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## LEAD ARTICLE

# Subspecies of Sri Lankan Mammals as Units of Biodiversity Conservation, with Special Reference to the Primates

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## ABSTRACT

Subspecies embody the evolution of different phenotypes as adaptations to local environmental differences in keeping with the concept of the Evolutionary Significant Unit (ESU). Sri Lankan mammals, being mostly of Indian-Indochinese origins, were honed, in part, by the events following the separation of Sri Lanka from Gondwana in the late Miocene. The emerging new Sri Lankan environment provided a varied topographic, climatic and biotic stage and impetus for new mammalian adaptations. This history is manifest nowhere as clearly as in the diversity of non-endemic and endemic genera, species and subspecies of Sri Lankan mammals that offer a cross-sectional time-slice (window) of evolution in progress: 3 of 53 genera (6%), and 22 of 91 species (24%) are endemic, but incorporating subspecies, the majority 69 of 108 (64%) Sri Lankan land-living indigenous mammal taxa are diversified as endemics. (Numerical details may change with taxonomic updates, but the pattern is clear). These unique forms distinguish Sri Lankan mammals from their continental relatives, and contribute to the otherwise strong biogeographic differences within the biodiversity hotspot shared with the Western Ghats. Regardless of the eventual fates of individual subspecies or ESU's they are repositories of phenotypic and genetic diversity and crucibles for the evolution of new endemic species and genera. Their importance is highlighted by recent taxonomic studies that have identified more than 20% of infra-specific populations as new endemic species. Such 'hidden species diversity' validates not only the policy to conserve the potential for evolutionary processes as manifest by infra-specific diversity, but also, to prioritize the conservation of subspecies over their precise taxonomic definitions. The conservation of biodiversity in practice, therefore, involves firstly the official acknowledgement of the existence and importance of infra-specific diversity, especially in taxa such as primates where it is well expressed; and secondly, the protection of highly threatened natural habitats that constitute the only realistic life-supporting environments for the conservation of Sri Lanka's diversity in mammals and many other life forms.

**Keywords:** Evolutionary Significant Units (ESUs), endangered endemics, infra-specific diversity, wildlife management, Western Ghats-Sri Lanka biodiversity hotspot.

## INTRODUCTION

The conservation of biodiversity entails safeguarding the survival of the many different manifestations of life forms. Stated simply, the task involves the taxonomic identification of different organisms, an assessment of their ecological requirements for survival and of the threats they face, and finally a decision by nations of how best to implement conservation actions in the light of competing economic and political pressures. Ignoring subspecies as units of conservation in the construction of Red Lists may be seductive practical simplification when faced with the complexities and daunting challenges of conservation (including political pressure). In effect, however, it is denying the known existence of the very thing that Red List tools are designed to help conserve. For taxa such as primates, where subspecies are often well defined and commonplace, turning a blind eye to their infra-specific diversity invites compromise in conservation and may lead to damaging management strategies.

This review was stimulated by newly adopted harmful wildlife management practices in Sri Lanka (discussed at the end of this article) that run parallel to the recent publication of the 'National Red List 2012 of Sri Lanka' (MOE, 2012). Overall, this book of 476 pages is an impressive compilation listing of more than 700 inland

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indigenous vertebrate species, 1400 invertebrates, and 3150 angiosperm plant species. Data summaries involved the expertise of 89 contributors of varying backgrounds. Given the enormity of the task and limitations in the availability of information for most species (not to speak of subspecies), the selected unit of conservation for IUCN standard assessments was chosen at the level of the species for all taxa. The book lists comprehensively the numerous species of plants and animals found in Sri Lanka. Sadly also, it underscores the island nation's status (in combination with the Western Ghats) as one of several global hotspots where the survival of most of its rich biological heritage is much threatened (Myers *et al.*, 2000, Brooks *et al.*, 2002; Wikramanayake *et al.*, 2002). Looking forward, the book is intended as a platform for future Red List revisions that are planned at 2-year intervals. In such a revision it would be productive to acknowledge the biodiversity inherent at the infra-specific level for mammals.

The objectives of this article are (a) to consider the theoretical and practical basis for selecting species or subspecies as units of conservation, (b) to review the diversity of Sri Lankan mammal species and subspecies, with (c) particular emphasis on the well-studied primates, (d) to draw attention to flawed management practices that can arise from ignoring infra-specific diversity, and (e) to point to some considerations in the implementation of conservation management of mammalian diversity.

## The unit of conservation: species versus subspecies

Consideration of which taxonomic level is the most appropriate unit of conservation in measuring diversity is not new, and the arguments for selecting species are well established (Mace, 2004): most people have an idea what a 'species' means, and many other measures are less intuitive. Species are also sensible units to choose from a biological perspective: they keep their genomes more or less to themselves, and to that extent have independent evolutionary trajectories and unique histories (Purvis and Hector, 2000). This view of species is often referred to as the "Biological Species Concept (BSC)" and arose primarily as a matter of taxonomic convenience for classifying phenotypic variation among organisms. Under this concept, species are defined as 'groups of actually or potentially interbreeding populations that are reproductively isolated from other such groups' (Mayr, 1942). 'Biological species' are viewed by many biologists as the units of evolution and thus, on theoretical grounds they are potentially an objective and unambiguous criterion on which to base a definition of conservation units. This concept, however, implies that the origin of reproductive isolation is the most important component of taxonomic diversification (i.e., of biodiversity) and its value as a unit of evolution and conservation has come into question, particularly for polytypic species (Cracraft, 1983). Also in practice, the biological species concept has shortcomings because of the fact that in many instances species designations are not actually based on the determination of reproductive isolation. Instead, more easily observed morphological attributes are used. This has given rise to an alternative, the Phylogenetic Species Concept (PSC), according to which conservation units are delimited by characters that diagnose clusters of individuals or populations to the exclusion of other such clusters (Faith and Baker, 2006; Nixon and Wheeler, 2006)

## The Evolutionary Significant Unit (ESU)

Species-oriented conservation objectives focus not merely on the species as a single taxonomic entity but also attempt to analyze and maintain intra-specific variation in order to maximally preserve biological diversity. The focus should be on preserving evolving populations in which adaptive diversity and potential for evolutionary processes are maintained. Traditionally, intra-specific variation in animals has been documented and taxonomically classified by the use of subspecies.

This subspecies category, however, has not been appreciated universally or applied consistently across all vertebrate taxa, and the recognition of a subspecies is, at least in part, a matter of taxonomic whim. In ichthyology and herpetology, for example, subspecies are almost never recognized. This is not because they do not "exist", but because taxonomists in these groups elevate them to species as a matter of routine, partly because they subscribe to the PSC, and partly because they see no point in naming infra-specific taxa even if they acknowledge that they exist. On the other hand, almost all ornithologists and mammalogists recognize subspecies.

In an attempt to reconcile and simplify divergent views on what constitutes a species and to give weight to intra-specific variation for the practice of conservation management, the idea of the Evolutionary Significant Unit (ESU) has been introduced (Ryder, 1986). It is an operational term designating unique groups of organisms that should be managed separately (Vogler and DeSalle, 1994). ESUs were originally intended to distinguish between populations that represented significant adaptive variation. The identification of ESUs was to be based on concordance between sets of data (genetic, morphological, ecological, behavioural) as outlined, for example, by Mortiz (1992). The emerging view (Hey *et al.*, 2003) accepts that ESU's should be chosen to maximize the potential for evolutionary success – and therefore to preserve adaptive diversity across the range of the taxon (Moritz, 2002). The ESU therefore is a population unit that merits separate management and has a high priority for conservation (Crandall *et al.*, 2000). Faith (1992) takes a flexible and practical view arguing that the unit of conservation for measuring phylogenetic diversity is useful across (e.g., sister species) or below (e.g., subspecies, populations) the level the species, depending on the availability of taxon information and other considerations. While genetic information is a desirable prop for deciding ESU identity, in practice it is rarely available, whereas historically traditional phenotypic descriptions and morphometric analyses often have been well documented for subspecies. Apart from the availability of phenotypic data, O'Brien and Mayr (1991) suggested that subspecies are logical conservation units because members of a subspecies share a unique geographic range or habitat, a group of phylogenetically concordant phenotypic characters, and a unique natural history relative to other subdivisions of the species. These qualities are in accord with the ESU concept.

The future survival of subspecies inherently is more uncertain than that of species because, being below the species level, different subspecies are reproductively compatible. An allopatric subspecies has four possible fates; it may: (i) go extinct; (ii) exchange genes with another subspecies and become a new 'mixed' subspecies; (iii) by evolutionary processes change its genetic character over time to become one or more new subspecies; and (iv) if effectively isolated, become a new species by acquiring genetic isolating mechanisms – following arguments of the BSC. Notwithstanding these differences in potential fates, a species with two or more subspecies manifests a greater genetic and morphological diversity than a monotypic one. Subspecies, or similarly unique populations, are the parent populations (incipient species) for fixating biological diversity through the evolution of new species. From the point of view of ESU considerations, subspecies, regardless of their fates and degree of development of reproductive isolation, constitute the adaptive diversity and potential for evolutionary change that most biologists consider important for conservation objectives.

### The importance globally of subspecies in primates and other mammals

O'Brien and Mayr's (1991) view has been applied particularly in mammals, which are arguably the best studied vertebrates globally, as well as in Sri Lanka (although most birds, too, are well defined). For example, the global 2004 IUCN Red List includes 2209 species and 718 subspecies among the evaluated mammal taxa, and the Order Primates has the highest number of subspecies (229) listed worldwide (Gippoliti, 2007). This, in itself, is a reflection of the importance of primate subspecies on a global scale, and this appreciation has gained momentum through recent studies of genetic differentiation among primate subspecies with an eye towards their conservation as ESUs (Gonder *et al.*, 1997; Andayani *et al.*, 2001; Blair *et al.*, 2013).

Considering primate taxa in the regional context, Sri Lanka represents less than 2% of South Asian land area, yet harbours 29% (12/42) of its primate subspecies (including nominate subspecies). Sri Lanka has the highest diversity of primate taxa in South Asia. It is instructive to view primates in the broader context of the diversity of other mammals in the region and within Sri Lanka.

