Tozetti, Oliveira & Pontes (2009) claim that a harmless colubrid hognose snake *Xenodon dorbignyi* mimics the viperid *Bothrops jararaca* not only by triangulating its head, but also by mimicking the viperid’s threat posture. Del-l’Aglia *et al.* (2012) in Brazil and Valkonen *et al.* (2011a) in Spain found that clay model snakes were attacked more often if they had the rounded head shape typical of non-venomous colubrids than if they had the triangular head shapes of venomous viperids, but Guimaraes & Sawaya (2011) found no support for the viper mimicry hypothesis in Brazil.

**Size**

In snakes, small clay models (representing juveniles) of the garter snake *Thamnophis sirtalis* (Colubridae) were attacked



**Figure 2** Clay models have been used to address four main, non-mutually exclusive, types of research question.

more often than were 'adult' models (Bittner, 2003). Steffen (2009), however, found that size of model lizards was less important than habitat in influencing attack rates. Predation in reptiles has been shown to be size dependent (e.g. Ferguson & Fox, 1984; Forsman, 1993), and so it is surprising that more studies with models do not explicitly test this.

### Colour

Many of the colour studies have tested differences in attack rate under particular environmental conditions. Colour as part of camouflage or crypsis is generally well-supported in clay model studies. Clay models of the mouse *Peromyscus polionotus* (Cricetidae) that did not match their substrate were attacked significantly more often than models that did match (Vignieri, Larson & Hoekstra, 2010), supporting the hypothesis that stabilizing selection through predation maintains very light and dark morphs that match their local substrate. Similarly, experiments with clay models of different coloured morphs (representing different populations) of the rattlesnake *Crotalus lepidus lepidus* (Viperidae) indicate that models contrasting in colour with local substrates are attacked by birds significantly more often (Farallo & Forstner, 2012).

In central Australia, models of two agamid lizard species *Ctenophorus isolepis* and *C. nuchalis* that have different types of cryptic colouration and are found in different habitat types (based on amount of cover) showed lower rates of attack for models placed out in the species' respective selected habitat (Daly, Dickman & Crowther, 2008). Models of both species under both habitat types were attacked more often in the open than under cover: therefore, predation appears to be only one of several ecological factors (e.g. thermal limits and diet divergence) influencing habitat divergence in these congeneric species.

### Colour polymorphism and sexual dimorphism

Models of the lizard *Norops (Anolis) humilis* (Polychrotidae) representing females with different natural back patterns were differentially attacked in different microhabitats, supporting a role for predation in maintaining polymorphism in this species (Paemelaere, Guyer & Stephen Dobson, 2013). By contrast, studies using clay models have also revealed no significant

difference in attack frequency for polymorphisms in other species, suggesting that the morphs have no defensive role. For example, a study of models mimicking the polymorphic garter snake *T. sirtalis* showed no difference in bird attacks on striped or melanistic models (Bittner, 2003), while there was also no significant difference in attack frequency for models of two morphs of the frog *Leptodactylus fuscus* (Leptodactylidae) – one with a pale vertebral line which is less common in the field and the more common morph without the stripe (Kakazu, Toledo & Haddad, 2010).

Intraspecific colour variations are often to do with sexual dimorphism. Slow worms *Anguis fragilis* (Anguidae) have a blue-spotted morph, usually male, that varies in frequency between populations. Clay models with blue spots were attacked more frequently by bird predators than unspotted models (Capula, Luiselli & Capanna, 1997). Furthermore, populations with a higher proportion of blue-spotted individuals had a higher proportion of individuals with broken tails (Capula *et al.*, 1997), which may reflect greater predation in those populations (although autotomy rates as an indicator of predation intensity should be viewed with caution; Bateman & Fleming, 2011). Using clay-covered plastic models of *Crotaphytus collaris* (Iguanidae) lizards, Husak *et al.* (2006) showed that the more brightly coloured males suffer greater predation than do females, and models made with the strongest colour contrast with the substrate were detected and attacked most often. Similarly, clay-covered epoxy models of *Lacerta agilis* (Lacertidae) that looked like males with neon-green nuptial colouration accumulated more attacks than did cryptic models (Olsson, 1993). Using plaster models of Australian *Ctenophorus* spp., Stuart-Fox *et al.* (2003) found that brightly coloured models representing males were attacked significantly more often than were duller models representing females. Interestingly, McLean, Moussalli & Stuart-Fox (2010) found that plastic models with coloured clay attached, representing female *C. maculatus*, were less likely to be attacked when on their back displaying bright orange colouration than when right side up and cryptic. Females flip on to their back to resist males attempting to mate and are much more conspicuous to predators when they do so; it is possible that females do this such short periods of time that they are not recognized as food or are avoided by neophobic predators.

