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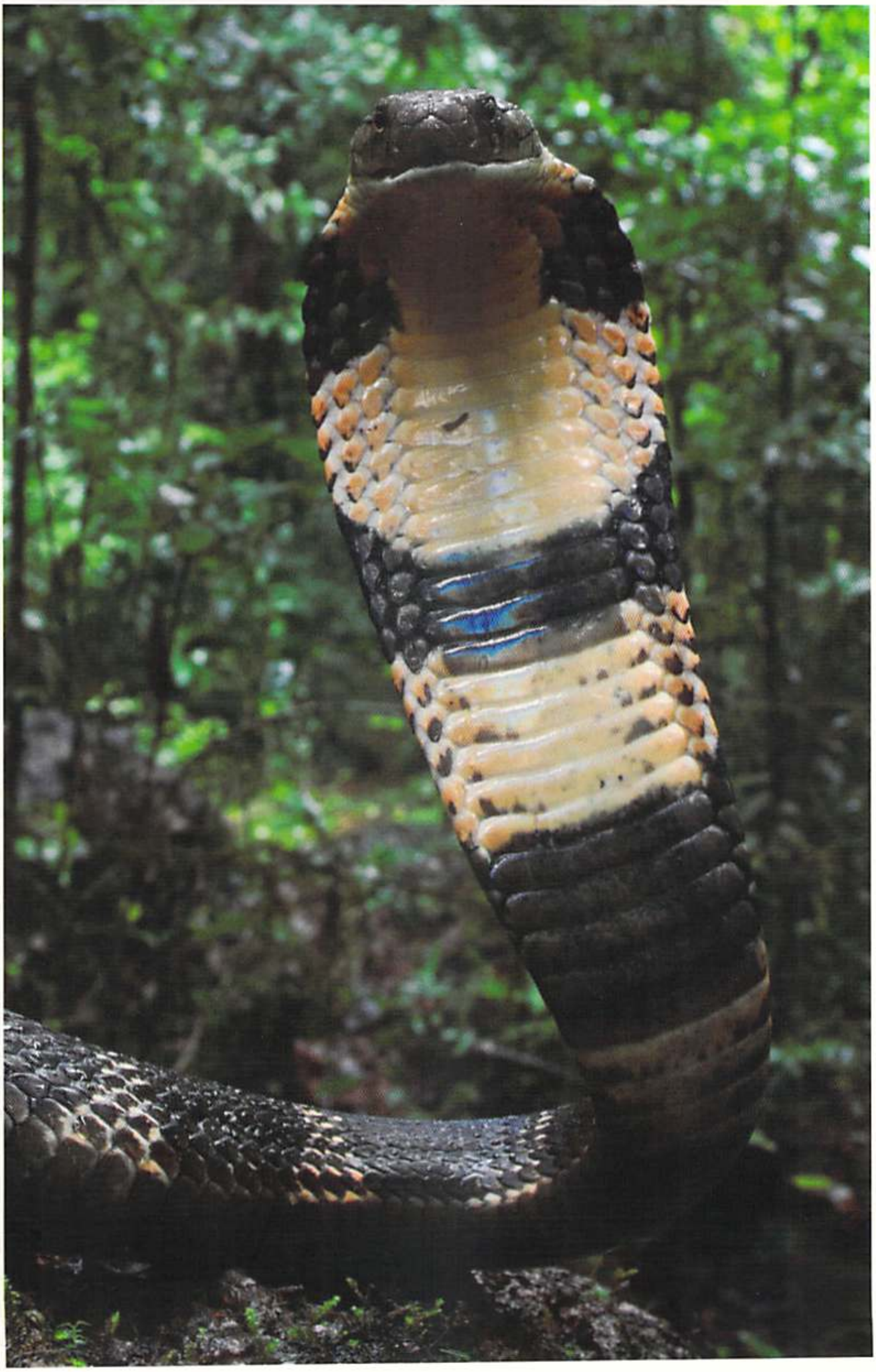

VOL. 36 NO. 2

King Cobra Special Issue

JUNE, 2013

HAMADRYAD

Journal of the Centre for Herpetology, Madras Crocodile Bank Trust

LAYOUT AND FORMAT: **Luk Gastmans**
EDITORIAL ASSISTANT: **Daniel Portik**

Front cover: *Ophiophagus hannah* (King Cobra) from Agumbe rainforest, Karnataka, India. This snake was rescued in July, during the monsoon, and was released after being photographed. The largest of all venomous snakes, the King Cobra is the subject of a series of papers in this issue of *Hamadryad*. Photographed with a Canon EOS Digital Rebel XTi (400D) body with a 18–55mm lens at f/8 without flash. Text and Photo: Gowri Shankar.

Back cover: *Feihyla kajau* (Jade Tree Frog) was originally described as *Rhacophorus kajau*. This small rhacophorid is widespread in the lowlands and midhills of western Borneo, and produces a jelly-coated egg mass. Hertwig et al. (2013. Mol. Phylogen. & Evol. 38) reallocated it to *Feihyla*, whose members were previously known from Indo-China. This individual is from the upper reaches (ca. 1000 m a.s.l.) of Gunung Penrissen, a mountain range that forms the boundary between western Sarawak (Malaysia) and Kalimantan Barat (Indonesia). Photographed with a Nikon D70 body and a 105 mm f/2.8 Micro Nikkor lens. A Nikon Speedlight SB80DX flash was used as a slave. Text and Photo: Indraneil Das.

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HAMADRYAD

A Journal of Tropical Asian Herpetology

INSTRUCTIONS TO CONTRIBUTORS

Hamadryad is a biannual hard copy (and soon to be electronic) journal that publishes original papers dealing with the herpetology of tropical Asia as broadly construed. Reviews of relevant books and major papers are also published. Systematic (phylogenetic and/or taxonomic), faunistic, ecological, and behavioural contributions are especially welcome. Purely clinical or laboratory-based manuscripts will not be accepted unless they pertain clearly and directly to the biology of the organisms investigated. Please contact the Editor in advance of submission if you wish to confirm that your subject matter is suitable for the journal. *Hamadryad* will shortly initiate the publishing of an online only journal, *Hamadryad Notes*, for shorter contributions including significant range extensions and natural history notes. These papers will undergo the same editorial procedure as all full length papers submitted to *Hamadryad*, but are published online once accepted and formatted. One continuously paginated volume will be published per calendar year. There is no charge for colour illustrations in *Hamadryad Notes* and all papers published in *Hamadryad Notes* are freely downloadable as .pdfs. Manuscripts deemed by the Editor as inappropriate for *Hamadryad* but suitable for *Hamadryad Notes* will be automatically considered for the latter journal.

Manuscripts should be only in English and submitted as email attachments to the Editor (at the address below). Authors are requested to submit text files as double-spaced Word (.doc) or Rich Text (.rtf) files (not .docx or other formats) with continuous line numbering. Please use Times New Roman 12 point font, with all genus and species names italicized. For review purposes authors should also submit a .pdf version (not to exceed 3 MB) of their manuscript with all figures included, numbered and in order of citation within the manuscript, at the end of the text, following any tables and appendices. Papers previously published or submitted for publication elsewhere should not be submitted. For general style, contributors are requested to examine the current issue of *Hamadryad*. Corresponding authors who are not current subscribers to *Hamadryad* are requested to pay US$ 5 or equivalent per printed page of their papers to help defray production costs. There are no page charges for subscribers, except for colour plates in *Hamadryad*, which will be charged at US $100 or equivalent per printed page. Hard copy reprints cannot be separately ordered, but all authors will receive a free .pdf file of their published papers which they may distribute for non-commercial purposes.

Major papers exceeding four pages (double spaced) of text, exclusive of literature cited, tables, figures and appendices, should contain the following headings: Title, name and address of author (but not titles and secondary affiliations), Abstract, Key Words (five to 10 words), Introduction, Material and Methods, Results, Discussion, Acknowledgements, Literature Cited (only the references cited in the paper). Appendices follow the main paper. Descriptions of new taxa will be considered as major papers regardless of size. Abstracts (up to 150 words) should summarize the important findings of the paper and should avoid the use of references. In case of descriptions of new taxa, abbreviated diagnoses should be provided in the abstract. Papers submitted as Notes do not require abstracts or key words and distributional or natural history notes intended for this journal do not require subdivisions of the body of the text into Introduction, Material and Methods, etc., although this may be appropriate for some types of shorter papers. Special attention should be paid to accents and diacritical marks. Manuscripts that do not meet these criteria will be returned to authors without review until revised accordingly.

Citations in the text should take the format Smith (1935) or (Smith 1935). Multiple references should be arranged chronologically and separated by a semicolon (Smith 1935; Deraniyagala 1953; Taylor 1962). Two authors should be connected by an ampersand (Biswas & Sanyal 1971) and three or more authors should be indicated by following the first author by "et al." (Das et al. 2006). When crediting authorship of a taxon name a comma should follow the author's name – Sharma, 1967. **The author and date of description should be given at the first use of each generic or specific name within a manuscript.** Such author—date combinations should not be included in the Literature Cited section unless they are otherwise cited in the text.

Literature Cited should be in the following format:

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Books:
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Chapters in books:
MURPHY, J. C. 1996. Crossing Bond's Line: The herpetofaunal exchange between the eastern Caribbean and mainland South America, pp. 207–216 *in* R. Powell and R. W. Henderson (eds.), Contributions to West Indian Herpetology: A Tribute to Albert Schwartz. Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Unpublished theses or reports:
MOODY, S. M. 1980. Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). Unpublished Ph. D. Dissertation, University of Michigan, Ann Arbor. 373 pp.

Publications in languages not using the Roman alphabet:
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Tables should be comprehensive without reference to the text. Tables should follow the main body of the paper, including references, and their desired location within the text should be indicated on the manuscript. Footnotes are not allowed except in special circumstances and by prearrangement with the Editor. Illustrations should be planned to fit either one column (6.5 cm) or one page (14 cm) width, after suitable reduction. All final figures should be provided as separate files in electronic format (.jpg, .tif, or .eps format) only once final acceptance has been indicated by the Editor. Minimum quality for final figures is 300 dpi at the actual size of reproduction. Colour figures will be accepted when necessary to adequately illustrate manuscripts (for example, species descriptions). A per page charge of US $100 applies to colour images, although this may be waived at the Editor's discretion when feasible. All manuscripts received for *Hamadryad* are sent to two or more referees. Authors of papers describing range extensions and descriptions of new taxa should deposit their material in established systematic institutions and cite museum registration numbers. Authors assume responsibility for assuring that all relevant legal requirements for collection, export, and animal welfare have been met. Range extensions not based on specimens, such as endangered or other protected species, may be based on voucher photographs that are deposited in a recognized systematic institution.

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King Cobra *Ophiophagus hannah* (Cantor, 1836) encounters in human-modified rainforests of the Western Ghats, India

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ABSTRACT.– We captured and relocated 106 King Cobras (*Ophiophagus hannah*) that were reported by villagers to the first author from human settlements. We report on their morphology, circumstances and possible reasons for their entering human settlements. Males were brownish to olive green with black tails, averaged 3.5 m (TBL) and 4.5 kg mass, whereas females were uniformly black or brown, 2.5 m (TBL) and 3.4 kg mass. King Cobras (*Ophiophagus hannah*) were usually seen as they were resting after a meal (as witnessed and reported by villagers) or foraging in paddy fields at 10.00–12.00 hrs, likely hunting for the ubiquitous Rat Snake (*Ptyas mucosa*) and Spectacled Cobra (*Naja naja*). We received most rescue calls between March and August, which coincides with their breeding season in southern India.

KEYWORDS.– King Cobra, spatio-temporal dynamics, sexual-dimorphism, removal, relocation, frequency, circumstances.

Introduction

Human encroachment on natural landscapes is a major cause of serious decline in global wildlife populations (McKee *et al.* 2003). Ever-changing land-use types cannot only eliminate fragile wildlife, but also force adaptive species to change their patterns of behavior (Brooks *et al.* 2002). Apex predators may be affected the most (Berger 1999).

Understanding the autecology of predators persisting in human-modified landscapes is the first step towards conserving these species (Elton 1927). Although anthropogenically-altered landscapes often do not support stable wildlife populations (Bender *et al.* 1998), some species may persist in certain human-dominated landscapes. Understanding the natural history of a species is essential to develop conservation measures to protect the habitat and the species alike.

While large mammals, especially carnivores, have received much research attention in this respect (Bekoff *et al.* 1984; Weaver *et al.* 1996; Wickramanayake *et al.* 1998), other taxa, such as snakes, have rarely been studied in such detail (but see Shine & Fitzgerald 2000). Herein, we report on the spatio-temporal dynamics of King Cobras persisting in a human-modified agro-forest ecosystem.

Material and Methods

Study Species.– Capable of growing up to 5.5 m in length, the King Cobra (Reptilia: Serpentes: Elapidae: *Ophiophagus hannah* Cantor, 1836) is the largest venomous snake in the world. This largely diurnal, actively foraging snake inhabits moist, forested tracts of southern Asia, where its diet consists primarily of other snakes. The King Cobra is oviparous, and it is the only snake that is known to build a nest (Aagaard 1924; Smith 1943; Whitaker 1978; Daniel 2002; Pfaff 2002; Whitaker & Captain 2004).

Study Area.– Agumbe (13°50.87' N, 075°09.59' E; 557 m a.s.l., Fig. 1) is an agricultural and Reserve Forest complex situated in the Malnad region of Karnataka, in the Western Ghats. The Western Ghats, identified by Myers *et al.* (2000) as a global biodiversity hotspot, was recently recognized as a World Heritage Site (UNESCO, 2012, Ref: 1342rev). In addition to agricultural land, Agumbe is covered mainly by tropical wet evergreen sub-montane and lowland rainforests. Agumbe is the wettest place in south India, receiving an average annual rainfall of over 8 m during the south-west monsoon season which occurs between the months of June and September (Champion & Seth 1968; Ramaswamy *et al.* 2001). Agumbe is a mosaic of land use types, containing human settlements, areca, coconut, acacia plantations and paddy fields, interspersed with stretches of forests in various stages of regeneration/degradation, depending on local human pressures and effectiveness of protection by the Forest Department.

Data Collection.– We obtained data on King Cobras from 2005 to 2009. Generally villagers here have high tolerance toward the King Cobra and seek help only after the snake is given ample time to move out on its own. We attended each King Cobra 'rescue' call and reassessed the situation and rescue operation was carried out only if it was close to their homes. We recorded complete details of the informant, locality of the house or other private holding into which the snake entered. We captured each snake using snake hooks and cloth bags (after Whitaker 1970) in the presence of local Forest Department authorities. We determined the sex of all captured individuals by probing and obtained masses using a calibrated spring balance (Pesola). Because we were unable to obtain permission to anesthetize snakes for processing, we visually estimated the total body length (TBL) length of each snake, relying on our prior experience measuring captive, sedated, and dead King Cobras. We also documented the colouration of each snake. Early in the study, we relocated the snakes a considerable distance away from the site of capture according to the wishes of the local people and instructions of the authorities. However, when it was inferred from our ongoing radiotelemetry study that the King Cobra has a clearly defined home range, we generally released snakes within one kilometer of the site of capture (Whitaker *et al.* 2011). We could not permanently mark released snakes because we were unable to obtain permission from the Forest Department.

Results

In a five year period from 2005 to 2009, we captured and relocated a total of 106 King Cobras (Table 1). Table 1 reveals that most King Co-

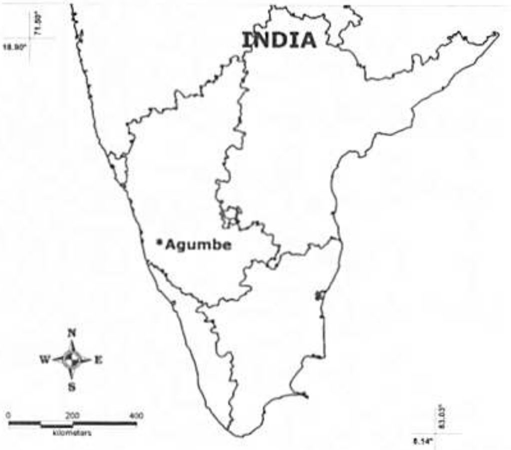

Figure 1. Location map of the study area, Agumbe, Karnataka, India.

Table 1. Monthly incidences of King Cobra captures by year. Bold numbers indicate the highest value in each year.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2005	—	1	**9**	1	1	1	—	1	2	2	1	1
2006	6	1	4	—	**7**	1	5	2	1	1	1	—
2007	3	2	**5**	1	—	—	—	1	—	—	—	—
2008	1	2	**6**	4	—	2	—	2	—	—	—	1
2009	1	3	4	1	2	1	2	**5**	2	1	4	1

bras were caught during the months of February, March (pre-monsoon season) and August (southwest monsoon season). King cobra encounters were on average lower during the months September through December. The lowest and highest frequencies per month ranged from 1–9 individuals. In 15 out of 60 months there were no King Cobra encounters reported.

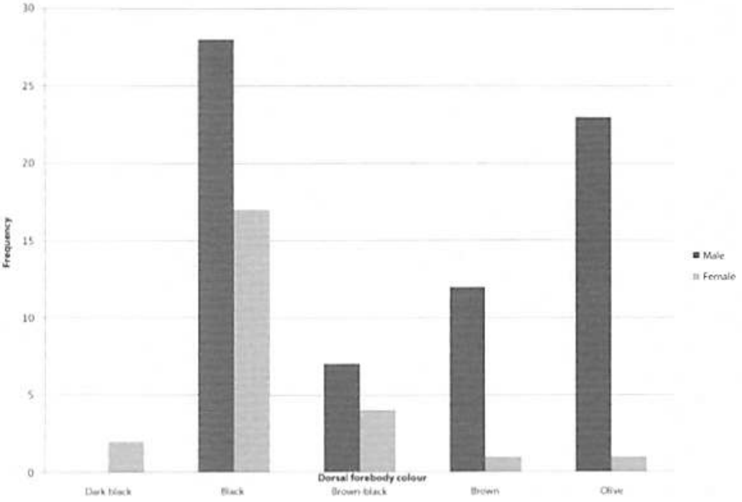

Figure 2. Dorsal fore-body colouration of male and female King Cobras.

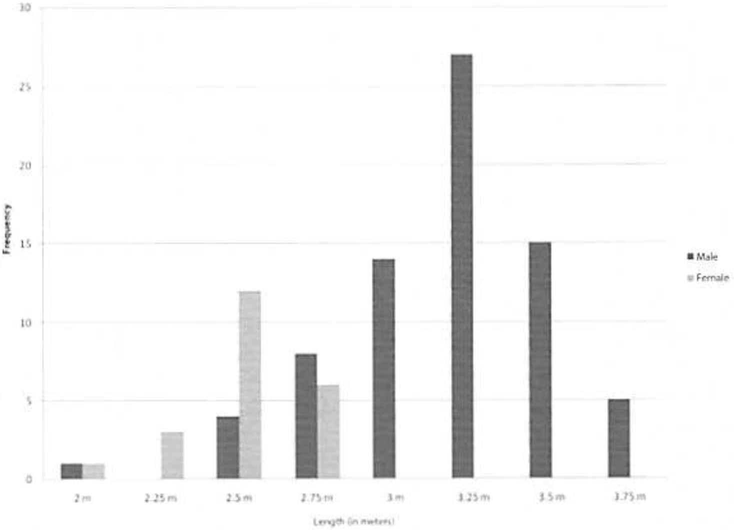

Figure 3. Length (m) of male and female King Cobras in the study.

In order to quantify sexual dimorphism, we compared the predominant dorsal fore-body color, length (m) and mass (kg) for males (n = 79) and females (n = 27) (Figs. 2, 3, 4).

We found that most snakes were reported in the late morning (10h00–12h00; Fig. 5), mainly from vegetation associated with paddy fields (Figs. 6, 7).

In an effort to understand why King Cobras enter human landscapes, we recorded behavioral observations on each snake we captured. After having been informed by villagers that the snake had been seen either foraging or feeding the previous evening or earlier that day we observed most King Cobras as they were resting after their meal or foraging in paddy fields typically from 10h00–12h00 (Fig. 8). Villagers confirmed that snakes commonly enter farms and settlements (Fig. 9) hunting for prey in paddy fields. These paddy fields contain high densities of rats, which presumably attract what appear to be unusually large numbers of Rat Snakes (*Ptyas mucosa*) and Spectacled Cobras (*Naja naja*) as compared to forest areas with a relative paucity of rodent prey. These are ideal prey items for King Cobras as they are both large, common snakes which we have often observed being preyed upon by King Cobras (pers. obs.).

Discussion

Our study demonstrates that females were smaller and darker in colouration, while males were larger and paler (Fig. 10) which is consistent with the literature (Leakey 1969; Pfaff 1995, 2002; Whitaker & Captain 2004). We found this difference in colouration to be more pronounced in the breeding season. Additionally, we observed males to be darker during wet seasons, which we believe may be a thermoregulatory adaptation (PGS & RW pers. obs.). In fact, sexual dimorphism in this species is so pronounced that Evans (1902) believed that males and females were two different species. In our work, males outnumbered females by nearly three to one, possibly because they have larger home ranges, require more prey and more actively search for mates during the breeding season (unpubl. data). Indeed, we received more King Cobra rescue calls during the breeding season.

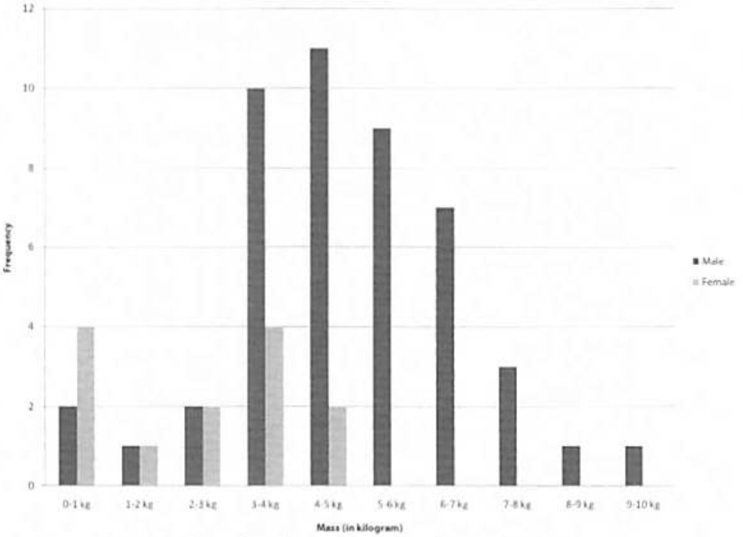

Figure 4. Mass (kg) of male and female King Cobras in the study.

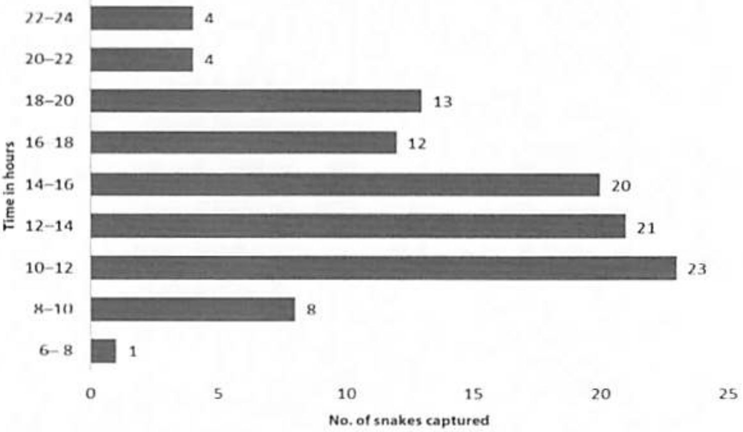

Figure 5. Time of day of captures of King Cobras from human habitations.

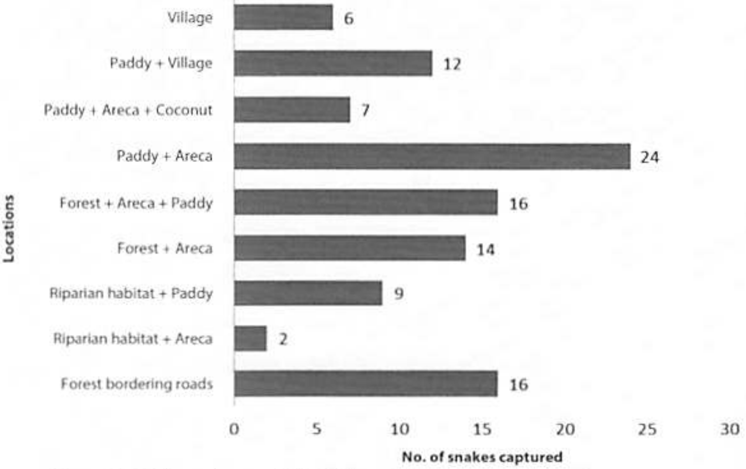

Figure 6. Habitats from which King Cobras were captured.

We captured several snakes from riparian habitat, which the snake has an apparent affinity for (Leakey 1969; Pfaff 1995, 2002; Whitaker & Captain 2004). Our study indicated that this species is active year round, moves freely in paddy fields, open clearings and thinly forested tracts. This is contrary to Daniel (2002), who remarks that it inhabits dense jungles in the hills or their vicinity in peninsular India. Our work revealed that an average of 21 snakes (range = 12-29) are 'rescued' per year in the Agumbe area, although some snake rescuers who work in nearby districts have reportedly rescued hundreds of King Cobras per year. These snakes were often released in our study site, having been relocated from around ca. 40-60 km radius. Such

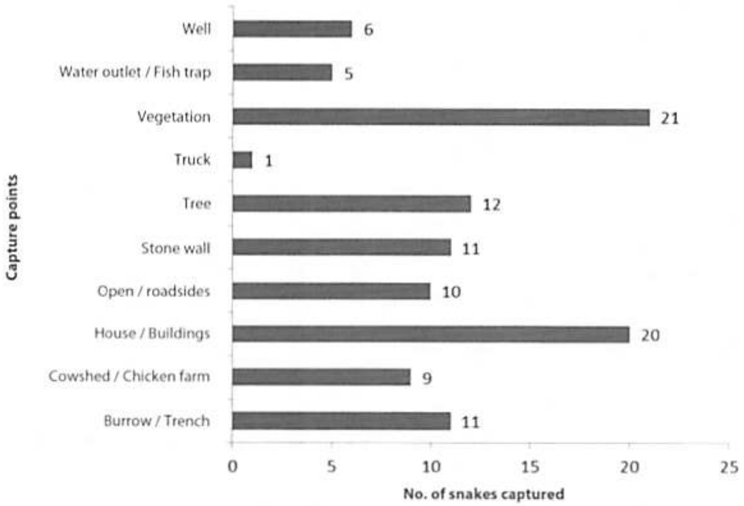

Figure 7. Location of King Cobra capture points.

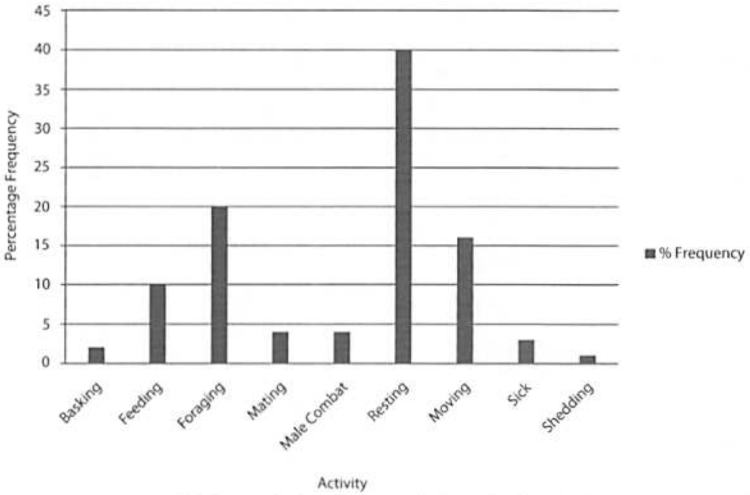

Figure 8. Activities and physical condition of King Cobras encountered around human settlements.

distantly relocated King Cobras could possibly be the ones noted by us to be 'sick' snakes, as our telemetry studies reveal that long-travelling snakes soon become evidently weak. Sick snakes were clearly discerned by an evidently visible vertebral column and ribs, resulting from malnutrition (Fig. 11). It is noteworthy to mention here that a long-term study on King Cobras has never been done (Das & Whitaker 1996), despite the fact that it is a charismatic species with a very high public awareness profile and a wide distribution in several south Asian countries (Smith 1943; Whitaker 1978; Daniel 2002; Whitaker & Captain 2004). This highlights the necessity of continued research on this unique snake. Insight into its natural history is vital to the conservation of this species. Considering that the King Cobra is persecuted throughout much of the rest of its range, it appears that the Malnad people's remarkable tolerance and reverential attitude toward the King Cobra is crucial to driving conservation of this potentially dangerous snake in a predominantly human-altered landscape.

Acknowledgements

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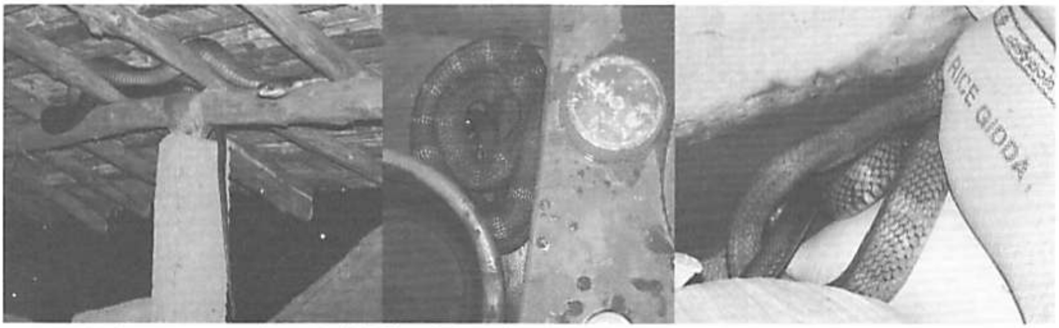

Figure 9. Various capture points of wild King Cobras in manmade structures in the Agumbe region.

Figure 10. Sexual dimorphism and dichromatism of Agumbe King Cobras showing a larger, paler (left) and a smaller, darker female (right).

Chief Conservator of Forests and Chief Wildlife Warden(Wildlife), N.B.Manjunath, Assistant Conservator of Forests, Brijesh Kumar, Conservator of Forests, N.H.Jaganath and H.S Suresha, Range Forest Officers of the Karnataka State Forest Department for permission to undertake the study and cooperation in the field. We are thankful to Sharmila Rajasegaran and all other staff of Agumbe Rainforest Research Station for their assistance. We thank Matt Goode and Mickey Parker for reviewing and sharing valuable editorial comments. We also thank S P Vijay for his critical comments. We are grateful to the citizens of Agumbe and surrounding villages who refrain from harming these snakes and cooperated with us whenever King Cobras entered into their houses and farms. Thanks to Mohammed Anees, J.Jagadeesh, Sandesh Kadur for their timely help in the field for rescue expertise, logistics and photography respectively. Thanks are also due to Nikhil Whitaker and Gowri Mallapur of Madras Crocodile Bank/ Centre for Herpetology and B. Vijayaraghavan, Chairman, Chennai Snake Park Trust for permitting library reference and literature collection in their care; the following organizations for their generous financial support: National Geographic Society (King Cobra Telemetry Project); National Geographic Television (A.R.R.S.); Whitley Fund for Nature (A.R.R.S.).

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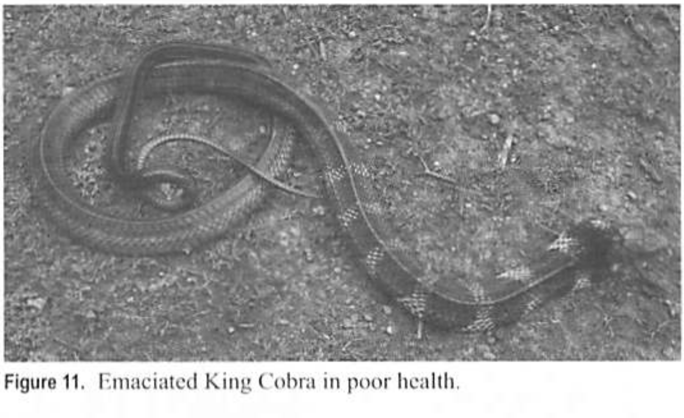

Figure 11. Emaciated King Cobra in poor health.

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Habitat use of King Cobra (*Ophiophagus hannah*) in a heterogeneous landscape matrix in the tropical forests of the Western Ghats, India

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ABSTRACT.– **King Cobras are the largest of all venomous snakes. Thus, they have a unique role in the ecosystem. We sampled habitat locations of five radio-tagged King Cobras in the Western Ghats of Karnataka, India, from December 2010 to April 2011. Habitat preferences were investigated based on use of retreat sites from radio-implanted animals. While sampling for known retreat sites, 30 additional sightings of wild adult non-radio-tagged King Cobras were recorded. Sex based differences in habitat use were studied by sampling nest sites. The data were analyzed using generalized linear models (GLM) for the binary presence dataset. We found King Cobra movement patterns are strongly influenced by ambient temperature, relative humidity and wind direction. King Cobras did not show strong preferences for any particular habitat type. King Cobras likely prefer areas close to streams with abundant fallen logs as retreat sites. Animal burrows were also used as shelter sites. Areas with a leaf litter depth of 10–17 cm were preferred sites for nest construction.**

KEYWORDS.– **King Cobra, habitat selection, snakes, *Ophiophagus hannah*, Western Ghats, Agumbe**

Introduction

Thermal environment has repeatedly been shown to be a strong driver in snake activity patterns (Schwaner 1989; Fitzgerald *et al.* 2002, 2003). Yet, snakes are highly adaptable, ranging from near arctic conditions to the tropics. Snakes, as poikilotherms, are intertwined with the surrounding thermal environment. Thus, they must adapt behaviorally depending upon the range of suitable temperatures of their habitats (Huey 1982). The effectiveness of this behavioral thermoregulation varies with thermal quality and evidence suggests that poikilotherms thermoregulate more effectively when the thermal quality is low (Blouin-Demers & Weatherhead 2001; Blouin-Demers & Nadeau 2005). Differences in thermal quality significantly influence site use on the canopy level in a forest, or open rock faces or underground burrows (Webb & Shine 1998). These are attributes of seasonal variation (Slip & Shine 1988; Goode *et al.* 2009). Habitat use in snakes varies with sex and between gravid and non-gravid females (Madsen 1984; Charland & Gregory 1995; Brown & Weatherhead 1999) In addition, prey availability has been observed to influence habitat use

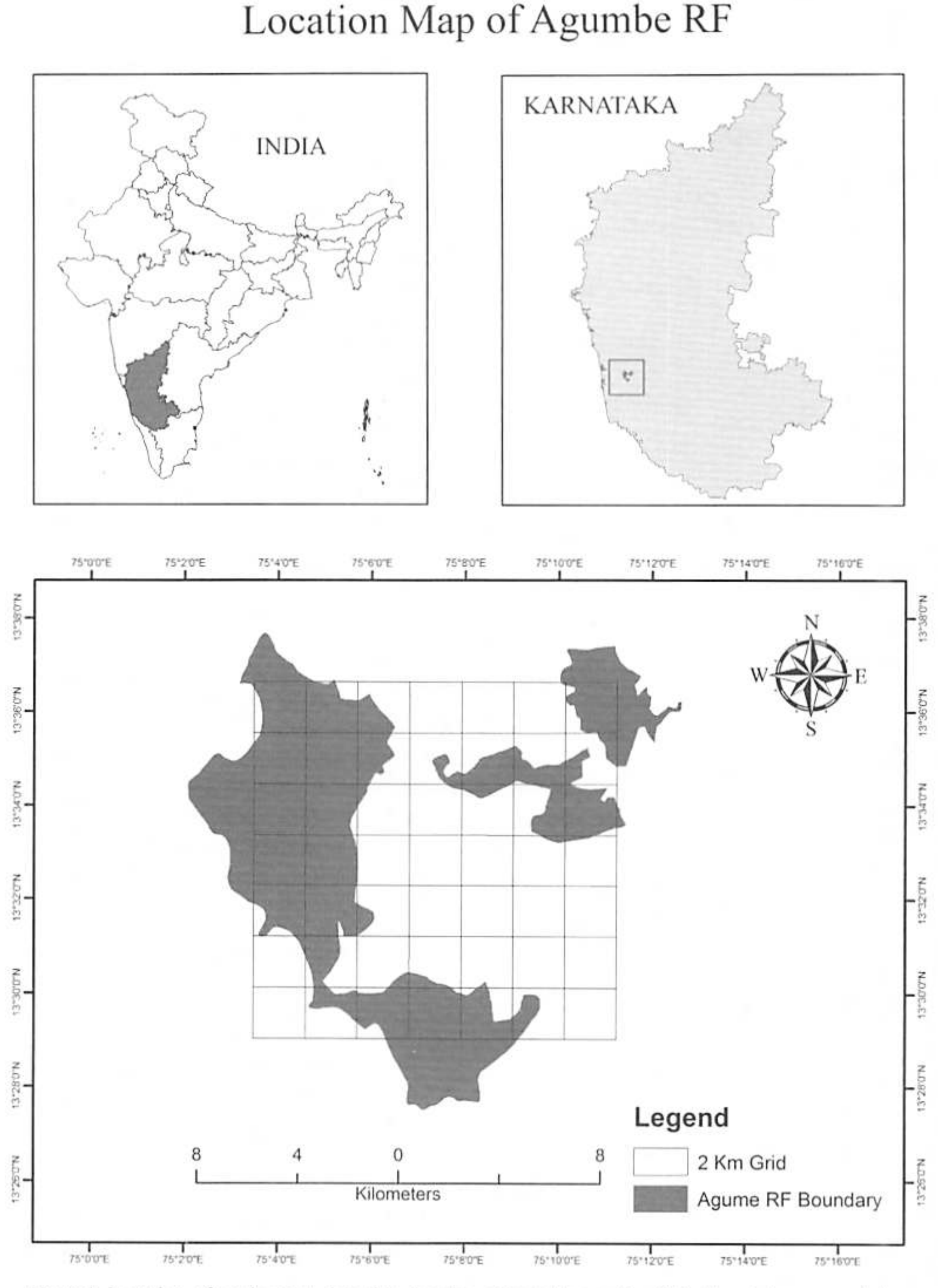

Figure 1. Location of study area; denoting the size of sampling grid within the study area and the subsequent reserve forest.

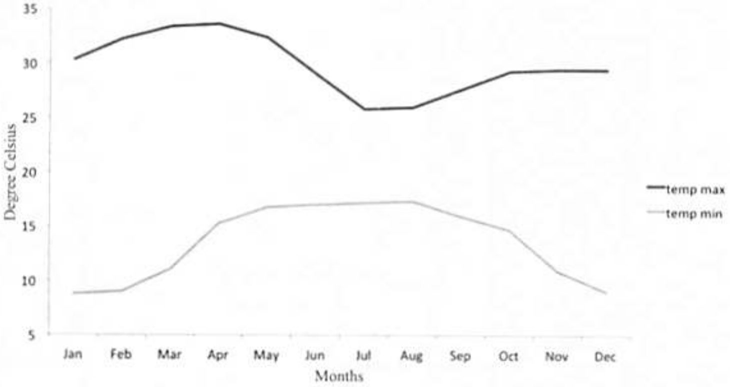

Figure 2. Annual temperature regime at Agumbe.

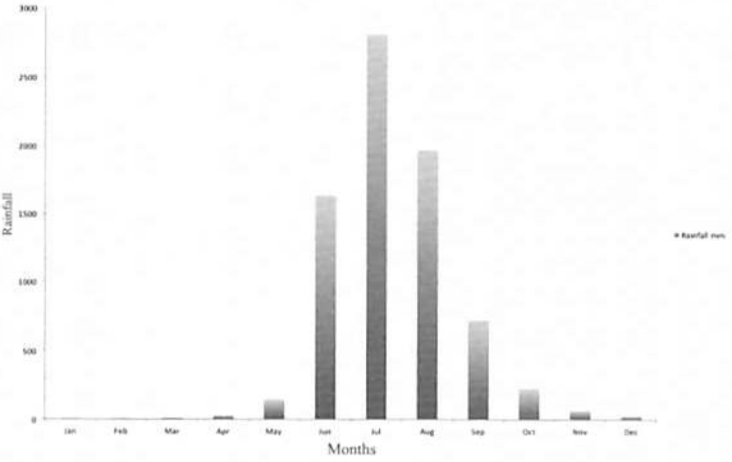

Figure 3. Annual rainfall regime in Agumbe. The peaks are mostly from June to August, measuring rain as high as 3000mm

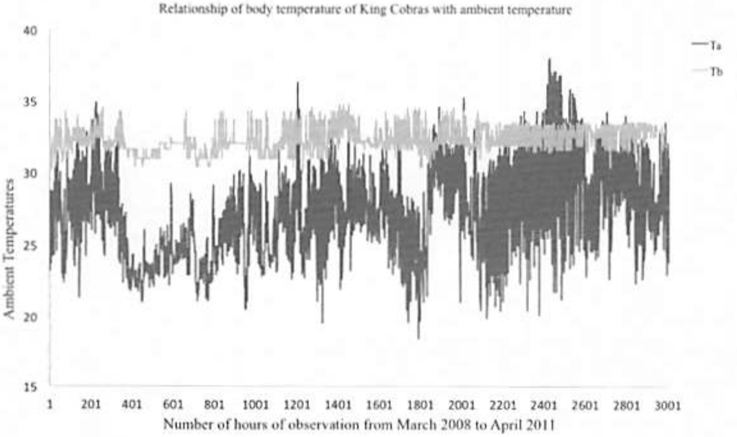

Figure 4. Body temperature (Tb) and ambient temperature graphs (Ta) for-OPHA ID snake F1; OPHA ID snake M1; OPHA ID snake M2; OPHA ID snake M3 and OPHA ID snake M4. The number of hours of observations is on the x-axis and temperatures are on the y-axis. Tb remains more-or-less constant despite fluctuations in Ta. Based on observations made from March 2008 to April 2011.

