



Snake life history traits and their association with urban habitat use in a tropical city

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Abstract

Urbanisation changes landscapes, often simplifying and homogenising natural ecosystems while introducing novel environments. Although this transformation often adversely impacts native wildlife, generalist species that exhibit broad dietary and habitat requirements can persist and take advantage of urban environments. To understand which life history traits most influence the occurrence of a diverse snake assemblage in an urban environment, we leveraged a dataset of 5102 detection records for 12 snake species in the tropical city of Darwin, Australia. By building ecological niche models, calculating urban niche hypervolume, and compiling life history data, we analysed the diversity of environments occupied by each species and determined which landscape components were most associated with occurrence data. In keeping with our hypothesis that generalist species would be more successful, we found that species with broader habitat and dietary preferences, as well as a penchant for arboreality, were associated with larger urban niche hypervolumes and more frequent human–snake interactions. Additionally, we found that colubrid snakes had significantly larger urban niche hypervolumes than elapid species. These findings contribute to understanding how life history traits aid wildlife persistence in, and adaptation to, urban ecosystems, and have implications for landscape design and conservation management.

Keywords Australia · Wildlife management · Human–wildlife conflict · Ecological niche · Distribution · Urban ecology

Introduction

Anthropogenic habitat modification, such as urbanisation and agricultural development, substantially alters spatial attributes of landscapes. These transformative processes fragment, degrade and/or remove natural ecosystems (Alberti 2016), creating novel environments and conditions (Mohanty et al. 2021), modifying resource availability and diversity (Lim et al. 2017), and introducing exotic species (Arazmi et al. 2022), pathogens (Mavroidi 2008) and toxic contaminants (Lettoof et al. 2022). As urbanisation increases at a rate and scale unmatched by background levels of

natural ecosystem change, native wildlife can (1) be extirpated, (2) persist in ‘islands’ of remnant habitat, or (3) adapt to the novel conditions (Lettoof et al. 2021; McDonnell and Hahs 2015; Theng et al. 2020). In response to global biodiversity declines, alongside an increase in human–wildlife conflict and zoonotic diseases, understanding the roles that physiological, behavioural and phylogenetic traits play in the persistence of species in urban environments is a focal area of research (Evans et al. 2011; Liu et al. 2021; Perrier et al. 2018; Santini et al. 2019).

The success of wildlife in urban spaces has often been attributed to taxa that express behavioural and phenotypic plasticity (Dykstra 2018; Lowry et al. 2013), and to species naturally occupying broader niches (i.e., generalists), rather than species that are adapted to a narrow range of environmental conditions (i.e., specialists) (Ducatez et al. 2018; Evans et al. 2011; Liu et al. 2021). Additionally, life history traits, such as high fecundity (Patankar et al. 2021; Saito and Koike 2015), larger body size (Liu et al. 2021), high dispersal and large home range size (Jung and Threlfall 2018), and larger cranial capacity (Santini et al. 2019), can increase the ability of species to adjust to urban life. Research into

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understanding functional traits of urban-adapted vertebrate species has been conducted on birds (Callaghan et al. 2019; Evans et al. 2011), mammals (Santini et al. 2019), and amphibians (Liu et al. 2021), but is broadly lacking for reptiles. Whilst some studies have investigated relationships between broad anthropogenic disturbances and life history traits in reptiles (Doherty et al. 2020; Hu et al. 2020), there is a dearth of literature investigating patterns associated with urbanisation gradients.

Despite reptiles being largely ignored in urban ecology (Collins et al. 2021), snakes—where they are diverse and abundant—may be a useful group with which to explore urban adaptation and space-use. Snake communities are usually comprised of species occupying several size classes and trophic levels (Sosa and Schalk 2016; Zipkin et al. 2020). Often these include top predators, which can act as indicators of environmental health (Beaupre and Douglas 2009; Sergio et al. 2008); and, where medically significant venomous species occur, snakebite can contribute a significant burden on human health systems (Chippaux 2017; Longbottom et al. 2018; Williams et al. 2019). Theoretically, larger snake species may be more prone to success in urban environments, as they generally have higher fecundity and larger home ranges, and the ability to exploit a wider variety of prey (Iverson 1987; Shine et al. 1998; Tamburello et al. 2015). However, larger species may also be more likely to be encountered by humans and, due to a general fear or dislike of snakes, may be more susceptible to relocation or persecution (Bateman et al. 2021; Burghardt et al. 2009). Moreover, components of the urban landscape likely restrict accessibility to snakes with particular traits. For example, heavily urbanised areas, such as industrial- or cityscapes, may be more accessible to arboreal species that can traverse artificially homogenous three-dimensional structures and access the limited shelter sites (Savidge et al. 2021; Slip and Shine 1988). Suburban areas, however, comprise complexes of housing structures, gardens, permanent water sources, and anthropogenic food subsidies, and may support high abundances of prey, such as frogs (Ernst et al. 2011; Liu et al. 2021) and rodents (Feng and Hims-worth 2013), favouring their predators. Thus, understanding how animal ecology and life history, and landscape traits influence urban snake persistence and success is crucial for urban conservation strategies, future urban landscape planning, and mitigating human–wildlife conflict.