### Coloured tails

Bright colour patterns not associated with sexual selection seem counter-intuitive as they will increase predatory attacks on an individual by making them more obvious to predators. For example, a number of studies have used clay models to show that red, blue or green tails on lizards attract more attacks from birds than monochrome models do (Castilla *et al.*, 1999; Watson *et al.*, 2012; Bateman *et al.*, 2014; Fresnillo *et al.*, 2015). Coloured tails induced attacks sooner and more often; however the location of attacks was telling – attacks were more likely to be diverted to the tail while monochrome models tended to be attacked on the ‘head’ or ‘body’, which would be lethal attacks on the lizards themselves (Bateman *et al.*, 2014; Fresnillo *et al.*, 2015). Coloured tails tends to be an ontogenetic stage found in younger lizards, and may reflect different predation pressures and habitat use by younger lizards (Hawlena *et al.*, 2006). Attracting such attacks has been called the ‘risky decoy’ hypothesis (Bateman *et al.*, 2014) and is likely to work well in lizards as they can autotomize their tail and are less likely to die during a predatory encounter (Bateman & Fleming, 2009b). These studies suggest that brightly coloured tails are therefore adaptive, in that they can decrease the likelihood of fatal attacks.

### Aposematism and mimicry

A distinct subset of studies explores variations in aposematic colouration and mimicry of other organisms that a predator might want to avoid. For example, dendrobatid frogs are well known as examples of aposematically-coloured organisms, and their bright colours have an adaptive role in warning predators of their unpalatability. Predators in Costa Rica attack brown-coloured clay models of the dendrobatid frog *Oophaga pumilio* at almost twice the rate of red models (Saporito *et al.*, 2007). Clay models painted to resemble the supposedly aposematic plethodontid salamander *Ensatina eschscholtzii xanthoptica* are attacked less often than models lacking aposematic colours, suggesting a benefit for the bright colouration in these salamanders, and supporting the idea that the salamanders mimic the colours of the highly toxic *Taricha* spp. newts (Salamandridae) (Kuchta & Reeder, 2005).

The banded patterns of venomous coral snakes (Elapidae) on clay models reduce predatory attacks in comparison to unbanded models (Brodie, 1993). An experiment with clay models of both the eastern coral snakes *Micrurus fulvius* and its non-venomous mimic the scarlet kingsnake *Lampropeltis triangulum elapsoides* (Colubridae) indicate that protection for the mimic is enhanced by more accurate mimicry in areas where the coral snake is rare, but where coral snakes are common and the chances of a lethal encounter for potential predators are therefore increased, a more general banded mimicry is sufficient to reduce attack frequency (Harper & Pfennig, 2007). Avoidance of banded patterns on snake models seems to be generalized, even if they do not accurately represent venomous coral snake patterns (Brodie & Janzen, 1995), while Madsen (1987) suggested that the yellow collar of juvenile grass snakes *Natrix natrix* (Colubridae) acts as a general aposematic mimic

of unpalatable insects, supported by higher levels of bird predation on melanistic clay models than on yellow-collared models.

Although we tend to think of aposematism as being linked mainly to colour, the pattern of colouration is also important. Experiments with clay models of snakes show that black zig-zag patterns on a grey background, typical of that of several old world viper species (Viperidae), is sufficient to reduce attack frequency by bird and mammal predators (Wüster *et al.*, 2004; Niskanen & Mappes, 2005; Valkonen *et al.*, 2011a).

Where it is not possible to move prey species around from site to site, using clay models allows us to test the responses of new suites of predators to coloured models and therefore examine whether bright, aposematic, colours are useful in warning predators in all situations. Noonan & Comeault (2009) found that predators attacked novel aposematic patterns on clay models of the dendrobatid *Dendrobates tinctorius* more than they did cryptic models or models reflecting local aposematic patterns. Amézquita *et al.* (2013), however, found that predators avoided aposematically-coloured clay models of the polymorphic dendrobatid *Oophaga histrionica* more than cryptic models, regardless of whether they reflected local aposematic pattern or not.

