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Dietary Habits and the Predators of the Bengal Monitor *Varanus bengalensis* in Sri Lanka

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Abstract - The Bengal monitor (*Varanus bengalensis*) is the second largest lizard species in Sri Lanka, and is well adapted to living in a variety of terrestrial habitats. *Varanus bengalensis* is a diurnal generalist predator, but sometimes function as a scavenger. Given the ecological plasticity and generalist foraging strategy of *V. bengalensis*, its feeding ecology and role in trophic networks could vary among different environments. Thus, in this study we documented the prey and natural predators of *V. bengalensis* across different landscapes along the urban-rural gradient and geo-climatic zones of Sri Lanka through field observations, literature surveys, and personal communications with other biologists. We documented 82 species of vertebrate prey in the diet of *V. bengalensis*, which included 20 mammals, 21 birds, 20 reptiles, 14 amphibians, and seven fishes. Although numerous invertebrates were recorded, their identification to species level was challenging. *Varanus bengalensis* also fed on road-killed animals and organic waste, such as rotting fruits and vegetables. Although *V. bengalensis* is largely terrestrial, our dietary analyses revealed that it also preys on aquatic prey; their predation on introduced species as well as threatened species was also remarkable. Our study confirmed that *V. bengalensis* has a greater dietary selection than *V. salvator* in Sri Lanka, which remained consistent across a diverse array of habitats. Our study also noted that *V. bengalensis* is predated by 24 species of vertebrates, including nine mammals, 10 birds, and five reptiles, which largely targeted juveniles. Neither the predator nor prey communities of *V. bengalensis* varied across the urban-rural gradient or across different geo-climatic zones of Sri Lanka.

Introduction

Varanid lizards, or monitors, are a highly diverse reptilian group that is broadly distributed throughout Africa, South and Southeast Asia, and Australasia (Pianka *et al.*, 2004). In general, varanids have a highly conservative body plan, but vary greatly in size, and have successfully colonized a wide range of habitats in various geo-climatic zones (Pianka & King, 2004). Their ecological success has frequently been attributed to elevated seasonal and daily activity levels, high stamina and metabolic rates, cardiovascular efficiency, respiratory efficiency due to gular pumping, and greater chemosensory perception (Pianka *et al.*, 2004).

With a few exceptions (*e.g.*, *Varanus bitatawa*, *V. olivaceus*, *V. indicus*), most varanids are highly-adaptive habitat generalists and opportunistic carnivores (Shine, 1986; Losos & Greene, 1988; Molnar, 2004). Certain species, such as, the Bengal monitor, *V. bengalensis*, have successfully established themselves in highly altered anthropogenic habitats, and also occur in a variety of natural landscapes including dense forests, sparse woodlands, grasslands, and thorny scrublands (Pianka, 2004). The geographic distribution of *V. bengalensis* extends from southeastern Iran through much of southern Asia, into the Malay Archipelago (Pianka, 2004). As in many wide-ranging varanids, the ecology and natural history of *V. bengalensis* vary remarkably throughout its range in response to the different habitats and geo-climatic zones they inhabit (Losos & Greene, 1988; Auffenberg, 1994; Pianka, 1995). In this study, we focused on the trophic ecology of *V. bengalensis* in Sri Lanka, an Indian oceanic island where varanid ecology still remains largely unexplored.

Two species of monitor lizard (genus *Varanus*) occur on Sri Lanka - *V. bengalensis* and *V. salvator* (de Silva, 2006). *Varanus bengalensis* has been recorded throughout Sri Lanka up to 500 m in elevation and across all geo-climatic zones (Das & de Silva, 2005). *Varanus bengalensis* is diurnal, and in Sri Lanka, due to year-round uniformly high temperatures, is active throughout the year. Daily activity is mostly limited to mid-day (1000 to 1400 h), and *V. bengalensis* is rarely observed during early mornings or late evenings (Deraniyagala, 1953; Wikramanayake & Dryden, 1993; Karunarathna *et al.*, 2012). Being a moderately large (average total length [TL] 100 cm) varanid, *V. bengalensis* is the second largest lizard species in Sri Lanka (Auffenberg, 1994), with the longest individual recorded measuring 174 cm TL at Hambegamuwa, a rural village in southern Sri Lanka (S. Karunarathna, pers. obs., 2013). *Varanus*

bengalensis is well adapted to occupy a variety of terrestrial habitats, and can also climb vertical surfaces and trees if necessary (Auffenberg, 1994). Although the species is found in floodplain woodlands, it tends to avoid aquatic habitats and is inept at swimming or diving (Pianka, 2004). In Sri Lanka, the thermoregulatory behavior, microhabitat use, metabolism (with respect to osmotic balance and energy), and behavioral aspects (particularly conspecific agnostic interactions) of *V. bengalensis* have been investigated (Wikramanayake & Green, 1989; Dryden *et al.*, 1992; Wikramanayake and Dryden, 1993); however, their trophic interactions remain largely unexplored. *Varanus bengalensis* are active generalist predators, feeding mostly on small invertebrate prey (Deraniyagala, 1953). They are also human commensals, and thrive in anthropogenic habitats such as home gardens and homesteads, and can even occupy households and built-up urban environments (Koch *et al.*, 2013).

Resource and microhabitat availability and environmental complexity differs remarkably across urban-rural gradients as well as geo-climatic gradients (Faeth *et al.*, 2005). Given the ecological plasticity and generalist foraging strategy of *V. bengalensis*, its feeding ecology and role in trophic networks could vary in different environments. Thus, documenting the diet and natural predators of *V. bengalensis* across different landscapes and geo-climatic zones are salient elements of ecological theory. In this paper, we studied the prey and predators of *V. bengalensis* in Sri Lanka.

Methods

Study Area

Sri Lanka is a tropical island (area: 65,610 km²) located in the Indian Ocean off the southern tip of peninsular India (5° 55' 0.12" – 9° 50' 60" N; 79° 40' 59.88" E – 81° 54' 0" E). The island consists of three elevation-based geographic zones (lowlands: < 300 m, uplands: 300-900 m, and highlands: > 900 m) and three major climatic zones based on average annual precipitation (dry zone: < 1900 mm, wet zone: > 2500 mm, and intermediate zone: 1900-2500 mm) (Survey Department of Sri Lanka, 2012).