### The diversity of Sri Lankan mammals in relation to phyto-climatic zones.

Most flora and fauna of Sri Lanka have their roots in the Indian and Indochinese regions. McKay (1984) analyzed Sri Lanka's mammal fauna and found an inverse relation between the number of shared genera and progressively more distant regions of the mainland. The greatest affinity among terrestrial forms is with the southern peninsula and the Deccan-Bengal areas of India. Some geographically widespread ubiquitous forms overlay this regional derivation (*e.g.*, *Suncus, Mus, Lutra, Sus, Canis, Hystrix, Lepus, Cervus*). Overall, in the region encompassing southern India and Sri Lanka there is no single factor which could explain the pattern of distribution of mammalian genera or species, but climatically-induced habitat diversification appears to play a role.

Within Sri Lanka itself, the topography and climate are highly variable within a relatively small area of 65,610 km$^2$, and the island's generally high biodiversity has been linked to localized floral and faunal trait adaptations (Eisenberg and McKay, 1970; Ashton *et al.*, 1997; Bossuyt *et al*., 2004; Gunatillake *et al.*, 2004; Weerakoon and Goonatilke, 2006; Kathriarachchi, 2012). Climate, and to some extent soil, interact to determine vegetation form which in turn influence mammalian ecology and faunal composition. Phillips (1935, and updated in 1980) is still a standard reference for detailed descriptions of mammalian species and subspecies. Eisenberg and McKay (1970) updated the nomenclature of Phillips (1935) and confirmed and extended the ranges of known named forms, basing their revisions on museum collections as well as on field observations. These authors also commented on the proposed validity of subspecies, and analyzed the distribution of mammalian fauna in relation to habitat types.

### *Phytoclimatic zones and mammalian niche partitioning*.

Following the climate maps of Mueller-Dombois and Sirisena (1967), Eisenberg and McKay (1970) recognized seven different phytoclimatic zones and related the distribution of terrestrial mammalian taxa accordingly. With reference to Fig. 1, the lowland arid zone (A) supports monsoon scrub jungles and grasslands that occur in the extreme north and northwest (A1) and extreme southeast (A2) of the island. The most extensive area (B) includes the lowland monsoon forest and grassland of what is commonly known as the ‘dry zone’. A belt of transitional inter-monsoon forest (C) separates the dry zone from the wet zone. Rainforests in the south-west and the central massif of the island occur below 1000 m (D1), between 1000 m to 1500 m (D2), and above 1500 m (D3). The boundaries between these habitat types are inexact (depending on measurement criteria applied) and local variations occur. For example, in zone D3, Wijesinghe *et al.* (1993) distinguish between an ‘intermediate’ and ‘wet’ montane zones, and Fernando (1968) confines the ‘arid zones’ much closer to the coasts. Floristic and habitat variations occur on a finer scale within the dry zone (*e.g*., Dittus, 1977a, 1985a; Perera, 2012), lowland wet zone (Gunatilleke *et al.*, 2006; Kathriarachchi, 2012) and montane wet zone (Wijesundara, 2012).

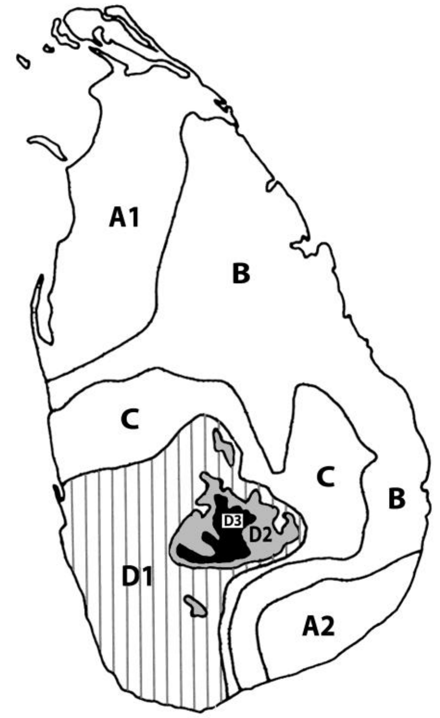

**Figure 1**. The climatic zones of Sri Lanka are: arid lowlands (A1 and A2), dry zone lowland (B), intermediate zone (C), rainforests of the lowland (D1, striped), midland (D2, dark gray) and montane regions (D3, black)

Regardless of zonal classifications, the contrasts and gradients in habitat constitute the different environmental contexts wherein mammalian phenotypic adaptations evolved. Eisenberg and KcKay (1970) pointed out that all of the major ecological feeding niches are filled by Sri Lankan mammals, but compared to that of South India the mammalian fauna of Sri Lanka is less diversified; there being fewer species to fill these niches (see also Eisenberg, 1981). This suggest firstly, that the ecological niches of Sri Lankan mammals are broader than those of subcontinent mammals, and secondly, that this greater niche breadth is subdivided among subspecies or ESUs. The latter proposition is examined more closely here.

### *The diversity of named mammals and their relation to habitat.*

Taking habitat type as a proxy for potential ecological niche specialization, it was instructive to examine mammalian phenotypic diversity at the level of the species and subspecies and its relation to this proxy. A compilation of this data (Appendix 1) was based primarily on Phillips (1980) and Eisenberg and McKay (1970) who considered subspecies in relation to habitat. Where these publications differ in subspecies designations, the more conservative application of Eisenberg and McKay (1970) was followed. The nomenclature for genera and species was updated to conform to recent taxonomic revisions as referenced by authors in Appendix 1. With a few exceptions, subspecies designations have not been closely scrutinized in the recent literature.

The data of Appendix 1 were summarized (Table 1). Among the 9 land-living orders of mammals of Sri Lanka, there are 91 species among 53 genera. Of these, 22 (24%) are endemic species. Among polytypic orders, the proportions of endemic species are highest among the insectivores (70%) and primates (60%), being nearly twice those found among rodents (32%) and Artiodactyla (33%), and more than among the carnivores (19%). The bats have the greatest number of genera and species, but there are no endemic species. McKay (1984) suggested that the lack of endemic bat species is the outcome of an absence of local effects owed to the bats' potentially high vagility. Endemicity in the Carnivora and Artiodactyla is confined to single families. Among the regionally widespread ungulates each genus is represented by only one species, two of which are endemic in Sri Lanka. There are no endemic species among the widespread monotypic orders or monotypic families.

Mammalian diversity and endemism come to the fore with a finer resolution incorporating subspecies in the compilation. There are 108 documented unique named taxa at the level of the species or subspecies and more than half (64%) of these are endemic (compared to only 24% of endemic species). The proportions of all endemic taxa below the level of the genus are the highest among primates (83% to 100%), moderately high (67% to 82%) in the insectivores, rodents, carnivores and ungulates, and relatively low (31%) among the bats. Among the monotypic orders, the elephant and hare are considered Sri Lankan subspecies. Similarly, among the monotypic genera of Artiodactyla, the spotted deer and possibly the sambar are peculiar subspecies.

The various habitat types described by Eisenberg and McKay (1970) and Phillips (1980), and applied in Appendix 1, can be combined into three major biotic zones (Table 2). McKay (1984) analyzed the distribution of mammals in relation to these three major zones and noted that all orders except the Insectivora have a reduced diversity in the high altitude wet zone. Typically widespread non-endemic forms (species or subspecies) are the most prevalent in the dry zone and the least in the montane wet zone. The dry zone (adding the intermediate zone), which occupies about two-thirds of the island's land area, is variable in forest structure and habitat type (summarized in Dittus 1977a, 1985a; Perera, 2006, 2012) and its northern aspects lie closest to India.

The origin for the high prevalence of non-endemic forms in the dry zone of Sri Lanka may reflect a combination of ecological preadaptation among continental ancestors, dispersal inertia and ecological barriers encountered at higher and wetter environments. The most differentiated forms, the endemic species, tend to cluster in the high altitude wet zone (Table 2). This is particularly true of the smaller mammals (insectivores and rodents) whose reproductive rates are high and specialized adaptations presumably evolved relatively rapidly, culminating in the evolution of at least three endemic genera *Solisorex, Srilankamys* and *Feroculus.* Wijesinghe's captive experiments (2001) and field studies (2006) suggested, however, that ecological specialization among the smallest endemic mammal species carries with it a reduced ability to compete with the more generalized non-endemic forms in disturbed habitats.

**Table 1.** The number of genera, species and subspecies among the orders of indigenous land-based mammals of Sri Lanka and the prevalence of endemics at different taxonomic levels (within brackets).

