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RESEARCH ARTICLE

Distribution, habitat associations and conservation implications of Sri Lankan freshwater terrapins outside the protected area network

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Abstract

1. Terrapins are integral to many freshwater ecosystems, yet are imperilled at a global scale. In Sri Lanka, terrapins are understudied; thus, much of their natural history and distribution status remain unknown. Such paucity of studies impedes conservation.
2. In this study, 79 freshwater habitats located outside the protected area network of south-western Sri Lanka were surveyed to document current population densities and habitat use of two terrapin species: Indian black terrapin (*Melanochelys trijuga thermalis*) and flap-shelled terrapin (*Lissemys ceylonensis*). Local inhabitants were interviewed to assess human threats towards terrapins.
3. Both species were recorded in low densities: 1–2 individuals ha^{-1}. Indian black terrapin was found in half of the surveyed sites while flap-shelled terrapin occurred in one-third of the surveyed sites. Highly urbanized river basins had the lowest densities for both species while rural basins supported higher numbers. Basking was the predominant behaviour of both species and large woody debris and boulders were preferred as basking substrates, together with sparse-canopy aquatic habitats with intact marshlands.
4. Overharvesting for meat was a major threat for terrapins. Most local inhabitants were unaware of legislation on terrapin conservation and the ecological importance of terrapins. Human threats such as pollution, modification of aquatic and wetland habitats, and loss of riparian forests were frequently observed in surveyed sites. Terrapin populations outside the protected area are at risk as evidenced by lower population densities and a multitude of human threats.
5. A landscape-scale ecosystem-based conservation approach is recommended for Sri Lanka's terrapins with incorporation of lands with different management regimes (privately owned, municipality managed) into the protected area network. Current environmental legislation should be revised to support buffer zone delineation for aquatic habitats, wetland restoration, and landscape-scale connectivity.

KEYWORDS
basking, chelonians, habitat use, management, overharvesting, wetlands

1 | INTRODUCTION

The Indian oceanic tropical island of Sri Lanka provides habitats for all three major clades of Chelonians (Class: Reptilia, Order: Testudines): marine turtles, land tortoises, and freshwater terrapins. The Indian star tortoise (*Geochelone elegans*) – a species widespread throughout southern Asia – is Sri Lanka's only terrestrial chelonian (Das & Bhupathy, 2009). Three species of terrapins have been recorded in Sri Lanka's freshwater habitats. The red-eared slider (*Trachemys scripta*) is considered an alien invasive species that has successfully established resident populations in Sri Lanka (Marambe et al., 2011). The flap-shelled terrapin (*Lissemys ceylonensis*) and two sub-species of the Indian black terrapin (*Melanochelys trijuga parkeri* and *Melanochelys trijuga thermalis*), have undergone insular radiation in Sri Lanka (Deraniyagala, 1939). Given long-term geographic isolation and ancient divergence, endemic species complexes are likely to exist within Sri Lankan terrapins and tortoises, especially in *Geochelone elegans* and *Melanochelys trijuga* (Mukherjee, Nixon, & Bhupathy, 2006; Praschag, Stuckas, Päckert, Maran, & Fritz, 2011).

Melanochelys trijuga thermalis occurs in both south-eastern India and Sri Lanka while Sri Lankan endemic *L. ceylonensis* is mostly found in the lowlands of Sri Lanka (Das & De Silva, 2005). These terrapins are generalists that are known to occupy a variety of aquatic and semi-aquatic habitats including wetlands, running water, and stagnant water (Das & Bhupathy, 2009; Deraniyagala, 1939; Karunarathna & Amarasinghe, 2011a). They feed on a wide variety of food including aquatic and semi-aquatic plants, fruits, many invertebrates (predominantly crustaceans and molluscs), and animal faeces (Das & Bhupathy, 2009; Deraniyagala, 1939). Throughout tropical wet climates these terrapins remain active year-round; their reproductive season extends from August to December (Das & Bhupathy, 2009).

Conservation of Sri Lankan chelonians is challenged by a deficiency of macroecological information since geographic distribution, habitat use, and conservation of Sri Lanka's terrapins are understudied (Karunarathna & Amarasinghe, 2011b). Moreover, scientific understanding of their seasonality in behavioural patterns and foraging ecology remain largely anecdotal or in grey literature (Dudgeon, 2003). In Sri Lanka, chelonian research and conservation efforts are overwhelmingly biased towards marine turtles (Hewavisenthi, 1993; Pernetta, 1993). Ecological research addressing population parameters, age structure, habitat use, microhabitat preferences, and behaviour has supported the conservation of terrapins in many other parts of the world – for instance, in the south-eastern United States and the Ozark mountain range of the US interior highlands (Fitzsimmons, Greene, Gibbons, Jeffrey, & Tucker, 2001; Pitt & Nickerson, 2012). Studies on community composition and population dynamics of freshwater terrapins have been reported from southern Asia as well (Safi & Khan, 2014).

In mainland Asia, consumption-based overexploitation both for international trade and for the local market is responsible for substantial population declines of terrapin communities (Cheung & Dudgeon, 2006; Krishnakumar, Raghavan, & Pereira, 2009). Water pollution, hydrological modifications, and extensive riparian deforestation have aggravated population decline of Asian terrapins, possibly leading to local extirpations (Cheung & Dudgeon, 2006; Dudgeon et al., 2006). Sri Lankan terrapins are also likely to suffer similar adversities. Nation-wide predicaments encountered by freshwater ecosystems and a paucity of ecological information make urgent the call for population surveys of Sri Lanka's terrapins to build up an ecological knowledge base, and for science-based conservation actions. The importance of monitoring terrapin populations has been underscored in many turtle conservation action plans (IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, 1989; Turtle Conservation Fund, 2002). The national conservation status of both these species is currently given as 'Least Concerned' owing to their 'purported' broad distribution; the IUCN Red List considers *M. trijuga* as 'Near Threatened' while *L. ceylonensis* remains unassessed (MOE, 2012).

