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Ecological and behavioural traits of the Sri Lankan water monitor (*Varanus salvator*) in an urban landscape of Western Province, Sri Lanka

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Abstract. The Asian water monitor *Varanus salvator* is one of the largest species of lizard in the world and is widespread on the island of Sri Lanka. In the present study, we conducted a 7-month survey within a 5-km stretch in the urbanised Attanagalu-Oya river area to study habitat associations, mesohabitat use and behaviour of *V. salvator* in urban landscapes. The greatest number of monitor sightings was made in aquatic habitats, followed by terrestrial and arboreal habitats within the riparian zone. Sightings of different life history stages of *V. salvator* across major habitat types varied significantly. The adults and subadults associated mostly with aquatic and terrestrial habitats, whereas hatchlings and juveniles associated mostly with aquatic and arboreal habitats. Given variable sighting frequencies of distinct life history stages across different major habitat types, it is likely that there is substantial age-structured niche partitioning in *V. salvator*. The urban population of *V. salvator* studied seemed to be fairly abundant, and resilient to anthropogenic stressors and adversity of urbanisation. In species-depauperate urban environments, ecosystem functions provisioned by *V. salvator* as generalist predators as well as scavengers are arguably significant and deserve further investigation. No direct anthropogenic threats were observed during the study.

Additional keywords: adaptability, conservation, habitat generalist, urban environment, varanid lizards.

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Introduction

The Asian water monitor *Varanus salvator* is widely distributed throughout the Oriental biogeographic realm, which includes south and south-eastern Asia, the mainland, Indian oceanic islands (e.g. Sri Lanka, Andaman Islands and Nicobar) and the Indo-Australian archipelago (Böhme 2003; Koch *et al.* 2010). Recent phylogenetic studies indicate that *V. salvator* represents a species complex with significant genetic variations across its large range (Koch *et al.* 2010, 2013; Welton *et al.* 2014). It is one of the largest extant lizard species in the world (on average, reaching 1.5-m total length and a weight of 10 kg; Gaulke *et al.* 2004), and the largest specimen known, a male measuring 3.21-m total length, was recorded from Sri Lanka (Randow 1932).

Two species of varanids are known from Sri Lanka, namely *V. salvator* and the much smaller Bengal monitor *Varanus bengalensis*. Both monitors have nearly sympatric, island-wide distributions: *V. bengalensis* occurs from the coast to an elevation of 500 m, whereas *V. salvator* occurs in most areas up to 1100-m elevation (Das and De Silva 2005; Somaweera and Somaweera 2009). *V. salvator* is frequently associated with many aquatic habitats (both inland and coastal) and terrestrial habitats adjoining water bodies (Koch *et al.* 2013). It is diurnally active and remains active from sunrise to sunset. *V. salvator* spends the morning and afternoon hours foraging and swimming. Its terrestrial habitat use is mostly restricted to thermally stable substrates and microhabitats in the riparian zone, such as dense vegetation, vegetated floodplain marshlands and burrows (Erdelen 1991; Gaulke *et al.* 2004; Koch *et al.* 2013).

In recent decades, scientific interest in monitors, particularly *V. salvator*, has undergone a renaissance. These studies have

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Fig. 1. (*a*) *Varanus salvator* (total length: 247.5 cm in, weight: 14.8 kg) in Attanagalu-Oya area. (*b*) *Varanus salvator* feeding on polythene-wrapped fish remains.

investigated taxonomy and phylogenetic affinities, biogeography and evolutionary radiation, local and regional distribution, thermal ecology, feeding habits, threats and conservation, as well as comparative ecophysiology and behaviour (Pianka 1969; Perry and Garland 2002; Sutherland 2011; Koch *et al.* 2013). Despite a regional and international increase in ecological research on these reptiles, similar studies in Sri Lanka have not progressed in the recent past. The limited number of existing studies on *V. salvator* of Sri Lanka have been conducted in forested, rural or ex-urban environments (Wikramanayake and Dryden 1993; Karunarathna *et al.* 2008), with very limited insight on the ecology of *V. salvator* in urban environments (Rathnayake *et al.* 2003; Karunarathna *et al.* 2008). Even these studies have been largely focused on thermal ecology or thermoregulatory behaviours (Wikramanayake and Green 1989; Wikramanayake and Dryden 1993; Rathnayake *et al.* 2003), whereas enumeration of population size or relative abundance, habitat associations or microhabitat preferences have not received adequate attention.

Studies conducted elsewhere on *V. salvator* have shown variable population-level and behavioural responses to urbanisation that suggest that ecological responses to urbanisation can vary across different geographies (Uyeda 2009; Kulabtong and Mahaprom 2014). Furthermore, resource distribution, microhabitat and macrohabitat availability and environmental complexity differ remarkably across urban–rural gradients (McKinney and Lockwood 1999; McKinney 2002). Declining richness in local and regional species pools, particularly for reptiles, due to variable intensities and extents of urbanisation has been demonstrated globally (Greenberg 2001; Ovaska *et al.* 2004; Barrett and Guyer 2008). Homogenisation of the biophysical environment, a disequilibrium state in community organisation and tremendous variation in energy and matter dynamics are the principal reasons for reduced biodiversity in urban environments (McKinney and Lockwood 1999; McKinney 2002). Thus, studying 'urban-adaptable' species will shed light onto the process of biotic homogenisation of urban and built-up environments. Moreover, *V. salvator* is semiaquatic; thus, its performance and physiology depend on the quality of both aquatic and riparian habitats. Owing to urban run-off, point-source pollution and inadequacy of vegetation cover across the watershed, the adverse effects of urbanisation are disproportionately high on aquatic habitats; therefore, water-dependent species may suffer greatly in built-up environments (Dudgeon 2000; Grimm *et al.* 2008).

