ISLAND-WIDE DISTRIBUTION OF SRI LANKAN PRIMATES BASED ON A QUESTIONNAIRE SURVEY OF RESIDENTS

Jennifer Pastorini[1,2*], M.K.C.R. De Silva[1], L.K.A. Jayasinghe[1], Prithiviraj Fernando[1]

[1]Centre for Conservation and Research, Tissamaharama, Sri Lanka. E-mails: channadesilva3@gmail.com; jayasinghe.lka@gmail.com; pruthu62@gmail.com

[2]Anthropologisches Institut, Universität Zürich, Zürich, Switzerland. E-mail: jenny@aim.uzh.ch

[*]Corresponding author

ABSTRACT

Five primate species, representing three genera and 12 subspecies, occur in Sri Lanka. We conducted an island-wide questionnaire survey of primate presence/absence, based on a 5x5 km grid with three questionnaires administered to residents in each cell. Respondents were queried on the presence of Slender Lorises, Toque Macaques, Sri Lankan Sacred Langurs and Purple-faced Langurs in their neighbourhood. Results indicated that Slender Lorises and Toque Macaques were distributed over 88% and 90% of Sri Lanka, respectively, including the wet and dry zones, but with patchy wet-zone distributions. Sri Lankan Sacred Langurs were present over 86% of the island but absent from large parts of the wet zone. Purple-faced Langurs were distributed over 53% of Sri Lanka with a disjunct distribution consisting of a patchy dry-zone presence and a more uniform wet-zone distribution. The maps presented are the first based on a systematic island-wide survey. We discuss the implications of the observed distributions for primate taxonomy and conservation.

Keywords: Distribution-map, *Loris tardigradus*, *Loris lydekkerianus*, *Macaca sinica*, *Semnopithecus priam*, *Semnopithecus vetulus*

INTRODUCTION

Sri Lanka is home to five primate species in three genera. Two species, *Loris tardigradus* (Linnaeus) and *Semnopithecus priam* Blyth are monotypic in Sri Lanka while the other three species together comprise ten subspecies (Table 1). Three species and all subspecies are endemic to the island. *Semnopithecus priam thersites* (Blyth) is Vulnerable (Dittus, 2020), the two subspecies *Semnopithecus vetulus nestor* Bennett (Rudran et al., 2020) and *Macaca sinica opisthomelas* Hill (Dittus & Gamage, 2020) are Critically Endangered, and the other nine Sri Lankan primate taxa are Endangered (IUCN, 2020).

Slender Lorises are strepsirhines and the only nocturnal primates in Sri Lanka. Hill (1953) recognised four subspecies of *Loris tardigradus* in Sri Lanka (*L. t. tardigradus* [Linnaeus], *L. t. grandis* Hill & Phillips, *L. t. nycticeboides* Hill and *L. t. nordicus* Hill) and two subspecies in India (*L. t. lydekkerianus* Cabrera and *L. t. malabaricus* Wroughton). Groves (1998) suggested recognising *L. t. tardigradus* as a full species and the other subspecies of *L. tardigradus* as subspecies of *L. lydekkerianus*. Groves (1998) also could not differentiate

between the subspecies *L. l. nordicus* and *L. l. grandis* on external morphology, including skull measurements. Therefore, he proposed subsuming *L. l. nordicus* under *L. l. grandis*. This leaves Sri Lanka with the endemic species *L. tardigradus* and two endemic subspecies of *L. lydekkerianus*, the latter with two additional subspecies in India (see also Brandon-Jones et al., 2004). Taxonomy of the Sri Lankan Slender Lorises remains in flux, some authors keeping *L. l. nordicus* (Dittus, 2013; Roos et al., 2014), some moving the subspecies *nycticeboides* from *L. lydekkerianus* to *L. tardigradus* (Nekaris & Jayewardene 2004) and some splitting the taxa into additional subspecies, *L. t. parvus* and *L. l. uva* (Gamage et al., 2017). The genetic data presented by Pozzi et al. (2015), confirms the existence of two species of Slender Loris (*L. lydekkerianus* and *L. tardigradus*) both of which occur in Sri Lanka; hence the main issue is the subspecific taxonomy.

The Toque Macaque *Macaca sinica* (Linnaeus) is endemic to Sri Lanka with up to four subspecies being described. Phillips (1935) identified two subspecies, *M. s. sinica* (Linnaeus) and *M. s. aurifrons* Pocock,

Table 1. Primate taxa in Sri Lanka.

Scientific name	Common name	IUCN Red List Status
Loris tardigradus tardigradus	Southwestern Red Slender Loris	Endangered
Loris lydekkerianus grandis	Highland Grey Slender Loris	Endangered
Loris lydekkerianus nordicus(?)	Northern Sri Lankan Grey Slender Loris	Endangered
Loris lydekkerianus nycticeboides(?)	Horton Plains Slender Loris	Endangered
Macaca sinica sinica	Dry-zone Toque Macaque	Endangered
Macaca sinica aurifrons	Pale-fronted Toque Macaque	Endangered
Macaca sinica opisthomelas(?)	Hill-zone Toque Macaque	Critically Endangered
Semnopithecus priam thersites	Sri Lankan Sacred Langur	Vulnerable
Semnopithecus vetulus vetulus	Southern Purple-faced Langur	Endangered
Semnopithecus vetulus monticola	Highland Purple-faced Langur	Endangered
Semnopithecus vetulus nestor	Western Purple-faced Langur	Critically Endangered
Semnopithecus vetulus philbricki	Northern Purple-faced Langur	Endangered

(?) The subspecies taxonomy is still debated.

distinguishing them by differences in bonnet hair colour and hair length of bonnet and back. Hill (1974) added a third subspecies, *M. s. opisthomelas*, in his monograph. Fooden (1979) studied 116 museum specimens of *M. sinica* across Sri Lanka but was unable to distinguish any subspecies morphometrically. However, he found the crown colour pattern exhibited a clear-cut geographic variation, justifying the recognition of two subspecies, *M. s. sinica* (north) and *M. s. aurifrons* (southwest). Fooden (1979) also expressed doubts about the stated origin of the two specimens based on which Hill (1974) described the third subspecies, *M. s. opisthomelas*. Fooden (1979) further stated that tail length, used as justification for a fourth subspecies, *M. s. longicaudata*, described by Deraniyagala (1965), is not a morphological feature used for taxonomy. While Groves (2001) and Brandon-Jones et al. (2004) recognised only two subspecies, Dittus (2013) and Roos et al. (2014) once again recognised *M. s. opisthomelas* as a valid taxon.