Data collection

We collected data on the prey and predators of *V. bengalensis* using various methods. Primarily, we made extensive field observations through opportunistic field

excursions conducted over a six-year (2010-2016) period in various regions of Sri Lanka representing different geo-climatic zones as well as habitats along the urban-rural gradient. Our field observations were made at distances of 2 to 20 m from the animals using 8×40 binoculars. Our field surveys were limited to periods of activity for *V. bengalensis*, between 0600 and 1800 h (Wikramanayake & Green, 1989; Wikramanayake & Dryden, 1993). We dissected ~12 fresh road-killed *V. bengalensis* from various parts of Sri Lanka and identified their stomach contents. Our direct feeding observations also included *V. bengalensis* feeding on road kills. During our field excursions, we also interviewed residents of local communities (~200 local residents) regarding their random observations on the trophic roles of *V. bengalensis*.

Additionally, we consulted veteran herpetologists and field biologists (a total of ~25) who have conducted field research in Sri Lanka in recent decades (1990-2016) on their experiences with *V. bengalensis* through in-person communication and social media. Whenever possible, we requested photographic evidence to validate their observations.

Finally, we conducted a comprehensive literature review utilizing online databases and scholarly search engines (Google Scholar, MEDLINE, Science Direct, Biological Sciences Collection, Academic Search Premier, EBSCOhost, JSTOR, and PubMed). We used a combination of the following keywords in the literature review: “*Varanus bengalensis*”, “Bengal monitor”, “Clouded monitor”, “Common Indian monitor”, “feeding”, “foraging”, “prey”, “predator”, “trophic”, “diet”, “Sri Lanka”, and “Ceylon”. We categorized the prey and predators based on their IUCN conservation status (Vulnerable, Endangered, and Critically Endangered) and residential status (endemic, residential, and non-native).

Results

Prey species

Our field-based observations, interviews with professional biologists, and review of the literature revealed a diverse array of prey consumed by *V. bengalensis* which included vertebrates, invertebrates, as well as dead organic matter including road-killed animals and household garbage and urban trash (Table 1; Fig. 1). We noted that the vertebrate prey of *V. bengalensis* was remarkably high in diversity: 20 mammals, 21 birds, 20 reptiles, 14 amphibians, and

7 freshwater fishes (a total of 82 species; Table 1). Among invertebrate prey, species-level identification was limited. Most of the invertebrate taxa predated by *V. bengalensis* were arthropods. Live prey included different life-history stages (eggs, larvae, juveniles, and adults). *Varanus bengalensis* appeared to consume animal carcasses of different stages of decomposition ranging from fresh carcasses (such as road-kills) to carrion (rotting animal flesh). Among live prey, these monitors consumed both endemic species (Sri Lankan toque monkey [*Macaca sinica*] and Sri Lankan yellow-fronted barbet [*Megalaima flavifrons*]) and non-native species including invasive species (1 species) as well as domesticated species (2 species). Moreover, 10 endemics and a total of 5 IUCN Red Listed species (2 critically endangered, 2 endangered, and 1 vulnerable) were also documented in our survey.

Predators

Our study revealed that *V. bengalensis* has several natural predators, including 9 mammals, 10 birds, and 5 reptiles (Table 2; Fig. 2). Among these predators, we found one endemic species (Sri Lankan grey hornbill [*Ocyrceros gingalensis*]) and one non-native species (domestic cat [*Felis catus*]). Of the 24 total records of predation we documented, juveniles were the victims in 14 (58.3%) instances, suggesting that juveniles are the most susceptible life-history stage (Table 2). In five instances, consumers of *V. bengalensis* were carrion feeders scavenging on road-killed individuals (jackal [*Canis aureus*], wild boar [*Sus scrofa*], and jungle crow [*Corvus leuallantii*]). Live, adult *V. bengalensis* suffered direct predation in a handful of instances (by five species). Most *V. bengalensis* predators were visually-oriented, active foragers (domestic cats, domestic dogs [*Canis familiaris*], leopards [*Panthera pardus*], mongoose [*Herpestes brachyurus*], birds of prey [e.g., *Spilornis cheela*], Indian cobra [*Naja naja*], and rat snakes [*Ptyas mucosa*]), while a few were sit-and-wait foragers (mugger crocodile [*Crocodylus palustris*], stork-billed kingfisher [*Pelargopsis capensis*], and lesser adjutant [*Leptoptilos javanicus*]). Moreover, one predator is a threatened species listed in the IUCN Red List (leopard, *Panthera pardus*) while another (Sri Lankan grey hornbill, *Ocyrceros gingalensis*) is an endemic species. Humans are also considered a key predator of *V. bengalensis*, and harvest these monitors from the wild for their flesh, hide, and fat. Neither the natural predators nor prey of *V. bengalensis* were restricted or specific to a particular geo-climatic zone of