In the present study we investigated the habitat associations, mesohabitat use and behaviour of *V. salvator* (Fig. 1) in an urban environment (Attanagalu-Oya) of Western Province, Sri Lanka. More specifically, the present study: (1) quantified sightings of *V. salvator* across different types of major habitats (aquatic, terrestrial and arboreal); (2) investigated differential patterns in occupancy of major habitats by different life history stages; (3) investigated life history stage-dependent mesohabitat associations; and (4) identified differences in types of behaviour among different life history stages.

Materials and methods

Study area

The study area, the Attanagalu-Oya river basin (Fig. 2), is an urbanised landscape found in Sri Lanka's lowland (5–20 m) wet zone (annual rainfall 2000–2500 mm, annual temperature ~28°C; Samarakoon and Renken 1999) and flanked by the Attanagalu-Oya River (7°5′33.29″–7°5′58.92″N, 79°57′23.11″–80°0′1.48″E). With an extent of 779 km^2, the Attanagalu-Oya River Basin is located between two larger river basins (Kelani and Maha Oya) in Western Province (Gampaha District), Sri Lanka (Pathirana *et al.* 2010). Over 40 km^2 of the riparian zone of the Attanagalu-Oya River has been used for commercial-scale paddy farming since historical times. In addition to riparian agriculture, built-up environments (industrialised areas, commercial development and multilane highways) and home gardens are the major land cover types in the region (Halwatura *et al.* 2013). With four major urban water supply intakes, the Attanagalu-Oya River also plays an important role in the national water supply. The river water is subturbid and shallow (maximum depth ~6 m, average depth ~3 m, during April–June), with few rapids along its length.

The research methods used in this study were approved by The Institutional Animal Care and Use Committee (IACUC) Committee of Bridgewater State University.

Field survey and data collection

The study site was visited 4–5 days per month for 7 months from September 2015 to March 2016. Collectively, three people spent 32 days at the study site (7–9 and 16 September, 12–13 and

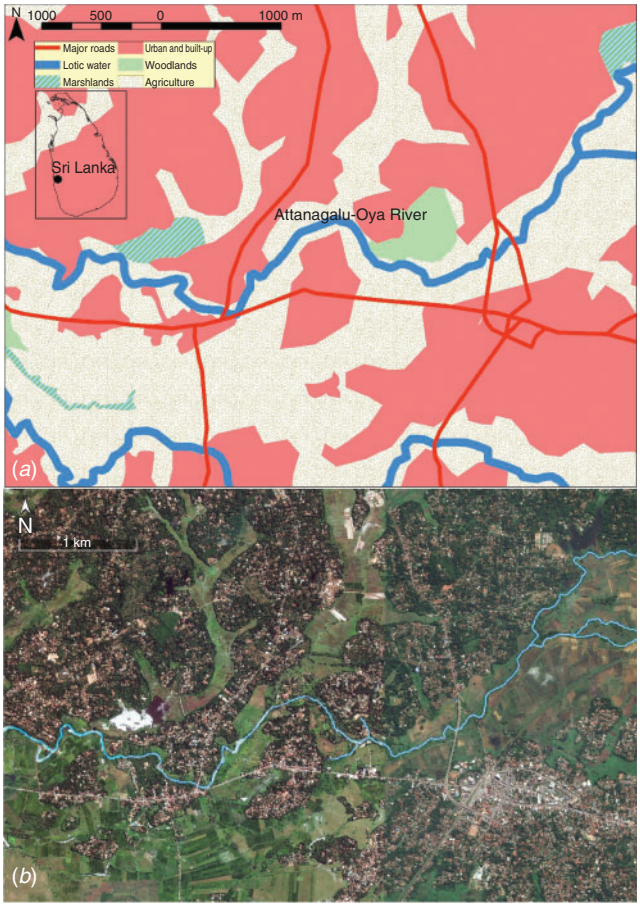


Fig. 2. (*a*) A land use land cover map of the study area around the Attanagalu-Oya River in Sri Lanka. The black circle on the inset map indicates the study area. (*b*) An aerial image of the study area.

21–22 October, 3–4 and 17–18 November, 9–10 and 21–23 December in 2015; and 6–8 and 25–26 January, 12–14 and 22–23 February, 2–4 and 14–15 March in 2016). The survey period overlapped both the south-western (May–September) and north-eastern (November–February) monsoon seasons, with intense torrential rainfall, as well as the relatively dry inter-monsoon season (March–April) to enable observations across different climatic conditions. During each day, the site was surveyed for 6 h at three different times: 0700–0900 hours in the morning, 1100–1300 hours in the afternoon and 1500–1700 hours in the evening. Previous studies have suggested that these are the general times when *V. salvator* is active (Wikramanayake and Green 1989; Wikramanayake and Dryden 1993). Direct observations were made along an approximate 5-km stretch of the river and ~500 m into either side of the riparian zone by walking, riding a motorbike on gravel and paved roads parallel to the river, and paddling a canoe on the river.

Once *V. salvator* individuals were found, we documented the major habitat type (aquatic, arboreal or terrestrial) and mesohabitat type (determine based on the substrate occupied and specific type of locality in which the individual was found) occupied, as well as the behaviour of the individual at the time of encounter. Based on body size, all *V. salvator* were categorised in the following life history stages: adults (snout to vent length, SVL, >65 cm), subadults (SVL 45–65 cm), juveniles (SVL 30–45 cm) and hatchlings (SVL <25 cm). In addition, the following environmental variables were documented at the point of encounter: (1) air temperature and relative humidity, evaluated using a QM-1594 multifunction environment meter (Digitech Instruments Co., Ltd, Hong Kong, PR China); (2) water temperature, determined using a standard thermometer; (3) pH measured using QM-1670 hand-held pH meter (Digitech Instruments QM–1670, Hong Kong, PR China); and (4) canopy cover, determined using a canopy densitometer. In addition, we accessed temperature and precipitation data for the general area through the Gampaha field station of the Meteorological Department of Sri Lanka, located 500 m north of the study area.