The nomenclature of the Sri Lankan Sacred Langur *Semnopithecus priam thersites* has changed over time. Initially classified as *S. entellus thersites* (Phillips, 1935; Groves, 1989; Brandon-Jones et al., 2004) it was subsequently changed to *S. priam thersites* (Groves, 2001; Dittus, 2013; Roos et al., 2014). *S. priam* is divided into three subspecies, with two (*S. p. priam* Blyth and *S. p. anchises* Blyth) occurring in south India. The third subspecies, *S. p. thersites*, is endemic to Sri Lanka. Also, the common name has changed between Hanuman, Indian Grey and Tufted Sacred Langur. In Sri Lanka it is also often referred to as the Grey Langur.

Regardless of the changes in nomenclature, *S. p. thersites* has always been considered to be a single taxon.

The Purple-faced Langur *Semnopithecus vetulus* (Erxleben), sometimes also called the Purple-faced Leaf Monkey, is endemic to Sri Lanka. The species initially was placed in the genus *Pithecus* (Phillips, 1935), then changed to *Trachypithecus* (Groves, 1989, 2001) and finally moved to *Semnopithecus* (Brandon-Jones et al., 2004; Roos et al., 2014). The placement of Sri Lanka's *S. p. thersites* and *S. vetulus* in the same genus was also confirmed by a genetic study (Karanth et al., 2008). Four subspecies of *S. vetulus* are recognised (Phillips, 1935; Groves, 2001; Brandon-Jones et al., 2004; Roos et al., 2014), which can be distinguished by their fur coloration (for illustrations see Pethiyagoda et al., 2012). *Semnopithecus v. vetulus* (Erxleben) is distributed in the south and southwest of the wet zone, south of the Kalu River; *S. v. nestor* in the lowland wet zone north of the Kalu River; *S. v. monticola* (Kelaart) in the central mountains and *S. v. philbricki* (Phillips) in the dry zone (north and east) (Molur et al., 2003; Roos et al., 2014).

Distribution maps depict the distribution of a taxon for communication and conservation planning and are a key component of species' spatial data (IUCN, 2018). Distribution maps can be developed by point-to-grid mapping of species occurrence data, expert drawn, or predicted with modelling programs such as Maxent which combine information from point occurrence data and environmental variables (Graham & Hijmans, 2006). Point-to-grid mapping can be

based on specimen collection data, direct or indirect detection of the species through physical surveys or questionnaire surveys. In physical surveys of large areas, only a very small fraction of each grid cell can be examined due to logistic constraints. Also, it is highly limited temporally, as surveyors are present at a given location only during the survey, hence the data approximate an instantaneous sample. In contrast, a questionnaire survey of residents investigates species occurrence over a wide spatio-temporal interval as it accesses observations respondents have accumulated over the years. Therefore, questionnaire surveys may have correspondingly higher detection probability. Questionnaire surveys have been used to assess the distribution of a wide range of species, including mountain lions (Berg et al., 1983), wolverines (Groves, 1988), chimpanzees (Sugiyama & Soumah, 1988), sika deer (Kaji et al., 2000), adders (Reading et al., 1996), squirrels (Teangana et al., 2000) and polecats (Baghli & Verhagen, 2003). However, the use of questionnaire surveys may not be effective with cryptic species and those unlikely to be accurately identified by respondents.

Previously published distribution maps for Sri Lankan primates (e.g., Molur et al., 2003; Pethiyagoda et al., 2012) were based on projections from locations where presence was known from expert knowledge and/or locations where presence was confirmed by physical surveys. Here we present the first distribution maps for Sri Lankan primates based on a systematic grid-based island-wide survey.

METHODS
Study area

Sri Lanka is an Indian Ocean island, situated approximately 50 km southeast from the southern tip of the Indian subcontinent. The area of Sri Lanka is 65,610 km^2. The topography is flat over most of the island, with central mountains reaching 2,500 m. The climate is tropical with precipitation from the southwest and northeast monsoons and inter-monsoonal thunderstorms. The southwest quarter receives rain from both monsoons and is considered the 'wet zone' and the rest of the island, with distinctly seasonal climate, the 'dry zone'. The natural vegetation in the wet zone is wet tropical evergreen forest, grading to montane forest in the mountains, and tropical dry evergreen forest in the dry zone. The wet zone, including the mountains, is densely populated and cultivated, while the dry-zone landscape includes agricultural areas, settlements, and natural forests. Most protected

areas are in the dry zone. Protected areas account for about 26% of Sri Lanka and are administered by the Department of Wildlife Conservation or the Forest Department. People can be legally resident in some protected-area categories such as sanctuaries and 'other state forest'.

Survey

The question of scale is an inherent issue with distribution surveys, with mapping at finer scales identifying smaller areas as occupied. Therefore, the finer the scale of a survey, the more 'accurate' will be the estimated distribution. However, decisions about survey scale must take logistical constraints into consideration, particularly in relation to the extent of the survey area. IUCN recommends scaling estimates of 'Area of Occurrence' (AOO) across all taxa using a grid size of 2x2 km for Red List assessments (IUCN, 2018). We selected a grid size of 5x5 km, as the primate survey was conducted in conjunction with a survey of elephant distribution, for which the grid size was chosen in consideration of elephant home range size and logistical constraints (Fernando et al., in press).

We divided Sri Lanka into 2,742 grid cells of 25 km^2, each measuring 5x5 km. From February 2011 to July 2015, we conducted a questionnaire survey across the island, interviewing three residents per grid cell. Interview locations within each grid cell were spread out as much as possible, keeping about 1 km away from the edges, to the degree permitted by road access and occurrence of residents. The GPS coordinates of the interview locations along with the answers were recorded on a datasheet. In selecting respondents, we visited each grid cell and chose persons who were long-time residents (>5 years) at the location the questionnaire was administered. Before administering the questionnaire, we engaged the persons in a discussion, asking questions about the area, climate etc. and made a subjective assessment of their knowledge of the surroundings and if they were truthful. If in doubt, the questionnaire was not administered, and a new respondent was selected.