## Predator variation and behaviour

### Responses of different predators

Clay model experiments can sometimes tell us about differences in behaviour of different potential predators. Colour-banded snake models mimicking the pattern of venomous snakes reduce predatory attacks by birds, particularly models mimicking local coral snake species (Brodie & Janzen, 1995), but colour-banded models are attacked more than monochrome models when the predator is a lizard *Ctenosaura similis* (Iguanidae) (Janzen & Brodie, 1995). Banded models were often torn apart and apparently partly ingested, presumably because the bright colours stimulated foraging behaviour by the herbivorous lizard rather than due to perception of the model as a snake (Janzen & Brodie, 1995).

### Why predators attack prey

Using clay models also allows examination of which cues are likely to be used by predators to detect their prey and the decision of whether to attack or not. Wall & Shine (2009) used black and white cylinders and spheres of clay, and black and white clay models of skinks to explore cues initiating predatory behaviour in Burton’s legless lizard *Lialis burtonis* (Pygopodidae), indicating that movement, shape and colour were important cues used by this saurophagous species. Similarly, Stuart, Dappen & Losin (2012) used familiar aposematic, novel aposematic, and cryptic clay models of dendrobatid frogs to test whether predators attack a certain prey type due to preference for that prey or because that prey type happens to be more conspicuous. Their data suggested that the predators (a range of bird species) make post-detection decisions on whether to avoid or attack particular prey items. These studies



demonstrate differences in predation due to relative conspicuousness as well as cognitive decisions by predators to recognize mimicry of dangerous or unpalatable prey (Kikuchi & Pfennig, 2010).

Shape as well as colour contributes to frog predation. Paluh, Kenison & Saporito (2015) found that red-coloured models of the dendrobatid *O. pumilio* were predated on by birds less than were brown frog models, or round balls of either red or brown plasticine (see 'Identifying predators – and is predator ID always required?'). Red balls, despite being the same colour as the 'aposematic' frog models, appeared to be perceived as fruit, and birds, particularly the Great Tinamou *Tinamus major*, foraged on them. This indicates that the same colour can be seen as both a negative and a positive stimulus when presented with different additional cues.

Familiarity with particular prey will allow predators to develop a particular search image, making them more efficient at prey detection. For example, models of the agamid *Ctenophorus vahnappa* were attacked more often than models of the congener *C. decresii*, even in *C. vahnappa*'s own range, despite the prediction that any species would be more cryptic in its home range (Stuart-Fox *et al.*, 2003).

### Where predators attack prey

A relatively simple experiment with undifferentiated clay models of the lizard *Podarcis sicula* (Lacertidae) on small islets in the Mediterranean revealed the predatory behaviour of the primary predators, yellow-legged gulls *Larus michahellis*, for these sites (Vervust, Van Loy & Van Damme, 2011). The authors recorded more attacks aimed at the heads of their models (Vervust *et al.*, 2011), which would translate to potentially fatal attacks in live lizards. Such behaviour by predators is likely to be the selective pressure that results in many species of lizard having brightly coloured tails (Vitt & Cooper, 1986; Castilla *et al.*, 1999; Bateman *et al.*, 2014) or behaviour such as tail waving (Cooper, 2011; Telemeco, Baird & Shine, 2011) that directs attacks towards autotomizable tails (Bateman & Fleming, 2009b), and may also select for longer tails (Fleming, Valentine & Bateman, 2013).

Clay models of garter snakes *T. sirtalis parietalis* are more likely to be attacked on the head than on the body (Langkilde, Shine & Mason, 2004). Comparing this observation with simulated 'pecking' attacks on the head or body of live snakes in the field resulted in different defensive responses: curling up and hiding the head or fleeing or gaping respectively. Anti-predator tactics and responses are likely to be flexible depending on the type of attack, that is, the level of vulnerability from such an attack (e.g. Bateman & Fleming, 2009a, 2013). Using clay models in combination with direct manipulation of responses is a potential method of exploring this.

Finally, clay models of snakes have also been used to explore the behaviour of potential prey. Models of snakes placed near ground squirrel *Spermophilus beecheyi* (Sciuridae) colonies indicated different responses by squirrels to snakes depending on size: smaller models were bitten more and more often on the head, while larger models were bitten more on the tail (Mitrovich, Cotroneo & Edwards, 2006).