Statistical analyses

Statistical analyses were performed using a combination of R Studio, ver. 1.0.136 (RStudio, Inc., Boston, MA, USA, see http://www.rstudio.com; R Foundation for Statistical Computing, Vienna, Austria, see http://www.R-project.org), PC-ORD ver. 6.21 (B. McCune and M. Mefford, MjM Software, Gleneden Beach, OR, USA), and SPSS, ver. 22 (IBM Corp., Armonk, NY, USA). The number of different sightings of *V. salvator* in four different life history stages was recorded, where each life history stage functions as a multiple response variable. Thus, the analyses were largely based on multivariate approaches, followed by univariate post hoc analyses whenever deemed suitable. Because only a handful of studies have explored habitat associations and other ecological attributes of *V. salvator*, our intention was to pursue multivariate-based exploratory analyses to address the study objectives.

Sightings across major habitats

Permutational multivariate analysis of variance (PERMANOVA) was run using distance matrices (R package: vegan; function: Adonis; 1000 permutations) where major habitat type (aquatic, arboreal, terrestrial) and the observation session (morning, afternoon, evening) were the predictor variables and the number of sightings of different life history stages (adults, subadults, juveniles, hatchlings) were the response variables, with the Julian Calendar date of the survey as the covariate. To construct the distance matrix for life history stages data, the Bray–Curtis index was used. PERMANOVA has been recommended for population and community-level analyses (Anderson 2001). If significant differences were found among major habitat types or observation sessions, a β-diversity (Bray–Curtis index) matrix was generated for monitor sightings using a multivariate homogeneity test of group dispersions (package: vegan; function: betadisper), followed by a Tukey honest significant difference test to investigate pairwise comparisons.

Occupancy patterns across major habitats by different life history stages

An ordination was constructed based on non-metric multidimensional scaling (NMDS) to summarise patterns in habitat occupancy of different life history stages using PC-ORD autopilot mode to avoid the problem of local minima. Distance

measures were calculated from the Sorenson index for life history stages and the distance matrix was rank transformed to reach multivariate normality. Two axes (of five maximum axes) were extracted with the lowest final stress that best ordinated the major habitats and observation sessions in species space through 500 iterations with random starting configurations. To select dimensionality with the lowest stress, a Monte Carlo test was ran (250 runs from real data, 250 runs from randomised data). An ordination plot was constructed with optimal axes to visualise patterns of habitat occupancy. The use of NMDS for analyses of habitat use across life history stages has been described elsewhere (Faunce and Serafy 2007).

Life history stage-dependent mesohabitat associations

Linear discriminant function analyses (DFA) (R package: MASS; function: lda) were performed to search for variations in mesohabitat use among life history stages. To extract discriminant functions, all different mesohabitats used by *V. salvator* and all environmental variables measured (air temperature, canopy cover, relative humidity) were used. Water temperature and pH were eliminated from the DFA because those measurements were only pertinent to monitors observed in water. All numerical variables were log transformed to reach multivariate normality. Using the two discriminant functions that best accounted for the proportional trace, an ordination plot was constructed to visualise the patterns of mesohabitat use by different life history stages of *V. salvator*. The use of DFAs to search for patterns in mesohabitat use within or among species has been described elsewhere (Johnson and Brown 2000).

Life history stage-dependent differences in major types of behaviour

Multivariate analysis of variance (MANOVA) was run to test for the effects of life history stages on behaviour (juveniles and hatchlings were combined into a single variable and considered juveniles for behavioural analyses). If significant differences were detected, Tukey's least significant difference tests were conducted to search for pairwise differences.

Results

During the survey, 287 sightings of *V. salvator* were recorded over 32 days, consisting of 108 (37.6%) adults, 139 (48.4%) subadults, 34 (11.8%) juveniles and 6 (2.1%) hatchlings. The number of sightings of *V. salvator* did not show any discernible pattern with regard to rainfall, but more sightings were made as the temperature increased from January to March (Fig. 3). The highest number of sightings was reported in March ($n = 58$) and the least in October ($n = 29$; Fig. 3). There were diurnal temporal differences, with most sightings during the mornings ($n = 113$), followed by evenings ($n = 92$) and afternoons ($n = 82$; Table 1). With regard to habitat, most sightings were in aquatic habitats

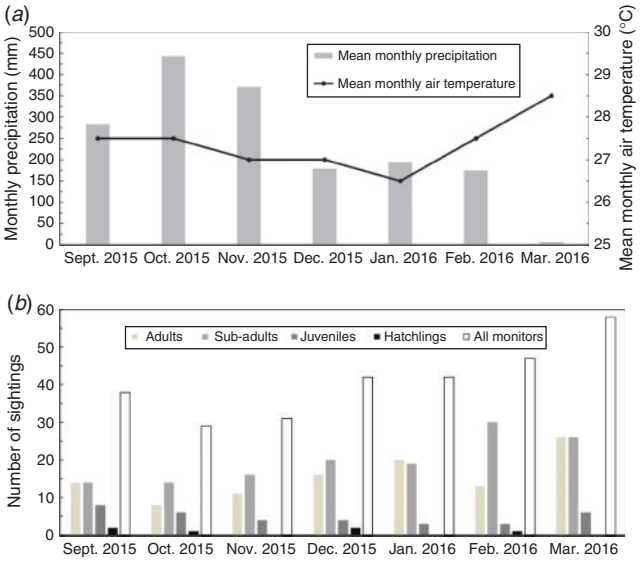


Fig. 3. (*a*) Mean monthly precipitation and air temperature during the study period. (*b*) Variation in the number of sightings of *Varanus salvator* (in total and per age class) throughout the study period in the Attanagalu-Oya area.