Here, we capitalise on an extensive dataset built from routine snake relocations across the city of Darwin, located in the wet–dry tropics of Australia, to investigate spatial ecology of a diverse snake fauna. We calculate niche hypervolumes (habitat utilisation) for each snake species and analyse the association between this measure of niche breadth and several morphological, reproductive, and ecological traits.

Additionally, we use ecological niche models to identify landscape attributes that are most strongly associated with the occurrence of each species in Darwin. We hypothesise that more generalist species (i.e., species with broad dietary and habitat requirements) should be favoured in highly modified urban environments. Such species should exhibit larger estimates of niche hypervolumes and will not be as reliant on the presence of natural bushland patches to persist.

Materials and methods

Study area and data collection

Darwin (12.46° S, 130.85° E) is the capital city of the Northern Territory, Australia. Darwin is a small city of about 146,000 people (Australian Bureau of Statistics, 2016), sprawling across a study area of 1041 km² of varying natural and anthropogenically modified environments. Mean monthly maximum temperatures are >30 °C in all months of the year, and mean monthly minimum temperatures are >20 °C for 10 months of the year. Annual average rainfall is high (1723 mm), with about 80% falling during a four-month monsoonal period (December to March; (Bureau of Meteorology, 2022).

Between 1st January 2011 to 31st December 2017, wildlife rangers and government contractors captured and relocated snakes from urban, industrial and rural areas of the Greater Darwin region, Northern Territory (Parkin et al. 2021). These relocations were typically initiated by members of the public calling a free 24-hour specialist callout service. Methods used have previously been described in Parkin et al. (2021). Snake catchers captured and moved snakes to a suitable nearby area of vacant bushland or urban parkland. Non-venomous snakes were relocated no more than 500 m from the capture site (typically <250 m, if suitable release sites were nearby), while dangerously venomous species were moved to the closest patch of natural bushland, to minimise danger to the public. For each individual snake, we identified the species, time and date of the callout, capture site and street address. Between September 2016 and December 2017, some species were also individually marked using scale-clipping to aid future identification and assess recapture rates (Parkin et al. 2021).

From a total of 7941 callout records, we removed any records for which (1) the species was not a snake, (2) the date was missing, (3) the location was not recorded, (4) the species name was missing or unable to be confidently deduced, (5) any records from prior to 2011 or after 2017 (due to incomplete or inconsistent data entry), and (6) species with less than 20 records (we consider these species to be very uncommon across the study area). Finally, because

Table 1 Life history and ecological traits for twelve species of snake found in Darwin, Northern Territory

Species	Body size		Clutch size (mean)	Diel activity	Lifestyle	Habitat breadth	Dietary breadth	Dominant prey taxa		Niche Hyper-volume
	SVL (mm)	Mass (g)						Species	Darwin	
Pythonidae										
Children's python (<i>Antaresia childreni</i>) <i>n</i> = 641	860	208	6.5	Nocturnal	Terrestrial	7.70	3.75	Mammals (36% of 42)	Birds (44% of 25)	15.42
Black-headed python (<i>Aspidites melanocephalus</i>) <i>n</i> = 32	1567	974	8.6	Both	Terrestrial	5.22	1.38	Reptiles (85% of 49)	Mammals (67% of 3)	0.04
Water python (<i>Liasis fuscus</i>) <i>n</i> = 640	1400	1259	12.9	Nocturnal	Terrestrial	8.72	1.73	Mammals (61% of 28)	Birds (85% of 110)	16.65
Olive python (<i>Liasis olivaceus</i>) <i>n</i> = 220	1830	1140	15.9	Nocturnal	Terrestrial	3.89	1.91	Mammals (53% of 17)	Birds (93% of 27)	10.44
Carpet python (<i>Morelia spilota</i>) <i>n</i> = 1084	1380	1592	11.5	Nocturnal	Arboreal	7.70	1.94	Mammals (72% of 141)	Mammals (59% of 49)	25.27
Colubridae										
Brown tree snake (<i>Boiga irregularis</i>) <i>n</i> = 267	1002	149	5.5	Nocturnal	Arboreal	5.49	4.09	Reptiles (34% of 96)	Birds (93% of 14)	28.94
Common tree snake (<i>Dendrelaphis punctulatus</i>) <i>n</i> = 1092	942	134	8.1	Diurnal	Arboreal	4.03	1.43	Frogs (76% of 74)	Frogs (95% of 37)	15.06
Slaty-grey snake (<i>Stegonotus cucullatus</i>) <i>n</i> = 805	916	247	11.7	Both	Terrestrial	6.34	4.78	Eggs (63% of 19)	Frogs (37% of 43)	22.64
Keelback (<i>Tropidonophis mairii</i>) <i>n</i> = 128	510	116	10.7	Both	Terrestrial	3.30	1.07	Frogs (97% of 149)	Frogs (100% of 3)	3.13
Elapidae										
Northern small-eyed snake (<i>Cryptophis pallidiceps</i>) <i>n</i> = 51	398	29	4	Nocturnal	Terrestrial	3.01	1.12	Reptiles (94% of 18)	-	1.26
Orange-naped snake (<i>Furina ornata</i>) <i>n</i> = 46	331	50	4.3	Nocturnal	Terrestrial	4.70	1.00	Reptiles (100% of 14)	-	0.28
Northern brown snake (<i>Pseudonaja nuchalis</i>) <i>n</i> = 96	878	444	12.2	Both	Terrestrial	3.47	2.10	Mammals (51% of 268)	Reptiles (66% of 3)	1.08

species identification for lesser black whipsnakes (*Demanisia vestigiata*) and greater black whipsnakes (*D. papuensis*) was not always confident due to their morphological similarity, we removed these two species from further analysis. This retained 12 species and 5102 callout records with high quality data (Table 1).

