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Ecological and zoological study of endemic Sri Lankan keelback (*Balanophis ceylonensis*): with implications for its conservation

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Abstract

The endemic Sri Lankan keelback (*Balanophis ceylonensis*) is a snake largely restricted to rainforests of the island. Based on an 11-years field survey covering 83 field sites and rescued specimens, we present an autecology of *B. ceylonensis*. We recorded 32 individuals of *B. ceylonensis* at 25 field sites. All snakes were found in 10–1000 m altitude range within or in close proximity of rainforests. This snake associated with canopy-shaded forest floor with sufficient leaf litter and a numerous other natural cover objects, and were active mostly during dusk. Our study indicated that *B. ceylonensis* is a rare species with a patchy distribution within the wet zone of southwestern Sri Lanka, and can be considered a rainforest specialist. The reproductive season spanned from November to February as evident by observations on copulation. The snake laid eggs in clutches of 3–4 underneath woody debris or inside the forest floor. Given its rarity, patchy distribution, and estimated extend of occurrence and area of occupancy, and continuing degradation of rainforests, we assessed the conservation status of *B. ceylonensis* as Endangered.

Key words

Behaviour, biogeography, biology, distribution, habitat loss, Natricinae, rainforests, snakes.

Introduction

The monotypic colubrid genus, *Balanophis* Smith, 1938, is endemic to the Indian Oceanic tropical island of Sri Lanka. Brief accounts of *B. ceylonensis* (Sri Lankan keelback) have been published by numerous authors, but most of them are historic records which recent literature has repeatedly cited (Günther, 1858; Haly, 1886; Wall, 1921; Nicholls, 1929; Smith, 1938; Deraniyagala, 1955; De Silva, 1980; de Silva & Aloysius, 1983; Mahendra, 1984; de Silva, 1990). The species is known from the wet zone lowlands (< 300 m), the mid-country hills (300–900 m), and some parts of the intermediate climatic zone (up to 1300 m) (Wall, 1921; de Silva, 1990; Somaweera & de Silva, 2010). It is considered a relict species that may previously have occupied a greater proportion of the humid tropical ecosystems of Sri Lanka (Günther, 1858). Based on morphological evidence,

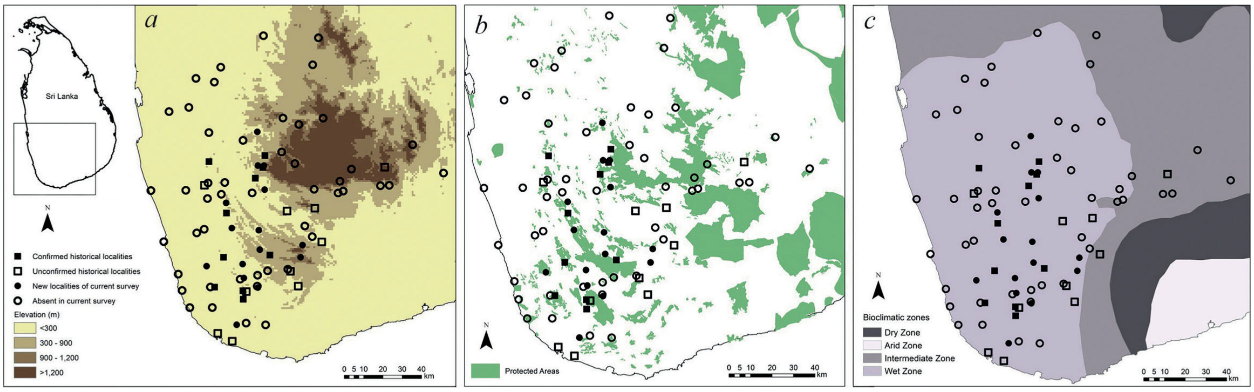

Fig. 1. Updated distribution records of *B. ceylonensis* along (*a*) the elevation gradient of Sri Lanka's wet zone, (*b*) with reference to the protected areas (most absent sites were located outside the protected area network), and (c) bioclimatic zones of Sri Lanka. Filled squares: confirmed historical localities (historical localities that were confirmed with live specimens found via field surveys in our study); open squares: unconfirmed historical localities (localities where *B. ceylonensis* was documented in previous surveys but not in our field surveys); filled circles: new localities (new localities where *B. ceylonensis* was found in our field surveys that was not historically documented); open circles: absent in current study (sites that were surveyed in our study but no live specimens were found). Elevation given as meters above sea level.

Malnate (1960) and Malnate & Minton (1965) considered *Balanophis* congeneric with *Rhabdophis*. However, this was questioned by Mahendra (1984) as well as several recent taxonomists, thus, de Silva (1990) resurrected the generic name *Balanophis*. While some molecular studies showed that *Balanophis* was strongly supported as the sister group of the Southeast Asian *Rhabdophis* in the subfamily Natricinae (Pyron *et al.*, 2013), others suggested that *Balanophis* is deeply nested within the genus *Rhabdophis* (Figueroa *et al.*, 2016).

Despite its restricted distribution within Sri Lanka, evaluations of the conservation status at national (Endangered: MOE, 2012) and global (Near Threatened: Somaweera & de Silva, 2010) levels are at disparity. Such contrasting listings of conservation status question the actual rarity and our knowledge on the distribution of *B. ceylonensis*. Moreover, disagreements between conservation assessments may also impede national conservation actions as well as policy decisions. Clarification of the species distribution and abundance requires spatially and temporally intensive surveys across its potential range. *B. ceylonensis* is an opisthoglyphous snake, having enlarged maxillary teeth and nuchal glands (Smith, 1938; Mori *et al.*, 2012). A brief account of mild case of envenoming (de Silva & Aloysius, 1983) and a detailed case report of a serious envenoming (Fernando *et al.*, 2015) have been reported.