Table 1. Number of sightings of *Varanus salvator* of different life history stages in the Attanagalu-Oya area across different habitat types and a different times of the day

Habitat types and time of day	Number of sightings				Total number of sightings (per habitat or time of day)
	Hatchling	Juvenile	Subadult	Adult	
Aquatic	3	27	92	75	197
Afternoon	3	20	12	0	35
Evening	0	7	33	21	61
Morning	0	0	47	54	101
Arboreal	2	7	18	11	38
Afternoon	0	0	13	6	19
Evening	2	5	5	5	17
Morning	0	2	0	0	2
Terrestrial	1	0	29	22	52
Afternoon	1	0	16	11	28
Evening	0	0	7	7	14
Morning	0	0	6	4	10

(197 individuals of all life history stages within the river channel), which is nearly fourfold greater than the equivalent figure for terrestrial habitats (52 individuals). The lowest number of sightings was recorded from arboreal habitats ($n = 38$) within the riparian zone.

Sightings across major habitats

The sightings of life history stages differed significantly across different major habitat types (PERMANOVA, $F = 20.29$, $P < 0.05$), with the interaction between observation session and the major habitat type being significant (PERMANOVA, $F = 10.28$, $P < 0.05$). The significance of the interaction term indicated that sightings of *V. salvator* across major habitat types varied significantly across the time of observation in a given day. Neither the observation session itself (PERMANOVA, $F = 1.73$, $P > 0.05$) nor the Julian Calendar date of the survey had any significant effect on *V. salvator* sightings (PERMANOVA, $F = 0.35$, $P > 0.05$). Pairwise comparisons revealed that the *V. salvator* were sighted significantly more in aquatic than in either terrestrial (Tukey test; mean difference = 0.068; $P < 0.04$) or arboreal (Tukey test; mean difference = 0.109; $P < 0.05$) habitats, whereas the difference in sightings between terrestrial and arboreal habitats was not significant (Tukey test; mean difference = 0.041; $P > 0.05$).

The NMDS ordination reached a stable solution (stress = 7.22) after 103 iterations and produced two orthogonal axes that accounted for 84% of the variability. The Monte Carlo randomisation also suggested that the two-axis solution was optimal (stress in randomised data = 13.89; $P < 0.05$). The ordination plots (Axes 1 and 2) indicated substantial segregation of the different life history stages based on the habitat occupied (Fig. 4). Adults and subadults associated mostly with aquatic and terrestrial habitats, whereas hatchlings and juveniles associated mostly with aquatic and arboreal habitats. In addition, adults and subadults clustered further apart from hatchlings and juveniles in the ordination space. The observation session of the day did not result in any discernible clustering of life history stages (Fig. 4).

Life history stage-dependent mesohabitat associations

V. salvator was recorded at 12 mesohabitats throughout the survey area (Table 2). The greatest number of lizards was found inside the open waters of the river channel ($n = 111$) and in canopy-shaded parts of the river channel ($n = 40$). Home gardens, canopy-shaded riverbanks and road verges had the lowest numbers ($n = 8$–10 individuals in each). Landward and river-leaning tree branches, shrub-dominant marshlands, exposed riverbanks, paddy fields and emergent water-borne substrates had moderate numbers of monitors ($n = 12$–20). The DFA produced three discriminant axes, the first two of which cumulatively explained 95% of the variability and were used to generate ordination plots. Among the environmental variables measured, air temperature had high loadings (−31.53) on the first axis, whereas relative humidity had a high loading on the second axis (−9.09). The frequency at which *V. salvator* occurred at marshlands, paddy fields and riverbanks had higher loadings on the first axis (2.12, 3.61 and −1.06 respectively), whereas monitor sightings at home gardens, open waters and road verges had high loadings on the second axis (−2.67, −0.83 and −1.28 respectively).

Different life history stages of *V. salvator* did not separate into distinct clusters in the ordination space (Fig. 5). The ellipses (denoting 95% confidence intervals) representing each life history stage overlapped with each other, indicating that mesohabitat use is consistently similar across different life history stages. Although both adults and subadults occurred across a greater number of mesohabitats ($n = 11$ and 12 respectively), they overwhelmingly concentrated in mesohabitats inside the