Snake life history traits

For each species in our dataset, we collected seven life history and ecological traits that may influence the ability for snakes to live in more urbanised environments (Table 1). For each species, we used the mean snout–vent length (SVL) for body size, and mean clutch size reported in Greer (1997).

We assigned each species an average body mass derived from the mean body mass of adult snakes collected during callouts between September 2016 and September 2018. Adequate adult body mass data was lacking for two species so, where possible, we used mean values from the literature (e.g., black-headed python *Aspidites melanocephalus*; (Bedford and Christian 1998). No published data exists for the northern brown snake (*Pseudonaja nuchalis*), so we substituted this with the mean mass for the related eastern brown snakes (*P. textilis*) (Whitaker et al. 2000). We classified each species diel activity as either ‘diurnal’, ‘nocturnal’ or ‘both’, and lifestyle as either predominantly ‘arboreal’ or ‘terrestrial’, based on Shine (1995) and our expert assessment of local snake ecology. To assess if a species’ urban

spatial occupancy was a product of broad species-level habitat specialisation, we calculated a habitat breadth index for each species. We used the index presented in Ducatez et al. (2014), extracting the habitat types and total number of co-occurring vertebrate species from the IUCN Red List database (IUCN, 2022) for each of our focal snake species. Higher values of this index represent more generalist species. We chose this method for several reasons, including (1) it is applicable across a large number of taxa, (2) it is a continuous variable and takes into account confounding factors, (3) it does not rely on detailed habitat usage data that is unavailable for our study species, (4) it uses standard habitat categories defined by the IUCN and recently reviewed for all Australian reptiles, and (5) the compositional diversity of co-occurring species is more meaningful than focusing on abiotic attributes.

To assess if a species' diet contributed to their spatial occupancy, we calculated the diet diversity of each species and assigned each species a dominant prey taxon. To determine diet diversity, we used Levins' index of diet breadth (Levins 1968) because it gives more weight to the abundant food categories. The food categories we used were: bird, mammal, reptile, frog, eggs (bird and reptile), and fish. Diet records for each snake species were collected using the R package *SquamataBase* (Grundler 2020), with records for *Cryptophis* supplemented from Shine (1984), combined with our own data collected from snake callouts. The Levins' index of diet breadth calculates a single value for a species, where 1 is low breadth (a single prey taxon is eaten) and higher values describe a variety of prey taxa eaten in similar proportions. To determine the dominant prey taxon for each species we used the prey taxon with the highest proportion of diet records, from records collated in *SquamataBase*. Because generalist snake species have been shown to have regional, seasonal or urban-induced shifts in diet (Capizzi et al. 2008; Hampton and Ford 2007; Luiselli 2006), we also assigned each snake a Darwin-specific dominant prey taxon. The Darwin-specific dominant prey taxon was determined from the highest proportion of prey taxon found with or regurgitated (post-capture) by each species during snake callouts.

The functional traits that govern ecological community composition, niche-partitioning among species, and organisms' capacity to respond to environmental change can be biased towards species sharing a common ancestry (phylogenetic history), as innovative traits conserved within a clade can arise faster than through convergent evolution in phylogenetically distant taxa (Cavender-Bares et al. 2009; Gallien and Carboni 2017; Webb et al. 2002). Thus, to assess potential phylogenetic drivers of trends, each species was also classified as a member of the families Pythonidae, Colubridae or Elapidae.

Landscape classification

To classify landscape variables around Darwin, we used the Northern Territory Land Use Mapping for Biosecurity 2016 (Staben and Edmeades 2017). This provided fine-scale and accurate polygons of the entire sampled study area. From satellite imagery and ground-truthing, we reclassified these polygons into six broad, ecologically relevant landscape types using QGIS v3.10.14 (QGIS, 2021). Landscape types (Fig. 1) included: permanent water bodies (Water), floodplains and ephemeral swamps (Wetlands), woodlands and vine forests (Forest), open grassland, agricultural vegetation, and bare ground (Plains), residential infrastructure with greenery/gardens (Suburban), and land dominated by concrete/asphalt infrastructure, roads and impervious surfaces (Urban).