(Klauber 1972; Weatherhead & Charland 1985; Daltry *et al.* 1998; Theodoratus & Chiszar 2000; Bhaisare *et al.* 2010). Behaviors such as mate selection, competition for natal areas, foraging, and reproduction (Brito 2003; Waldron *et al.* 2006) are ecological influences on habitat site selection of snakes. Habitat use may vary extensively amongst sympatric species (Keller & Heske 2000). Within a particular sex, as observed by Pattishall & Cundall (2009), there is often site fidelity with respect to nesting sites. Certain snakes seem to use suitable ambush sites, depending upon the thermal situation and relative humidity (Daltry *et al.* 1998; Oliveira & Martins 2001). Many snakes use underground burrows as hibernacula or for nesting (Steen *et al.* 2007; Ramesh & Bhupathy 2010a). In human modified landscapes, snakes use retreat sites such as abandoned construction sites and utilize roads as thermoregulatory surfaces (Daltry *et al.* 1998). Most importantly, habitat use of snakes is usually multidimensional and habitats are used in a complex manner (Hebrard & Mushinsky 1978).

The King Cobra (*Ophiophagus hannah* Cantor, 1836) is a largebodied snake occurring in South and Southeast Asia (Aagaard 1924). Throughout its range, the King Cobra occurs in a wide variety of habitats from littoral, mangrove swamps to broadleafed alpine forests (Bashir *et al.* 2010). Although much anecdotal information has been recorded as reviewed by Das & Whitaker's (1996), detailed studies are lacking for this species. The King Cobra is considered an apex predator occurring in a variety of habitats, however, the nature of its habitat selection strategy is poorly understood. The diurnal and seasonal eco-geographical requirements for predation and other life history traits are unknown. Much of the Western Ghats biodiversity hotspot is under threat of deforestation. Currently, the effects of deteriorating forest quality and the expanding human habitations on King Cobra ecology are unknown. This was one of the major pretexts for the King Cobra Telemetry Project in South India and for this study in particular.

Material and Methods

Study Site.– Fieldwork was performed in Agumbe (13.5087° N, 75.0959° E; 716 m a.s.l.), located in the Central Western Ghats of the Shimoga District, Karnataka, India (Fig. 1). The Agumbe Rainforest Research Station (ARRS) has been conducting King Cobra research through the King Cobra Telemetry Project (KCTP) since March 2008. The area is considered tropically seasonal but has a heavy rainfall bout and cold winter and hot summer regimes. Monsoons occur from June to September and the area receives 1500–3000 mm of rain during the monsoon season (Fig. 2) and humidity levels are high and relatively stable at above 75%, reaching 95% during the monsoon. The cold season lasts from December–February and has a temperature range from 15–35°C (Fig. 2). The hot dry season is usually from March–May and is characterized by lower humidity and temperatures that are above 35°C. Champion & Seth (1968) classified these forests as the West Coast Tropical Evergreen forest (1/A-C/4). Forest areas are dominated by tree species of the genera *Dipterocarpus*, *Diospyros*, *Humboldtia* and *Artocarpus* (Pascal 1988). However, many areas surrounding the Agumbe reserve forest have been converted to plantations (Acacia, Areca nut and Banana), or rice and wheat paddy fields. Thus, the landscape is a complex mosaic of habitat types, including natural forests, paddy fields and plantations.

Table 1. GLM values of coefficients with their standard errors at a population level for King Cobras.

Variables	coefficients
TA	7.7e10-1 ± 0.06
RH	1.25 ± 1.14
SW-NE	1.19 ± 2.6e10+3
S-N	0.21 ± 0.42
SE-NW	-5.36 ± -0.54
E-W	-4.77 ± 3.31e10+2
W-E	-4.69 ± 3.5e10+2
N-S	-4.57 ± 1.6e10+3
NE-SW	-4.517 ± 1.9e10+3
NW-SE	-3.99 ± 1.5e10+3

The Intensive Study Area (ISA) of 96 km^2 encompasses previous presence location records of these radio tagged snakes. The ISA was divided into 49 grids of 2 km^2 each (Fig. 1) and was sampled for habitat variables relating to the presence of King Cobras. Secondary records of

Table 2. Habitat use vs. availability results of the four radio tagged King Cobras.

Rank	Habitat type	Average	LCL	UCL	Standard Error
1	Evergreen Forest	0.19	-0.1	0.48	0.02
2	Deciduous Forest	-0.1	-0.48	0.29	0.1
3	Plantation/Orchard	-0.16	-0.83	0.51	0.34
4	Scrub/Deg Forest	-0.33	-1.09	0.43	0.38
5	Agriculture	-0.53	-1	-0.04	0.18
6	Grassland	-0.65	-1.21	-0.09	0.28
7	Water bodies	-0.72	-1.27	-0.18	0.27

LM with microhabitat variables with presence as a response variable to different microhabitat vari- a retreat site during the present study. Significant values (< 0.05) are indicated in bold.

	Estimate	Std. Error	z value	Pr(>|z|)
ept)	1.16e+00	4.4e-01	2.667	0.00766
w	-7.24e-01	4.31e-01	-1.682	0.09249
e of Stream	1.67e+01	1.33e+03	0.013	0.98997
e Trunk	1.69e+01	1.76e+03	0.010	0.99230
amboo Thicket	1.69e+01	2.509e+03	0.007	0.99463
Distance from stream	7.51e-03	3.310e-03	2.266	0.02344
Dead Vegetation	-2.05e-02	6.712e-03	-3.043	0.00234
Fallen Logs	2.333e+00	5.113e-01	4.551	5.35e-06

Table 4. Final GLM for King Cobra nest site with presence as a response to various microhabitat variables. Significant values (< 0.05) are indicated in bold.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-7.35	2.86513	-2.565	0.0103
SC	0.022	0.02247	0.945	0.3445
CC	0.039	0.03320	1.169	0.2426
LL_DEP	0.65	0.30998	2.073	0.0381

110 wild non-tagged King Cobras from March 2008 to October 2010 as well as points located within the grid were used for presence analysis. All habitat points were recorded using a Garmin 72H GPS.

Retreat sites sampling.– Retreat sites were identified as areas where tracked King Cobras remained stationary for an entire night, in addition to sites revisited more than once by the animal. All retreat sites were within the intensive study area grid boundaries. We located additional retreat sites, along with the locations of tagged animals, based on sightings from December 2010 to April 2011. Ambient temperature (TA) (Schwaner 1989; Row & Blouin-Demers 2006) and relative humidity (RH) (Daltry *et al.* 1998) as well a wind speed and direction were measured within a 10 m radius of each retreat site with a Kestrel 3000 Wind Meter. We also attempted to categorize and quantify habitat covariates, habitat type, percentage shrub cover (Madsen 1984; Weatherhead & Charland 1985), and percentage dead vegetation on site. Canopy cover was measured using a spherical densitometer. We recorded land characteristics including: burrows (BURR), fallen logs (F_LOG), leaf litter depth (LL_DEP), distance from nearest water source (DIST_STREAM), distance to nearest burrow (DIST_BURR), distance to the nearest fallen log (DIST_FLOG), and distance to the nearest rock (DIST_ROCK) using a flexible field measuring tape

Nest site sampling.– Our field study period partially coincided with the King Cobra breeding season from March to late April 2011. Because King Cobra females are the only snakes in the world that make a nest, we wanted to find out whether any particular habitat parameter influenced nest site selection. We also engaged the local people to search for King Cobra nests i the area. At each nest site location (n = 13), hab itat covariates within a 10 m radius were sam pled. Recorded variables were GPS location i Universal Transverse Mercator (UTM) forma habitat type (HAB_TYPE), shrub cover (SC dead vegetation (DV) and canopy cover (CC Measurements were also taken at four rando locations at 50 m distances from each nest site

Radio Telemetry.– The KCTP collected dat from March 2008 until April 2011. Five snake (ID: F1, M1, M2, M3 and M4) were tagge and followed. The transmitters (Holohil sy tems; model AI-2T, weight 24 grams) used fo the snakes varied in frequency. The transmi ters were implanted into the coelomic cavit (Weatherhead & Anderka 1984).

Snakes were tracked for varying amounts o time; only one snake ID OPHA M4 was suc cessfully tracked to the study completion. Body temperatures of the snakes were recorded using an inbuilt thermal sensor in the transmitter. Wind direction, ambient temperature (TA) and relative humidity (RH) were also recorded during tracking using a Kestrel 3000 Wind Meter. At each retreat site selected by M4, location in UTM coordinates and the major habitat type, and microhabitat variables were recorded. These data were collected from 08h00–16h00, depending upon the activity period of the animal for the given day. If the snake moved then it would be followed and monitored until it selected a retreat site.

Land Use Land Cover (LULC) Map.– A 1:250 000 land use land cover map was derived from the Indian Remote Sensing Satellite (IRS 1D) Linear Imaging Self-scanning Sensor (LISS) III image. The spatial resolution was degraded from 23.5 m to 62.5 m. The LISS III data for the year 2005 was used to classify land use land cover (LULC) map. The classified habitat types in the LULC map are as follows (IIRS report 2002): evergreen forest, deciduous forest, plantations/ orchards, scrub forest, agriculture — mostly rice and wheat cultivation, grassland — areas mostly covered by grass species or clearings and water bodies. This map was later used to analyze habitat use by radio tracked King Cobras.

Retreat and Nest Site Selection Data Analysis.– We used generalized linear models (GLM) with a logit link function (for binomial errors) to analyze the data, as appropriate for a binary dataset with categorical variables (Crawley 2007). To investigate the factors influencing retreat site selection, presence/absence (binary response) data along with habitat predictors were collected from 262 presence points.

Microhabitat sites (n = 262) and nest sites (n = 13) were checked for correlations using a Spearman Correlation test. Of the highly correlated variable pairs, the ecologically less meaningful and redundant variables were removed from the models. Variable correlated above a value of 0.4 were removed from all models. A full logistic regression model with linear predictors (microhabitat variables) was constructed and then reduced using backward selection. The AIC (Akaike Information Criterion) was used to select the most parsimonious model. The regression coefficients were verified using univariate logistic regression of predictors (variables) to infer direction size eff nificance of microhabitat variables o ability of King Cobra presence/absen

Habitat Use vs. Availability: Analyzing Pattern.– Habitat use of radio tagged s computed using Jacob's Index (1974). alized linear model framework (GLM- l and binomial error, i.e., logistic regressi computed. Movement vs. no movement ry response) was modeled with environ parameters such as ambient temperature relative humidity (RH), wind speed and direction and their combinations/interact to understand movement patterns. Movem data were used from tagged snake M4. To i prove the sample size, datasets from the KC (March 2008–December 2010), were also use All analyses were performed in *R* version 2.11. (R Development Core Team 2008).

Results

Using generalized linear models to predict the influencing variable on movement pattern we selected the most parsimonious model using AIC values (see Table 1). Ambient temperature (7.7e10-1 ± 0.0545, P < 0.001; range 20–35°C) has the greatest influence on movement, followed by relative humidity (1.25 ± 1.14, P = 0.01; range 70–90%). Since King Cobras are chiefly diurnal, 87% of activity was observed from 10h00 hours (thermoregulation) to 18h00 hours (return to retreat sites), although when they would seek cover in their retreat sites at approximately ~12h00. Some observations (n=3) were during night hours, primarily when the snake was foraging.

Habitat use was ranked with significance values derived from the index as per their average values (see Table 2). The ranked habitats were as follows: evergreen forest (~83%) > plantation/orchard (~7%) > scrub/degraded forest (~4%) > agriculture (~3%) > (grassland ~1%) > water bodies (~1%) (P < 0.001). Here water bodies imply major reservoirs, rivers and canals, and excludes forest streams and rivulets. During the breeding season, March to April of 2011, we encountered a higher number of King Cobras around human habitations (n= 21).

We sampled a total 262 presence locations in which Fallen Logs (0.02, Z= 4, P < 0.001), Dead vegetation (P = 0.002) and distance to streams (P = 0.02) show the maximum influence on the presence of a King Cobra at a site. A large number of occurrences of King Cobras in burrows was also documented (n=57, 21%). These microhabitat sites were distributed across the landscape of the study area. However, presence locations were higher (>70%) in sites located close to forests or in the forests. We observed one active nest during the sampling session wherein we could see that areas with higher leaf litter were chosen as suitable sites for building nests. Also from the generalized linear model, LL_DEP (Leaf Litter Depth) proved to be a significant factor influencing nest site selection (0.65, $Z = 2$, P = 0.03; leaf litter depth of 10–17 cm).

Discussion

Movement Pattern: Behavioral Thermoregulation.– Numerous studies on habitat use or activity patterns of ectothermic animals have highlighted the importance of behavioral thermoregulation (Schwaner 1989; Fitzgerald et al. 2002). Body temperatures often show distinct variation in summer and winter seasons in the temperate region (Schwaner 1989). However, the biology of snakes in thermally stable environments, such as warm water bodies or the humid tropics, has rarely been investigated. Shine & Lambeck (1985) demonstrated that aquatic filesnakes, Acrochordus arafurae, maintain a mean body temperature of 26–30°C by passively thermoconforming. A radio-telemetric study of water pythons, Liasis fuscus, concluded that they maintained body temperatures of around 30°C, again without apparent thermoregulatory behaviour (Shine & Madsen 1996). King Cobras show a considerable response to ambient temperatures. In this case, individuals were observed maintaining their body temperatures within a fixed range (max of about 30°C) (Fig. 4). These results concur with the findings in some other snake studies in tropical ecosystems (Lilywhite 1987; Shine 1987; Schwaner 1989; Shine & Madsen 1996; Ramesh & Bhupathy 2010a).

While the relation of snakes with their ambient temperature is well understood, relative humidity has been found to be a factor of greater influence on King Cobra movements. Similar results have been seen in Malayan Pit Vipers (*Calloselasma rhodostoma*) which exhibit no basking thermoregulatory behavior and are primarily influenced by relative humidity (Daltry et al. 1998). A direct influence of humidity on King Cobras may be answered by the fact that many areas of the Western Ghats show very high levels of humidity. Thus proximity to water may be important for avoiding desiccation thanks to highly humid conditions (Huey 1982). Reptiles, especially species in dry tropical areas, can lose a substantial amount of water through their skin (Heatwole 1976). High water loss was also observed during ecdysis in snake M4, as is typical for many reptiles (Heatwole 1976; Shankar & Whitaker 2009).

The influence of wind direction on movement pattern may in part, be due to the predatory strategy of King Cobras (S. Rachakonda, pers. obs). King Cobras have excellent cognitive abilities and have been observed to use scent trails to search for and locate prey in addition to finding mates (pers. obs.).

The apparent influence of relative humidity and wind direction on King Cobra movement patterns sheds new light on the ecology of this tropical species. Most snake behaviour studies have been conducted in areas with greater temperature extremes, where behavioural thermoregulation may be extremely important (Blouin-Demers & Weatherhead 2001; Blouin-Demers & Nadeau 2005). Shine & Madsen (1996) rightly pointed out that the vast majority of species inhabit the tropics, and further studies in this region may ultimately negate the common assumption that thermoregulation is of paramount importance in the daily life of most reptiles.

Habitat Use In Relation to Thermoregulation.– Snake habitat use is a function of many factors operating on a micro-scale (Prior & Weatherhead 1994). These factors influence snakes even at population levels (Reinert 1984). The empirical results for habitat utilization show that King Cobras use a variety of habitats opportunistically and the Jacob's Index shows most habitats as 'neutral'. King Cobras did not actively prefer or avoid any particular habitat type in the study area, which is a mosaic of habitat types. Diversified habitat types typically have a diversity of snake species (Shine & Fitzgerald 1996; Blouin-Demers & Weatherhead 2001).

Since King Cobras prey exclusively on other snakes, it can be assumed that they move mostly in search of prey, even in the human dominated landscape. Coinciding with this is the fact that a prey species favored by King Cobras; the Indian rat snake, *Ptyas mucosa*, was the most observed snake within the habitat mosaic.

King Cobras select retreat sites based on the availability of basking and cover. The amount of sunlight varied significantly during the course of the day. However, these snakes only came out during certain times of the day (forenoon and late afternoons), likely avoiding midday and early afternoon basking, thus exhibiting bimodal thermoregulation. Nevertheless, these snakes are very alert during most of the time spent basking and would retreat immediately beneath a fallen log or into dead vegetation at the slightest hint of disturbance. Indeed, a number of snake studies have highlighted the importance of behavioural thermoregulation. For example, snakes are often observed spending extended periods basking or exploiting cool micro-habitats. Thus, maintaining body temperature within a narrow range (Schwaner 1989). Broad-headed snakes, *Hoplocephalus bungaroides*, are restricted to sandstone rock outcroppings in Australia, where exfoliated boulders of different sizes and thicknesses provide a suite of retreat-sites with variable thermal characteristics. Sheltering snake body temperatures under rocks are determined by the degree of shading and the thickness of the rock (Webb & Shine 1998). The Indian Rock Python (*Python molurus molurus*), during a study performed in Keoladeo Ghana National Park in India by Bhupathy & Vijayan (1989), showed bimodal activity patterns with respect to external temperature. These animals however, used burrows, coming out in the morning hours to bask and retreating during evening hours. They also were found to use different burrows or hibernacula (as winter hibernating sites) and some individuals were seen using tree tops to perhaps reach the desired body temperature, as observed in Carpet Pythons, *Morelia spilota*, in coastal eastern Australia (Shine & Fitzgerald 1996).

Our research is limited to adult individuals. Juvenile King Cobras are likely to use habitats differently as they face a higher risk of mortality due to predation and starvation. Since the external temperature remains more or less constant, fallen logs may provide excellent cover and basking sites as they may provide the appropriate thermal quality and camouflage (Row & Blouin-Demers 2006). Hiding within the dead vegetation can also be an ambush predatory tactic as seen in vipers. A preference for fallen logs that provide a linear hiding place was observed, and often they exhibited basking behavior with their body sprawled rather than coiled (pers. obs.). King Cobras observed near human habitations quickly disappeared inside burrows when disturbed. However it should be noted that these observations made are only of adult king cobras. These results cannot be inferred for juvenile king cobras, as their habitat requirements owing to predation pressure may be entirely different.

Most species of snakes lay their eggs either in burrows (Ramesh & Bhupathy 2010a), leaf litter, or under rocks/fallen logs (Burger & Zappalorti 1988). King Cobras however, are the only species that builds a mound nest comprised of fallen vegetation. Thus, there is a significant predilection in King Cobra females for sites with higher levels of dead vegetation and leaf litter (a range of 10–17 cm) for nest building (Table 5). Leaf litter and other dead vegetation form the perfect substrate for the nest chamber (Dattatri 1987). King Cobra females start building nests in late April and may continue until the first week of May at the study site (G. Shankar, pers. obs). Since these areas receive very high rainfall, it is an important priority for the females to select sites with enough substrate to keep the nest chamber dry. However, certain disturbance factors such as proximity of village, human and livestock presence (Kannan 1993) have not been accounted for while testing habitat preference of these nest sites. Female King Cobras occurring in the north Indian state of Uttarakhand have been observed to begin nest construction in June and remain at the nest site longer compared to the females in the Western Ghats. Nests observed in the state of Mizoram have been found to be different in size and shape (bottle shaped) but interestingly nest-building starts by late April and May, similar to populations occurring in the Western Ghats (G. Shankar, pers. obs).

Fortunately, despite the proximity of the snakes to human dominated areas, there is evidence of high tolerance by the local people towards King Cobras and they refrain from killing them. This stems from the religious belief that people have towards the King Cobra, which is worshipped in Agumbe. This is evident through presence of snake idols across the landscape. Such tolerant attitudes can be important catalysts in aiding the conservation of this fascinating apex level predator. Since the Western Ghats is a unique landscape, it would also be interesting to know how King Cobras live in other areas of their distribution and how the ecology varies geographically. It would be useful to study King Cobra populations occurring in other habitats such as littoral forests and broad-leaved forests (Bashir *et al.* 2010). This would enable us to understand the adaptability of this species to gradual events such as climate change as well as the rapid deterioration of their habitats.

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A preliminary study on translocation of "rescued" King Cobras (*Ophiophagus hannah*)

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ABSTRACT.– **Translocation of "nuisance" snakes is a common practice in India. We investigated effects of translocation on movement patterns and home range characteristics of King Cobras (*Ophiophagus hannah* Cantor, 1836) living in the rainforests of the Western Ghats, Karnataka, India. We radiotracked one translocated snake and two non-translocated snakes. The translocated snake exhibited significantly greater movement frequency, distance moved per day, and total distance moved, and its home range was significantly larger than non-translocated snakes. We present our findings on the potentially deleterious effects of long-distance translocation on King Cobras, and we provide information on the scale of the snake translocation problem in India based on information obtained from snake "rescuers."**

KEYWORDS.– **King Cobra, *Ophiophagus hannah*, translocation, movement patterns, spatial ecology, snake rescue, radiotelemetry**

Introduction

Rapidly expanding human populations, and associated acceleration of habitat destruction and degradation, have led to a dramatic increase in human-wildlife conflicts worldwide (Conover 2002). These conflicts can be classified into four broad categories: 1) competition for space; 2) destruction of crops, gardens or landscaping; 3) depredation of livestock, and; 4) injury or death of humans (Smith 2007). Human-snake conflicts are especially important, because they may result in the deaths of both humans and snakes. In India, an estimated 800 000 snake bites cause as many as 50 000 human deaths and tens-of-thousands of amputations every year (Mohapatra *et al.* 2010). The widespread nature of human-snake conflicts in India is largely due to encroachment on snake habitats by humans, and persistence of snakes in human-dominated environments that provide suitable habitat for snakes (e.g., agricultural developments that attract rodent prey).

The last decade has seen a considerable increase in the number of "snake enthusiasts" or "sarpa-mitra" across India. These "activists" have been successful in safely removing thousands of snakes from houses, where they otherwise would have been killed. The number of "rescue" calls has undoubtedly risen steadily across the country, but reliable data documenting this increase are scant. One NGO in the Delhi region, Wildlife SOS, has received more than 300 rescue calls per month for reptiles, most of which were snakes (http://www.wildlifesos.com/rprotect/repthome.html). The Gujarat Society for Prevention of Cruelty to Animals has rescued up to 1000 snakes per year from the Vadodra region alone (Athreya 2006). Approximately 320 people, who were officially recognized by the Maharashtra State Forest Department, have rescued more than 2000 snakes per year from in and around Mumbai, and many more snake rescues remain undocumented (Nandvikar 2010). Interviews with snake rescu-

Table 1. Estimated number of snakes "rescued" and distances translocated based on interviews of four prominent snake rescuers at four sites in Karnataka, India.

Rescuer	Time Period	No. Snakes	Location	Distance Translocated (km)
Mohan	1997–2010	8000	Bangalore	20–50
Snake Shyam	1997–2010	23000	Mysore	15–60
Kiran	2005–2010	2500	Shimoga	20–30
Naresh	2006–2010	7000	Chikmaglur	15–20

ers in Karnataka have also produced startling figures (Table 1). Although largely anecdotal, we believe that the above estimates provide a fair indication of the scale and frequency of the snake-human conflict problem in India. The sheer magnitude of snake-human confrontations is undoubtedly due to human encroachment on relatively natural areas; however, the dramatic increase in well-intentioned people who "rescue" snakes may be a positive sign of increased awareness of snakes and their plight. After capture, it is normal practice in India to release rescued snakes into the nearest forested area away from human habitation, and release sites are often designated by local forestry department officials. However, there is usually very little thought given to the suitability of release sites or to the fate of translocated snakes. Therefore, translocation is primarily used as a "quick fix" to mitigate "nuisance" snakes, and other wildlife species (Athreya 2006); this is true not only in India, but throughout the world as well. The effect of translocation on snakes has been studied in other countries like Australia, the United States, and England (Germano & Bishop 2008), but not in India, where the number of translocated snakes is undoubtedly much higher than the above-mentioned countries. Many snake species are known to have fixed home ranges, and snakes inhabiting temperate areas are known to use the same hibernacula throughout their lives. However, translocated individuals tend to exhibit aberrant movement patterns, often exhibiting long-distance, fixed-angle movements, in an apparent effort to find their original home range. In some cases, individuals may fail to locate suitable hibernacula, cease reproductive activities and feeding, and even die (Reinert & Rupert 1999). We present a case study on the effects of translocation on King Cobras (*Ophiophagus hannah* Cantor, 1836) by comparing radiotelemetry data from one translocated and two non-translocated snakes in the Western Ghats of southern India.

Figure 1. Location of study site in the Agumbe region of the Western Ghats, Karnataka, India.

Material and Methods

The study area was located in the Malnad region of Karnataka in the vicinity of the Agumbe Rainforest Research Station (ARRS), from where our operations were based. The area was characterized by a large tract of wet evergreen upland forest situated on the edge of the Western Ghats plateau. The rainforest has become increasingly fragmented due to anthropogenic impacts, including rice (*Oryza* spp.) paddies, areca nut (*Areca catechu*) and *Acacia* spp. plantations, and towns and villages interspersed with small forest fragments and sacred groves. The region receives heavy rainfall (8000–10 000 mm annually) during the monsoon season (June–September), followed by an eight-month long dry season.

Table 2. Minimum convex polygon (MCP) and 95%, 50% active kernel (AK) home range estimates and total distance traveled (in 6 months) of one translocated (M1) and two non-translocated (M2, M4) King Cobras from the Agumbe region of the Western Ghats, Karnataka, India.

Snake ID	MCP (km²)	95% AK (km²)	50% AK (km²)	Total distance traveled (km)
M1	91.3	83.9	8.4	83
M2	14.8	15.3	2.2	45.5
M4	30.0	15.0	6.5	30.5

Tolerance of, and even reverence for, snakes, especially King Cobras, is an important aspect of local beliefs and culture. People seldom kill King Cobras, even if they are found in homes. Respect for King Cobras in the region has been crucial to the success of the project, because local inhabitants inform our research team immediately when a snake is encountered, which led to 143 rescues from 2005–2010 (G. Shankar *et al.*, unpubl. data).

We surgically implanted radio transmitters (model AI-2T, Holohil Ltd., Ontario, Canada) into the coelomic cavities of three King Cobras. We obtained all three snakes from houses or private property. We translocated one male snake (M1) approximately 40 km from his original capture site and released him in the vicinity of ARRS. We released two other male snakes (M2 and M4) at their original capture sites, also near ARRS. We tracked M1 from March–December 2008, M2 from July 2009 to July 2010 and M4 from December 2009–September 2011. Initially, we tracked each snake daily, following it around the clock, until we determined that they were primarily diurnal; subsequently, we tracked each snake throughout its entire diurnal activity period from dawn to dusk, which averaged 10.6 hrs/day. Although we observed snakes continuously when possible, we only recorded exact locations if the snake moved more than 100 m from its last recorded location. We always maintained a minimum distance of 10 m (usually much greater) from snakes to minimize disturbance. We also collected data on a suite of environmental variables, including temperature, humidity, and a variety of habitat parameters.

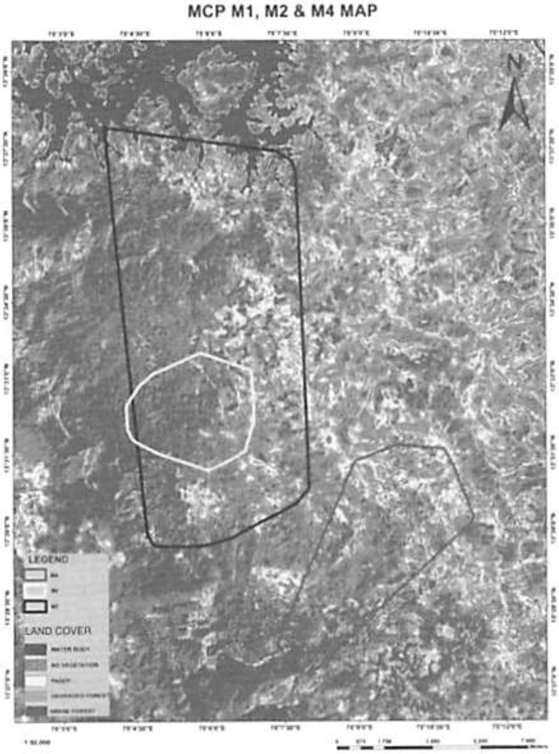
MCP M1, M2 & M4 MAP

Figure 2. Minimum convex polygon home ranges for one translocated (M1) and two non-translocated King Cobras (M2, M4) from the Agumbe region of the Western Ghats, Karnataka, India.

We analyzed home range and movement patterns using the Animal Movement Analysis extension (Hooge *et al.* 1999) for ArcView 3.2 (ESRI, Inc.). We carried out 5% outlier removal, an in-built function in the program that removes the most disparate points to increase the precision of the calculated home range before analyses. We compared total movement over a six-month period (month 2–month 7) and average daily movement distances among snakes. Total distance was calculated by summing the aerial distance between successive points recorded for each snake. Because data were not normally distributed, we used a non-parametric Mann-Whitney U test to examine differences

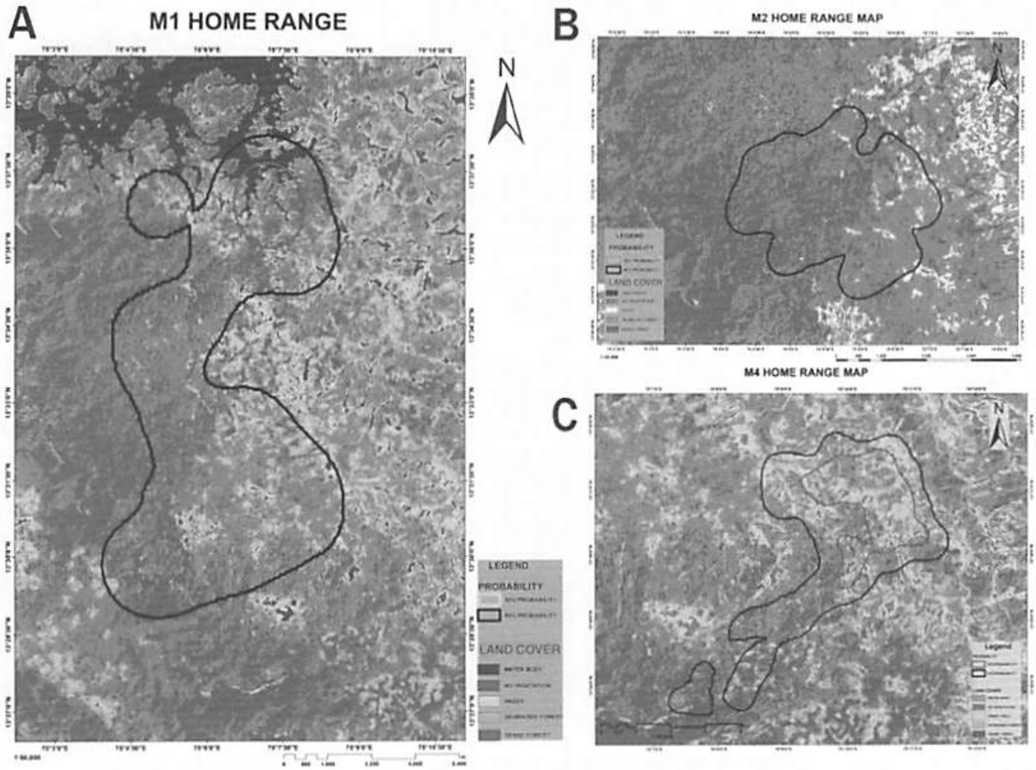

Figure 3. (A) Map depicting home range of translocated King Cobra, M1, red polygons enclose intensively used areas making up 50% of locations, from the Agumbe region of the Western Ghats, Karnataka, India. (B) Map depicting home range of nontranslocated King Cobra, M2, orange polygons enclose intensively used areas making up 50% of locations, from the Agumbe region of the Western Ghats in Karnataka, India. (C) Map depicting home range of nontranslocated King Cobra, M4, red polygon encloses intensively used areas making up 50% of locations, from the Agumbe region of the Western Ghats in Karnataka, India.

in average daily movement. We also compared 95% and 50% active kernel (AK) and minimum convex polygon (MCP) home range estimates to examine potential differences in space use between the translocated snake and the two non-translocated snakes.

Results

Total distance traveled varied greatly between M1, the translocated snake and the two non-translocated snakes, M2 and M4. Over the course of one six-month period, M1 moved a total of 83 km, compared to 45.5 km and 30.5 km for M2 and M4, respectively. A Mann-Whitney U test revealed that average daily movement of M1 (330 m ± 536 m, N = 205) was significantly greater than M2 (201 m ± 307 m, N = 364) (Z = 5.58, P = 0.001) and M4 (194 m ± 144 m, N = 427) (Z = 7.07, P = 0.001). The average daily movement distances between M2 and M4 were not statistically significant (Z = 1.11, P = 0.26).

Home range analyses revealed striking differences in home range size and use between M1 and the two non-translocated snakes. The MCP of M1, the translocated snake, was approximately three times larger than the MCPs of the two non-translocated snakes (Fig. 2). The 95% AK home range of M1 was more than five times greater than that of the other two snakes (Table 2, Fig. 3A–C). Although the 50% AK core use area of M1 was greater than the two translocated snakes, the differences were not as great as the 95% AK (Table 2, Fig. 3A–C).

Discussion

Analyses of King Cobra movement patterns revealed important individual differences in habitat use between translocated and non-translocated snakes. M2 utilized primarily forested and forest-fringe habitat (Fig. 3B), moving greater total distance than M4, whose home range was comprised largely by human-dominated landscape with very little forest cover (Fig. 3C). However, M2's core home range (50% AK) was only about one third that of M4, even though estimated home ranges of the two snakes were almost identical. Habitat type may have affected prey consumed, which in turn, may have affected movement distances. For example, M2 often fed almost exclusively on small Malabar pit vipers (*Trimeresurus malabaricus*; Bhaisare *et al.* 2010), which are encountered more often in dense forests, while M4 fed primarily on much larger spectacled cobras (*Naja naja*) and Indian rat snakes (*Ptyas mucosa*), which are found more often in edge habitats and associated with human disturbance. Perhaps M2 moved farther to obtain the greater number of smaller snakes needed to meet its energy requirements.

We also found a striking difference in use of shelter sites between the translocated snake and the two snakes that were not translocated. For example, M4 reused six burrows 17 times, and M2 reused 8 burrows 19 times, with up to 11 months between visits of the same burrow. We never observed M1 reusing burrows. Clearly, the two snakes that were not translocated had established home ranges, and were able to home back to particular sites that apparently provided them with a secure, thermally suitable site, often during vulnerable periods, such as ecdysis. Detailed knowledge of home ranges and homing behavior, likely mediated by chemosensory reception has been documented in other snake species (e.g., Reinert & Rupert 1999; Goode *et al.* 2008).

Despite small sample sizes, our results are congruent with other studies on snake translocation. Significant increases in home range size, and average daily and total distance travelled are widespread effects seen in the relatively small number of species that have been studied (Nowak *et al.* 1999; Butler *et al.* 2005). The translocated King Cobra (M1) also showed other anomalous behavior typical of translocated snakes such as ceasing reproductive activities and even feeding. Because King Cobras are often apex predators in the ecosystems within which they occur, it is possible that translocation may not only affect individual snakes, but may also have unknown trophic cascade effects (Estes *et al.* 2011). Although the focus of our study was the King Cobra, we speculate that the magnitude of the translocation problem may be greater in species commonly found near human habitation, such as the rat snake (*P. mucosa*) and spectacled cobra (*N. naja*), both of which are regularly rescued and translocated, often large distances. Although snakes that are translocated short distances (i.e., within their established home ranges) appear to fare better than when moved long distances (e.g., Reinert & Rupert 1999), this does not necessarily solve the problem, because individuals often remain in the area of conflict (Brown *et al.* 2009). Considering the magnitude of snake translocation in India, there is an urgent need to educate "snake rescuers," not only about the likelihood of direct negative impacts on individuals, but also the potential for population-level effects.

Animal translocation has been a tool used for management of "nuisance" or "problem" animals for decades, often in the absence of any scientific evidence to support its use. However, there is a growing volume of scientific literature documenting the complexity of translocation, including studies on a large diversity of taxa (e.g., mammals, Linnel *et al.* 1997; birds, Richardson *et al.* 2006; tortoises, Field *et al.* 2007). The complexity of translocation is compounded by the fact that "success" or "failure" may be difficult to define (Wolf *et al.* 1998). The importance of combining information on survival and reproduction with behavior and physiology of translocated animals in comparison to animals that have not been translocated is gradually being realized (Wollman *et al.* 2009).

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Cannibalism in wild and captive King Cobras *Ophiophagus hannah* (Cantor, 1836)

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ABSTRACT.– In a review of cannibalism in snakes, 101 species were reported to eat their own kind, some on a regular basis; such as King Cobras (*Ophiophagus hannah*) Cantor, 1836 and American kingsnakes (*Lampropeltis* sp.). Reports (mostly anecdotal) from zoos and collections around the world, point to the fact that King Cobras in particular commonly feed on their own kind. Here we report five instances of cannibalism in King Cobras in south India, of which two instances were recorded for captive snakes and three were observed in wild. We briefly discuss possible reasons for this apparently 'ordinary' behaviour in this species.

KEYWORDS.– King Cobra, *Ophiophagus hannah*, cannibalism, breeding

Introduction

Several snake species are largely ophiophagic, such as the King Cobra (*Ophiophagus hannah*) from South and Southeast Asia and the Mussurana (*Clelia clelia*) from Central and South America (Gasc 1994). King Cobras feed mainly on snakes, both non-venomous and venomous species, and they are not averse to devouring monitor lizards (*Varanus* spp.). They have also been reported to feed on their own kind (Smith 1943). In most reptile species, cannibalism can be an aberrant behaviour or may occur opportunistically as a by-product of normal predatory behaviour (Fox 1975; Polis 1981; Polis & Myers 1985; Mitchell 1986). Lourdais *et al.* (2005) reported adaptive maternal cannibalism in Rainbow Boas (*Epicrates cenchria maurus*) indicating that cannibalism may be common and important in the ecology of some species. Captive individuals of several species are known to eat their cage mates (Mitchell 1986; R. Whitaker, pers. obs.). Acharyjo *et al.*(1983) mentioned agonistic behaviour between two female King Cobras housed together in the same enclosure. Here we review five observations of cannibalism in King Cobras in southern India both in captivity as well as in the wild, confirming that this is common behaviour for the species.

Methods

Captive breeding studies.– During the course of a captive breeding project undertaken at the Madras Snake Park in 1985 and Madras Crocodile Bank in 1996, several pairs of King Cobras were obtained on breeding loan from other zoos and imported from zoos in Malaysia and Thailand. Adult male and female King Cobras were at first housed separately and then cautiously introduced to each other at the start of the breeding season, generally around March each year. If the pairs seemed compatible with no agonistic behaviour toward each other, they were allowed to stay together in the same enclosure, except during nesting time when the females were isolated in nesting chambers with the requisite leaf litter and controlled temperature and humidity.

Telemetric studies.– After implanting the radio transmitters and releasing King Cobras in the wild, the snakes were not disturbed nor interfered with. This study was conducted in Agumbe, located in Central Western Ghats, Karnataka, South India. This was done to record their natural behaviour, about which virtually little is known.

Rescue operations.– A rescue operation, where a snake was removed and relocated, was carried out if a King Cobra was reported close to human habitation and if it was a cause of concern to people. Between 2005 and 2008 more than 100 King Cobras were rescued within a radius of 30 km from Agumbe Reserve Forest, Shivamogga district, Karnataka.

Results

At Madras Snake Park, a pair of King Cobras received in 1972 from a zoo in Thailand were introduced to each other in a spacious circular enclosure (8 m diameter) constructed especially for the purpose. They initially showed no signs of aggression toward each other, however, after about 15 days, the female (length about 250 cm) was found dead and from the appearance of the carcass we could infer that she had been killed, swallowed, and then regurgitated by the male (length about 350 cm). Both snakes had been feeding normally on rat snakes (*Ptyas mucosa*) up to that point, which rules out starvation as a motive (R. Whitaker, pers. obs.).

At the Madras Crocodile Bank, juvenile King Cobras produced during the breeding programme of 1996 were housed together and reared for several years (Whitaker *et al.* 2005). When they reached a length of 200 cm, they were housed separately. One pair of captive bred King Cobras from different parents was kept with the goal of breeding them. In 2005, the pair was put together in March, the normal breeding season, and a 24 h watch was kept to make sure they were compatible. Because they did not display any aggression toward each other, they were left undisturbed in the hope that they would breed. After ten days, upon routine cage checking we found that the male King Cobra (280 cm) had killed and half swallowed the female (225 cm). Perhaps due to disturbance by the keeper, the male regurgitated the female and did not touch her again.

During the course of a routine King Cobra rescue, the first author was called to a cattle shed in Shedgar Reserve forest (13.64'007 N, 075.35'391 E), where it had been reported that two large King Cobras were seen fighting and that the larger individual had bitten the smaller individual. Apart from that, the larger snake had bitten a 1 ½ year old buffalo calf present in the shed which died in 20 to 25 minutes. As male combat in snakes usually means 'wrestling' and not biting, this was probably not a case of classic male combat. Upon arrival at the shed, we observed a single large male King Cobra with about 60 cm of the tail of another large King Cobra sticking out of its mouth. There had apparently been a considerable fight between the two large snakes, one succumbing to the venom of the other and then being completely consumed in 2 h 15 min. The larger individual weighed 11.9 kg (almost half of which was the consumed snake) and measured approximately 4 metres total length (Fig. 1).