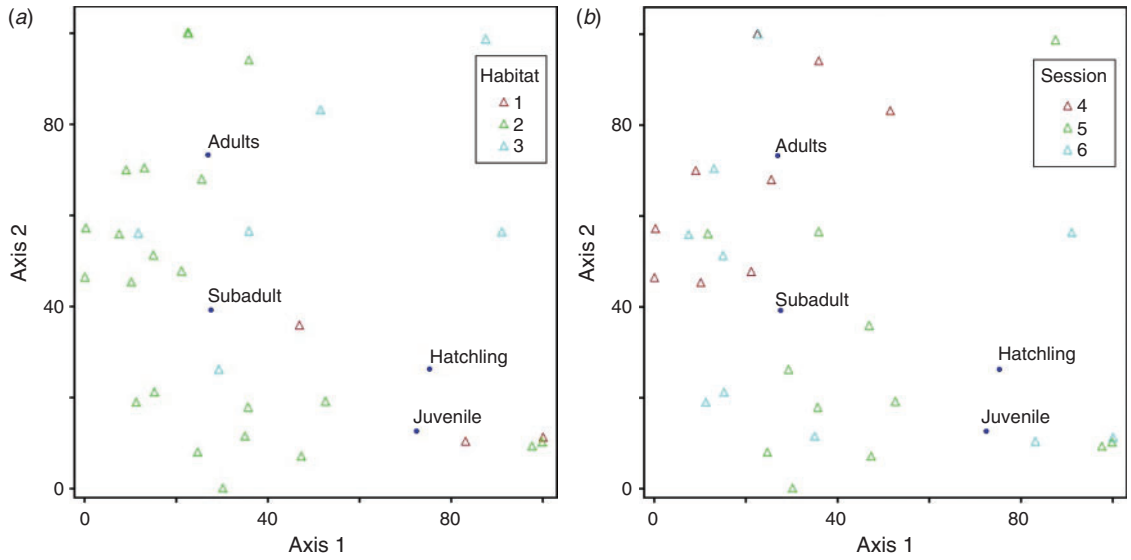


Fig. 4. Non-metric multidimensional scaling ordination plots. The two ordination axes accounted for 84% of the variability in the number of *Varanus salvator* sightings. Ordination of the number of sightings across (*a*) different major habitat types (1, arboreal; 2, aquatic; 3, terrestrial) and (*b*) different observation times during the day (4, morning; 5, afternoon; 6, evening).

Table 2. Mesohabitat use of *Varanus salvator* and the environmental variables associated with their presence in the Attanagalu-Oya area
Data are presented as the mean ± s.d. or as *n* (%)

Mesohabitat	Adults	Subadults	Juveniles	Hatchling	All monitors
Landward tree branches	6 (5.6)	6 (4.3)	6 (17.6)	2 (33.3)	20 (7.0)
Tree branches overhanging the river	5 (4.6)	12 (8.6)	1 (2.9)	0 (0.0)	18 (6.3)
Scrub-dominated marshlands	4 (3.7)	2 (1.4)	6 (17.6)	0 (0.0)	12 (4.2)
Open river banks with no woody vegetation	5 (4.6)	11 (7.9)	0 (0.0)	0 (0.0)	16 (5.6)
Open home gardens with lawns and low shrubs	4 (3.7)	5 (3.6)	0 (0.0)	0 (0.0)	9 (3.1)
Open water of the river	54 (50.0)	49 (35.3)	7 (20.6)	1 (16.7)	111 (38.7)
Paddy fields	0 (0.0)	4 (2.9)	8 (23.5)	2 (33.3)	14 (4.9)
Road verges	5 (4.6)	5 (3.6)	0 (0.0)	0 (0.0)	10 (3.5)
Canopy-shaded riverbanks	5 (4.6)	4 (2.9)	0 (0.0)	0 (0.0)	9 (3.1)
Shaded home gardens with woody vegetation	3 (2.8)	4 (2.9)	0 (0.0)	1 (16.7)	8 (2.8)
Canopy-shaded portions of the river	12 (11.1)	25 (18.0)	3 (8.8)	0 (0.0)	40 (13.9)
Emergent substrates inside the river channel	5 (4.6)	12 (8.6)	3 (8.8)	0 (0.0)	20 (7.0)
Environmental variables					
Air temperature (°C)	31.75 ± 0.74	31.77 ± 0.72	31.40 ± 0.85	31.10 ± 1.27	31.71 ± 0.77
Water temperature (°C)	28.8 ± 0.5	28.8 ± 0.5	28.9 ± 0.6	28.6 ± 0.1	29.0 ± 0.4
Water pH	4.91 ± 3.65	4.44 ± 3.78	5.44 ± 3.59	3.93 ± 4.32	4.72 ± 3.72
Relative humidity (%)	45.91 ± 9.07	46.04 ± 9.72	46.76 ± 9.31	58.17 ± 13.38	46.33 ± 9.62
Canopy cover (%)	14.58 ± 23.93	16.65 ± 23.07	15.29 ± 24.74	29.17 ± 32.00	15.98 ± 23.75
Monitor body surface temperature (°C)	10.07 ± 13.74	11.98 ± 14.28	7.51 ± 12.71	14.32 ± 15.68	10.78 ± 13.91

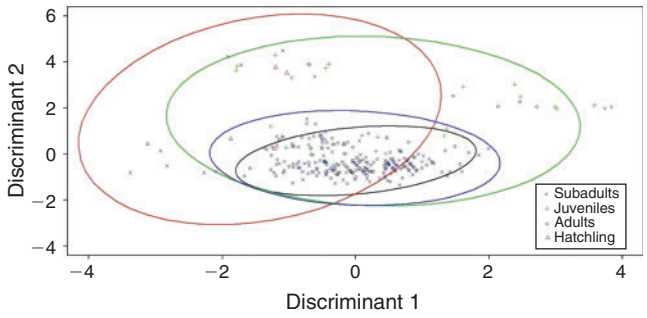


Fig. 5. Discriminant function analyses plot ordinating mesohabitat use of different life history stages of *Varanus salvator*. The two discriminant axes accounted for 95% of the variability in *V. salvator* sightings in different mesohabitats. The ellipses represent the 95% confidence intervals for each life history stage.

river channel. In contrast, juveniles and hatchlings occurred in a fewer number of mesohabitats ($n = 7$ and 4 respectively), but were rather uniformly distributed across those mesohabitats (Fig. 5). Although *V. salvator* occurrences in paddy fields and marshlands ordinated distinctly from each other as well as from other mesohabitats, this separation did not correspond to any distinct life history stage.