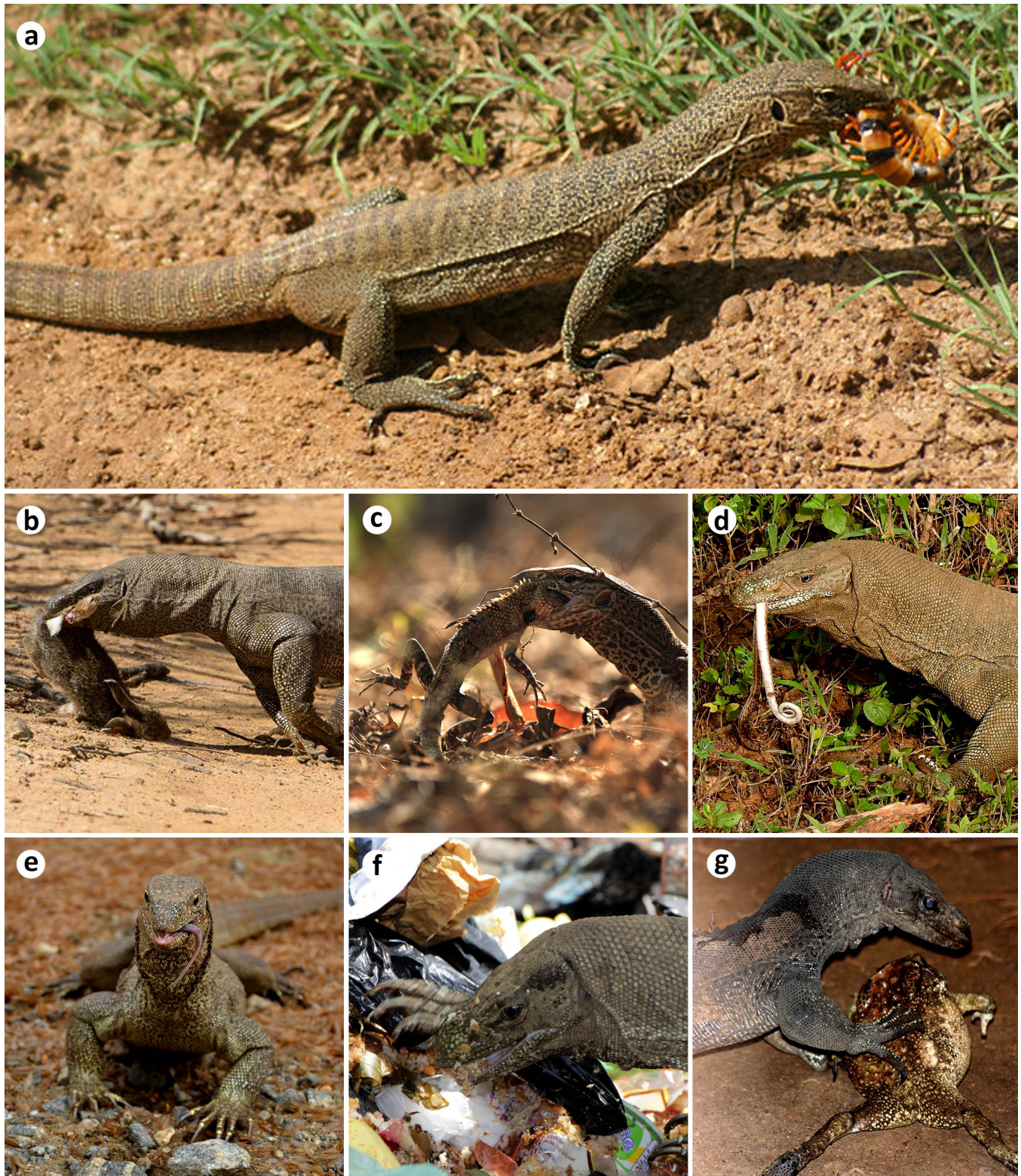


Fig. 1. *Varanus bengalensis* preying on an (a) Indian tiger centipede (*Scolopendra hardwicki*), (b) juvenile black-napped hare (*Lepus nigricollis*), (c) adult common garden lizard (*Calotes versicolor*), (d) adult variegated kukri snake (*Oligodon taeniolata*), (e) flying termites, (f) household trash, and (g) adult Asian common toad (*Duttaphrynus melanostictus*). Photographs by **Craig Moore**, **Mevan Piyasena**, **Senehas Karunarathna**, **Nilupul Rangana**, and **Bushana Kalhara**.

Table 1. Currently known prey items of *Varanus bengalensis* in Sri Lanka and their current status in Sri Lanka in terms of IUCN national conservation status, endemism, and residential (native vs introduced) status. Abbreviations used: E = Endemic; NA = not applicable; NV = native; NN = non-native; VU = Vulnerable; EN = Endangered; CR = Critically Endangered. Non-native species include domesticated species (domestic cats and dogs), naturalized alien species, and invasive species.

Prey Class	Prey taxon	Common name	Species Status	Description of Prey	Geo-climatic Zone	Location (Habitat)	References
Mammalia	<i>Bandicota bengalensis</i>	Mole rat	NV	Freshly killed by home owner	Lowland wet zone	Ramallana (Urban)	This study
	<i>Bandicota indica</i>	Malabar bandicoot	NV	Road kill	Lowland wet zone	Kelaniya (Residential)	This study
	<i>Bubalus bubalis</i>	Buffalo	NV	Scavenged from slaughter houses and carcasses	Lowland wet zone	Aluthgama (Residential)	M. Wickramasinghe, pers. comm.
	<i>Canis familiaris</i>	Domestic dog	NN	Road kill	Lowland wet zone, Lowland arid zone	Beruwala (Urban), Hambantota (Forest)	M. Wickramasinghe, pers. comm.
	<i>Crocidura</i> sp.	Shrew sp.	NV	Live adult	Lowland wet zone	Kudawa (Residential)	This study
	<i>Felis catus</i>	Domestic cat	NN	Live juveniles, road-killed carcass	Lowland wet zone	Kalutara (Forest)	M. Wickramasinghe, pers. comm.
	<i>Funambulus palmarum</i>	Palm squirrel	NV	Juveniles hunted from the nest, road kill	Lowland intermediate zone, Lowland dry zone, Upland wet zone	Hambegamuwa (Residential), Yala (Forest), Thammimalai (Residential)	S. Kumara, M. Karunarathna & T. Kusuminda, pers. comm.
	<i>Kerivoula picta</i>	Painted bat	NV	Road kill	Lowland dry zone	Polonnaruwa (Residential)	This study
	<i>Lepus nigricollis</i>	Black-napped hare	NV	Live subadult	Lowland dry zone	Yala (Forest)	M. Piyasena, pers. comm.
	<i>Macaca sinica</i>	Sri Lankan toque monkey	E	Juvenile carcass	Lowland wet zone	Dombagaskanda (Forest)	This study
	<i>Manis crassicaudata</i>	Pangolin	NV	Adult carcass	Lowland dry zone	Galoya (Forest)	D. Kulathunga, pers. comm.
	<i>Mus booduga</i>	Field mouse	NV	Freshly killed by homeowner	Lowland intermediate zone	Tanamalwila (Residential)	S. Kumara, pers. comm.
	<i>Mus musculus</i>	Indian house mouse	NV	Freshly killed by homeowner	Lowland wet zone	Ambalangoda (Urban)	This study
	<i>Pteropus giganteus</i>	Flying fox	NV	Electrocuted carcass	Lowland wet zone	Piliyandala (Urban)	This study
	<i>Rattus rattus</i>	Black rat	NN	Freshly killed by homeowner	Lowland wet zone	Ramallana (Urban)	This study
Aves	<i>Rusa unicolor</i>	Sambur deer	NV	Adult carcass	Lowland wet zone	Sinharaja (Forest)	This study