In March 2008, at Agumbe Reserve Forest (13°50.87 N, 75°09.59 E) one female King Cobra (292.5 cm) was implanted with a radio transmitter and followed for 46 days (11 March 2008 to 27 April 2008), yielding valuable first time data on the movements of a wild adult female King Cobra. During the last two weeks of tracking this snake, it was seen with an adult male on several occasions and we inferred that the two had mated and we waited expectantly for nesting behaviour to begin. On 27th April, a foul smell emanated from the bushes where the two snakes had been staying and closer examination revealed the dead female. The head and neck portion showed signs of deterioration and it was evident that the male had killed the female, swallowed her and after some time regurgitated the carcass.

Within a few weeks of this incident in 2008, another female King Cobra was observed along with a male and the pair was watched for 30 days at Chokodbailu (13.61410° N, 75.18862° E). The male was seen leaving the vicinity and returning on a regular basis. Researchers were able to observe the female as she was resting/settled in a burrow close to a house in a patch of forest. However, another male King Cobra came to where this pair was resting and engaged in ritual combat with the resident male. Although it is difficult to be sure, the resident male was apparently chased away by the 'intruding' male, who then turned his attention to the female. The researchers observed (and documented on video) the male initially court the female and then suddenly bite her on the neck. The male killed

Figure 1. Adult King Cobra after swallowing another adult male, with body diameter nearly doubled.

and partially swallowed the female, only to regurgitate it after 50 min (Figs. 2–4).

Figure 2. Female King Cobra in the jaws of a male conspecific.

Discussion

Cannibalism has been reported in over 100 species of snakes worldwide (Polis 1981; Polis *et al.* 1985; Mitchell 1986). It is a common phenomenon in King Cobras, initially reported in captive snakes, but now conclusively shown to be part of the species normal behaviour in the wild. Intraspecific predation is observed in several species for reasons like hunger, environmental stress, nutritional requirements, and high conspecific density (Fox 1975; Kaplan & Sherman 1980; Polis 1981, 1985). Oliver (1957) reported that, one of his curators was trying to feed 35 young King Cobra babies with dead snakes which they refused; however, they did feed on their cage mates.

Our personal interaction with zoo and serpentarium keepers who rear King Cobras have reported that bigger individuals sometime feed on smaller ones, hence they are kept separately and housed together only during the mating season (February to April). Several such reports of King Cobras feeding on their own kind in captivity exists but, until our study, not in the wild. It was surmised that unless a wild male King Cobra is unable to find its normal prey species of snakes, cannibalism may be a usual behaviour. Another case in Burma (Evans 1902) mentions that a King Cobra measuring 3.45 m in length and 7 ¼" girth was carrying another King Cobra in its mouth, which measured 2.6 m in length and 5 1/8" girth. It apparently meant to make a meal of the smaller one. The complete feeding sequence was not recorded because the author and his assistants killed both the snakes (Evans 1902).

King Cobras are large predators that feed almost solely on other snakes and are solitary

Figure 3. Male King Cobra swallowing female.

Figure 4. Male King cobra regurgitating female.

throughout most of the year (authors' pers. obs.). Here we documented five cases of cannibalism in the species: a male eating a male in one case and males eating females in four cases. One possible explanation for males eating females is that the breeding season was just ending (the females were already gravid) and the hormonal state in the males, which inhibit them from feeding during the mating season — the one time when king cobras actually cohabitate, would have reverted to the non-breeding condition). This suggests that the males were ready to eat and they judged the females to be acceptable prey. It seems likely that as the field study progresses, we will find cannibalism will be recorded more commonly in wild King Cobras than hitherto reported or expected.

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Factors influencing human hostility to King Cobras (*Ophiophagus hannah*) in the Western Ghats of India.

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ABSTRACT.- **This paper investigates people's perceptions toward King Cobras in the tropical rainforests of the Western Ghats ecoregion of southern India. We built logistic regression models to test if people's perceptions (to kill/not to kill the snake) were influenced by factors such as the snake's size and defensiveness, whether the snake was found near human habitation, the time of encounter and season. The model correctly classified over 80% of instances when people expressed an inclination to kill the snake. Results support our expectation that the snake's defensiveness escalates the probability that the snake will be killed, but are contrary in that smaller snakes are more likely to be killed than larger ones, especially when encountered away from human habitation. Findings suggest a need for slight refocusing of King Cobra conservation outreach efforts towards smaller snakes, especially in regions where sizeable human habitations exist near fragmented King Cobra habitat.**

KEYWORDS.- **Agumbe, ARRS, King Cobra, logistic regression, mortality risk.**

Introduction

There is consensus that a variety of direct and indirect anthropogenic stressors may be linked to biodiversity loss worldwide (Ehrlich 1994; Pimm *et al.* 1995). Although direct persecution and habitat destruction contributes more to extinction risks in the majority of the species (Dodd 1987; Caughley & Sinclair 1994; Bonnet *et al.* 1999), intentional but non-exploitative killing of wildlife (i.e., retaliatory killing) could be an important but overlooked stressor (Mishra 1997; Kissui 2008; Liu *et al.* 2011). It is clear that formulating conservation strategies for species that are perceived as dangerous to humans can be difficult given the need to balance human and wildlife welfare. This is especially true for snakes, against which humans harbor deep-seated prejudices (Ohman & Mineka 2003; Prokop *et al.* 2009; Fita *et al.* 2010; Prokop & Fancovicova 2010).

From a biological standpoint, studies have identified combinations of behavioral and life-history traits and seasonal factors that affect mortality patterns in snakes. Reed & Shine (2002) found extinction risk in Australian elapid snakes to be related to foraging habit and combat behavior wherein ambush predators and snakes that do not engage in male-male combat were at a higher risk of extinction. Bonnet *et al.* (1999) found that snakes that dispersed over long distances were more at risk than their more sedentary conspecifics, and were more likely to be killed during the mating season. Although a number of studies have investigated patterns of

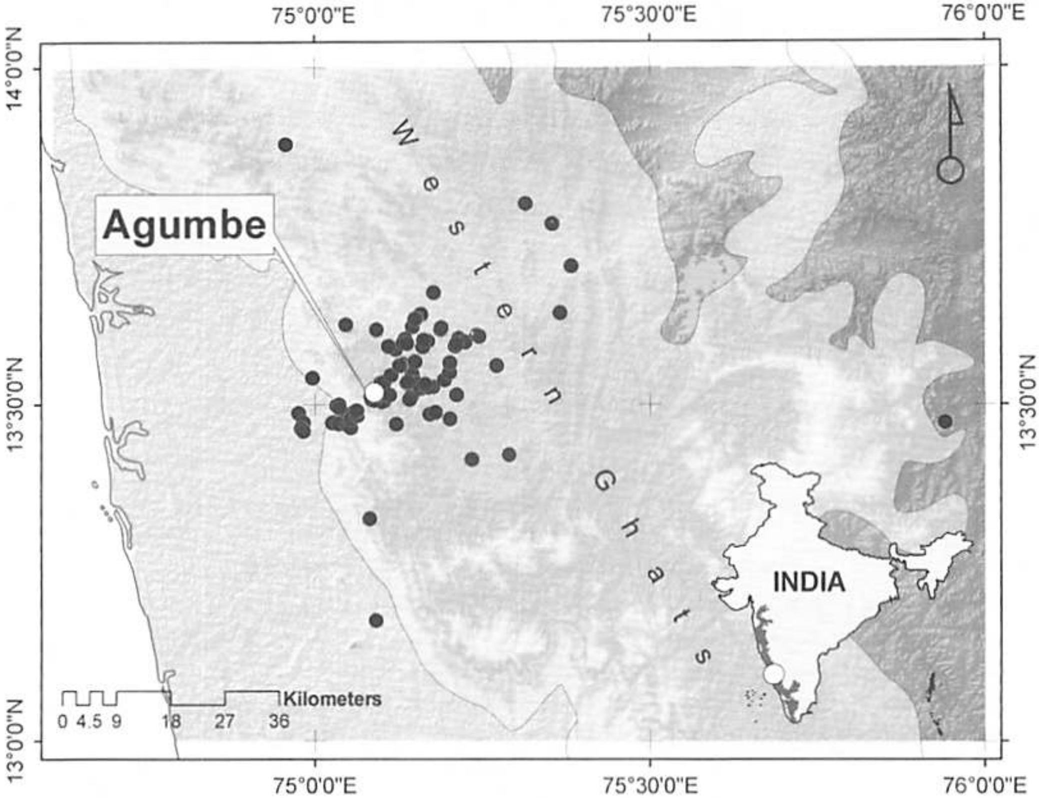

Figure 1. Location of Agumbe (○) in the Western Ghats of South India overlaid on a terrain-shaded map. Locations where encounters were reported from are shown as filled circles (●).

human-caused mortality in snakes (Bonnet *et al.* 1999; Lode 2000; Whitaker & Shine 2000; Akani *et al.* 2002; Ciesiolkiewicz *et al.* 2006), most have focused on factors influencing indirect or accidental mortality, such as via vehicular accidents. For example, Row *et al.* (2007) estimated road mortality to cause an increase in extinction probability from 7.3% to 99% over 500 years for black rattlesnakes in Ontario, Canada. Whereas estimates for intentional anthropogenic mortality are generally rare (Bonnet *et al.* 1999), Akani *et al.* (2002) could attribute ca. 50% of cases of snake mortality to intentional killing by humans in the Niger Delta. Akani *et al.* (2002) also found a significant seasonal pattern to snake encounters in human habitat wherein most events were related with rainfall events that forced snakes from their natural refuge to places inhabited by humans.

From the human standpoint, negative perceptions of snakes are believed to have evolutionary roots (Ohman & Mineka 2003) and have been observed as behavioral manifestations across countries and cultures (Prokop *et al.* 2009; Fita *et al.* 2010). As a result, conservation programs focused on snakes have to deal with two distinct issues: 1) patterns of snake behavior that put snakes in direct contact with humans and, 2) overcoming inherent human responses to encounters with snakes that make outreach and sensitization difficult. Sensitization is especially difficult when the species involved are venomous and easily identified as such. The issue is further compounded in developing countries where large human populations exist in close proximity to wildlife habitat and where the largest number of cases of envenomation occur (Harrison *et al.* 2009). Factors that affect the ability of snakes and humans to cohabitate are therefore important both from snake conservation and human welfare standpoints. This is especially important for a mega diverse country like India that reports a disproportionate number of snake envenomation cases globally (mortality estimates ranging widely from about 1300 to 50 000; Mohapatra *et al.* 2011)

The focus of this study, the King Cobra (*Ophiophagus hannah*, Cantor 1836) is the largest venomous snake in the world (Tin-Myint *et al.* 1991; Das 1996; Whitaker & Captain 2004; Inger *et al.* 2009). Largely diurnal, the snake can reach up to 5.5 m in length, feeds mainly on snakes, is oviparous, and is the only snake that builds a nest (Aagaard 1924; Smith 1943; Whitaker 1978; Daniel 2002; Whitaker & Captain 2004). Classified 'Vulnerable' by the IUCN (Inger *et al.* 2009), King Cobras are mostly found in and around the tropical rainforests of India, southern China and southeast Asia. They also inhabit a variety of microhabitats such as mangrove swamps, agricultural fields, and have been reported from degraded semi-evergreen and deciduous forest fragments in India. Although data on population trends of King Cobras in India are insufficient, it is thought that continuing habitat destruction and degradation may be negatively influencing their numbers (Inger *et al.* 2009).

Although many communities in India consider snakes (especially cobras, *Naja* spp.) sacred due to religious beliefs (Joshi & Joshi 2010), King Cobras are often killed when they come in contact with humans. Although the exact reasons are unknown, King Cobras in the region likely enter human habitations to seek other snakes (their major prey), which in turn, are probably attracted to a higher relative density of rodents around agricultural fields and household granaries. Human reactions to King Cobra encounters in India and elsewhere may be a complex combination of societal and situational factors. Such factors could include the behavior of the snake (i.e., level of defensiveness), the location where the snake is encountered (e.g., inside sleeping quarters of a dwelling), seasonal factors (such as during monsoons when burrows used as refuge by snakes are flooded, and during the mating season) or socio-cultural factors (religious beliefs, levels of formal education, prior exposure to sensitization).

This study investigates factors influencing people's perceptions (intention to kill, or leave a snake alone) in events of encounters with King Cobras in and around villages situated in tropical rainforests in southern India. We hypothesize that 1) people would be more hostile to highly defensive snakes, as a highly defensive snake may pose a greater immediate danger to people in the vicinity; 2) people would be more hostile to larger and healthier snakes, as a large (and healthy) snake could be perceived as more dangerous with respect to quickness, strength and perceived venom delivery than a smaller (or sicker) one; 3) people would be more inclined to kill a snake when encountered inside or near human habitation because of the perceived direct danger posed to humans and 4) people would be more inclined to kill a snake when encountered in the dark, as darkness could be perceived to confer an elevated opportunity to the snake to either escape or evade detection. Although societal and/or educational factors may strongly influence people's perceptions, we do not currently have data on socio-economic or cultural factors.

We believe that information on what shapes people's reactions to King Cobra encounters could be invaluable from both public welfare and management standpoints. Such information could aid King Cobra conservation by improving management of snake-human encounters, as well as for retooling conservation, education and first-response strategies. To the extent of our knowledge, this is the first study of its kind in the Indian subcontinent.

Material and Methods

Study area.– Agumbe is situated in a reserve forest in the Western Ghats Ecoregion of India (13°30'15" E, 75°5'25" N, Fig.1). The region harbors high levels of biodiversity, much of which is endemic. Not only is the Western Ghats ecoregion a global biodiversity hotspot (Mittermeier *et al.* 1998; Myers *et al.* 2000; Myers 2003) it was also recently designated a UNESCO World Heritage Site (UNESCO 2012). The physiography consists of forested hills, tropical evergreen rainforest (Champion & Seth 1968; Ramaswamy *et al.* 2001) and floodplains characterized by a mosaic of agriculture (paddy) and plantations (areca, coconut, plantain, acacia). The region is one of the wettest regions in southern India and receives an annual rainfall of ca. 8000 mm during the southwest monsoon (June–September). Terrain elevation ranges from 150 m to 800 m.

Data collection.– A research program initiated by the Agumbe Rainforest Research Station (hereafter ARRS) has been monitoring human-

Table 1. Number of total King Cobra rescue calls (2005–2009) received at ARRS, cross-tabulated by location where snake was encountered. Rescue calls in the breeding season are shown in bold typeface.

Month	Field	House	Forest	Plantation	Settlement	Total
Jan	**4**	**7**				**11**
Feb	**3**	**6**		**1**		**10**
Mar	**12**	**9**	**3**	**3**	**2**	**29**
Apr		3	2		1	6
May	1	6	1	1		9
Jun	1	3			1	5
Jul	1	5				6
Aug	2	1	4	1		8
Sep	1	4	1	2		8
Oct	2		1	1	1	5
Nov	3	3				6
Dec		1			2	3
Total	30	48	12	9	7	106

King Cobra encounters since 2005. Data for this study were collected over a five-year period from 2005–2009. The ARRS conducts long-term ecological research into the biology of the King Cobra as well as provides educational and outreach programs to village communities in the region. The outreach program at ARRS has ensured that most, if not all, King Cobra-human encounters are immediately reported and responded to. For each 'rescue' call received at the ARRS, a team comprised of a trained snake catcher and community outreach specialists were immediately dispatched. On arrival, the team evacuated all people from the immediate location and outreach specialists conducted a semi-structured interview of the first responders and the owners of the property. Outreach specialists also delivered a comprehensive "snake-talk" to people present at the location. In the meantime, the snake rescue specialist safely captured the snake using hooked sticks and cloth bags (Fig. 2, following the protocol by Whitaker 1970). The rescue specialist took length and weight measurements to the nearest centimeter and gram respectively, determined its gender, deposited it in custom-made bags, and prepared it to be safely released in a forested region at least a kilometer away from the capture locality. A brief health assessment of the snake was also carried out. We termed the health 'good' when the snake had a more or less circular body cross section and the vertebral column not visible through the skin, 'moderate' when the snake had a more or less round body with slightly evident vertebral column and 'poor' when the snake had a tented body with the vertebral column and rib bones easily visible. For each such call, details of the physical environment and the (pre-capture) opinion of the responders towards either killing or not killing the snake were also recorded.

The behavior of the snake was assessed by taking into consideration the objective opinion of the first responders, and by observations made by the team before the rescue commenced. The behavior was judged 'very defensive' when the snake reared up hooded, hissed and charged when first approached; 'defensive' when the snake reared up hooded, hissed and charged once disturbed during capture; 'moderate' when the snake showed moderate resistance to handling and 'docile' when the snake did not exhibit any signs of vigorous resistance during the course of rescue.

Statistical analysis.– As the response of responders (intention to kill/ not kill) was best modeled as a binary (1/0) choice, we built logistic regression models to model the response as a function of the variables: snake defensiveness (categorical: five levels: very defensive to very

Figure 2. An adult King Cobra being rescued from a well near Agumbe. Photo P. Gowri Shankar.

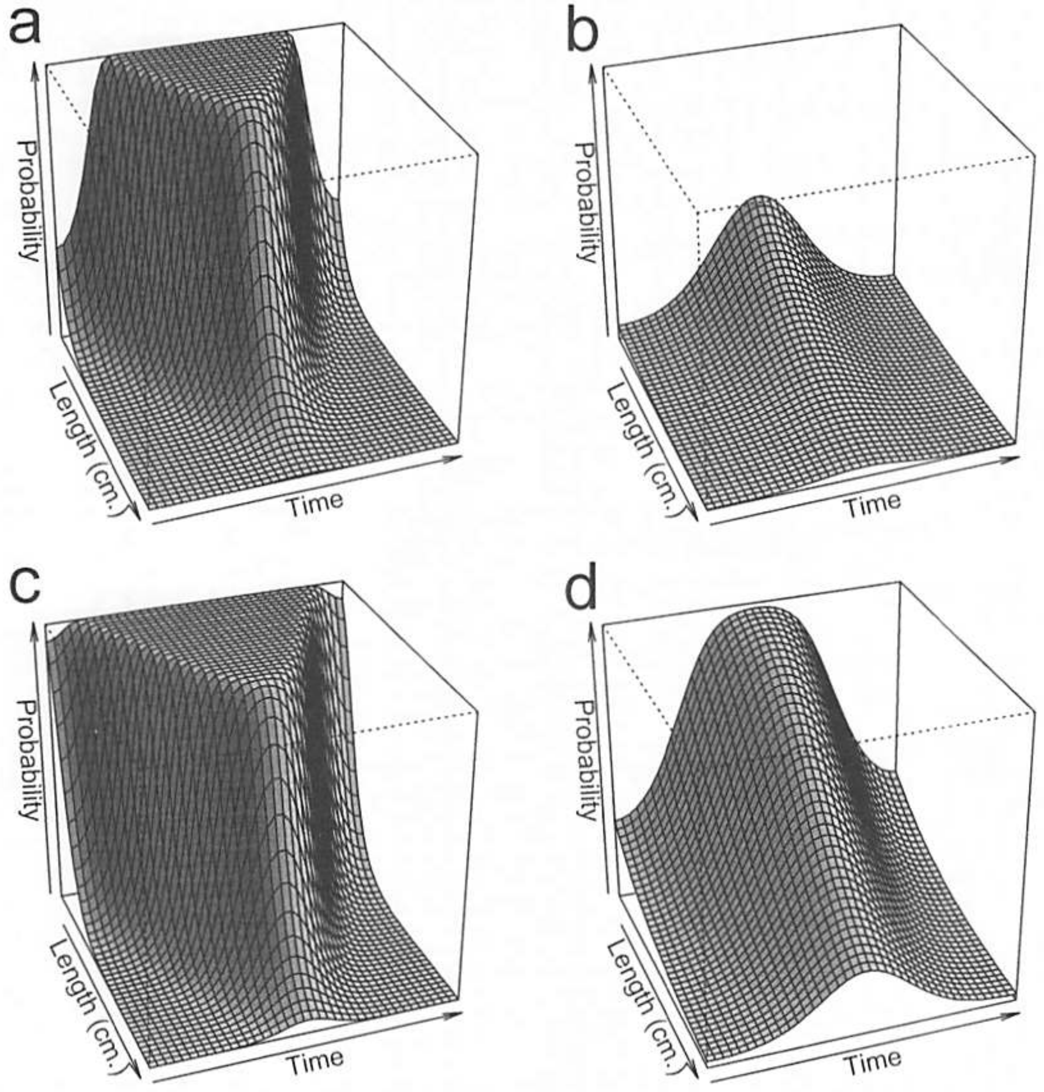

Figure 3. Surface plots showing the probability that a snake would be killed (on the z-axis) as a function of snake length (y-axis: min = 55cm, max = 400cm.) and time-of-day (x-axis; extremes denote midnight, axis midpoint denotes midday). Note: the z-axis is scaled from 0 to 1 in all subplots, probabilities are symmetric about the midpoint of the time (x) axis. Subplots grouped by combinations of whether a snake was defensive (subplot a, c) or docile (subplot b, d); if it was found in human habitation (subplot a, b) or in an open area (subplot c, d).

docile), health (categorical: three levels; bad, moderate, good), month (categorical), snake size (length in cm.), location (binary, near or inside house, well, shed or granary = 1, 0 elsewhere) and time of encounter (sine-transformed to scale midday to 1.0 and midnight to -1.0). We did not use the snake's mass as a proxy for size because 1) mass is highly correlated with length and 2) people would most likely find it easier to estimate length as opposed to mass as a proxy for size. Being a perception study, the gender of the snake was excluded as a predictor as none of the interviewees could give consistent guesses on the gender of the snake, and it likely did not influence their eventual perception. We sequentially tested all main and all possible two-way interaction effects between all variables for significance. We sequentially dropped all non-significant effects until only significant interaction effects and associated main effects remained. Preliminary analyses revealed that defensiveness was better modeled as a binary variable

Table 2. Results from a logistic regression model investigating factors affecting people's opinions (kill = 1, not kill = 0) on encounters with King Cobras in the Western Ghats of India ($n = 106$, Wald $\chi^2 = 19.28$, df = 6, $P < 0.0037$). The model used a complementary log-log link function. The model correctly classified 83.8% of all cases where people wanted to kill Cobras (AUC = 0.839).

Parameter	df	β	S.E.	P
Intercept	1	0.607	1.670	0.7160
Defensive	1	6.129	2.056	0.0029
Length (cm)	1	-0.008	0.005	0.1672
Length*defensive	1	-0.026	0.007	0.0004
Habitation	1	-1.890	0.535	0.0004
Time	1	1.227	0.983	0.2122
Time*defensive	1	2.613	1.006	0.0094

and was thus recoded as such (very defensive or defensive = 1, moderate or docile = 0). Because the snake's defensiveness could be a major factor determining public perception, we separately modeled the snake's defensiveness as a function of size, month (or March = 1 as a binary variable denoting the end of breeding season), time of day and location. Finally, we used Moran's I (Moran 1950) to test for spatial autocorrelation in standardized residuals from the final model. All statistical analysis was conducted using SAS software, Version 9.2 (SAS System for Windows © 2002–2008, SAS Institute, Inc. Cary, North Carolina, USA).

Results

A total of 107 rescue calls were attended to between 2005 and 2009 (mean: 21 ± 7SD Year^{-1}). The maximum number of rescues were conducted in 2006 (N = 29) and 2009 (N = 28). Reporting patterns did not follow any predictable trend across years ($P > 0.1$). Across months however, rescue calls increased significantly in post-winter months (Jan–March mean: 16.66 ± 10.69 SD) in comparison to the rest of the year (Apr-Dec: mean: 6.33 ± 1.87 SD, $P < 0.001$). Rescue calls peaked in March, when there were approximately seven times as many rescues as the annual average (mean excluding March: 7.09 ± 2.3 SD). It should be noted that the breeding season for King Cobras starts around January, peaks in March, and culminates with hatching of the young near late July or early August. As expected, the majority of snakes were reported from around human habitation (88.68% in any human use area, 45.28% of total inside houses, Table 1). Although no trend was apparent for non-breeding months, a large majority of the calls during the early breeding season (Jan–Feb) involved snakes encountered in houses (>60%) and in agricultural fields or plantations in March (~40%). Around 80% of the snakes were found in good health, and on average measured 297.05 ± 6.38 cm in length (N = 107, range: 55.5–396.24 cm) and weighed 4464.54 ± 286.03 g (N = 63, range: 22–12 000 g). Responders expressed an inclination to kill the snake in only 14% of the cases.

We used a complementary log-log link function to fit the logistic regression model as response proportions were skewed (14% kill, 86% not kill). One observation did not have sufficient information on covariates and was dropped from all subsequent analyses. After removing all non-significant effects, the logistic regression model retained only four variables (Table 2), and correctly classified 83.8% of all instances where people wanted the snake killed. The main effect of the variable coding for human habitation was significant ($P = 0.002$) as were the interaction effects of length of snake and defensiveness ($P = 0.001$), and the time of day and defensiveness ($P = 0.02$). Tests for spatial autocorrelation in residuals were not significant (Moran's I, $P > 0.1$) indicating no significant spatial clustering in public perceptions and encounter reporting patterns. As independent examination of individual variables was difficult due to the presence of two interaction effects, we built 'kill-probability' response surfaces by segmenting the model by the categorical variables 'habitation' and 'de-

Table 3. Results from logistic regression investigating factors affecting King Cobra defensiveness (Wald $\chi^2 = 10.63$, df = 1, $P < 0.01$). The model correctly classified only 37.7% of all cases where King Cobras displayed defensive behavior (AUC = 0.656).

Parameter	df	β	S.E.	P
Intercept	1	-0.715	0.255	0.005
Breeding season	1	1.757	0.539	0.001

fensiveness' and by varying continuous predictors (length of snake and time of day) across the range of the respective measurements.

Results indicate that defensive snakes (Fig 3a, 3c) are at a disproportionately higher risk of being killed than their relatively docile counterparts (Fig 3b, 3d) regardless of whether they are encountered around habitation or in open areas. Also, smaller snakes are more likely to be killed than larger ones regardless of the snake's level of defensiveness or the location where the snake is encountered. Results also indicate that the probability a snake will be killed is generally higher during the day than in the night (Fig 3). A logistic regression model built to explain snake defensiveness retained only 'month = March' as a significant explanatory variable but explained only 37.7% of all cases where the snake was found defensive (Table 3).

Discussion

Our intent was to investigate factors that influence people's opinions on harming King Cobras when encountered in and around human habitation. A logistic regression model relating situational factors with people's opinions successfully predicted over 80% of all cases where people wanted the snake killed rather than left alone. In spite of the apparent good fit of the model, it should be noted that this study is limited to situations when rescue calls are actually made, it may well be that a larger number of snakes are killed (often of the genus *Naja*) and never reported back to the conservation team.

While our expectation that defensive snakes would attract more hostile reactions was supported by the data we collected, none of the other hypotheses were supported. Specifically, when controlling for the size of the snake and the location of encounter, the model confirmed that defensive snakes were far more likely to be killed than ones that were relatively docile. In contrast, for the second hypothesis (larger snakes would be more at risk) the model suggested the opposite. We found that smaller snakes were far more likely to be killed than larger ones across all levels of defensiveness and location of the encounter. While this finding is counterintuitive, we suspect that elevated hostility of people towards smaller King Cobras may be related to the higher apparent likelihood of successfully subduing an 'aggressive' but smaller-sized and identifiably dangerous snake. We speculate that it is likely traditional knowledge in the region that the young of the King Cobra hatch with enough venom to cause mortality in humans. Elevated defensiveness in younger King Cobras has been observed in the field, and has also been widely reported for a number of other species (for example, see Brodie & Russell 1999; Shine *et al.* 2002). Our expectation that people would be more hostile towards snakes found in and around habitation was also not supported by the data. We found that snakes encountered in the open were significantly more likely to be killed than left alone. This finding indicates a potentially elevated mortality risk for King Cobras around forest edges and fragments. Whereas the model showed a significant time-of-day effect, in that people would likely want to have the snake killed when encountered during daytime, we suspect this may be an artifact of the confounding effects of the diurnal nature of the King Cobra coinciding with general activity patterns of humans. In combination, discounting time-of-day as a confounding factor, the model suggests the possibility of the 'ease of subduing' hypothesis to be the leading factor shaping people's perceptions in typical King Cobra encounters. It is likely that smaller snakes are more likely to be killed when encountered in areas where they can be tracked and pursued easily, especially when they display elevated defensive behavior.

The only factor that was a significant predictor for snake defensiveness was the binary variable coding for the month of March. This may indicate a seasonal pattern to snake defensiveness related to breeding and nesting phenology of King Cobras. In general, defensiveness in snakes has been related to antipredator behavior (in this case, likely a response to humans, also see: Bonnet *et al.* 2005; Aubret *et al.* 2011), seasonal weather patterns (Schieffelin & Dequeiroz 1991; Brodie & Russell 1999; Mori & Burghardt 2004), reproductive status (Brodie & Russell 1999; Brown & Shine 2004) and body condition (Shine *et al.* 2000; Shine *et al.* 2002). Although we currently do not have data to test these theories specifically for the King Cobra, they are a subject of ongoing research at ARRS.

From a conservation standpoint, the finding that smaller snakes are more likely to be killed could lead to the possibility of a population bottleneck occurring, especially if increasing habitat degradation and fragmentation drives more snakes into human habitation. Increased intentional anthropogenic mortality may pose an additional stressor to King Cobra populations when compounded with persecution from domesticated mesopredators (such as dogs, pigs) around forest edges. Further, such direct anthropogenic stressors may aggravate reproductive losses King Cobras suffer from nest-raiding mesopredators such as monitor lizards (*Varanus* spp.) and mongooses (*Herpestes* spp.).

From a human welfare and conservation standpoint, the findings point to a need for a slight retuning of outreach focus. Although the current outreach program has focused on educating people on the ecological importance of snakes in general, the focus on protecting smaller snakes could probably be emphasized. There is also the possibility of implementing sensitization programs and classes to train affected people in the safe handling of smaller snakes for removal from houses. Overall, these findings could be utilized to design better conservation and outreach strategies in India; and perhaps in other regions with extant King Cobra populations.

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Nesting ecology of the King Cobra (*Ophiophagus hannah*) in India

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ABSTRACT.– Here we present the results of a nest survey of the King Cobra in the states of Karnataka, Mizoram, and Uttarakhand, with data collected between the 2004 and 2010 nesting seasons. We collected data on thermal and hydric conditions in addition to the impact of rainfall, clutch survival, hatchling size, and incubation periods. Of 15 nests located, eight had temperature profiles recorded. Thirteen of 15 nests had a female King Cobra present upon location. The majority of nests (13) recorded were from the Shivamogga district of Karnataka, with a single nest each from Mizoram and Uttarakhand. Clutch size averaged 25 ± 0.5 (7–43) eggs with an average of 23 ± 8.7 (6–38) eggs surviving to term. We used a previously published regression equation to relate clutch size to female size. We also report on the lowest nest temperatures known in this species, the Uttarakhand nest, which averaged 23.0°C. All nests were located between April and June, with eggs at various stages of development.

KEYWORDS.– King Cobra, *Ophiophagus hannah*, nesting ecology, nest temperatures

Introduction

The reproductive biology of the King Cobra, *Ophiophagus hannah*, apart from an in depth study by Leakey (1969) in Thailand, is little known. Other related subjects that have been reported on for this species include nest desertion by a female (Kannan 1993), captive breeding and husbandry (Burchfield 1977; Dattatri 1987), and sporadic reports on nests observed in the wild (Mustill 1936; Whitaker 1977). This is the only species within the Class Reptilia, apart from the Crocodylia, that actively constructs a nest (Evans 1902).

Material and Methods

King cobra nests were located 2004–2010 using information given by residents living in and around King Cobra nesting habitat. Local residents (areca nut plantation owners, shop-owners, local wildlife enthusiasts) were also encouraged to provide information on location of nests.

Temperature profiles of nests were recorded with automatic temperature loggers (Onset Instruments CORP, Pocasset, MA 02550, USA) that were pre-launched at 1h intervals, and placed within the nest chamber. Temperatures for other nests were recorded with manual mercury thermometers inserted in 2.5 cm diameter PVC tubes that were further pushed through a basket and carefully placed within the nest. During the period 2004–2010 nests were located between mid-April and the beginning of June — the onset of the south-west monsoon in Karnataka, but a relatively dry season in the North East, Mizoram, and North India at the foot-hills of the Himalayas, Uttarakhand. Each nest is presented on a case-by-case basis, due to the large variation in availability of temperature loggers, rain gauges and hygrometers, which limited the degree of information collected from each particular nest. The initial two years of nest data, 2004–2005, have detailed information on temperature/hydric conditions, whereas the remainder had nest chamber temperature recorded. Rainfall was measured with two 10 mm rain gauges in one nest, N1-2004, with one placed over the nest, and one in an open area adjacent to the nest. Nest width, length, and height were measured to the closest 3 cm, and flora associated with the nest and immediate surroundings were noted. Incubation period used here is measured from the date of location of the nest until hatching. We examined a total of 15 nests for predicted female total length (FTL), using an equation from Whitaker *et al.* (2005): FTL= 126.457 + 5.244 x CS (r^2 = 0.79; N = 23; SEE = 21.8), with a 95% confidence limit (Student's T-test, t = 2.080; df = 21).

Abbreviations used in the text are KA (Shivamogga district of Karnataka), TL (total length), SVL (Snout-vent length), in centimeters (cm) and wt (weight). Rainfall, where recorded, is given in millimeters (mm). Relative humidity (RH) is given as a percentage. Paired sample T-tests were used when identical numbers of observations were available for comparison, and ANOVA was used when two variables had different numbers of observations. Standard deviations are presented following the mean of temperature, humidity, and hatchling lengths and weights, followed by the range of values, and number of samples. All analyses were carried out using SPSS v.10 on a Windows Platform.

Results

2004, Nest One. Yedagaaru Hamlet, KA: The nest, comprised of dry leave litter, was found on 25 April 2004, at the base of a tree. Environmental variables at this nest were recorded from 15 May to8 August 2004, when the first eggs hatched. Temperature within the nest chamber (X = 24.3 ± 0.72°C) differed significantly from temperature at 5 cm above the forest floor (X = 22.6 ± 1.06°C, t = 30.80, df = 199, P > 0.0001) and 1 m above the forest floor (X = 22.7 ± 1.14°C, t = 30.39, df = 207, P > 0.001). Nest temperature was observed to peak between 12h30 and 17h30. RH was observed to differ significantly between the nest chamber (X = 94.56% ± 5) and outside of the nest (X = 93.57% ± 5.52, t = 4.823, df = 165, P > 0.0001). Rainfall over the nest (X = 5.01 mm) was lower than rainfall in an adjacent open area (X = 5.72 mm), although the two did not differ significantly. The female was observed on the date of discovery of this nest only, after which she was not seen.

Eggs in this nest hatched after an observed incubation period of approximately 105 days, resulting in 16 hatchlings from 17 eggs, a hatching success of 94%. The average TL was 47.8 ± 2.1 cm (range 43.2–50.1 cm), and wt averaged 21.6 ± 2.8 gms (range 17–26 gms).

2005, Nest One. Agsarskone Hamlet, KA: This nest was constructed on 22 April 2005, as the owner of the hamlet had not seen the nest the day before. Ambient temperature outside the nest was measured manually from 1 May to16 June, and temperature within the nest chamber was measured manually from 12 May to16 June. The logger measured temperature from 10 June to21 July, when the eggs hatched. Nest chamber temperature (X = 24.6 ± 1.4°C) differed significantly from ambient temperatures recorded near the nest (X=28.1 ± 2.6°C; ANOVA, F = 46338.73, df = 70, P < 0.0001). This nest exhibited the greatest difference between nest chamber and outside temperature. Both nest chamber and outside ambient temperatures peaked at 10h30. Nest construction was observed first hand up until 4 May, after which the female was not seen again. Eggs in this nest hatched on 21 June at 13h00, with 23 of 24 eggs hatching for a hatching success of 96%, after an observed incubation period of 90 days. The TL of the hatchlings averaged 56.1 ± 1 cm (range 54–58 cm), while wt averaged 24.4 ± 1.3 gms (range 21–26 gms).

2005, Nest Two. Kamar Kodige, KA: This nest was first observed on 14 May 2005. Disturbed forest and plantation surrounded the nest, and a stream flowed nearby. Nest chamber and nearby ambient temperatures were recorded 20 June–28 July. Temperature within the nest chamber averaged 23.48 ± 1.28°C, and was significantly different from outside ambient temperature, which averaged 24.77 ± 1.6°C (t = -7.98, df = 114, P < 0.0001). Temperatures within the nest chamber peaked at 17h30 and at 08h30 for outside ambient temperature. The female was observed until 4 June, a period of twenty-two days, and disappeared with the onset of the south-west monsoon in mid-June.

Hatching occurred on 28 July, all 39 eggs following an incubation period of 76 days. The TL of the hatchlings averaged 54.9 ± 1.2 cm (range

52–57 cm), and wt averaged 20.5 ± 2 gms (range 16–23 gms).

2005, Nest Three. Koradi Village, KA: The site was visited on 26 June 2005, and it was found through local informants that the nest was seen in the last week of March, and an *O. hannah* was seen until sometime in April after which she abandoned the nest. No temperatures were measured in this nest. A visit on 11 July revealed that the eggs had hatched. The nest chamber was dry with hatchlings within, although the presence of shed skins indicated that snakes may have hatched 3–4 days earlier. Clutch size was seven eggs, with one egg apparently infertile. The TL of the six hatchlings averaged 55.8 ± 1.2 cm (range 55–58 cm).

2006, Nest One. Souli, Kalmane, KA: This nest was first observed on 4 May 2006. A data logger was placed in the nest cavity on 10 May. Temperature averaged 27.0 ± 0.7°C (24.6–30.5°C). The female was observed on the nest for a period of three days in early May. Out of 28 eggs counted, 25 (89%) hatched on the 19 July after an observed incubation period of 77 days. Three eggs were rotten.

2006, Nest Two. Magundi, KA: This nest was first observed on the 13 May 2006. A logger was placed in the nest on 17 June, and remained in place until hatching on 29 July. Mean nest temperature was 26.6 ± 1.5°C (22.1–30.9°C). The female was observed on the nest 10 May–13 May. Clutch size was 25 eggs, of which 24 (96%) hatched on the 29 July, after an observed incubation period of 77 days.

2008, Nest One. Kerebailu, Hallibidargodu, KA: This nest was first observed on 21 May 2008. A data logger was inserted within the nest chamber on 24 May. Another logger measured ambient temperature (at 1 m above the nest) from 24 May–14 August, the date of hatching. Temperature within the nest averaged 24.1 ± 2.8°C (13.4–34°C), whereas temperature outside the nest averaged 25.4 ± 5.7°C (3.3–43.6°C). Out of 20 eggs, 13 (65%) hatched following an 85 day observed incubation period.

2008, Nest Two. Kokodu, near Nallur, KA: The nest was first observed on 24 May. The nest hatched on 13 August, with a total of 28 eggs hatching out of 29, for a 97% hatch success, and an incubation period of 81 days. The TL of the 27 hatchlings averaged 55.6 ± 2 cm (range 49.5–58.5 cm), SVL averaged 45.5 ± 1.6 cm (range 45.5–47.5 cm), and wt averaged 34.3 ± 2.6 gms (range 26–38 gms).

2009, Nest One. Thaluve, Thirthahalli, KA: Thanks to information from the Karnataka Forest Department, this nest was first visited on 26 April 2009. The nest was located in a small patch of forest on a slope, close to a path frequented by people and cattle. It was surrounded by acacia plantation, areca and paddy fields. A data logger was put in the nest from 28 May to 3 August. Nest chamber temperature averaged 27.1 ± 2.2°C (22.1–37.4°C). The female on this nest was observed from 26 April to11 May. The observed incubation period was 107 days. Clutch size in this nest was 34, of which 32 (94%) hatched on 9 August. Two eggs were found to be rotten upon opening the nest.

2009, Nest Two. Billgadde, Hulugaru, KA: First observed on 28 April 2009. The nest was located next to a path used regularly by people and surrounded by a disturbed community forest with dense forest ca. 100 m from the nest. The female was observed from 28 April to11 May on the nest, during which period active nest construction was observed. Clutch size was 30 eggs, of which 28 (93%) hatched on 18 August, after an observed incubation period of 113 days. A sample of hatchlings measured comprised eight females and ten males. The TL averaged 50.2 ± 2.7 cm (range 41.2–53.2 cm), SVL 41.5 ± 1.4 cm (range 37.5–44 cm), and wt averaged 25.1 ± 2.3 gms (range 19–28 gms), with no observed gender differences in morphology. Two eggs deemed rotten were found within the nest

2009, Nest Three. Thanikodu, Kudremukh, KA: The nest was observed by a plantation worker in the last week of May. It was found under a tree close to a pedestrian mud path, surrounded by banana, areca and acacia plantations. A perennial river with thick forest stands was ~150 m from the nest. No female was observed in the vicinity of the nest. Eggs in the nest hatched on 13 August, and the nest was excavated on 15 August to determine clutch size. Of 43 eggs, 38 (88%) hatched successfully, 3 were rotten and 2 hatchlings were fully formed but found dead within their eggs. The TL of 37 hatchlings averaged 51.57 ± 2.1 cm (range 45.4–56.5 cm), SVL averaged 42.2 ± 1.8 cm (range 37.2–46.5 cm), and wt averaged 22.8 ± 2.5 gms (range 13–26 gms).