| Mammal Order/Family | No. of genera (endemic) | No. of species (endemic) | % of species endemic | No. of subspecies endemic | No. of unique species or subspecies (endemic) | % of unique taxa endemic |
|---|---|---|---|---|---|---|
| ***Polytypic Orders*** | | | | | | |
| **Insectivora** | 4 (2) | 10 (7) | 70 | 2 | 11 (9) | 82 |
| **Chiroptera** | | | | | | |
| Pteropodidae | 3 (0) | 4 (0) | 0 | 1 | 4 (1) | 25 |
| Rhinolophidae | 1 (0) | 2 (0) | 0 | 1 | 2 (1) | 50 |
| Hipposideridae | 1 (0) | 4 (0) | 0 | 2 | 4 (2) | 50 |
| Megadermatidae | 1 (0) | 2 (0) | 0 | 1 | 2 (1) | 50 |
| Vespertilionidae | 8 (0) | 12 (0) | 0 | 3 | 12 (3) | 25 |
| Emballonuridae | 2 (0) | 3 (0) | 0 | 0 | 3 (0) | 0 |
| Molossidae | 2 (0) | 2 (0) | 0 | 1 | 2 (1) | 50 |
| Subtotal Chiroptera | 18 (0) | 29 (0) | 0 | 9 | 29 (9) | 31 |
| **Primates** | | | | | | |
| Lorisidae | 1 (0) | 2 (1) | 50 | 4 | 4 (4) | 100 |
| Cercopithecidae | 2 (0) | 3 (2) | 67 | 8 | 8 (8) | 100 |
| Subtotal Primates | 3 (0) | 5 (3) | 60 | 12 | 12 (12) | 100 |
| **Rodentia** | | | | | | |
| Histricidae | 1 (0) | 1 (0) | 0 | 0 | 1 (0) | 0 |
| Sciuridae | 4 (0) | 6 (2) | 33 | 7 | 10 (9) | 90 |
| Muridae | 9 (1) | 15 (5) | 33 | 7 | 18 (12) | 67 |
| Subtotal Rodentia | 14 (1) | 22 (7) | 32 | 14 | 29 (21) | 72 |
| **Carnivora** | | | | | | |
| Mustelidae | 1 (0) | 1 (0) | 0 | 0 | 1 (0) | 0 |
| Canidae | 1 (0) | 1 (0) | 0 | 1 | 1 (1) | 100 |
| Ursidae | 1 (0) | 1 (0) | 0 | 1 | 1 (1) | 100 |
| Viverridae | 3 (0) | 9 (3) | 33 | 5 | 11 (8) | 73 |
| Felidae | 3 (0) | 4 (0) | 0 | 2 | 4 (2) | 50 |
| Subtotal Carnivora | 9 (0) | 16 (3) | 19 | 9 | 18 (12) | 67 |
| **Artiodactyla** | | | | | | |
| Suidae | 1 (0) | 1 (0) | 0 | 0 | 1 (0) | 0 |
| Tragulidae | 1 (0) | 2 (2) | 100 | 0 | 2 (2) | 100 |
| Cervidae | 3 (0) | 3 (0) | 0 | 2 | 3 (2) | 67 |
| Subtotal Artiodactyla | 5 (0) | 6 (2) | 33 | 2 | 6 (4) | 67 |
| ***Monotypic Orders*** | | | | | | |
| **Philodota** | 1 (0) | 1 (0) | 0 | 0 | 1 (0) | 0 |
| **Lagomorpha** | 1 (0) | 1 (0) | 0 | 1 | 1 (1) | 100 |
| **Proboscidae** | 1 (0) | 1 (0) | 0 | 1 | 1 (1) | 100 |
| **TOTALS** | **53 (3)** | **91 (22)** | **24** | **51** | **108 (69)** | **64** |

**Table 2.** The numbers of native terrestrial mammals of non-endemic unique taxa (named species or subspecies), endemic species and endemic subspecies occurring in the major biotic zones of Sri Lanka.

| | **Non-endemic taxa** | | | | **Endemic species** | | | | **Endemic subspecies** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Oder /Family | Total No. of Taxa | Dry A,B,C | Low Wet D1 | High Wet D2, D3 | Total No. of Species | Dry A,B,C | Low Wet D1 | High Wet D2, D3 | Total No. of Sub-species | Dry A,B,C | Low Wet D1 | High Wet D2, D3 |
| Insectivores | **2** | 1 | 1 | 2 | **7** | 0 | 1 | 7 | **2** | 0 | 1 | 2 |
| Chiroptera | **20** | 17 | 16 | 11 | **0** | 0 | | | **9** | 6 | 7 | 8 |
| Primates | **0** | | | | **3** | 4 | 3 | 4 | **12** | 5 | 5 | 3 |
| Pholidota | **1** | 1 | 1 | 1 | **0** | 0 | | | **0** | | | |
| Rodentia | | | | | | | | | | | | |
| Histricidae | **1** | 1 | 1 | 1 | **0** | | | | **0** | | | |
| Sciuridae | **1** | 1 | 0 | 0 | **2** | 1 | 2 | 2 | **7** | 3 | 3 | 4 |
| Muridae | **6** | 6 | 4 | 2 | **5** | 1 | 0 | 4 | **7** | 4 | 5 | 6 |
| Lagomorpha | **0** | | | | **0** | 0 | | | **1** | 1 | 1 | 1 |
| Carnivora | | | | | | | | | | | | |
| Mustelidae | **1** | 1 | 1 | 1 | **0** | | | | **0** | | | |
| Canidae | **0** | | | | **0** | | | | **1** | 1 | 1 | 0 |
| Ursidae | **0** | | | | **0** | | | | **1** | 1 | 0 | 0 |
| Viverridae | **3** | 3 | 2 | 2 | **3** | 3 | 1 | 2 | **5** | 3 | 3 | 3 |
| Felidae | **2** | 2 | 1 | 0 | **0** | | | | **2** | 2 | 2 | 2 |
| Artiodactyla | **2** | 2 | 2 | 2 | **2** | 1 | 1 | 2 | **2** | 2 | 1 | 1 |
| Proboscidea | **0** | | | | **0** | | | | **1** | 1 | 1 | 1 |
| **Totals** | **39** | **35** | **29** | **21** | **22** | **10** | **8** | **21** | **50** | **29** | **30** | **31** |

Most species occupied more than one climatic zone indicating their tolerance to a wide range of habitat conditions. This broad tolerance, however, appears to have given rise to local specialization as manifest by endemic subspecies (Appendix 1). Within any order of mammals the trend for the evolution of endemic species is accentuated by further differentiation at the level of the subspecies (Tables 1 and 2). Orders and families with no endemic species also tend to show endemic differentiation as subspecies, a prime example of this being the polytypic bats. In contrast to endemic species, the endemic subspecies are distributed in about equal numbers across contrasting habitats or exhibit clinal variations with respect to climate (arid to humid) and altitude (Table 2). In addition to environmental effects, McKay (1984) points to unexplained polymorphism in some rodents.

### Taxonomy: The importance of ESUs as potential endemic species

Given clinal phenotypic variations among different populations of a species, and the often fuzzy boundaries between subspecies has led to taxonomic quandaries in classification. The original authors for describing subspecies (Appendix 1) sometimes qualify the taxonomic status of a subspecies (or species). Modernization of nomenclature aside, recent studies reveal several taxonomic changes where subspecies and local phenotypic variants of a species have been ‘upgraded’ to endemic species status. The list includes: *Suncus montanus*, *Suncus zeylanicus, Suncus fellowesgordoni*, *Crocidura hikmiya, Funambulus layardi, Funambulus obscurus*, and *Vandeleuria nolthenii*. The endemic species, *Rattus ohiensis*, has been given its own endemic genus *Srilankamys ohiensis*. Eisenberg and McKay (1970) suggested that two subspecies of rats, *Rattus rattus kandianus* and *R. r. kelaarti*, may represent two new endemic species.

In the Viverridae, local populations of the endemic species *Paradoxurus zeylonensis* have been shown to represent at least three (possibly five) new endemic species: *P. aureus*, *P. montanus* and *P. stenocephalus* (Groves *et al.*, 2009). Similarly, in the ungulates, the chevrotain, which was formerly considered as a single non-endemic species, is now recognized as two endemic species: *Moschiola meminna* and *M. kathygre* (Groves and Meijaard, 2005).

Turning to primates, the earlier classification of the slender loris (e.g., Eisenberg and McKay, 1970) recognized four subspecies under one endemic species, *Loris tardigradus*. One of these subspecies is now recognized as an endemic species (*Loris tardigradus*) (Groves, 2001), whereas the other three subspecies are subsumed under *Loris lydekkerianus*, a species that occurs also in India (Brandon-Jones *et al*., 2004). The montane loris (*L. l. nycticeboides*) had been considered a subspecies of *L. tardigradus* (Nekaris and Jayewardene, 2004), but its distinctive morphology strongly suggest a closer affinity to the other two subspecies of *L. lydekkerianus* (Groves, 2001); indeed, it may represent an additional or third endemic species of loris altogether. The other subspecies of loris, *L. l. nordicus* and *L. l. grandis*, occur in the dry zone lowlands and intermediate zone hilly regions, respectively (Perera, 2008). [Subspecies of loris and of other primates are well illustrated with photographs by Nekaris and de Silva Wijeyeratne (2009) and Pethiyagoda *et al*. (2012)].

Taxonomic decision can sometimes be controversial. For example, retraction of ‘endemic genus’ status for Keelart’s long-clawed shrew (*Feroculus*) (MOE, 2012) is likely to be reversed (as in Appendix 1), because the alleged identical morph described from southern India (Pradham *et al*., 1997), lacks empirical support and awaits verification (Pethiyagoda, 2012).

The exact numbers of subspecies and their geographic boundaries, as compiled in Appendix 1, are likely to change with new information or as a matter of interpretation. Notwithstanding, the trend of these observations suggests that new taxonomic knowledge is likely to enhance rather than diminish the biological significance of infra-specific phenotypic variation: twelve (about 22%) of named and previously unnamed infra-specific forms have been shown to represent new endemic species.

### Reading the genes

Genetic information available for Sri Lankan mammals is spotty, but instructive with regard to ESU populations. For example, molecular studies of elephants point to significant differentiation of mitochondrial DNA (mtDNA) between India and Sri Lanka, as well as among different geographical regions within the island (Fernando *et al.*, 2000). Sri Lankan leopards *Panthera pardus kotiya,* on the other hand, are less diverse genetically than their Indian counterparts, suggesting a bottleneck or founder effect, and there is little evidence for regional genetic differences among Sri Lankan leopard populations (Miththapala *et al.*, 1991, 1996).

Analyses using mtDNA have been particularly useful in clarifying the phylogenetic relationships among small mammals. For example, the Sri Lankan and Indian populations of the mountain shrew are morphologically very similar and were thought to represent a single species. Using molecular analyses, Meegaskumbura and Schneider (2008) showed them to be separate endemic species; *Suncus montanus* in Sri Lanka and *S. niger* in India. Similarly, Meegaskumbura *et al.* (2007) discovered a new species *Crocidura hikmiya* (in the lowland and midland rainforests) that is genetically distinct from *C. miya* of the montane wet forest. Dissanayake and Oshida (2012) distinguished a new endemic species of squirrel *Funambulus obscurus*.

At the level of the genus, Phillips (1980) had assigned the purple-faced langur to the genus *Trachypithecus*, but recent genetic studies (Karanth, 2010; Karanth *et al*., 2010) suggest a closer affinity with the genus *Semnopithecus* as had been suggested earlier on morphological grounds alone (Brandon-Jones *et al*., 2004).