	<i>Semnopithecus priam</i>	Grey langur	NV	Adult carcass	Lowland dry zone	Wilpattu (Forest)	D. Ramasinghe, pers. comm.
	<i>Semnopithecus vetulus</i>	Sri Lankan Purple-faced langur	E/EN	Electrocuted carcass	Lowland wet zone	Awissawella (Urban)	S. Kolambage, pers. comm.
	<i>Suncus murinus</i>	Common musk shrew	NV	Adult carcass	Lowland wet zone	Ganemulla (Urban)	This study
	<i>Tandeleuria oleracea</i>	Long-tailed tree mouse	VU	Live adult	Lowland dry zone	Karawalagawewa (Forest)	This study
	<i>Acridotheres tristis</i>	Common myna	NV	Nestlings	Lowland wet zone	Ganemulla (Urban)	This study
	<i>Amaurornis phoeniceus</i>	White-breasted waterhen	NV	Road kill	Lowland dry zone	Tissamaharamaya (Residential)	This study
	<i>Chalcophaps indica</i>	Emerald dove	NV	Adult carcass	Lowland wet zone	Aluthgama (Residential)	This study
	<i>Columba livia</i>	Rock pigeon	NV	Adult carcass	Lowland wet zone	Ramallana (Urban)	This study
	<i>Copsychus saularis</i>	Oriental magpie robin	NV	Eggs	Lowland intermediate zone	Bibila (Residential)	This study
	<i>Dinopium benghalense</i>	Black-rumped flameback	NV	Hatchlings from the nest	Lowland dry zone	Polonnaruwa (Residential)	L. Dayaratne, pers. comm.
	<i>Eudynamis scolopaceus</i>	Asian koel	NV	Juvenile carcass	Lowland wet zone	Kadawatha (Urban)	R. Saranga, pers. comm.
	<i>Francolinus pictus</i>	Painted francolin	CR	Leftover meat discarded by hunters	Lowland intermediate zone	Nilgala (Forest)	D. Kulathunga, pers. comm.
	<i>Halcyon smyrnensis</i>	White-throated kingfisher	NV	Hatchlings from the nest	Lowland wet zone	Galle (Residential)	M. Dahanayake, pers. comm.
	<i>Megalaima flavirostris</i>	Sri Lankan yellow-fronted barbet	E	Live chicks from the nest	Lowland wet zone	Dombagaskanda (Forest)	This study
	<i>Megalaima zeylanica</i>	Brown-headed barbet	NV	Live chicks from the nest	Lowland dry zone	Polonnaruwa (Forest)	L. Dayaratne, pers. comm.
	<i>Pentelura asiatica</i>	Jungle bush-quail	CR	Trash body parts discarded by hunters	Lowland intermediate zone	Mahiyanganaya (Forest)	D. Kulathunga, pers. comm.
	<i>Psittacula calthropae</i>	Sri Lankan emerald collared parakeet	E	Dislodged live hatchlings and eggs	Lowland wet zone	Deraniyagala (Forest)	M. Wickramasinghe, pers. comm.
	<i>Psittacula krameri</i>	Rose-ringed parakeet	NV	Dislodged live hatchlings and eggs	Lowland wet zone	Mideripitiya (Forest)	M. Wickramasinghe, pers. comm.
	<i>Pycnonotus cafer</i>	Red vented bulbul	NV	Dislodged hatchlings	Lowland wet zone	Matara (Residential)	N. Rangana, pers. comm.
	<i>Pycnonotus luteolus</i>	White browed bulbul	NV	Road kill carcass	Lowland wet zone	Ingiriya (Residential)	This study
	<i>Saxicola leucurus</i>	Indian robin	NV	Eggs and hatchlings	Lowland dry zone	Rajanganaya (Forest)	D. Ramasinghe, pers. comm.
	<i>Stigmatopelia chinensis</i>	Spotted dove	NV	Adult carcass	Lowland dry zone	Chilaw (Urban)	A. Kumarsinghe, pers. comm.
	<i>Turdoides affinis</i>	Yellow billed babbler	NV	Injured adult	Lowland wet zone	Panadura (Urban)	This study
	<i>Turnix suscitator</i>	Barred buttonquail	NV	Trash body parts discarded by hunters	Lowland dry zone	Giradurukotte (Forest)	D. Kulathunga, pers. comm.
	<i>Vanellus indicus</i>	Red-wattled lapwing	NV	Live fledglings and eggs from the nest	Lowland wet zone	Seenigama (Residential)	S. de Soya, pers. comm.