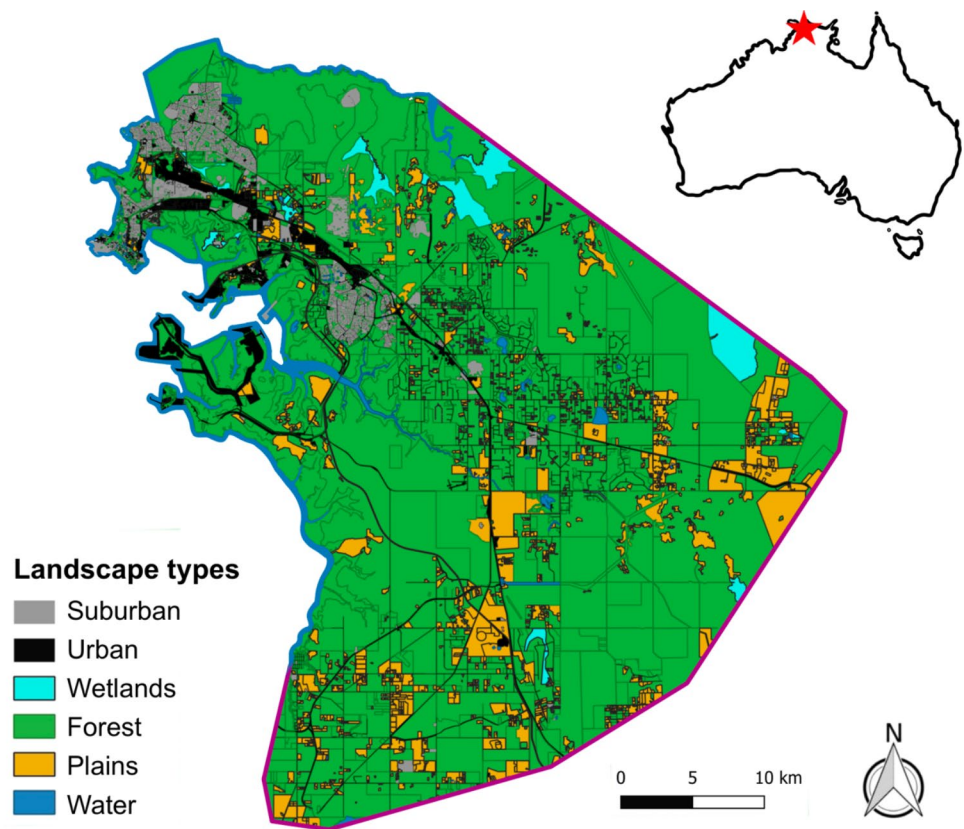
Niche hypervolume estimation

In addition to the range-wide habitat breadth index calculated above, we quantified the local range of landscape types utilised by each species through the construction of a multidimensional hypervolume (Blonder and Harris 2018). This represents the niche breadth of each species within the study area. We first calculated the area of each landscape type for a buffer zone around every snake capture location. This buffer zone represents potential/assumed space use by an individual snake. Most studies use an arbitrary area around records (e.g., from 25 m to 1 km buffers) (Giraudeau et al. 2014; Liu et al. 2021; MacGregor-Fors and Schondube 2011; Meillere et al. 2015); however, we roughly calculated a more biologically relevant area using estimates of species-specific home-range size. As home-range estimates were non-existent for almost all the study species, we used the known positive correlation between body size and home-range size (Fiedler et al. 2021; Tamburello et al. 2015) to estimate home-range sizes for each species. After controlling for energy use, Tamburello et al. (2015) determined the home-range area estimates for snakes to be the regression of:

$$2.17 + 1.18 \times \log_{10}(M)$$

Where M is body mass in grams. As species could easily be categorised into two body mass sizes: small (<500 g) and large (>500 g), we used the regression equation to determine the buffer zone around each record for these two categories. This prevented over-fitting home-range sizes to species based on a general rule-of-thumb. Home range estimates were 6.76 ha (134 m radius) around records of species with a small (mean \pm SE: 172.1 \pm 46.6 g) body mass, and 66.41 ha (457 m radius) around records of species with

Fig. 1 Map of Darwin, Northern Territory, Australia overlaid with the six landscape types that were classified from a modified version of the Northern Territory Land Use Mapping for Biosecurity (2016). The study area boundaries are delimited in purple and by the Arafura Sea to the north-west



a large (mean \pm SE: 1241.3 ± 130.7 g) body mass. We then converted the area of each landscape type within an individual's buffer zone to a percentage of the total area of that buffer zone, so that values were comparable between the two size categories.

We calculated the niche hypervolumes of each species from the area of each landscape type in the buffer zones around each occurrence point. These hypervolumes measure the multidimensional space (volume) defined within the bounds of scaled and centred environmental predictor variables (Blonder et al. 2017; Tingley et al. 2014). Hypervolumes were constructed using a one-class support vector machine method, via the *hypervolume_svm* function (with default γ value of 0.5) of the “hypervolume” package (Blonder and Harris 2018). The support vector machine method was chosen because it allows for outlier inclusion while generating a smooth boundary around the data. Before calculating each hypervolume, we thinned the records for each species so that just one record was present within a 250 m x 250 m pixel, minimising bias from localized survey effort.

We used the niche hypervolume as the single continuous variable to represent a species' urban niche occupation, with higher hypervolume values signifying a greater use of the urban landscape. To identify whether snake niche hypervolume was a product of life history traits, we ran

multiple univariate generalised linear models (GLMs) with species hypervolume as the response variable and each trait (Table 1) as the predictor variable. Due to the sample size of 12, we had insufficient power to create multivariate models or use random effects. Collinearity for continuous traits was compared, but, other than SVL and mass, no two variables were strongly correlated ($r^2 < 0.7$). For analyses of snake body size, we used SVL as the predictor variable. All models were fitted with the most appropriate error distribution family determined by distribution of the model residuals.