Toque macaques show a high level of genetic heterogeneity in nuclear genes across the island (Shotake *et al.*, 1991) but within a local population at Polonnaruwa, mtDNA haplotypes are unusually divergent even among neighboring social groups (Hoelzer *et al*., 1994). The mtDNA suggest a rapid rate of evolution among matrilines resulting from frequent extinctions among ecologically competing matrilineal social groups (Dittus, 1987, 2004). High rates of group (mtDNA haplotype) extinctions appear to be in step with frequent drastic changes in forest structure owed to regular cyclonic activity affecting dry zone forests' floristic composition (Dittus 1985a, b) that in turn impact primate demography and genetic population structure (Dittus, 2004).

Genetic data, when integrated with behvioural and ecological data, contribute a valuable perspective to our understanding of evolutionary processes (De Salle and Amato, 2004). From a purely taxonomic outlook, Baker and Bradley (2006) estimate that genetic investigation of mammals will uncover >2,000 new and 'cryptic species' worldwide. By and large, however, genetic studies have not contradicted taxonomic relationships as determined by 'old school' morphological analyses alone; Losos *et al*., (2012) caution that we should reconsider whether DNA is always inherently superior for inferring life's history.

**The significance of ESUs in relation to phylogeography and hotspot boundaries.**

Are the phylogeographic trends noted in other faunas also present in mammals? The mammals of the low and high altitude rainforests, like many sympatric amphibians, reptiles, fish and invertebrates (Crusz, 1973; Senanayke *et al*., 1977; Bossuyt *et al*., 2004) appear also to have differentiated in isolation from South Indian taxa. This happened even though land bridge connections (providing the potential for faunal exchanges) existed between India and Sri Lanka in the Pleistocene during recurrent episodes of sea-level low-stands in the last 500,000 years (Rohling *et al.,* 1998) (Fig. 2). Going back further in geological time, Crusz (1973) as well as Senanayake *et al*., (1977) considered the amphibians and reptiles of Sri Lanka's wet montane regions to harbor relic fauna with affinities to Madagascar, Africa and Indochina, and recent molecular studies support their view (Bossuyt and Milinkovitch, 2001; Datta-Roy and Karanth, 2009). Sri Lanka lay at the center of Gondwana, abutting areas that now are separated as Madagascar, Africa, India, Indochina and other land masses (Dissanayake and Chandrajith, 1999), lending credence to ancient biological links that may be read in present day relic faunas (Karanth, 2009). Evidence for Gondwana origins for Sri Lankan mammals is mostly conjectural (at present), but it stands to reason that the earliest mammals would have accompanied other fauna in dispersing by way of shifting tectonic plates. Intriguingly, the montane endemic mammalian genus *Solisorex*, may have its roots in Africa (Meegaskumbara, 2007 cited in Pethiyagoda, 2012).

Compared to the montane wetzone, the lowland dry zone is home to fewer endemic species and a greater number of non-endemic taxa (species and subspecies), implying a more recent derivation from continental ancestors. Notwithstanding, a trend towards the evolution of endemism is apparent even in the dry zone lowlands insofar as the number of endemic subspecies is on par with that in the other zones (Table 2). These data are consistent with the idea that evolutionary differentiation is apparent in the mammalian assemblage of the dry zone, but, with its potentially more recent influence from continental ancestors, appears to be lagging behind in degree of endemicity (*i.e*., fewer endemic genera and species) as found particularly in the montane area.

Sri Lanka and the Western Ghats (Fig. 2) are considered together as a single biodiversity hotspot, its boundaries determined by ‘biological communalities’. It is distinguished from other global hotspots by a separate biota or community of species that fits together as a biogeographic unit (Myers *et al*., 2000). The strong degree of endemism among the Sri Lankan mammal ESUs (64%) distinguishes it from Indian and other continental ancestors, and contradicts the concept of a single biogeographic unit (Prendergast *et al*., 1993) as pointed out by Bossuyt *et al*. (2004) in reference to other Sri Lankan faunal assemblages. In short, Sri Lanka might be considered a biodiversity hotspot in its own right; given the high number of endemics among its fauna together with almost 1,000 endemic angiosperm species (listed by Wijesundara *et al*., 2012).

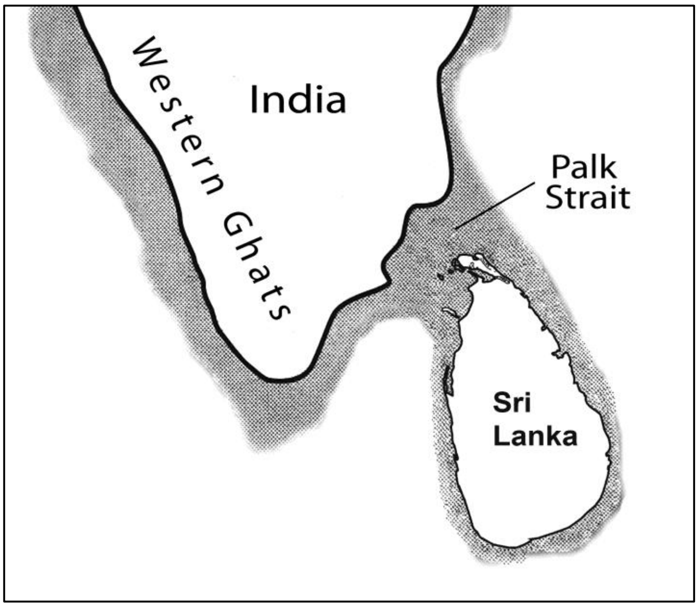

**Figure 2**. The Western Ghats-Sri Lanka hotspot is divided by the Palk Strait. The continental shelf (light gray), at a maximum depth of 70m, ties Sri Lanka to India and during recurrent periods of sea-level low-stands, during the Pleistocene, provided a land bridge at the present day Palk Strait

Taking the wide view, the rich biogeography and evolutionary history of this region is written nowhere as dramatically as in the non-endemic and endemic genera, species and subspecies of Sri Lanka, that, in a true sense, offer a cross-sectional time-slice (window) of evolution in progress. Regardless of the eventual fates of individual subspecies or ESUs, they are the crucibles for the evolution of new endemic species diversity.

## The model case of subspecies of toque macaques and other primates among Sri Lankan mammals

Each order of mammals has its own special appeal, knowledge base and challenges to conservation and it is beyond the scope of this article to treat each one in detail. The focus here is on primates because they are a well-studied group, and principles derived from their study have broader taxonomic relevance.

Recognition and description of the infra-specific diversity of Sri Lankan primates has a long history summarized by Phillips (1935), Hill (1939), Eisenberg and McKay (1970) and updated by Groves (2001) and Brandon-Jones *et al*. (2004). Brandon-Jones *et al*. (2004) endorsed the taxonomic certainly of seven out of the 12 described subspecies among five species of primates (Table 3). These endorsements were based almost entirely on museum collections.

All 12 subspecies (among five species) listed in Table 3 are endemic to Sri Lanka, the populations of the gray langur (*Semnopithecus priam*) and one of the two species of slender loris (*Loris lydekkerianus*) have species counterparts in South India. Whether these last two populations are subspecies peculiar to two regions because they are genetically and geographically separated by the Palk Strait, or as potentially different morphs under the Phylogenic Species Concept requires taxonomic clarification (Brandon-Jones *et al*., 2004). Sri Lanka is home to 12 distinct subspecies (among five species) of primates, or 10 subspecies if one were to adopt a more conservative conceptual approach. Subspecies of uncertain status have also been described; *Macaca sinica longicaudata* (Deraniyagala, 1965) and *Semnopithecus vetulus harti* (Deraniyagala, 1954), but they were not compiled here. In addition, white or leucistic sets of individuals have been noted over several centuries among the purple-faced langurs (*T. v. vetulus*) of the midland and lowland wet zone rainforests (de Silva *et al*., 2011; Pethiyagoda *et al*., 2012). Phenotypic variation among Sri Lankan primates is far more extensive than suggested by a simple species list, and that is true of other mammals as well (Appendix 1).

The taxonomic or ESU status of the subspecies of toque macaque warrants special consideration. Basing assessments on museum specimens only, Brandon-Jones *et al*. (2004) as well as Groves (2001), following Fooden (1979), dismiss Hill's (1942) identification of the montane toque macaque (*M. s. opisthomelas*) as a taxon intermediate between *M. s. sinica* and *M. s. aurifrons*. On the other hand, observations of numerous live specimen over four decades by the author and his co-workers, as well as investigations of live and museum specimen by other biologists resident in Sri Lanka (Phillips, 1935; Eisenberg and McKay, 1970) confirm the validity of *M. opisthomelas*. It is a distinct morphological variant apical in the higher elevations of the montane zone. It is not an intermediate type between *M. s. sinica* and *M. s. aurifrons* as had been as suggested by Brandon-Jones *et al*. (2004). If an intermediate type were to be sought at all, it would better apply to *M. s. aurifrons* rather than *M. s. opisthomelas*.

Several salient morphological traits distinguish the subspecies of toque macaques (Table 4, Fig. 3 and Fig. 4) and especially tail length differences. Following the theoretical framework of the phylogenetic species concept, conservation units (argued to be subspecies here) are delimited by clusters of characters to the exclusion of other such clusters provided they can be inferred to be genetically heritable. Drawing on genealogical histories spanning over 25 years, Cheverud and Dittus (1992) have demonstrated a high degree of heritable variation (average 0.51 to 0.56 heritability) in 25 of 27 different body measurements of toque macaques (*M. s. sinica*) at Polonnaruwa. These authors' results indicate sufficient genetic variation for a quick response in selection on body size and tail length. These are the very traits that Hill (1942), as well as Deraniyagala (1965), emphasized as diagnostic for subspecies phenotypic differentiation among toque macaques as well as among species of macaques in general (Hill, 1974; Fooden, 1979). In fact, the entire family of Cercopithecidae (Old World Monkeys) shows a remarkable consistency and uniformity in skeleto-muscular anatomy, in most bodily characters and in basic mode of locomotion. The major morphological differences in this group are the widely distributed differences in tail length and a remarkable variety of specific and subspecific differences in the coloration and patterns of their coats (Schultz, 1970). Subspecies of toque macaques are a model example of this family characteristic: not only do they differ in heritable differences in tail length (and many other traits), but population differences in head hair, or toque, (Fig. 3) and pelage (Fig. 4) are striking and diagnostic.