Table 1 (continued).

Prey Class	Prey taxon	Common name	Species Status	Description of Prey	Geo-climatic Zone	Location (Habitat)	References
Reptilia	<i>Amphisma solutum</i>	Buff striped keelback	NV	Live adult, Road kill	Lowland intermediate zone, Lowland dry intermediate zone, Lowland wet zone	Thamalmvila (Residential), Kumana (Forest), Waga (Residential)	This study, G. Jayantha & M. Wickramasinghe, pers. comm.
	<i>Calotes calotes</i>	Green garden lizard	NV	Live adults	Lowland dry zone, Lowland wet zone	Anuradapura (Residential), Maharagama (Urban)	This study
	<i>Calotes versicolor</i>	Common garden lizard	NV	Live adult, road-killed specimen	Lowland dry zone, Lowland arid zone	Mihintale (Forest), Yala (Forest)	This study, S. Karunarathna, pers. comm.
	<i>Chamaeleo zeylanicus</i>	Sri Lankan chameleon	EN	Live adults	Lowland dry zone	Vanatavilluwa (Residential)	Karunarathna <i>et al.</i> , 2009
	<i>Crocodylus palustris</i>	Mugger crocodile	NV	Carcass	Lowland dry zone	Kanadara (Residential)	This study
	<i>Daboia russelii</i>	Russell's viper	NV	Live juvenile	Lowland intermediate zone	Udawalawe (Forest)	S. Kumara, pers. comm.
	<i>Eutropis carinata</i>	Common skink	NV	Live adults	Lowland intermediate zone	Ham begamuwa (Residential)	This study
	<i>Geochelone elegans</i>	Star tortoise	NV	Live juvenile	Lowland dry zone	Eluwankulam (Residential)	D. Ramasinghe, pers. comm.
	<i>Hemidactylus frenatus</i>	Common house-gecko	NV	Live adults	Lowland wet zone	Ganemulla (Residential)	This study, M. Wickramasinghe, pers. comm.
	<i>Hemidactylus parvimaculatus</i>	Spotted housegecko	NV	Live adults	Lowland wet zone	Ganemulla (Residential)	This study
	<i>Hypnale hypnale</i>	Merren's hump nose viper	NV	Killed by villagers	Lowland wet zone	Nittambuwa (Residential)	This study
	<i>Indotyphlops</i> sp.	Blind snake species	NV	Live adults	Lowland wet zone	Ganemulla (Residential)	This study
	<i>Lycodon aulicus</i>	Wolf snake	NV	Live adults	Lowland dry zone	Gampaha (Urban)	This study
	<i>Melanoechys trijuga</i>	Black turtle	NV	Live juvenile	Lowland wet zone	Maharagama (Urban)	This study
	<i>Oligodon amensis</i>	Common kukri snake	NV	Road kill	Lowland dry zone	Padaviya (Forest)	This study
	<i>Oligodon taeniolata</i>	Variagated kukri snake	NV	Live adults	Lowland dry zone	Yala (Forest)	This study
	<i>Otocoryps nigrisigma</i>	Black spotted kangaroo lizard	E	Live adults	Lowland intermediate zone	Nilgala (Forest)	This study
	<i>Pygas mucosa</i>	Rat snake	NV	Live juvenile	Lowland wet zone	Ragama (Urban)	This study
	<i>Sitana devakai</i>	Devaka's fanthroat lizard	E	Live adults	Lowland dry zone	Vanatavilluwa (Residential)	This study
	<i>Xenochrophis piscator</i>	Checkered keelback	NV	Live adults	Lowland wet zone	Dediya (Forest)	M. Wickramasinghe, pers. comm.
Amphibia	<i>Duttaphrynus atukoralei</i>	Aukoral's toad	E	Live adults	Lowland wet zone	Matara (Residential)	This study
	<i>Duttaphrynus melanostictus</i>	Common house toad	NV	Live adult, road kill	Lowland wet zone	Kalutara (Residential), Polgasovita (Urban)	This study, B. Kalhara & T. Ranasinghe, pers. comm.
	<i>Duttaphrynus scaber</i>	Schneider's toad	NV	Live adults	Lowland dry zone	Jaffna (Residential)	This study
	<i>Euphyctes cyanophytis</i>	Indian skipper frog	NV	Live adults	Lowland intermediate zone	Ham begamuwa (Forest)	This study
	<i>Euphyctes hexadactylus</i>	Indian green frog	NV	Live adults	Lowland intermediate zone	Ham begamuwa (Residential)	This study
	<i>Fekervarya limncharis</i>	Common paddy field frog	NV	Live adults	Lowland intermediate zone	Hettipola (Residential)	Jolley & Meek, 2006
	<i>Hoplobatrachus crassus</i>	Jurdon's bullfrog	NV	Live adults	Lowland dry zone	Yala (Forest)	S. Roelofs, pers. comm.
	<i>Uperodon taprobanica</i>	Sri Lankan bullfrog	NV	Live adult, road kill	Lowland dry zone, Lowland wet zone	Puttalam (Urban), Dambulla (Residential), Matugama (Forest)	This study, M. Wickramasinghe, pers. comm.
	<i>Polypedates maculatus</i>	Spotted tree frog	NV	Live adults, road kill	Lowland intermediate zone, Lowland arid zone	Monaragala (Forest), Hambantota (Residential)	This study, M. Wickramasinghe, pers. comm.
	<i>Pseudophilautus popularis</i>	Common shrub frog	E	Live adults	Lowland wet zone	Ganemulla (Urban)	This study
	<i>Uperodon variegatus</i>	Variagated ramanella	NV	Live adults	Lowland arid zone	Hambantota (Residential)	M. Wickramasinghe, pers. comm.
	<i>Sphaerotheca breviceps</i>	Short-headed burrowing frog	NV	Live adults	Lowland dry zone	Yala (Forest), Puttalam (Urban), Hambantota (Residential)	This study, M. Wickramasinghe, pers. comm.
	<i>Sphaerotheca rolandae</i>	Roland's burrowing frog	NV	Live adults	Lowland dry zone, Lowland arid zone	Karawalagaswewa (Forest), Mannar (Urban)	This study, M. Wickramasinghe, pers. comm.
	<i>Uperodon systoma</i>	Marbled balloon frog	NV	Live adults	Lowland dry zone	Yala (Forest), Anuradapura (Residential), Wilpattu (Forest)	This study, M. Wickramasinghe, pers. comm.
Pisces	<i>Davkinsia singhala</i>	Sri Lankan filament Barb	E	Live specimens trapped in small pools	Lowland dry zone	Udawalawe (Forest)	S. Atapattu, pers. comm.
	<i>Devario malabaricus</i>	Giant danio	NV	Live specimens trapped in small pools	Lowland dry zone	Udawalawe (Forest)	S. Atapattu, pers. comm.
	<i>Esomus thermoicos</i>	Sri Lankan flying barb	E	Live specimens trapped in small pools	Lowland dry zone	Udawalawe (Forest)	S. Atapattu, pers. comm.
	<i>Etiopis suratensis</i>	Green chromide	NV	Live specimens trapped in small pools	Lowland dry zone	Udawalawe (Forest)	S. Atapattu, pers. comm.
	<i>Oreochromis mossambicus</i>	Tilapia	NN	Live specimens trapped in small pools	Lowland dry zone	Udawalawe (Forest)	S. Atapattu, pers. comm.
	<i>Puntius dorsalis</i>	Long-snouted barb	NV	Live specimens trapped in small pools	Lowland dry zone	Udawalawe (Forest)	S. Atapattu, pers. comm.
	<i>Rashora dandiya</i>	Broad line Strip rasbora	NV	Live specimens trapped in small pools	Lowland dry zone	Udawalawe (Forest)	S. Atapattu, pers. comm.

Table 1 (continued).