Terrapins play a critical role in wetlands and other inland aquatic ecosystems. They are effective seed dispersing agents for aquatic plants. Being consumers (herbivores, carnivores, and scavengers) at multiple levels in aquatic and semi-aquatic food webs, they support nutrient cycling as well as maintaining trophic dynamics (Harden, DiLuzio, Gibbons, & Dorcas, 2007). Such environmental services performed by terrapins also underline the need for their conservation and for ecological research.

To document distribution of the two species of Sri Lankan freshwater terrapins, *L. ceylonensis* and *M. trijuga thermalis*, surveys were conducted in less explored landscapes of south-western Sri Lanka outside the protected area network. In Sri Lanka, the protected area network comprises state-owned lands such as national parks, forest reserves, conservation forests, and sanctuaries. A greater proportion (~70%) of Sri Lanka's protected area network lies in the dry and intermediate bioclimatic zone (annual average rainfall <2000 mm) of Sri Lanka (Bambaradeniya, 2006); yet >90% of the nation's biodiversity is found in the south-western wet zone (annual average rainfall >2000 mm), where the protection afforded is inadequate (Gunatilleke & Gunatilleke, 1990). Protected areas in south-western Sri Lanka are smaller (40–70 km^2) and are isolated (Gunawardene et al., 2007; MFE, 1999). Given inadequate protection, adverse human impacts on natural landscapes are growing in this region. Although, statutory protection prohibits collection, killing, and trade of terrapins or their eggs, the enforcement of these regulations outside the protected area network is non-existent (Parliament of the Democratic Socialist Republic of Sri Lanka, 2009). Therefore, it is both timely and appropriate to focus this survey in south-western Sri Lanka. The objectives of this research were to (1) compare the population density of the two terrapin species among different administrative districts and river basins; (2) investigate microhabitat use (based on the substrates occupied) and general behaviour of the species; (3) study the influence of local environmental variables on the density of each species; (4) document threats endangering populations and habitats of species; and (5) provide recommendations to conserve these species and their habitats.

2 | METHODS

2.1 | Field surveys

Seventy-nine inland aquatic habitats (streams and lakes) and associated riparian habitats representing seven river basins (Attanagaluoya, Kelani, Kalu, Bentara, Gin, Nilwala, and Walawe) (Figure 1) were surveyed during a 6-month period (November 2014–April 2015). The sampling period covered both the active period and reproductive season of the species. All sampling sites were located outside the protected area network and covered six administrative districts (Gampaha, Kalutara, Galle, Matara, Hambantota, and Colombo). An average of eight transects per day were surveyed involving three field biologists. To capture variation in the daily activity of the terrapins, a given site was surveyed at different times of the day: mornings (07.00–11.00), afternoons (13.00–15.00), and evenings (17.00–19.00).

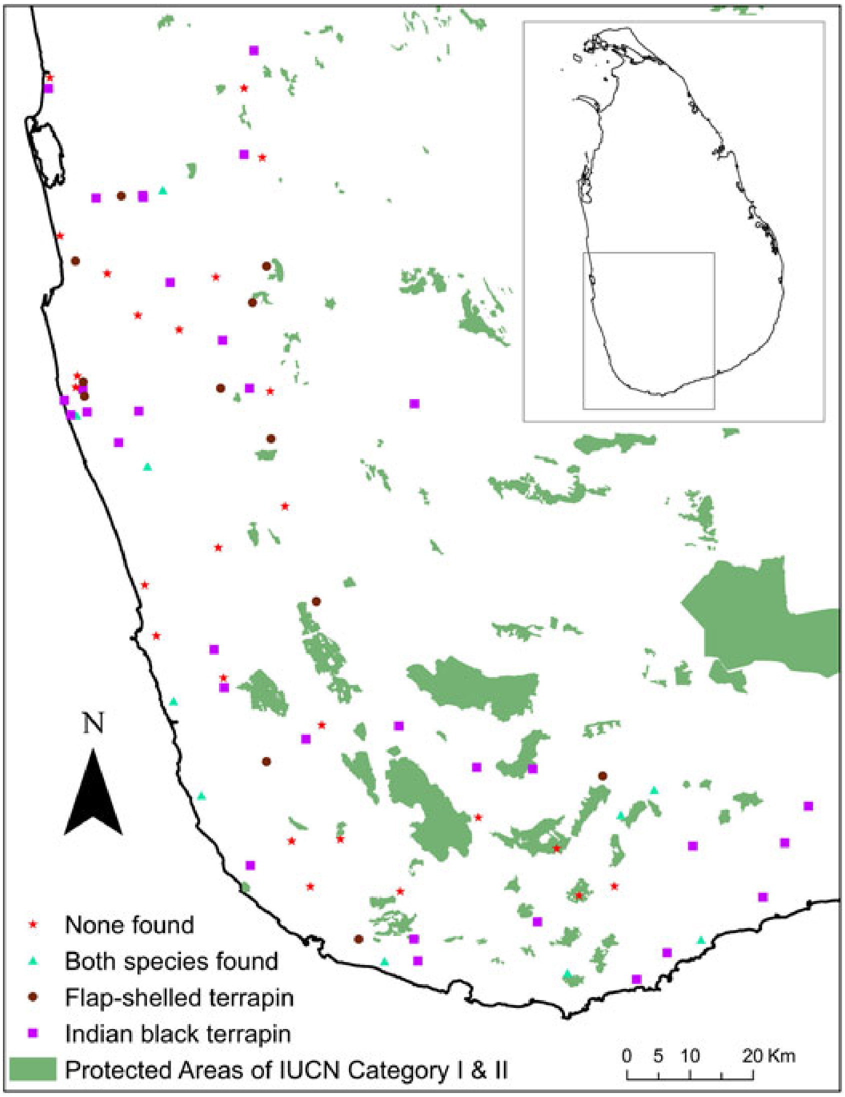

FIGURE 1 Sampling locations of Indian black terrapin (*Melanochelys trijuga thermalis*) and Sri Lanka flap-shelled terrapin (*Lissemys ceylonensis*) from south-western Sri Lanka during the present study

At each location, the surveys were based on both active search and visual scanning of 200 m × 20 m belt transects where each transect covered both standing-water habitats and adjoining terrestrial habitats. Sampling locations were at least 1 km apart from each other, thus were spatially independent. Terrapins inside the transects were captured by hand, and the species identity and the stage of maturity (adult, subadult or juvenile) were recorded based on their body sizes (adults ≥21 cm, subadults 16–20 cm or juvenile ≤15 cm). In addition, specific behavioural acts (i.e. specific behaviour performed by each turtle, such as sunning, moving, and foraging) at the time of observation were also documented.