We asked residents about the presence of 'Lorises', 'Macaques', 'Sri Lankan Sacred Langurs' and 'Purple-faced Langurs' in their neighbourhood. As these are morphologically distinct (Fig. 1), and people were universally familiar with their vernacular names, we assumed them to be capable of distinguishing between them. Interviews were conducted in the vernacular Sinhala or Tamil as both languages have specific names for the four taxa. We did not expect people
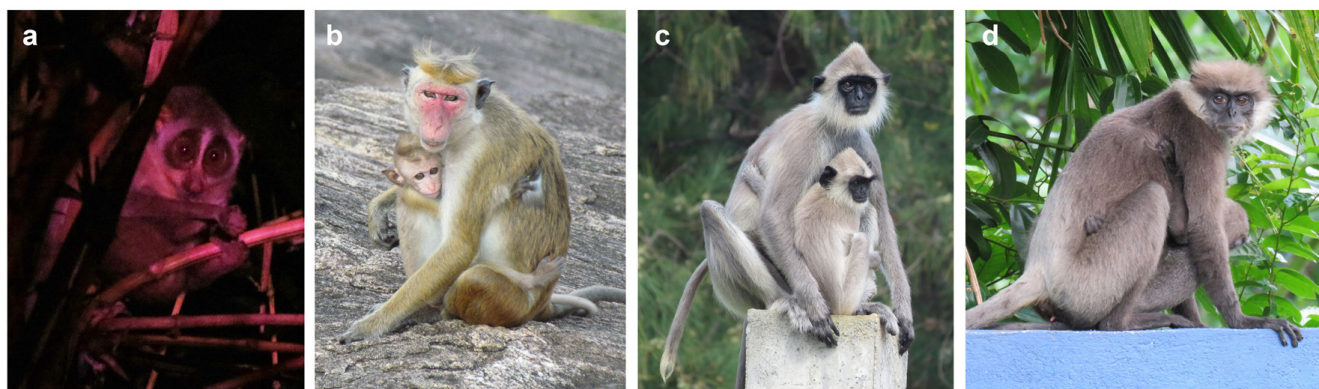
Fig. 1. Primate taxa surveyed in Sri Lanka. (a) *L. lydekkerianus*; (b) *M. sinica*; (c) *S. p. thersites*; (d) *S. vetulus*.

to be able to reliably differentiate the two species of Slender Loris or between any of the subspecies; hence terms identifying them were not included in the query.

The data were analysed in Microsoft Excel and the maps were compiled in QGIS 3.4.7 (QGIS Development Team, 2018). A grid cell with 1–3 positive answers for a species' presence was categorised as 'species present', assuming that heterogeneity of responses reflected spatial heterogeneity within the mapping unit of 25 km² (see Fernando et al., in press, for additional discussion on sampling and interpretation).

A cell without resident people to be interviewed was assigned a state based on the four cells sharing a common boundary with it (first-order neighbourhood). Accordingly, if any of the four adjoining cells had the species, the cell in question was categorised as having the species. Cells assigned states were subsequently considered the same as cells categorised on survey data.

We conducted an additional survey from 10–17 October 2019 to assess error due to respondents confusing *S. p. thersites* and *S. vetulus*. We administered a questionnaire based on a 2x2 km grid to one person per grid, asking about the presence/absence of *S. p. thersites* and *S. vetulus* in their area. After recording their answers, we showed them photographs of the two species and observed if the responses then changed.

RESULTS

Data for the four taxa were collected in a total of 2,209–2,213 grid cells where 6,558–6,583 interviews were conducted for each taxon (Table 2). In 2,150–2,166 grid cells (>97%), three interviews were done. In 38–49 grid cells only two people and in 9–10 grid cells only one person could be interviewed. In 13–17 grid cells, no data was collected due to error (Table 2). In

498 grid cells there were no resident people.

Slender Loris

In 85.3% of the 2,209 grid cells with interview data at least one respondent affirmed the presence of *Loris* sp. in their neighbourhood (Table 3). In 1,234 of these grid cells (65.5%) all three people interviewed reported *Loris* sp. while in 650 grid cells (34.5%) one or two interviewees stated that *Loris* sp. was absent or fewer than three people could be interviewed (Fig. 2). All 498 grid cells without resident people were assigned *Loris* sp. presence, based on first order neighbourhood. Thus, a total of 2,382 grid cells were found to have *Loris* sp., which is 88.0% of Sri Lanka or an area of 59,550 km² (Fig. 3a).

Toque Macaque

In 1,951 grid cells (88.2% of cells from which data were available), at least one person stated that *M. sinica* was present (Table 3), while in 262 grid cells (11.8%) *M. sinica* was absent. In 1,591 grid cells (81.5% of cells in which *M. sinica* presence was reported) all three respondents reported *M. sinica* presence, while in 360 grid cells (18.5%) one or more stated that *M. sinica* was absent or fewer than three people could be interviewed (Fig. 2). All but one of the 498 grid cells without resident people were assigned as *M. sinica* present (Fig. 3b).

Sri Lankan Sacred Langur

Semnopithecus p. thersites was reported from 1,827 grid cells (82.6% of cells from which data were available). In 1,511 cells (82.7%) all three respondents stated that *S. p. thersites* was present (Table 3). In the other 316 grid cells (17.3%) one or two said that *S. p. thersites* was absent or fewer than three people could be interviewed (Fig. 2). In 386 grid cells (17.4%) all respondents stated that *S. p. thersites* was absent. All but two of the 498 grid cells without people were assigned as having *S. p. thersites* (Fig. 3c).

Table 2. Data collected for the four primate taxa.

Taxon	Interviews	Cells	Interviews per cell			Missing cells
			1	2	3	
L. tardigradus & *L. lydekkerianus*	6,558	2,209	10	49	2,150	17
M. sinica	6,583	2,213	9	38	2,166	13
S. p. thersites	6,583	2,213	9	38	2,166	13
S. vetulus	6,578	2,212	9	40	2,163	14

Table 3. Results from the interviews and assignment of grid cells without resident people (forest).