2009, Nest Four. Mundagaru village, Matholli, Kudremukh, KA: This nest was located in thick forest, ~10 m from a pedestrian mud road on a slope with a perennial stream ~50 m from the nest, in May 2009. A local resident observed the female add leaf litter to the nest. The nest was visited on 3 June, by which time the female had left. A second visit on 13 August revealed that hatching had already taken place. Clutch size was 29 eggs, of which all hatched successfully based on egg-shell counts.

2009, Nest Five. Nainital Forest Division, Uttarakhand: this nest was found on 30 June 2009, and was located in an oak dominated forest, at 1980 m a.s.l. It was beside a path that residents frequented to collect fodder for their livestock. On 16 July, 15 days after the nest was found, a data logger was placed within the nest chamber, until the eggs hatched. Nest temperature averaged 23 ± 1.95°C (18.3-31.1°C). At this nest, 8–10 % of nest temperature readings were in the 23–24°C range (Fig. 1). The female was observed on the nest from 30 June to12 July. Of 32 eggs, 28 hatched on 7 October, after an observed incubation period of 99 days. The TL of the 28 hatchlings averaged 50 ± 3.8 cm (range 37.5–55.9 cm), and wt averaged 21.79 ± 3.7 gms (range 9–25 gms).

2010, Nest One. Aizwal, Mizoram: The nest was located on 28 May 2010, in a bamboo thicket between a jhum ("slash and burn") cultivation area and coffee plantation, about 30 m on the upper side of slope of a footpath linking these two plantations. The female was observed with the nest from 28 May to 3 August. Of a clutch of 16 eggs, 4 hatched on 2 August, for an observed incubation period of 95 days. Seven eggs had been destroyed by local miscreants. A number of empty egg sacs were visible on the nest, and 5 hatchlings were given to the local Forest Department for release.

2010, Nest Two. Hasirumane, Ilimane, KA: This nest was located on 2 June 2010. The nest was situated adjacent to an areca plantation, 50 m from a perennial stream encompassed by secondary forest. A data logger was placed inside the nest on 20 June and removed from the nest on 18 July 2010 when the eggs hatched. The female was not observed on the nest. Mean temperature was 25.6 ± 0.8°C (range 23–33°C). This nest contained 34 eggs, of which 24 (71%) hatched.

Discussion

Predicted FTL averaged 268.7 ± 49 cm (range 163–352 cm; Fig. 2). The CS averaged 25 ± 0.5 eggs (range 7–43), with an average of 23 ± 8.7 eggs (range 6–38) surviving to term. Early and late embryonic deaths and/or infertile eggs (eggs not surviving to term) averaged 11 ± 0.8 (range 1–10). A report on captive breeding of *Ophiophagus hannah* at Brownsville Zoo yielded the largest clutch size known to date, 53 eggs, of which 39 hatchlings were produced (Burchfield 1977). Incubation period in this study averaged 86 ± 12.76 days (range 66–105 days, N = 9). This is similar to a report of captive bred *Ophiophagus hannah* at the Madras Crocodile Bank hatching in 57–63 days (Whitaker *et al.* 2005), a shorter incubation period than reported in other instances of captive breeding (70–75 days) (Oliver 1956; Burchfield 1977; Dattatri 1987). Wall (1925) reported clutch sizes ranging from 21–33 eggs from six nests. Wasey (1892) observed a clutch size of 33 eggs, although it is unclear if Wall in his report included Wasey's clutch size as his maximum number of eggs.

Interestingly, the smallest clutch size (2005, Nest Three) produced seven eggs yielding six hatchings, perhaps by a female nesting for the first time. A six year old captive bred female (MCBT ID K-7) nesting for the first time (measured 13 February 2001, TL = 184 cm, wt = 700 gms), laid a clutch of 4 viable eggs (2 eggs were normal and 2 very small) at the Madras Crocodile Bank Trust on 10 May 2001 (pers. obs.).

Mean temperatures experienced by the eggs differed among nests (23–27.1°C), as did mean maxima (27.8–37.4°C), and mean minima (13.5-24.6°C) (Fig. 3). The volume of eight nests averaged 2.25 ± 1.4 m^3 (range 0.4–4.6 m^3) (Fig. 4), however compaction of the nest by rain and the addition of leaf litter by the female may have affected nest volume. The period that a female *Ophiophagus hannah* was observed in the vicinity of the nest averaged 29 days (range 2–77 days). We did not consider fluctuation in nest temperature related to the presence/absence of the female, unlike within the family Pythonidae wherein rhythmic contractions of the female's musculature generate heat to increase egg temperatures (Charles *et al.* 1985; Slip & Shine 1988). However, the presence of females on nests during rainfall may have reduced the amount of free water from rain reaching the eggs.

It would presumably be a challenge for King Cobra nests to maintain temperatures suitable for incubation at high elevation. The highest nest observed was 1980 m a.s.l. at the Nainital nest site (2009, Nest Five), where temperatures ranged from 18.3 to 31.1°C. This may reflect that *Ophiophagus hannah* eggs have adapted to develop at low temperatures. Other high altitude nests have been observed at Talla Ramgarh, 1500 m a.s.l., and at Jeolikote, at around 1300 m a.s.l. (Wild Himalayas 2011), both also within the Nainital Forest Division, Uttarakhand. Sangha *et al.* (2011) reported finding a juvenile *Ophiophagus hannah* at an altitude of 2005 m. Perhaps a colony of *Ophiophagus hannah* in captivity could be bred and nests manipulated, i.e. with the female and without, at different times of incubation, different number of eggs (to gauge metabolic heat production) and different ambient temperatures (hence nest temperatures), similar to the work of Aubert *et al.* (2003) on *Python regius*. The highest altitudinal record for a King Cobra was reported by Waltner (1975) who mentioned a specimen he obtained from a site located at an altitude of 2181 m at Mussoorie in 1967.

One hundred eighty-nine hatchlings were measured following emergence from the nest. Hatchling TL, not taking nest site into factor, averaged 53.1 ± 3.5 cm (range 37.5–58.5 cm, N = 176). Hatchling SVL averaged 43.6 ± 2.4 cm (range 37.2–47.5 cm, N = 64), and wt averaged 25 ± 5.3 gms (range 9–38 gms, N = 170). This is similar to other published values, including those reported in a study by Chanhome *et al.* (2001), who recorded an average TLof 47.8 cm and wt of 12 gms in captive bred Thai King Cobras. Similarly, Chanhome (2007) reported a length of 48–65 cm and wt of 12.2–24 gms. Burchfield (1977) reported a ca. 4 m long female producing 19 hatchlings, averaging 47.9 ± 3.5 cm (range 40–55 cm) TL, and 25.8 ± 3.3 gms (14.7–29.8 gms) wt.

Previously thought to be a semi-evergreen specialist, *Ophiophagus hannah* is now known to occupy a wide variety of niches. The forests in the Shivamogga District of Karnataka are classified as West Coast Tropical Evergreen forest (1/A-C/4) by Champion & Seth (1968). Dominant plant types are *Dipterocarpus indicus*, *Diospyros candolleana; Humboldtia brunonis, Artocarpus hirsutus* (Pascal 1988). The landscape also contains an irregular mosaic of *Acacia auriculiformis*, *Areca catechu*, Banana *Ensete superbum* plantations and paddy fields. The forests of Mizoram are classified as 'Cachar Tropical Evergreen (IB/C3)' and 'Cachar Semi Evergreen (2B/C2)' (Champion & Seth 1968). In Uttarakhand's Temperate Zone, where one King Cobra nest was observed, the flora is typically dominated by oak species, (*Quercus leucotrichophora*, *Q. semecarpifolia*, & *Q. dilatata*). Coniferous forests also occur on slopes here. A summary of flora found around five nests from Shivamogga is presented in Table 1. Further studies on the reproductive biology across the range of the King Cobra within India would prove fruitful, especially with detailed environmental records from nests located at high elevations.

Table 1. Flora associated with five King Cobra nests.

Nest ID	Location/State	Flora around the nest site
2008, Nest One	Kerebailu, Hallibidargodu, Karnataka	*Strychnos wallichaiana, Syzygium gardaneri, Nothopigia beddomii, Diospyros malabarica, Sarcanthus pauciflorus*
2008, Nest Two	Kokodu, Nallur, Karnataka	*Dichapetalon gelonioides, Myristica dactyloides, Amoora cararana, Humboltia brunonis, Lansium anamallayanum*
2009, Nest Three	Mundagaru village, Matholli, Kudremukh, Karnataka	*Litsea ghatica, Syzygium zeylanicum, Memesylom ubmellatum, Symlex zeylanica, Gymnacranthera* sp.
2010, Nest One	Hasirumane, Ilimane, Karnataka	*Madhuca longifolia (neriifolia), Garcinia gummigutta, Zanthoxylum ovalifolium, Allophylus cobbe, Nilgirianthus heyneaunus, Justicia symplex*
2010, Nest Two	Mualpui (Soth East Aizawl), Mizoram	*Bambusa vulgaris, Bambusa nutans*

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Forest secondary succession and patterns of anuran recolonization of abandoned tea plantations in Sri Lanka: The effects of time and distance

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ABSTRACT.- **Habitat alteration and destruction have been implicated in the decline of anuran species in various parts of the world. In areas in which forest habitat is cleared to make way for the planting of crops, suitable habitat for anurans is removed. In some such situations this cleared land is abandoned once its agricultural productivity is exhausted. We used these circumstances to investigate the effects of time and distance from likely source populations on the recolonization of such patches by anurans from the virgin sub-montane forest (potential source) in Sri Lanka. Our findings indicate that secondary successional climax vegetation takes between 100 and 150 years to become established, and that colonization of the successional stages (from early to late) involves substantive species turnover, with anurans exhibiting replacement patterns as the secondary succession continues. It also indicates that only the late stages of secondary succession harbour anuran communities that have a strong compositional overlap with that of the virgin sub-montane forest community. Distance of the exploited patches from the potential source for recolonization further impact the rate at which re-establishment of the original community structure takes place.**

KEYWORDS.- **Anurans, Knuckles Mountain Forest Range, Secondary succession, Sri Lanka, Stage–for–time model.**

Introduction

Multiple lines of evidence document the drastic decline of anuran species in various parts of the world during recent historical times (Houlahan *et al.* 2000; Meegaskumbura *et al.* 2002). Some regions appear to have been more greatly affected by anthropogenic activities than others (Kiesecker *et al.* 2004; Lannoo 2005). One of the major factors implicated in these declines has been habitat destruction and alteration (Kiesecker *et al.* 2004; Stuart *et al.* 2004).

Many factors have led to habitat destruction, and anthropogenic conversion of land has resulted in significant reductions in the availability of the natural environment of many anuran species (Dodd & Smith 2003). Several studies have explored the effects of habitat destruction on biodiversity, and the deforestation of tropical regions has figured prominently among them (Denslow 1980; Uhl *et al.* 1981, 1982; Purata 1986; Duncan 2000; Wickramaratne *et al.* 2009). Whereas some of the impacts of deforestation are of very broad scale and thus appear to be irreversible in the short term, other effects may be more localized and less permanent, and offer the possibility of habitat and faunal recovery after anthropogenic activities have ceased. Such recovery is only possible, however, if source populations of flora and fauna are located in reasonably close proximity to the disturbed lands.

Little is known of recovery and recolonization patterns following deforestation of tropical areas. Most studies exploring this have focused on more overtly visible taxa such as birds (Bowman *et al.* 1990; Raman *et al.* 1998; Raman 2001; Renjifo 2001; Williams *et al.* 2001; Dunn 2004) and insects (particularly, butterflies) (Southwood *et al.* 1979; Brown 1984; Bowman *et al.* 1990; Watt *et al.* 1997, 2002; Dunn 2004). Fewer have documented herpetofaunal (Bowman *et al.* 1990; Perman 1997; Pawar *et al.* 2004; Rios-López & Aide 2007) or small mammal (Fox & McKay 1981) recovery. The majority of such investigations have explored patterns over short time spans, and most do not incorporate replication, limiting their ability to reveal general patterns (Dunn 2004). Studies that have examined recovery patterns of both flora and fauna have focused mainly on successional gradients and have explored the relationships between flora and their consumers (Southwood *et al.* 1979; Brown 1984; Raman *et al.* 1998; Raman 2001; Dunn 2004). The relationship of distance to recolonization has only occasionally been investigated (Simberloff & Wilson 1970), and extended periods of time have generally not been explored in this regard.

Extrinsic factors that may influence anurans and their ability to recolonize regenerating areas include the structure of the vegetational community, the distance to the nearest source habitat, time elapsed since regeneration began, and the physical features of the sampling site. Intrinsic factors that may be differentially expressed will be characteristic of particular species, such as abundance, body size, and mode and rate of reproduction. Anuran diversity can be either negatively (Bonin *et al.* 1997; Hecnar 1997) or positively (Knutson *et al.* 1999; Virginia 2004) affected by agricultural practices. Abandoned agricultural land can be recolonized by pioneer species, but this may be slow if the lands are located far from the natural habitats that serve as sources for the colonists (Bonin *et al.* 1997; Hecnar 1997).

We sought a situation for investigating the potential recovery of anuran communities over more protracted time periods under circumstances in which habitat alteration has been followed by prolonged periods of floral regeneration. We selected Sri Lanka, a global amphibian hotspot (Meegaskumbura *et al.* 2002; Bossuyt *et al.* 2004) harbouring a large human population in which habitat alteration related to subsistence and commercial crash crop cultivation has persisted for relatively long periods of time.

Deforestation has been dramatic in Sri Lanka (Pethiyagoda & Manamendra-Arachchi 1998; Manamendra-Arachchi & Pethiyagoda 1999; Pethiyagoda 2005; Meegaskumbura *et al.* 2007). The process was initiated in the 18th century on a large scale and has continued to the present. In the early 1900s Sri Lanka boasted 70% forest cover, but by 2005 this had fallen to 20%, and by 2010 was only 14% (Maheepala 2010). Only about 800 km^2 of relatively undisturbed virgin forest now remains in the wet zone, and this is severely fragmented. The three largest fragments (Knuckles Mountain Forest Range (KMFR), the Sinharaja World Heritage Site, and the Peak Wilderness Area) collectively account for about half of this, with the balance being distributed among approximately 100 enclaves of varying size (Pethiyagoda *et al.* 2006).

From an agricultural standpoint, the hilly areas of Sri Lanka were originally exploited for the cultivation of coffee (*Coffea arabica*), this industry reaching its peak in about 1860 (Marby 1972). Coffee rust, caused by *Hemileia vastatrix*, resulted in the annihilation of the coffee industry (Forrest 1967), and plantations were abandoned (Marby 1972). In 1867 tea (*Camellia sinensis*) plantations began to replace coffee plantations, and these were intermixed with cardamom (*Elettaria cardamomum*) plantations in the wet mountainous areas (700–1300 m above sea level). By 1967 over 24,000 ha were devoted to tea plantations (Forrest 1967; Jayaraman 1975), including about 2800 ha in the KMFR, the latter having been established in the period 1874 to 1875.

In our research, we focus on abandoned tea plantations in the KMFR, where large areas have been cleared of the virgin forest to make way for cultivation of cash crops, and where other human activities, such as fuel wood collection, gem mining, and soil erosion have also extensively impacted the region.

Within the KMFR, the virgin sub-montane forest has been fragmented by the clearing of land for tea and cardamom. Cleared areas used for cultivation remain productive for only a limited period before the soil is exhausted (Fareed 1996), or before disease and insect attack (Marby 1972) render the patch unproductive. Once this occurs, the plots are abandoned and secondary succession occurs, the plots becoming increasingly occupied by native flora. Within a few years of abandonment, dominance shifts to fast growing tree species of intermediate to high shade tolerance (Soulé *et al.* 1998). These grow taller than the general mass of vegetation, resulting in stratification of the newly-forming forest, developing a similar configuration to that of the primary forest (Soulé *et al.* 1998). Over periods of 100 years or more these abandoned plots return to a semi-natural pattern of vegetation.

We used this sequence of successional change in a stage-for-time model to investigate the recolonization patterns of anurans in the parts of the KMFR that have been heavily exploited for tea and cardamom production. Anurans are closely associated with vegetation, are not highly mobile over broad distances, and are environmentally sensitive animals (Ash 1997; Alford & Richards 1999; Collins & Storfer 2003; Lannoo 2005; Wells 2007; Collins & Crump 2009; Jepson & Ladle 2010).

Material and Methods

Study area.– The KMFR (07°21'N; 81°45'E, covering an area of approximately 21,000 ha) resides in the Intermediate Zone of Sri Lanka (Fig. 1) and experiences a wide range of rainfall (de Rosario 1958) and temperature. The KMFR acts as a climatic barrier because it is oriented perpendicular to the two principal wind currents that bring rains (the South-west and North-east monsoons). The highlands of the KMFR are extremely wet throughout the year, with an annual rainfall of about 5000 mm, whereas the lower eastern slopes experience less than 2500 mm (Ekanayake & Bambaradeniya 2001; Bambaradeniya & Ekanayake 2003). Mean monthly temperature ranges from 15° to 25°C (de Silva *et al.* 2005).

The range of climatic and landscape features of the KMFR result in the presence of a variety of natural vegetation types, from lowland semi-evergreen forests, to sub-montane forests, to montane forests (de Rosario 1958), and there is a high level of floral endemism (Aston & Gunathilake 1987). In the KMFR, the virgin sub-montane forest represents a transitional biological belt between highlands and lowlands, and typical patches occur in Cobert's Gap, Kelabokka, and the Riverstone Estate, at elevations between 600 and 1300 m. Our field studies were conducted at Riverstone Estate (07°44'22.45"N, 80°46'32.17"E; 1000–1200 m elevation) (Fig. 1). Trees in the virgin sub-montane forest are stunted, much-branched, and aerodynamically shaped as a result of strong wind action. The forest has three strata, the herb/shrub layer (2 m); the sub-canopy (5 m); and the canopy (15 m). Each layer has its own unique plant species (Bambaradeniya & Ekanayake 2003).

Selection of sampling stages.– Our sampling approach incorporated five vegetational communities. The virgin sub-montane forest (VF) was used as baseline for establishing anuran abundance and diversity because we postulated that the VF harbours the composition of leaf-litter and arboreal anuran communities representative of the area before disturbance. Tea plantations currently in production (CIP) were sampled for documentation of anuran community structure in the maximally disturbed and most human-impacted environment. We also sampled tea plantations that had been abandoned and that possessed structural vegetational characteristics that enabled them to be characterized as either early (ES—relatively recently after abandonment), middle (MS), or late (LS—fully established secondary forest structure) successional stages (Table 1, Fig. 2). These served as proxies for time in the successional continuum. Based upon vegetational regrowth characteristics, information about land-use patterns from local villagers and farmers, and similar information from forest officers of the region, we estimate that the early (ES) successional stage represents a period of about 10–15 years since abandonment, the middle (MS) stage 40–50 years, and the late (LS) stage 100–150 years.

To examine the effects of distance from the potential source community (VF) we examined our experimental stages (CIP, ES, MS and LS) at different distances from the closest VF: less than 10 m; between 10 m and 100 m; and between 100 m and 500 m.

Table 1. Sampling design for examination of anuran communities in the KMFR, Sri Lanka (n= no. of sampling sites, * = Sampling site number, see Fig. 2 for representation of sample site distribution).

Vegetation type	Distance from virgin sub-montane forest		
	< 10m	10m – 100m	100m – 500m
Tea plantations currently in production (CIP): Dominated by tea plants, few grasses and ferns	n = 10, Site designation 0–10* Acronym CIP^{10}	–	n = 10, Site designation 61–70* Acronym CIP^{500}
Early successional stage (ES): Dominated by herbs—chiefly grasses and surviving tea plants.	n = 10, Site designation 11–20* Acronym ES^{10}	–	–
Middle successional stage (MS): Dominated by secondary shrubs that have eliminated pioneer herbs by shading, fewer surviving tea plants.	n = 10, Site designation 21–30* Acronym MS^{10}	n = 10, Site designation 41–50* Acronym MS^{100}	n = 10, Site designation 51–60* Acronym MS^{500}
Late successional stage (LS): Dominated by taller secondary trees with an established canopy. Forest dense. 1–2 vertical vegetational strata.	n = 10, Site designation 31–40* Acronym LS^{10}	–	–
Virgin sub-montane forest (VF): Dense, multi-storey, dominated by woody trees.		n = 10, Site designation A–J* Acronym VF	

We tested the following predictions: (1) abandoned tea plantations at different successional stages but equidistant from the VF will show evidence of recolonization by anurans indicative of an increasing resemblance to the source community structure with time (as indicated by successional stage); (2) Abandoned tea plantations at the same successional stage (in this case, MS) will exhibit patterns of similarity to the source community structure in direct relation to the distance from the source (indicating that distance affects recolonization dynamics). The sampling design is presented in Table 1 and Fig. 2.

Period of sampling.– Each successional stage is represented by ten sites, and each stage was sampled five times (phases), as follows: first inter-monsoon (March 2008 to April 2008); South-west monsoon (May 2008 to September 2008); Second inter-monsoon (October 2008 to November 2008); North-east monsoon, (December 2008 to February 2009) and a repeat of the first inter-monsoon (March 2009 to April 2009).The first inter-monsoon season entailed two bouts of sampling to allow us to test for completeness of sampling before proceeding to the other sampling phases. This protocol enabled us to include both of the annual monsoon and inter-monsoon seasons, and to accommodate for any season–specific activity of anurans. Field work was conducted from 600h–1000h (day sampling), and from 1800h–2200h (night sampling), coinciding with the daily-peak-activity periods of tropical anurans (Duellman & Lizana 1994).

Sampling methods effort.– Quadrat sampling was employed for leaf-litter and arboreal anurans in our field locations (Jaeger & Inger 1994). We used ten, 10 m x 10 m quadrats at each site and for each season sampled. Thus, we sampled one quadrat per site per season, and ten quadrats per successional stage (Table 1), yielding a total of 80 sampled quadrats per sampling period and 400 quadrats for the entire duration of the study. For each sampling period a fresh quadrat was sampled at each study site. We laid quadrats randomly as independent replicates to avoid pseudoreplication (Hurlbert 1984). Sampling was conducted both during the day and at night.

Four field workers searched for leaf-litter (occurring among leaf-litter, vegetation, within and under logs, in rock crevices, and under rocks) and arboreal (up to 1.5 m above the ground, among leaves, on twigs and on the bark of trees) anurans within all microhabitats within each quadrat. One person on each side of the quadrat removed all litter from a 30 cm broad-strip along the outer perimeter of the quadrat and watched for escaping animals (Jaeger & Inger 1994). Litter and ground cover was removed in strips inside the quadrat, parallel to the boundary twine, working successive strips from the perimeter toward the centre until the entire area had been sampled. Individual anurans were collected and identified to the species level. To avoid recounting the same individual, release of collected anurans did not occur until the sampling of that quadrat was complete. All anurans were released at their original location of capture once sampling at that site and for that sampling period was completed. All litter and rocks were replaced. All sampling procedures were conducted in accordance with University of Calgary Animal Care Protocol No. BI 07R-51.

Data analysis.– Samples of anurans obtained during diurnal and nocturnal collecting bouts were assessed to check for any daily patterns of occurrence that differed between the two. This revealed that no anuran species encountered were unique to only one of these sampling regimes. As a result, anurans collected in both time periods were pooled for analysis. All observations of anurans within quadrats were used to determine species richness, cumulative species richness, abundance, evenness, and diversity.

All data were tested for normality before analyses proceeded. The complete count of the number of anuran species for a successional stage was used to calculate species richness of that stage for each season. The cumulative number of species recorded for all seasons for each successional stage was plotted against the sampling phase to produce a species accumulation curve for each respective stage, revealing trends associated with sampling effort (Magurran 2004). The abundance of each anuran species was recorded as number of individuals per species per successional stage (Krebs 1999, 2009; Brown *et al.* 2009) and average abundance per m^2 for each successional stage was calculated. Species evenness was calculated using Simpson's E (Krebs 1999). Alpha diversity was calculated using the Shannon Information Index (Krebs 1999; Magurran 2004; Kingsolver 2006). Beta diversity (i.e., species turnover) (Magurran 2004), comparing species diversity along environmental gradients, was explored in relation to the sampling of data obtained from the successional stages.

One-way analysis of variance was used to test for significant differences among successional stages in relation to species richness and diversity. The abundance of anurans (when comparing two successional stages) was tested using the Kolmogorov-Smirnov Two Sample Test (Rohlf & Sokal 1995; Sokal & Rohlf 1995; Krebs 1999; Magurran 2004). Two Sample t-tests (Watt 1997; Grafen & Hails 2002; McClearly *et al.* 2007) were used to investigate whether species richness and diversity of anurans of MS^{10} sites were greater than those of MS^{500} sites (Fig. 2), and whether species richness and diversity of anurans of LS^{10}sites were greater than those of ES^{10} sites (Fig. 2). The Jaccard Coefficient of Community Similarity Index (Krebs 1999; Gibbs *et al.* 2008) was used to test whether the anuran community of LS^{10} sites differed from that of ES^{10} sites; and whether that of MS^{10}sites differed from that of MS^{500} sites. Before comparison between successional stages, each stage was compared with the VF in relation to its species richness, and this result was used for subsequent comparisons. Cluster Analysis (Krebs 1999; Magurran 2004) was used to group successional stages according to their degree of similarity. Similarity measures were used to investigate the distance (based on the distribution of anuran species among sampling sites) between all pairs of successional stages. All statistical analyses were performed using MINITAB version 15 for WINDOWS (2007).

Results

In total, 237 post-metamorphic anurans, representing 21 species arrayed among the families Bufonidae, Microhylidae, Nyctibatrachidae, Ranidae and Rhacophoridae were collected (Table 2).

We hypothesized that abandoned tea plantations representing different successional stages (ES^{10} and LS^{10}) equidistant from the VF would be recolonized by anuran species in accord with vegetational structure, such that species richness, abundance, and diversity would

Table 2. Species, number of individuals, and relative abundance (in parentheses) of anurans collected in this study, (unid. spp = unidentified species).

Family	Species	Sampling phases (see text for details)					Total
		1	2	3	4	5	
Bufonidae	*Duttaphrynus melanostictus*	3	6	0	5	6	20 (8.4%)
Microhylidae	*Kaloula taprobanica*	2	0	3	2	0	7 (3.0%)
	Ramanella obscura	1	0	3	3	2	9 (3.8%)
Nyctibatrachidae	*Lankanectes corrugatus*	2	2	3	0	3	0 (4.2%)
Ranidae	*Rana temporalis*	3	1	2	5	4	15 (6.3%)
Rhacophoridae	*Pseudophilautus cavirostris*	2	2	4	2	2	12 (5.1%)
	P. fergusonianus	0	0	3	2	1	6 (2.5%)
	P. fulvus	2	4	7	5	2	20 (8.4%)
	P. hoffmani	0	0	1	2	0	3 (1.3%)
	P. macropus	2	2	3	0	1	8 (3.9%)
	P. mooreorum	2	2	3	2	2	11 (4.6%)
	P. cf. ocularis	0	1	0	3	0	4 (1.7%)
	P. sarasinorum	4	2	1	4	1	12 (5.1%)
	P. cf. silus	1	1	0	2	1	5 (2.1%)
	P. steineri	5	4	7	4	2	22 (9.3%)
	P. stuarti	2	3	3	4	3	15 (6.3%)
	P. unid. spp. I	0	1	0	0	0	1 (0.4%)
	P. unid. spp. II	0	0	1	0	0	1 (0.4%)
	P. unid. spp. III	0	0	0	1	0	1 (0.4%)
	Polypedates cruciger	7	7	10	4	8	36(15.2%)
	Taruga cf. eques	7	4	4	2	2	19(8%)
	Total = 21	45	42	58	52	40	237(100%)

be greater for LS^{10} sites than for ES^{10} sites. In agreement with this prediction, we found that species richness ($P < 0.05$) and diversity ($P < 0.05$) were greater at sites representing LS^{10} sites than ES^{10} sites (Table 3). Although anuran abundance in LS^{10} sites was greater than that for ES^{10} sites, the difference was not statistically significant ($P > 0.05$).

We also hypothesized that MS^{10} sites would be recolonized by anuran species sooner than MS^{500} sites. We further predicted, on this basis, that the species richness, abundance, and diversity of anuran species of MS^{10} sites would be greater than those for MS^{500} sites. These predictions were borne out (Tables 4 & 5). Although abundance at MS^{10} sites was greater than it was at MS^{500} sites, this difference was not statistically significant ($P > 0.05$) (Table 3).

Species richness.– Measures of species richness provide a broad indication of whether the target group varies between habitats (Pearman 1997). Table 4 provides summary data for species richness for all sampling phases across all successional stages, and includes both diurnal and nocturnal encounters. The conversion of primary forest to cultivated land and its subsequent recovery to secondary forest is accompanied by changes in species richness as well as abundance. The pattern of species richness of anurans along the successional gradient from CIP^{10}sites to VF is shown in Figure 3. These patterns reveal a non-uniform trend, with a reversal in species richness occurring for the MS^{100} and MS^{500} sites, before increasing again in the LS^{10} and VF situations. The richest stages yielded eight anuran species at their peak, whereas the

Table 3. Results of comparisons of anuran species richness, abundance and diversity between the different successional stages sampled in this study (* = T value; ** = D value). See Table 1 for information about successional stages.

Measurement	LS^{10} vs. ES^{10}	MS^{10} vs. MS^{500}
Species richness	Two sample T-test df = 7, T = 6.40*, P <0.05	Two sample T-test df = 7, T = 2.75*, P <0.05
Abundance	Kolmogorov-Smirnov two sample test D=13.24**,P>0.05	Kolmogorov-Smirnov two sample test D=5.13**,P>0.05
Species diversity	Two sample T-test df = 7, T = 4.68*, P <0.05	Two sample T-test df = 7, T = 3.22*, P <0.05

most depauperate stages yielded only a single anuran species in a given sampling phase (Table 4). All species encountered in diurnal surveys have been reported elsewhere to be day active (de Silva 2009). Twenty-one species of anurans were encountered during nocturnal sampling periods, with species richness ranging from three to 11 species per successional stage (Table 4). The currently in production stages (CIP^{10}; CIP ^{500}) exhibited the lowest species richness (Table 4). The successional stages sampled differed significantly from each other in species richness (One Way ANOVA, $F_{7,32} = 32.39$, $P < 0.05$). Appendix 1 summarizes habitat occupancy, period of activity, and conservation status-relevant data for all anuran species encountered.

Species accumulation curves and variation of species richness among successional stages.– Species accumulation data are presented in Table 4. Trends are distinct among successional stages. The CIP^{10}, CIP^{500} and MS^{500} stages reached their species accumulation asymptote by the end of the third sampling phase, whereas the remainder of the successional stages reached their asymptote at the end of the fourth sampling phase (Fig. 3).

Species abundance.– We examined the patterns of average abundance of anurans during the five sampling phases employed in this study (Fig. 4). Across the study, the lowest abundance was recorded from CIP^{10} sites, followed by ES^{10} sites. The CIP^{500} sites yielded a relatively higher abundance of anurans than did all other sites except for LS^{10} and VF sites, even though it was located between 100 and 500 m from the VF (Fig. 4). The greatest number of anurans was collected from the VF, followed by LS^{10} sites (Fig. 4). The abundance of anurans exhibited significant differences among successional stages across the five sampling phases (One Way ANOVA, $F_{7,32} = 18.46$, $P < 0.05$).

Species evenness.– We examined species evenness among all successional stages. The highest value is recorded for the MS^{100} sites, whereas the lowest is recorded for CIP^{10} sites (Appendix 2). The remainder of the successional stages show a relatively equal value for species evenness (Appendix 2).

Species diversity.– The lowest index of alpha diversity is evident for CIP stages, and the highest value is evident for the VF (Appendix 2). Highly significant differences among successional stages in regard to species diversity of anurans were observed across the five sampling phases (One Way ANOVA, $F_{7,32} = 14.96$, $P < 0.05$).

Species composition.– Species composition data are provided in Table 5. Differences in species composition were evaluated for each successional stage over all five sampling phases. The proportional representation of different families of anurans differed among the different successional stage categories, and among the five sampling phases. Species composition is less diverse in the early successional stages than it is in later successional stages. This was expected, because the natural vegetation of the VF had been removed to make way for the planting of tea. In the later successional stages some of the original plant species had recolonized the abandoned plantations.

A major difference in species composition is evident between the remainder of the successional stages when compared to the VF. Additionally, substantial differences are evident within the same successional stage (MS^{10}, MS^{100} and MS^{500}) at different distances from the VF (Table 5). The species composition of anurans in CIP^{10}, and CIP^{500} sites was relatively simple (three and four species respectively), whereas LS^{10} and VF sites had a complex species composition (eight and 11 species, respectively) (Table 5). Several species of anurans were restricted to a particular successional

Table 4. Species richness (number of species) by stage and sampling phase, and by time of sampling (D/N* = indicates diurnal / nocturnal; cumulative species richness data by sampling period in parentheses; Total = Cumulative species accumulation data for each successional stage; No. Ind. = Total number of individuals). For acronyms identifying successional stages see Table 1.

Stage	Sampling phase															Total # of species	Total # of specimens
	1			2			3			4			5				
	D/N*	Total	No. Ind.	D/N	Total	No. Ind.	D/N	Total	No. Ind.	D/N	Total	No. Ind.	D/N	Total	No. Ind.		
CIP^{10}	0/1	1(1)	2	0/2	2(1)	2	0/3	3(1)	6	0/2	2(0)	2	0/1	1(0)	1	3	13
CIP^{500}	1/3	3(3)	6	1/2	2(0)	7	1/2	3(1)	7	1/4	4(0)	9	1/3	3(0)	9	4	38
ES^{10}	0/3	3(3)	3	0/3	3(0)	4	0/2	2(1)	2	0/3	5(1)	5	0/2	2(0)	3	5	17
MS^{10}	0/4	4(4)	7	0/4	4(0)	5	0/4	4(1)	9	0/6	6(1)	7	0/4	4(0)	4	6	32
MS^{100}	0/3	3(3)	4	0/3	3(0)	4	0/3	3(0)	4	0/4	4(2)	6	0/3	3(0)	4	5	22
MS^{500}	0/3	3(3)	4	0/2	2(0)	3	0/4	4(2)	6	0/3	3(0)	3	0/3	3(0)	3	5	19
LS^{10}	1/5	5(5)	8	1/5	5(1)	7	0/6	6(1)	10	0/7	7(1)	9	0/5	5(0)	6	8	40
VF	1/7	7(7)	11	2/8	8(2)	10	0/7	7(1)	14	1/8	8(1)	11	1/7	7(0)	10	11	56
Total	2/15	15	45	3/15	15	42	1/15	16	58	2/17	17	52	2/15	15	40	21	237

stage, yielding different patterns of species composition (Table 5).

Marked changes in beta diversity are evident, ranging from 0.429 (between CIP^{10} and CIP^{500} sites) to 0.857 (between CIP^{10} and VF sites), and from 0.200 (between MS^{100} and MS^{500} sites) to 1.000 (between MS^{100} and VF sites) (Appendix 3). The highest values for these indices were attained when stages were compared with LS^{10} or VF stages (ranging from 0.714 to 1.000), because the anuran species of these two successional stages differs markedly from the remainder (Appendix 3).

Assessment of anuran communities using Cluster Analysis.– We employed cluster analysis to explore the association patterns of anurans found in the various successional stages investigated (Fig. 5). This revealed patterns of similarity between successional stages based on shared community elements.

The most distinctive assemblage is that recorded from the CIP^{500} stage. The remainder of the successional stages are linked at the 28% similarity level. These further resolve into two major clusters at the 45% level. One of these links the LS^{10} and VF stages of anuran assemblages at the 65% similarity level. The other segregates into two branches, with the CIP^{10} and ES^{10} stages linked at the 78% similarity level. The three middle successional stages form a cluster at the 69% similarity level, with the MS^{500} stage assemblage being segregated from MS^{10} and MS^{100} assemblages, the latter being linked at the 80% similarity level (Fig. 5).

These data indicate that the CIP stage most distant from the VF (CIP^{500}) shows the greatest difference from the anuran assemblages in all other successional stages. The CIP stage closest to the VF (CIP^{10}) shows considerably more similarity to those of ES^{10} stage that are also closer to VF. The MS stages cluster as an assemblage, as do LS^{10} and VF (Fig. 5).

Individual species responses.– Abundance patterns of anuran species among

Table 5. Presence and abundance of anuran species by successional stage (see Table 1 for designation data pooled for all sampling phases; * = restricted to a particular stage; ** = known distribution restricted to the KMFR; For the "Total" row the numbers refer to number of species/number of individuals). Shaded designations (CIP^{10}, ES^{10}, MS^{10}, and LS^{10}) represent the time axis examined in this study. The unshaded CIP^{500}, MS^{100}, and MS^{500} designations represent distance axis, unid. sp = unidentified species.

Species	Successional stages and location								
	CIP^{10}	CIP^{500}	ES^{10}	MS^{10}	MS^{100}	MS^{500}	LS^{10}	VF	Total
Duttaphrynus melanostictus	-	20*	-	-	-	-	-	-	20
Kaloula taprobanica	-	7*	-	-	-	-	-	-	7
Ramanella obscura	-	-	-	-	-	-	4	5	9
Lankanectes corrugatus	-	-	-	-	-	-	-	10*	10
Rana temporalis	-	-	-	-	-	-	6	9	15
Pseudophilautus cavirostris	-	-	-	-	-	-	6	6	12
P. fergusonianus	2	4	-	-	-	-	-	-	6
*P. fulvus***	5	-	2	4	-	-	5	4	20
*P. hoffmani***	-	-	1	1	1	-	-	-	3
*P. macropus***	-	-	-	-	-	8*	-	-	8
*P. mooreorum***	-	-	-	-	-	-	5	6	11
P. cf. *ocularis*	-	-	-	-	-	-	1	3	4
P. sarasinorum	-	-	2	5	2	3	-	-	12
P. cf. *silus*	-	-	5*	-	-	-	-	-	5
*P. steineri***	-	-	-	7	7	4	4	-	22
*P. stuarti***	-	-	-	7	7	1	-	-	15
P. unid. spp. I	-	-	-	-	-	-	-	1*	1
P. unid. spp. II	-	-	-	-	-	-	-	1*	1
P. unid. spp. III	-	-	-	-	-	-	-	1*	1
Polypedates cruciger	6	7	7	8	5	3	-	-	36
Taruga cf. *eques*	-	-	-	-	-	-	9	10	19
Total (# species / # individuals)	3/13	4/38	5/17	6/32	5/22	5/19	8/40	11/56	21/237

the successional stages differed. On aggregate, the most common species was the arboreal hourglass frog, *Polypedates cruciger,* with 36 individuals collected throughout the sampling phases (Table 2). These were collected from CIP^{10}, CIP^{500}, ES^{10}, MS^{10}, MS^{100}, and MS^{500} sites (Table 5). Some of these successional stages were close (< 10 m) to the VF (CIP^{10}; ES^{10}; MS^{10}) whereas others (CIP^{500}; MS^{500}) were located between 100 and 500 m from the VF. *Polypedates cruciger* was not encountered in LS^{10} or the VF (Table 5).

Polypedates cruciger was followed in terms of abundance, by Steiner's shrub frog, *Pseudophilautus steineri*, the Knuckles shrub frog, *Pseudophilautus fulvus*, and the common toad, *Duttaphrynus melanostictus*, with 22, 20 and 20 specimens collected respectively (Table 2). The arboreal species, *Pseudophilautus fulvus*, was collected from all successional stages that were physically close (< 10 m) to the VF, but none were collected at successional stages more distant (100 m or more) from the VF (Table 4).

The greatest number of individuals of a species collected from an individual successional stage was 20 for *Duttaphrynus melanostictus* (CIP^{500}) (Table 5), and this species had likely invaded the CIP^{500} sites from neighbouring anthropogenically-altered habitats.

Muller's shrub frog, *Pseudophilautus sarasinorum*, was encountered in ES^{10}, MS^{10}, MS^{100}, and MS^{500} sites (Table 5), but Hoffman's shrub frog, *Pseudophilautus hoffmani*, was not encountered in MS^{500} sites. Similarly, Stuart's shrub frog, *Pseudophilautus stuarti*, was restricted in occurrence to all of the MS stages, whereas Steiner's shrub frog, *Pseudophilautus steineri*, was encountered in all of the MS as well as in the LS^{10} site (Table 5).

Several species of anurans were restricted to a particular successional stage, yielding different patterns of species composition (Table 5). For example *Duttaphrynus melanostictus* and *Kaloula taprobanica* are unique to the CIP^{500} sites, whereas *Pseudophilautus macropus* is restricted to MS^{500} sites. *Duttaphrynus melanostictus* is considered to be a disturbed habitat specialist (Pethiyagoda & Manamendra-Arachchi 1998, de Silva 2009) and *P. macropus* is a wet large boulder habitat specialist (Manamendra-Arachchi & Pethiyagoda 2006; de Silva 2009). The CIP^{500} and MS^{500} sites were located between 100 and 500 m from VF, where disturbance of habitat is likely to be the greatest of all the habitat locations investigated here. *Pseudophilautus* cf. *silus* (Table 5) is restricted to ES^{10} sites, in which the occurrence of grasses is relatively high. *Lankanectes corrugatus* and the three unidentified species of *Pseudophilautus* were encountered only in the VF (Table 5). *Lankanectes corrugatus* is a forest habitat specialist and depends upon canopy cover (Manamendra-Arachchi & Pethiyagoda, 2006; Weerawardhena & Russell 2012).