Prey Class	Prey taxon	Common name	Species Status	Description of Prey	Geo-climatic Zone	Location (Habitat)	References
Arachnida	<i>Buthoscorpio sarasinorum</i>	Scorpion	NV	Live adults	Lowland dry zone	Eluwankulm (Residential)	A. Kumara, pers. comm.
	<i>Heierometrus gravimanus</i>	Scorpion	NV	Live adults	Lowland wet zone	Anbalangoda (Residential); Akuressa (Residential)	This study; S. Karunaratna, pers. comm.
Chilopoda	<i>Heterometrus serratus</i>	Scorpion	NV	Live adults and juveniles	Lowland intermediate zone	Nilgala (Forest)	This study
	<i>Reddyanus jayaratnei</i>	Scorpion	NV	Live adults	Lowland wet zone	Kanneliya (Forest)	S. Akmeemana, pers. comm.
	<i>Reddyanus loebli</i>	Scorpion	NV	Live adults	Lowland dry zone	Sangamankande (Residential)	This study
	<i>Rhyida</i> sp.	Common centipede	NV	Live adults	Lowland dry zone	Bibila (Urban)	This study
Gastropoda	<i>Scelopendra haradwicki</i>	Indian tiger centipede	NV	Live adults	Lowland dry zone	Yala (Forest)	C. Moore, pers. comm.
	<i>Cryptazona biserialis</i>	Common translucent snail	NV	Live adults	Lowland wet zone	Ganemulla (Urban)	This study
	<i>Lissachatina fulica</i>	Giant African snail	NN	Live adults	Lowland wet zone	Ganemulla (Urban), Gampaha (Urban)	This study; T. Ranasinghe, pers. comm.
Malacostraca	<i>Oziohelphusa</i> sp.	Freshwater crab	E	Live adults	Lowland dry zone	Mihintale (Forest)	This study
	<i>Oziohelphusa hippocastanum</i>	Freshwater crab	E/EN	Live adults, road kill	Lowland dry zone	Jaffna (Residential)	This study
	<i>Perbrinckia</i> sp.	Freshwater crab	E	Live adults	Lowland intermediate zone	Nilgala (Forest), Pokunnetma (Forest)	This study; M. Wickramasinghe, pers. comm.
Insecta	Suborder: Caelifera	Grasshoppers	NV	Live adults	Lowland intermediate zone, Upland wet zone	Sigiriya (Residential), Peradeniya (Urban)	This study
	Family: Scarabaeidae	Dung beetles	NV	Live adults	Lowland dry zone	Mihintale (Forest), Udawalawe (Forest)	This study; M. Wickramasinghe, pers. comm.
	Infraorder: Isoptera	Termites	NV	Live adults, flying and larvae	Lowland dry zone, Lowland dry zone	Mihintale (Forest), Suriyawewa (Residential), Sigiriya (Residential), Dambulla (Forest)	N. Rangana & M. Rathnayake, pers. comm.
Malacostraca	Subfamily: Formicinae Order: Coleoptera	Black ants Beetle species	NV NV	Live adults	Lowland dry zone	Mihintale (Forest)	This study
	Family: Gryllidae	Crickets species	NV	Live adults and juveniles	Lowland wet zone, Lowland dry zone	Moratuwa (Urban), Yala (Forest)	A. Godahewa & M. Wickramasinghe, pers. comm.
	Suborder: Oniscidea	Doodlebug	NV	Live adults and larvae	Lowland dry zone, Lowland wet zone	Ganemulla (Urban), Hambegamuwa (Residential)	This study
	Order: Blattodea	Wild cockroaches	NV	Live specimens	Lowland wet zone	Habarana (Residential), Galle (Residential)	This study; T. Ranasinghe, pers. comm.
	<i>Heteropoda venatoria</i> <i>Gryllotalpa</i> sp.	Huntsman spider Mole cricket	NV NV	Live specimens	Lowland wet zone	Aluthigama (Urban), Nittambuwa (Residential)	This study
	Suborder Megadrilacea	Earthworm	NV	Live specimens	Lowland intermediate zone, Lowland dry zone	Elpitiya (Forest)	This study
						Nilgala (Forest), Ampara (Urban)	D. Kulathunga, pers. comm.
Garbage	n/a	Cooked anchovy	NA	Household trash	Lowland dry zone	Homagama (Urban), Ratmalana (Urban)	This study
	n/a	Cooked chicken	NA	Household trash	Lowland wet zone	Higurakgoda (Residential)	This study
	n/a	Cooked shrimps	NA	Household trash	Lowland dry zone	Kururita (Forest)	This study
	n/a	Fruits	NA	Road-killed specimen (from inside the stomach)	Lowland dry zone	Yala (Forest)	C. Anarasinghe, pers. comm.
						Trincomalee (Urban)	M. Rathnayake, pers. comm.

Table 2. Currently known predators of *V. bengalensis*, in Sri Lanka. Abbreviations used: E = Endemic; NV = native; NN = non-native; EN = non-native; EN = Endangered.

Predatory Class	Predator Taxon	Common name	Species Status	Prey Description	Location	References
Mammalia	<i>Homo sapiens</i>	Human	NV	Hunting on juveniles subadult, and adult stages, eats tongue and heart, skin use for drums, fat to make an oil	Lowland wet zone: Galle; Lowland intermediate zone: Kurunegala, Nilgala; Lowland dry zone: Jaffna	This study; Deraniyagala (1953), de Silva (1996)
	<i>Panthera pardus</i>	Leopard	EN	Live subadult	Lowland dry zone: Yala, Wilpattu	D. Ramasinghe & M. Piyasena, pers. comm.
	<i>Canis familiaris</i>	Domestic dog	NN	Live adult	Lowland wet zone: Raddolugama, Ambalangoda	This study; S. Atapattu pers. com.
	<i>Felis catus</i>	Domestic cat	NN	Live juvenile	Lowland wet zone: Rambukkana	This study
	<i>Canis aureus</i>	Jackal	NV	Carcass	Lowland intermediate zone: Illukkumbura; Lowland wet zone: Mirigama	This study
	<i>Herpestes brachyurus</i>	Brown mongoose	NV	Live juvenile	Lowland wet zone: Galle	M. Dahanayake, pers. comm.
	<i>Herpestes edwardsii</i>	Grey mongoose	NV	Live juveniles	Lowland wet zone: Ganemulla	This study
	<i>Herpestes smithii</i>	Ruddy mongoose	NV	Live juveniles	Lowland wet zone: Yala	M. Piyasena & S. Karunaratna, pers. comm.
	<i>Sus scrofa</i>	Wild boar	NV	Road kill	Lowland dry zone: Wilpattu, Galoya	This study; D. Kulathunga, pers. comm.
	<i>Oryzopsis gingalensis</i>	Sri Lankan grey hornbill	E	Live juveniles	Lowland dry zone: Mahiyanganaya	D. Kulathunga, pers. comm.
	<i>Pelargopsis capensis</i>	Stork-billed kingfisher	NV	Live juveniles	Lowland dry zone: Chilaw	A. Kumarasinghe, pers. comm.
	<i>Centropus sinensis</i>	Greater coucal	NV	Live juveniles	Lowland dry zone: Pannala	This study
	<i>Spilornis cheela</i>	Crested serpent-eagle	NV	Live juveniles	Lowland dry zone: Yala, Girtale; Lowland intermediate zone: Udawalawe	This study; C. Amarasinghe, pers. comm.
	<i>Accipiter badius</i>	Shikra	NV	Live juveniles	Lowland wet zone: Panadura, Kalutara	S. Dayananda, pers. comm.
	<i>Spizaetus cirrhatus</i>	Changeable hawk-eagle	NV	Live adult	Lowland dry zone: Yala	S. Karunaratna, pers. comm.
Reptilia	<i>Mycteria leucocephala</i>	Painted stork	NV	Live juvenile	Lowland wet zone: Maharagama	K. Buddika pers. comm.
	<i>Leptopitios javanicus</i>	Lesser adjutant	NV	Live juvenile	Lowland dry zone: Pokunutenna	N. Perera, pers. comm.
	<i>Corvus splendens</i>	House Crow	NV	Road kill	Lowland intermediate zone: Nilgala, Thanamalwila;	This study
	<i>Corvus leuicollis</i>	Jungle crow	NV	Road kill	Lowland dry zone: Eluwankulam	This study
	<i>Crocodylus palustris</i>	Mugger crocodile	NV	Live adult	Lowland intermediate zone: Thanamalwila; Lowland dry zone: Nilgala	D. Ramasinghe & N. Kamalgoda, pers. com.
	<i>Python molurus</i>	Rat snake	NV	Live juveniles	Lowland dry zone: Wilpattu; Lowland dry zone: Yala	This study, S. Kumara, pers. comm.
	<i>Python molurus</i>	Indian python	NV	Live adult	Lowland intermediate zone: Udawalawe; Lowland dry zone: Yala, Wilpattu; Upland wet zone: Kundsale	D. Jayantha, N. Kamalgoda & S. Karunaratna, pers. comm.
	<i>Naja naja</i>	Indian cobra	NV	Live juveniles	Lowland intermediate zone: Bulupitiya; Lowland dry zone: Polonnaruwa	This study; D. Kulathunga, pers. comm.
	<i>Varanus salvator</i>	Water monitor	NV	Road kill	Lowland wet zone: Kandana	This study