Taxon	Interviews		Forest		Total	
	present	absent	present	absent	% present	% absent
L. tardigradus and *L. lydekkerianus*	1,884	325	498	0	88.0	12.0
M. sinica	1,951	262	497	1	90.3	9.7
S. p. thersites	1,827	386	496	2	85.7	14.3
S. vetulus	954	1,258	479	19	52.9	47.1
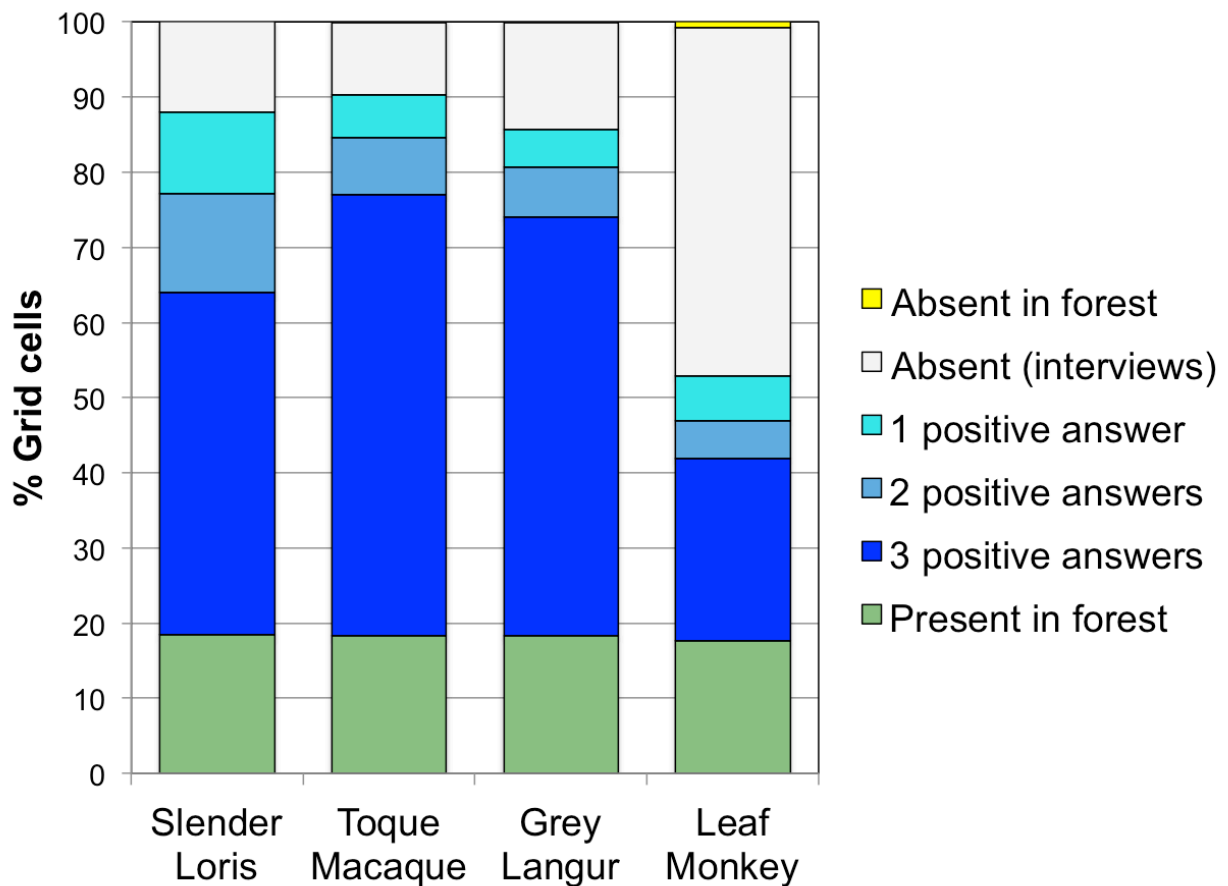
Fig. 2. Presence/absence in grid cells, based on interviews (absent, 1, 2 or 3 positive answers) or assigned based on neighbouring cells for grid cells without residents (absent or present in the forest). "Forest" refers to grid cells without resident people.
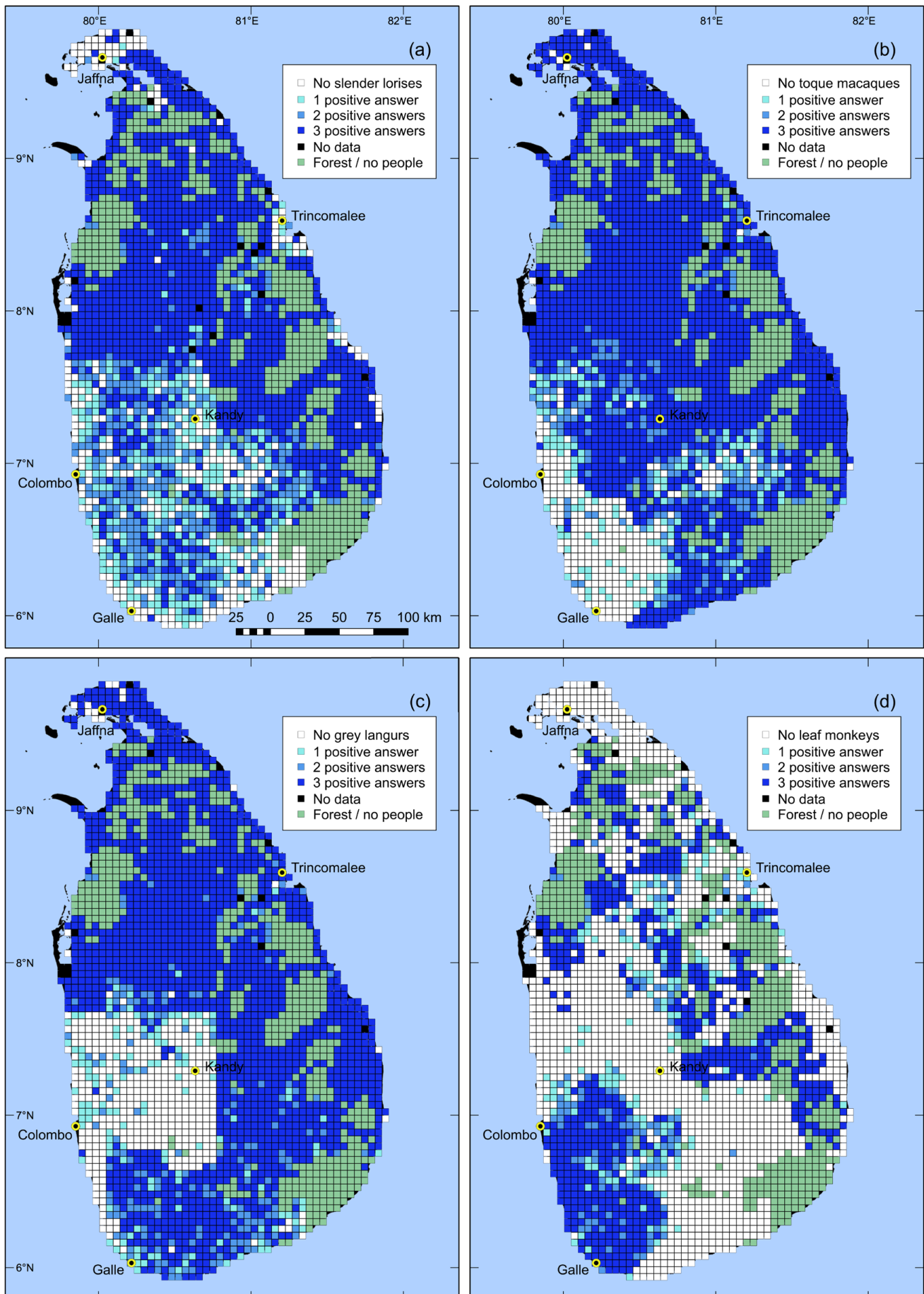
Fig. 3. Distribution maps for (a) *L. tardigradus* and *L. lydekkerianus*; (b) *M. sinica*; (c) *S. p. thersites*; (d) *S. vetulus*.