## The conservation of infra-specific variation as a prerequisite to taxonomic study

In reviewing mammals in the National Red List of Sri Lanka, Weerakoon (2012) acknowledged the special status of the subspecies of primates inhabiting the montane wet forests (zone D3). In keeping with the species-only format of the volume, however, an assessment of subspecies was omitted on grounds of their unclear taxonomic status, and recommendations for conservation efforts at this level were deferred to the future. To be sure, more taxonomic data are certainly welcome for these and many other taxa, assuming that they will not be driven to extinction before their genuine status can be appraised with modern technology (Costello *et al*., 2013). It has been argued that the urgency of conservation must precede taxonomy.

In particular, the reliable assessment of the numbers of genera and species requires the effective conservation of as many subspecies as possible (Stanford, 2001; Brandon-Jones *et al*., 2004, Brandon-Jones, 2006). Grantham *et al*. (2009) have shown how the benefits of additional taxonomic knowledge are outweighed by costs of delays in conservation action. The ideal of greater resolution in the status of one or two taxa alone cannot justify ignoring the majority whose subspecific status is unambiguous or worse yet, implementing adverse conservation practices on such a premise (O'Brien and Mayer, 1991; Rodriguez *et al*., 2013).

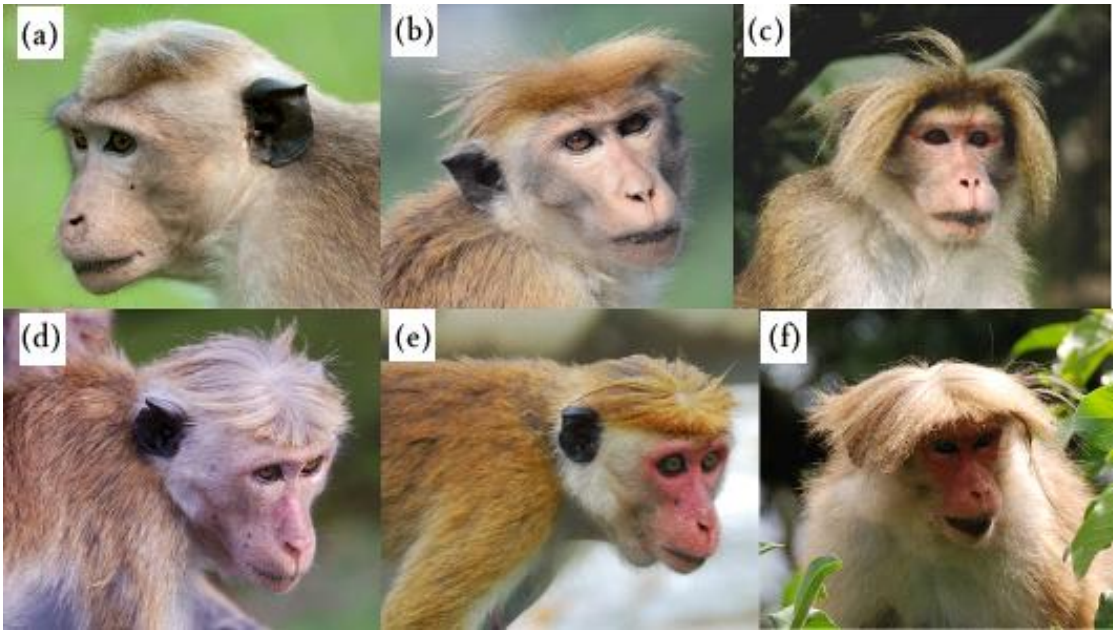

**Figure 3.** Comparison of differences in the colour and length of the head hair (toque) as evident among individuals representing three subspecies of toque macaques: *Macaca sinica sinica* male (a) and female (d); *M. s. aurifrons* male (b) and female (e); and *M. s. opisthomelas* male (c) and female (f). [Photos by Barney Wilczak (a), and the author (b) - (f).]

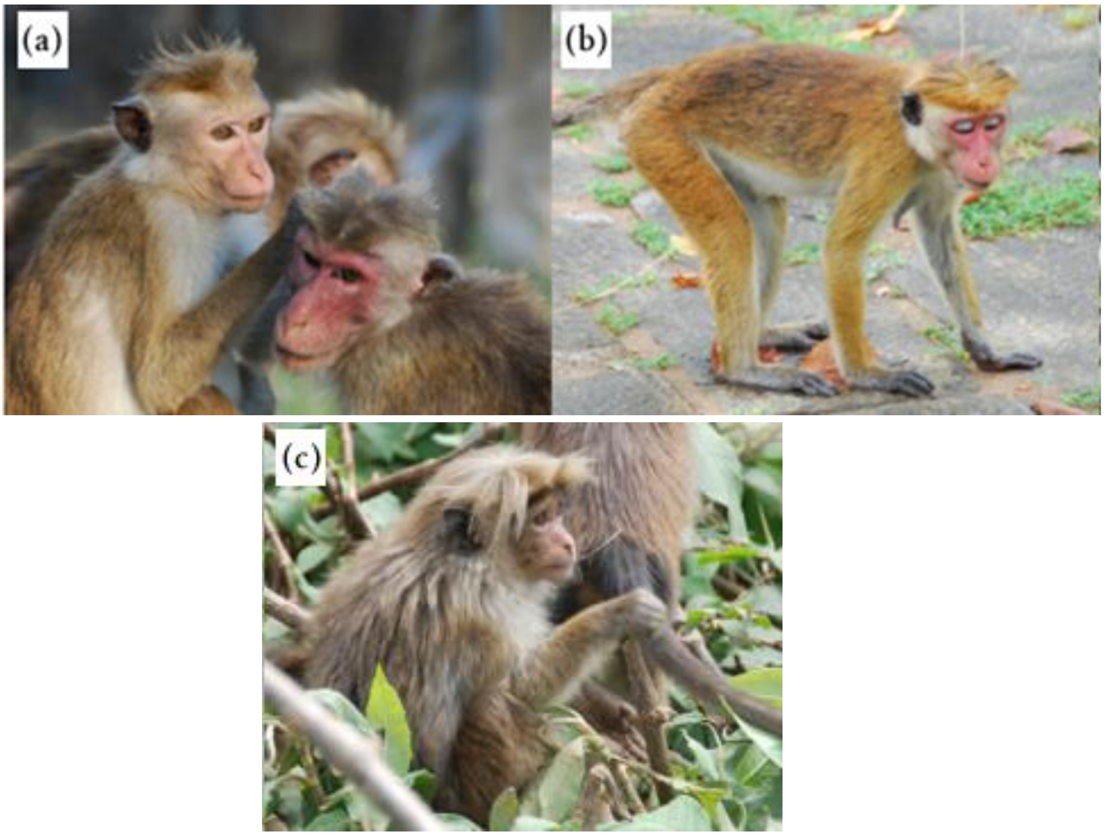

**Figure 4**. Comparison of differences in the colour, length and density of body fur among the three subspecies of toque macaque: (a) *Macaca sinica sinica*, (b) *M. s. aurifrons*, and (c) *M. s. opisthomelas*. [Photos by the author]

**Table 3.** Comparison of Red List assessments of Sri Lankan primates, according to IUCN defined categories of threat to extinction: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Not Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE).

| **Taxon** | **Distribution** | **IUCN 2012.2, version 3.1** | **Brandon-Jones *et al*. 2004** | **Sri Lanka National Red List 2012** |
|---|---|---|---|---|
| Lorisidae | | | | |
| 1. *Loris tardigradus* (Linnaeus, 1758) | D1 | EN C2a(i) | | VU B1ab(iii) |
| a. *L. t. tardigradus* (Linnaeus, 1758)* | D1 | EN A2cd + 4cd; C1 | EN A1c | |
| 2. *Loris lydekkerianus* (Cabrera, 1908) | | LC | | NT |
| a. *L. l. grandis* (Hill & Phillips, 1932)* | C, D2 | EN A2cd+4cd B1ab(i, ii, iii, iv, v) + 2ab(i, ii, iii, iv, v) | EN A1c | |
| b. *L. l. nordicus* (Hill, 1933)* | A, B | EN A2cd+4cd | EN A1c | |
| c. *L.l. nycticeboides* (Hill, 1942)* | D3 | EN A2cd+4cd B1ab(i, ii, iii, iv, v) | ENA1c | |
| Cercopithecidae | | | | |
| 3. Macaca *sinica* (Linnaeus, 1771) | | EN A2cd | | LC |
| a. *M. s. sinica* (Linnaeus, 1771)* | A,B,C | EN A2cd+3cd | VU A1c | |
| b. *M. s. aurifrons* (Pocock, 1931)* | D1, D2 | EN A2cd+3cd | VU A1c | |
| c. *M. s. opisthomelas* (Hill, 1942) | D3 | EN A2cd+3cd B1ab(i, ii, iii, iv, v) + 2ab(i, ii, iii, iv, v) | | |
| 4. *Semnopithecus priam* | | NT | | LC |
| a. *S. p. thersites* (Blyth, 1844) | A,B | En 4cd | VU A1cd | |
| 5. *Trachypithecus vetulus* | | | EN A2cd+3cd+4cd | EN B2ab(iii) |
| a. *T. v. philbricki* (Phillips, 1939)* | A,B | EN A2cd+4cd | EN A1cd | |
| b. *T. v. vetulus* (Erxleben, 1777)* | D1-south | EN A2cd+4cd | EN A1cd | |
| c. *T. v. nestor* (Bennett, 1833)* | D1-north | CR A2cd+3cd+4cd | EN A1cd | |
| d. *T. v. monticola* (Kelaart, 1850)* | D3 | EN A2cd+3cd+4cd B1ab(i, ii, iii, iv, v) | EN A1cd | |

*Brandon-Jones *et al*. (2004) considered these subspecies as well established with a high credibility rating.

