

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·km² 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⁻² 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_{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 ($F_{2,106} = 1.7$; $P = 0.093$).

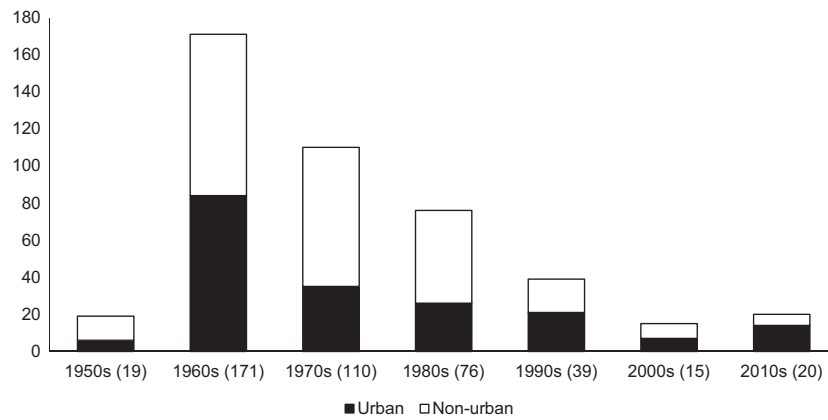


Figure 2. Comparison of urban and non-urban specimens collected over time. Only 3 snakes were collected prior to the 1950s: 2 urban snakes in the 1920s and 1 non-urban snake collected from the 1930s. Data represented as Decade (n).

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 (β) 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

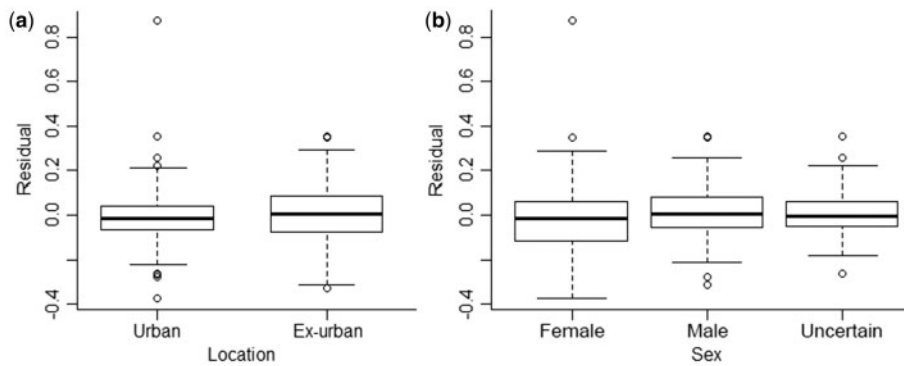


Figure 3. Residual body mass (compared with SVL) for a) urban and non-urban dugites and b) specimens of each sex. Residuals were calculated using a linear regression of log-SVL against log-body mass.

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 ± 2.6 cm for females and 108.5 ± 2.7 cm for males, no significant difference (n.s.), Shine 1989; SVL = 90.8 ± 2.8 cm for females and 104.3 ± 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 km², 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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