Ecological niche modelling

We constructed ecological niche models to identify which of our six landscape types were most strongly associated with the occurrence of each snake species. From across the entire study area, a set of 10,000 random background (pseudo-absence) points were sampled. To compensate for spatial sampling bias in the occurrence data for each species, we modified our sampling of background points by incorporating a probability function that corresponded to the bias in sampling effort (von Takach et al. 2020). Sampling effort across the study area was estimated by producing a two-dimensional Gaussian kernel density grid of all 5102 snake occurrence records. The kernel density grid was created using the *kde2d* function of the “MASS” package (Ripley

et al. 2013), with the default normal reference bandwidth calculation. This bias reduction method allows for sampling proportionally more background points from geographic areas that have been subjected to a greater survey effort, and fewer background points from less well surveyed regions, and is commonly used to account for spatial bias in sampling effort (Molloy et al. 2017; Phillips et al. 2009; Syfert et al. 2013). We used the “Maxent” algorithm (Phillips et al. 2006, 2017a) to create ecological niche models. Maxent was chosen because its predictions have been shown to perform well when accounting for sampling bias and by utilizing many background points from the landscape (Elith et al. 2011; Syfert et al. 2013). The default output of Maxent is a habitat suitability value that has undergone a logistic post-transformation. The *maxent* function of the “dismo” package (Hijmans et al. 2017), with five cross-validation runs, was used to create the ecological niche model. Mean values of all cross-validation runs for two metrics were extracted from the model output. These metrics included (a) the area under the curve (AUC) of a receiver operating characteristic, which estimates overall model fit via a threshold-independent measure of predictivity, and (b) permutation importance, a measure of the relevance of each predictor variable to the response variable. To calculate permutation importance, the values of a predictor variable are first randomly permuted among the occurrence and background points, the model is re-evaluated, and the resulting drop in the AUC value is calculated and normalized to a percentage (Phillips et al. 2017b; Searcy and Shaffer 2016).

Results

Diet

The diet breadth of snake species captured throughout Darwin ranged between 1.00 (*Furina ornata*) and 4.78 (*Stegonotus cucullatus*; Table 1). Five species, *Antaresia childreni*, *Aspidites melanocephalus*, *Liasis fuscus*, *Liasis olivaceus* and *Boiga irregularis*, all exhibited a difference in dominant prey taxa in Darwin compared to the dominant prey taxa known from their species more generally (Table 1). For three species, *Antaresia childreni*, *Liasis fuscus* and *Liasis olivaceus*, birds were the dominant prey taxa in Darwin, whereas their natural diet is dominated by mammals. Domestic chickens and caged birds contributed to a large proportion of prey items taken by these species (Table S1). *Pseudonaja nuchalis* and *Aspidites melanocephalus* also exhibited a shift in their dominant prey taxa; however, sample sizes, and thus confidence in this shift, were limited.

Urban niche hypervolumes

The urban niche hypervolumes varied among species by two orders of magnitude: 0.04 in *Aspidites melanocephalus* to 28.94 in *Boiga irregularis* (Table 1). Niche hypervolumes were highest in *Boiga irregularis*, *Morelia spilota* and *Stegonotus cucullatus*, and lowest in *Aspidites melanocephalus*, *Furina ornata*, *Pseudonaja nuchalis* and *Cryptophis pallidiceps*, broadly reflecting the frequency with which the species was captured in the study area. There was a significant positive relationship between a species urban niche hypervolume and both their diet breadth ($r^2=0.46$, $X^2=9.55$, $df=1$, $p=0.002$; Fig. 2a) and habitat breadth ($r^2=0.37$, $X^2=6.35$, $df=1$, $p=0.011$; Fig. 2b). Arboreal species had a significantly higher urban niche hypervolume than terrestrial species ($r^2=0.73$, $X^2=38.54$, $df=1$, $p<0.001$; Fig. 2c), and species in the colubrid family had a significantly higher urban niche hypervolume than species in the elapid family ($r^2=0.37$, $X^2=6.32$, $df=2$, $p=0.042$; Fig. 2d).

Urban ecological niche modelling

Ecological niche modelling using Maxent produced moderate to high AUC values (0.82–0.94), suggesting that model fits were suitable for analysis. The AUC values for the testing data were typically close to, but slightly lower than the values for the training data, as expected.

Most snake species did not appear to avoid highly modified urban landscapes across our study area, with importance values for the urban landscape type >30% for all species except *Tropidonophis mairii* and *Pseudonaja nuchalis* (Table 2). For those two species, the percentage of natural woodland and forest space was overwhelmingly important (74.6% and 46.1%, respectively). Similarly, many species, including *Antaresia childreni*, *Stegonotus cucullatus*, *Dendrelaphis punctulatus*, *Liasis fuscus* and *Aspidites melanocephalus*, were common in suburban landscapes (importance values >20%). Forested landscapes were moderately important (>15%) for *Morelia spilota*, *Boiga irregularis*, *Dendrelaphis punctulatus*, *Liasis fuscus*, *Liasis olivaceus* and *Furina ornata*, and open grassland and agricultural (plains) landscapes were moderately important (>20%) for *Tropidonophis mairii*, *Furina ornata* and *Cryptophis pallidiceps*. Wetland and water landscapes were generally not important for any species except *Tropidonophis mairii* (wetland importance=13.64%) and possibly *Furina ornata* (wetland importance=8.76%).