### Does habitat variation influence 'attack' rate?

Models have been used to test vulnerability of prey under different habitats. Placing uniform models across a range of habitats allows direct comparison of detection and attack rates. For example, Steffen (2009) found that clay models shaped to look like *Anolis* lizards (Polychrotidae) were attacked by birds (assessed by beak marks) three times more frequently in the canopy of trees than on the trunks of the trees. Differences in predation risk between canopy and trunk may contribute to the lower diversity of canopy-dwelling species compared to trunk-ground-dwelling ecomorph anole species at this site. A similar result was recorded by Schneider & Moritz (1999) who found that clay model lizards in the Australian wet tropics were attacked by birds over five times more frequently in open-forest sites than closed-rainforest sites. Similarly, McMillan & Irschick (2010) found that clay models of green anoles *Anolis carolinensis* were attacked more by predators in fragmented (urban) habitats than in continuous (natural swamp) habitats. However, at sites in the Dominican Republic, there was no correlation between habitat openness (as a proxy of predation intensity) and predatory damage to clay lizard models, even though populations of *Leiocephalus* spp. lizards (Leiocephalidae) vary in predator response behaviour: having longer flight initiation distances, faster sprint speed, and longer limbs at more open sites (Gifford, Herrel & Mahler, 2008).

A body of research has used placement of nests of artificial bird eggs to explore the influence of habitat on egg predation. Studies with false nests to explore predation on bird eggs have usually relied on using a combination of real eggs (usually quail or finch eggs) and plasticine eggs (sometimes rubber coated to reduce olfactory cues, Purger *et al.*, 2012b) to both induce and record predation events. Vetter, Rucker & Storch (2013) carried out a meta-analysis of edge effects on nest predation in tropical forests, using studies that made use of over 9000 artificial nests and eggs and found support for more predation along forest edges. Similar support has been recorded for studies in other biomes, such as forests (e.g. Nour, Matthysen & Dhondt, 1993; Taylor & Ford, 1998; Vergara & Simonetti, 2003), reed beds (e.g. Schiegg, Eger & Pasinelli, 2007), oceanic islands (e.g. Stirnemann *et al.*, 2015), tropical woodlands (e.g. Noske, Fischer & Brook, 2008), urban bushland (e.g. Matthews *et al.*, 1999) and agricultural landscapes (e.g. Gardner, 1998), indicating the broad applicability of the artificial nest and egg method.

Microhabitat also plays a part in influencing the visibility of eggs in nests: artificial ground nests in the Amazon, with quail and plasticine eggs were attacked more if the leaf litter had been cleared around them than if left undisturbed. Other variables (distance from trail, understorey density, etc.) did not influence predation rates (Michalski & Norris, 2014). Even the nest type can have an effect: plasticine eggs in artificial nests mimicking open-type nests were predated more than were eggs in artificial domed-type nests (Noske *et al.*, 2008).

Different body forms can also be tested for their vulnerability across habitats. In Brazil, Shepard (2007) deployed clay-

covered plastic model lizards representing a variety of body shapes across a range of habitats, varying in structural complexity. There was a greater frequency of attack in the most structurally-complex habitat, but within that habitat there was a greater probability of being attacked in microhabitats that were more open. Intriguingly, attack frequencies did not differ between the lizard model shapes, indicating that habitat complexity (and potentially predator diversity) is more important than body shape.

Repeating model studies across time can indicate where vulnerability to predation is influenced by temporal factors. For example, Castilla & Labra (1998) found that season as well as habitat had an effect on predation risk: not only were clay model *Podarcis hispanica* lizards (Lacertidae) on the Columbretes islands of Spain attacked by yellow-legged gulls *Larus michahellis*, more frequently when far from vegetation, but also attacks were more intense when models were near gull nests or, out of the breeding season, near gull roosts. Proximity to territories of corvid species increases predation risk on eggs in artificial nests mimicking red-backed shrike *Lanius colurio* nests (Roos & Pärt, 2004).