Recent studies on this species mostly investigated the snake's taxonomy, phylogenic affinities, nuchal gland anatomy, and venom physiology (Mori *et al.*, 2012, 2016). Species autecology, behaviour, distribution, and habitat associations have not been researched adequately. Being a rare endemic snake, studying such aspects of *B. ceylonensis* is imperative to consolidate or scientific information base as well as to promote informed conservation planning. Furthermore, a scientific foundation on this snake's habitat preferences, behaviour, and other aspects of natural history may also help improve knowledge on the medical importance of *B. ceylonensis* to humans. In this study, our objectives are to (1) refine the distribution of *B. ceylonensis* based on new locality records, and report new ecological, morphological, and behavioural information on *B. ceylonensis* and (2) produce a habitat suitability model for the focal species.

Methods and materials

Field methods

Investing over 960 person-hours between October 2005 and December 2016, we opportunistically surveyed 83 sites for herpetofauna throughout southwestern Sri Lanka (Fig. 1), encompassing both the lowland wet zone and the intermediate climatic zone of the island. Survey sites were at least 1 km apart. In each year, our sampling efforts covered both the monsoon (May–September) and the inter-monsoon (October–January) seasons. We surveyed each of the 83 sites in the morning (07:00–11:00 hrs) as well as in the evenings (16:00–19:00 hrs). Fourteen of these sites were also surveyed at nights (21:00 and 23:00 hrs). We visited each site at least twice in two different years during the 11-year survey period. Our surveys covered a wide variety of habitats, including open woodlands, primary and secondary forests, pine plantations, home gardens, and various agricultural lands (coconut, rubber, tea, cardamom, cinnamon, oil palm plantations, and paddy fields). At each sampling site, we actively surveyed by visually scanning the ground (Visual Encounter Survey) and by searching through all movable cover objects, such as logs, rocks, and leaf-litter piles. We also searched through understory vegetation, saplings, rocky surfaces, and other vertical structures. On average, a given site was surveyed for two hours per visit.

At each capture site, we recorded six environmental variables to characterize the environmental preferences of the species recorded: ambient temperature, relative humidity, light intensity (all measured using a Digitech QM 1594, 6-in-1 multifunction environment meter; Digitek Instruments Co., Ltd, Hong Kong, China), ground surface temperature (infrared thermometer: N19-Q137, Dick Smith Electronics, Shanghai, China), percent canopy cover (canopy densiometer), and leaf-litter depth (ruler). We georeferenced each site where the focal species was found. We also made opportunistic observations on feeding behaviours and predation.

For each captured snake, we determined the sex by everting the hemipenes or by cloacal probing. We recorded the following morphometric characters using a 0.1 mm digital Vernier caliper and a measuring tape: head length, distance between the posterior edge of mandible and the tip of snout; head width, maximum width of head; jaw length, distance between the tip of snout to the gape; snout length, distance between the anteriormost point of ocular scale and the tip of snout; snout-vent length, measured from the tip of snout to the anterior margin of vent; interorbital width, least distance between the upper margins of orbits; tail length, measured from the anterior margin of vent to the tail tip. We also recorded the following meristic data (aided by a × 10 hand lens when needed): supralabials and infralabials, first labial scale to last labial scale bordering gape; dorsal scale row, counted around body from one side of ventrals to the other in three positions, on the neck, at midbody and at one scale anterior to the cloacal scale; ventral scales, counted from the first ventral scale (which is distinctly wider than gular scales) to the cloacal scale; subcaudal scales, counted from the first postcloacal scale to the tip of the tail, excluding the terminal scale. Afterward, all snakes we captured were released back to the site of captured except for the individuals used for captive observations.

Captive studies

We received five live individuals of *B. ceylonensis* (two males and three females) that were originally collected within forest habitats by local inhabitants. We housed each snake separately for 4–6 days in a glass tank (40 cm long, 20 cm wide, and 20 cm high) prior to relocating them into suitable habitats. The tanks contained loose soil up to 2 cm in depth, 2.5 cm-thick leaf-litter layer on top of soil, and a log that is 2.5 cm in diameter and 15 cm in length. Water was provided ad-lib in a container (8 cm diameter, 4 cm height) buried into the substrate so that the container opening levelled with the litter surface. The materials placed into the tank were changed and the tank was cleaned between introductions of different snakes. During this period, we fed each snake once with a gecko for the entire captive period (either *Hemidactylus pieresii*, *H. frenatus*, *H. depressus*, or *H. parvimaculatus*). In addition to captive snakes, we collected two clutches of eggs and incubated those under room temperature (28.5 °C) inside the same mesocosm (one clutch at a time, eggs buried into the substrate) setup used for captive snakes. We continued incubation until hatching and released the neonates back to the wild.

Table 1. Egg dimensions of *B. ceylonensis* from two rainforests, Sri Lanka (measurements in millimetres, weight in grams, & mean ± standard deviation).

Eggs no. & Loc.	Length	Width	Weight
1. Atweltota	19.6	11.2	1.4
2. Atweltota	18.8	10.6	1.1
3. Atweltota	20.2	11.6	1.5
4. Atweltota	19.5	11.3	1.2
5.Beraliya	19.8	11.5	1.5
6. Beraliya	20.1	12.1	1.7
7. Beraliya	19.6	11.5	1.2
Mean ± SD	19.7±0.4	11.4±0.4	1.4±0.2

Habitat suitability modelling

We used *B. ceylonensis* occurrence data from the southwestern of Sri Lanka to predict the distribution of the species using maximum entropy distribution modelling or MaxEnt (Kumara & Stohlgren, 2009; Elith *et al.*, 2011). A total of 83 locations of *B. ceylonensis* occurrence and nine bioclimatic variables (seven bioclimatic variables, land-use land cover types, and elevation) were used to predict the species distribution in different habitats. The environment variables were obtained from WorldClim (Hijmans *et al.*, 2005; http://www. worldclim.org/bioclim.htm), DATA.GOV (2015) and Diva GIS (2018) web sites. We used the freely available MaxEnt software, version 3.3 (www.cs.princeton.edu/~schapire/maxent), to generate probability of species occurrence in Sri Lanka.