Purple-faced Langur

Semnopithecus vetulus was scored as present in 954 grid cells (43.1%). Of these, in 657 grid cells (68.9%) all three respondents affirmed the presence of *S. vetulus* (Fig. 2). In the other 297 grid cells (31.1%) one or two people stated that *S. vetulus* was absent or fewer than three people could be interviewed (Table 3). Of the 498 grid cells without residents, 479 grid cells were assigned as *S. vetulus* present (Fig. 3d).

Supplementary survey

Of 82 respondents, 42 (51.2%) stated that neither *S. vetulus* nor *S. p. thersites* were present and three (3.7%) that both species were present. None in either group changed their opinion after the photographs were shown. Seven respondents (8.5%) stated that only *S. vetulus* was present and 30 (36.6%) only *S. p. thersites*. Of these, three people (3.7%) changed their mind after seeing the photographs. One person switched from *S. p. thersites* to *S. vetulus* and the other two changed from *S. vetulus* to *S. p. thersites*.

Discussion
Slender Loris

We found *Loris* sp. range in Sri Lanka to be mostly continuous, with only eight grid cells with the presence of *Loris* sp. (0.3%) not having first or second-order neighbourhood contiguity with other cells with *Loris* sp. presence (Fig. 3a). The somewhat greater proportion of grid cells without unanimous indication of presence may be due to characteristics of the species, such as small size and nocturnal and arboreal behaviour, which may make it less noticeable than the other primate species.

We found that the range encompassed almost the entire island; hence *Loris* sp. was more widespread than previously recognised. The first published distribution map for Sri Lankan *Loris* sp. (Hill, 1953) also showed a continuous range, but with two large vacant areas in the west (Colombo - Kurunegala - Chilaw - along the coast back to Colombo) and east (Trincomalee - Polonnaruwa - Badulla - Ambalantota - along the coast back to Trincomalee). Hill's (1953) map was updated in a review of Lorises by Schulze & Meier (1995), who maintained the two gaps, but expanded the range a little towards the east in the mountains.

From 2001 to 2002 Nekaris & Jayewardene (2004) surveyed 31 sites across Sri Lanka and found *Loris* sp. in 13 locations. One site with *Loris* sp. (Maimbulakanda Nature Reserve) was in the western vacant area and another (Maduru Oya National Park) in the eastern vacant area of the maps from Hill (1953) and Schulze & Meier (1995). Perera (2008), in a map depicting all historic and recent records of *L. lydekkerianus*, included around a dozen locations in southeast Sri Lanka, suggesting its occurrence over almost the entire eastern vacant area, which was confirmed by our survey.

Toque Macaque

Based on our map, *M. sinica* has a continuous distribution over most of Sri Lanka (Fig. 3b). However, in the Southwest (wet zone) the distribution is very fragmented. This patchy part encompasses almost the entire distribution of the subspecies *M. s. aurifrons* (Fooden, 1979).

The distribution map from Hill (1974) showed *M. sinica* to be present throughout Sri Lanka with parapatry of the two subspecies *M. s. sinica* and *M. s. aurifrons*. The third subspecies *M. s. opisthomelas* was shown as occurring only in Horton Plains, encircled by *M. s. aurifrons* range. In contrast, Fooden's (1979) coarse-grained map depicted a broad intermediate zone not assigned to either, between the two subspecies *M. s. sinica* and *M. s. aurifrons*. It also showed the presence of *M. sinica* all over Sri Lanka.

Molur et al. (2003) presented separate maps for the three subspecies of *M. sinica*. The distribution of the disputed *M. s. opisthomelas* was drawn as a very small area within *M. s. aurifrons* range. They depicted a gap between *M. s. aurifrons* and *M. s. sinica* and also made the range of *M. s. sinica* much smaller than in Fooden (1979). *M. sinica* was shown as absent along the western coast from Colombo to Jaffna in their maps (Molur et al., 2003).

Our map confirms *M. sinica* presence in northwestern Sri Lanka, as indicated by Hill (1974) and Fooden (1979). Although subspecies boundaries are unclear, our distribution data suggest that *M. s. aurifrons* with its smaller and fragmented range, is more threatened than *M. s. sinica*. Since the range of *M. s. opisthomelas* is considered to be extremely small, if a valid taxon, it of course would be the most endangered.

Sri Lankan Sacred Langur

Semnopithecus p. thersites has a continuous distribution throughout the dry zone (Fig. 3c). We found few published studies on *S. p. thersites*. Hardly any distribution maps have been published. Molur et al. (2003) give a rudimentary map showing one continuous range across Sri Lanka's dry zone, leaving out the entire wet zone and most of the North Western

Province (dry zone). Our map shows a much wider distribution of *S. p. thersites*, including parts of the wet zone and the entire North Western Province.

A large part of the wet zone range in our map contains isolated grid cells with within-cell variance in response (Fig. 3c). Our control survey showed that 8.1% of people with only one of the two langur species in their neighbourhood made errors in species assignment. Therefore, the isolated cells in the wet zone indicating *S. p. thersites* presence in our survey may be suspect. The coexistence of two colour morphs has been reported in some *S. vetulus* populations in the southwest of the wet zone (De Silva et al., 2011). Such occurrence may also have caused false positives for *S. p. thersites* in our survey. However, our overall results suggest that Molur et al. (2003) considerably underestimated *S. p. thersites* distribution.