**Table 4.** Key traits of the three subspecies of toque macaques, *Macaca sinica*

| Trait | *M. s. sinica* | *M. s. aurifrons* | *M. s. opisthomelas* |
|---|---|---|---|
| **Pelage, general colour of the dorsal region and outer limbs** | Variable; light to mid brown, light grey and yellowish, reddish or chestnut especially on thighs and shoulders | Dusky chestnut-orange, dusky yellowish or golden. Darker at higher elevations. | Greyish-olive, dark brown, little or no rufescence. Black lower rump. |
| **Pelage hair** | Short, not dense | Moderately long and dense | Long and dense |
| **Radiating hairs of the cap or toque** | Short, with tips of hairs brown or pale–buffy | Longer, with tips of hairs reddish, or yellowish | Extremely long (up to 12 cm), with tips of hairs straw-coloured |
| **Black pigment of lower lip and eyelids** | Variable; sometimes barely noticeable | Moderate | Conspicuous and common. |
| **Skin of ventral surfaces** | Light blue often with white patches | Moderately blue | Deeper blue than other subspecies. White patches are rare. |
| **Crown-rump length (mm)** | 415-449 (male, n=44) | 495 (male, n=3) | 456 (male, n=1) |
| | 379-388 (female, n=71) | 429 (female, n=4) | 426 (female, n=1) |
| **Body weight (kg)** | 5.0-5.7 (male) | 5.0 (male); | 6.1 (male) |
| | 2.9-3.3 (female) | 3.1 (female) | 3.4 (female) |
| **Tail length (mm)** | 573 -606 (male) | 604 (male) | 498 (male) |
| | 531-543 (female) | 458 (female) | 448 (female) |

### Ignoring infra-specific diversity in Red List assessments leads to misguided conservation policy and management

The many challenges to conservation in Sri Lanka have been reviewed and most often involve loss of habitat (Senanayake *et al*., 1977; Wikramanayake and Gunatilleke, 2002a, b, c; Bambaradeniya, 2006; Wijesinghe, 2006; MOE, 2012). In Red-List assessments the level of threat to a taxon is highly dependent on the population numbers, the geographic 'Extent of Occurrence' and 'Areas of Occupancy'. As a general rule, the larger these areas are, the greater are the population numbers and the lesser is the threat of extinction, other factors being equal. It follows that any species in its entirety is less vulnerable to extinction than its constituent subpopulations. The effect of this simple arithmetic relationship is evident in different Red List assessments that had been made for primates, for example (Table 3).

Assessment at the level of the species (as opposed to the subspecies) is inimical to the conservation of biodiversity for the following reasons. The message to policy makers and managers is that genotypic and phenotypic differences as manifest by subspecies (primate or otherwise) and other population variants (*e.g*., leucistic leaf monkeys) are of no consequence to the preservation of diversity. Not only does this stance contradict scientific fact and widely held professional opinion, but also fails to fulfill the government's published objective of the Red List – namely to preserve Sri Lankan nation's biodiversity for generations to come (page xv, National Red List 2012 of Sri Lanka). You cannot preserve biodiversity by denying its very existence.

The 'species only' Red List approach also can encourage adverse wildlife management. An endemic species, *Macaca sinica* has been assessed at the national level as 'Least Concern (LC)', whereas its subspecies, notably the montane *M. s. opisthomelas*, are 'Endangered' (Table 3). Furthermore, this endemic species has been declared a 'pest' because they can be destructive and come into conflict with people. It is the only endemic mammal species explicitly not protected under the Fauna and Flora Protection Ordinance (Act No. 22 of 2009). Official management practice involves trapping large numbers of toque macaques of different subspecies (*M. s. opisthomelas* as well as *M. s. aurifrons*) and releasing them into rural areas and national parks with incompatible habitats (e.g., Maduru Oya and Uda Walawe). Purple-faced langurs have been shifted about similarly between 'foreign' subspecies environments. Quite apart from ethical issues and the adverse effects on biodiversity of this type of action (e.g., Templeton, 1986), the entire process of trans-locating pest monkeys is illegal in most nations because they can be ineffective as a method of control, economically harmful to people, biologically fallacious and inferior to better methods of pest control (Singh *et al.,* 2005; Dittus, 2012). Fernando *et al.* (2012) brought similar arguments against the translocation of 'problem' elephants. Sri Lanka's fauna and flora contribute to its economic development in tourism (de Silva Wijeyeratne, 2006). Destroying any portion of its biodiversity, especially among charismatic species like primates, runs afoul not only of the nation's economics but also of its cultural and religious traditions. The ancient kings of Sri Lanka might be credited with having established the world's first officially proclaimed nature sanctuaries, as documented in the Mahavamsa (Geiger, 1912), but that prestige has been losing its luster in modern times (Dittus and Gunathilake, 2013).

## The way forward

The first step to safeguarding Sri Lanka's mammalian biodiversity is to acknowledge its existence. The more challenging aspect involves the identification and safeguarding of habitats that are suitable for sustaining it (Moritz, 2002). It is beyond the scope of this article to review such areas; they have been outlined elsewhere (Wikramanayake *et al*., 2002; Kathriarachchi, 2012; Perera, 2012; Wijesundara, 2012). Notwithstanding, some observations pertaining to conservation management are noteworthy.

In Red List assessments, Areas of Occurrence and Occupancy for primates and other mammals overestimate the available ecologically suitable habitat. Most mature natural forests are found in protected areas (including Forest Reserves), and the most extensive of these are confined to the unproductive arid and dry zones in which primates (and other water-bound mammals) either cannot be sustained at all, or only at very low densities localized near permanent water sources (Eisenberg and Lockhart 1972; McKay, 1973; Dittus 1977b). This is particularly true of the dry zone subspecies of toque macaque, purple-faced langur and loris. The gray langur is somewhat more drought tolerant (Ripley, 1965; Ripley and Schikele, 1970) and may inhabit dry scrub forest. The protected areas at Kaudulla and Angamedilla, with their riparian forests, are welcome additions for the protection of dry zone faunas.The limited areas of highland natural rainforest and related habitats which sustain many of the nation's endemic flora and fauna are under the greatest threat of destruction by humans (Wijesundara, 2012). Illegal felling continues and authorities flout effective wildlife management practices by translocating 'troublesome' primates out of the sanctuary of the Hakgala Botanical Gardens.

Marris (2009) euphemistically referred to secondary habitats as 'havens of biodiversity' which Pethiyagoda (2012) considered 'valuable conservation opportunities' in the Sri Lankan context. While this approach has some merit and historical precedents, it also has serious drawbacks. For instance, given the complexities of phenotypic adaptation to varied environments, it would seem that many species would be ill-adapted (*e.g*., Brook *et al*., 2003), principally mammals with restricted distributions and niche specializations (Ceballos *et al*. 2005; Wijeinghe and Brooke, 2005; Collen *et al*., 2011). An example of appropriate and inappropriate habitats for an endemic mammal is illustrated in Fig. 5. While it is true that some typical forest edge species and ecological generalists may well thrive in disturbed environments (Richard *et al*., 1989), others may develop into pests (Dittus, 2012). The choice is not between secondary habitat and 'old growth forest', as it is often argued, but between habitat with and without the environmental qualities suited to a taxon's ecological niche. In setting priorities for limited political and financial capital for conservation the best investment would target extant natural areas that harbor threatened taxa (Prendergast *et al*., 1993; Hendry *et al*., 2010). Promotion of secondary habitats as conservation landscapes detracts from the difficult and crucial task of conserving natural ancestral niche habitats – the only realistic long-term life-support system for most taxa.

Figure 5. The camouflaged pelage colour pattern of the chevrotain (*Moschiola meminna*) is well suited to hide this immature individual from detection by predators in its ecological niche in the undergrowth of the dry zone forest (a); but this protective colouration loses its effect in disturbed secondary habitat (b). [Photos by the author]

## SUMMARY AND CONCLUSIONS

In order to maximally preserve the diversity of Sri Lankan mammals, conservation objectives must focus not just on the species as a single taxonomic entity, *per se*, but also on intra-specific variation. The diversity of mammals is most readily observed among its named and documented subspecies that can be taken as units of conservation in accord with the concepts of Phylogenetic Species and Evolutionary Significant Units (ESUs). The focus on subspecies as units of conservation involves the preservation of evolving populations in which adaptive diversity and potential for evolutionary change are maintained. They represent Sri Lanka's best estimate of mammal diversity.

Considering land-living indigenous taxa, Sri Lanka has 108 uniquely named species or subspecies of which 69 or 64% are endemic to Sri Lanka, compared to only 22 endemic species (24% of species). The degree of endemism varies by taxonomic order, family and habitat type. Depending on the criteria used for defining endemism, 83% to 100% of primate taxa are endemic, followed by 67% to 82% endemism among the insectivores, rodents, carnivores and ungulates, relatively low 31% endemism among the bats. Most non-endemic taxa are distributed in the extensive and habitat-diverse dry zone (comprising about two-thirds of Sri Lanka's land area). Presumably these taxa were derived relatively recently from continental (mostly Indian) ancestors as endemic species are few (compared to the montane zone), but an evolutionary trend towards endemism is nevertheless indicated by the numbers of dryzone subspecies. Endemic species tend to cluster in the montane wet zone, especially the fast-reproducing insectivores and rodents among which three genera are endemic. Endemic mammals of the highlands appear to share some phylogeographic trends known from other faunal groups (reptiles, amphibian, fish and some invertebrates). The high endemicity (64%) among Sri Lankan mammals, along with that among other Sri Lankan faunas and its flora, sets Sri Lankan apart as a separate unit of biodiversity within the Western Ghats–Sri Lanka hotspot.

The importance of focusing on subspecies, or ESUs, as units of conservation is buttressed by recent taxonomic studies, which have identified 12 new endemic species representing 22% of infra-specific named forms among the orders of: Insectivora, Rodentia, Primates, Carnivora and Artiodactyla. Field observation of wild toque macaques point to the existence of three endemic subspecies, whereas studies of museum skins had led taxonomists to recognize only two. Threats of extinction indicate that the conservation of mammal ESU populations is an urgent priority over their precise taxonomic definitions.

Effective conservation needs first: to officially acknowledge the existence and importance of mammal subspecies (*e.g.*, in Red List assessments) and secondly, to preserve habitats that are critical to their survival. To this end, the promotion of disturbed habitats and captive settings as refugia for Sri Lankan mammals potentially misdirects limited resources away from the urgent priority of preserving native habitats to which mammals with distinct phenotypes have been ecologically adapted. Furthermore, the official disregard of infra-specific mammal diversity invites adverse wildlife management practices, such as the translocation of some primates (considered as pests) to hostile habitats. Such translocation is illegal in most countries and is inimical to the Sri Lankan government's publicized goal of biodiversity conservation for future generations.