Model studies can also indicate potential conflicting selective pressures acting on animals. For example, a study of microhabitat use by juvenile broad-headed snakes *Hoplocephalus bungaroides* (Elapidae) was couched in terms of thermoregulation and whether risk of predation deters snakes from basking. Clay models exposed in the sun (representing basking snakes) were attacked significantly more often by bird predators than were models underneath small stones (inside a refuge, where a snake would face thermal costs), suggesting that juvenile *H. bungaroides* trade heat (basking) for safety (Webb & Blumstein, 2005).

### Social interactions

A very different use of clay models is for studying social interactions between conspecifics. Because this topic does not pertain to predation, we shall provide only a brief review of the topic here. Realistic clay models have been used to elicit responses in captive *Egernia whitii* skinks (Sinn, While & Wapstra, 2008; While, Sinn & Wapstra, 2009; While *et al.*, 2010; McEvoy *et al.*, 2013) and it is encouraging to note that even conspecifics outside of a predator-prey situation are sufficiently convinced by clay models that they will react to them as to real animal. In the field, McMillan & Irschick (2010) found that clay models of green anoles *A. carolinensis* were bitten by male green anoles (identified by distinctive bite patterns) and that there was both a habitat and seasonal influence, with more models bitten by anoles in urban areas and more bites occurring during spring and autumn, suggesting peaks in competitive selection pressures.

### Interpretation and problems

There are a number of assumptions around using clay models to draw conclusions about predation. These include assumptions about confirming 'attacks', being able to identify the predators and the accuracy of the models.

### Confirming attacks

The marks left on clay models are used to identify the predators and clear unambiguous marks can allow identification of the attacker to species level in some cases. For example, McMillan & Irschick (2010) were able to record green anole attacks on model anoles by their distinctive bite marks, and Webb & Whiting (2006) were able to identify Superb Lyrebird *Menura novaehollandiae*, bush rat *Rattus fuscipes* and the marsupial carnivore *Antechinus agilis* as predators of their plasticine snake models.

### Identifying predators – and is predator ID always required?

Not only are some predator species unidentifiable from marks on models, but one must also be cautious in inferring predation events at all. Such ambiguity is – perhaps understandably – not recorded in papers, but personal experience once showed us that what appeared to be predatory marks left on model lizards turned out to be simply footprints of Australian Wood Ducks *Chenonetta jubata* that accidentally trod on the models when foraging across the paddock in which the models had been placed.

Pietz & Granfors (2000) set up cameras on artificial nests mimicking those of a ground-nesting bird to record predators and filmed an array of species: rodents, mustelids, canids, deer, cowbirds and hawks. Paluh *et al.* (2015) used cameras on a subset of their model frogs *O. pumilio* and associated round controls, and identified tinamous as predators. Willink *et al.* (2014) set cameras over models of cryptic and aposematic dendrobatid frogs *O. granulifera* and although they were set to high sensitivity, trials showed that they were rarely activated by reptiles and forest crabs. Consequently, the cameras were set to intermittent video mode to try and capture as many visitors to the models as possible. Predators recorded included birds, lizards and crabs and the video data also showed attraction to the models by coatis *Nasua narica*, a capuchin monkey *Cebus capuchinus* and a peccary *Pecari tajacu*. Surprisingly, there has been little other use of cameras in conjunction with clay models, but it is likely that, for some experiments, cameras would prove useful in not only identifying predators (particularly when models are removed entirely), but also in recording potential predators that find and visit models but are not, in the end, motivated to attack them (Willink *et al.*, 2014).

It is, of course, entirely possible that the experimental question and design is set up such that predator identification and the other issues above do not matter. Regardless of the would-be predator, we learn whether the models are being found and attacked. Regardless of the accuracy of the model in appearance and behaviour, we learn if general traits (e.g. body size, microhabitat use) influence attack rates on a broadly 'prey-shaped' object. Few papers have included whether predators will approach and interact with modelling clay or other materials in the field as a control. The salamander *S. s. gallaica* models prepared by Velo-Antón & Cordero-Rivera (2011) were distributed in the field together with round plasticine lumps as controls. All of the models were chewed by rats, but none of

the round lumps were, suggesting that the visual appearance of the models induced predatory attacks. However, in south-west Australian woodlands, of paired clay model lizards and undifferentiated lumps of clay, it was the lumps which were predated on most, often being removed completely (Bateman, unpublished data). If, as suspected, emus *Dromaius novaehollandiae* were the predators, this could be a similar result to that recorded by Paluh *et al.* (2015), where tinamous preferentially preyed on plasticine balls that were perceived as fruit.