Purple-faced Langur

Our survey shows *S. vetulus* having two geographically disjunct distributions. One range covers large parts of the wet zone in the southwest of Sri Lanka and the other spreads across the dry zone in the east and north of Sri Lanka (Fig. 3d). The dry zone range shown in our map coincides with the distribution of *S. v. philbricki*. The wet zone range would include both, *S. v. nestor* and *S. v. vetulus*, with no obvious boundary between the two. Our survey did not detect *S. vetulus* over most of the distributional range of *S. v. monticola*, as indicated by the localities in the map from Pethiyagoda et al. (2012), which was based on sightings by biologists.

Areas without human presence

Questionnaire surveys depend on the presence of residents and hence cannot be used to sample areas without residents, such as many protected areas. The assignment of presence/absence to grid cells based on first-order neighbourhood was adopted on the premise that species occurrence was not dependent on anthropogenic habitat change. Nekaris & Jayewardene (2004) reported significantly higher sightings of *Loris* sp. outside protected areas than within. Macaques may display human commensalism (Mangalam & Singh, 2013). *Semnopithecus p. thersites* and *S. vetulus* may also benefit from some types of anthropogenic habitat change and adapt to some human-dominated habitats (Ahamed & Dharmaretnam, 2003; Moore et al. 2010). However, none of them can be viewed as synanthropes. Therefore, we feel that the assumption that a species occurring in a grid cell with humans would also occur in a contiguous cell without humans is justified. However, in very large protected areas encompassing regions

significantly different in climatic or physical factors from surrounding areas, some areas may be uninhabitable by particular species. For example, the Wilpattu complex in the northwest and the Yala complex in the southeast have coastal dunes, areas of dense cover, and arid areas. Our survey may have over-estimated primate presence in such situations. Since grid cells without resident people amounted to only 18% of Sri Lanka and the species surveyed are known to be present in many of the protected areas, we assume any consequent error would be slight. Surveying such areas by direct methods would be a useful addition to the data presented here.

Use of questionnaire surveys for assessing the distribution

In determining species distribution, questionnaire surveys assume respondents' knowledge of species presence, violation of which results in false negatives. Awareness of presence is likely to vary by species. Those that are conspicuous, large, diurnal, likely to come in contact with people or are adapted to anthropogenic habitats are more likely to be detected. Correspondingly, cryptic, small, nocturnal species that avoid human habitats and contact are more likely to be missed. In our survey, false negatives are most likely to have occurred with the *Loris* sp. and perhaps some populations of *S. vetulus*.

The occurrence of false positives in questionnaire surveys can occur if the taxon in question is confused with another, which may have been an issue with the distributions of *S. p. thersites* and *S. vetulus* in our survey. Presenting photographs and confirming identity in the survey would decrease such bias.

Another possible source of false positives or negatives would be untruthful responses. Such incidents could occur if respondents perceive positive or negative consequences in admitting presence or absence of the species. For example, if a particular species' presence could result in altering the status or management of an area or people's access to resources. Additionally, people may give fictitious answers due to personal reasons or attitudes towards those administering the questionnaire.

Conducting multiple interviews per mapping unit decreases the impact of false negatives and positives. If one or more positive responses per mapping unit are adopted as the standard of presence, as was done in our survey, the impact of false negatives is minimised. Conversely, taking unanimity of responses to indicate presence reduces the impact of false positives but entails a trade-off due to geographic variation of

presence within a mapping unit. We chose to accept any bias due to false positives, as geographic variation in presence within a grid cell was likely given the relative sizes of our mapping unit and primate home ranges and the importance of detection, rather than non-detection, for conservation.

Taxonomy

Twelve Sri Lankan primate taxa have been described at subspecies level. With the exception of two populations of *S. vetulus*, we did not detect any discontinuities in a distribution consistent with subspecies designations. However, the ability to detect breaks in distribution is related to home range size and the scale of surveying. Home ranges reported for Slender Lorises in India (*L. l. lydekkerianus*) are around 0.9–3.8 ha (Radhakrishna & Singh, 2002; Nekaris, 2003) and those of *S. vetulus* 1–16 ha (Rudran, 1973; Moore et al., 2010; Kumara et al., 2019). We did not find any published home range estimates for *M. sinica*, but home range sizes of other macaque species are in the low hundreds of ha (Izumiyama et al., 2003; Richter et al., 2013; Erinjery et al., 2015; José-Dominguez et al., 2015). Reported home range sizes for *S. priam* have ranged between 7.8 and 9.4 ha in Sri Lanka (Ahamed & Dharmaretnam, 2003; Vandercone et al., 2012) and 45–350 ha in India (Sommer et al., 2002; Chhangani & Mohnot, 2006). Thus, the home range sizes of the species surveyed may extend from less than one ha up to a few hundreds of ha. Given the large disparity between our minimum mapping unit (25 km^2 or 2,500 ha) and the possible home range sizes of the species surveyed, we may not have detected isolation, particularly in the case of *Loris* sp. and *S. vetulus*.

Genetic connectivity between populations depends on the movement of individuals between them. Dispersal distances could be much higher than the dimensions of home ranges. For example, while the home ranges of *S. entellus* (*S. priam*) groups vary from about 45–350 ha, individual males can move over areas of more than 2,000 ha (Sommer et al., 2002). Gene flow via the transfer of a single reproductive individual per generation (OMPG, one migrant per generation rule) prevents genetic divergence between populations (Mills & Allendorf, 1996). If no breaks in distribution precluding dispersal are present, whether subspecies characters could be maintained is questionable. On the other hand, if parapatric or sympatric populations maintain different suites of morphological characters, it could indicate reproductive isolation, hence specific rather than subspecific differentiation.

Our results emphasise the need to verify Sri Lankan primate taxonomy by conducting comprehensive genetic studies including samples from across their distribution. Similarly, radio-tracking studies could provide accurate information on dispersal and home range size.

Conservation

While our survey shows large and continuous distribution ranges for most of the primates, it is important to keep in mind that the minimum mapping unit was 25 km^2 and that the maps indicate only the distributional range of the species. It in no way suggests that there are viable populations of the species over the entire distribution range. Nor does our survey provide any indication of densities, hence the abundance, of species. For conservation and management, taking the observed distribution as a baseline, finer scaled surveys should be conducted to obtain higher resolution distribution maps of taxa of concern. Given the extent of overall distributions detected by our survey, the logistics of such an initiative will be formidable and may not be practical for island-wide surveys of any primate species. Therefore, finer scale surveys for conservation efforts directed at specific sites and populations could commence with point locations with known presence and expand outward to assess connectivity and population boundaries.