Life history stage-dependent differences in major types of behaviour

Seven types of behaviour were observed among *V. salvator* (Table 3). Foraging was the most common behaviour across all life history stages (123 sightings), followed by resting (54 sightings) and swimming (45 sightings). Sunning and roaming were observed 29 and 16 times respectively. Observations of mating and aggression were the most infrequent (10 signings per each behavioural type). The type of behaviour performed by monitors varied significantly across different life history stages (MANOVA, Wilks' $\lambda = 0.559$, $F = 4.196$, $P < 0.05$). Among different types of behaviour, life history stages had significant effects on foraging, resting, swimming, sunning and roaming. Foraging was significantly more predominant among subadults than among adults or juveniles (Tukey test; Table 4). Resting, sunning and roaming were observed significantly more among subadults than among juveniles, with the level of significance for the latter being marginal ($P = 0.049$). Swimming was significantly predominant in both subadults and adults compared with juveniles. Although mating and aggression did not contribute significantly to the variation in types of behaviour among life history stages (Table 4), aggression and mating were observed more frequently among adults than other life history stages (Tables 3, 4).

Discussion

The present study revealed that *V. salvator* is fairly common throughout the urban landscapes of Attanagalu-Oya. This 7-month survey covered an area of 5.18 km^2 and recorded 287 sightings. The number of sightings per month was consistent throughout the study period (mean ± s.d., 41.0 ± 9.8), although there was a greater number of sightings in warmer months. The study area experiences a wet tropical climate where seasonality is less pronounced and water bodies are perennial; therefore, variations were not detected in either abundance or activity rhythms among monitors during the study period. In contrast, seasonality in activity patterns has been observed elsewhere in monsoon-influenced subtropical and tropical dry climates (Dryden *et al.* 1992; Auliya and Erdelen 1999; Gaulke *at al.* 1999)

A greater proportion of the *V. salvator* encountered belonged to younger life history stages (all but adults) (62.4%), although the proportion of hatchlings only accounted for ~2% of total sightings. This could have been due to increased predation on

Table 3. Types of behaviour of *Varanus salvator* in the Attanagalu-Oya area across different habitat types and different times of day
Types of behaviour were defined on the basis of actions performed by the monitors at the time of observation. Data are given as *n* (%)

Behaviour	Description of behaviour	Adults	Subadults	Juveniles	Hatchlings	All monitors
Foraging	Swimming or walking while constantly flicking the tongue	14 (38.0)	58 (41.7)	21 (61.8)	3 (50.0)	123 (49.2)
Aggression	Charging at potential threats (natural predators or conspecifics)	7 (6.5)	3 (2.2)	0 (0.0)	0 (0.0)	10 (3.5)
Mating	Males mounting females for copulation	7 (6.5)	3 (2.2)	0 (0.0)	0 (0.0)	10 (3.5)
Resting	Motionless; lying on a substrate with limbs stretched out, ventrum in contact with substrate in sheltered environments	18 (16.7)	26 (18.7)	8 (23.5)	2 (33.3)	54 (18.8)
Swimming	Moving through water using either or both limbs and tail	19 (16.7)	23 (16.5)	3 (8.8)	0 (0.0)	45 (15.7)
Sunning	Motionless; lying on a warm substrate exposed to direct sunlight with limbs stretched out, ventrum in contact with substrate	9 (8.3)	18 (12.9)	2 (5.9)	0 (0.0)	29 (10.1)
Roaming	Moving on land without constant tongue flicking	7 (6.5)	8 (5.8)	0 (0.0)	1 (16.7)	16 (5.6)

Table 4. Variability in the different types of behaviour among different life history stages of *Varanus salvator*
The test statistics are based on multivariate analysis of variance (MANOVA); pairwise comparisons between life history stages of *V. salvator* are based on Tukey's honestly significant difference test as a post hoc test to the MANOVA. $P < 0.05$ was considered significant. SS, sum of squares

Behaviour	Type III SS	*F*-value	*P*-value	Partial η^2	Age classes	Pairwise comparisons of life history stages	
						Mean difference	*P*-value
Foraging	18.063	6.596	0.002	0.124	Adults–juvenile	0.53	0.170
					Adults–subadults	−0.53	0.170
					Subadults–juveniles	1.06	0.001
Pursuit	0.771	2.941	0.058	0.059	Adults–juvenile	0.22	0.046
					Adults–subadults	0.12	0.355
					Subadults–juveniles	0.09	0.556
Mating	0.771	2.941	0.058	0.059	Adults–juvenile	0.22	0.046
					Adults–subadults	0.13	0.355
					Subadults–juveniles	0.09	0.556
Resting	4.000	3.603	0.031	0.072	Adults–juvenile	0.25	0.376
					Adults–subadults	−0.25	0.376
					Subadults–juveniles	0.50	0.023
Swimming	7.000	9.325	0.000	0.167	Adults–juvenile	0.50	0.004
					Adults–subadults	−0.12	0.694
					Subadults–juveniles	0.62	0.000
Sunning*	4.021	7.720	0.001	0.142	Adults–juvenile	0.22	0.205
					Adults–subadults	−0.28	0.076
					Subadults–juveniles	0.50	0.000
Roaming*	0.896	3.349	0.039	0.067	Adults–juvenile	0.19	0.106
					Adults–subadults	−0.03	0.938
					Subadults–juveniles	0.22	0.049

early life history stages, as suggested for taxa with Type III survivorship curves, with higher mortality among younger life history stages (including eggs) observed among varanids in general (Pepin 2001), or impaired detectability due to smaller bodies, crypsis, the occupancy of subterranean microhabitats and secretive behaviour (Gaulke *et al.* 1999; Smith and Ballinger 2001; Nichols *et al.* 2008; Bozec *et al.* 2011). However, variable age structures have been documented among different *V. salvator* populations throughout Sri Lanka. For example, Karunarathna *et al.* (2008) reported a nearly 1 : 1 ratio between adult and non-adult *V. salvator* in a free-roaming population within the premises of a zoo, whereas Amarasinghe *et al.* (2009) found a 1 : 2.3 ratio of adults to non-adults in a population inhabiting a human-settled coastal area comprising mangroves and home gardens.