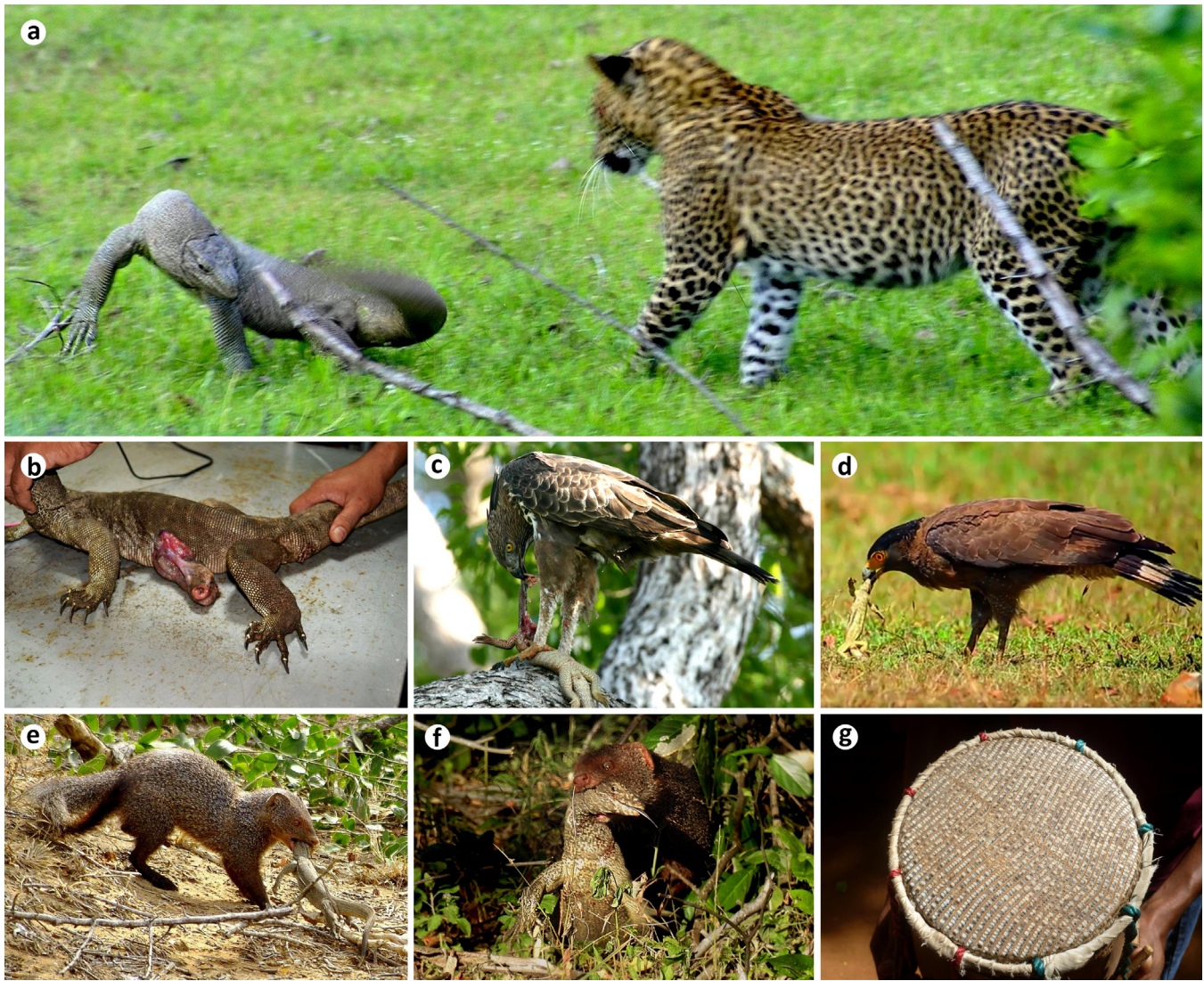


Fig. 2. Predators of *V. bengalensis*: (a) Sri Lankan leopard (*Panthera pardus*), (b) domestic dog attack (*Canis familiaris*), (c) changeable hawk-eagle (*Spizaetus cirrhatus*), (d) crested serpent-eagle (*Spilornis cheela*), (e & f) grey mongoose (*Herpestes edwardsii*), (g) local drum using the skin of *V. bengalensis*. Photographs by Mevan Piyasena, Sanjaya Atapattu, Mendis Wickramasinghe, and Dinesh Silva.

Sri Lanka or habitat type.

Discussion

Our study confirmed that *V. bengalensis* is a widely-foraging generalist predator that can also function as an opportunistic scavenger (Auffenberg, 1994; Pianka, 2004). Broad dietary niches have been reported for several other varanids throughout the Indo-Malayan and Australasian realms (Sutherland, 2011). In Sri Lanka, *V. bengalensis* seems to forage mostly as an active predator, and most of its prey are vertebrates. In

contrast, studies conducted elsewhere have suggested that invertebrates (flying insects, annelids, arachnids, mollusks, and crustaceans) comprised the primary diet, while vertebrates were an alternative prey depending on their availability (Auffenberg, 1994; Pianka, 2004). The dietary bias we noted in our study can be an artifact of biased sampling and detectability since predation on vertebrates is more noticeable to an opportunistic observer. *Varanus bengalensis* is also considered an egg predator of both reptiles and birds (Deraniyagala, 1953; Somaweera & Somaweera, 2009); however, our study only confirmed *V. bengalensis* predation of bird

eggs in Sri Lanka. Dietary studies on varanids have suggested a strong positive correlation between prey size and the monitor's body size, with large-bodied monitors foraging predominantly on vertebrate prey such as mammals while smaller-sized monitors practice insectivory (Arbuckle, 2009). Gut content analyses of *V. bengalensis* have supported this notion, where juvenile monitors feed nearly exclusively on insects such as orthopterans and coleopterans (Auffenberg & Ipe, 1983). However, vertebrate prey may account for a greater caloric (energetic) intake by monitors irrespective of the relative proportion of vertebrates in monitor diets (Arbuckle, 2009).