REFERENCES

Ahamed, R. and Dharmaaretnam, M. 2003. Ranging pattern, feeding and time budget of langurs (*Semnopithecus entellus*) in a recently established home range at Eastern University Campus, Batticaloa, Sri Lanka. *Journal of Science Eastern University of Sri Lanka* **3**(1): 1–10.

Baghli, A. and Verhagen, R. 2003. The distribution and status of the polecat *Mustela putorius* in Luxembourg. *Mammal Review* **33**(1): 57–68. https://doi.org/10.1046/j.1365-2907.2003.00006.x

Berg, R.L., McDonald, L.L. and Strickland, M.D. 1983. Distribution of mountain lions in Wyoming as determined by mail questionnaire. *Wildlife Society Bulletin* **11**(3): 265–268.

Brandon-Jones, D., Eudey, A.A., Geissmann, T., Groves, C.P., Melnick, D.J., Morales, J.C., Shekelle, M. and Stewart, C.-B. 2004. Asian primate classification. *International Journal of Primatology* **25**(1): 97–164. https://doi.org/10.1023/B:IJOP.0000014647.18720.32

Chhangani, A.K. and Mohnot, S.M. 2006. Ranging behaviour of Hanuman langurs (*Semnopithecus entellus*) in three different habitats. *Primate Conservation* **21**: 171–177. https://doi.org/10.1896/0898-6207.21.1.171

Deraniyagala, P.E.P. 1965. A new subspecies of macaque, *Macaca sinica longicaudata* from Ceylon. *Spolia Zeylanica* **30**(2): 261–262.

De Silva, M.A., Hapuarachchi, N.C. and Krishantha, P.A.R. 2011. Southern purple-faced leaf langur (*Semnopithecus vetulus vetulus*) – a new colour morph. *Zoo's Print* **26**(12): 4–7.

Dittus, W.P.J. 2013. Subspecies of Sri Lankan mammals as units of biodiversity conservation, with special reference to the primates. *Ceylon Journal of Science (Bio Sci)* **42**(2): 1–27. http://dx.doi.org/10.4038/cjsbs.v42i2.6606

Dittus, W. 2020. *Semnopithecus priam ssp. thersites.* The IUCN Red List of Threatened Species 2020: e.T39841A17982835. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T39841A17982835.en Downloaded on 29 January 2021.

Dittus, W. & Gamage, S.N. 2020. *Macaca sinica ssp. opisthomelas*. The IUCN Red List of Threatened Species 2020: e.T39800A17985750. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T39800A17985750.en Downloaded on 29 January 2021.

Erinjery, J.J., Kavana, T.S. and Singh, M. 2015. Food resources, distribution and seasonal variations in ranging in lion-tailed macaques, *Macaca silenus* in the Western Ghats, India. *Primates* **56**(1): 45–54. https://doi.org/10.1007/s10329-014-0447-x

Fernando, P., De Silva, M.K.C.R., Jayasinghe, L.K.A., Janaka, H.K. and Pastorini, J. 2021. First country-wide survey of the endangered Asian elephant: Towards better conservation and management in Sri Lanka. *Oryx* **55**(1): 46-55. https://doi.org/10.1017/S0030605318001254

Fooden, J. 1979. Taxonomy and evolution of the *sinica* group of macaques: I. Species and subspecies accounts of *Macaca sinica. Primates* **20**(1): 109–140. https://doi.org/10.1007/BF02373832

Gamage, S.N., Groves, C.P., Marikar, F.M.M.T., Turner, C.S., Padmalal, K.U.K.G. and Kotagama, S.W. 2017. The taxonomy, distribution, and conservation status of the slender loris (Primates, Lorisidae: *Loris*) in Sri Lanka. *Primate Conservation* **31**: 83–106.

Graham, C.H. and Hijmans, R.J. 2006. A comparison of methods for mapping species ranges and species richness. *Global Ecology and Biogeography* **15**(6): 578–587. https://doi.org/10.1111/j.1466-8238.2006.00257.x

Groves, C.P. 1989. *A Theory of Human and Primate Evolution*. Oxford University Press, Oxford.

Groves, C.P. 1998. Systematics of the tarsiers and lorises. *Primates* **39**(1): 13–27. https://doi.org/10.1007/BF02557740

Groves, C.P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.

Groves, C.R. 1988. Distribution of the wolverine in Idaho as determined by mail questionnaire. *Northwest Science* **62**: 181–185.

Hill, W.C.O. 1953. *Primates: Comparative Anatomy and Taxonomy. Vol. I: Strepsirhini*. Edinburgh University Press, Edinburgh.

Hill, W.C.O. 1974. *Primates: Comparative Anatomy and Taxonomy. Vol. VII: Cynopithecinae: Cercocebus*, *Macaca, Cynopithecus.* Edinburgh University Press, Edinburgh.

IUCN 2018. *Red List Mapping Standards and Data Quality for the IUCN Red List Categories and Criteria Version 1.16*. https://nc.iucnredlist.org/redlist/resources/files/1539098236-Mapping_Standards_Version_1.16_2018.pdf Accessed 9 April 2020.

IUCN 2020. *The IUCN Red List of Threatened Species. Version 2020-1*. http://www.iucnredlist.org. Accessed 9 April 2020.

Izumiyama, S., Mochizuki, T. and Shiraishi, T. 2003. Troop size, home range area and seasonal range use of the Japanese macaque in the Northern Japan Alps. *Ecological Research* **18**(5): 465–474. https://doi.org/10.1046/j.1440-1703.2003.00570.x

José-Dominguez, J.M., Savini, T. and Asensio, N. 2015. Ranging and site fidelity in Northern pigtailed macaques (*Macaca leonina*) over different temporal scales. *American Journal of Primatology* **77**(8): 841–853. https://doi.org/10.1002/ajp.22409

Kaji, K., Miyaki, M., Saitoh, T., Ono, S. and Kaneko, M. 2000. Spatial distribution of an expanding sika deer population on Hokkaido Island, Japan. *Wildlife Society Bulletin* **28**(3): 699–707.