Multiple environmental variables were measured at each transect: percentage canopy cover (spherical densiometer), substrate occupied by terrapins, elevation (Garmin Etrex 10), ambient temperature (hand-held thermometer), relative humidity, and physicochemical water quality variables such as water depth, water temperature, and pH (6-in-1 environmental digital meter). For each individual captured, the body surface temperature (laser beam thermometer) was recorded. At each survey location, the riparian vegetation type was assigned to one of three possible categories: bushlands (predominantly woody vegetation with a height of 1–3 m), scrublands (predominantly herbaceous vegetation mixed with scattered woody patches of shrubs, highest vegetation <1 m), and marshlands (predominantly grasses and sedges growing in saturated soil or standing water).

At each transect, all observable threats for terrapin populations and their habitats were documented. Based on a questionnaire survey, interviews were conducted in person with 183 inhabitants of local communities across all survey sites to assess the human impacts on terrapin populations. The questionnaire asked the following: (1) Have you seen either species in the wild? (2) Have you killed/consumed species regularly? If so how many? (3) Do terrapins confer environmental/economic benefits? (4) Are terrapin populations declining? (5) Have you seen terrapin road-kills? (6) Are you aware of state-mandated legislation on terrapin conservation? All questions had binary responses except for the questions on numbers of animals killed.

2.2 | Data analysis

All analyses were conducted using *R* statistical software version 3.2.2 (*R* Core Team, 2016) based on non-parametric tests since the data collected did not meet normality. Since the relative abundance of each maturity stage of both terrapin species was small, all statistical analyses were conducted per species, not per stage of maturity.

Based on the relative abundance, the population density of each species was calculated per hectare at each sampling site. Differences in density of each species was assessed among all surveyed administrative districts as well as different river basins using a Kruskal–Wallis test. For each sampling location, all point observations of major behavioural acts per species were tallied. Based on a Wilcox sign rank test, the frequencies of all behavioural acts per species were compared to test which behavioural act is more frequent during their active period. The number of instances each species was recorded at a given substrate (irrespective of the behaviour) were tallied. Any significant differences in substrate use for each species were examined using a Kruskal–Wallis test. If significant differences were detected, pairwise post hoc tests were conducted. A non-parametric Pearson's partial correlation test was performed between each species density and each of the environmental variables measured. In the same analyses, the density of one species was correlated with the density of the other species to test how density of one species affects that of the other. To assess the influence of riparian vegetation type on density of species, a Kruskal-Wallis test was performed. If significant differences were detected, pairwise post hoc tests were performed.

All binary responses from the interview survey were analysed using a paired Wilcox sign rank test. The total numbers of respondents for each binary option were considered the numerical response variables while the questions asked were considered the factors.

3 | RESULTS

3.1 | Differences in population density

In total, 68 *M. t. thermalis* and 35 *L. ceylonensis* were reported during this survey, with an average density of 2.15 (S.E. ±0.28) and 1.11 (S.E. ±0.22) ha^{-1}, respectively. *Melanochelys trijuga thermalis* was found in 53.16% of the surveyed locations; the equivalent figure for *L. ceylonensis* was 27.85%. Neither was recorded from 31.65% of the surveyed sites; both were found in 12% of the surveyed sites. These numbers reported were based on surface-active terrapins. Detection of underwater terrapins was impossible owing to high turbidity; the survey did not account for subterranean terrapins either.

On average, the density of *M. t. thermalis* and *L. ceylonensis* per administrative district was 2.3 (±1.2) ha^{-1} and 1.2 (±0.4) ha^{-1}, respectively (Table 1). The equivalent numbers per river basin were 2.3 (±1.1) ha^{-1} and 1.2 (±0.3) ha^{-1} (Table 1). The Kruskal–Wallis test revealed a significant difference in density of *M. t. thermalis* across administrative districts ($H = 12.73$, $P < 0.05$) but not across river basins ($H = 9.73$, $P > 0.05$). No significant differences were detected for density variation of *L. ceylonensis* across administrative districts ($H = 1.16$, $P > 0.05$) or river basins ($H = 1.37$, $P > 0.05$). The greatest density of both species was recorded from Hambantota district followed by Galle and Matara districts (Table 1). The lowest density of *M. t. thermalis* was reported from Kalutara district whereas Gampaha district had the lowest density of *L. ceylonensis*. For both species, the second lowest density was recorded from Colombo district (Table 1). Most of the captured individuals of both *M. t. thermalis* (59%) and *L. ceylonensis* (63%) were adults.

Among all the administrative districts surveyed, *M. t. thermalis* was the dominant species with the exception of Kalutara district where both species occurred in equal numbers. Comparable observations were made across different river basins where *M. t. thermalis* dominated all surveyed river basins with Kalu basin being the exception where dominance was reversed (Table 1). Walawe basin had the greatest density of *M. t. thermalis* followed by Gin basin; the same basins had the greatest density of *L. ceylonensis* (Table 1). Kalu and Maha river basins had the lowest density of *M. t. thermalis* and *L. ceylonensis*, respectively.

3.2 | Comparison of behaviour

Two major behavioural acts were observed for both species – basking and foraging. For both species, the number of basking individuals was significantly higher than that for foraging (*M. t. thermalis*, $U = 861$, $P < 0.05$; *L. ceylonensis*, $U = 484$, $P < 0.05$). The behavioural observations reported were limited to surface (above water) activities. Terrapins mostly foraged on both aquatic and riparian plants, but high turbidity of the water prevented observations being made under water. Although the survey period overlapped with the breeding season of both species, no reproductive behaviour (mating, egg-laying) was observed.