Results

General findings

During our 11-year survey, we encountered only 32 individuals of *B. ceylonensis*, of which 19 were males and 13 were females. The total number included 27 snakes we captured in the survey and another five snakes originally captured by local inhabitants within the forest and subsequently handed over to us. We did not find any juveniles in the wild, but we found a total of seven eggs in two clutches (3 and 4 eggs per clutch) (Table 1). Of 83 sites we surveyed, we documented *B. ceylonensis* only at 25 locations. Among these locations, 10 sites were historic localities where the focal species was documented previously while 15 were new localities (Fig. 1). We failed to document *B. ceylonensis* from 11 sites where the snake was previously recorded by other authors (Anthonisz,

Table 2. Morphometric and meristic data (mean ± standard deviation) for three male and five female specimens of *B. ceylonensis* found in southwestern Sri Lanka in the current study (measurements in mm).

Location	Kukulugala	Kanneliya	Yagirala	Gilemale	Morningside	Mean ± SD	Sinharaja	Beraliya	Atweltota	Mean ± SD
Sex	Female	Female	Female	Female	Female		Male	Male	Male	
Jaw length	12.2	12.0	11.8	12.2	12.4	12.1 ± 0.2	8.9	9.3	12.3	10.2 ± 1.9
Head length	14.5	14.2	13.9	14.6	14.9	14.4 ± 0.4	10.8	11.5	14.8	12.4 ± 2.1
Head width	7.8	7.3	7.2	7.7	7.8	7.6 ± 0.3	6.2	6.5	6.7	6.5 ± 0.3
Snout length	4.8	4.2	4.1	4.7	4.8	4.5 ± 0.3	3.6	3.8	3.9	3.8 ± 0.2
Inter orbital width	4.1	3.8	3.9	4.1	4.2	4.0 ± 0.2	3.3	3.5	3.6	3.5 ± 0.2
Snout vent length	287.3	268.5	268.3	285.5	293.4	280.6 ± 11.5	186.5	194.8	198.7	193.3 ± 6.2
Tail length	72.5	69.7	68.9	71.4	74.1	71.3 ± 2.1	54.3	56.2	57.1	55.9 ± 1.4
Supralabials	8	8	8	8	8	8.0 ± 0.0	7	8	7	7.3 ± 0.6
Infralabials	7	8	8	7	8	7.6 ± 0.5	8	7	8	7.7 ± 0.6
Ventral scales	134	132	131	135	145	135.4 ± 5.6	145	137	139	140.3 ± 4.2
Subcaudal scales	44	45	42	46	43	44.0 ± 1.6	55	57	53	55.0 ± 2.0
Midbody scales	19	19	19	19	19	19.0 ± 0.0	19	19	19	19.0 ± 0.0

Table 3. Environmental variables recorded at each capture of *B. ceylonensis* (mean ± standard deviation).

Environmental variables	**Mean ± SD**
Ambient temperature (°C)	27.4 ± 0.8
Ground surface temperature (°C)	26.1 ± 0.5
Canopy cover (%)	65.0 ± 10.3
Relative humidity (%)	67.3 ± 9.6
Light intensity (lux)	775.8 ± 177.1
Leaf–litter depth (mm)	58.8 ± 14.1

1885; Haly, 1886; Boulenger, 1890; Wall, 1921; Deraniyagala, 1955; De Silva, 1969; De Silva, 1980; De Silva & Aloysius, 1983; Mahendra, 1984; de Silva, 1990; Somaweera, 2004; Karunarathna & Amarasinghe, 2011, 2012; Botejue & Wattavidanage, 2012; Peabotuwage *et al.*, 2012). Of all the locations where we found the species, 16 were in the lowland rainforest biome, five were at sub-montane rainforests while the rest were in forests of central highlands or foothills of the central highlands.

Morphometric and meristic data

Measurement data were recorded only for three males and five females. Females were larger than males in terms of morphometric variables, particularly in snout-vent length (Table 2). Although infralabial, supralabial, and mid-body scales did not differ much between sexes, the number of ventral and subcaudal scales were greater in males than females. Both meristic and morphometric data were similar among survey sites.

Microhabitat use and environmental correlates

Most individuals (27) were encountered during dusk (17:00 – 19:00 hrs) while the rest were found in the morning hours (08:00 – 09:00 hrs). All individuals were captured under conditions of moderately high air temperature ($\bar{x} = 27.4$ °C), in habitats with relatively high canopy cover (65%), moderately high relative humidity (65%), and thick leaf-litter cover (60 mm) (Table 3). We observed this species under decaying logs, within dense, moist leaf litter, under rocky rubble, and woody debris in and around granite caves near streams. *Balanophis ceylonensis* appeared to be a sub-fossorial snake that uses a variety of microhabitats within the forest floor. We did not find any specimens in disturbed understory or in woodlands with sparse canopy, or on any vertical structure above the forest floor.