Karanth, K.P., Singh, L., Collura, R.V. and Stewart, C.-B. 2008. Molecular phylogeny and biogeography of langurs and leaf monkeys of South Asia (Primates: Colobinae). *Molecular Phylogenetics and Evolution* **46**(2): 683–694. https://doi.org/10.1016/j.ympev.2007.11.026

Kumara, H.W.R., Nahallage, C.A.D. and Huffman, M.A. 2019. Study on home range size and pattern among three diurnal non-human primates in Mihintale Wildlife Sanctuary in Sri Lanka. *International Journal of Multidisciplinary Studies* **6**(1): 56–63 http://doi.org/10.4038/ijms.v6i1.92

Mangalam, M. and Singh, M. 2013. Flexibility in food extraction techniques in urban free-ranging bonnet macaques, *Macaca radiata. PLoS ONE* **8**(12): e85497. https://doi.org/10.1371/journal.pone.0085497

Mills, L.S. and Allendorf, F.W. 1996. The one-migrant-per-generation rule in conservation and management. *Conservation Biology* **10**(6): 1509–1518. https://doi.org/10.1046/j.1523-1739.1996.10061509.x

Molur, S., Brandon-Jones, D., Dittus, W., Eudey, A., Kumar, A., Singh, M., Feeroz, M.M., Chalise, M., Priya, P. and Walker, S. 2003. *Status of South Asian Primates. Conservation Assessment and Management Plan (C.A.M.P.)* Workshop report. Coimbatore, India.

Moore, R., Nekaris, K.A. and Eschmann, C. 2010. Habitat use by western purple-faced langurs (Colobinae: *Trachypithecus vetulus nestor*) in a fragmented suburban landscape. *Endangered Species Research* 12: 227–234. **12**(3): 227–234. https://doi.org/10.3354/esr00307

Nekaris, K.A.I. 2003. Spacing system of the Mysore slender loris (*Loris lydekkerianus lydekkerianus*). *American Journal of Physical Anthropology* **121**(1): 86–96. https://doi.org/10.1002/ajpa.10189

Nekaris, K.A.I. and Jayewardene, J. 2004. Survey of the slender loris (Primates, Lorisidae Gray, 1821: *Loris tardigradus* Linnaeus, 1758 and *Loris lydekkerianus* Cabrera, 1908) in Sri Lanka. *Journal of Zoology* **262**(4): 327–338. https://doi.org/10.1017/S0952836903004710

Perera, M.S.J. 2008. A review of the distribution of grey slender loris (*Loris lydekkerianus*) in Sri Lanka. *Primate Conservation* **23**: 89–96.

Pethiyagoda, R., De Silva, M. and Hapuarachchi, N. 2012. *Sri Lankan Primates. An Enthusiasts' Guide*. Wildlife Conservation Society, Galle.

Phillips, W.W.A. 1935. *Manual of the Mammals of Ceylon*. Colombo Museum, Ceylon.

Pozzi, L., Nekaris, K.A.I., Perkin, A., Bearder, S.K., Pimley, E.R., Schulze, H., Streicher, U., Nadler, T., Kitchener, A., Zischler, H., Zinner, D. and Roos, C. 2015. Remarkable ancient divergences amongst neglected lorisiform primates. *Zoological Journal of the Linnean Society* **175**(3): 661–674. https://doi.org/10.1111/zoj.12286

QGIS Development Team 2018. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.org/.

Radhakrishna, S. and Singh, M. 2002. Home range and ranging pattern in the slender loris (*Loris tardigradus lydekkerianus*). *Primates* **43**(3): 237–248. https://doi.org/10.1007/BF02629651

Reading, C.J., Buckland, S.T., McGowan, G.M., Jayasinghe, G., Gorzula, S. and Balharry, D. 1996. The distribution and status of the adder (*Vipera berus* L) in Scotland determined from questionnaire surveys. *Journal of Biogeography* **23**(5): 657–667. https://doi.org/10.1111/j.1365-2699.1996.tb00026.x

Richter, C., Taufiq, A., Hodges, K., Ostner, J. and Schülke, O. 2013. Ecology of an endemic primate species (*Macaca siberu*) on Siberut Island, Indonesia. *Springer Plus* **2**e137. https://doi.org/10.1186/2193-1801-2-137

Roos, C., Boonratana, R., Supriatna, J., Fellowes, J.R., Groves, C.P., Nash, S.D., Rylands, A.B. and Mittermeier, R.A. 2014. An updated taxonomy and conservation status review of Asian primates. *Asian Primates Journal* **4**: 2–38.

Rudran, R. 1973. Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. *Folia Primatologica* **19**(2-3): 166–192. https://doi.org/10.1159/000155537

Rudran, R., Dittus, W., Gamage, S.N. & Nekaris, K.A.I. 2020. *Semnopithecus vetulus*. The IUCN Red List of Threatened Species 2020: e.T22042A17959452. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T22042A17959452.en Downloaded on 29 January 2021.

Schulze, H. and Meier, B. 1995. The subspecies of *Loris tardigradus* and their conservation status: A review. **In**: *Creatures of the Dark.* L. Alterman, G. Doyle, and M.K. Izard (eds.), pp. 193–209. Springer, Boston, MA. https://doi.org/10.1007/978-1-4757-2405-9_13

Sommer, V., Denham, A. and Little, K. 2002. Postconflict behaviour of wild Indian langur monkeys: Avoidance of opponents but rarely affinity. *Animal Behaviour* **63**(4): 637–648. https://doi.org/10.1006/anbe.2001.1897

Sugiyama, Y. and Soumah, A.G. 1988. Preliminary survey of the distribution and population of chimpanzees in the Republic of Guinea. *Primates* **29**(4): 569–574. https://doi.org/10.1007/BF02381144

Teangana, D.O., Reilly, S., Montgomery, W.I. and Rochford, J. 2000. Distribution and status of the red squirrel (*Sciurus vulgaris*) and grey squirrel (*Sciurus carolinensis*) in Ireland. *Mammal Review* **30**(1): 45–56. https://doi.org/10.1046/j.1365-2907.2000.00054.x

Vandercone, R.P., Dinadh, C., Wijethunga, G., Ranawana, K. and Rasmussen, D.T. 2012. Dietary diversity and food selection in Hanuman langurs (*Semnopithecus entellus*) and purple faced langurs (*Trachypithecus vetulus*) in the Kaludiyapokuna Forest Reserve in the dry zone of Sri Lanka. *International Journal of Primatology* **33**(6): 1382-1405. https://doi.org/10.1007/s10764-012-9629-9