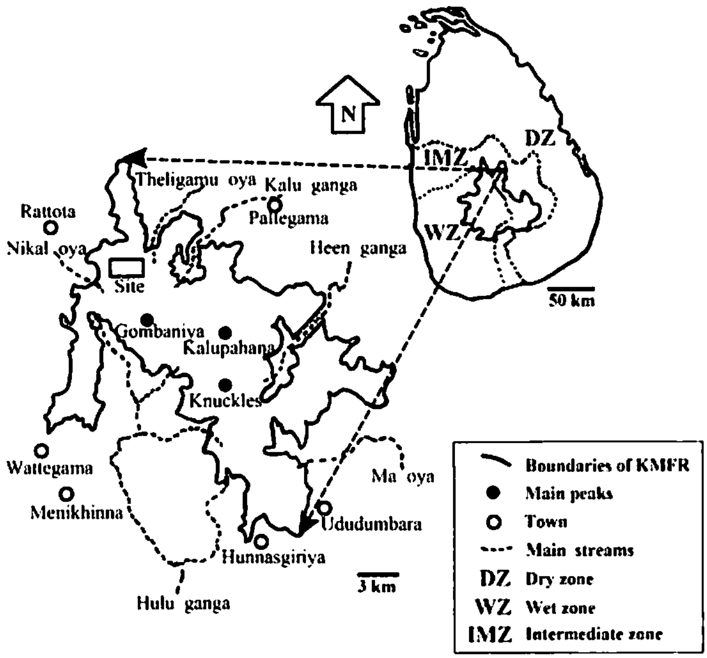

Figure 1. Map depicting the location of the Knuckles Mountain Forest Range within Sri Lanka, and the location of the study site (rectangle) within the KMFR (inset).

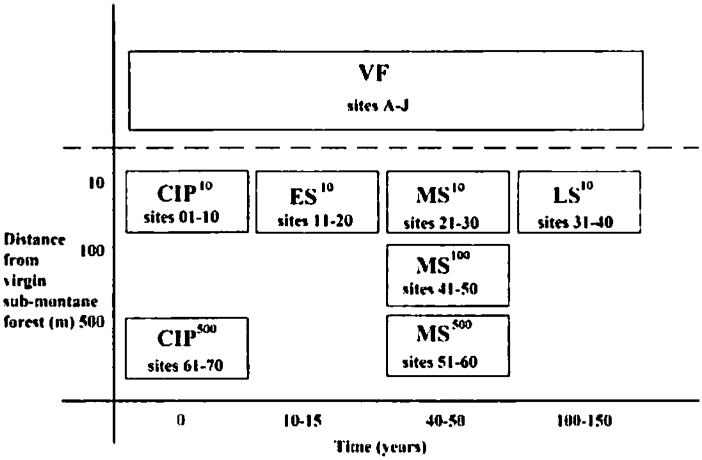

Figure 2. Experimental design for analysis of the dynamics of recovery of abandoned tea plantations by anuran species in the KMFR, Sri Lanka. The virgin sub-montane forest (VF) represents the "permanent" habitat type to which others are compared. For the successional stages [currently in production (CIP), Early (ES), Middle (MS), and Late (LS)] the horizontal axis represents a time axis, and the vertical axis represents distance axis (with reference to the VF). For further details see Table 1.

No anurans were encountered in diurnal surveys of CIP^{10}sites, but two species (*Duttaphrynus melanostictus* and *Kaloula taprobanica*) were found to be diurnally active at CIP^{500} sites. No diurnally active anurans were encountered in MS^{10}, MS^{100} or MS^{500} surveys. Diurnal sam-

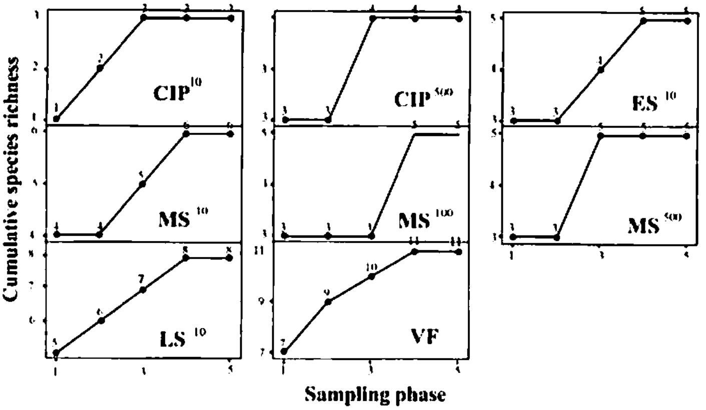

Figure 3. Number of anuran species against sampling phases of all successional stages (Y axis = Cumulative species richness; X axis = Sampling phase; ● = sampling season (see text for details) – season 1 is to the left, season 5 to the right; The cumulative number of species encountered in each successional stage following each sampling phase is stated above each plotted point).

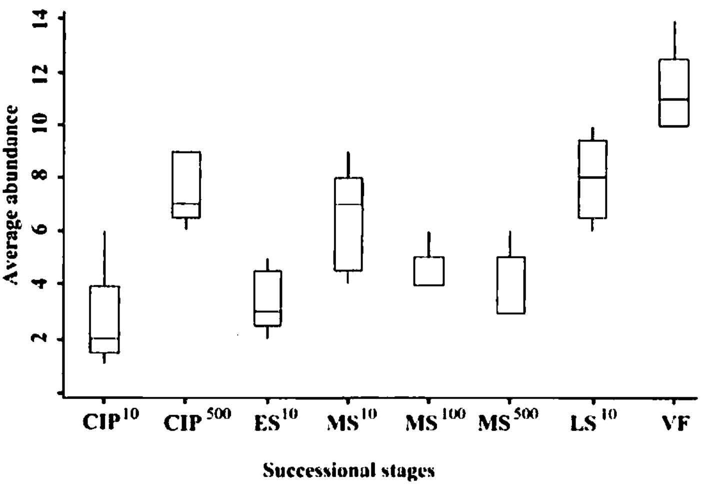

Figure 4. Patterns of average abundance of anuran species among all successional stages (see Table 1) for all sampling phases (see Text for details).

pling resulted in encountering *Taruga* cf. *eques* in LS^{10} sites, and three species were encountered diurnally in the VF (*Lankanectes corrugatus*, *T.* cf. *eques*, and *Rana temporalis*).

Discussion

Our findings concerning the recolonization patterns of abandoned tea plantations by leaf-litter and arboreal anurans were consistent with our hypotheses, both in terms of time and distance. The structure of anuran communities is closely associated with the pattern of secondary succession investigated in this study.

In our stage-for-time model we designated a number of successional communities that represent a time axis. This is most evidently displayed in Figure 2, in which the time axis is represented by the various versions of tea plantations (successional stages): CIP, ES, MS and LS. Employing the successional stages that lie within 10 m of the VF, we were able to examine a successional sequence in which time is the variable. Table 5 shows the anuran species composition of the CIP^{10}, ES^{10}, MS^{10}, LS^{10}, and VF sites, and Figure 5 depicts community affinities based upon similarity of included anuran taxa. These are used to interpret broad scale trends.

For the CIP stages that are located close to the VF (within 10 m), the anuran fauna is species-poor, harbouring only two species of *Pseudophilautus* (*P. fergusonianus* and *P. fulvus*), plus *Polypedates cruciger*. Of these, only *P. fulvus* is also encountered in the VF (Table 5). Overlap between these two extremal communities is thus minimal. Clearing the VF to make way for tea plantations almost totally eliminates the native anuran community.

For the CIP category, we compared anuran communities in tea plantations close to the VF (CIP^{10} site) and at distances considerably further away (CIP^{500} site). Species diversity was only slightly higher for the CIP^{500} than for the CIP^{10} site (Appendix 2), but Table 5 shows that relative abundance was much greater for the CIP^{500} site. At the CIP^{500} sites, *Duttaphrynus melanostictus* and *Kaloula taprobanica* were encountered. Collectively these two species account for 71% of specimens found at the CIP^{500} sites, and these species were found nowhere else (Table 5). By contrast, *Pseudophilautus fulvus*, which was encountered at the CIP^{10}, ES^{10}, MS^{10}, LS^{10}

Appendix 1. Habitat, period of activity, IUCN status (IUCN, 2007), and endemism (Pethiyagoda *et al.*, 2006; Stuart *et al.*, 2008) of anurans sampled in this study (Habitat: T = terrestrial; AQ = aquatic; AR = arboreal; Period of activity: D = diurnal; N = nocturnal; DN = active day and night; IUCN Red list categories: CR = critically endangered; EN = endangered; VU = vulnerable; NT = near threatened; LC = least concern; NE = not evaluated; Endemism: Y = endemic to Sri Lanka; N = not endemic).

Species	Habitat	Period of activity	IUCN status	Endemism
Duttaphrynus melanostictus	T	DN	LC	N
Kaloula taprobanica	T	DN	LC	N
Ramanella obscura	T	N	NT	Y
Lankanectes corrugatus	AQ	DN	VU	Y
Rana temporalis	AQ	DN	LC	Y
Pseudophilautus cavirostris	AR	N	EN	Y
P. fergusonianus	T	N	LC	Y
P. fulvus	T	N	EN	Y
P. hoffmani	AR	N	EN	Y
P. macropus	T	N	CR	Y
P. mooreorum	AR	N	EN	Y
P. cf. *ocularis*	AR	N	EN	Y
P. sarasinorum	T	N	EN	Y
P. cf. *silus*	AR	N	EN	Y
P. steineri	AR	N	EN	Y
P. stuarti	AR	N	EN	Y
P. unid. spp. I	AR	N	NE	N
P. unid. spp. II	AR	N	NE	N
P. unid. spp. III	T	N	NE	N
Polypedates cruciger	AR	N	LC	Y
Taruga cf. *eques*	AR	DN	EN	Y

Appendix 2. Species evenness and alpha diversity values of anuran species collected from all successional stages over the five sampling phases (For designation of these phases see text) (^{a} = the lowest value and ^{aa} = the highest value for α – diversity). For successional stages see Table 1.

Stage	Evenness	Sampling phase				
		1	2	3	4	5
CIP^{10}	0.70	0.0000 ^{a}	0.6931	1.0114	0.6931	0.0000
CIP^{500}	0.94	0.0114	0.4101	1.0789	1.1490	0.8487
ES^{10}	0.91	1.0986	1.0398	0.6932	1.0549	0.6365
MS^{10}	0.92	1.3516	1.3322	1.3688	1.7474	1.3864
MS^{100}	0.99	1.0398	1.0398	1.0398	1.3296	1.0398
MS^{500}	0.90	1.0398	0.6365	1.2424	1.0986	1.0986
LS^{10}	0.95	1.4941	1.5495	1.7482	1.8889	1.2620
VF	0.96	1.7678	2.0253 ^{aa}	1.9085	1.9722	1.8354

Appendix 3. Beta diversity values for successional stages (based on anuran species collected from all stages over the five phases). For successional stages see Table 1.

Stage	CIP^{500}	ES^{10}	MS^{10}	MS^{100}	MS^{500}	LS^{10}	VF
CIP^{10}	0.429	0.500	0.555	0.750	0.750	0.818	0.857
CIP^{500}	-	0.555	0.600	0.778	0.778	0.833	0.867
ES^{10}	-	-	0.273	0.400	0.600	0.846	0.875
MS^{10}	-	-	-	0.091	0.273	0.714	0.882
MS^{100}	-	-	-	-	0.200	0.846	1.000
MS^{500}	-	-	-	-	-	0.846	1.000
LS^{10}	-	-	-	-	-	-	0.263

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Ecdysis in free-ranging Indian rock pythons: a case study

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ABSTRACT.– The annual pattern of ecdysis in free ranging Indian rock pythons, *Python molurus*, was studied in Keoladeo National Park, Bharatpur, India from October 2007 to September 2009. Though number of snakes undergoing ecdysis was high during colder months, the proportion of them in ecdysis was high during warmer months. Number of snakes undergoing ecdysis was positively influenced by monthly mean variation of temperature and relative humidity and negatively by number of snakes feeding in a month. Other factors such as reproductive status of the snake, feeding, basking and tick infestation appear to influence the ecdysis in free ranging pythons independently or in combination. A study using temperature sensitive radio-telemetry is required to have better understanding on the ecdysis and other activities of Indian rock pythons in relation to various abiotic and biotic factors and age/size classes under natural conditions.

KEYWORDS.– Environmental factors, Indian rock python, National Park, Sloughing in snakes

Introduction

The reptilian integument functions to prevent the body from dehydration as it is largely made up of keratinized scales (Lillywhite 2006). The epidermis of lepidosaurian reptiles is periodically renewed by the synchronized proliferation of new cells and the shedding older ones (Lillywhite 1989), which is variously known as ecdysis, moulting, sloughing and skin shedding. Ecdysis involves a significant expenditure of energy (Semlitsch 1979), which is about 3% in *Elaphe guttata* and 11% in *Heterodont platyrhinos* (Smith 1976). This process is influenced by various factors such as the health of individuals, food consumed, reproductive status, endocrine cycles, parasites and local environmental factors (Loomis 1951; Chiu & Lynn 1970; Semlitsch 1979; Naulleau & Brule 1981; Bauwens *et al.* 1989; Verveen 2010). The frequency of shedding may increase with growth rate and therefore would decrease with body size. Synchrony in mating and ecdysis has been reported in both lizards and snakes (Andren 1982). Ling (1972) reported that much time and effort is needed to measure temporal patterns of ecdysis in free ranging animals. To date, most of our understanding of snake ecdysis is based on observations in captivity (Stabler 1939; Ling 1972; Semlitsch 1979; Hoser 1982; Banks 1985; Lillywhite 1989; Verveen 2010).

The Indian rock python *Python molurus* has a wide distribution in most parts of the Indian subcontinent and Southeast Asia (Whitaker 1993; Whitaker & Captain 2004). Available information on the ecdysis of pythons is based on observations in captivity (Stabler 1939; Biswas & Acharjyo 1976; Rathinasabapathy & Kalaiarasan 1995; Vyas 1999). Considerable information on the ecdysis of other Indian snakes in captivity is also available (Biswas & Acharjyo 1976; Acharjyo *et al.* 1978; Naulleau & Brule 1981; Rathinasabapathy & Kalaiarasan 1995; Vyas 1999; Shankar & Whitaker 2009). In captivity, small sample sizes and variation in husbandry make findings incomparable with studies in natural conditions. In the present paper, we provide data on the ecdysis of free ranging Indian rock pythons *Python molurus* based on observations in Keoladeo National Park, Bharatpur, Rajasthan state, India.

Material and Methods

Keoladeo National Park (KNP; 27°10' N, 77°31'E, Fig. 1), Bharatpur, a World Heritage and Ramsar site, has an area of about 29 km^2 including 8.5 km^2 wetland. The vegetation of KNP is dominated by a mixture of xerophytic and semi-xerophytic species such as *Acacia nilotica*, *Prosopis juliflora*, *Salvadora persica*, *S. oleoides*, *Capparis decidua* and *C. sepiaria* (Prasad *et al.* 1996). Currently, the terrestrial vegetation of KNP is highly altered due to the proliferation of the weed, *P. juliflora*, and control measures initiated by the Rajasthan Forest Department during 2007 (Ramesh, unpublished data). Major terrestrial fauna of the park include Golden jackal *Canis aureus*, Indian porcupine *Hystrix indica* and Spotted deer *Axis axis*. Climate of the area is sub-humid to semi-arid, and monthly mean maximum and minimum temperatures varied between 30.8 °C and 35.1 °C and 16.9 °C and 22.4 ° C respectively (Ali & Vijayan 1986). The monsoon season extends from late June to September, and the average rainfall of Bharatpur is 655 mm (Ali & Vijayan 1986). Descriptions on the general ecology of KNP and Indian rock pythons are available in Bhupathy & Vijayan (1989), Vijayan (1991) and Ramesh & Bhupathy (2010). An estimated 100–200 adult Indian rock pythons inhabit KNP (Bhupathy & Vijayan 1989; Krishnan *et al.* 2009; Bhupathy & Ramesh 2010).

In KNP, pythons live in underground burrows dug by the Indian porcupines. Burrows may provide safe retreat to pythons from some predators and from extreme climatic conditions. A burrow was considered as a python burrow when live snakes or signs of their presence (body marks, sloughs and scats) were seen at the entrance or nearby (Krishnan *et al.* 2009). The terrestrial area of KNP was extensively surveyed on foot and the burrows occupied by pythons were recorded using a GPS and marked on a map (Fig. 1).

Python burrows were examined biweekly between October 2007 and September 2009 to locate snakes. An area within approximately a 50 m radius of each burrow was searched for

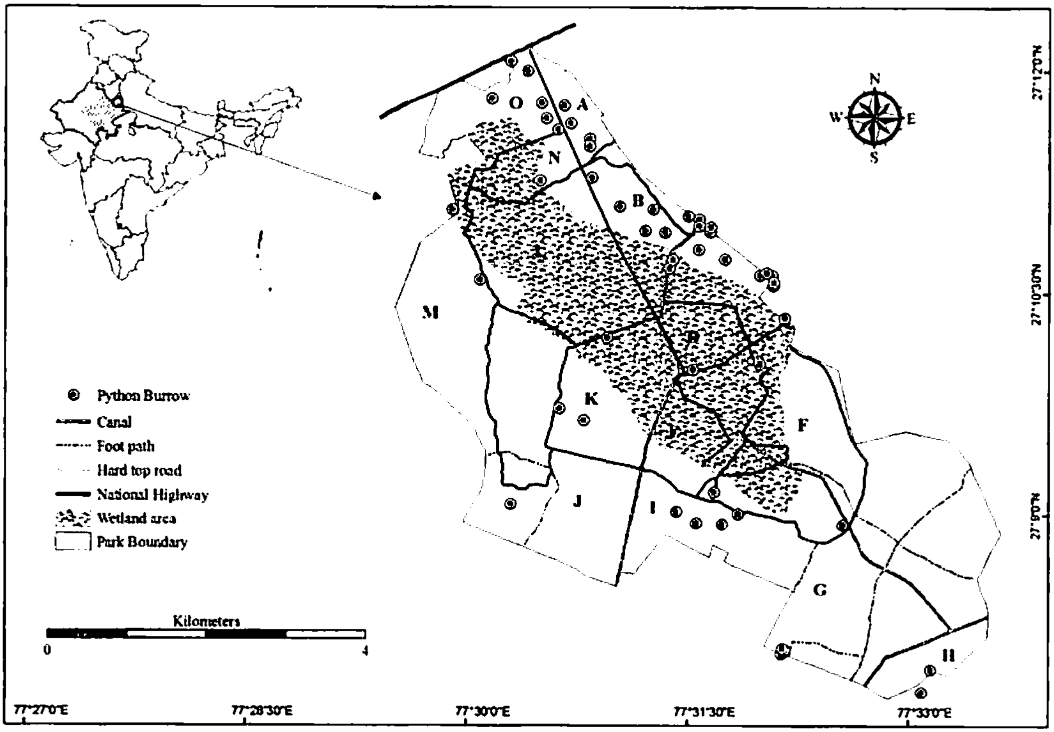

Figure 1. Distribution of burrows occupied by Indian rock pythons in Keoladeo National Park, Bharatpur, Rajasthan, India during October 2007–September 2009.

snakes during each survey. Each encountered snake was visually examined at close range (within 2–3 m) for the presence of shedding skin attached to its body. As the inter-survey period was at least 15 days, each observation (i.e., snake with attached sloughed skin) was considered as new. Snakes were also identified based on natural markings (Bhupathy 1990) and monitored in subsequent surveys. Sloughs found in pieces, or intact, outside the burrows were not considered for analysis as this could lead to double counts. Only a few snakes were observed outside the burrows during fortnightly surveys after May. Hence, surveys were also carried out in dried wetlands during May–July 2009 to locate snakes and record ecdysis. In addition, 29 random plots (100 x 100 m) about 200–1000 m away from python burrows were examined for snakes. Porcupines maintain the burrows by periodic excavation, and the excavated soil was examined for the presence of sloughed skins, especially during summer, when snakes were rarely observed. The number of snakes that had eaten was recorded based on direct (visual confirmation of prey ingestion) and indirect (distended stomach) observations. Other activities of Indian rock pythons such as mating and incubation of eggs during the period were recorded opportunistically.

Daily data on temperature, relative humidity and rainfall were collected from government managed meteorological station at Bharatpur and monthly average of the same was considered for analysis. Variation of temperature was calculated based on the difference between monthly mean maximum and minimum temperatures. A Generalized Linear Model (GLM) with Poisson log link function was applied to examine bio-climatic factors, namely temperature and relative humidity, as well as the number of snakes that had fed, and their influence number of snakes undergoing ecdysis. A chi-square (2 X 2 contingency test) was used to detect significant variation in the number of snakes observed and undergoing ecdysis between the warmer (April–September) and colder (October–March) seasons.

Results

In all, 362 free ranging Indian rock pythons were observed during the present study, i.e., 48 surveys carried out biweekly covering 50 burrows from October 2007 to September 2009. Eighty-one snakes had pieces of shedding skin attached to their body. This might include shedding of the skin by a single snake on several occasions. Ecdysis in Indian rock pythons was observed in all months barring September. The highest number of pythons undergoing ecdysis (22 out of 77) was observed during January followed by December (17 out of 61 snakes, Fig. 2), which are the coldest months.

Only a few snakes were observed outside the ground burrows during warmer months, April–October (Fig. 2). However, the proportion of snakes undergoing ecdysis was high during these months. These snakes included nesting and incubating snakes. An attempt was made to confirm the activity of snakes away from burrows (200–1000 m) in dried wetlands during warmer months, but yielded no snakes. Sloughed skins of Indian rock pythons were also not found along with soil freshly excavated by porcupines during this period, indicating that pythons did not shed. No snake was observed in surveys conducted in 29 plots placed (200–1000 m) away from burrows during May–July. These indicate that snakes were most likely aestivating during this period. However further studies are required to determine the

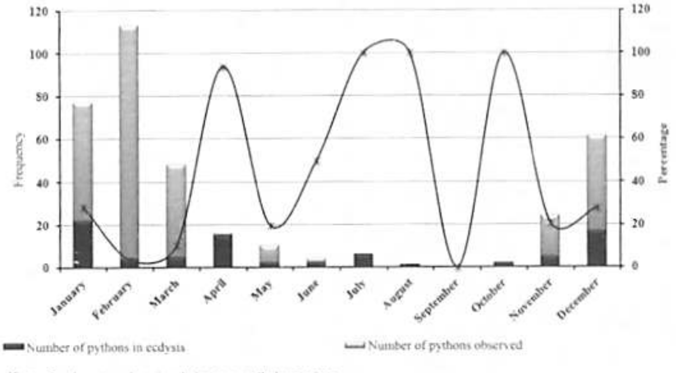

Figure 2. Number of Indian rock pythons observed outside the burrows in relation to snakes undergoing ecdysis in Keoladeo National Park, Bharatpur during October 2007–September 2009.

extent of aestivation of Indian rock pythons in KNP.

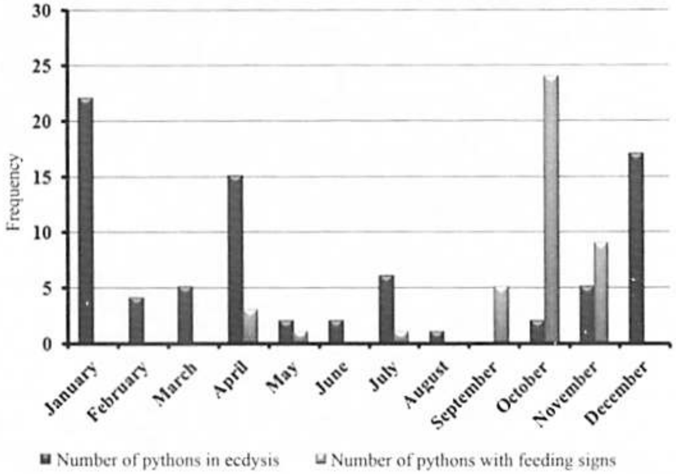

Figure 3. Monthly frequency of Indian rock pythons undergoing ecdysis and feeding in Keoladeo National Park from October 2007–September 2009.

High frequency of feeding by Indian rock python was observed during September–November (relatively warmer months), and feeding was not recorded during December–March (colder months; Fig. 3). The incidence of ecdysis in snakes was higher in months subsequent to feeding. Analysis using the Generalised Linear Model (GLM) showed that number of snakes undergoing ecdysis in a month was positively influenced by monthly mean variation of temperature ($\beta = 0.207$; $P = < 0.01$) and relative humidity ($\beta = 0.047$; $P = < 0.01$), and negatively influenced by number of snakes feeding in a month ($\beta = -0.081$; $P = < 0.01$). A significantly higher proportion of snakes observed outside the burrows were in the process of ecdysis during the dry season as compared to the colder season ($\chi^2 = 266.34$, df = 3, $P < 0.05$).

During the present study, 10 records of mating and two nests of Indian rock pythons were obtained. Both male and female snakes underwent ecdysis prior to courtship and mating, which was clear from the bright and shining skins of all those individuals (10 pairs). Nesting females underwent ecdysis about one week prior to laying eggs and starting of incubation. Pieces of sloughed skins were found in the vicinity of the nest, and bright skin of the incubating snakes also confirmed recent ecdysis. In KNP, Indian rock pythons incubate the eggs for about 60–70 days, and no ecdysis was observed during this period. Snakes shedded their skin soon after terminating incubation (number of nests monitored= 2). Proliferation of external parasites (*Amblyomma* sp. and *Aponomma* sp.) was observed at about 8–10 days prior to the hatching of eggs (i.e., July–August 2008) during this study.

Discussion

In KNP, ecdysis of Indian rock pythons was observed in all months barring September. This could be due to the presence of various age/size classes of snakes in the population (Krishnan *et al.* 2009). However, due to small sample size, ecdysis in relation to various size/age classes could not be analysed in the present study. It has been reported that juveniles may slough frequently, whereas older individuals would shed their skin only once or twice in a year (Verveen 2010). Females (lengths: 3.9 m and 3.3 m) that nested during the present study shed their skin at least thrice within one year, i.e., prior to mating, egg deposition, and completion of incubation. It has been reported that frequency of sloughing decreased with age among six (two male and four female) captive juvenile *Python molurus molurus* (6, 5.3 and 4.5 times during the first, second and third year respectively, Vyas 1999). *Python m. bivittatus* moulted nine times during the first year, which reduced to six, five and four times during the second, third and fourth year respectively (Jacobson 1977 cited in Vereveen 2010).

The highest number of Indian rock pythons undergoing ecdysis was observed during December–January. However, the proportion of snakes in ecdysis was high during warmer months (April–September). Vyas (1999) reported higher frequency of sloughing in Indian rock pythons during warmer months (June–July) in the Sayaji Baugh Zoo (Vadodara, Gujarat). On the other hand, at Chennai Snake Park, a captive facility, ecdysis in *Python reticulatus* was more frequent during colder months (Rathinasabapathy & Kalaiarasan 1995). Variations in the observed differences in the ecdysis of free ranging Indian rock pythons and those studied in captivity and could largely be due to controlled temperature, lower numbers of experimental animals and regular feeding in captivity as compared to natural conditions.

Only a few pythons were observed outside the burrows during the warmer months, April–October (Fig. 2) and most of them were undergoing ecdysis. During this period, no sloughed skin was observed in the excavated soil near porcupine burrows, which indicated that most of the snakes were not active or did not shed their skin. No snake was observed in dried wetlands and 29 (100 X 100 m) plots surveyed during May–July, which further supports the view of aestivation of Indian rock pythons during dry season. Aestivation of Indian rock pythons in northern parts of their distribution has been reported by Murphy (2013).

Semlitsch (1979) reported that shedding frequency in snakes has some temperature dependency, which is independent of growth rate. The present study area is relatively colder and Indian rock pythons stopped feeding by November. Perhaps maintaining the body temperature at a certain level is important for snakes to digest and assimilate the prey consumed (Alexander *et al.* 2012), and hence, they could have basked extensively during colder months (December–January). Feeding (prior to December) and subsequent basking might have facilitated growth, which resulted in ecdysis during these (colder) months.

It was found that a higher incidence of ecdysis in Indian rock pythons in KNP coincided with reproductive activity; prior to mating (February–March) and egg laying (April) and on completion of incubation (end of July; Ramesh & Bhupathy 2010). Similar to this study, pre-nuptial moulting has been reported in vipers (Nilson 1980). According to Ling (1972), breeding phenology has an influence on ecdysis of reptiles. In captivity, it is reported that ecdysis appears to stimulate courtship in *Python molurus* (Walsh & Murphy 2003). Synchrony in mating and ecdysis has been reported both in lizards and snakes. The shedding of skin prior to mating reportedly facilitates the release and spread of pheromones through the skin (Andren 1982).

Pre-egg laying shedding is reportedly common in pythons (Walsh & Murphy 2003; Lourdais *et al.* 2008) and colubrids (Markel 1990) and the reason for the same is not clear. The physiological significance of skin-shedding in squamate reptiles is unknown (Maderson *et al.* 1970). Bauwens *et al.* (1989) reported certain endocrine mechanisms that affect both reproductive physiology and ecdysis. This might indicate that the phenomenon of skin-shedding has been evolutionarily selected to account for hormonal associations in different reptile taxa. We do not have supporting data for this and further studies are required in this direction.

Verveen (2010) reported that parasitic mites *Ophionyssus natricis* accelerate sloughing frequency in snakes due to mechanical damage to the epidermis. Ramesh & Bhupathy (2010) reported proliferation of ectoparasites and shedding of skin by the female pythons upon termination of incubation in KNP, Bharatpur. It was presumed that skin shedding helped the snake to get rid of ectoparasites. Two genera of ticks, *Amblyomma* and *Aponomma*, have been reported from pythons in the same study area (Bhupathy & Vijayan 1989). It is reported that while brooding, Indian rock pythons maintained a narrow range of nest temperatures and did not feed for several months following copulation (Ramesh & Bhupathy 2010). This could have weakened the health of the snake and influenced the proliferation of ectoparasites.

The relationship between ecdysis in Indian rock pythons and monthly mean variation in ambient temperature and relative humidity was positive, but was negatively significant with frequency of feeding snakes. The significant relationship of the number of snakes in ecdysis to monthly mean variation of ambient temperature in KNP shows the influence of temperature on ecdysis, which augments the findings of Semlitsch (1979).

The present study showed that frequency of ecdysis in Indian rock python was higher during post-feeding months, i.e. December–January. These months are relatively colder, and several snakes were observed basking outside their ground burrows in KNP (Krishnan *et al.* 2009). Naulleau & Brule (1981) reported that the process of renewing the epidermis is influenced more by temperature than by food intake.

Verveen (2010) reported that digestion and renewal of epidermis often occur in combination. Moulting is also synchronized with the seasonal cycle according to the availability of energy resources and time to complete the essential functions (Ling 1972). Based on the results of the present study, factors such as reproductive status of the snake, climatic conditions especially temperature variation, relative humidity, feeding, basking and tick infestation appear to influence the ecdysis in free ranging Indian rock pythons independently or in combination. A detailed study is required using radio-telemetry to have a better understanding on the ecdysis and other activities of pythons in relation to various abiotic and biotic factors under natural conditions.

Acknowledgements

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Habitat selection and habitat characteristics of *Clinotarsus alticola* (Boulenger, 1882) tadpoles in Rosekandy Tea Estate, Cachar District, Assam, India

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ABSTRACT.- A study on the Rosekandy Tea Estate in the Cachar District, Assam, India revealed the presence of five species of anuran tadpoles in different aquatic habitats, including permanent and temporary lentic bodies and slow flowing lotic habitats in the form of streams. The tadpoles detected were *Clinotarsus alticola, Euphlyctis cyanophlyctis, Leptobrachium smithi, Fejervarya* aff. *limnocharis* and *Microhyla ornata.* The tadpoles of *Clinotarsus alticola* where found in two permanent lentic water bodies which were relatively undisturbed and surrounded by secondary forest. Water depth, size of the ponds, and vegetation as well as physico-chemical characteristics of the water from these water bodies were recorded. The presence of *C. alticola* in permanent lentic water bodies contrasts with earlier findings. A lack of disturbance and proximity to forested areas may have prompted the selection of this habitat by the breeding frogs.

KEYWORDS.- *Clinotarsus alticola* tadpole, distribution, lentic water body, microhabitat use.

Introduction

Amphibians form an important component of the biodiversity of tropical ecosystems. The ecology of tadpoles is complex and is important in understanding the structure of anuran communities. The type of water body occupied and their location can be helpful in establishing the species identity of tadpoles, as larvae typically occupy specific niches (Malkmus *et al.* 2002).

Habitat selection of amphibian tadpoles has been widely documented (Waringer-Loschenkohl 1988) at the global level, but in Northeast India, it has not been studied extensively. Distribution and habitat selection may vary with the physical and biotic environment (Holomuzki 1986; Wollmuth *et al.* 1987; Lawler 1989). Diversity in the size and shape of the tadpoles and in their life duration are related to feeding adaptations, habitat types and social behaviour (Tyning 1990). According to Inger (1966), the major factors that ultimately limit the distribution of tropical amphibians are ecological factors such as temperature, total rainfall, vegetation, competition, geographic and geological factors.

The ranid frog species *Clinotarsus alticola* (Boulenger, 1882) is widely distributed. It is known from all seven states of Northeast India (Dutta 1997) as well as from Bhutan, Nepal, Bangladesh, Thailand and Myanmar (Ahmed *et al.* 2009). It is considered to be of Least Concern in the IUCN Red List, with no apparent threats. In Assam, adults have been reported from Barail Wildlife Sanctuary (Das *et al.* 2009). In the present investigation, the occurrence of *Clinotarsus alticola* tadpoles is reported from Rosekandy Tea Estate in the Cachar District of Assam. It was found breeding in lentic habitats.

Material and Methods

The study was conducted at Barjalenga (24°42'29"–24°41'31" N, 92°41'52"–92°42'39" E), Rosekandy Tea Estate, Cachar District, Assam, 25 km from Silchar town, the district headquarters of Cachar, and ca.3.5 km from the

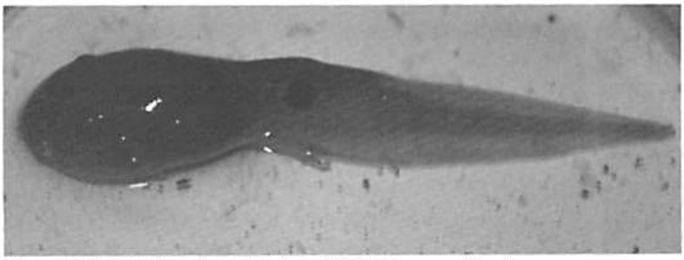

Figure 1. The distinctive tadpole of *Clinotarsus alticola*.

Assam University Campus. The maximum monthly temperature in the study area ranges from 23–34.4°C, minimum temperatures 11.4–26°C and relative humidity from 60.4–96%. The total area in the tea estate is about 1702.01 hectares, of which 562.80 ha area is used for tea plantation. The remainder comprises uncultivated lands, secondary forest growth and water reservoirs. The topography of the area is primarily a combination of uneven plains, low lying areas and occasional small hillocks. Tea plantations are generally established on uplands and surrounding hillocks. There are a number of permanent and temporary lentic and lotic water bodies (in the form of nullahs or drains) inside the tea gardens. The permanent standing water bodies are situated in disturbed as well as undisturbed areas and are adjacent to the forest and tea plantation area. The disturbed area contains human settlements, factories and tarred roads.

Field sampling was done over a period of approximately 10 months between March to December 2011. The stations were selected at random to cover the study area and to define the distribution of tadpoles. Water samples and tadpoles were surveyed and collected from a variety of habitats including moving and standing bodies of water. The tadpoles were collected during the day using hand nets (mesh size 1mm, diameter 30 cm). Unidentified tadpoles were reared in laboratory conditions until they reached an identifiable juvenile stage. Tadpole species were classified based on morphology, structure of mouth parts, vent position and other data (Inger 1966; Malkmus *et al.* 2002). Water samples were collected from tadpole occurrence stations and physico-chemical parameters were analysed by using standard methods (e.g., Trivedy & Goel 1984; APHA 2005). Measurements of the habitat and water depth were taken and vegetation was also recorded, as they are important for understanding individual species requirements (Sir 2005).

Results

A total of 12 different sites were surveyed within the Rosekandy Tea Estate for presence of tadpoles. Of these sites, tadpoles were found in five and tadpoles of *Clinotarsus alticola* (Figs. 1–2) were found at two stations during the survey period. At the other stations four species of tadpoles were found: *Fejervarya* aff. *limnocharis*, *Microhyla ornata*, *Leptobrachium smithi* and *Euphlyctis cyanophlyctis* (Table 1). Tadpoles of more than one species were not found to coexist at any one water body during the same period of sampling, which may be due to different breeding seasons.

Table 1. Habitat used by tadpoles of five species of anuran amphibians from Rosekandy Tea Estate, Cachar, India.

Station	Habitat types	Tadpole sp.	Month of occurrence
R_1	Stream	*Leptobrachium smithi* *Euphlyctis cyanophlyctis*	September–November Year around
R_2	Temporary water bodies	*Fejervarya* aff. *limnocharis* *Microhyla ornata*	March, August April–August,November
R_3	Pond	*Clinotarsus alticola*	March, July–December
R_4	Fishery	—	—
R_5	Stream	*Microhyla ornata*	April–August,November
R_6	Pond	*Clinotarsus alticola*	March, July–December

Figure 2. Metamorphosing *Clinotarsus alticola* reared from tadpoles collected at the Rosekandy Tea Estate, Assam.

Table 2. Physico-chemical parameters of surveyed water bodies in Rosekandy Tea Estate. X±SD (range in parentheses).

Station	Parameters							
	Air Temp (°C)	Surface Water Temp (°C)	pH	D.O.(mg/L)	Free CO_2 (mg/L)	TA(mg/L)	Nitrate (mg/L)	Phosphate (mg/L)
R_1	28.63±1.049 (26.5–29.9)	26.7±0.658 (25.2–27.5)	6.67±0.052 (6.60–6.67)	10.31±0.99 (8.98–12.08)	8.78±2.040 (6.60–11)	42.45±10.98 (26.5–63)	0.0607±0.0027 (0.058–0.065)	0.0244±0.0031 (0.019–0.028)
R_2	28.4±1.646 (24–29.9)	26.09±1.741 (22–27.5)	5.82±0.329 (5.48–6.22)	10.08±1.702 (9.11–14.7)	33.73±3.217 (30.3–40.2)	24.02±9.11 (13–36.5)	0.0272±0.0075 (0.013–0.035)	0.0026±0.0021 (0.011–0.042)
R_3	28.1±1.791 (24–29.9)	25.04±2.932 (19–27.5)	6.67±0.073 (6.54–6.75)	3.861±0.880 (2.73–5.33)	10.10±2.770 (6.53–14.52)	30.19±1.88 (26.5–31.5)	0.03±0.0033 (0.026–0.037)	0.0483±0.0085 (0.050–0.063)
R_4	28.73±1.078 (26–29.9)	26.83±0.732 (25–27.9)	6.65±0.071 (6.58–6.75)	6.922±0.533 (6.10–7.56)	15.78±5.203 (9.92–20.46)	49.45±5.267 (44.1–56.5)	0.0451±0.007 (0.028–0.053)	0.0382±0.005 (0.031–0.046)
R_5	28.3±1.504 (25–29.9)	25.33±3.370 (19–27.9)	6.78±0.069 (6.70–6.87)	7.30±1.590 (4.35–8.98)	8.202±1.917 (6.60–13.2)	41.09±9.207 (31–63)	0.0415±0.0031 (0.038–0.045)	0.0215±0.0063 (0.011–0.031)
R_6	28.13±1.620 (25–29.9)	25.33±2.832 (19–27.9)	6.78±0.069 (6.70–6.87)	12.10±2.527 (8.17–15.36)	12.35±1.757 (9.46–14.55)	37.47±7.203 (30–48)	0.0583±0.0032 (0.055–0.064)	0.0535±0.0021 (0.051–0.057)

Physico-chemical studies were carried out at six sites. Table 2 presents physico-chemical parameters of surveyed water bodies. Among the physico-chemical variables the pH in all water bodies was acidic and fluctuated between 5.48 and 6.87. Surface water temperature ranged from 27.0 to 29.5°C. Alkalinity ranged between 13 and 63 mg/L. Among the other parameters, dissolved oxygen and free CO_2 ranged between 2.73–15.36 mg/L and 6.53–40.2 mg/L, respectively Nitrates and phosphates ranged between 0.013–0.065 mg/L and 0.011– 0.063 mg/L, respectively. The results of a One-Way ANOVA revealed that there was no significant difference ($P < 0.05$) between air and water temperatures, but significant differences ($P < 0.05$) between stations were observed in CO_2, DO, pH, total alkalinity, nitrate, and phosphate (Table 3).

Both stations with *C. alticola* tadpoles are permanent lentic systems in rural settings, with no lotic system or waterfalls near the ponds. Tadpoles were found in large numbers and actively moving in aggregations (Fig. 3). The dimensions of the ponds were 25×8 m with a maximum depth of 2.0 m and 30×35 m and a maximum depth of ca. 2.5 m, and both had muddy bottoms. Trees provided shade to the ponds and the systems were undisturbed (Fig. 4). One side of each pond was covered with thick vegetation and trees such as *Bombax ceiba, Albizia lebbeck, Albizia odoratissima, Pterygota alata,*

Table 3. Significance of differences between physico-chemical parameter among six stations as revealed by one-way ANOVA ($P<0.05$). Significant differences indicated by an asterisk (*).