Defensive behaviour

We observed several defensive responses during our surveys. When threatened, the snakes coiled the body and

Fig. 2. Focal species, behavior and feeding events observed: (*a*) raising its forebody (up to one third of overall body length); (*b*) full body coloration of subadult; (*c*) swallowing *Duttaphrynus kotagamai* in the field; (*d*) feeding on *Fejervarya kirtisinghei* under captivity; (*e*) natural habitat with thick leaf litters in lowland rain forest in Beraliya.

sometimes hid the head within the coils and became immobile. Sometimes the cephalic region and the forebody were flattened to display white, light green, or light blue skin between the scales (Fig. 2). In a few instances, small adults raised their forebody (up to one third of overall body length) off the ground to expose the reddish patch with black border on the neck. In four instances we observed that snakes feigned death for up to 20 minutes during handling and capture where the snake instantly froze and became completely immobile. We did not observe any nuchal glands-related displays, such as neck arch and neck butting, during the experiment with rescued snakes. During our survey, *B. ceylonensis* bit occasionally when captured or handled, especially during the breeding season (November to February). Only one bite incidence resulted in serious medical complications which was reported in Fernando *et al*. (2015). The other bites did not result in any medically critical outcome.

Predators

We observed four incidents of native vertebrates preying on *B. ceylonensis* in the wild. Once, a green-billed coucal (*Centropus chlororhynchus*) stealthily approached the snake along the forest floor, snatched it with the beak at one attempt, and immediately flew away. Another instance, we observed blue magpie (*Urocissa ornata*) grasping *B. ceylonensis* off the forest floor with its beak and immediately flew away with the prey. One of the captive females held in mesocosms was predated by a pipesnake (*Cylindrophis maculata*); the latter was introduced into the mesocosm and predation occurred 14 hours after the introduction where the pipesnake struck *B. ceylonensis* head first, and gradually ingested it. The entire prey ingestion process took approximately 45 mins. In another occasion, we found parts of the tail of a *B. ceylonensis* among other leftovers immediately beneath the nest of a grey hornbill (*Ocyceros gingalensis*). In all direct observations, the snakes predated were subadults (30 cm in length, with prominent orange patch on the head); all observations were made during the morning hours (08:00–09:00 hrs). We did not observe any immediate and apparent deterrent effects of the nuchal glands on the predators.

Prey items

In the field, *B. ceylonensis* was observed feeding on a variety of amphibians (*Adenomus kelaartii*, *Duttaphrynus kotagamai* (Fig. 2), *D. melanostictus*, *D. noellerti*, *Microhyla mihintalei*, *Minervarya kirtisinghei*, *Fejervarya limnocharis*, *Indosylvirana serendipi*, and *I. temporalis*), skinks (*Lankascincus gansi*, *L. greeri*, and *Eutropis carinata*), and an agamid lizard (*Otocryptis wiegmanni*). Larger prey with tough (thick and rough) skin, such as skinks and agamids, were held in the mouth for 8–15 mins after insertion of the fangs, but frogs and toads were swallowed 2–3 mins after fang insertion. In all instances, the snake gradually ingested the prey and chewedthe prey to ensure proper insertion of the rear fangs into the prey. The predatory tactic can be described as active pursuit where *B. ceylonensis* slowly move around in search of prey. We observed no attempts to constrict the prey or ambush the prey from a vantage point. Under captivity, *B. ceylonensis* accepted all native geckos offered (*Hemidactylus pieresii*, *H. frenatus*, *H. depressus*, and *H. parvimaculatus*), and 25–45 minutes were taken to swallow the geckos completely.

Reproduction

We observed copulation twice, both in rainforests: 1) 29th December 2011 at Kalugala (6.407347 N 80.248189 E) and 2) 14th January 2014 at Kitulgala (6.991014 N 80.405653 E). Both observations were made at dusk (17.00–18.00 hrs), and each copulation event lasted 20–30 minutes. During the December–January period these snakes were more active and attempted to bite more frequently. Two clutches of eggs found on the forest floor in 15th April 2006 from two lowland rainforests, Atweltota (6.543208 N and 80.286783 E) and 23 may 2009 from Beraliya (6.268336 N and 80.206558 E) turned out to be those laid by *B. ceylonensis* upon hatching in captivity. One clutch (four eggs) was deposited 27 mm beneath the soil surface and the other clutch (three eggs) was found underneath a decaying log, in a canopy-shaded site. The eggs in each clutch were firmly adhered to one another. These oviposition sites had well-drained, loose soil where accumulation of rainwater would have been unlikely. Eggs were oblong-shaped, with a mean mass of 1.4 g (range: 1.1–1.7 g) and mean length and diameter of 19.7 × 11.4 mm, respectively (length range: 18.8–20.2 mm; diameter range: 10.6–12.1 mm). The eggs from Atweltota hatched after 8 days in captivity and those from Beraliya after 6 days in captivity.

Habitat associations

Balanophis ceylonensis was found in 25 of the 83 sites surveyed (Fig. 1). Encounters with *B. ceylonensis* were limited to relatively undisturbed, mature, closed-canopy forests. The elevational range extended to approximately 1000 m above mean sea level. No individuals were found within any of agricultural landscapes (home gardens, plantation or estate-based croplands, paddy-fields) or pine plantations.

Habitat suitability modelling

We estimated the distribution extent of *B. ceylonensis* in each predicted probability class. The core area of the lowland wet zone is predicted as the most suitable habitats for *B. ceylonensis* where the probability of occurrence was greater than 0.6 (Fig. 3) followed by the wet zone periphery and the central massif (probability of occurrence: 0.4–0.6). The intermediate zone appeared to be comparatively lower in suitability (probability of occurrence: 0.1–0.4). The dry zone and the arid zone of Sri Lanka are the least suitable (probability of occurrence < 0.1). The MaxEnt model's internal Jackknife test