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**Appendix 1.** List of naturally occurring land-living mammals of Sri Lanka, excluding introduced taxa†. Definitions of climatic zones follow Eisenberg and McKay (1970). Taxon nomenclature and distributions by climate zone follow cited references (additional references are found in those cited here). Asterisks denote ***endemic genus, **endemic species, and *endemic subspecies.

[Colour photographs of many mammals are found in popular guides (de Silva Wijeyeratne, 2008; Pethiyagoda, 2012; Pethiyagoda *et al*., 2012; Yapa and Ratnavira, 2013]

| Native land-living mammal of Sri Lanka | Distribution by Climatic Zone | Reference |
|---|---|---|
| **Order Insectivora** | | |
| **FAMILY SORICIDAE (Shrews)** | | |
| *Suncus murinus murinus* (Linnaeus, 1766)<br>Common Indian Musk Shrew | A,B,C,D1 | 1,2,3,4 |
| ***Suncus montanus* (Kelaart, 1850)<br>Highland Shrew | D3 | 1,4 |
| **Suncus murinus kandianus* (Kelaart, 1853)<br>Kandyan Shrew | D2 | 1,2,4 |
| ***Suncus zeylanicus* (Phillips, 1928)<br>Sri Lanka Jungle Shrew | D2 | 1,3,4 |
| ***Suncus fellowesgordoni* Phillips, 1932<br>Ceylon Pigmy Shrew | D3 | 1,4 |
| *Suncus etruscus* (Savi, 1822)<br>Pigmy Shrew | D1,D2,D3 | 4,5 |
| **Crocidura horsfieldi horsfieldi* (Tomes, 1856)<br>Horsfield’s Shrew | D2,D3 | 1,2,3,6 |
| ***Crocidura miya* Phillips, 1929<br>Sri Lanka Long-tailed Shrew | D2,D3 | 1,2,3,6,7 |
| ** *Crocidura hikmiya* Meegaskumbura *et al.* , 2007 | D1,D2 | 6 |
| ****Solisorex pearsoni* Thomas, 1924<br>Person’s Long-clawed Shrew | D2,D3 | 1,2,3,7 |
| ****Feroculus feroculus* (Kelaart, 1850)<br>Kelaart’s Long-tailed Shrew | D3 | 1,2,5,24 |
| **Order Chiroptera** | | |
| **FAMILY PTEROPIDAE (Fruit Bats)** | | |
| *Pteropus giganteus giganteus* (Brunnich, 1782)<br>Flying-fox | A to D2 | 1,2 |

| **Native land-living mammal of Sri Lanka** | **Distribution by Climatic Zone** | **Reference** |
|---|---|---|
| **FAMILY PTEROPIDAE (Fruit Bats)** (contd.) | | |
| *Cynopterus sphinx sphinx* (Vahl, 1797)<br>Indian Short-nosed Fruit Bat | all zones | 1,2, 3, 5 |
| **Cynopterus brachyotis ceylonensis* (Muller, 1838)<br>Sri Lanka Short-nosed Fruit-bat | all zones | 1,2,3,8 |
| *Rousettus leschenaulti* (Desmarset, 1820)<br>Fulvus Frit-bat | (A, B, C), D1, D2 | 1,2,3,5 |
| **FAMILY RHINOLOPHIDAE (Horseshoe bats)** | | |
| **Rhinolophus beddomei sobrinus* (Anderson, 1918)<br>Great Horse-shoe Bat | A, B, D1 | 1,2,5 |
| *Rhinolophus rouxi rouxi* Temminck, 1835<br>Rufous Horse-shoe Bat | all zones | 1,2,5 |
| **FAMILY HIPPOSIDERIDAE (Leaf-nosed Bats)** | | |
| **Hipposideros lankadiva lankadiva* Kelaart, 1850<br>Great Sri Lanka Leaf-nosed Bat | A to D2 | 1,2 |
| *Hipposideros speoris speoris* (Schneider, 1800)<br>Schneider’s Leaf-nosed Bat | C, D1, D2 | 1,2 |
| *Hipposideros galeritus brachyotus* (Dobson, 1874)<br>Dekhan Leaf-nosed Bat | C, D1, D2 | 1,2 |
| **Hipposideros bicolor ater* (Templeton, 1848)<br>Sri Lanka Bi-coloured Leaf-nosed Bat | A, B, D1 | 1,2,3,8 |
| **FAMILY MAGADERMATIDAE (False Vampire Bats)** | | |
| **Megaderma spasma ceylonese* Anderson, 1918<br>Sri Lanka False Vampire Bat | A to D2 | 1,2 |
| *Megaderma lyra lyra* Geoffroy, 1810<br>Indian False Vampire Bat | D1, D2 | 1,2 |
| **FAMILY VESPERTILLIONIDAE** | | |
| *Falsistrellus affinis* (Dobson, 1871)<br>Chocolate Bat | D3 | 1,2,3,5,8 |
| **Pipistrellus ceylonicus ceylonicus* (Kelaart, 1853)<br>Kelaart’s Pipistrel | C, D1, D2, D3 | 1,2 |
| *Pipistrellus coromandra* (Gray, 1838)<br>Indian Pipistrel | A, B, C | 1,2, |
| *Pipistrellus tenuis mimus* (Temminck, 1840)<br>Indian Pigmy Pipistrel | D1 (B, C) | 1,2,5,8 |
| *Hesperoptenus tickelli* (Blyth, 1851)<br>Tickell’s Bat | A, B, C, D1 | 1,2 |
| *Scotophilus heathi heathi* (Horsfield, 1831)<br>Greater Yellow Bat | C, D1 | 1,2 |
| *Scotophilus kuhli wroughtoni* Leach, 1821<br>Lesser Yellow Bat | A, B, C, D1 | 1,2,3,5,8 |
| *Myotis hasselti* (Temminck, 1840)<br>Brown Bat | A, B | 1,2,3,5,8 |
| **Murina cyclotis eileenae* (Phillips, 1932)<br>Sri Lanka Tube-nosed Bat | D2 , (D1) | 1,2, |
| *Kerivoula picta* (Pallas, 1767)<br>Painted Bat | B, C, D1, D2 | 1,2,8 |
| **Kerivoula hardwickei malpasi* (Phillips, 1932)<br>Malpas’s Bat | D2 (D1) | 1,2 |
| *Miniopterus schreibersi fuliginosus* (Hodgson, 1935)<br>Long-winged Bat | B, C, D1 | 1,2 |

| Native land-living mammal of Sri Lanka | Distribution by Climatic Zone | Reference |
|---|---|---|
| **FAMILY EMBALLONURIDAE (Sheath-tailed Bats)** | | |
| *Taphozous longimanus* Hardwicke, 1825<br>Long-armed Sheath-tailed Bat | A, B, C, D1 | 1,2,8 |
| *Taphozous melanopogon* Temminck, 1841<br>Black-bearded Sheath-tailed Bat | B, D1 | 1,2,8 |
| *Saccolaimus saccolaimus* Temminck, 1838<br>Pouch-bearing Sheath-tailed Bat | A, B, C, D1 | 1,2,5,8 |
| **FAMILY MOLOSSIDAE (Free-tailed Bats)** | | |
| *Tadarida aegyptiaca thomasi* Wroughton, 1919<br>Indian Wrinkled-lipped Bat | D2, D3 | 1,2,3,5 |
| **Chaerephon plicatus insularis* (Phillips, 1935)<br>Sri Lanka Wrinkle-lipped Bat | D2 | 1,2,3,5 |
| **Order Primates** | | |
| **FAMILY LORISIDAE (Slender Loris)** | | |
| ***Loris tardigradus tardigradus* (Linnaeus, 1758)<br>Red Slender Loris | D1 | 1,2, 9,10,11,15 |
| **Loris lydekkerianus nycticeboides* (Hill, 1942)<br>Montane Slender Loris | D3 | 1,2,9,10,12, 15,16 |
| **Loris lydekkerianus grandis* (Hill and Phillips, 1932)<br>Gray Slender Loris | C, D1, D2 | 1,2,9,10,13,14,15 |
| **Loris lydekkerianus nordicus* (Hill, 1933)<br>Northern Slender Loris | A, B, C | 1,2,9,10,13,14,15 |
| **FAMILY CERCOPITHECIDAE (Macaques and Langurs)** | | |
| ***Semnopithecus vetulus vetulus* (Erxleben, 1777)<br>Southern Purple-faced Langur | D1, D2 | 1,2,9,15 |
| ***Semnopithecus vetulus nestor* (Bennett, 1833)<br>Western Purple-faced Langur | D1 | 1,2,9, 15,16,17 |
| **Semnopithecus vetulus monticola* (Kelaart, 1850)<br>Bear Monkey | D3 | 1,2,9, 15 |
| **Semnopithecus vetulus philbricki* (Phillips, 1927)<br>Northern Purple-face Langur | A, B, C | 1,2,9, 15 |
| **Semnopithecus priam thersites* (Blyth, 1844)<br>Hanuman or Grey Langur | A, B, C | 1,2,9, 15,16, 17 |
| ***Macaca sinica sinica* (Linnaeus, 1771)<br>Dry-zone macaque | A, B, C | 1,2,9, 15,16 |
| **Macaca sinica aurifrons* (Pocock, 1931)<br>Wet-zone Macaque | D1, D2 | 1,2,9,15,16 |
| **Macaca sinica opisthomelas* (Hill, 1942)<br>Montane Macaque | D3 | 1,2,9,15,16,18 |
| **Order Philodota** | | |
| **FAMILY MANIDAE (Pangolins)** | | |
| *Manis crassicaudata* Gray, 1827<br>Pangolin | A, B, C, D1, D2 | 1,2 |