3.3 | Comparison of microhabitat associations (substrate use)

The species exclusively used three types of microhabitats: woody debris and boulders that emerged from the water, and riparian habitats such as river banks. Significant differences in microhabitat associations were found for both species (*M. t. thermalis*, $H = 7.12$, $P < 0.05$; *L. ceylonensis*, $H = 7.18$, $P < 0.05$). While there was no significant difference in microhabitat occupancy for either terrapin species between woody debris and boulders, both species showed a significant preference both for boulders and woody debris over riparian habitats (*M. t. thermalis* mean difference = 2.75, $P < 0.05$; *L. ceylonensis* mean difference = 2.75, $P < 0.05$).

3.4 | Correlation between density and local environmental variables

Among the environmental variables (Table 2), canopy cover had a significant negative correlation with the density of both terrapin species (*M. t. thermalis* $r = -0.62$, $P < 0.05$; *L. ceylonensis*, $r = -0.33$, $P < 0.05$). The density of each species had a significant, but weak negative correlation with the other ($P < 0.05$, $r = -0.22$). The density also varied significantly across different riparian vegetation types (*M. t. thermalis*, $H = 8.43$, $P < 0.05$; *L. ceylonensis*, $H = 17.72$, $P < 0.05$). Both species occurred in significantly higher densities in marshlands than in bushlands (*L. ceylonensis* mean difference = 4.27, $P < 0.05$) or scrublands (*M. t. thermalis*, 4.87, $P < 0.05$). Neither species significantly differed in density between scrublands and bushlands (*L. ceylonensis*, mean difference = 1.07, $P > 0.05$; *M. t. thermalis*, 1.85, $P > 0.05$). None of the

TABLE 1 Distribution of Indian black terrapin (*Melanochelys trijuga thermalis)* and Sri Lanka flap-shelled terrapin (*Lissemys ceylonensis*) within each administrative district and river basin: percentage occurrence [(total abundance per stage of maturity in each species ÷ total abundance of both species at all stages of maturity) * 100], and population density

	Melanochelys trijuga thermalis				*Lissemys ceylonensis*			
District	**Adult**	**Subadult**	**Juvenile**	**Total**	**Adult**	**Subadult**	**Juvenile**	**Total**
Percentage occurrence								
Gampaha	35.29	29.41	5.88	70.58	17.65	11.76	0.00	29.41
Kalutara	37.50	12.5	0.00	50	37.5	12.5	0.00	50
Galle	40.74	25.92	0.00	66.66	29.63	3.70	0.00	33.33
Matara	50.00	16.67	0.00	66.67	16.67	16.67	0.00	33.34
Hambantota	23.81	38.10	9.52	71.43	4.76	19.05	4.76	28.57
Colombo	44.44	16.67	0.00	61.11	22.22	16.67	0.00	38.89
Population density (animals ha^{-1})								
Gampaha	0.89	0.74	0.15	1.78	0.44	0.29	0.00	0.73
Kalutara	0.75	0.25	0.00	1	0.75	0.25	0.00	1
Galle	1.71	1.10	0.00	2.81	1.25	0.16	0.00	1.41
Matara	1.50	0.50	0.00	2	0.50	0.50	0.00	1
Hambantota	1.56	2.50	0.62	4.68	0.31	1.25	0.31	1.87
Colombo	1.11	0.42	0.00	1.53	0.56	0.42	0.00	0.98

	Melanochelys trijuga thermalis				*Lissemys ceylonensis*			
River basin	**Adult**	**Subadult**	**Juvenile**	**Total**	**Adult**	**Subadult**	**Juvenile**	**Total**
Percentage occurrence								
Benthara	40	20	0	60	40	0	0	40
Gin	33.33	33.33	0	66.66	26.67	6.67	0	33.34
Kalu	40	0	0	40	40	20	0	60
Kelani	37.5	20.83	0	58.33	25	16.67	0	41.67
Maha	38.46	30.77	7.69	76.92	15.38	7.69	0	23.07
Nilwala	41.67	25	4.17	70.84	12.5	12.5	4.17	29.17
Walawe	33.33	33.33	8.33	74.99	0	25	0	25
Population density (animals ha^{-1})								
Benthara	1.25	0.63	0.00	1.88	1.25	0.00	0.00	1.25
Gin	1.56	1.56	0.00	3.12	1.25	0.31	0.00	1.56
Kalu	0.62	0.00	0.00	0.62	0.62	0.31	0.00	0.93
Kelani	1.12	0.62	0.00	1.74	0.75	0.50	0.00	1.25
Maha	0.89	0.71	0.18	1.78	0.36	0.18	0.00	0.54
Nilwala	1.56	0.94	0.16	2.66	0.47	0.47	0.16	1.1
Walawe	2.00	2.00	0.50	4.50	0.00	1.50	0.00	1.5

TABLE 2 Average physico-chemical parameters of sampling sites (79) associated with the presence of Indian black terrapin (*Melanochelys trijuga thermalis)* and Sri Lanka flap-shelled terrapin (*Lissemys ceylonensis*). The standard deviations are provided in parentheses

Environmental variable	*M. t. thermalis*	*L. ceylonensis*
Canopy cover (%)	1.96 (2.95)	0.04 (0.04)
Body surface temp. °C	28.54 (0.42)	27.13 (0.35)
Water temperature (°C)	28.70 (0.23)	28.72 (0.19)
Air temperature (°C)	31.29 (0.48)	31.38 (0.42)
Water pH	7.34 (0.17)	7.35 (0.22)
Water depth (m)	2.98 (0.93)	3.05 (1.13)
Relative humidity (%)	60.05 (6.27)	59.64 (5.94)
Elevation (m)	33.60 (43.67)	41.85 (64.84)

other environmental variables showed any significant correlations with the density of either species.