### Accuracy of models – does accuracy of the models' appearance, smell and 'behaviour' matter?

It is safe to assume that some aspects of the models will influence how predators detect and respond to them. The appearance, smell and behaviour of the models are all likely to be important. Do predators see the model as they would actual prey? And does a non-moving clay model elicit the same reaction from predators as mobile, reactive, live prey?

Sometimes accuracy of appearance is vital, when the models are intended to look, to predators, like a particular species or local variant of a species. Marshall, Philpot & Stevens (2015) used reflectance spectrometry measurements of Aegean wall lizards *Podarcis erhardii* to alter the colour of the clay used to make lizard models in an effort to mimic the colour as part of their test for the contribution of sexual dimorphism and local variation to predation rates by birds. Similarly, Stuart-Fox *et al.* (2003) created clay models of Australian agamid lizards that matched as closely as possible the reflectance spectra of their target species, together with sex and individual differences. This sort of attention to detail can be important because birds, the main predator taxon considered in most such studies (Fig. 1), have different visual acuity to humans (Hart, 2001), which may affect their predatory behaviour and success (Håstad, Victorsson & Ödeen, 2005). For some taxa that are modelled, visual accuracy is less of an issue. For example, Saporito *et al.* (2007) report that dendrobatid frogs lack significant UV reflectance and hence clay colours can be matched to frogs by eye (Noonan & Comeault, 2009), something also reported for dorsal colouration of the lacertid *Acanthodactylus erythurus* (Fresnillo *et al.*, 2015).

Another criticism of models is the role of olfactory cues in influencing predation. This has been identified as a particular issue for experiments involving plasticine eggs in artificial ground nests (Rangen, Clark & Hobson, 2000). Purger *et al.* (2012b) recommend coating clay eggs with a thin layer of rubber to mitigate high scent cues and to reduce the unnaturally high nest predation recorded from artificial nests with plasticine eggs (e.g. Maier & Degraaf, 2001; Purger *et al.*, 2012a). The sense of smell in birds has traditionally not been considered highly developed (Katz & Dill, 1998), although many birds almost certainly do have a good sense of smell (e.g. Steiger *et al.*, 2008). Olfactory cues are probably more likely to influence predation by small mammals (e.g. Pärt & Wretenberg, 2002) and as modelling clay has a strong, non-animal odour, this may influence attack rate. A similar caveat is the lack of a heat signature from models –

this is likely to influence predation rates by snakes which have never been unequivocally recorded as predators on models (Fig. 1b).

Clay models of frogs, lizards, snakes and mammals lack one criterion that is not a problem for clay model eggs: they do not move, and hence are unlike live animals in this important way. Again, this may not be important if the experimental design is only interested in broad habitat or trait differences; however, crypsis, for example, can be broken when an animal moves (Cooper, Caldwell & Vitt, 2009) and the effect of this on predation is an interesting research area. Paluh, Hantak & Saporito (2014) explored movement disruption of camouflage with brown and red clay models of *O. pumilio* frogs that were attached to the second hand of a clock mechanism hidden beneath leaf litter, such that it appeared that the frog moved in a small circle. Moving brown models were attacked significantly more than were stationary ones, while moving red models were attacked significantly less than were stationary ones, indicating an important role of movement for both aposematic and non-aposematic individuals.

### Does experimental design matter?

Aspects of the methodology that can vary markedly between studies include how many models were used, how long the models were out in the field, and how often were they checked for evidence of attack. There is much variability in how many models are put out and for how long: there may be no optimum number of models and number of days as this will be dependent on the question asked, but the higher the number of variables to be considered, the more models will be required, and an adequate knowledge of the potential predators in the study area is needed when deciding on how long to deploy models. A single check at the end of the study provides information on total number of attacks, but nothing on how soon predators found the models, when they were found (e.g. day vs night), or which models were attacked first, or by what predators. These are variables that could have profound effects on conclusions drawn. An equal final number of attacks on models of two types might be deceptive if one type was found by predators later than the other but received more attacks in each encounter. Collecting data as often as possible and creating an accumulation curve may be one the most useful approaches.