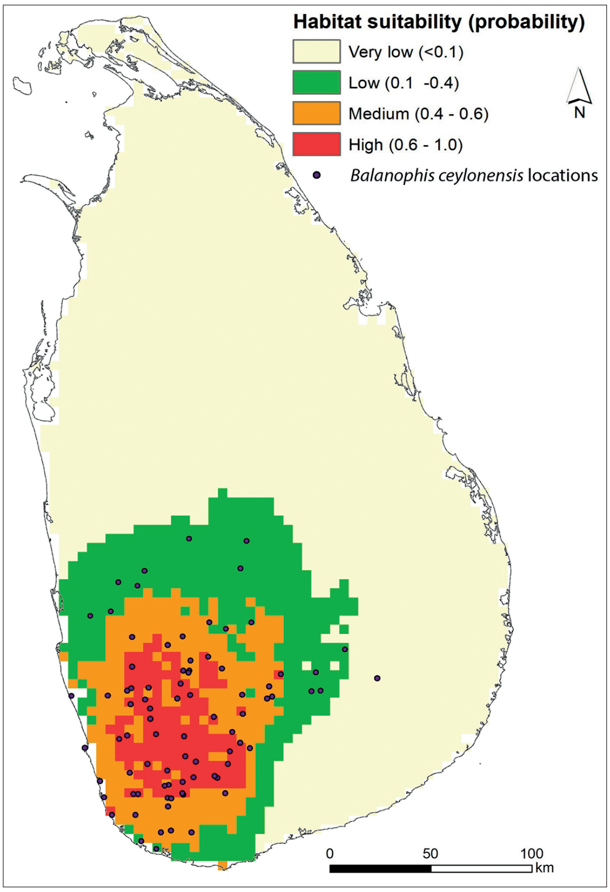

Fig. 3. Predicted potential suitable habitats for *B. ceylonensis* in Sri Lanka based on nine bioclimatic variables.

of variable importance showed that precipitation of driest month (Bio14) as the most important predictor (55%) of *B. ceylonensis*'s distribution (Table 4; Fig. 4) followed by The next important variable the precipitation of warmest quarter (Bio18), which contributes 20% for the MaxEnt Model. In addition, both temperature seasonality (Bio4) and mean temperature of driest quarter (Bio9) were also critical determents of the snake's occupancy.

Discussion

Distribution

Previously published localities of *B. ceylonensis* are limited to 23 locations (Fig. 1) (ANTHONISZ, 1885; HALY, 1886; BOULENGER, 1890; WALL, 1921; DERANIYAGALA, 1955; DE SILVA, 1969; DE SILVA, 1980; DE SILVA & ALOYSIUS, 1983; MAHENDRA, 1984; DE SILVA, 1990; KARUNARATHNA & AMARASINGHE, 2011, 2012; BOTEJUE & WATTAVIDANAGE, 2012; PEABOTUWAGE *et al.*, 2012; SOMAWEERA, 2004). The species is poorly represented in the National Museum of Sri Lanka by only four preserved female specimens from two lowland wet zone localities (Kuruvita and Kegalla) (as of February 2016).

Table 4. Selected environmental variables and their percent contribution in MaxEnt model for *B. ceylonensis* in Sri Lanka.

Environmental variable	Percent contribution	Source/Reference
Precipitation of driest month (Bio14)	55.2363	WorldClime: Hijmans *et al.* (2005)
Precipitation of warmest quarter (Bio18)	20.0595	WorldClime: Hijmans *et al.* (2005)
Temperature seasonality (standard deviation *100, Bio4)	9.2370	WorldClime: Hijmans *et al.* (2005)
Mean temperature of driest quarter (Bio9)	8.1184	WorldClime: Hijmans *et al.* (2005)
Annual precipitation (Bio12)	3.0620	WorldClime: Hijmans *et al.* (2005)
Elevation (m)	2.2468	DIVA-GIS (2018)
Precipitation seasonality (coefficient of variation, Bio15)	1.8346	WorldClime: Hijmans *et al.* (2005)
Precipitation of driest quarter (Bio17)	0.1976	WorldClime: Hijmans *et al.* (2005)
Landuse	0.0078	data.gov (2015)