3.5 | Trends in the questionnaire survey

More respondents have seen *M. t. thermalis* in the wild than those who have seen *L. ceylonensis* (Table 3). The number of respondents who have seen *M. t. thermalis* in the wild were significantly higher than those who have not ($U = 1$, $P < 0.05$); in contrast, no such significant differences were found for *L. ceylonensis* ($U = 4.5$, $P > 0.05$). The number of respondents claimed to have killed either species did not differ significantly from those who did not (Table 3, *M. t. thermalis*, $U = 15$, $P > 0.05$; *L. ceylonensis*, $U = 15$, $P > 0.05$). However, significantly more respondents (70%) seemed to have

TABLE 3 Results of the questionnaire-based interview with the local communities (MTT = *Melanochelys trijuga thermalis*; LC = *Lissemys ceylonensis*; FFPO = Fauna and Flora Protection Ordinance)

	Administrative districts (number of people interviewed)						
Questions	**Hambantota (32)**	**Matara (29)**	**Colombo (45)**	**Gampaha (23)**	**Kalutara (18)**	**Galle (36)**	**Total**
Have you seen MTT in the past 10 years?							
Yes	27	21	26	17	16	22	129
No	5	8	19	6	2	14	54
Have you seen LC in the past 10 years?							
Yes	14	11	23	9	11	22	90
No	18	18	22	14	7	14	93
Have you ever killed MTT?							
Yes	15	10	21	9	8	24	87
No	17	19	24	14	10	12	96
If yes, how many did you kill in the past 10 years?	260	320	170	280	220	370	1620
Have you ever killed LC?							
Yes	12	14	17	11	8	26	88
No	20	15	28	12	10	10	95
If yes, how many did you kill in the past 10 years?	150	200	180	90	220	260	1100
Do you regularly consume MTT?							
Yes	27	26	35	15	16	27	146
No	5	3	10	8	2	9	37
Have you ever eaten LC?							
Yes	24	21	38	18	14	25	140
No	8	8	7	5	4	11	43
The benefit of terrapins:							
For environment functions	2	7	9	4	5	11	38
For meat	30	22	36	19	13	25	145
Are terrapins protected by FFPO?							
Yes	5	8	16	7	4	14	54
No	27	21	29	16	14	22	129
Are terrapins declining?							
Yes	30	24	39	19	16	32	160
No	2	5	6	4	2	4	23
Have you seen roadkilled MTT?							
Yes	13	22	31	15	12	27	120
No	19	7	14	8	6	9	63
Have you seen roadkilled LC?							
Yes	9	19	22	12	10	17	89
No	23	10	23	11	8	19	94

eaten either species compared with the number of those who have not (Table 3, *M. t. thermalis*, $U = 0$, $P < 0.05$; *L. ceylonensis*, $U = 0$, $P < 0.05$).

Only one-fifth of respondents believed in environmental benefits of terrapins, which was significantly lower than the number considering that meat consumption is the only use of terrapins (Table 3, $U = 0$, $P < 0.05$). Moreover, a significantly higher proportion of respondents (70%) was unaware that native terrapins were protected by Fauna and Flora Protection (Amendment) Ordinance (Table 3, $U = 21$, $P < 0.05$). A significantly greater proportion of the local inhabitants (87%) believed that terrapins are declining based on their opportunistic observations (Table 3, $U = 0$, $P < 0.05$). A significantly higher number of local inhabitants have seen roadkills of *M. t. thermalis* but not *L. ceylonensis* (Table 3, *M. t. thermalis*, $U = 1.5$, $P < 0.05$; *L. ceylonensis*, $U = 11$, $P > 0.05$).

3.6 | Threats observed

The human threats documented through direct observations included hydrological modifications, littering, point-source and nonpoint-source pollution, overharvesting terrapins, clearance of riparian vegetation, road mortality, and filling and draining wetlands (Figure 2, 3). Nearly 82% of the surveyed sites suffered at least two forms of human-induced impacts. Draining and reclamation of wetlands for infrastructure, industrial, and residential development or agriculture were the commonest types of impacts and recorded at >82% of the sites.

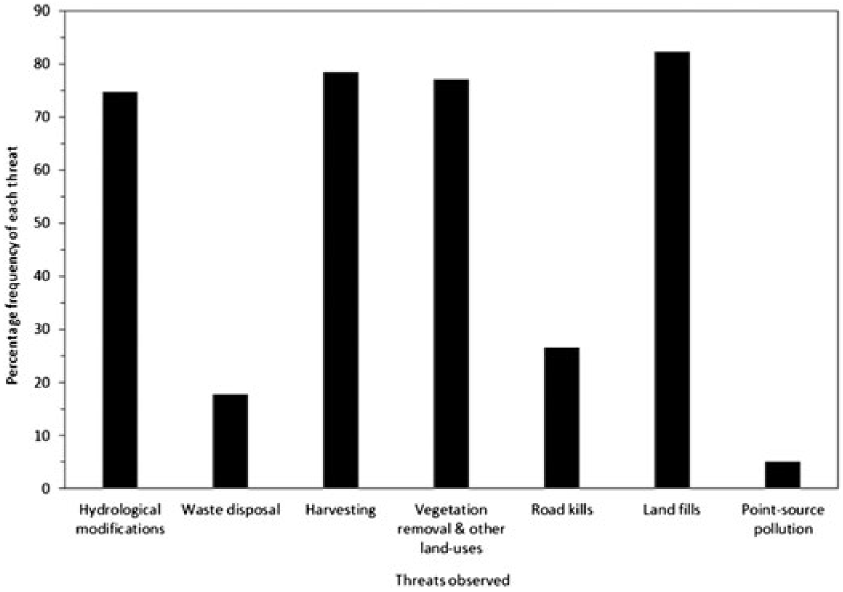

FIGURE 2 Major threats documented in and around surveyed locations in south-western Sri Lanka

FIGURE 3 Species, habitats surveyed, and threats observed: (a) Indian black terrapin (*Melanochelys trijuga thermalis*); (b) flap-shelled terrapin (*Lissemys ceylonensis*); (c) intact riparian vegetation found in rural river basins; (d) large woody debris and large boulders in river channel; (e) wetland drainage and reclamation; and (f) loss of riparian habitats, development, and pollution in urban river basins

Hydrological modifications, overharvesting, and loss of riparian vegetation were also commonly observed at more than 75% of the surveyed sites (Figure 3). Impoundment, diversion, and channelization were the most prominent forms of hydrological modifications. Improper disposal of solid waste (household garbage and municipal waste) was recorded at 18% of the surveyed sites. Riparian habitats have been encroached on for arable farming (mostly to cultivate edible green leaves) as well as for illicit human settlements and tourist hotels. Although observed at relatively low frequency (5% of sites), industrial and municipal effluents were discharged directly into aquatic habitats. Industrial effluvia were mostly discharged from crude oil refinery plants, garment factories, and battery and asbestos manufacturing plants.