Association with major habitats

Although *V. salvator* were recorded in terrestrial and arboreal riparian habitats, the monitors largely occupied aquatic habitats (the river channel and marshlands associated with the river). Most individuals that occupied the terrestrial habitats were found closer to the river channel. These observations are in agreement with those of previous studies across different landscapes and bioclimatic regions in which monitors' major activity centres were positioned around the immediate proximity of water bodies (Dryden *et al.* 1992; Auliya and Erdelen 1999; Gaulke *et al.* 1999). A few studies conducted in natural and seminatural habitats indicated that *V. salvator* is semi-aquatic in habitat selection given their reliance on riparian forests (Pianka 1969; Gaulke and De Silva 1997; Weijola 2010).

V. salvator is well adapted to exploit different types of aquatic habitats, ranging from inland fresh water (rivers, swamps, lakes, tanks) to brackish water habitats (lagoons, tidal streams, mangroves, coastal marshes) to man-made waterbodies (drainage canals, ponds, abandoned mining pits) and paddy fields (Erdelen 1991; Lauprasert and Thirakhupt 1999). The present study indicates that *V. salvator* can also occur in highly altered urban rivers, confirming the catholic habitat use of these monitors. Their association with water could be due to abundant foraging benefits (Pandav and Choudhury 1996; Shine *et al.* 1996; Gaulke *et al.* 2004), thermoregulatory benefits (Træholt 1995) or even spatial niche segregation from the sympatric conger *V. bengalensis*, which is xeric adapted (Wikramanayake and Dryden 1993; Gaulke and De Silva 1997).

The present and previous studies have also reported an association between *V. salvator* and arboreal and terrestrial habitats in the vicinity of water (Horn *et al.* 2004; Pianka *et al.* 2004; Cota *et al.* 2009). However, although *V. salvator* was recorded ~400 m away from the river channel in the present study, individuals were rarely encountered beyond 200 m from a water body in south-eastern Asia, despite suitable habitat been present (Cota *et al.* 2009). Varanids are excellent climbers; in particular, the younger life history stages use arboreal habitats as an antipredation measure (Horn *et al.* 2004; Pianka *et al.* 2004). Association of non-aquatic habitats, such as riparian forests, littoral forests, dried wetlands, subterranean burrows and primary and secondary forests, by *V. salvator* for thermoregulation, foraging, oviposition and refuge and night-time shelter have been documented throughout its biogeography (Træholt 1995; Gaulke *et al.* 2004; Amarasinghe *et al.* 2009).

We found no effects of time of observation on the number of sightings of *V. salvator*. Nonetheless, *V. salvator* shifted its habitat type as the day progressed, whereby individuals were found swimming and foraging in the river channel in the morning (0700–0900 hours), moving to terrestrial and arboreal habitats in the afternoon and evening hours (1100–1700 hours) for resting and sunning. In contrast, in arid and dry climates of Asia, foraging and other activities in the water continued into afternoon hours, with an initial basking period in the terrestrial habitats (Wikramanayake and Green 1989; Pandav and Choudhury 1996). Gaulke (1992) reported bimodal daily activity peaks of *V. salvator* in the Philippines. These variations are likely due to local differences in water temperature and solar radiation. Among varanids, *V. salvator* has the lowest active body temperature, which may enable it to commence critical biological activities early in the day and remain active in water for prolonged periods with little need to frequently return to land for basking (Wikramanayake and Dryden 1993; Rathnayake *et al.* 2003). Activity patterns of varanids vary in response to temperature, whereby their activity plummets at the hottest time of the day, leading to variable habitat choices at different times of the day (Pandav and Choudhury 1996; Guarino 2002). Different habitat types embedded in the same landscape may offer different environmental optima in terms of microclimate, predator avoidance, food availability, energetics and mating grounds (Pianka 1969; Wikramanayake and Dryden 1993; Perry and Garland 2002; Sutherland 2011). Therefore, differential niche dimensions of *V. salvator* may have led to daily shifts among different habitats. Such variations in habitat associations, microhabitat use and daily activity patterns of *V. salvator* are similar to those of other semiaquatic monitors, such as *V. niloticus* and *V. mertensi* (Pianka *et al.* 2004; Mayes 2006).

Partial segregation in use of major habitat types (aquatic, arboreal, and terrestrial) among life -history stages was evident, indicating partial age-structured niche partitioning in *V.* salvator; late life history stages (adults and subadults) seemed to mostly occupy aquatic and terrestrial habitats, whereas early life history (hatchlings and juveniles) stages mostly occupied arboreal and terrestrial habitats. Habitat partitioning may have evolved as a consequence of intraspecific competitive exclusion of juveniles, as well as conspecific agnosticism exhibited by competitively superior adults (who tend to be much larger in body size). Alternatively, age-structured ecological needs, such as maximum size of ingestible food, preferred food type, foraging station and foraging period, may also have resulted in the observed habitat partitioning (Polis 1984). As individuals age, their body dimensions, morphology, survivorship and physiology can vary considerably (Guarino 2002); consequently, different life history stages of a population vary in reproductive status, metabolism, energetics, nutritional requirements, behaviour, food choice and foraging tactics (Pianka *et al.* 2004; Sutherland 2011; Uyeda *et al.* 2015). Therefore, different life history stages can attain optimal fitness by occupying the habitat most conducive to their ecological requirements, which can lead to within-population habitat partitioning.

Life history stage-dependent mesohabitat associations and behaviour

Our observations on mesohabitat use also highlighted the water dependency of our focal species, because *V. salvator* overwhelmingly associated with mesohabitats in aquatic and wetland environments (68.7% of all sightings). Both air temperature and relative humidity were influential variables in the DFA, suggesting that thermal properties and microclimate may drive mesohabitat selection in *V. salvator*. Being poikilotherms, air temperature is a critical element in metabolism, physiology and behaviour of *V. salvator* (Wikramanayake and Dryden 1993; Pianka *et al.* 2004). However, the DFA in the present study indicated that there is no describable variation in mesohabitat use among different life history stages. The study site was embedded in an urban landscape where novel and altered ecological processes, such as the ‘heat island effect’, may have substantially homogenised the microclimate differences, with environmental gradients only existing at the macro scale across the major habitat types (McKinney and Lockwood 1999; McKinney 2002).