Parameters	F value
Air Temp	$0.305_{5, 54}$
Surface Water Temp	$1.099_{5, 54}$
pH	$^{*}61.50_{5, 54}$
DO	$^{*}38.23_{5, 54}$
CO_2	$^{*}100.11_{5, 54}$
TA	$^{*}13.72_{5, 54}$
Nitrate	$^{*}80.66_{5, 54}$
Phosphate	$^{*}137.37_{5, 54}$

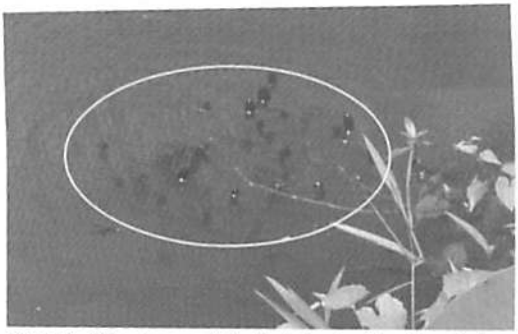

Figure 3. *Clinotarsus alticola* tadpoles (in elipse) clustering near the surface of the pond at study site R3.

the opposite bank was dominated by tea plants. *Pogonatherum crinitum*, *Monochoria* sp., *Cyperus* sp., *Eupatorium* sp., *Eupatorium odoratum* and *Mimosa pudica* as well as several unidentified species of ferns were present at the stations where *C. alticola* were found.

Discussion

The physico-chemical parameters of the selected water bodies studied showed variation as revealed by One-Way ANOVA, although this did not relate to the presence or absence of tadpoles of *C. alticola*. The other ponds are also reasonably large and have human settlements nearby. The presence of predators such as carnivorous fishes like *Wallago attu*, *Cirrhinus mrigala* and *Bagarius bagarius* may be a reason that tadpoles were absent in these ponds.

The documentation of *C. alticola* in permanent lentic water bodies in the present study contrasts with earlier findings, which reported the species from lotic systems in association with tropical forest, shrubland and grasses in hilly areas. Sahu & Khare (1980) reported that the tadpoles are generally found in mountain torrents. Grosjean *et al.* (2003) likewise collected them from large pools under a waterfall of a river (ca.10 m wide) running through a primary forest, where as Sailo (unpublished data) reported that the tadpoles were found in both lentic and lotic water systems. The stations from which the tadpoles were collected in the present study are permanent water bodies situated in undisturbed secondary forest areas. There are no streams or waterfalls near the ponds. It was also found that the tadpoles aggregated at the surface of the pond where temperatures varyed between 19.0 and27.9°C.

Figure 4. Study site R6 showing the habitat of one of the undisturbed ponds containing *C. alticola* tadpoles.

The undisturbed nature of the ponds and their location near forested areas adjacent to the tea plantation may have promoted the selection of microhabitat by the frog. Further study on water parameters, vegetation and habitat characteristics in other habitats will contribute to a better understanding of the utilization of microhabitat by this species.

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Terrestrial locomotion in the marine filesnake, *Acrochordus granulatus* (Schneider, 1799)

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ABSTRACT.- Acrochordids are a fully aquatic radiation of snakes characterized by loss of the ventral scutes. These snakes are commonly described as virtually helpless on land. We observed the terrestrial behavior and locomotion of one acrochordid species, the marine file snake (*Acrochordus granulatus*). On land these snakes exhibited typical exploratory behavior, including pronounced head elevation. They probed the substrate with their head (using marked neck arching for additional force application) and performed vertical burrowing. The animals moved chiefly by concertina locomotion. While all of these behaviors were performed at relatively slow speed, they are hard to reconcile with the popular depiction of these animals as either "unable to support themselves" or "helpless" on land.

KEYWORDS.- Locomotion, behaviour, snake, *Acrochordus*

Introduction

Snakes, being limbless, move over land exclusively by using their body surface to push against contact points on the substrate. The interactions between the snake's body surface and the substrate can be highly repetitive and even rhythmic (as in sidewinding, e.g., Gans & Mendelssohn 1972) or more sporadic and irregular (as in concertina, e.g., Jayne & Davis 1991). The snake's lateral body surface can be used against substrate contact points (particularly during lateral undulation, e.g., Gray 1946; Moon & Gans 1998); however, most terrestrial locomotion is achieved using the expanded ventral scales or scutes (Mosauer 1932). In most snakes the cranial margin of the scute is "fixed" while the caudal margin is free, making it well-suited to push back against the substrate. Since each scute is under voluntary muscle control; the snake can both displace the scute relative to the vertebral column (as in rectilinear locomotion, e.g., Lissman 1950) or change the angle of the scute to elevate the free caudal edge and increase the available surface area for contact (Gans 1962; Hu & Shelley 2012).

One of the classic lines of evidence for the importance of scutes during terrestrial locomotion is the fact that there are (independent) lineages of fully aquatic snakes which lack scutes and are generally described as "helpless" on land (e.g., Greene 1997). One such aquatic lineage is the filesnakes which morphological and molecular analyses have shown to be a long isolated sister-taxon to the large caenophidian radiation (Cundall *et al.* 1993; Slowinski & Lawson 2002; Vidal *et al.* 2007; Sanders *et al.* 2010). In recognition of their unusual features and phylogenetic position, the three species of filesnakes are generally placed in their own family (Acrochordidae) or Superfamily (Acrochordoidea). Acrochordids, while charaterized as aquatic snakes, generally inhabit ephemeral pools and traverse overland during low tides (e.g., Lillywhite & Sanmartino 1993), establishing a clear ecological importance to terrestrial locomotion.

In addition to their lack of scutes, acrochordids are frequently described as having a greatly diminished body tone of rigor; Mehrtens (1987, pp. 79) states that when *Acrochordus* is removed from the water it feels like, "a deflated tire tube." Smith (1943, pp. 133-134) stated that, "On land it is quite out of its element, and its movements are slow and clumsy, progressing more like a gigantic worm than a snake." Numerous "classic" and modern authors have offered similar accounts, often describing these snakes as "helpless" on land, or "virtually incapable" of terrestrial locomotion. Jayne (1986), in the only study of terrestrial locomotion in an acrochordid, reported that *Acrochordus javanicus* performed concertina over linoleum at a rate (in terms of body lengths per second) that was faster than that of *Nerodia fasciata* performing concertina in either a narrow or wide tunnel. Rick Shine, who has done extensive field studies of acrochordids (e.g., Madsen & Shine 2000), noted (Shine & Houston 1993, pp. 2–3) that, " ...individuals of *A. arafurae* have been observed moving short distances overland...Underwater, filesnakes move about both by crawling on the bottom and swimming". This seeming contradiction in the literature motivated the present study, which is intended primarily as a description of the terrestrial behaviors, including locomotion, in one acrochordid (*A. granulatus*).

Materials and Methods

Four long-term captive specimens of *Acrochordus granulatus* were obtained commercially; all four were within the adult size range (snout-vent lengths of 57–65.5 cm; masses 54–111 g) for this species (Cogger 1975; O'Shea 1996). Specimens were kept individually in 100 l aquaria with a sand substrate ~8 cm deep; a combination of submerged hide boxes, large rocks, and anchored artifical plants provided multiple hiding places within each tank. The tanks were individually filtered, and aerated with an air stone. The water was loaded with tannins (from cork bark) and left discolored and slight acidic, approaching the Southeast Asian "blackwater" condition (Adey & Loveland 2007). The tanks were kept in a heated (25–29.5° C) reptile room, under a 12:12 light cycle. The snakes were maintained on a diet of live goldfish (*Carassius auratus*). All care and use of these animals was approved by the Institutional Animal Care and Use Committee of the University of Massachusetts Lowell.

Some locomotion trials were conducted by placing the snake on a large pane of glass, but all of the data presented herein were obtained with the snake moving freely in a 120 cm diameter enclosure. The floor of the enclosure was covered with an approximately 7 cm deep layer of wetted topsoil; there was no standing water in the enclosure, and the topsoil did not contain any large aggregates or foreign material.

An individual specimen was placed in the enclosure and allowed to move freely; minimal contact and/or motivation of the snakes was employed, as such the velocities we report herein may not represent the maximum achievable by this species. In light of the unusual energy-balance of acrochordids (Shine 1986) we terminated all trials within two minutes, gave the animals at least 10 minutes between trials, and never attempted more than three trials in a 24 hour period.

Locomotor performance was recorded using a digital camera and high-speed digital video system consisting of a Troubleshooter 1000S camera (Xcitex, Inc.) filming at 125 fps, and the MaxTrak analysis software (Innovision Systems, Inc.). The only behavior quantified was concertina locomotion; the video files were exported to ImageJ (NIH) for quantification and EXCEL for statistical summary. During the observed sequences of concertina locomotion, the position of the tip of the snout was digitized, the number of lateral body loops was recorded, and the maximum lateral amplitude of each loop measured. Herein locomotion velocity is defined as the distance covered by the tip of the snout divided by the duration of the locomotion sequence; as such this is mean, not maximal velocity; the temporal duration is defined as the period between the first onset of a lateral loop and the cessation of forward progress by the head.

Results

Head Elevation.– When placed in the filming enclosure *Acrochordus granulatus* exhibited fairly typical (if slower) ophidian exploratory behavior characterized by lateral sweeps of the head and tongue flicks. As part of this exploratory behavior the specimens would elevate their head and approximately 10% of their snout-vent length (Fig. 1). The snakes were capable of moving forward while holding their head and anterior trunk off the ground.

Head Probing and Body Arching.– As part of their exploratory behavior, the snakes would probe

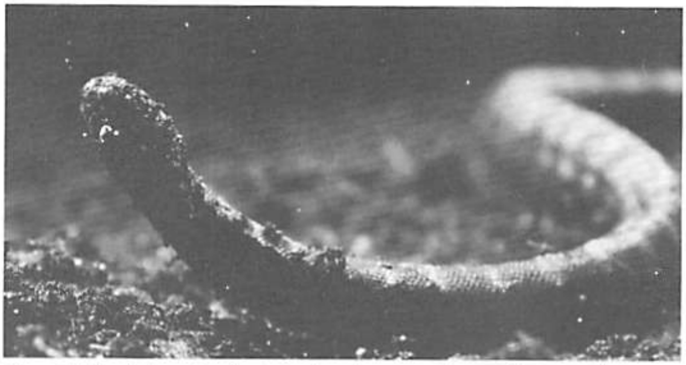

Figure 1. Head elevation in *Acrochordus granulatus*. These snakes were able to move forward while elevating roughly 10% of their body off the substrate.

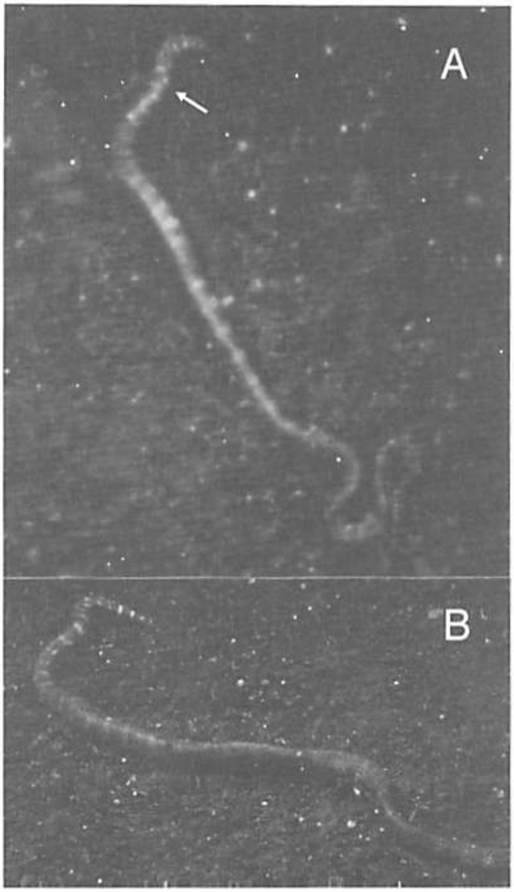

Figure 2. Head Probing and Neck Arching in *Acrochordus granulatus*. In both this still from the digital video record (A) and this digital photograph (B) the snake's head is in the substrate and the neck and forebody is arched and elevated (the arrow in A is pointing at the shadowing under the elevated forebody).

the substrate with their head. The snout was placed at a steep angle (often nearly perpendicular) to the ground and wiggled slightly in an attempt to push the head into the substrate. This head probing was frequently accompanied by vertical arching of the neck and forebody, a position sometimes held for several seconds (Fig. 2).

Vertical Burrowing.– This behavior was only observed on two occasions. The snakes first formed their body into a loose horizontal "coil." Using lateral elevation of the ribs (clearly visible on the surface of the snake) and what appeared to be long-axis rotation of the vertebrae (inferred from observed movements of the dorsal midline of the snake) these acrochordids were able to displace enough substrate to lower themselves vertically (Fig. 3). On both occasions the snakes were immobile in this "burrowed" position for only a few minutes before moving again. While there was a clear vertical displacement of these snakes relative to the surface of the substrate, much of their body remained above the substrate level and they did not cover their body with loose substrate.

Unique Acrochordid Terrestrial Locomotion.– A novel form of terrestrial locomotion was observed, this locomotor sequence had two distinct phases. First, the "loose" skin of *Acrochordus granulatus* coalesced (or was compressed cranio-caudally) in one region of the body. This increased quantity of skin formed what resembled an isolated annular segment; increased skin was visible all around the snake, and because of the folding or pleating of the coalesced skin there was a localized increase in the diameter of the snake. Second, this expanded cutaneous "segment" was used as a contact point on the substrate and the snake's body advanced relative to the cutaneous segment; visually, the cutaenous segment was displaced caudally along the snake's body.

Only four bouts of this locomotion were observed. In all four the cutaneous segment was displaced for less than 20% of the length of the snake. This resulted in slow locomotion over a limited distance. Categorizing this behavior as "locomotion" is based on three key features: 1) in every case it was observed shortly after or

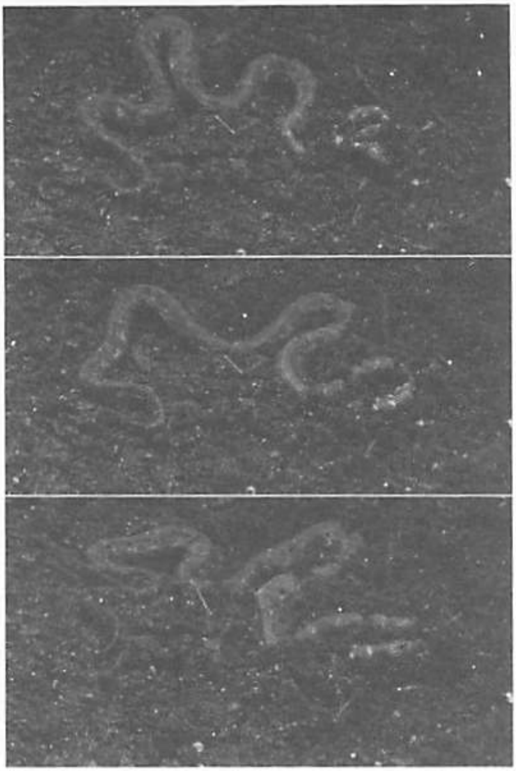

Figure 3. Vertical Burrowing in *Acrochordus granulatus*. These three photographs are from a single vertical burrowing episode (total time between the photographs was less than a minute) and show the movement of the head and body into the substrate.

before concertina locomotion; 2) the behavior did result in forward displacement of the head and snake; and 3) the formation of the localized cutaneous segment was pronounced and consistent enough to suggest that it is a functional specialization, not simply an epiphenomenon. Our video camera was positioned far enough away from the animal that the sequences of this behavior were not distinctive.

Concertina Locomotion.– This was the most common form of terrestrial locomotion observed in *Acrochordus granulatus*. The basic kinematics resembled what has been described for concertina in other snakes: initially the head and forebody are "fixed" and the snake creates lateral body loops by advancing the caudal end of the body, then the caudal end of the snake is "fixed" and the head and forebody advanced by compression of the lateral body loops (Fig. 4).

These filesnakes did not exhibit a preference or "handedness" for the lateral body loops. The lateral body loops formed by *A. granulatus* were rather small; the mean maximum amplitude (measured from the long axis of the body) was only 4% of the snout-vent length (S.D. = 1.6%, N = 25). The locomotor velocity was rather slow; the 25 bouts of concertina locomotion had a mean velocity of 0.022 body lengths per s (S.D. = 0.013). Despite moving over a substrate (wetted topsoil) that provided ample contact

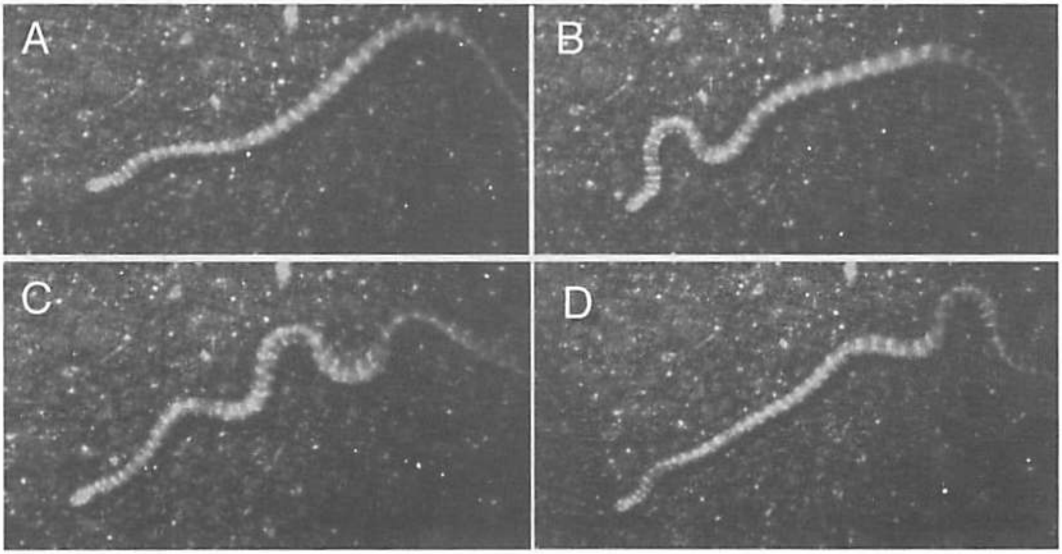

Figure 4. Concertina locomotion in *Acrochordus granulatus*. Four frames from a digital video sequence show the phasic movement and lateral body loops that typify concertina. Note the relatively small lateral body loops formed by *A. granulatus*.

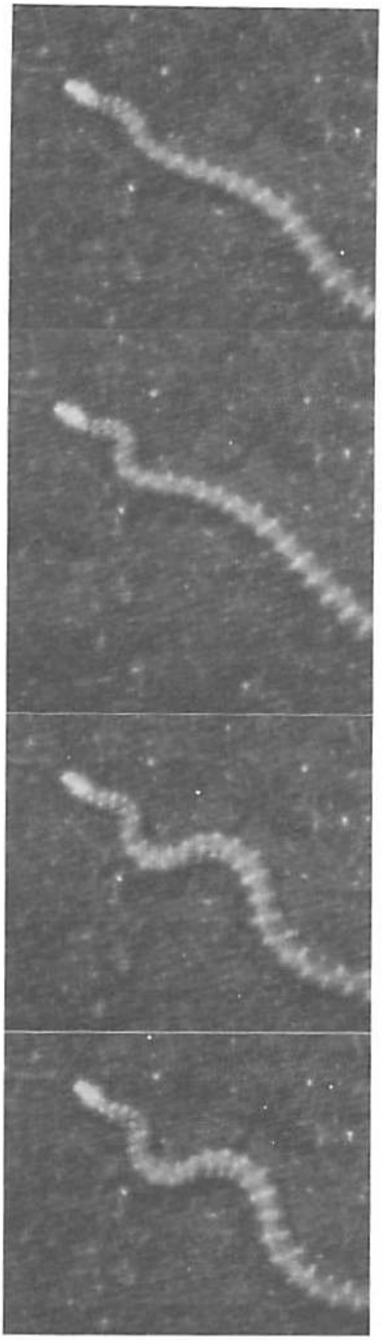

Figure 5. Concertina locomotion showing the "slippage" of the head. In this sequence a blue line has been placed on the same spot on the substrate in each frame. As the lateral body loops are expanding, the head can be seen to "slip" caudally relatively to the substrate reference point, reducing forward progress and locomotion efficiency.

points, these acrochordids would "slip" while performing concertina. By "slipping" we mean that the head, instead of remaining fixed during the initial phase of the locomotion, actually displaced caudally as the lateral loop was expanded (Fig. 5). This slipping was pronounced enough that it could easily be detected on the video records in 8 of the 25 trials (32%); the total incidence is likely higher.

Discussion

We observed three non-locomotor terrestrial behaviors in *Acrochordus granulatus*; head elevation, head probing with neck arching, and vertical burrowing. The level of head elevation we observed (~ 10% of body length), while less than what is found in either arboreal species (Byrnes & Jayne 2012) or during vertical posturing/defensive displays (e.g., Johnson 1975), is far greater than what we have observed in either the burrowing *Xenopeltis* or the large heavy-bodied viper, *Bitis arietans* (Young, pers. obs.). Aquatic head substrate probing by *A. granulatus* has been previously described (Lillywhite 1996); however, this appears to be the first description of the prominent neck-arching that accompanied the terrestrial head probing (Fig. 2). Similar probing behavior, with neck arching, has been described for some terrestrial snakes (e.g., Wake 1993; Kochva 2002). The vertical burrowing we observed in *A. granulatus* appeared to be kinematically similar to that of *Cerastes* (Young & Morain 2003), though unlike *Cerastes*, *A. granulatus* never achieved complete submersion.

Investigators commonly remark that acrochordids simply "feel different" when you are holding them (e.g., Mehrtens 1987), and that has certainly been our experience with *A. granulatus*. While there are definitely unusual features to the skin of *Acrochordis* (Schmidt 1918), extrapolating from the skin to the broader issue of body tone or body support must be done with caution. Statements that can be found online and in popular works that acrochordids can not support their body on land are hard to reconcile with the snake's ability to perform either head elevation (Fig. 1) or neck-arching to enhance cephalic probing (Fig. 2).

Our observations of concertina locomotion in *Acrochordus granulatus* are in good agreement with the earlier study conducted by Jayne (1986). Jayne reported instantaneous velocity, not mean locomotor velocity as was done in the present study; averaging the peak velocities he reported (~0.2 body lengths / s) over the course of the locomotor cycle would produce a value very similar to the mean velocity (0.02 body lengths / s) reported herein. By comparison in a recent study of terrestrial locomotion in sub-adult yellow anacondas (*Eunectes notaeus*) we found mean velocities for concertina locomotion of 0.07 body lengths/s (Young, pers. ob.) or roughly three times the velocity achieved by *Acro-*

chordus. The relatively low locomotor velocities achieved by *A. granulatus* presumably result, at least in part, from the relatively small lateral loops formed, and from the "slippage" that was observed against the substrate (Fig. 5). The caudal slippage of the head suggests that the snake is unable to establish robust anisotropic frictional contact points along its ventral surface. This may reflect the absence of scutes in acrochordids, the relative symmetry of the scale ornamentation of these snakes (which is present on the ventral surface), or the "loose" connection between the skin and the underlying body wall. In this context it is interesting to note that *A. granulatus* achieved very similar locomotor speeds when performing concertina locomotion over low friction (linoleum; Jayne 1986) and high friction (wetted topsoil, present study) substrates.

Herein we offer a brief description of a form of terrestrial locomotion that may be unique to acrochordids. We hypothesize that when these snakes form localized coalesced segments of their (loose) skin, the ventral skin forms a fold or "keel" as is seen when these animals move through the water (e.g., Lillywhite 1996). If the ventral skin forms a fold or keel (even if it is much smaller than is seen during aquatic locomotion), it would substantially increase the friction with the substrate. In this hypothesis, the peristaltic-like movements of the coalesced region of skin would be analogous to the rhythmic movements of the ventral scutes during rectilinear locomotion (Lissman 1950). Additional observations, particularly of the ventral surface of the animal, will be required to elucidate the functional basis and locomotor significance of this behavior.

Despite their local abundance and economic significance (e.g., Houston & Shine 1994; Shine et al. 1995), acrochordids are rarely studied in the field. These interesting snakes tend to do poorly in captivity, and are rarely kept for long periods (Banks 1989). Thus, understandably, many of the popular accounts of *Acrochordus* are not based on personal experience. This may have led to an exaggeration of the "unique" aspects of these animals as they relate to terrestrial locomotion. While *A. granulatus* will never be confused with *Coluber*, we found this species to exhibit typical (if slow) terrestrial exploratory behavior and locomotion.

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Comments on *Xenochrophis cerasogaster* (Cantor, 1839) (Serpentes: Natricidae) with remarks on its natural history and distribution

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ABSTRACT.– Additional morphometric data on the little known snake species *Xenochrophis cerasogaster* is provided and the hemipenis is described in detail. Natural history is discussed and data from newly collected specimens are incorporated with existing information. The distribution of this species is within a narrow geographic range and is obviously limited to wetlands. Despite having been previously included by some workers in the fauna of Malaysia, this species not been recorded reliably from this country and it is consequently delisted from the Malaysian herpetofauna.

KEYWORDS.– *Xenochrophis cerasogaster*, Assam, Malaysia, wetland habitat

Introduction

The natricid snake genus *Xenochrophis* Günther, 1864 is represented by thirteen valid species worldwide (Uetz 2011; Vogel & David 2012). It was erected by Günther (1864) for the species *Psammophis cerasogaster* Cantor, 1839 (type species by monotypy). Later Malnate & Minton (1965) compared the members of the genus *Fowlea* Theobald, 1868 (type species *Tropidonotus punctulatus* Günther, 1858) namely *F. piscator, F. vitatta* (Linnaeus, 1758) and *F. punctulatus* with *X. cerasogaster* and concluded that *X. cerasogaster* and species of *Fowlea* are congeneric and thus the genus *Fowlea* was synonymised with *Xenochrophis*. Recently, although with a very shallow taxon-sampling, it was shown that the genus *Xenochrophis* is not monophyletic (Dubey *et al.* 2012), and that *X. vittatus* seems to be more closely allied to *Rhabdophis* Fitzinger, 1843 (Pyron *et al.* 2011; Guo *et al.* 2012).

In India seven species of this genus have been recorded (Das 2003). Ahmed *et al.* (2009) have reported *Xenochrophis piscator* (Schneider, 1799), *X. flavipunctatus* (Hallowell, 1860), *X. schnurrenbergeri* (Kramer, 1977), *X. sanctijohannis* (Boulenger, 1890) and *X. cerasogaster* (Cantor, 1839) from Northeastern India, whereas Sanyal & Gayen (2006) reported *X. punctulatus* (Günther, 1858) from Arunachal Pradesh. The records of *X. flavipunctatus* from northeastern India are doubtful and the validity of *X. sanctijohannis* as a species distinct from the widespread *X. psicator* is still questioned (Vogel & David 2012).

Although formally named and described as early as 1839, *X. cerasogaster* is still rather

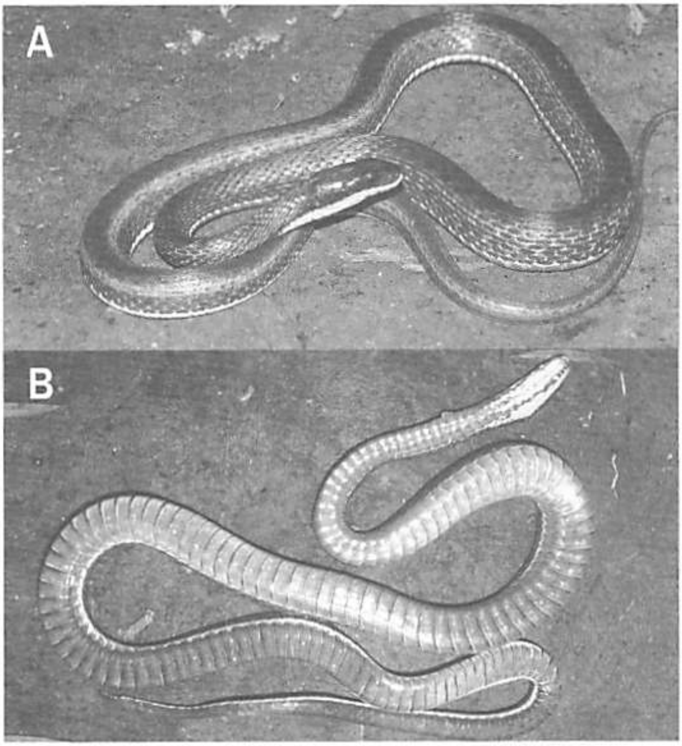

Figure 1. Dorsal and ventral view of live *Xenochrophis cerasogaster* from Deeporbeel wetland, Assam.

poorly known. *Amphiesma schistaceum* Jan, 1865 originating from "Indes Orientales" is considered a subjective junior synonym (fide Smith 1943). The species is distributed within a narrow geographic range and is known to occur in the following countries and localities: Pakistan. *Sindh Province* (Manchar Lake, Dadu and Sanghar Districts; Mirpur Sakro, Hyderabad District, Gharo, Tatta District; Jati Sindh District). Nepal. *Rupandehi* (Devanandpur). India. *Assam* (Goalpara and Guwahati); *Bihar* (Purnia); *Meghalaya* (Khasi Hills, previously mentioned from the state of Assam); *Uttar Pradesh* (Fyzabad); *West Bengal* (no locality); as well as in the Ganges Valley. Bangladesh. *Barisal Division* (Char Kajal) (Günther 1864; Boulenger 1899; Wall 1923; Smith 1943; Minton 1966; Mertens 1969; Khan 1988; Mathew 1995; Schleich & Kästle 2002; Khan 2004; Shah & Tiwari 2004; Khan 2006; Kabir *et al.* 2009; Sourav & Purkayastha 2011). It has also been reported from Perak and Penang Island in Peninsular Malaysia (Cantor 1847; Günther 1864; Boulenger 1912; Smith 1930). Most of our knowledge on this snake is based on preserved specimens and the natural history is still largely unknown. We present a summary of morphological and distributional information along with notes on its natural history based on new observations made on freshly collected specimens.

Materials and Methods

Our field study was conducted in Deeporbeel, (26°07'47.71" N, 91°39'16.42" E), the lone Ramsar site in the state of Assam. Deeporbeel is a wetland with a water-holding capacity of 10.1 km^2 that extends up to 40.1 km^2 during floods. It is a proposed bird sanctuary. It is situated at about 18 km from the capital city of Assam, Guwahati, on the north bank of river Brahmapu-

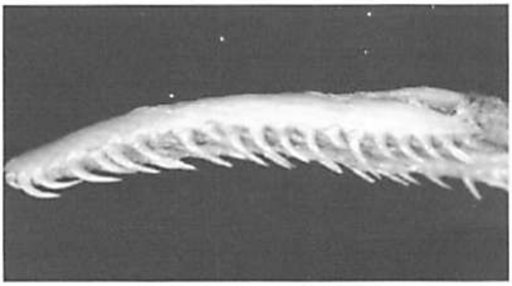

Figure 2. Maxillary dentition of *Xenochrophis cerasogaster.*

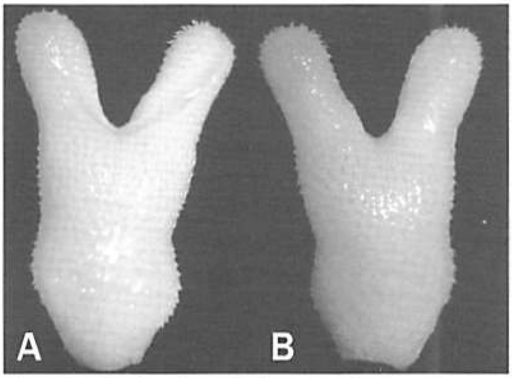

Figure 3. Hemipenis (sulcal and asulcal surface) of *Xenochrophis cerasogaster.*

Table1. Mensural and meristic characteristics of examined specimens of *Xenochrophis cerasogaster*.

Sp no.	**JP0020**	**JP0018**	**JP0022**	**JP0096**	**JP0117**	**JP0021**	**JP0131**	**JP132**	**JP0130**	**MNHN 1962-224**	**MNHN 1962-223**	**MNHN 822**
LOCALITY	Guwahati, India	Guwahati, India	Guwahati, India	Guwahati, India	Guwahati, India	Guwahati, India	Guwahati, India	Guwahati, India	Guwahati, India	Mirpur sakro, Pakistan	Mirpur sakro, Pakistan	Indes Orientales
SEX	M	F	M	F	M	M	M	M	F	M	M	M
VEN	144	147	149	147	139	142	147	149	150	151	149	143
SC	49+	62	78	71	69+	70	52+	68	66	80	78	78
SL	9/9	9/9	9/9	9/9	9/9	9/9	10/9	9/9	9/9	9/9	10/9	9/9
SLTE	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/4
IL	9/9	9/9	9/9	9/9	9/9	9/9	9/9	10/9	9/10	9/9	10/10	10/10
DSR	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17
TEMP	1+2/2+3	2+2/2+2	2+2/2+2	2+2/2+2	2+2/2+3	2+2/2+2	2+3/2+3	2+2/2+2	2+2/2+2	2+3/2+3	2+3/2+2	2+2/2+2
PREO	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
POSTO	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	4/3	3/3
SVL	485	654	470	655	349	445	540	565	550	335	432	400
TL	120	170	139	210	114+	165	130	145	160	117	150	156

tra and also is an important flood plain lake of Assam (Fig. 4A). The vegetation in the wetland is characterized by water hyacinth (*Eicchornia crassipes*), fox nut (*Euryale ferox*), esthwaite waterweed (*Hydrilla verticillata*), azolla (*Azolla pinnata*), with water cashewnut (*Trapa bispinosa*) being the dominant plant.

The morphological study is based on 24 specimens of which three are from the collections of Muséum national d'Histoire naturelle, Paris (MNHN), seven from the Natural History Museum (London) (BMNH), five from the Naturkundemuseum *Senckenberg*, Frankfurt (SMF) and the remainder were collected during our field survey at Deeporbeel. All the freshly collected specimens were preserved in 10% formaldehyde and are in the personal collection of Jayaditya Purkayastha (JP). Measurements were taken using Mitutoyo dial calipers with 0.02 mm precision. Ventral scales were counted following Dowling (1951) and the subcaudals were counted excluding the terminal scute. Detailed structure of the hemipenis was studied after eversion by injecting water through the 15th subcaudal scale. Abbreviations used are: Sp no. (Specimen number); Ven (number of ventrals); Sc (number of subcaudals); SVL (snout to vent length); TL (tail length); ToL (total length); SL (number of supralabials); IL (number of infralabials); SLTE (supralabials touching the eye); Temp (number of temporals); PreO (number of postoculars); DSR (dorsal scale rows).

Results

Description and variation.– The morphological characterization of *Xenochrophis cerasogaster* is based on 24 specimens (Table.1). The species is moderately sized (SVL up to 655 mm), body slender and cylindrical; head slightly distinct from the neck; dorsal scales strongly keeled, in 19 (anterior) /19 (midbody) /17 (posterior) rows. Eye moderate, rostral wider than high, pupil round, nostril lateral, 9, rarely 10 supralabi-

Sp no.	BMNH 60.3.19.1223	BMNH 53.8.12.42	BMNH 1907.2.14.2	BMNH 1907.2.14.5	BMNH 1907.2.14.8	BMNH 51.5.9.2	BMNH 52.9.13.252	SMF 57344	SMF 63045	SMF 57343	SMF 50463	SMF 63046
LOCALITY	Pinang, Malaysia	Khasi hills, India	Fyzerabad, India	Fyzerabad,	Fyzerabad, India	"India"	"India"	Jati, Sind, Pakistan	Jati, Sind, Pakistan	Jati, Sind, Pakistan	Gharo, Pakistan	Jati, Sind, Pa-kistan
SEX	M	M	M	F	F	F	F	F	F	F	F	M
VEN	141	139	144	149	149	146	143	154	153	154	155	148
SC	67	76	72 +	63	66	70	65	71	65	71	inc.	inc
SL	10/9	9/9	9/9	9/9	9/9	9/9	9/9	9/9	9/9	9/9	9/10	9/9
SLTE	5/6	4/4	4/4	4/4	4/4	4/4	4/4	4/4	4/5	4/4	4/4	4/4
IL	10/11	10/10	10/10	11/12	10/10	12/11	9/9	9/11	10/11	11/11	10/11	11/11
DSR	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17	19/19/17
TEMP	2+2/2+3	2+4/ 2+3	2+3/3+3	2+2/2+2	2+2/1+2	2+2/2+3	2+3/2+3	2+2/2+3	2+3/2+3	2+3/2+3	2+2/2+3	
PREO	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	
POSTO	4/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	3/3	
SVL	448	359	391	467	382	497	474	703	604	705	581	502
TL	150	133	135+	136	111	157	136	214	177	217	inc	inc

als, 4th touching the eye (except in specimen BMNH 60.3.19.1223 where 5/6 were touching the eye in right and left sides respectively), 9–10 (rarely 11 or 12) infralabials. Chin shields in two pairs, posterior one bigger, mental groove present. Temporals usually 2+2 (other occasional combinations are 1+2, 2+3, 2+4, 3+3), 1 large preocular, 3 (rarely 4) postoculars; Ventrals 139–151 in males and 143–155 in females; Subcaudals 67–80 in males and 62–71 in females.

Colouration in life.– Anterior part of body reddish brown, gradually fading off posteriorly, where it is rather blackish brown with a red tinge. Two light brown streaks parallel to each other run along the body axis. Streaks are not prominent in the anterior part but become so posteriorly (Fig. 1). Ventrals with a marbled lusture, reddish black in colour with white spots which gradually become indistinct towards the posterior part of the body (Fig. 1). Margins of the ventrals yellow with red spots, also becoming indistinct on posterior of the body. Subcaudals reddish black.

Dentition.– The nine specimens from Guwahati have 21–25 subequal maxillary teeth (Fig. 2).

Hemipenial morphology.– The hemipenis of *X. cerasogaster* is bilobed and spinose. The lobes are distinct and the apex is elongated (Figure 3). An uneverted hemipenis extends to the 4th subcaudal and a fully everted one extends to the 7th subcaudal. Spines cover the entire lobe margin and are scattered along the main body with very few or no spines near the basal region. It is longer than broad with the lobe width being 1/4th of the maximum hemipenial width. The sulcus spermaticus bifurcates much below the apex, thereby providing the structure with a distinct lobe, which is 1/3rd of the total hemipenis length. The sulcus spermaticus enters into the apical lobes almost up to its tip. There is no other ornamentation present on the hemipenis. However, the base of the structure is comparatively swollen and rounded.

Natural history.– *Xenochrophis cerasogaster* specimens encountered during the study were entirely aquatic. We never en-

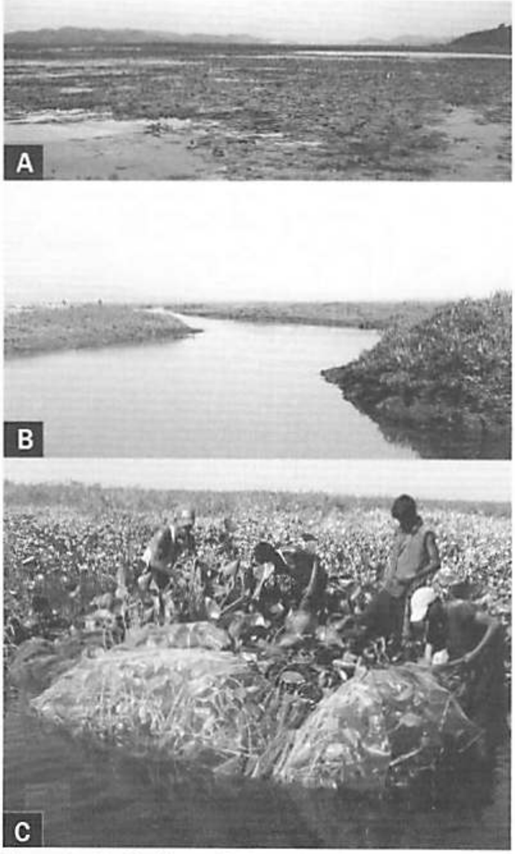

Figure 4. A) Habitat of *Xenochrophis cerasogaster*, wetland with aquatic vegetations, Deeporbeel, Assam, India. B) Manmade boat navigable waterways by clearing the vegetations, Deeporbeel. C) Indigenous fishing practice locally known as "sitki mara" practiced in Deeporbeel.

countered an individual on land, not even adjacent to the water body. The snakes were found to be active throughout the day. As seen from two events and also stated by fishermen in the study site, it ambushes its prey and occasionally is seen to assume a position in aquatic vegetation with the anterior part of its body raised. It uses a characteristic vertical lunging motion that cannot be unambiguously interpreted as a prey strike. Locally, the snake is called Bat-feti (Assamese: bat- path, feti- hooded), which literally means "a hooded snake in the way". This is based on the fact that it is often encountered on the manmade boat-navigable waterways in the course of clearing the vegetation (Fig. 4B) and since it raises its anterior part of the body when waiting for prey, which is often misconstrued as hooding. Contrary to previous records (Cantor 1847; Boulenger 1899) specimens in the study area were found to be rather gentle and timid as noted by Smith (1943) and Minton (1966).

A fishing technique locally known as "Sitki Mara" refers to a method in which the fishing net is placed below a mass of overhanging vegetation mostly comprising of water hyacinths (Fig. 4C). The vegetation is then slowly drawn towards the bank where the hyacinths are removed from above the net to get to the fishes. It has been observed that this snake most commonly gets trapped by this type of fishing along with another sympatric water snake species, *Enhydris enhydris* (Schneider, 1799), leading us to believe that both species prefer almost the same type of microhabitat. In the study area *X. cerasogaster* was found to be sympatric with its congeners *X. piscator* and *X. schnurrenbergeri*. We did not observe obvious niche segregation among these three species.