Fig. 2 Association between snake (a) dietary and (b) habitat breadth, (c) lifestyle, and (d) phylogeny and their urban niche hypervolume for twelve species of snake caught in Darwin, Northern Territory

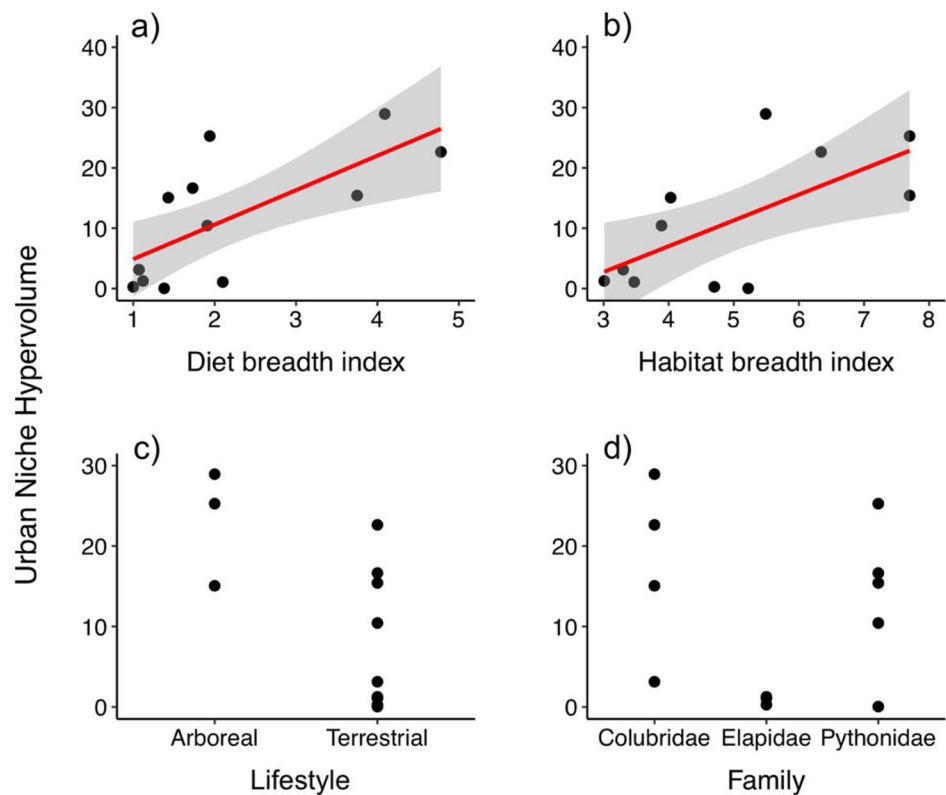


Table 2 Permutation importance values for urban landscape ecological niche models for twelve species of snake caught in Darwin, Northern Territory

	Urban	Suburban	Forest	Plains	Wetland	Water
Pythonidae						
<i>Antaresia children</i>	48.17	33.03	7.89	7.35	2.73	0.82
<i>Aspidites melanocephalus</i>	47.79	43.29	3.88	2.49	0.51	2.03
<i>Morelia spilota</i>	54.93	16.59	17.79	6.61	1.82	2.26
<i>Liasis fuscus</i>	42.09	29.05	18.74	6.55	2.28	1.30
<i>Liasis olivaceus</i>	48.28	18.50	15.26	13.81	3.29	0.86
Colubridae						
<i>Boiga irregularis</i>	47.77	16.10	18.20	13.00	1.43	3.51
<i>Dendrelaphis punctulatus</i>	37.01	30.51	18.79	8.20	3.15	2.34
<i>Stegonotus cucullatus</i>	58.05	27.06	5.13	4.32	4.37	1.07
<i>Tropidonophis mairii</i>	4.03	12.84	46.17	21.39	13.64	1.93
Elapidae						
<i>Cryptophis pallidiceps</i>	52.20	3.63	7.18	35.90	0.19	0.90
<i>Furina ornata</i>	30.17	16.74	17.59	20.78	8.76	5.95
<i>Pseudonaja nuchalis</i>	7.78	9.39	74.57	2.61	3.47	2.19

Discussion

In support of our hypothesis that urbanisation should favour generalists, we found that habitat and dietary breadth, as well as arboreality, was associated with larger urban niche hypervolumes in snakes in a tropical urban landscape. Additionally, we found that colubrid snakes had significantly higher urban niche hypervolumes than elapid species. The traits we identified as associated with urban success in

snakes are broadly paralleled in other taxa (Evans et al. 2011; Santini et al. 2019), but we provide the first explicit example of generalist snakes being favoured in more urbanised landscapes. Because our findings equally suggest that more specialised species are less likely to be able to exploit urban ecosystems, and specialist species tend to have higher extinction risk (Davies et al. 2004), this research has implications for conservation of urban biodiversity. Additionally, understanding the urban land-use preferences of snake

species can help inform management of urban ecosystems and biodiversity, snake relocation policies, and mitigate human–snake conflict.