| Native land-living mammal of Sri Lanka | Distribution by Climatic Zone | Reference |
|---|---|---|
| **Order Rodentia** | | |
| **FAMILY SCIURIDAE (Squirrels)** | | |
| **Petaurista philippinensis lanka* (Wroughton, 1911)<br>Large Sri Lanka Flying-Squirrel | D1, D2, D3 | 1,2,5 |
| **Petinomys fuscocapillus layardi* (Kelaart, 1850)<br>Small Sri Lanka Flying-Squirrel | D1, D2 | 1,2 |
| **Ratufa macroura macroura* (Pennant, 1769)<br>Highland Sri Lanka Giant-Squirrel | D2, D3 | 1,2 |
| **Ratufa macroura melanochra* Thomas and Wroughton, 1915<br>Black and Yellow Giant Squirrel | D1 | 1,2 |
| *Ratufa macroura dandolena* Thomas and Wroughton, 1915<br>Common Sri Lanka Giant Squirrel | A, B, C | 1,2 |
| **Funambulus palmarum brodiei* (Blyth, 1849)<br>Northern Sri Lanka Palm Squirrel | A | 1,2 |
| **Funambulus palmarum kelaarti* (Layard, 1851)<br>Southern Sri Lanka Palm Squirrel | A, B, C | 1,2 |
| **Funambulus palmarum olympius* Thomas and Wroughton, 1915<br>Highland Sri Lanka Palm Squirrel | D2, D3 | 1,2 |
| ***Funambulus layardi* (Blyth, 1849)<br>Flame-striped Jungle Squirrel | B, C, D1, D2, D3 | 1,2, 19 |
| ***Funambulus obscurus* (Pelzen and Kohl, 1886)<br>Ceylon Dusky-striped Palm Squirrel | D1, D2, D3 | 1,2,19 |
| **FAMILY HYSTRICIDAE (Porcupine)** | | |
| *Hystrix indica* (Kerr, 1792)<br>Porcupine | all zones | 1,2 |
| **FAMILY MURIDAE (Rats and Mice)** | | |
| **Tatera indica ceylonica* (Wroughton, 1906)<br>Sri Lanka Gerbil | A, B,C, (D1) | 1,2 |
| *Bandicota indica malabarica* Hill, 1939<br>Greater Bandicoot Rat | B, C, D1, D2 | 2, |
| **Bandicota bengalensis gracilis* (Nehring, 1902)<br>Lesser Bandicoot Rat | A, B, C, D1, D2 | 1,2 |
| *Mus musculus urbanus* (Hodgson, 1845)<br>House Mouse | all zones | 1,2 |
| **Mus booduga (cervicolor) fulvidiventris* (Blyth, 1852)<br>Sri Lanka Field Mouse | A, B, C, D | 1,2,5 |
| ***Mus fernandoni* (Phillips, 1932)<br>Sri Lanka Spiny Mouse | A, B, C | 1,2,3,8 |
| ***Mus mayori mayori* (Thomas, 1915)<br>Highland Spiny Rat | D2, D3 | 1,2,7,8 |
| **Mus mayori pococki* Ellerman, 1947<br>Bi-coloured Spiny Rat | D1, D2 | 1,2 |
| **Rattus rattus kandianus* (Kelaart, 1850)<br>Common Sri Lanka House Rat | A, B, C, D1, D2 | 1,2 |
| **Rattus rattus kelaarti* (Wroughton, 1915)<br>Sri Lanka Highland Rat | D2, D3 | 1,2 |
| *Madromys blanfordi* (Thomas, 1881)<br>White-tailed Rat | A, B, C | 1,2,8 |

| Native land-living mammal of Sri Lanka | Distribution by Climatic Zone | Reference |
|---|---|---|
| **FAMILY MURIDAE (Rats and Mice)** (contd.) | | |
| ****Srilankamys ohiensis* (Phillips, 1929)<br>Sri Lanka Bi-coloured Rat | D2, D3 | 1,2,3,7,8 |
| ***Rattus montanus* Phillips, 1932<br>Nelu Rat | D3 | 1,2,3,7,8 |
| *Golunda ellioti ellioti* Gray 1837<br>Indian Bush Rat | A, B, C, D | 1,2 |
| **Golunda ellioti nuwara* (Kelaart, 1850)<br>Sri Lanka Highland Bush Rat or “Coffee Rat” | D2, D3 | 1,2 |
| *Millardia meltada meltada* (Gray, 1837)<br>Soft-furred Field Rat | A, B | 1,2 |
| *Vandeleuria oleracea rubida* (Thomas, 1914)<br>Long-tailed Tree Mouse | A, B, C, D1 | 1,2,3 |
| ***Vandeleuria nolthenii* Phillips, 1929<br>Sri Lanka Long-tailed Tree Mouse | D2, D3 | 1,2,3,7,8 |
| **Order Lagomorpha** | | |
| **FAMILY LEPORIDAE (Hares)** | | |
| **Lepus nigricollis singhala* Wroughton, 1915<br>Sri Lanka Black-naped Hare | all zones | 1,2 |
| **Order Carnivora** | | |
| **FAMILY MUSTELLIDAE (Otter)** | | |
| *Lutra lutra nair* (F. Cuvier, 1923)<br>Sri Lanka Otter | all zones | 1,2 |
| **FAMILY CANIDAE (Jackal)** | | |
| **Canis aureus lanka* (Wroughton, 1916)<br>Sri Lanka Jackal | A, B, C, D1, D2 | 1,2 |
| **FAMILY URSIDAE (Bear)** | | |
| **Melursus ursinus inornatus* (Pucheran, 1855)<br>Sri Lanka Sloth Bear | A, B, C | 1,2 |
| **FAMILY VIVERRIDAE (Civets and Mongoose)** | | |
| **Viverricula indica mayori* Pocock, 1933<br>Sri Lanka Small Civet-cat | A, B ,C, D1, D2 | 1,2 |
| *Paradoxurus hermaphroditus* (Pallas, 1777)<br>Common Indian Palm Civet or Toddy Cat | all zones | 1,2 |
| ***Paradoxurus aureus* Cuvier, 1822<br>Wet-zone Golden Palm Civet | C, D1, D2, D3 | 20 |
| ***Paradoxurus montanus* Kelaart, 1853<br>Sri Lanka Brown Palm Civet | B, D2, D3 | 20 |
| ***Paradoxurus stenocephalus* Groves *et al*., 2009,<br>Dry-zone Golden Palm Civet | B | 20 |
| **Herpestes edwardsi lanka* (Wroughton, 1915)<br>Grey Mongoose | A, B, C | 1,2 |
| **Herpestes fuscus flavidens* (Kelaart, 1850)<br>Highland Sri Lanka Brown Mongoose | D2, D3 | 1,2 |
| **Herpestes fuscus rubidior* (Pocock, 1937)<br>Western Sri Lanka Brown Mongoose | D1 | 1,2 |
| *Herpestes fuscus maccarthiae* (Gray, 1851)<br>Northern Sri Lanka Brown Mongoose | A, B | 1,2 |

| Native land-living mammal of Sri Lanka | Distribution by Climatic Zone | Reference |
|---|---|---|
| **FAMILY VIVERRIDAE (Civets and Mongoose)** (contd.) | | |
| **Herpestes smithi zeylanicus* Thomas, 1921<br>Sri Lanka Ruddy Mongoose | A, B, C, D1, D2 | 1,2 |
| *Herpestes vitticollis* Bennett, 1835<br>Striped-necked Mongoose | A, B, C, D2, D3 | 1,2 |
| **FAMILY FELIDAE (Cats)** | | |
| **Prionailurus rubiginosus phillipsi* Pocock, 1939<br>Sri Lanka Rusty-spotted Cat | all zones | 1,2 |
| *Prionailurus viverrinus* (Bennett, 1833)<br>Indian Fishing Cat | A, B, C, D1 | 1,2,5 |
| *Felis chaus affinis* (Gray, 1830)<br>Sri Lanka Jungle Cat | A, B | 1,2 |
| **Panthera pardus kotiya* (Meyer, 1794)<br>Sri Lanka leopard | all zones | 1,2,21 |
| **Order Proboscidea** | | |
| **FAMILY ELEPHANTIDAE (Elephant)** | | |
| **Elephas maximus maximus* Linnaeus, 1758<br>Elephant | all zones | 1,2,22 |
| **Order Artiodactyla** | | |
| **FAMILY SUIDAE (Pig)** | | |
| *Sus scrofa cristatus* (Wagner, 1839)<br>Wild Boar | all zones | 1,2 |
| **FAMILY TRAGULIDAE (Chevrotain)** | | |
| ***Moschiola meminna* Erexleben, 1777<br>Sri Lanka Chevrotain (or Mouse-deer) | A, B, C, D1, D2 | 1,2, 23 |
| ***Moschiola kathygre* Groves and Meijaard, 2004<br>Sri Lanka Pigmy Chevrotain (or Mouse-deer) | D3 | 1,2, 23 |
| **FAMILY CERVIDAE (Deer)** | | |
| *Muntiacus muntjak malabaricus* Lydekker, 1915<br>Barking Deer | A, B, C, D1, D2 | 1,2 |
| **Axis axis ceylonensis* Fischer, 1829<br>Spotted Deer | A, B, C | 1,2 |
| **Rusa unicolor unicolor* Kerr, 1792<br>Sambur | all zones | 1,2, 8 |

1 Phillips (1980), 2 Eisenberg and McKay (1970), 3 McKay (1984), 4 Meegaskumbura and Schneider (2008), 5 Weerakoon and Goonatilake (2006), 6 Meegaskumbura *et al*. (2007), 7 Wijesinghe (2006), 8 Weekaroon (2012), 9 Molour *et al*. (2003), 10 Nekaris and Jayewardene (2004), 11 Gamage *et al*. (2009), 12 Gamage *et al*. (2010), 13 Perera (2008), 14 Perera *et al*. (2009), 15 Brandon-Jones et al. (2004), 16 Groves (2001), 17 Karanth (2010), 18 Hill (1942), 19 Dissanayake and Oshida (2012), 20 Groves *et al*. (2009), 21 Miththapala (2006), 22 Fernando *et al*. (2000), 23 Groves and Meijaard (2005), 24 Pethiyagoda (2012).

† Introduced forms normally cited in lists of Sri Lankan mammals include the following taxa: *Rattus rattus rattus, R. r. alexandrinus, R.r. rufescens, Rattus norvegicus, Axis porcinus porcinus, Bubalus bubalis bubalis, Equus caballus.*