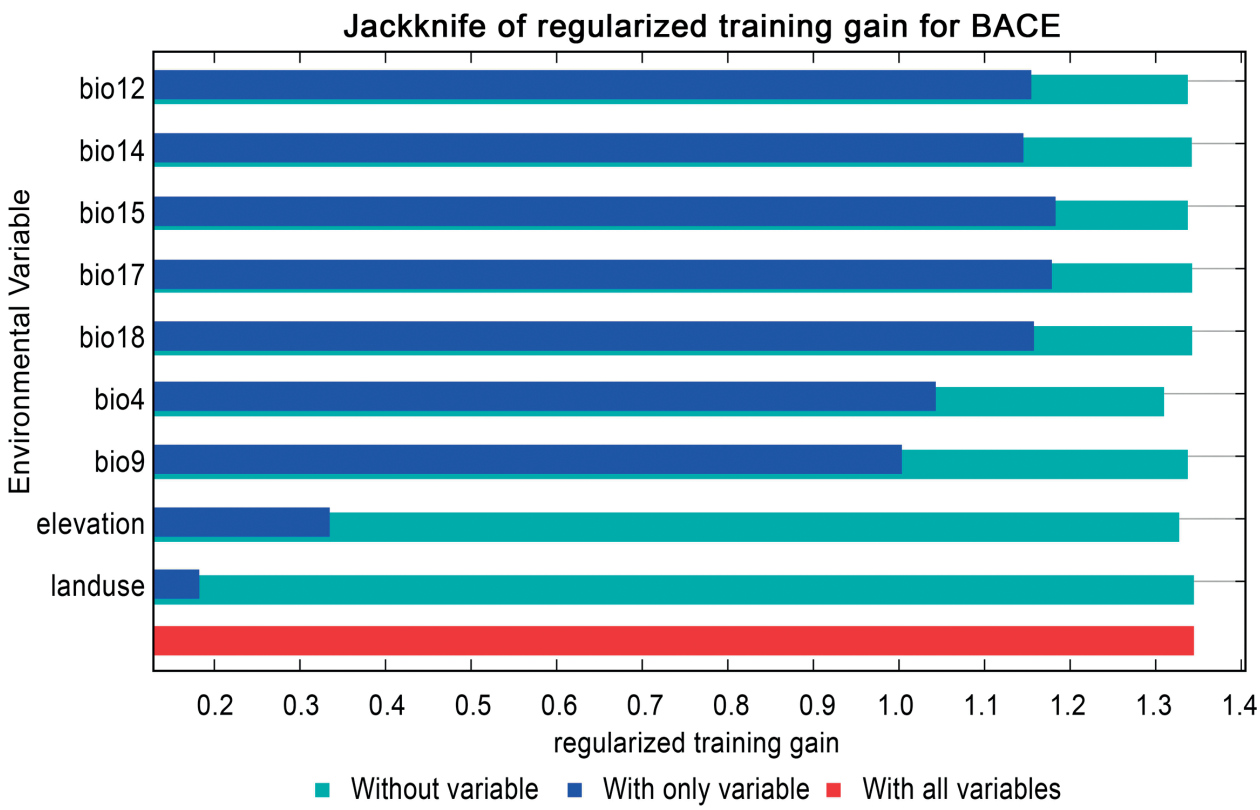

Fig. 4. Results of Jackknife evaluations of relative importance of predictor variables for *B. ceylonensis* Maxent model. Note: 'Bio12' is annual precipitation, 'Bio14' is precipitation of driest month, 'Bio15' is precipitation seasonality, 'Bio17' is precipitation of driest quarter, 'Bio18' is precipitation of warmest quarter, 'Bio 4' is temperature seasonality, 'Bio 9' is mean temperature of driest quarter, elevation and land use.

Given the limited number of snakes we encountered in our spatially and temporally extensive survey, *B. ceylonensis* appears to be a secretive species that might exhibit limited surface activity. Moreover, the survey also suggested that *B. ceylonensis* may also be a rare species with a patchy distribution. The snake was not found at 58 of the sites we surveyed, although all survey sites were located within the species' presumed range (Fig. 1; Appendix 1). Recent evaluations suggested that its purported rarity could reflect detection bias due to its secretive nature, cryptic coloration, and/or use of shelters (Somaweera & de Silva, 2010). Nonetheless, our study supports its low abundance, although our survey added 15 new localities to the species' distribution records. An occupancy modelling approach that accounts for detectability and environmental complexity is imperative in order to ascertain its true abundance.

Ecology and biology

Our study reinstated that *B. ceylonensis* occupies primary rainforests of the southwestern lowland wet zone and some parts of the intermediate zone of Sri Lanka, within a broad elevational range of 10–1000 m (Fig. 1). We also noted that a dense, mature canopy and microhabitats that provide shelter, such as decaying, moist leaf litter and coarse, woody debris are critical requirements of *B. ceylonensis*, in agreement with previous reports (WALL, 1921; DE SILVA, 2009). *B. ceylonensis* is a forest specialist that is likely sensitive to human disturbance and habitat alteration. We did not document this snake from the dry zone habitats, high-altitude montane forests, nor from monoculture plantations, clear-cut areas, or highly disturbed habitats. *Balanophis ceylonensis* also was not found in any arboreal habitats, rock outcrops, or other vertical structures.

Our observations on the feeding ecology of the *B. ceylonensis* match previous records. Adults consume frogs and skinks, whereas captive neonates reportedly preyed on orthopterans (DERANIYAGALA, 1955; DAS & DE SILVA, 2005; SOMAWEERA, 2006). Of the four specimens (three subadults and one adult) preserved in the Colombo National Museum, one had a partially digested frog (species not recorded) in the gut (DE SILVA, 1969). Our study provides the first record of predation on toads (*Adenomus kelaartii*, *Duttaphrynus kotagamai*, *D. melanostictus* and *D. noellerti*) and an agamid (*Otocryptis wiegmanni*) in wild and geckos under captivity. The bufonids consumed by *B. ceylonensis* possess parotoid glands that secrete bufadienolide toxins that deter many other predators. The ability of *B. ceylonensis* to ingest toxic prey is noteworthy. However, it is consistent with the widespread occurrence of genetic resistance to bufadienolides among natricine colubrids (MOHAMMADI *et al.*, 2016), and the presence of enlarged and sexually dimorphic adrenal glands is shared with several other toad-eating snakes, including the natricine *Rhabdophis tigrinus* (MOHAMMADI *et al.*, 2013, 2017). Such evolutionary adaptations may reduce interspecific competition for prey. Both, our observations and the previous literature indicated that the diet of *B. ceylonensis* is substantially biased towards small vertebrate prey, and that it is an active forager rather than a sit-and-wait predator. Prey selections of snakes are known to change ontogenetically as well as seasonally so that both *in-situ* and *ex-situ* observations are required to learn more about the shifts in prey selection and foraging strategies of these snakes (MUSHINSKY *et al.*, 1982). Previous studies suggested that *B. ceylonensis* is a slow-moving, largely diurnal snake, but that it is occasionally active at night (DERANIYAGALA, 1955; SOMAWEERA, 2006).While we did not find any snakes during our nocturnal surveys, our observations confirmed that these snakes are sluggish and surface-active mostly during dusk.