Microhabitat use and the daily activities of varanids have often been linked to thermal inertia (Auliya and Erdelen 1999; Pianka *et al.* 2004). Studies conducted in forested and rural habitats of dry and intermediate climatic zones of Sri Lanka have shown that basking does not constitute a substantial proportion of the daily activity budget of *V. salvator* (Wikramanayake and Dryden 1993): the body temperature of inactive or resting *V. salvator* is maintained below ambient temperature and thus they occupy shaded, cooler mesohabitats with stable temperatures. Because of their large body mass, these lizards tends to have higher caloric needs to maintain their daily physiological functions and daily movements. Thus, most

monitors encountered in the present study were actively foraging. Our observations are supported by natural history accounts where *V. salvator* are considered as '[widely foraging] lizards that roam actively in search of live prey or carcasses' (Deraniyagala 1953). Moreover, the lower physiological optima of *V. salvator* preclude the need for frequent basking; thus, these monitors can effectively exploit different aquatic habitats where loss of body heat is not a liability (Wikramanayake and Green 1989; Dryden *et al.* 1992; Wikramanayake and Dryden 1993).

Type of behaviour also differed substantially among different life history stages, particularly with regard to foraging, resting, swimming, sunning and roaming, which supports our previous assertion of partial niche partitioning among life history stages. Effects of life history stage on type of behaviour can be attributed to several reasons. Reptiles, in general, have a deterministic growth and thus the body size of *V. salvator* increases with age (Gaulke *et al.* 1999), whereas fecundity and reproductive fitness vary with age (Pianka *et al.* 2004). Therefore, different life history stages may differ in metabolic needs, energy demands, fitness costs and adaptive responses to environmental change, and may even belong to different social hierarchies.

Signs of aggression, such as pursuit, are overwhelmingly exhibited by domineering older life history stages, a condition prevalent among many lizard taxa (Uyeda *et al.* 2015). Although not territorial, varanids are known for a multitude of antagonistic displays, such as charging, chasing, bipedal clinch phase and tail slapping, where larger adults are the aggressors and the smaller young are submissive (Horn *et al.* 2004; Uyeda *et al.* 2015). Although older life history stages in the study area were remarkably aggressive, displays were limited to short pursuits. Interestingly, mating-related behaviour, such as mounting and courting, were not limited to sexually mature adults because subadults attempted mating. The evolutionary significance of subadult mating attempts is unclear and may be analogous to play behaviour oriented towards learning and experiencing.

V. salvator *as a habitat generalist*

Despite urban development, high-density human occupancy, a dense network of roads, impervious surfaces and intensive agricultural practices, *V. salvator* sightings in the urban study area were comparatively infrequent (mean 55.41 sightings km^{-2}). As the most widespread varanid in the world (Koch *et al.* 2007), *V. salvator* is known to maintain healthy populations, even in altered, human-affected habitats such as homesteads, urban and suburban settings, industrial areas and croplands (Horn *et al.* 2004). Karunarathna *et al.* (2008) surveyed a non-captive population of *V. salvator* at an urban zoological garden in Sri Lanka and reported a density of 500 individuals km^{-2}. Similarly, a survey conducted in human-dominated area of West Java revealed a density of 1400 individuals km^{-2} (Uyeda 2009). Elsewhere in south and south-eastern Asia, highly variable density estimations have been reported for *V. salvator*, ranging from 4.5 to >250 individuals km^{-2} (Shine *et al.* 1996).

Population effects

There is no reliable evidence for human exploitation of monitor lizards at the present study site or in Sri Lanka in general. In fact, the increasingly urbanising landscape may benefit monitors through human-assisted food supplementation. However, exploitation for the leather industry, deliberate killings (mainly as a precaution to prevent poultry predation) and hunting for bush meat are known anthropogenic effects on this species within urban environments elsewhere (Erdelen 1991; Shine *et al.* 1996).

V. salvator is also not deterred by anthropogenic effects such as pollution, sand mining or other hydrologic alterations. The Attanagalu-Oya River is surrounded by intensively managed, commercial-scale paddy fields and a built-up environment, likely sources of non-point-source pollution (Halwatura *et al.* 2013; Sudasinghe *et al.* 2015). Unregulated disposal of domestic and industrial wastes has also led to deteriorating water quality in this river. Recent water quality assessments indicated that the surface water of the Attanagalu-Oya River had low pH (4–5), high conductivity (3500–8500 $\mu S\ cm^{-1}$) and high faecal coliform counts, and was contaminated with heavy metals (0.01–0.02 ppm; Wijesekara and Kudahetty 2009). As a species with high tolerance to disturbances and plasticity in behaviour, *V. salvator* seems to have adapted well to use this urban environment.

Quantification of the occurrence of *V. salvator* in the present study was based on the number of sightings, not identification of individuals. Use of mark and recapture techniques and occupancy modelling to account for imperfect detections may enable more accurate estimates of population parameters. Further, the types of behaviour we defined may not be mutually exclusive, and substantial overlaps are possible among different types of behaviour. Focal animal sampling techniques will also help identify behavioural patterns that are composites of multiple interrelated behavioural acts, and thus reveal the true ethological intricacies of *V. salvator*. Moreover, the viability and stability of *V. salvator* populations in urban landscapes should be investigated based on long-term studies where survey durations extend beyond the generation time of these long-lived monitors.

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