Plasticity in food selection and the catholic dietary habits of *V. bengalensis* have previously been documented from southeastern and southern Asian mainland, Indo-Malayan island, and Indian oceanic island populations (Jolley & Meek, 2006). Although predominantly terrestrial, a minor proportion of the diet of *V. bengalensis* consists of both aquatic and semi-aquatic prey (freshwater fish, amphibians, waterfowl, crocodiles, and freshwater crabs) in aquatic and riparian environments (S. Karunarathna, pers. obs.). Therefore, *V. bengalensis*, like many other varanids, may even shift its prey choice in response to seasonal and spatial variation in food availability, ontogeny, and intensity of competitive interactions (Shine, 1986; Losos & Greene, 1988; Sutherland, 2011). In Sri Lanka, the diversity of large lizards (only two species of *Varanus*) is lower than other regions within the natural range of varanids such as the Indo-Malayan region; thus, inter-specific competition is lower, which may have enabled *V. bengalensis* to retain a generalist diet. The other extant Sri Lankan monitor species, *V. salvator*, is predominantly aquatic, which further minimizes niche overlap with *V. bengalensis* (Karunarathna *et al.*, 2012).

Although *V. bengalensis* is mostly terrestrial, we have documented that the species can forage in arboreal habitats, where individuals feed on birds (common myna [*Acridotheres tristis*]; Jolley & Meek, 2006). Sometimes, *V. bengalensis* forages in vegetation alongside river banks or at the land-water interphase of rivers, lakes, and wetlands. When feeding on larger vertebrate prey, these monitors are known to kill their prey by violently shaking it or slamming it against hard substrates, then swallow the prey head first by pushing the prey against the ground and then using inertial movements until ingestion is complete (Loop, 1974; Jolley & Meek, 2006; Rahman *et al.*, 2015). When handling or capturing larger prey, these monitors can dismember their prey by holding them with forelimbs;

they are also known to dig in search of prey with their forelimbs and jaws (Auffenberg & Ipe, 1983; Rahman *et al.*, 2015). Moreover, when feeding on invertebrates with hard exoskeletons, the monitors masticate the shells first prior to ingestion (Jolley & Meek, 2006). We noted that *V. bengalensis* forages in multiple habitat types, including forests and woodlands with trees of variable trunk densities, home gardens and homesteads, urban and suburban environments, lotic and lentic aquatic habitats of both natural and anthropogenic origins, and brackish water habitats.

Our study indicates that *V. bengalensis* is capable of feeding on live prey as well as dead organic matter, including both native and introduced species. Carrion feeding has been observed throughout its range (Karunarathna *et al.*, 2012). Populations inhabiting homestead environments are known to spend nearly 50% of their activity budget on scavenging among household garbage, particularly kitchen trash where they feed on cooked and uncooked vegetables, grains, and fruits (Rahman *et al.*, 2015). The ability of several varanid species to scavenge human-generated trash is a remarkable feature which has enabled them to successfully exploit built-up environments and as a human commensal (Uyeda, 2009). Human-assisted food subsidies for varanids could have profound ecological effects on wild populations, such as increased abundance, altered community and intraspecific interactions, modified social hierarchies, and aggravated human-wildlife conflicts. Dramatic changes in wildlife behavior and community structure have been recognized among many other human commensals such as coyotes, crows, raccoons, mongoose, and gulls upon "supplementary feeding" (O'Connor, 2013).

Our study also established the fact that *V. bengalensis* may not be a top predator in Sri Lanka's ecosystems, although we only documented a few predators of *V. bengalensis*. Throughout its biogeographic range, a number of predators including pythons and other large snakes, eagles, mongooses, wild and domesticated dogs, feral cats, humans, and other varanids are known to predate on *V. bengalensis* (Auffenberg, 1994; Pianka, 2004). Similar to our findings in Sri Lanka, predation mostly occurs in early life-history stages (eggs, hatchlings, and juveniles), with only a small portion of predation involving fully-grown adults (Auffenberg, 1994; Pianka, 2004). Although cannibalism has been cited elsewhere, we do not have any evidence for active intraspecific predation of *V. bengalensis* in Sri Lanka (Auffenberg, 1994; Pianka, 2004).

Humans' role as a predator of *V. bengalensis* in

Sri Lanka is noteworthy. The human exploitation of *V. bengalensis* for food in Sri Lanka has historically been recorded as far back as 800 BC - 200 AD, and continues today to a greater extent and includes both consumption and trade (Abayaratna & Mahaulpatha, 2006; de Silva, 2006). Human exploitation of *V. bengalensis* has also been reported from South and Southeast Asia (Koch *et al.*, 2013). The hunting pressure on *V. bengalensis* in Sri Lanka as well as in some other parts of its range have led to localized population declines and reductions in their former ranges and habitats (Amarasinghe *et al.*, 2009; Koch *et al.*, 2013). In some rural parts of Sri Lanka such as Hambegamuwa (southeastern Sri Lanka), local inhabitants use the hides of *V. bengalensis* for making drums (Fig. 2).

Given its broad dietary preferences, which include many insects and rats, *V. bengalensis* can be considered a biological pest control agent (Karunarathna *et al.*, 2008; Karunarathna *et al.*, 2012). Moreover, as scavengers, these monitors contribute to organic matter cycling and the removal of carrion (Somaweera & Somaweera, 2009; Karunarathna *et al.*, 2012). Their role as a mesopredator provisions many ecosystem services which involves regulating populations in lower trophic levels while also serving as prey for top predators. Behavioral studies have suggested that *V. bengalensis* allocate a greater portion of their daily activity budgets to foraging, where they roam extensively over great distances exploring profitable foraging grounds (Losos & Greene, 1988; Sweet & Pianka, 2007). Thus, their contribution to energy flow and nutrient cycling is salient for proper ecosystem functioning. Quantifying their role in food webs based on gut content surveys and carbon isotope analyses using network theory (carbon and energy flow across different trophic nodes) may provide considerable insight on their ecological role. Moreover, our study has indicated that *V. bengalensis* feeds on non-native species; therefore, these monitors could have some impacts on controlling invasive species. This potential requires further investigation.

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