NICHOLLS (1929) considered *B. ceylonensis* to be a non-venomous snake. However, several species of the related genus *Rhabdophis* are known to generate clinically significant bites in humans, sometimes resulting in death (MATHER *et al.*, 1978; OGAWA, 1986; WEINSTEIN *et al.*, 2011; HIFUMI *et al.*, 2014). As a rear-fanged (opisthoglyphous) snake, *B. ceylonensis* is considered mildly venomous to humans, and medical complications from envenomation have been reported elsewhere (DE SILVA & ALOYSIUS, 1983; FERNANDO *et al.*, 2015). When bitten, patients developed a severe occipital headache, photophobia, chills, transient loss of consciousness, and vomited blood-stained gastric contents (FERNANDO *et al.*, 2015). Since *B. ceylonensis* is rear-fanged, severe complications may only develop if the victim's body parts lock fully into the snake's jaws during the biting process; a quick strike may not render the same effect. Biochemical assays and pathophysiological experiments are required to understand the chemical composition and potency of the venom of *B. ceylonensis*, and further study of the storage and delivery mechanism is warranted, especially in light of the unusual grooving of the fangs.

Defensive displays of *B. ceylonensis* have been documented by several authors. For example, WALL (1921) described expansion of the body, exposing scarlet coloration of the skin between the scales. We observed several typical defensive responses, such as head-hiding (in body coils) and neck flattening in wild snakes, and GREENE (1988) reported the same. We also presented the first documentation of death feigning in *B. ceylonensis* upon been handled. This could be an anti-predatory defence to mislead its predators. This behaviour have been reported from several colubrids (particularly *Rhabdophis tigrinus*, a related species to *B. ceylonensis*) as well as other snakes (GEHLBACH, 1970; MUTOH, 1983; VOGEL & HAN-YUEN, 2010). This could be effective defence as many predators only attack live prey, and this strategy is considered resistant to predator-learning (GEHLBACH, 1970). Most often, death-feigning behaviour is initiated by a tactile stimuli (such as being attacked by a predator) and can be associated with other adaptive anti-predatory responses, such as erratic (vigorous writing and body snapping) or stereotyped (head-cocking, defecation and cloacal discharge) behaviour (GEHLBACH, 1970; MUTOH, 1983). During death-feigning, respiration seemed to become shallow or arrested and the body becomes limp for many snakes (MUTOH, 1983). Although our confirmation of the exploitation of toads as diet and the reported presence of the nuchal glands in *B. ceylonensis* (SMITH, 1938) imply the possession of sequestered toxic chemicals in the glands, which has been demonstrated in *R. tigrinus* (HUTCHINSON *et al.*, 2007), reconfirmation of the presence of the nuchal glands and analysis of chemical components of the nuchal gland fluids, if any, are essential to determine the defensive tactics of *B. ceylonensis*. Although we did not document any nuchal gland display behaviour in *B. ceylonensis*, related natricine snakes such as *Rhabdophis* species, are known to perform neck arching (chin directed towards the substrate and the neck bent upward) and neck butting (the arched neck swings so that the neck is thrusted against the stimulus) both of which involves displaying the nuchal glands to the predators (FRY, 2015; MORI *et al.*, 2015). More observations in both natural and manipulated settings are needed to confirm the ability of *B. ceylonensis* to perform specific behaviours associated with nuchal gland display.

Documentation of the reproductive biology of *B. ceylonensis* is limited. WALL (1921) recorded that these snakes lay up to seven eggs per clutch during March. DERANIYAGALA (1955) reported observations on a clutch of seven adherent eggs found inside a decaying log. The clutch size recorded in our survey is much smaller than the numbers recorded previously (3.5 eggs per clutch of two clutches, range: 3–4). Moreover, although Deraniyagala (1955) found eggs inside decaying logs, we found eggs underneath a decaying log. The eggs we hatched in mesocosms hatched relatively early (6–8 days). This suggested that those eggs would have been laid a few weeks earlier (Fitch, 1970).

Our habitat suitability model (Fig. 3) also revealed the importance of long-term climate conditions on this snake's distribution and habitat selection. Although this species is considered endemic to southwestern Sri Lanka (De Silva, 1980), our habitat suitability model indicated non-uniform distribution of *B. ceylonensis* throughout the wet zone (Fig. 3). The model also indicated that the optimal habitats for *B. ceylonensis*is much smaller than its potential extent of distribution where the suitability is much greater in lowland rainforests compared to montane forests. Precipitation of driest month as well as that of the warmest quarter was the most important environmental predictors for *B. ceylonensis* (Fig. 4). Similarly, temperature seasonality as well as temperature of driest quarter were also influential parameters of habitat suitability (Fig. 4). Such patterns of habitat suitability can be attributed to being predominantly crepuscular as well as fossorial habits. In general, when physiological optima of a given species is limited by seasonality and extremities of temperature and precipitation, such species tend to adapt niches characterized by moist habitats with stable microclimatic features, a condition widely observed in reptiles (Huey, 1982; Guyer, 1994; Dodd, 2016). The habitat suitability model further justifies that *B. ceylonensis* is likely a specialist snake of Sri Lanka's tropical humid forests, which agrees with the current consensus on this snake's distribution range.

Implications for conservation

Habitat loss and fragmentation continue to occur throughout southwestern Sri Lanka, even in rural areas, given agricultural expansion, infrastructure development, construction of transportation networks, establishment of new human settlements, and many other rural development programs (Karunarathna & Amarasinghe, 2011, 2012). Given its preference for forested habitats, *B. ceylonensis* could be a species under threat from such habitat alternation. Within these fragmented landscapes, individuals are also subjected to road mortality (Karunarathna & Amarasinghe, 2012). Intentional killings by humans are a substantial threat to most Sri Lankan snakes, including *B. ceylonensis* (de Silva, 2006). The vivid colour pattern displayed by this species may mislead people to assume that it is highly venomous species. Lack of safety wear when working outdoors and the lack of effective first aid knowledge, results in high snakebite mortality in Sri Lanka. These issues culminate in an inherent fear for snakes among local people, which has unfortunately lead to indiscriminate killing of snakes (Alirol *et al.*, 2010).