Harvesting terrapins – both adults and eggs – was mostly evident by observing the presence of terrapin carapaces, plastrons, and egg shells in and around homesteads, and via the questionnaire-based interview with local inhabitants. The primary purpose of harvest seemed to be local consumption as a delicacy (especially around Hambantota and Galle districts). Local villagers capture terrapins with cast nets, hoop net turtle traps, baited hooks, or manually by actively searching. Terrapins in burrows are collected by probing the earth with an iron-tipped stick.

4 | DISCUSSION

4.1 | Variation in population density

The survey covered a substantial extent of Sri Lanka's south-western lowlands (Figure 1). The density recorded for both species was remarkably low: only 103 individuals were found over a total area of 316 000 m^2. Terrapin densities recorded in this study are comparable with declining freshwater turtle populations throughout Indo-Malayan and Indo-Chinese biogeographical realms (Van Dijk, 2000). For each species, density ranged between 1 and 2 individuals per ha. *Melanochelys trijuga thermalis* was nearly twice as abundant as *L. ceylonensis*. The abundance of sexually immature individuals was also low for both species (31 of *M. t. thermalis* and 13 of *L. ceylonensis*); this suggests reduced recruitment of younger age classes either through high mortality or reduced reproductive effort. Chelonians are long-lived species with longer generation times, prolonged growth periods, delayed reproductive maturity, and high juvenile mortality (Congdon, Dunham, & van Loben Sels, 1993; Gerlach, 2008).

Although both species occur in stable, relatively large populations in protected areas of Sri Lanka, and hence considered ‘Least Concerned’ in national conservation assessments (Das & Bhupathy, 2009; IUCNSL & MOENR, 2007; MOE, 2012), this survey found that their status outside state-mandated conservation lands is bleak. Lower abundance, low densities, and long-term population reductions have been observed in many chelonians in other tropical areas, especially in Continental Asia and Indian Oceanic Islands (Das, 1990; Gerlach, 2008; Krishnakumar et al., 2009; Safi & Khan, 2014). Declining populations of terrapins have also been reported from biodiversity-rich New World eco-regions such as the Ozark-Ouachita Mountains and the south-eastern coastal plains of North America (Pitt & Nickerson, 2012; Pittman & Dorcas, 2006).

This study revealed variable terrapin population densities among different administrative districts. The lowest densities were recorded from highly-urbanized, western coastal districts – Colombo, Gampaha, and Kalutara – where high human population densities and industrial development have endangered terrapin habitats (Department of Census & Statistics, 2012; Survey Department of Sri Lanka, 2012). The southern districts – Hambantota, Galle, and Matara – are mostly rural, with lower human population growth rates, so terrapin habitats experience less pressure (Department of Census & Statistics, 2012; UNDP Sri Lanka, 2012). Although differences in terrapin densities across river basins were non-significant, southern river basins overlapped spatially with rural southern districts where the pressures on aquatic habitats are low, thus supporting higher terrapin densities. Likewise, western river basins supported lower terrapin densities which coincided with urbanized western districts. Basin-scale urban development is known to induce declines in population sizes, reduced reproductive fitness and recruitment, slowed growth, and altered community interactions. In Australia, urbanization at a catchment scale led to inhibition of niche partitioning among sympatric turtles, ultimately leading to intensification of competition for habitats and other critical resources (Burgin & Ryan, 2008).

Inferences on terrapin densities, and subsequent analyses on microhabitat associations and behaviour, were limited to surface-active terrapins. The survey techniques used accounted neither for subterranean terrapins (those that remain in burrows) nor submerged terrapins. Therefore, density estimations in this study may be underestimations owing to partial detection. Thus, replicating surveys within and between years, and occupancy modelling that accounts for habitat heterogeneity (presence of terrain burrows, subterranean tunnels, and water turbidity) would have enhanced detectability.

4.2 | Variation in behaviour and microhabitat associations

Basking was the major behavioural act observed for both species, emphasizing the importance of behavioural thermoregulation for terrapins. Being poikilotherms, they rely on exposure to solar radiation to regulate their internal body temperature to maintain optimal metabolism. Allocation of a greater portion of their activity budget for behavioural thermoregulation (both basking and immersing in water) has been reported elsewhere (Harden et al., 2007; Lindeman, 1999; Moll & Moll, 2004). Maintaining their metabolic optima is crucial for maximizing their overall fitness through active foraging, efficient digestion, blood circulation, nutrient and energy assimilation, optimal immunity, efficient growth and higher reproductive success (Polo-Cavia, López, & Martín, 2012). Basking also helps skin conditioning to eliminate epibionts and parasites (Lindeman, 1999).

Microhabitat selection of terrapins was also linked to basking as both species were associated with emergent substrates such as boulders and large fallen logs and tree stumps. These substrates provide optimal exposure to solar radiation while minimizing predation risk. Terrapins use a variety of other basking substrates including roots of standing vegetation, rocks, sandy beaches, and grassy or muddy banks (Boyer, 1965). The boulders and fallen logs were drier and dark-coloured compared with the damp riparian habitats; therefore they had higher IR-absorption capacity (Boyer, 1965) so were the most preferred basking substrates. Numerous previous studies have made similar observations on the use of rocks and woody debris for basking (Nickerson & Pitt, 2012; Pitt & Nickerson, 2012).