### Application and future directions

Models have been used to test for the presence of potential predators and are a useful test for the effectiveness of pest eradication programmes. Velo-Antón & Cordero-Rivera (2011) made accurate clay models of the salamandrid *Salamandra salamandra gallaica* to assess presence and potential predation by invasive non-native mink *Neovison vison* (Mustelidae) and black rats *Rattus rattus* (Muridae) on small islands off the north-west coast of Spain. Similarly, Jones *et al.* (2005) used paired chicken eggs and brown model eggs to monitor predation on Xantus's murrelet *Synthliboramphus hypoleucus scrippsi* nests by black rats both before and after a rat eradication programme on Anacapa Island (California). In a similar

**Table 1** Suggestions for standardisation of methods, and for future applications

## Experimental design:

- Consideration of potential importance of olfactory cues, movement and accuracy of models
- Check models as frequently as possible and/or use cameras to assist with identification of (a) predation events and (b) predators
- Use of controls where suitable for the experiment

## Reporting:

- Describing model accuracy and including a photograph within the report
- Clearly describe the brand and colour of the clay used and comment on how well it worked (e.g. whether melted or hardened, etc.)

## Future applications:

- Generating 3D digital models that can be shared and printed
- Conservation-relevant questions
- Assessing impacts of urbanization
- Do predators learn to avoid clay models after a time?

conservation-oriented approach, Sato *et al.* (2014) found that development of ski runs in Australian alpine areas resulted in a reduction in vegetation structural complexity and higher predation rates on lizard models by corvids. Santos *et al.* (2013) found the opposite: less predation on snake models in human-altered areas than in grassland reserves in Brazil due to lower density of predators in human-altered areas.

Clay models may similarly help elucidate the impact of other habitat disturbance on predator–prey interactions, such as urbanization. Urban habitats provide benefits such as anthropogenic food resources, resulting in high densities of urban-adapted predator taxa compared with natural areas (Bateman & Fleming, 2012) and therefore increased predation pressure in urban or semiurban environments (Prugh *et al.*, 2009). Urban-adapted reptiles therefore face an assemblage of generalist predators that vary in predation efficiency (Bateman & Fleming, 2011). The use of clay models to explore differences in predation between urban and non-urban areas is surprisingly rare; McMillan & Irschick (2010) considered predation rates on model green anoles in urban and non-urban areas and found that predation was lower in urban areas, suggesting differences in predation pressure.

As part of this review, we noted that there have been few studies that have used controls as part of their experimental design. The use of controls would support interpretations regarding the mechanism (e.g. visual, olfactory) by which predators locate and identify potential prey (e.g. Velo-Antón & Cordero-Rivera 2011). With improved methods of creating models, including 3D printing, it may be possible in the future to standardize the appearance of models and allowing researchers to share the same models across different sites/continents. Additional materials (e.g. soft plastic) may also speed up construction, while the addition of battery-operated mechanisms could add lifelike movement. Coupling this method with the use of camera traps will further test the effectiveness of clay models, improve knowledge about the predators involved, and allow us compare interpretations about predation and predator attraction to models when considering camera data or relying solely on bite marks.

Other technical issues include providing precise information of modelling clay make and colour in each publication. We note that different makes of modelling clay have different melting points and some are highly susceptible to almost

complete dissolution after exposure to sun, blurring or obliterating potential predator marks.

Castilla *et al.* (1999) noted that 81% of deployed model lizards disappeared completely; while potentially indicating predation, this provides no information on the type of predator. To counter this, Bateman *et al.* (2014) tethered their model lizards to a paper plate that was then buried under sand and leaf litter on which the model lizard sat. Similar tethering of models could be used whenever the risk of losing models is likely.

The use of clay models is biased towards visually-oriented predators, but scent is likely to play an important role, as indicated by higher nest predation at artificial nests with plasticine eggs providing an odour cue (e.g. Maier & Degraaf, 2001; Purger *et al.*, 2012a). Coating eggs with a thin layer of rubber may partially counter this (Purger *et al.*, 2012b). We suggest that the use of clay models with associated natural or synthetic prey odour cues may be a fruitful area, for example, either to mask the smell of the modelling material or through the preparation of scent trails culminating in a clay model versus the deployment of clay models without scent trails.

In conclusion, clay models are a useful way to assess predation without the use of live prey animals, and this method is likely to continue to be used in more sophisticated ways in the future. We have identified several areas (Table 1) where standardization of this technique will assist with the experimental design, reporting of projects using clay models, and future applications.

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