Currently, *B. ceylonensis* is listed as "Endangered" in national conservation assessments (MOE, 2012), and as "Near Threatened" in the Red List (Somaweera & de Silva, 2010). Given the updated distribution records of *B. ceylonensis* based on our study, the area of occupancy is 1617 km^2 while the extent of occurrence is 3164 km^2; the current populations are severely fragmented (Fig. 1). In addition, continuing habitat loss, particularly deforestation and degradation of habitat quality of smaller forest patches, may further contribute to both declining area of occupancy and extent of occurrence. Thus, based on IUCN Red List Criteria (IUCN, 2012; B1 ab(i)(ii) and B2 ab(i)(ii)), conservation status of *B. ceylonensis* should be retained as "Endangered".

Although we have shown that *B. ceylonensis* has a greater spatial occurrence than previously known, its sensitivity to habitat alteration, specific habitat requirements (dense, mature, closed-canopy forest), and endemicity to Sri Lanka, also emphasizes the importance of retaining its current conservation status as "Endangered". Nevertheless, a combination of intensive repeated surveys of "absent sites" spatially-explicit population viability analyses, and occupancy modelling are needed to re-assess the species' actual conservation status. Through formal education and well-planned informal nature awareness programs, the general public in rural areas should be informed of the importance of all snakes and on safety precautions that can prevent injury from highly venomous species. Better regulation of rural development and infrastructure improvement programs within lowland wet-zone biodiversity hotspots of Sri Lanka is required to ensure a sustainable future for species restricted to forested habitats, including *B. ceylonensis*.

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Appendix 1.

Surveyed locations of *B. ceylonensis*: **NL** – new localities in our study; **HR** – historical site confirmed by our study; **CH** – historical site that are not confirmed by our study; **AL** – other location we surveyed where snakes were not found.

Location	North	East	Status
Atweltota	6.543208	80.286783	NL
Belilena	6.833972	80.436158	NL
Erathna	6.833972	80.408442	NL
Gilimale	6.721867	80.439669	NL
Huniduma	6.310731	80.342814	NL
Kalawana	6.533100	80.412267	NL
Kitulgala	6.991014	80.405653	NL
Kottawa	6.093186	80.309425	NL
Kudawa	6.442617	80.417347	NL
Kukuleganga	6.660378	80.260414	NL
Lankagama	6.375567	80.337056	NL
Morningside	6.407083	80.607350	NL
Opatha	6.266356	80.408117	NL
Rakwana	6.463906	80.616342	NL
Yagirala	6.365964	80.169150	NL
Beraliya	6.268336	80.206558	HR
Kalugala	6.407347	80.248189	HR
Kanneliya	6.251289	80.338425	HR
Kukulugala	6.613258	80.261800	HR
Kuruwita	6.775425	80.396364	HR
Labugama	6.852447	80.180286	HR
Sinharaja	6.417739	80.464164	HR
Sri Padha	6.825483	80.431150	HR

Udamaliboda	6.880494	80.440994	HR
Udugama	6.212250	80.339789	HR
Balangoda	6.636147	80.673242	CH
Bandrawela	6.827006	80.998731	CH
Deniyaya	6.342436	80.559475	CH
Galle	6.053803	80.220769	CH
Ingiriya	6.742928	80.158561	CH
Kegalle	6.247906	80.354033	CH
Knuckles	6.479208	80.705556	CH
Pelmadulla	6.623025	80.543697	CH
Peradeniya	6.273311	80.595617	CH
Uva Patana	6.799811	81.272722	CH
Yatiyantota	6.017053	80.288169	CH
Agalawatte	6.538133	80.157644	AL
Ahungalla	6.328922	80.036761	AL
Akuressa	6.093242	80.444050	AL
Alawwa	7.292297	80.234781	AL
Ambalangoda	6.253172	80.054800	AL
Ambuluwawa	6.723997	80.670122	AL
Anduragala	6.719564	80.072008	AL
Baddegama	6.173769	80.195642	AL
Belihuloya	6.707075	80.781444	AL
Beruwala	6.480422	79.969519	AL
Bulatsinhala	6.681203	80.172817	AL
Dellawa	6.344964	80.453108	AL
Diyadawa	6.351792	80.547678	AL
Elkaduwa	7.428978	80.690142	AL
Gampaha	7.085636	79.993847	AL
Godakawela	6.504008	80.661189	AL
Gommalgama	6.951700	80.338678	AL

Hiniduma	6.305928	80.325614	AL
Ingiriya	6.753428	80.175600	AL
Kalubovitiyana	6.324314	80.406519	AL
Katepola	6.700922	80.237578	AL
Koslanda	6.742497	81.020050	AL
Kotmale	7.025589	80.598681	AL
Labugama	6.269339	80.186761	AL
Mahausakanda	6.755433	80.253453	AL
Makandura	6.553125	80.626578	AL
Maskeliya	6.843431	80.580461	AL
Matugama	6.520919	80.123056	AL
Mawathagama	7.438819	80.433972	AL
Mirigama	7.240239	80.119264	AL
Mitirigala	6.987903	80.179519	AL
Namunukula	6.931228	81.129206	AL
Nanperial estate	6.761669	80.790478	AL
Nawalapitiya	7.055600	80.524747	AL
Nikapotha	6.740728	80.978978	AL
Nortonbrige	6.897806	80.518956	AL
Ohiya	6.817864	80.844044	AL
Opatha	6.273239	80.405108	AL
Panadura	6.718336	79.909364	AL
Pilikuttuwa	7.105319	80.086053	AL
Ramboda	7.054869	80.711753	AL
Rassagala	6.715792	80.805342	AL
Ratnapura	6.707269	80.381408	AL
Telwatta	6.173344	80.090725	AL
Udawattekale	7.303489	80.663378	AL
Warakapola	7.222758	80.204856	AL
Yakkalamulla	6.101672	80.353164	AL