Discussion

Cantor (1839) explicitly mentioned *X. cerasogaster* from Bengal and Assam. He gave the scutellation of a single specimen. Smith (1943) noted the type to be a specimen figured in a colored sketch in the Bodleian Library, Oxford and the type locality to be situated near Calcutta (now Kolkata, West Bengal State, India) which is in all likelihood a presumption based on Cantor's handwritten note which states that the only live specimen that he observed was from near Calcutta in July 1836. Obviously this specimen served as a model for his drawing and is thus the holotype (Malnate & Minton 1965). MNHN 0822 is *X. cerasogaster* which is labeled as holotype of *Tamnosophis delesserti* (Fig. 5). Interestingly, as far as we know, the name *Tamnosophis delesserti* (MNHN822) was never published in the sense of the 4th edition of the International Code of Zoological Nomenclature (1999) and it is thus deemed to be an unavailable name.

The few distributional records of *X. cerasogaster* from India, Bangladesh, Nepal and Pakistan give the impression that the snake has a patchy distribution. The snake is also mentioned from the Malay Peninsula (Günther 1864; Boulenger 1899). Smith (1930) also listed *X. cerasogaster* from this region, but later deleted it (1943). Several workers have followed Tweedie

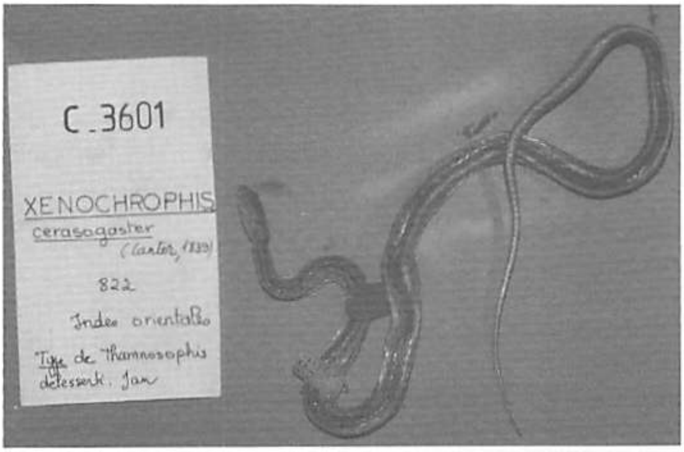

Figure 5. MNHN 822, specimen labeled as type of '*Tamnosophis delesserti*'.

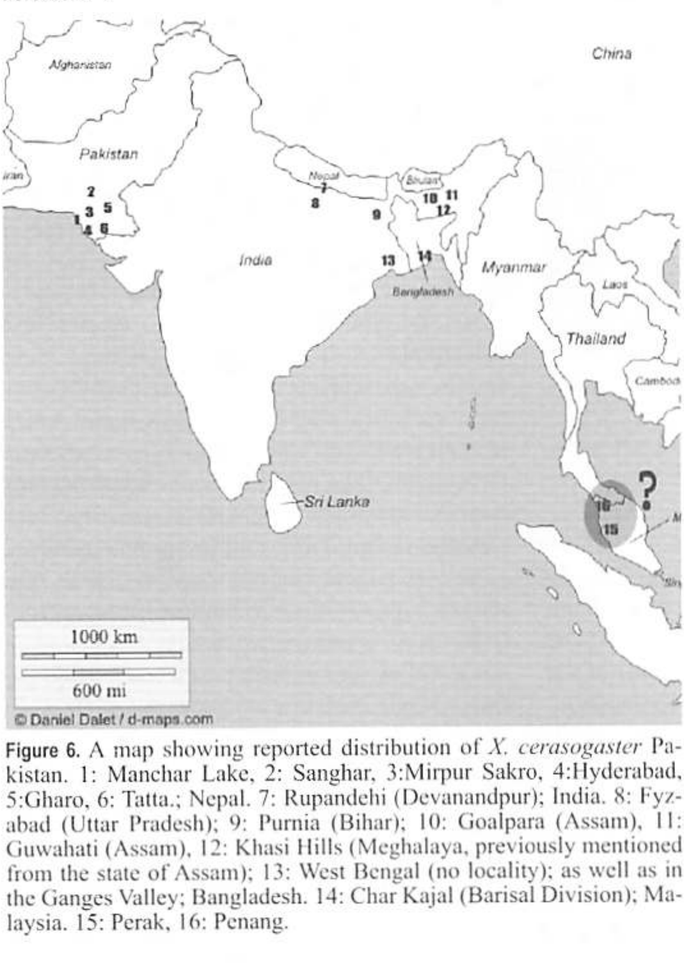

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Figure 6. A map showing reported distribution of *X. cerasogaster* Pakistan. 1: Manchar Lake, 2: Sanghar, 3:Mirpur Sakro, 4:Hyderabad, 5:Gharo, 6: Tatta.; Nepal. 7: Rupandehi (Devanandpur); India. 8: Fyzabad (Uttar Pradesh); 9: Purnia (Bihar); 10: Goalpara (Assam), 11: Guwahati (Assam), 12: Khasi Hills (Meghalaya, previously mentioned from the state of Assam); 13: West Bengal (no locality); as well as in the Ganges Valley; Bangladesh. 14: Char Kajal (Barisal Division); Malaysia. 15: Perak, 16: Penang.

(1953) in excluding it as member of the West Malaysian herpetofauna. However, the species was recently again included in the list of Malaysian species (Grismer *et al.* 2010) who mentioned it, following Cantor (1847), based on specimen BMNH 60.3.19.1223, and Boulenger (1912), based on specimen BMNH 53.8.12.42. The former specimen is from Penang Island and the later from Perak Province.

If we eliminate these two distantly allopatric Malayan specimens of *X. cerasogaster,* all other records of the species are restricted to a narrow, more northerly latitudinal range of 27° N–22.5° N. The Malaysian records of Penang (05°15'47.64" N) and Perak (04°48'26.26" N) are well out of this range (Fig. 6). All other locality records are in the vicinity of major river systems originating in the Himalayas — the Brahmaputra, Ganges, Indus. Obviously these river systems may have played a vital role in the dispersal of this riparian snake.

Biogeographically the occurrence of *X. cerasogaster* in the Malaya Peninsula is highly unlikely. A possible explanation for the two records could be erroneous locality data. Such confusion, in which locality records were mixed or lapsus calami were introduced, is common and has been noted, for example, by Schulz & Entzeroth (1996) and Klauber (1956). The problem is especially acute with respect to many earlier naturalists (Bailey 1933). Cantor's collections of specimens labeled as from Penang Island have been shown to originate partly from other localities (Adler 2007). At the time of Cantor's activity material dispatched to Britain from this part of the world used to travel along the "silk route" and the goods that went from peninsular Malaya may have made an intermediate stop at Kolkata (= Calcutta), India. Goods from peninsular Malaya and from India were often interchanged. There have been no other records of this snake from Malaysia for over a century. Thus, Malaysia in all likelihood, should not be included in the range of this Himalayan river system species and Assam (India) and Sind (Pakistan) should be considered the easternmost and westernmost extents of its distributional range, respectively.

Our field observations accord with those from Pakistan reported by Minton (1966), who found these snakes to be abundant in quite shallow water with much emergent vegetation such as lotus, *Ipomoea* and water-lily. He further noted that *X. cerasogaster* are usually found in grass at the edge of marshes or resting on lily pads or other plants and swim away rapidly when alarmed. They are plentiful from the end of the rains until mid-November. Wall (1907) mentioned shrimp as major food for this species in Fyzabad (now Fyzerabad), India, but Minton (1966) found fish in the stomachs of two specimens. He reported that two specimens laid clutches of 20 eggs each during the first week of April. The eggs were slightly smaller and more globular than those of *X. piscator*. A juvenile 250 mm in total length was collected May 31 (Minton 1966).

This species is restricted to marshlands, a habitat which is today quite limited in extent in South Asia. Thus, the need to conserve remaining wetlands should be emphasized as a means of conservation action for this poorly-known water snake.

Acknowledgements

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Sexual dimorphism in leaf-toed gecko *Asaccus elisae* (Werner, 1895) (Sauria: Gekkonidae) from western Iran

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ABSTRACT.- Sexual size dimorphism occurs when the sexes of a species or a population differ in morphometric characters and in the body size. So far, sexual size dimorphism in the Iranian leaf-toed gecko, *Asaccus elisae*, is undocumented. In this study 75 specimens were collected from Kermanshah, Ilam, and Lorestan provinces in western and southwestern regions of the Iranian Plateau. The uni-and multivariate analyses performed on the morphometric data demonstrated that males are relatively larger than females.

KEYWORDS.- *Asaccus elisae*, Sexual dimorphism, Statistical analysis, Morphology, Iran

Introduction

The genus *Asaccus* Dixon and Anderson, 1973 is distributed in some parts of the Middle East region and also in the Arabian Peninsula and and parts of southwestern Asia, like Turkey. A characteristic of this genus is the absence of cloacal sacs and postanal bones (Dixon & Anderson 1973). *Asaccus* includes at least 16 species of which *A. elisae*, Werner's leaf-toed gecko, is the most widespread nominal taxon with populations occurring in Iran, Iraq, Turkey, and Syria (Papenfuss *et al.* 2010). Sexual dimorphism in *A. elisae* has previously been undocumented, hence the investigation of the degree of sexual size dimorphism in this species is of interest.

Sexual dimorphism (SD), defined as a phenotypic difference between males and females of a species and sexual dimorphism in body size, which is the result of a variety of selective forces, is a common phenomenon affecting the body size or other morphological characteristics, has been reported in numerous lizard species (Darwin 1871; Halliday & Verrell 1986; Andersson 1994; Braña 1996; Kratochvíl & Frynta 2006; Olsson *et al.* 2002). Sexual size dimorphism (SSD) is a fundamental and widespread biological phenomenon in which individuals of one sex are characteristically larger than those of the other sex for a given population or species (Cox *et al.* 2003). Numerous surveys have been carried out on sexual dimorphism in lizards (Trivers 1976; Stamps 1983; Carothers 1984; Rocha 1996; Molina-Borja 2003; Baird *et al.* 2003; Verrastro 2004; Bruner *et al.* 2005; Kaliontzopoulou *et al.* 2007; Fathinia *et al.* 2011). Sexual dimorphism in animals is expressed in three different aspects: behavior, size and shape (Selander 1972).

In this paper sexual size dimorphism in the leaf-toed gecko, *Asaccus elisae*, collected from western and southwestern Iran have been investigated and are discussed.

Material and Methods

We examined 75 (48 males and 27 females) adult specimens of *Asaccus elisae*. Five adult specimens (two males and three females) were borrowed from Hamedan Museum of Natural History, and the 70 remaining specimens were collected by hand during field work from September 2008 to September 2011 with the aid of an electric torch at night on the walls and ceiling of buildings and rocky areas of the Zagros Mountains in Naft-Shahr (33°59' N, 45°30'

E), Qasr-e-Shirin (34°31' N, 45°35' E), and Sarpol-e-Zahab (34°24' N, 45°52' E), in Kermanshah Province, Darr-e-Shahar (33°09' N, 47°24' E) in Ilam Province, and Pol-e-Dokhtar (33°09' N, 47°42' E) in Lorestan Province, in western and southwestern Iran. Many of specimens (20 male and 15 female) were dissected to determine sex based on the presence of testes or ovaries. The examined specimens are deposited in the Razi University Zoological Museum (number code specimens dissected RUZM-GA20.11–44, and intact specimens RUZM-GA20.45–71).

Using the SPSS 16 and S-PLUS 8 statistical packages, and employing a principal component analysis (PCA), all the specimens were initially examined based on 13 morphological characters. The characters used in this study are as follows: SVL: snout to vent length; HW: head width; HL: head length; HH: head height; EED: eye-ear distance; NED: nostril-eye distance; NL: neck length; LFL: length of forelimb; LHL: length of hind limb; SL: number of supralabials; IL: number of infralabials; NDT: number of dorsal tubercles at midbody; SDLT: subdigital lamellae under the fourth toe. Morphometric measurements were taken by digital calipers model Shoka Gulf to the nearest 0.01 mm, and for meristic characters a stereo microscope was used.

Results

Values for the metric characters as well as the direction of differences and the significant characters ($P < 0.05$) are summarized in Table 1.

One-way ANOVA.– Clear differences in the value of metric variables are observed between the sexes (Table 1). Males have relatively higher values for nine metric characters than the females. Males have a mean value of SVL 50.83 mm versus females 47.88 mm. Also head dimensions show significant differences between the sexes. Males have 9.22 mm, 13.16 mm, 5.79 mm, for HW, HL and HH respectively. For EED and NED males have mean values of 3.31 mm and 4.45 mm while females have 2.99 mm and 3.87 mm respectively. In LFL and LHL, these characters are significantly different between males and females, so that males have significantly higher mean values for LFL (20.41 mm) and LHF (28.40 mm) than females (LFL = 18.69 mm; LHF = 26.16 mm) ($P < 0.05$). All metric variables are male-biased. In the meristic variables there were no significant differences ($P > 0.05$) between the sexes (results not shown here).

Principal Component Analysis (PCA).– The results of the PCA for metric characters show that the first three axes collectively represent 72.08% of the total variation (Table 2). Of this, 57.75% is explained by PC1, with SVL, WH, HL, NED, LFL, and LHL mainly responsible for the observed variation, and 8.26% is explained by PC2, in which the NL had the highest value, and 6.06% is explained by PC3, in which HH has the most important role.

Discussion

Comparative studies of sexual dimorphism should generally encompass body size as a

Table 1. Results of the one way ANOVA test in the measured morphological characters in males and females of *Asaccus elisae*. N: Number of individuals; SEM: Standard error of the Mean; D of d: Direction of difference. All measurements in millimeters (mm).

		SVL	HW	HL	HH	EED	NED	NL	LFL	LHL
	Mean	50.83	9.22	13.16	5.79	3.31	4.15	8.45	20.41	28.40
Male	N	48	48	48	48	48	48	48	48	48
	SEM	0.81	0.19	0.21	0.13	0.07	0.08	0.14	0.48	0.60
	Mean	47.88	8.54	12.27	5.27	2.99	3.87	7.76	18.69	26.16
Female	N	27	27	27	27	27	27	27	27	27
	SEM	0.92	0.21	0.22	0.14	0.07	0.09	0.15	0.56	0.74
D. of d.		M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F	M>F
F-value		5.87	5.44	8.02	6.79	9.06	4.86	10.53	5.17	4.36
P-value		0.018	0.022	0.006	0.011	0.004	0.031	0.002	0.026	0.040

Table 2. Loadings from principal component analysis of metric and meristic characters of *A. elisae*. Variables loading strongly on each principal component are shown in bold.

Variables	PC1	PC2	PC3
SVL	**0.971**	-0.052	-0.079
WH	**0.961**	0.006	0.066
HL	**0.966**	-0.047	-0.133
HH	**0.822**	0.086	**0.550**
EED	**0.889**	-0.168	-0.136
NED	**0.944**	-0.028	0.002
NL	**0.698**	**0.699**	-0.139
LFL	**0.937**	-0.152	0.030
LHL	**0.932**	-0.161	-0.132
Eigenvalues	12.128	1.735	1.274
% of Variance	57.75	8.26	6.06
Cumulative%	57.75	66.01	72.07

potential determinant (Fairbairn *et al.* 2007). The evolutionary result of selection acting differently on body size and rest of male and female traits is sexual size dimorphism (Andersson 1994). Rensch's rule (Rensch 1950) states that females tend to be larger than males in small species, whereas males are larger than females in large species, also Rensch's rule states that sexual size dimorphism characteristically increases with size when males are the larger sex and decreases with size when females are the larger sex (Fairbairn 1997, Abouheif & Fairbairn 1997; Colwell 2000; Cox *et al.* 2007; Fairbairn *et al.* 2007). In some lizards the SVL in males is greater than in females, because larger males are more likely to survive or mate with females (Anderson & Vitt 1990). In other lizards, for example *Mediodactylus heteropholis* (Minton, Anderson, and Anderson, 1970) (Červenka *et al.* 2010) and *Tropiocolotes helenae fasciatus* (Schmidtler & Schmidtler, 1972), this is not the case (Madsen & Shine 1993; Torki 2007; Fathinia *et al.* 2011).

Sexual dimorphism is widespread in lizards, with the most consistently dimorphic traits being head size (males have larger heads) and trunk length (Torki 2007; Fathinia & Rastegar-Pouyani 2011). This is the case for *Asaccus elisae*. Both sexes have evolved different body or head sizes to use different niche dimensions, such as microhabitat type, perch height, or diet (Smith & Nickel 2002). In *A. elisae* sexual size dimorphism occurs in general body size and several body parts, with males being significantly larger than females in nine out of thirteen studied characters. In the snout-vent length, length of forelimbs, and length of hind limbs, the males of *A. elisae* have higher values than those in females. Long limbs increase maximum sprint speed, allowing lizards to catch prey or escape predators more efficiently. However, shorter limbs are favored on narrow perches because they enhance agility relative to longer limbs (Calsbeek & Smith 2003). Males tend to have longer limbs, which can increase sprint for an escape from predators or facilitate chasing females for successful mating (Fathinia & Rastegar-Pouyani 2011). Head width in males is usually greater than in females (Smith & Nickel

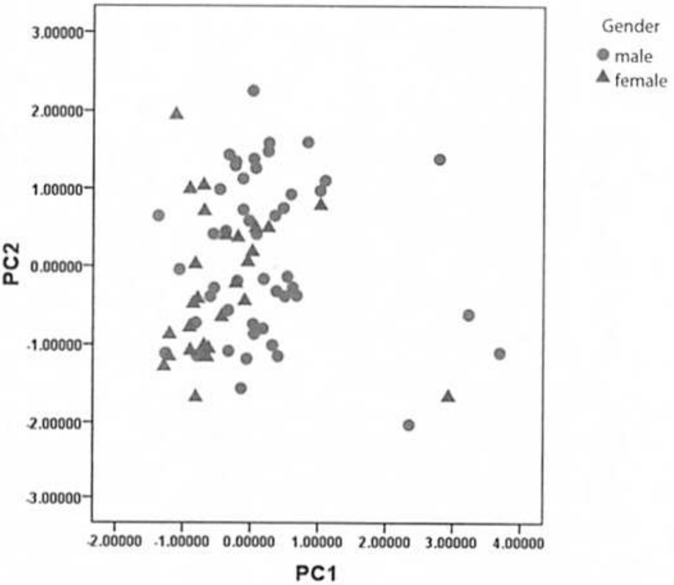

Figure 1. Ordination of the individual males and females of *Asaccus elisae* on the first two principal components. Note the relative separation of males and females along PC1.

2002). This is true for *A. elisae* as well as for the two additional characters (HL and HH).

Sexual selection may favor large females, because female fecundity is proportional to body size (Darwin 1871; Shine 1988; Braña 1996). Accordingly, clutch size indeed usually increases with female body size among lizards (e.g. Braña 1996; Cuadrado 1998). The Gekkonidae have invariant clutches of one to two eggs with relatively large size (Anderson 1999) and so selection for large female size cannot be attributed to increased fecundity. This is also the case with *A. elisae* as there is no clear-cut difference between the males and females in body parts and proportions as well as in meristic characters, though the males generally tend to be more slender than females.

In conclusion, based on this study it was shown that there is no distinct pattern of sexual dimorphism in meristic characters in *Asaccus elisae*. However, in metric characters the sexes are, to some extent, separated as revealed by the PCA (Fig. 1), therefore, Rensch's rule is not fully applicable for *Asaccus elisae*.

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New locality records of the recently described gecko *Hemidactylus aaronbaueri* Giri, 2008 with additional notes on natural history

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ABSTRACT.– A new gecko, *Hemidactylus aaronbaueri* Giri, 2008 was recently described from the northern Western Ghats of Maharashtra, India. This is a chiefly rupicolous species and only known from the type locality and type series. Recently we recorded this species from a few new localities in the northern Western Ghats. This appears to be a habitat specific gecko and is mostly seen on rocky cliffs. Our observations from these new localities provide new insights into habitat and natural history of this species. Morphological and meristic data is largely consistent with the data published along with the original description on this species.

KEYWORDS.– *Hemidactylus aaronbaueri*, new locality, natural history, habitat, distribution.

Introduction

Hemidactylus aaronbaueri is one of the largest Indian *Hemidactylus*, reaching a snout-vent length of at least 128 mm (Giri 2008). Giri described this species in 2008 based on a series of four adult and one sub-adult specimens collected from near Ghatghar, Taluka Junnar, District Pune, Maharashtra, India (19°17'28 N, 73°40'36 E; 248 m a.s.l.).

According to the original description *H. aaronbaueri* is a rock dwelling, nocturnal and very active gecko which is usually found on rocky cliffs. The species is currently only known from the type locality and type series. During recent survey work, we recorded the occurrence of this species from six new localities, all of which are hill forts surrounded by mixed deciduous forest in the northern Western Ghats. The rocky walls and caves of these forts are inhabited by this species. Apart from this a few individuals were also observed on rocks near a small stream in forest.

In spite of its large size and occurrence at a well frequented tourist spot, this gecko was overlooked as it was long subsumed under *Hemidactylus giganteus* Stoliczka, 1871 (Soman 1966; Chopra 1968), a species mostly known from the Eastern Ghats. *Hemidactylus aaronbaueri* has also been confused with its sympatric but much more widespread congener *H. maculatus* Duméril & Bibron, 1836, which is commonly found in the northern Western Ghats. Thus, *H. aaronbaueri* still remains a very poorly known species. Here we provide ancillary information on new localities, habitat and natural history of this gecko based on recent observations.

Material and Methods

Specimens of *Hemidactylus aaronbaueri* were collected from Peth Fort (BNHS 1872), near

Ambivili village, Raigad District; Gorakhgad (BNHS 1874), Taluka Murbad, Thane District; Sudhagad (BNHS 1893), Taluka Pali, Raigad District and Naneghat (CESL 092, CESL 128 and CESL 130), Taluka Junnar, Pune District, Maharashtra, India by Saunak Pal, Prathamesh Ghumare and Mrugank Prabhu. Apart from this, we have also added three previously collected individuals of *H. aaronbaueri* housed in the ZSI (Kolkata) collection in this study. These specimens were collected from Bhairavgadh Fort (ZSI 21648A, ZSI 21648B and ZSI 21648C), Karjat Taluka, Pune District (formerly Kolaba District), Maharashtra, India (19°19'06.24" N; 73°42'51.13" E; 680m msl) on 27 January 1965 by P. W. Soman. The data is gleaned based on material in the collection of the Bombay Natural History Society (BNHS), Mumbai; Zoological Survey of India (ZSI), Kolkata and Centre for Ecological Sciences (CES), Bangalore.

Hand collected specimens of *Hemidactylus aaronbaueri* were euthanized, fixed in 10% formalin, and transferred into 70% ethanol. Measurements were taken with a Mitutoyo dial caliper (to the nearest 0.05 mm) following Giri (2008). Scale counts and external observations of morphology were made using a Wild M5 dissecting microscope.

Results

All the new localities for *Hemidactylus aaronbaueri* are situated in the northern Western Ghats and are surrounded by mixed deciduous forests (Fig. 1). Raigad Fort is ca. airline 130 km south-west of Ghatghar, the type locality, and represents the southernmost locality for *H. aaronbaueri*. In most of these new localities *Hemidactylus aaronbaueri* is abundant and is found in hill forts, except at Bhimashankar Wildlife Sanctuary, in the Pune District, Maharashtra, where it was observed on rocks near a small stream.

Peth/Kotligad (Fig. 2A) is a small fort located in the Raigad District, Maharashtra (18°59'55" N, 73°30'73" E; 650 m.) with a small cave at its base. On 28 June 2008 the first author (SP) observed five large geckos on the rocky cliff of this fort at 12h40. An adult male was collected (BNHS 1872) and confirmed as *Hemidactylus aaronbaueri*. Most of the geckos were found motionless near crevices in the rocky cliffs and moved inside when approached. Although *H. maculatus* was also seen sharing this habitat with *H. aaronbaueri*, it was found about 5 m away on a stone arch (gate) of the fort. *Hemidactylus* cf. *brookii* was also seen in the same habitat.

Sudhagad is another fort near Pali in the Raigad district, Maharashtra (18°32'24" N, 73°19'12" E; 645 m). On 7 August 2008, five individuals of *Hemidactylus aaronbaueri* were observed in a hole in the rocky arch (Mahadarvaja) of Sudhagad. More individuals were observed on the ceiling of an old rocky water tank situated on the slopes of the hill (Fig. 2C). A single individual (BNHS 1893) was positioned upside down under a large rock adjacent to the tank and was collected at 13h30. No other gecko species were seen in the vicinity.

Gorakhgad (Fig. 2B) is a fort in the Thane District, Maharashtra, India (19°11'50" N, 73°32'44" E; 620 m.). On 26 June 2008 SP observed an adult male gecko on a rocky cliff adjacent to the trail towards the fort. Another six individuals were observed at 13h10 on the rocky walls of a small cave at the base of this fort. Of these, one (BNHS 1874) was collected and identified as *H. aaronbaueri*. All others escaped inside crevices when disturbed. Three eggs, each ca. 20 mm long, along with an adult female (Fig. 2D) were observed in June 2008 at Gorakhgad, inside a crevice in a small cave ca. 2.5 m above the floor. These geckos were found sympatrically with *H.* cf. *brookii*.

Naneghat is a mountain pass in the Western Ghats near Vaishakhare village in the Thane District, Maharashtra, India (19°17'32" N, 73°40'29" E; 744 m msl). On 27 July 2010, 17 individuals of *Hemidactylus aaronbaueri* were observed on the rocky cliffs near the man-made caves in the vicinity of the pass at 19h50. One individual was also observed inside a cave. Three individuals were collected, of which two were male and one female (CESL 092, CESL 130 and CESL 128, respectively). One individual of *H. maculatus* was also collected from a nearby rocky boulder (CESL 094) and another one was seen on a tree trunk. These geckos were found sympatrically with *H.* cf. *brookii*.

On 25 October 2008, two geckos (*H. aaronbaueri*) were observed on rocks near a small stream in Bhimashankar Wildlife Sanctuary,

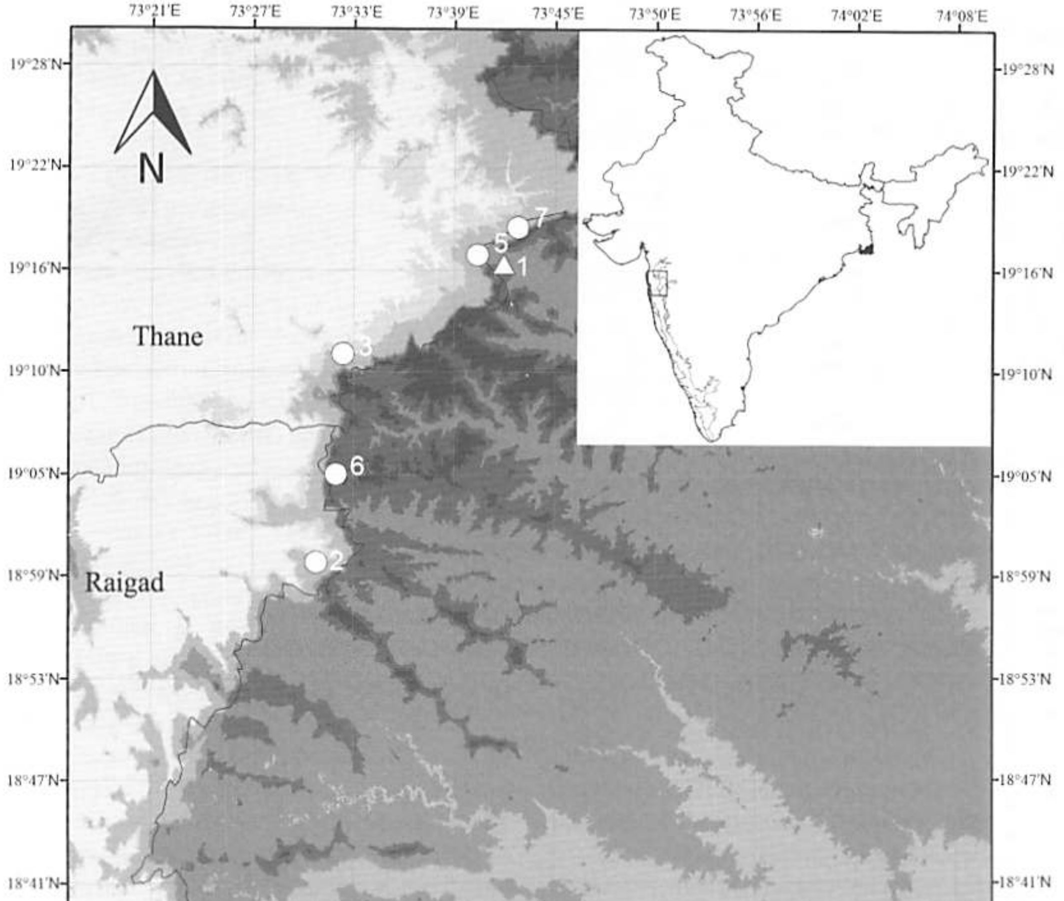

Figure 1. Topographic map of the localities of *Hemidactylus aaronbauerii.* Inset map of India showing the enlarged region of Northern Western Ghats. Numbers indicate each locality as follows: 1. Ghatghar; 2. Peth fort; 3. Gorakhgad; 4. Sudhagad; 5. Naneghat; 6. Bhimashankar; 7. Bhairavgadh and 8. Raigad.

Pune District, Mahrashtra, India (19°08'06" N; 73°53'81" E; 983 m msl) at about 16h40. One of these geckos was captured, measured, photographed and then released. No other gecko species were seen in the area but three Brahminy Skinks, *Eutropis carinata* (Schneider, 1801), were found sharing the same habitat.

On 8 October 2011, five *H. aaronbaueri* were seen hiding inside crevice of a stone arch of Raigad Fort, Raigad District, Mahrashtra, India (18°14'09" N; 73°25'45" E; 466 m msl) at about 11h20. One of these geckos was captured, photographed and then released.

Night searches to Gorakhgad and Peth on 22 November 2008 and 9 December 2008, respectively revealed nine and seven geckos, respectively. Almost all of these were observed to be most active between 18h20 to 23h30. The geckos were stationary or moving slowly on the rocky walls foraging on insects. They would crawl rapidly for a short distance when approached, and then remained still. When an insect landed near a gecko it would move quickly towards it. The prey species observed in these two localities included mainly orthopterans and lepidopterans. One individual was also seen feeding on an odonate. A large *H. aaronbaueri* in Gorakhgad was seen eating a juvenile of *H.* cf. *brookii*. In Peth five *H. maculatus* were also seen, but were restricted to the forest floor and nearby tree trunks. On previous occasions two *H. maculatus* were found to be sharing a similar habitat to *H. aaronbaueri* during day (one in a cave, another on a stone arch).

The specimen collected from Sudhagad on 7 August 2008 (BNHS 1893) was retained in captivity for brief observations for a week. It was kept in a wooden box with small stones as a substrate and provided with grasshoppers, mantises and moths, which it readily fed on at night. The gecko hid under the rocks during the day and became active at dusk.

Our morphological data of the new specimens from the BNHS, CES and ZSI collection is largely in consistent with the data published by Giri (2008) in the original description of this species. The only variation observed was related to the specimen from Sudhagad (BNHS 1893), which has 14 lamellae under fourth toe of right pes.

Discussion

Our new records and observations of *Hemidactylus aaronbaueri* from Peth, Gorakhgad, Sudhagad, Naneghat, Bhimashankar and Raigad, Maharashtra suggest that this gecko appears to be common in appropriate habitat. Because of its superficial resemblance to the Rock gecko *H. maculatus* or other large geckos (*H. giganteus*), this species might have been overlooked until now. In Maharashtra, *H. giganteus* has been reported from Pandava Caves, Kolaba District (Soman 1966) and Ozar, Nasik District (Chopra 1968). Giri (2008) mentioned that as these related specimens were not traceable and fresh material from these two localities, needs to be examined to determine if indeed the geckos found here are *H. giganteus*, or actually *H. aaronbaueri*. Interestingly P. W. Soman deposited three specimens of *Hemidactylus* in the collection of Zoological Survey of India, Kolkata, which were collected from Bhairavgadh Fort, Karjat Taluka, Kolaba District (now Pune District), Maharashtra, India on 27 January 1965. These specimens were eventually identified as *H. giganteus* and were mentioned in a note published by Soman (1966). These specimens are indeed *H. aaronbaueri* and are included in this publication. The other locality mentioned by Chopra (1968), Ozar in Nashik district is also close to the type locality of *H. aaronbaueri* and shares a similar habitat. Given the habitat preference, this species may also be present in other suitable regions of in the Northern Western Ghats.

Despite its distinctive coloration/pattern and high local density, the species has escaped the notice of herpetologists and has remained unknown. This situation parallels that of the *Calodactylodes aureus* Beddome, 1870 a large, brightly colored and highly vocal gecko of the Eastern Ghats; *Hemidactylus giganteus* Stoliczka, 1871 another large, widespread gecko in Peninsular India; *Hemidactylus prashadi* Smith, 1935 yet another large, conspicuous, widespread gecko in central and northern Western Ghats; *Hemidactylus albofasciatus* Grandison & Soman, 1963 a small ground dwelling gecko from southern Maharashtra; and *Hemidactylus scabriceps* Annandale, 1906 a recently rediscovered medium sized gecko from the eastern coast of Tamilnadu. Despite their conspicuousness and occurrence near human settlements,

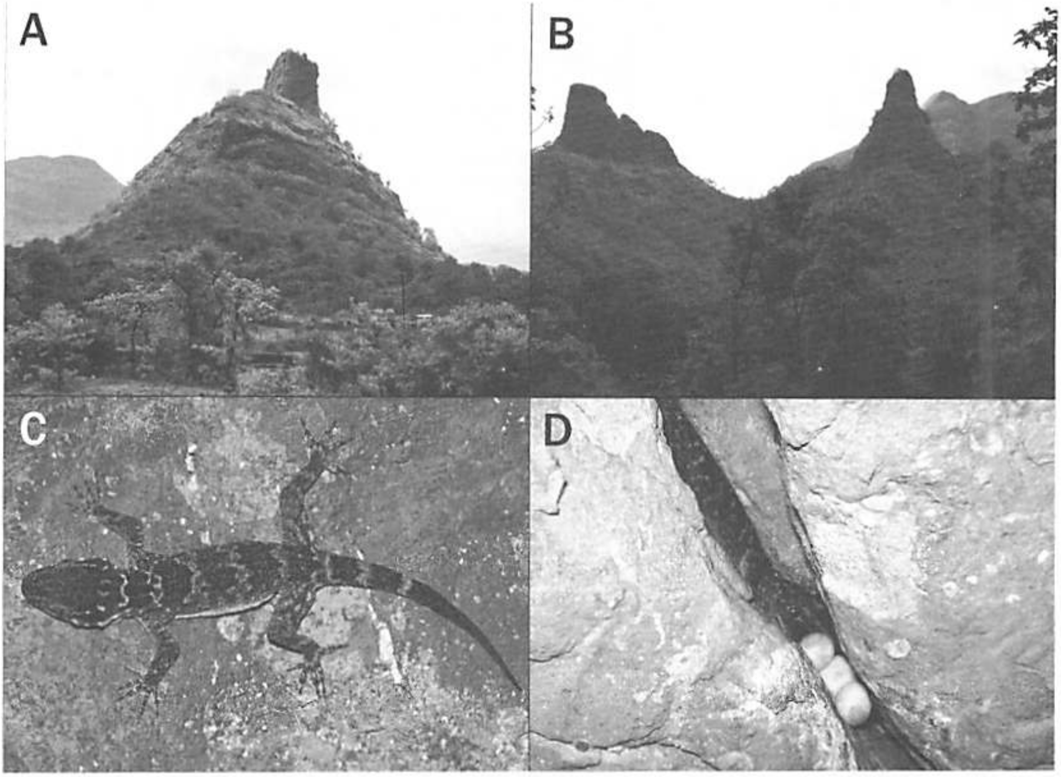

Figure 2. Habitat of *Hemidactylus aaronbauerii* surrounded by deciduous forest at (A) Peth Fort and (B) Gorakhgad (at right of photo). (C) Life photograph of adult *Hemidactylus aaronbauerii* seen on the ceiling of an old rocky water tank in Sudhagad (D) A female H. *aaronbaueri* with three eggs inside a crevice in a cave at Gorakhgad.

these species were until recently considered as among the rarest of Indian geckos (Bauer & Das 2001; Giri *et al.* 2003; Giri & Bauer 2006; Gaikwad *et al.* 2010; Ganesh & Chandramouli 2010).

The landscape in Peth, Gorakhgad and Sudhagad comprises altered habitats of forts with rocky ruin walls surrounded by patches of deciduous forests. The specimens from Bhimashankar were found between boulders near a small stream surrounded by semi-evergreen forest. A nearly exclusive association with rocky surfaces suggests that *H. aaronbaueri* is habitat specific and strictly rupicolous.

The forests in Peth, Gorakhgad, and Sudhagad are mixed deciduous and have huge rocky outcrops and caves, whereas that in Bhimashankar is of semi-evergreen type with boulders and streams. This shows that *H. aaronbaueri* may exist in different kinds of forests. We observed three eggs in June 2008 at Gorakhgad, inside a crevice in a small cave. The eggs were ca. 20 mm long. This shows the breeding season of these geckos to coincide with the monsoon. The occurrence of the adults throughout the year shows that this gecko is active throughout the year.

As a result this paper presents new additional localities for this gecko in the recently described, restricted-range species. However this data is preliminary and additional information on natural history, distribution and threats should be collected from throughout the range for the conservation of this large, regionally endemic gecko.

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Reproduction of Bowring's Supple Skink, *Lygosoma bowringii* (Scincidae) from Thailand

Lygosoma bowringii (Günther, 1864) is widespread in South East Asia and occurs in parts of West Malaysia, Philippines, Indonesia, China (Hong Kong), Singapore, India, Indochina west to Myanmar, and Australia (Christmas Island) (Uetz 2012). It is diurnal, terrestrial, subfossorial and has a diet of small insects (Das 2010). Information on reproduction of *L. bowringii* is limited and consists mostly of numerous reports of females laying clutches of 2–4 eggs (Smith 1935; Tikader & Sharma 1992; Manthey & Grossman 1997; Cox *et al.* 1999; Malkmus *et al.* 2002; Das 2004, 2006, 2007, 2010; McKay 2006). However, Pongsapipatana (1975), based on individuals from Sakaerat, northeastern Thailand, provided data on two egg clutches, sizes (respectively one and four eggs), egg size (12.4 x 7.3 mm, n = 1) and other characteristics, hatchling size (SVL 22.0–23.0 mm, n = 3) and incubation period. He provided a photograph of a clutch, described the environment in which eggs are laid (leaf litter) and correlated the egg deposition date with the monthly rainfall and average soil moisture in Sakaerat (eggs were collected in the wild from early July to end of August). Grismer (2011) presented observations suggesting *L. bowringii* is a year-round breeder in the Seribuat Archipelago, Malaysia. Information on the reproductive biology of lizards such as time of egg and sperm production, clutch size, and number of clutches produced are useful in formulating conservation policies (Gibbons 1994). Due to the difficulty in justifying collections of large monthly samples, utilization of museum collections for obtaining reproductive data has become increasingly important. The purpose of this paper is to present more detailed information on reproduction of *L. bowringii* from northeastern Thailand. Comparisons are made between the reproductive cycle of *L. bowringii* and other South Asian skinks.

A sample of 90 *L. bowringii* from Sakaerat (14.6000°N, 102.0327°E), 234 m elevation, Amphoe Pak Thong Chai District, Nakhon Ratchasima Province, Thailand collected in 1969, including 49 females (mean snout vent length, SVL = 56.37 mm ± 7.9 SD, range = 43–82 mm), 40 males (mean SVL = 51.1 mm ± 4.1 SD, range = 43–58 mm) and one subadult male (SVL = 38 mm) was examined from the herpetology collection of the Field Museum of Natural History (FMNH), Chicago, Illinois (Appendix).

For histological examination, the left testis was removed from males and the left ovary was removed from females. Enlarged yolking follicles (> 3 mm length) or oviductal eggs were counted. No histology was done on them. Tissues were embedded in paraffin and cut into sections of 5 µm. Slides were stained with Harris hematoxylin followed by eosin counterstain (Presnell & Schreibman 1997). Histology slides were deposited in FMNH. Slides of testes were examined to determine the stage of the spermatogenic cycle. Slides of ovaries were examined for the presence of yolk deposition or corpora lutea. The relationship between female clutch size and body size was examined using linear regression analysis; an unpaired *t*-test was used to compare male and female mean body sizes (SVL) using Instat (vers. 3.0b, Graphpad Software, San Diego, CA).

Four stages were observed in the testicular cycle (Table 1): (1) Regression, the seminiferous tubules contain spermatogonia with interspersed Sertoli cells (2) Early recrudescence, renewal of germinal epithelium for the next period of spermiogenesis has commenced. Primary spermatocytes are present; (3) Recrudescence, renewal of germinal epithelium has progressed, primary and secondary spermatocytes are present; (4) Spermiogenesis, lumina of seminiferous tubules are lined by clusters of sperm or metamorphosing spermatids. Spermiogenesis was observed in November through July (Table 1). The presence of 4/8 (50%) males in regression and 0/8 (0%) undergoing spermiogenesis in October indicates males do not produce sperm during this month. My finding of males from November exhibiting recrudescence or sper-

Table 1. Monthly distribution of stages in the testicular cycle of 40 *L. bowringii* males from Thailand.