Our observations also emphasized the importance of large woody debris (LWD) in aquatic and wetland habitats, which is regularly removed from navigable and constructed waterways; such management activities can have a detrimental impact on terrapin populations (Lindeman, 1999; Nickerson & Pitt, 2012). Presence of mature riparian vegetation is essential for ensuring a continuous supply of LWD; reduced availability and lower abundance of terrapins have been observed in drainage basins with highly developed shorelines (Lindeman, 1999). Large woody debris also provides habitats for terrapin prey such as molluscs and aquatic insect larvae (Nickerson &

Pitt, 2012; Pitt & Nickerson, 2012); thus, a reduced supply of LWD can also lead to food depletion for terrapins. Although not documented in this study, recreational motor boating causes significant physical damage and mortality to terrapins through direct collisions. In addition, impeded intraspecific communication, as well as disturbance to life-history functions such as sunning, foraging, and mating can result from recreational boating (Bulté, Carrière, & Blouin-Demers, 2010). Although uncommon in Sri Lankan inland waterways, with burgeoning tourism and outdoor leisure activities recreational boating may affect rivers and lakes in Sri Lanka in the near future (Simon, De Jesus, Boonchuwong, & Mohottala, 2001).

4.3 | Effects of local environmental variables on terrapins populations

The presence of canopy openings was an important environmental feature for both species. This can be attributed to their basking behaviour which requires exposure to solar radiation. Yet, a closed canopy should not be interpreted as a cause of declining terrapin populations; rather, sparse canopy is an environmental correlate of larger aquatic ecosystems such as large-sized sluggish rivers, swamps, and lakes that are conducive to terrapins (Bour, 2008; Deraniyagala, 1939; Sethy, Samantasinghar, & Pramanik, 2015).

The strong positive association observed between terrapin density and the presence of intact marshlands underscored the importance of wetlands for these species. Terrapins are known to aestivate in marshlands during droughts (Sethy et al., 2015). Wetlands retain sediments, inorganic and organic matter, and subsequently recycle and redistribute such allochthonous material and thereby detoxify surface runoff before it reaches the core aquatic habitat. Thus, marshlands function as a buffer to regulate optimal water quality and other hydrological features (discharge) of the core aquatic habitat (Dudgeon et al., 2006). Wetlands are among the most productive inland ecosystems, and can be ideal feeding grounds for terrapins (Dudgeon, 2000). Marshlands between aquatic habitats may function as effective corridors facilitating landscape-scale connectivity, metapopulation interactions, and gene flow (Turtle Conservation Fund, 2002). As wide-ranging species that move among multiple aquatic habitats during their lifetime, functional connectivity is crucial for terrapins (Burke, Lovich, & Gibbons, 2000; Carter, Haas, & Mitchell, 1999). Improperly constructed river crossings (culverts and bridges) and impoundments can impede terrapin movements, which may impair their dispersal and migration and culminate in reduced genetic diversity across different populations (Ihlow et al., 2014; Jackson, 2003).

The correlation between the densities of the two species suggested interspecific competition. These species, along with their oriental congeners, are largely sympatric and occur in similar habitats, and thus may have overlapping niches (Das & De Silva, 2005; Sethy et al., 2015). Higher abundance of *M. t. thermalis* relative to *L. ceylonensis* in all the river basins except the Kalu basin suggested that the former could be competitively superior. With the evident habitat modifications and concomitant resource scarcity, the competitively subordinate species may suffer further population decline (Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007). However, these inferences on interspecific competition assume comparable behaviour and activity patterns between the two species. Different activity patterns may have led to differential detection of surface-active terrapins, and thereby may have biased density estimations. The reversed dominance status of *L. ceylonensis* was noteworthy and could be an artefact of a density-dependent environmental factor, reduced recruitment due to dispersal limitations, or ecological disturbances that selectively operate on *M. t. thermalis* (see also Harden et al., 2007; Spencer, 2002). Addressing such interspecific interactions between these two species requires a deeper understanding of these species' niche dimensions and long-term observations to understand their population dynamics.

4.4 | Public awareness, knowledge, and perceptions

The local inhabitants (questionnaire respondents), based on their opportunistic observations, have seen *M. t. thermalis* more frequently than *L. ceylonensis* which is in agreement with these survey results. More than 60% of respondents have seen one or other species in the wild indicating that despite the low density, these terrapins are still broadly distributed across south-eastern Sri Lanka. Nearly half of the respondents have killed at least one of the two species, and the total number killed exceeded 2500. Consumption of terrapin meat was alarmingly high throughout the study area where nearly two-thirds of respondents claimed to have eaten terrapin meat regularly. Elsewhere, local bushmeat trade has led to marked population declines among south Asian terrapins (Krishnakumar et al., 2009; Turtle Conservation Fund, 2002).

Ecological understanding and conservation awareness were poor among the respondents. Only one-fifth were aware of the ecological importance of terrapins while the vast majority viewed terrapins as a meat source. Such consumption-driven viewpoints are common among many local communities across southern and eastern Asia (Chen, Chang, & Lue, 2009; Cheung & Dudgeon, 2006; De Silva, 1999). Although Sri Lankan chelonians are protected by the Fauna and Flora Protection (Amendment) Ordinance, less than 30% of the respondents were aware of this.

Although terrapin abundance in this survey was substantially lower compared with historical records (Das & Bhupathy, 2009; Deraniyagala, 1939), nearly 90% of the respondents were incognizant of decline. Poor science-based knowledge, apathy towards nature, and cynicism towards wildlife conservation is rampant in southern Asia (Kirupakaran & Thiruchelvam, 2011; Safi & Khan, 2014). Poverty, lack of educational opportunities, scientific illiteracy, and cultural misinformation may also have played a significant role in the local inhabitants' apathy on chelonian conservation (Hemson, Maclennan, Mills, Johnson, & Macdonald, 2009; Kirupakaran & Thiruchelvam, 2011).