Ecological traits and snake urban space use

The diversity of habitats occupied by a vertebrate species is typically related to their (1) dietary breadth (Terraube and Arroyo 2011; Terraube et al. 2014), (2) physiological range and flexibility (Bonier et al. 2007; Gilchrist 1995; Nowakowski et al. 2018), (3) behavioural plasticity (Overington et al. 2011) and (4) functional morphology/locomotion (Ferry-Graham et al. 2002; Santini et al. 2019; Webb 1984). Thus, more generalist vertebrate species (i.e., those with a larger habitat breadth) likely possess advantageous traits for colonising, occupying and persisting in modified habitats (Ducatez et al. 2018; Liu et al. 2021). Here, we found a positive relationship between snakes' habitat breadth and the hypervolume of their urban niche, as well as greater urban niche hypervolumes in arboreal species. The three arboreal snakes—carpet pythons, common tree snakes, and brown tree snakes—have also successfully exploited urban areas in other regions of Australia, and are frequently found using human structures to access both prey and shelter (Fearn et al. 2001; Parkin et al. 2021; Shine and Koenig 2001). Where arboreal species are present, arboreality may contribute to success in urban areas because arboreal snakes have an improved ability to exploit novel three-dimensional structures and are potentially less restricted by barriers to dispersal (e.g., roads, fences, buildings) and threats (e.g., dog and cat predators) compared to more terrestrial species (Akani et al. 2002; Holderness-Roddam and McQuillan 2014; Lettoof et al. 2021; Quintero-Ángel et al. 2012).

In Darwin, snake species with broader dietary breadth occupied a broader range of environmental conditions. Broad diets are likely to be advantageous over specialised diets in novel urban ecosystems if species can opportunistically exploit locally abundant and/or novel prey. Indeed, some urban snake species are known to capitalise on different and novel prey species in urban areas. For instance, brown tree snakes (*Boiga irregularis*) exploit introduced birds and rodents in urban Guam (Savidge 1988), African rock pythons (*Python sebae*) predominantly feed on domestic poultry, pet dogs and introduced rats in suburban Nigeria (Luiselli et al. 2001), and carpet pythons depredate domestic pets and caged birds in suburban Brisbane, Australia (Fearn et al. 2001). In Darwin, of the five python species found, four were frequently recorded depredating non-native prey species, such as pet caged birds, poultry, and black rats (*Rattus rattus*), resulting in a shift away from the known dominant prey taxa of these pythons. Although urban landscapes tend to favour fewer faunal species, those that do prosper can be

abundant (Faeth et al. 2011; McKinney 2008; Shochat et al. 2015; Sullivan et al. 2016). It is, therefore, unsurprising that opportunistic and flexible predatory snake species exploit locally abundant urban prey resources, a pattern reflected in dietary shift observed in carnivorous birds and mammals (Dykstra 2018; Larson et al. 2015). Furthermore, species with the innate ability to feed on a broader diet often have a greater capacity to exploit novel or abundant resources in more urbanised environments (Moller 2009; Patankar et al. 2021).

We did detect a potential signal of phylogenetic bias—colubrid species had significantly larger urban niche hypervolumes than elapids. However, this bias may genuinely reflect colubrid snakes' ability to colonise novel habitats (Ivanov 2000; Rodda et al. 1992; Weiperth et al. 2014), rather than a sampling bias. Colubrids are arguably the most successful radiation of snakes on the planet, boasting the widest phylogenetic diversity and geographic distribution of any snake family (Figueroa et al. 2016; O'Shea 2018; Pincheira-Donoso et al. 2013). Regarded as a global megaradiation, the success of colubrids has been attributed to the diversity of arboreal species within the family, providing access to a wider variety of prey (Harrington et al. 2018) and, thus, an ability to exploit otherwise underutilised ecological opportunities (Grundler and Rabosky 2021). Despite their international success, however, colubrids are comparatively recent arrivals to Australia, having emigrated to a land where most terrestrial snake niches were already filled by pythons and elapids (Shine 1991). This appears to explain the lack of diversity and endemism in the family in Australia—there are only five species of Australian colubrid, none of which are endemic (cf. 109 terrestrial elapid species; (Wilson and Swan 2021). Additionally, Australian colubrids are confined to wetter, forested parts of the continent, having failed to penetrate southern and interior regions (Cogger 1981; Greer 1997). Thus, colubrids are not considered a successful radiation of snakes in Australia (Shine 1991). Despite this, all of the region's colubrid species were frequently collected in the study area across the duration of the study, compared to most local elapid species (62% of species) that were not or only very rarely encountered during the study (Parkin et al. 2021). Presumably because of their broad habitat requirements, dietary breadth/plasticity and exploitation of arboreal lifestyles, Australian colubrids have a preadapted advantage over elapids to exploit urban environments, as they have done throughout Darwin. However, elapids exhibiting arboreality in many other regions of the world (e.g., *Bungarus caeruleus*, *Naja spp.*, *Ophiophagus hannah*, *Dendroaspis jamesoni*, and *D. polylepis*; (Hauptfleisch et al. 2020; Ingle et al. 2019; Marshall et al. 2019; Widodo et al. 2019; Zassi-Boulou et al. 2020) are regularly found in urban areas, often exploiting human structures and

roof spaces. Therefore, urban exploitation may be a function of lifestyle traits shared by these species and not entirely explained by phylogeny.