Month	n	Regressed	Early Recrudescence	Recrudescence	Spermiogenesis
January	2	0	0	0	2
February	2	0	0	0	2
March	4	0	0	0	4
April	5	0	0	0	5
May	5	0	0	0	5
June	4	0	0	0	4
July	3	0	0	0	3
October	8	4	2	2	0
November	6	0	0	4	2
December	1	0	0	0	1

miogenesis suggests sperm production begins in this month. The smallest reproductively active male (spermiogenesis underway) measured 43 mm (FMNH 182313) and was collected in January. One smaller male (SVL = 38 mm) from December exhibited early recrudescence and was considered a sub-adult.

Mean body size (SVL) of female *L. bowringii* was significantly larger than that of males (unpaired t-test, t = 4.1, df = 87, P = < 0.0001). Five stages were observed in the ovarian cycle (Table 2); (1) Quiescent, no yolk deposition; (2) Early yolk deposition, basophilic yolk granules in the ooplasm; (3) Enlarged ovarian follicles (> 3 mm); (4) Oviductal eggs; (5) Oviductal eggs with concurrent yolk deposition. As no traces of embryos were noted, I concluded *L. bowringii* is oviparous, confirming previous observations available in the literature cited above. *Lygosoma bowringii* females were reproductively active March, May to July. There was a prolonged period August to December when a total of 25 females exhibited quiescent ovaries (Table 2). Three females (Table 1) (one each from March, May and June) exhibited concurrent yolk deposition for a subsequent clutch, indicating *L. bowringii* may produce multiple clutches in the same reproductive season. Mean clutch size for 17 females was 3.1 ± 0.90 SD, range = 2–5. Five is a new maximum clutch size for *L. bowringii*. The smallest reproductively active female (2 enlarged follicles, 4 mm each) measured 43 mm and was collected in June (FMNH 182119). A linear regression analysis revealed a significant positive correlation between female body size, SVL and clutch size for 17 *L. bowringii* females.

Table 2. Monthly distribution of stages in the ovarian cycle of 49 *L. bowringii* females from Thailand.

Month	n	Quiescent	Early yolk deposition	Follicles > 3 mm	Oviductal eggs	Oviductal eggs and yolk deposition
January	1	1	0	0	0	0
March	4	0	0	1	2	1
May	6	1	0	2	2	1
June	9	2	0	4	2	1
July	4	2	1	0	1	0
August	2	2	0	0	0	0
September	7	7	0	0	0	0
October	12	12	0	0	0	0
November	2	2	0	0	0	0
December	2	2	0	0	0	0

This is shown by the regression equation: $Y = -0.70 + 0.07X$, $r = 0.60$, $P = 0.01$.

The reproductive cycle of *L. bowringii* differs from those of other tropical skinks, which exhibit prolonged or continuous reproductive cycles (Inger & Greenberg 1966; Goldberg 2010; Fitch 1982). Female *L. bowringii* from August to December exhibited quiescent ovaries. Although no *L. bowringii* samples from August and September were available, no males from November were producing sperm, suggesting both sexes were reproductively inactive the latter part of the year. An examination of yearly variations in temperature and rainfall in Sakaerat, Thailand (worldweatheronline 2012) revealed mean monthly maximum temperatures varied slightly from maximum highs of 36°C in March and 37°C in April to 30°C in November and December. There was a downward trend in mean monthly maximum temperatures (33°C to 30°C) during the August to December period of reproductive inactivity. Considering precipitation, August (165 mm) and September (225 mm) were the two months with maximum rainfall (worldweatheronline 2012) that corresponds with the start of the *L. bowringii* period of reproductive inactivity. Whether increased precipitation has a negative impact on *L. bowringii* reproduction will require additional study.

In conclusion, my data, as well as the data from Pongsapipatana (1975), suggest that *L. bowringii* ceases reproduction in the latter part of the year in Nakhon Ratchasima Province, Thailand. Also, a new maximum clutch size of five is reported, hence the currently known clutch size variation is 1–5 eggs. Considering the extensive geographic range of *L. bowringii* (Uetz 2012) and the suggestion that it breeds throughout the year in the Seribuat Archipelago, Malaysia (Grismer 2011) further investigations on additional populations are needed to ascertain geographic variations in the reproductive cycle.

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Appendix

The following specimens of *L. bowringii* from Nakhon Ratchasima Province, Thailand comprise the basis for this study: FMNH 181847, 181856, 181864, 181865, 181886, 181917, 181925, 181936, 181944, 181945, 181948, 181965, 181968, 181970, 181972, 181976, 181983, 181986, 181993, 181996, 182016, 182043, 182049, 182052, 182054, 182056, 182059, 182066, 182069, 182072, 182075, 182077, 182088, 182095–182097, 182102, 182116, 182118–182120, 182124–182126, 182132, 182134, 182139, 182144, 182149, 182151, 182155, 182170, 182173, 182176, 182178–182180, 182183, 182184, 182188, 182190, 182202, 182205, 182207, 182208, 182218, 182225, 182234, 182235, 182237–182239, 182241, 182242, 182246, 182250, 182256, 182258, 182267, 182286, 182287, 182294, 182304, 182313, 182318, 182322, 182329, 182331, 182333, 182340.

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The status of the dorsal snake scale lophate microdermatoglyphic pattern

The first studies on the snake scale microstructure were presented by Leydig (1868, 1873). No other work on the subject appeared before that of Picado (1931), who announced the major importance of this character in snake systematics, confirmed by the works of Holtzinger-Tenever (1935) and Pockrandt (1937), also done with light microscopy. The first study of snake scale microstructure by electron microscope (T.E.M.) was done by Hoge & Souza Santos (1953). The term "microdermatoglyphics" was used for the first time by Dowling *et al.* (1972) who used a Scanning Electron Microscope (S.E.M.), and defined for the first time by Price (1981: 5) as "all features of snake scale surface sculpturing too small to be seen with the naked eye but which are resolvable under the scanning electron microscope". The first attempts to define the nomenclature of the microdermatoglyphic patterns were by Price (1981, 1982).

The terminology adopted by the (rare) authors currently working on the study of the dorsal snake scale microdermatoglyphics is still mainly based on that coined by Price (1982) who was himself inspired by the palynological nomenclature of Kremp (1965). Price's (1982) work, in which he enumerated and defined most of the major patterns and the pattern subtypes he had observed, was a very abbreviated version of his unpublished Ph.D. thesis defended in 1981. The pictures accompanying the pattern definitions by Price (1982) were very stereotyped. In order to really grasp the variation that Price understood for each pattern, it is actually necessary to examine all pictures presented in both works of 1981 and 1982 for each pattern, but this variation was however not expressed in the very laconic definitions of his 1982 work. A redefinition of all the patterns, presenting the variation within each one, seems necessary for future studies, as well for systematic works as for the study of the relation between the microstructure and the ecology of a given taxon.

A very important aspect of dorsal scale microstructure, not dealt with in Price (1981, 1982), but only later by Price & Kelly (1989), is the variation of the microstructure along the surface of the scale itself, following an antero-posterior axis. Price (1981, 1982) did not specify at which place on the scale the photographs were taken, and, as he himself noted (Price, 1989: 90), the existence of a transition between a basal and an apical pattern through a "microdermatoglyphic transition zone" (MTZ) was discovered by him only after his 1981 and 1982 works. Thus, the eleven patterns defined by Price in 1982 might not have been all based on the observation of the posterior part of the scales. Nevertheless, these eleven patterns are sufficient to classify most of the snake apical patterns known to date, except the scolecophidian patterns, since Price never observed them, and those of sea snakes, some of which were examined by Price for his Ph.D., but not mentioned in his 1982 work.

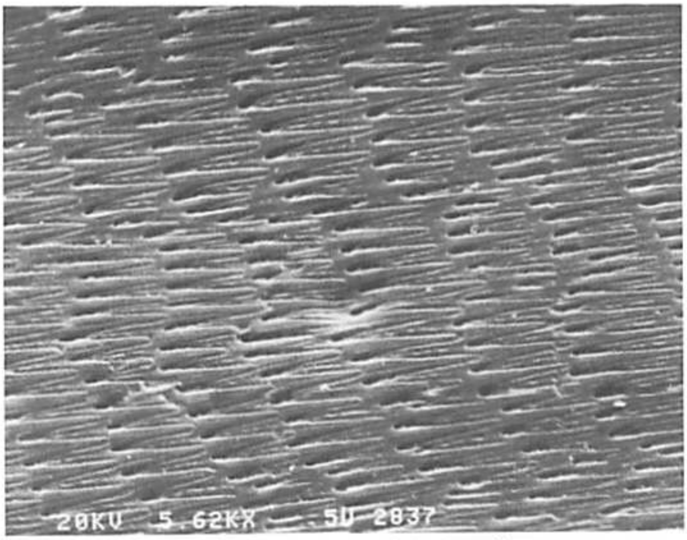

Figure 1. Echinate pattern, a member of the lamellate patterns group (here the central part of a mid-dorsal scale of an adult *Lycodon laoensis*, MNHN 1998.8549 from Chiang Mai, Chiang Mai Province, Thailand; for photography methodology, see Pauwels et al. 2000).

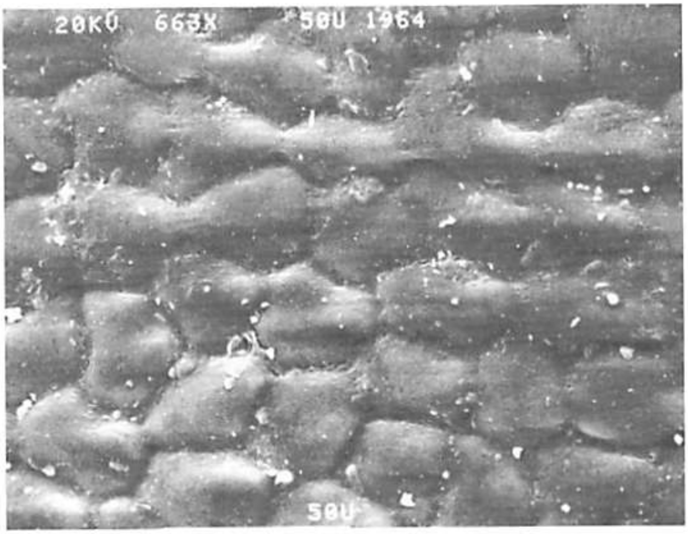

Figure 2. Tessellate pattern, a member of the tessellate patterns group (here the central part of a mid-dorsal scale of an adult *Trimeresurus albolabris*, MNHN 1998.0569 from Ban Salakern, Ban Lat District, Phetchaburi Province, Thailand).

In order to stabilize the nomenclature of the dorsal scale microdermatoglyphics, an ultimate reference should be chosen, as with type specimens for the definition of taxa in systematic zoology. The pictures presented by Price (1982) could logically serve as 'types' for each pattern. In the case that a pattern is not represented in that work, I would suggest to select it among the pictures presented in his Ph.D. thesis, in order to stay loyal to Price's conception of the patterns. Price himself (1990) noted that some authors (in particular Chiasson & Lowe 1989) wrongly interpretated his terminology, and appealed for "standardization and use of pre-existing terminology" (i.e., his own).

Many pattern subtypes were very briefly defined but unfortunately not illustrated by Price (1982): cristate striocristate, echinate echinulate, echinate subechinate, foveate foveoreticulate, lophate striolophate, papillate "secondarily microreticulate", and reticulate echinoreticulate. Among the major patterns, a single one was not illustrated by Price (1982), nor in all his subsequent works: the lophate pattern. It was vaguely defined as following: "having smooth longitudinal ridges" (Price, 1982: 296). The definition given for this pattern in his Ph.D., "with the outer surface thrown into ridges" (Price, 1981: 145) refers to his Fig. 158, which represents the microstructure of *Candoia carinata* (Schneider, 1801) (Boidae). According to the above mentioned processes, I regard this picture as the primary reference for the lophate pattern. A thorough examination of this picture, however, does not reveal any difference between this pattern and that illustrated on the same page for *Acrantophis madagascariensis* (Duméril & Bibron, 1844) (Boidae) (loc. cit.: fig. 157) which Price qualified as "strioreticulate". Likewise, there is no difference between the pattern said to be "striolophate" for *Phyllorhynchus browni* Stejneger, 1890 and *P. decurtatus* (Cope, 1868) (Colubridae) by Price (1981: 16, 67-68, figs. 6–7) and the pattern "reticulate, subtype strioreticulate" illustrated for *Xenochrophis piscator* (Schneider, 1799) and *Virginia striatula* (Linnaeus, 1766) (Colubridae) in his 1982 publication. Price (1981: 47) stressed the similarities between the striolophate pattern of *P. decurtatus* and the "strioreticulate" pattern of *Gloydius himalayanus* (Günther, 1864) (Viperidae).

As to the "subechinolophate" pattern of *Helicops danieli* Amaral, 1938 (Colubridae) (Price, 1981: 124), it is best described as a plicate pattern, exactly like that illustrated in Price (1982), which is fully consistent with the fact that Price (1983: 294) identified the microstructure of the closely related species *Helicops angulatus* (Linnaeus, 1758) as being "plicate". A comparison of the pictures illustrating the microstructure of these two species moreover shows that they are absolutely identical. Price (1981: 42) stressed the similarity between the pattern of *H. danieli* and those of *Regina rigida* (Say, 1825) (loc. cit., fig. 45, "echinoreticulate") and *Liodytes alleni* (Garman, 1874) (loc. cit., fig. 46, "echinoplicate and punctate"; qualified as "plicate, secondarily punctate" by Price, 1982, as "plicate" by Price, 1983: 293, and as "plicate (punctate)" by Price & Kelly, 1989). Price did not mention the echinoplicate and subechinolophate patterns in his 1982 work.

I hence conclude that the lophate pattern is a composite and artificial pattern, that should be abandoned. A number of patterns (corrugate, foveolate, granulate, lamelliform, rugulate, striate) quoted and defined by Price in 1981 were not listed in his 1982 paper. On the other hand, a plethora of new terms naming apical morphotypes (patterns) was provided by Price & Kelly (1989) without definitions. Price's patterns were divided in two major groups by Pauwels *et al.* (2000) on the basis of the elementary units visible through S.E.M. at the surface of the scales: either very elongated units perpendicular to the antero-posterior axis of the scale (lamellate patterns group, see Fig. 1), or sub-polygonal, typical cell-shaped, units (tessellate patterns group, see Fig. 2). Now that the lophate pattern is definitely eliminated from the microdermatoglyphic jargon, the group of the lamellate patterns comprises the following major patterns: canaliculate, echinate, fimbriate, papillate, plicate and reticulate. The tessellate patterns group includes the cristate, foveate and verrucate patterns. The acrochordate pattern is represented only by the genus *Acrochordus* Hornstedt, 1787 (Acrochordidae). Further studies are necessary for the classification of the scolecophidian and the sea snake patterns.

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A new record of *Pseudoxenodon inornatus* (Boie In: Boie, 1827) from Gunung Gedeh National Park, West Java, Indonesia (Squamata: Pseudoxenodontidae)

The genus *Pseudoxenodon* (Family Pseudoxenodontidae) comprises six nominal species from east and south-east Asia (Uetz 2012): *Pseudoxenodon bambusicola* Vogt, 1922 (distribution: southern China and northern Vietnam; Bourret 1936; Orlov *et al.* 2000); *Pseudoxenodon baramensis* Smith, 1921 (distribution: Sarawak, East Malaysia [Borneo]; Smith 1921); *Pseudoxenodon inornatus* Boie in Boie, 1827 (distribution: Java; Manthey & Grossmann 1997); *Pseudoxenodon jacobsonii* van Lidth de Jeude, 1922 (distribution: Sumatra; David & Vogel 1996; sometimes considered a subspecies of *inornatus* but considered distinct here on account of its diagnosability and disjunct distribution); *Pseudoxenodon karlschmidti* Pope, 1928 (distribution: southern China and northern Vietnam; Smith 1943; Nguyen *et al.* 2009); *Pseudoxenodon macrops* (Blyth, 1855) (distribution: Nepal, eastern India, south-western China, Myanmar; Thailand, Peninsular Malaysia, Vietnam, Laos; Manthey & Grossmann 1997; Zhao & Adler 1993); and *Pseudoxenodon stejnegeri* Barbour, 1908 (distribution: southern China; Barbour 1908; Zhao & Adler 1993). One additional taxon, *P. buettikoferi*, has been described from Ka-

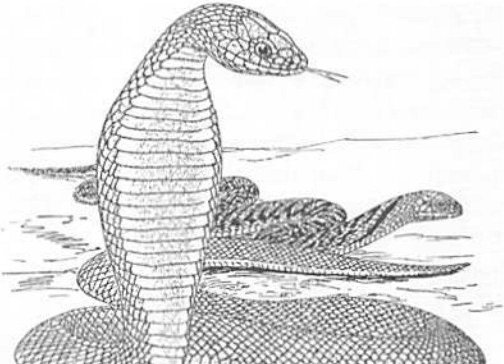

Figure 1. Line art showing a pair of *Pseudoxenodon inornatus* (reproduced from de Rooij 1917).

Figure 2. Live individual of *Pseudoxenodon inornatus* from Gunung Gede, showing lateral view of anterior aspect of body.

limantan, Borneo (Brongersma & Helle 1951), and was treated as a subspecies of *P. inornatus* by David and Vogel (1996), but its status requires reevaluation. Little has been recorded of the natural history of *Pseudoxenodon* of the Greater Sundas (Das 2010), with published data deriving chiefly from their respective holotypes.

The scarcity of biological information on *Pseudoxenodon inornatus*, the 'Dull Bamboo snake' or 'Javanese False Cobra', is the result of the small number of specimens known. No images of the species have been published in the scientific literature to the best of our knowledge, apart from a line drawing in de Rooij (1917), reproduced here as Fig. 1. The species has been assessed as Least Concern in the IUCN Red List (Vogel *et al.* 2012). Brongersma (1950) reviewed previous data on the species, including: the holotype of Boie (1827), which was from Cihanjawar (06°50'01" S; 106°49'02" E), at the foot of Gunung Pangrango, Jawa Barat Province, collected by Salomon Müller and two additional specimens that were sent to the Zoological Museum Amsterdam (now merged with the National Centre for Biodiversity Naturalis, Leiden, The Netherlands), by J. C. Bauwens, from "Sumadra Estate near Garut" (07°23'00" S; 107°43'00" E), also in Jawa Barat Province. No further specimens have been recorded.

On 14 April 2012, at 1530 h, En. Firman photographed a snake that could be identified as *Pseudoxenodon inornatus*. It was found at the Selabintana Resort, Sukabumi (06°52'19" S; 106°56'57" E), at the base of the 2929 m Gunung Gumuruh, within the Gunung Gede Pangrango National Park, Jawa Barat Province. It was found near an ephemeral stream within submontane forests dominated by *Altingia excelsa* (Altingiaceae) and *Schima wallichii* (Theaceae), at ca. 1200 m asl. The snake was released after it was photographed. Provided here are scale counts made from images reproduced here as Figs. 2–3, arguably the first of the species in life. Given in parentheses are scale counts from de Rooij (1917) and Brongersma (1950), counts

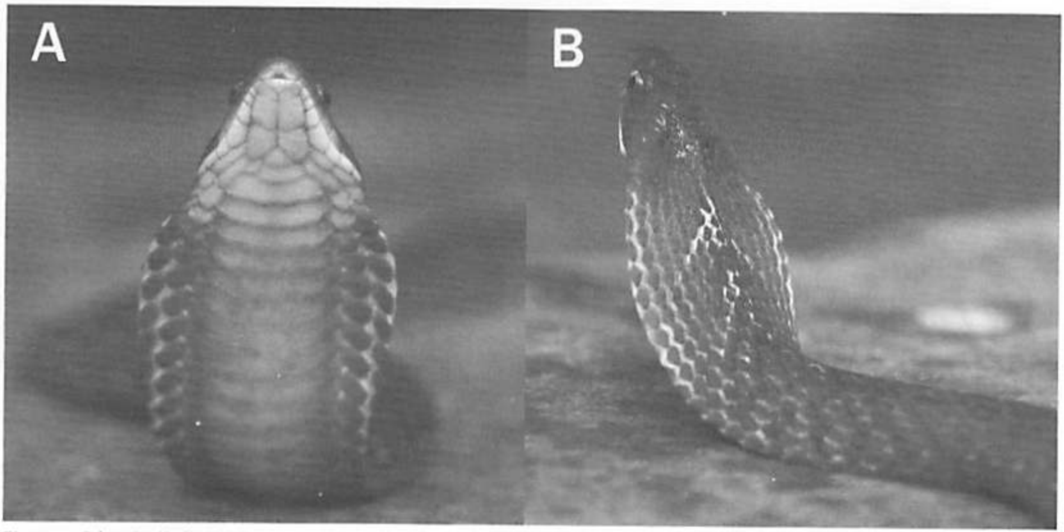

Figure 3. Live individual of *Pseudoxenodon inornatus* from Gunung Gede, with raised head and flared neck in frontal (A) and posterolateral (B) views, showing extent of flaring of neck and 'hood' pattern.

separated by a slash ('/'), '?' being unspecified values.

Midbody scale row 19 (19/19); loreal present; 3 (2–3/2-4) preoculars; 1 presubocular; 3 (3/3) postoculars; 2 internasals; 2 prefrontals; 2 anterior chin shields; 2 posterior chin shields; 8 (8/7–8) supralabials (supralabials VI and V contact orbit); 8 (?/9–10) infralabials. Head is short, neck is distinct, eyes are large, pupil is rounded; prefrontal ca. twice as large as internasal. Total length of the new specimen was estimated to be 500–600 mm. Body is subtriangular in cross-section. Dorsum is olive brown, with three cream-coloured chevron marks on neck, the anteriormost being most distinct; upper labials are slightly paler than sides of head; lower labials are cream coloured; vertebral region is slightly darker; venter is pale yellow, except for the dark brown paired row of enlarged scales on sides of throat that form the hood.

The rediscovery of this rare snake emphasizes the potential for discoveries on the densely populated Indonesian island of Java, which still has sizeable forested areas, especially in the uplands.

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First description of male *Hemidactylus sataraensis* Giri & Bauer 2008 (Sauria: Gekkonidae) with notes on its natural history, distribution and conservation status

The genus *Hemidactylus* is represented in India by 27 species (Uetz 2012) and it is likely that with the increasing attention paid to this group, the number of species will increase (Giri & Bauer 2008; Mahony 2009; Agarwal *et al*. 2011).

Giri & Bauer (2008) described *Hemidactylus sataraensis* based on two female specimens (BNHS 1742–1743) from Chalakewadi (17°34'40" N, 73°49'28" E) in the Satara District in the Western Ghats of the Indian state of Maharashtra. The type locality is characterized by extensive lateritic rock outcrop and by relatively extreme conditions with highly patchy and temporally variable resources and an average elevation of over 1200m above mean sea level. The microclimatic conditions vary from almost xeric to water-logged during the course of a year (Watve & Thakur 2006). This creates an extremely harsh physical environment for biodiversity inhibiting the area. Under these harsh conditions, this species takes refuge under boulders on the plateau. The landscape is dominated by numerous windmills and attracts tourists and therefore is under tremendous anthropogenic pressure. In spite of being described almost four years ago, *H. sataraensis* remains known only from female specimens. Data on important taxonomic characters like number and nature of pores restricted to males (Smith 1935) is not known. Additionally, it is not possible from the few specimens thus far reported to assess the rarity of the species, but this data deficiency alone warrants its assessment.

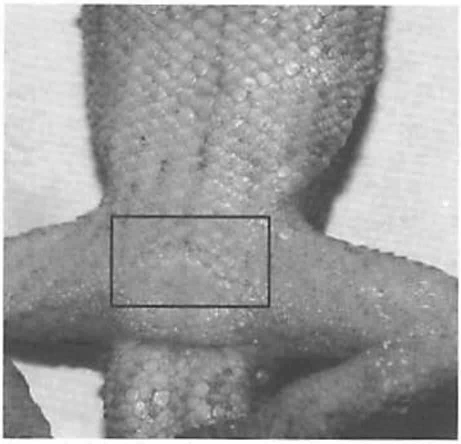

Figure 1. *Hemidactylus sataraensis* male (BNHS 2288) ventral view of trunk and cloacal region showing precloacal pores in the black square.

Recent herpetological investigation in the area has resulted in the discovery of males of this species as well as several additional females and juveniles. This permits us to add valuable data on morphological variation in this species along with a first description of males. Observations and specimens were collected on several trips made to the type locality over a period of two years. Measurements were taken with digital calipers (to the nearest 0.1 mm) following Giri & Bauer (2008)

Material examined.– The female holotype (Bombay Natural History Society – BNHS 1743) and paratype (BNHS 1742) (data in Giri & Bauer 2008) were examined by Harshal Bhosale. Additional material: BNHS 2288 (male), BNHS 2289 (female), Chalakewadi, Satara District, Maharashtra, India (17°34'40" N, 73°49'28" E) on 22 July 2012. Collected by Harshal Bhosale. BNHS 2290 (male), BNHS 2291 (female), same locality as above, on 18 June 2012. Collected by Zeeshan Mirza, Ashish Jadhav, Nilesh Mane & Vishal Deshpande.

Variation.– Apart from morphometric and merestic variation presented in Table 1, the species also exhibits a great deal of colour variation with respect to its size. Larger individuals are more conspicuously marked as opposed to juveniles and subadults (Fig. 2). Juveniles are dark brown with a tinge of tan to them with diffused

Table 1. Measurements (mm) and scale counts for recently collected specimens of *Hemidactylus sataraensis*. Abbreviations follow Giri & Bauer (2008). * = tail incomplete, ** = regenerated tail.

Characters	BNHS 2288	BNHS 2289	BNHS 2290	BNHS 2291
Sex	Male	Female	Female	Male
SVL	37.90	33.61	35.80	26.74
TRL	19.39	14.52	19.01	12.32
BW	7.32	5.77	6.35	4.64
CL	5.03	4.81	5.62	4.66
TL	50.27	35.10**	1.50*	1.54*
TW	5.91	4.82	3.64	2.20
HL	12.82	9.88	12.64	9.45
HW	7.34	6.50	7.97	6.25
HH	4.08	3.80	5.08	3.40
FL	4.78	4.60	5.39	3.60
OD	2.20	2.01	2.30	1.80
NE	2.97	2.43	2.62	2.05
SE	3.80	3.65	3.82	3.03
EE	3.01	2.85	2.69	2.42
IN	0.96	0.80	1.30	0.90
IO	5.15	3.90	4.17	3.22
Lamellae				
Right manus	6-7-8-8-7	5-7-7-8-8	6-7-8-8-8	6-7-7-8-8
Right pes	5-8-8-10-8	6-7-8-10-8	6-7-8-10-9	6-7-8-10-8
Upper labials	10	8	9	9
Lower labials	8	7	7	6

markings typical to the species (Fig. 3). Males differ from the females only in (i) possessing precloacal pores (6 pores present in males vs. absent in females), (ii) distinct hemipenial bulge (hemipenial bulge absent in females making the caudal constriction appear deeper) and (iii) shape of post cloacal spur (large and conical with a pointed tip in males vs. small with a rounded tip in females).

Natural History, Distribution and Conservation Status.– All specimens were collected during the daytime from piles of rocks. Individuals often retained their 'S'-shaped body posture as noted by Giri & Bauer (2008) and made no attempts to escape. The habitat was shared by *Hemidactylus* cf. *brookii*, *Echis carinatus*, *Sitana* sp. and several predatory arthropods which include theraphosid spiders, scorpions and scolopendran centipedes. The geckos were mostly found on the plateau and on a few occasions on the slopes of the plateau. It was observed that most specimens took refuge under a pile of rocks as opposed to isolated boulders. Likely prey species observed include termites, crickets and spiders which were also found under boulders. Specimens were retained in captivity for three days during which they accepted termites and jumping spiders as food. The species is abundant at the type locality from April to June but their numbers decrease with time, being notably absent in the late monsoon (October) and winters (November to March). Individuals were found at a distance from each other and no more than one specimen was found in a pile of rocks, indicating territorial behaviour as seen in *Hemidactylus albofasciatus* (Mirza & Sanap 2012). One of us (HB) found two eggs under a boulder with the female in the last week of May. Giri & Bauer (2008) reported the holotype containing two eggs in the body cavity collected in the month of January. Juveniles have been encountered from May to June. Considering the above points, it is likely that this species breeds more than once per year. Juveniles have a bright orange tail as seen in *H. albofasciatus*. It is likely that this species uses its tail for signalling conspecific individuals which aids in maintaining territory, a parallel situation observed in its sister species *H. albofasciatus*. All specimens encountered between 2011 and 2012 were found only at the type locality and the surrounding plateau, which covers an area of less than 8 km^2. Although there are similar plateaus in the Satara district which share similar floral and faunal elements with the type locality of *H. sataraensis*, this species has only been found on this particular plateau and its environs. The type locality is under strong pressure from various anthropogenic activities like tourism. Boulders, which are used by the geckos for refuge, are being increasingly moved to construct dams. This might lead to increased competition for scarce shelter sites.

Hemidactylus sataraensis closely resembles *H. albofasciatus* in most aspects. Apart from its

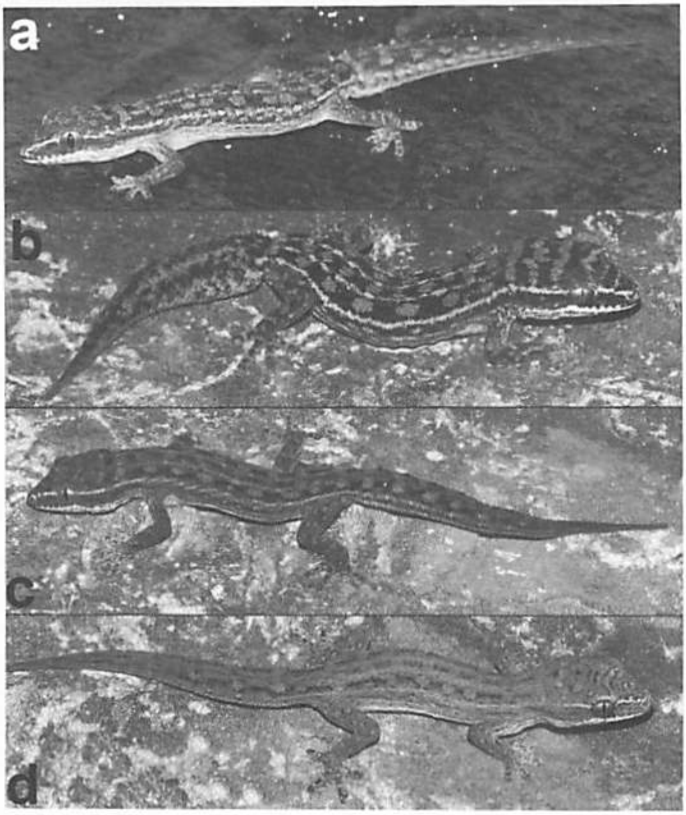

Figure 2. *Hemidactylus sataraensis* colouration in life. (a) male BNHS 2288, (b) female BNHS 2290, (c) male BNHS 2291, (d) uncollected female. Photo (a) by Harshal Bhosale, (b–d) by Zeeshan Mirza.

Figure 3. Uncollected juvenile of *Hemidactylus sataraensis*. Photo by Harshal Bhosale.

similar habitus and other morphological characters, the juveniles of the two species are very similar (Fig. 3). However, different ecological parameter preferences distinguish the two species; *H. albofasciatus* is known from several localities in two districts of coastal Maharashtra at an elevation of 50 m a.s.l. (Gaikwad *et al*. 2009) whereas *H. sataraensis* is known only from the vicinity of the type locality at 1159 m a.s.l.

Considering the currently available data for this species, it should be listed as 'Critically Endangered' based on IUCN criteria. Hence, immediate and substantial efforts are needed to protect the unique habitat which this species inhabits. Additionally, more research may be needed to confirm its 'Critically Endangered' conservation status, especially pertaining to its geographic distribution.

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Notes on reproduction of the skink *Scincella melanosticta* (Squamata: Scincidae) from Thailand

Scincella melanosticta is known from all of Thailand, eastern Myanmar, southern Vietnam, Laos and Cambodia (Ouboter 1986; Nguyen *et al.* 2009). It occurs to 1300 m elevation (Manthey & Grossmann 1997) and in Cambodia it is known to live in evergreen forests (Stuart and Emmett 2006). Grismer *et al.* (2007) reported gravid females of *S. melanosticta* from August. The purpose of this paper is to report on the reproductive cycle of *S. melanosticta* from a histological analysis of museum specimens collected in Thailand as part of an ongoing study on the reproductive biology of Southeast Asian lizards.

A total of 37 *S. melanosticta* including 18 adult males (mean snout vent length, SVL = 50.5 mm ± 3.4 SD, range = 43–55 mm), one subadult male (SVL = 38 mm), 17 adult females (mean SVL = 48.6 mm ± 4.2 SD, range = 41–53 mm) and one subadult female (SVL = 36 mm) from Thailand were examined from the herpetology collection of the Field Museum of Natural History (FMNH), Chicago, Illinois (Appendix). *Scincella melanosticta* were collected from the following years: 1957, 1969–1971, 1977.

For histological examination, the left testis was removed from males and the left ovary was removed from females. Oviductal eggs were counted. Tissues were embedded in paraffin and 5 µm sections cut. Slides were stained with Harris hematoxylin followed by eosin counterstain (Presnell & Schreibman 1997). Slides of testes were examined to determine the stage of the spermatogenic cycle. Slides of ovaries were examined for the presence of yolk deposition or corpora lutea. Histology slides were deposited in the FMNH herpetology collection. An unpaired t-test was used to compare *S. melanosticta* male and female mean body sizes and linear regression analysis was used to examine the relationship between female SVL and clutch size using Instat (vers 3.0b, Graphpad Software, San Diego, CA).

There was no significant size difference in mean SVL between males and females of *S.*

Table 1. Monthly distribution of stages in the ovarian cycle of 17 *Scincella melanosticta* females from Thailand.

Month	n	Quiescent	Early yolk deposition	Follicles > 3 mm	Oviductal eggs	Oviductal eggs and yolk deposition
January	2	1	1	0	0	0
March	1	0	0	0	0	1
April	2	0	0	0	1	1
May	4	1	0	1	1	1
June	1	0	0	0	0	1
July	2	0	0	2	0	0
August	1	0	0	0	0	1
September	1	0	0	1	0	0
October	1	1	0	0	0	0
November	1	1	0	0	0	0
December	1	0	0	1	0	0

melanosticta (unpaired t-test, t = 1.50, df = 33, P = 0.144). Two stages were observed in the testicular cycle: (1) Recrudescence which occurs prior to spermiogenesis (sperm formation) and is characterized by a renewal of germinal epithelium with primary and spermatocytes present; (2) Spermiogenesis, seminiferous tubules are lined by clusters of sperm and/or groups of metamorphosing spermatids. Males undergoing spermiogenesis (sample size in parentheses) were collected during the following months: January (2), February (2), March (3), April (2), May (1), June (3), July (2), November (2). The smallest reproductively active male measured 43 mm SVL (FMNH 191478) and was from November. The testis of one male from December (SVL = 38 mm) was undergoing recrudescence (FMNH 181044) and was considered a sub-adult. One male from September (FMNH 181023), which measured 47 mm SVL, exhibited recrudescence. Whether this single finding indicates a period of renewal in the testicular cycle is not clear. To answer this question will require examination of additional males of *S. melanosticta*.

Five stages were observed in the ovarian cycle (Table 1): (1) Quiescent, no yolk deposition; (2) Early yolk deposition, basophilic yolk granules in the ooplasm; (3) Enlarged ovarian follicles (> 3 mm); (4) Oviductal eggs; (5) Oviductal eggs with concurrent yolk deposition (Table 1). As no traces of embryos were noted, I conclude *S. melanosticta* is oviparous. In contrast the congener *Scincella reevesii* is ovoviviparous (Goldberg, 2011). Female *S. melanosticta* were reproductively active in all months sampled except October and November (Table 1). Five females (Table 1) with oviductal eggs exhibited concurrent yolk deposition for a subsequent clutch, indicating *S. melanosticta* may produce multiple clutches in the same reproductive season. Mean clutch size for 12 gravid females was 3.0 ± 0.96 SD, range = 1–4. The smallest reproductively active female measured 42 mm (early yolk deposition) and was from January (FMNH 216016). One smaller female from October (SVL = 36 mm) was reproductively inactive (FMNH 181027) and was considered a subadult. A linear regression analysis revealed a significant positive correlation between female body size, SVL and clutch size for 12 *S. melanosticta* females. This is shown by the regression equation: $Y = -8.4 + 0.23 X$, $r = 0.71$, $P = 0.004$.

In conclusion, the reproductive cycle of *S. melanosticta* appears similar to those of other tropical skinks, which exhibit prolonged or continuous reproductive cycles (Fitch 1982), including, for example, *Tropidophorus brookei* from Borneo (Inger & Greenberg 1966; Goldberg 2010). With at least 45 other species of skinks occurring in Thailand (Nguyen *et al.* 2009, Nabhitabhata *et al.* "2000" 2004, Chanard *et al.* 2011) additional studies are needed before the reproductive cycles of the Scincidae of Thailand can be ascertained.

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Appendix

The following specimens of *S. melanosticta* from Thailand (by province) comprise the basis for this study: Chiang Mai: FMNH 176970; Chantaburi: FMNH 191478, 216015, 216016; 216020; Nakhon Ratchasima: FMNH 180941, 180943, 180945, 180946, 180953, 180955, 180959, 180962, 180964, 180966, 180970, 180972, 180973, 180975, 180978, 180979, 180984, 180986, 180987, 180995, 180997, 181000, 181010, 181023, 181027, 181030, 181038, 181040, 181044, 181049–181051.

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On the identity of two *Oligodon* species in the collection at Zoological Survey of India, Kolkata

The genus *Oligodon* (Fitzinger, 1826) has a widespread distribution throughout central and tropical Asia, and contains about 70 valid species (Green *et al.* 2010). The Zoological Survey of India at Kolkata holds collections from a vast geographic area in tropical Asia, including several name bearing type specimens (Das *et al.* 1998). *Oligodon travancoricus* was first described by Beddome (1877) from the Travancore hills in Western Ghats of South India. Subsequent reports on the species were in the southern Western Ghats (Smith 1943; Whitaker 1978; Ferguson 1985; Murthy 1990; Sharma 2003; Hutton & David 2008; Ganesh *et al.* 2009). A single record of the species from Northern Nallamala hills, Eastern Ghats by Sanyal *et al.* (1993) drew our interest. This record of *O. travancoricus* by Sanyal *et al.* (1993) was subsequently cited by Srinivasulu & Das (2008). Sanyal *et al.* (1993) deposited two specimens in Indian Museum, Kolkata. The exact locations of these two specimens are Pullareddyguden village, Guntur District, Andhra Pradesh. These two specimens were re-examined. Meristic characters include: dorsal scales (counted on the mid-body, corresponding to half the number of ventrals), and ventral counts following Dowling (1951). The terminal scute (tip) is excluded from the number of subcaudals. Photographs of the specimen were taken with high-resolution digital cameras (> 8 megapixels).

There were two specimens tagged as *Oligodon travancoricus* with the same tag number, ZSI 21338. Both had 15 scale rows at mid-body and the anal divided. The larger individual had 191 ventrals,47 subcaudals and measured 523 mm total length. The smaller individual, measuring 443 mm total length, was badly damaged which made it impossible to count the ventrals. These scale counts clearly match with *O. taeniolatus* (Daudin, 1803). *Oligodon travancoricus* has mid-body scale rows of 17, a lower number of ventrals (150–155) and fewer subcaudals (31–39). The colouration of these two specimens has faded but the faint streaked markings also match with *O. taeniolatus*. Our re-examination suggests that these two specimens of *O. taeniolatus* were misidentified as *O. travancoricus*.

Oligodon sublineatus (Duméril, Bibron, and Duméril, 1854) is a species endemic to Sri Lanka (Wall 1921; Smith 1943). There exists a collection of nine specimens of this species stored together in a single bottle in the collection of Zoological Survey of India, Kolkata. For two of these specimens, viz., ZSI 8899 and ZSI 8900, the collection locality according to the label is "Camorta, Nicobars". The other seven specimens are from Sri Lanka. The only *Oligodon* species known to occur in the Nicobar Islands is *O. woodmasoni* (Sclater, 1891), which is endemic to the Andaman and Nicobar group. The two specimens of *O. sublineatus* that are supposedly from the Nicobar Islands are clearly not *O. woodmasoni*. Scale counts of the two specimens – mid-body scale counts 15 (17 in *O. woodmasoni*), seven supralabials, presence of loreal, ventrals 134 and 135, subcaudals 37 and 35, respectively for ZSI 8899 and ZSI 8900 – clearly identify the specimens as *O. sublineatus*. According to the labels, these two specimens were collected by Frederick Adolph de Roepstorff, Officer in Charge of the British Camp at Nancowry harbour from 1882 onwards (Krishnan 2008). It should be noted that several past authors have raised doubts regarding the collection localities of some of Roepstorff's specimens from the Andaman and Nicobar Islands. These include *Calotes andamanensis* (Boulenger, 1891) (Krishnan 2008) and *Sibynophis bistrigatus* (Günther, 1868) (Smith 1943). Some other species, such as *Amphiesma nicobarensis* (Sclater, 1891) collected by Roepstorff from Camorta in the Nicobar Islands, have never been recorded from these islands since. It seems that the two specimens of *O. sublineatus* are clearly mislabelled as regards their locality.

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