4.5 | Current threats and conservation actions

The threats documented can be summarized as: (1) loss of core (aquatic) and peripheral (riparian) habitats and landscape impermeability (reduced or absences of habitat connectivity), and dredging and draining wetlands; (2) alien invasive species; (3) point-source (industrial effluents, sewage, and municipal outlets) and nonpoint-source pollution (garbage disposal, soil erosion, and agrochemical runoff); (4) hydrological modifications (channelization, diversions, and water over-abstraction); (5) consumptive over-exploitation; and (6) ineffective state policies and poor governance outside the protected area network. Similar threats have been documented elsewhere in southern Asia (Das, 1990; Das & Bhupathy, 2009; De Silva, 1999; Geekiyanage, Vithanage, Wijesekara, & Pushpakumara, 2015). Road mortality, predation on eggs and hatchlings by human commensals (feral pigs, village crows, cats, and dogs) are also notable threats (De Silva, 1999). Sand and gem mining, eutrophication, and climate change (increased intensity and frequency of droughts) could exacerbate these current pressures (De Silva, 1999; Geekiyanage et al., 2015).

The survey found that a significant proportion of the range of Sri Lankan terrapins fell outside the protected area network; these areas receive no sanctuary from habitat loss, pollution, or illicit collectors. Only 30% of Sri Lanka's wetlands are protected; a greater proportion lies outside the protected areas, and are threatened by human activities (IUCN Sri Lanka and Central Environmental Authority, 2006). National legislation (Fauna and Flora Protection Ordinance, Forest Amendment Act, National Policy on Wetlands, and National Environmental Policy) can only mitigate wetland loss in state-mandated protected areas (Dela, 2009; Parliament of the Democratic Socialist Republic of Sri Lanka, 2009). Other national legislation focusing on natural resource management, such as the Water Resource Board Act, Fisheries and Aquatic Resources Act, Urban Development Authority Act, and Town and Country Planning Act do not advocate protection of terrapins or their habitats. Moreover, these policies operate in isolation with no integration of the different environmental legislation. The interagency communication among mandating government authorities is also weak.

Adults, juveniles, and eggs of terrapins throughout the Asian mainland have been collected for meat, medicinal purposes, and aphrodisiacs (Chen et al., 2009; Das, 1990). Marine turtles of Sri Lanka have been exploited historically for the international food trade (De Silva, 2006), and are suffering from a burgeoning shell industry (making curios, collectors' trophies) (IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, 1989). If proper regulations are not enforced, Sri Lanka's terrapins could become victims of the shell industry as well as international trade.

Terrapins depend on multiple habitats for a variety of life-history functions; thus we recommend an ecosystem-wide approach that protects native biodiversity while sustaining vital ecological services. Undeveloped public lands in south-western Sri Lanka must be incorporated into conservation as a multi-purpose protected area network. These undeveloped lands may even function as landscape-scale habitat connectivity corridors by facilitating terrapin dispersal and migrations. Terrapin habitats confer numerous other environmental and socioeconomic benefits: flood mitigation, water purification, nutrient retention and recycling, groundwater recharge, and freshwater fish conservation (Gibbons, 2003; Sharitz, 2003). Such values must be highlighted to local municipalities to promote terrapin conservation beyond the protected area network. Conservation programmes that benefit private landowners (easements, community-based conservation, and conservation reserve programmes) have succeeded in North America, Europe, and Southern Africa in expanding the protected area network; therefore, similar approaches can be implemented in Sri Lanka (Meffe, 2002; Rissman et al., 2007). Habitat-based conservation efforts must be strengthened by captive breeding and *ex situ* conservation (Turtle Conservation Fund, 2002).

The present national legislation must be integrated into a national biodiversity conservation action plan (Geekiyanage et al., 2015). Under the umbrella of National Environmental Policy, all national legislation on wildlife, forestry, and natural resource management must be networked into a single cohesive unit with lucid communication among regulating agencies with a broader focus on ecosystem-scale or landscape-scale natural resource management and biodiversity conservation (Dela, 2009). Policy innovations should include: allocating buffer zones; delineating core aquatic and terrestrial habitats; restoration of degraded terrapin habitats, including provision of large woody debris; removal of invasive species and controlling the populations of human commensals; and establishing ecoregion-wide landscape-scale connectivity among terrapin habitats (Bodie, 2001; Boyer, 1965; Semlitsch, 2000; Semlitsch & Bodie, 2003). It is also imperative to inform the general public, educators, natural resource and land managers, and private entrepreneurs about environmental legislation through printed and electronic media and outreach activities. International treaties ratified by the Sri Lankan government – the Ramsar Convention on Wetlands of International Importance, the Convention on Biological Diversity, and the Convention on International Trade in Endangered Species (CITES)– must be used as guidelines to revise current policies on the conservation of terrapins (IUCN Sri Lanka and Central Environmental Authority, 2006). Captive populations with the original genetic diversity of wild populations must be maintained that subsequently can be used for reintroduction (Horne, Poole, & Walde, 2012). We recommend that *M. trijuga* be listed in CITES appendix II (*L. ceylonensis* is already listed) as a precautionary approach to impede potential international scale explorations in future (Horne et al., 2012). Deraniyagala (1939), recognized many subspecies of Sri Lankan terrapins; therefore, the national conservation assessments should evaluate these terrapins below species level (subspecies, genetically distinct populations, or ecotypes). Universities and environmental enthusiasts should play a substantial role in enhancing public awareness of terrapin conservation.

Inadequacy of science-based research and continuous monitoring have greatly hampered terrapin conservation efforts in Sri Lanka. The last comprehensive chelonian survey was carried out more than 75 years ago (Deraniyagala, 1939), so the taxonomy and systematics of Sri Lankan inland chelonians need to be revised based on molecular phylogenetics and population genetics. Future research should focus on documenting spatially explicit patterns of threats and island-wide terrapin distribution. The proposed action plan for Testudines and their habitats in Sri Lanka suggested continuous monitoring of chelonian populations and human threats –especially wildlife trafficking and harvesting for the pet-trade and food (De Silva, 1999). Yet, no such systematic monitoring has been implemented regionally or nationwide in Sri Lanka. Therefore, island-wide surveys of chelonians are needed urgently. We hope that this study will be a first step towards regional assessments that will later culminate in country-wide surveys, and that the results will enhance the current knowledge of Sri Lanka's terrapins. This increased understanding should enable national wildlife authorities to implement conservation actions, including expansion of the existing protected area network.

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DISCLOSURE/CONFLICT OF INTEREST

The authors have no conflicts of interest on this research.

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