Snake landscape utilisation

Our ecological niche models suggested that many native tropical snake species are capable of persisting in or near to urban and suburban areas in Darwin. Some species potentially move between the natural and urbanised habitats, and may be more reliant on connectivity with habitat or gene flow outside of the urban matrix. Such patterns have been shown in *Morelia spilota*, where individuals exhibit seasonal shifts between natural environments and urban dwellings (e.g., roof spaces; (Shine and Fitzgerald 1996; Slip and Shine 1988). Partitioning of dietary resources has been shown to be a stronger structuring agent for syntopic (i.e., coexisting without interference) snakes than habitat resources (How and Shine 1999), and we speculate that differences in preferential prey, in combination with anthropogenically maintained prey availability (e.g., introduced black rats, cage birds, and poultry), among species allows the diversity of Darwin snakes to simultaneously use similar landscape types.

The ‘urban’ landscape of our study is comprised primarily of impervious, smooth surfaces (roads), homogenous three-dimensional structures (buildings), and relatively high-density human activity—characteristics that are generally unfavourable or risky for snakes (Bauder et al. 2020; Wagner et al. 2021). However, these landscapes can provide high densities of commensal rodent prey (Aplin et al. 2003) and thermally favourable refugia and nesting sites (French et al. 2018; Zappalorti and Mitchell 2008). Previous studies have demonstrated that some North American snakes exploit these resources by using the edges of heavily urbanised or disturbed areas (Anguiano and Diffendorfer 2015; Bauder et al. 2018; Row and Blouin-Demers 2006). Considering snakes in Darwin were rarely collected from the cores of these areas (e.g., industrial complexes, city CBD), we suspect the species we found to have high affinity for proximate urban areas are likely utilising the edges of these landscapes as opposed to living within the most heavily urbanised areas. Although comprising of similar features, the ‘suburban’ landscape is also intersected with modified green areas (e.g., gardens, mowed grass, vegetated parks) and permanent water sources (e.g., taps, reticulation, ponds and pools); supporting abundant prey, such as frogs, rodents, lizards (Bartholomaeus 2010; Hamer and McDonnell 2009; Liu et al. 2021), and domestic animals, as well as providing novel refugia (e.g., roofing spaces, compost heaps, concrete slabs and scrap piles) (Zappalorti and Mitchell 2008). Moreover, these suburban landscapes may

provide more stable prey, water, and shelter resources than the surrounding forests and savannas, where populations of native species are subjected to a range of challenging and threatening processes (Leahy et al. 2015; Penton et al. 2021; von Takach et al. 2022).

Management implications

Urban planning and landscape design is increasingly considering the conservation and enrichment of wildlife (Hess et al. 2014), including predators, such as snakes, that play fundamental roles in ecosystem food webs. With increasing landscape homogenisation resulting from the process of urbanisation, it is difficult to maintain or rehabilitate ecosystem components for species such as dietary and habitat specialists; however, focussing efforts on establishing a broader diversity of habitat or prey species may increase the likelihood of specialists persisting in urban ecosystems. For example, properly designed stormwater retention ponds (Hamer et al. 2012) and artificial frog ponds (Bartholomaeus 2010; Moor et al. 2022; Oertli and Parris 2019) can increase connectivity and abundance of urban frogs, which may support anurophagous snakes. Moreover, terrestrial snake species could benefit from adequately sheltered habitat patches or corridors; ground vegetation cover (longer native grasses and shrubs), complex rock or log piles, and appropriate canopy tree species distributed through the urban matrix could encourage and support terrestrial snake diversity (Kjoss and Litvaitis 2001; Nordberg et al. 2021; Zappalorti and Mitchell 2008). In contrast, human–snake conflict is a globally significant issue (Chippaux 2017; Shine and Koenig 2001; Williams et al. 2019) with impacts ranging from harmless species entering a home or backyard, the predation of domestic pets, poultry and livestock, to morbidity or mortality from dangerously venomous snake bites. Understanding the ecological and life history traits, and landscape preferences of urban snakes may assist in developing strategies that help mitigate the most severe impacts of human–snake conflict on communities living with high urban snake populations. Increasing awareness, via public education on snake-proofing cages and aviaries, may reduce pet and poultry predation from snakes, minimising the unnecessary killing of harmless snakes by distressed residents, and alleviate human–snake conflict in Darwin, elsewhere in Australia and across the Globe.

Conclusion

As urbanisation expands at an ever-increasing rate across the planet, biodiversity will continue to be degraded, filtered, and/or lost. Snakes can represent a substantial

proportion of local biodiversity, contributing to ecosystem function, and potentially indicating long-term changes in ecosystem health (Beaupre and Douglas 2009). Inevitably, some snakes are imperilled by increasing urbanisation, while other snakes persist or are even advantaged by novel urban resources. Understanding the life history and ecological traits that dictate species' responses to urbanisation are crucial to conservation efforts, as well as mitigating human–snake conflict and snakebite risk. This research would be complemented by additional global studies comparing the abundance, or success, of snakes in urban areas with similar life history and ecological traits.

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Code availability Code created for this study is available on request from the corresponding author.

Declarations

Conflict of interest The authors declare they have no conflicts of interest.

Ethics approval Scientific research permits and permits to interfere with protected wildlife were approved by the PWCNT under permit numbers: 61117 and 61617. Ethics approval was given by the Curtin University Ethics committee (Approval number: ARE2017-18).

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