ECOLOGICAL, MORPHOLOGICAL AND DEMOGRAPHICAL VARIATIONS OF HANUMAN LANGUR (*SEMNOPITHECUS SPP*) SPECIES COMPLEX IN PENINSULAR INDIA AND THEIR IMPLICATIONS TO TAXONOMY

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In

Zoology

By

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CERTIFICATE

This is to certify that the thesis, entitled "Ecological, Morphological and Demographical variations of Hanuman langur (*Semnopithecus spp)* species complex in peninsular India and their implications to taxonomy ", submitted to the Bharathiar University, in partial fulfillment of the requirements for the award of the Degree of Doctor of Philosophy in Zoology is a record of original research work done by Mr. Chetan Nag.K.S during the period July 2008 to November 2011 of his study at Sálim Ali Centre for Ornithology and Natural History, Coimbatore, under my supervision and guidance and the thesis has not formed the basis for the award of any other Degree/Diploma/Associateship/Fellowship or other similar title to any candidate of any University.

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DECLARATION

I, ChetanNag.K.S., hereby declare that the thesis entitled " Ecological, Morphological and Demographical variations of Hanuman langur (*Semnopithecus spp)* species complex in peninsular India and their implications to taxonomy " submitted to the Bharathiar University, in partial fulfillment of the requirements for the award of the Degree of Doctor of Philosophy in Zoology is a record of original and independent research work done by me during July 2008 to November 2011 under the supervision and guidance of Dr. P. Pramod, Sálim Ali Centre for Ornithology and Natural History, Coimbatore and it has not formed the basis for the award of any Degree/Diploma/Associateship/Fellowship or other similar title to any candidate in any other University.

Signature of the Candidate

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PUBLICATIONS

List of peer reviewed publications

1. Nag, K. S. C., Pramod, P and Karanth, K. P. 2011. Taxonomic Implications of a Field Study of Morphotypes of Hanuman Langurs (*Semnopithecus entellus*) in Peninsular India. *International journal of Primatology.*32:830–848. Published online: 5th March 2011 (DOI: 10.1007/s10764-011-9504-0).

2. Nag, K.S.C., Pramod.P and Karanth, K.P. 2011. Natural range extension, sampling artifact, or human mediated translocations? Range limits of Northern type *Semnopithecus entellus* (Dufresne, 1797) (Primates: Cercopithecidae: Colobinae) in peninsular India. *Journal of Threatened Taxa* 3(8): 2028–2032.

3. Nag, K.S.C., Karanth, K.P., Gururaja, K.V. 2011. Understanding the ecological requirements of Hanuman langurs (*Semnopithecus entellus*) of peninsular India by ecological niche modeling approach. (To be submitted).

4. Nag, K.S.C., Shenoy, P.A., Karanth, K.P. 2011. Variations in troop structure and compositions of Hanuman langur species complex of peninsular India. (To be submitted).

THESIS ABSTRACT

The Hanuman langur (*Semnopithecus spp*) is one of the most widely distributed and morphologically diverse non-human primates in South Asia. Even though it has been extensively studied, the taxonomic status of this species remains hugely debated. Most authors consider Hanuman langurs to be a single species, *Semnopithecus entellus*, but divide this species into 14, 15, and 16 subspecies while others split the Hanuman langurs to as many as two, four, seven distinct species. The incongruence in the taxonomic status of Hanuman langurs are largely attributed to practice of conventional taxonomy. In addition, recent molecular phylogenetic works also do not support the monophyly of Hanuman langurs (Karanth et al. 2008, 2010; Osterholz et al. 2008) suggesting that Hanuman langurs consist of multiple species. This ambiguous taxonomic status has serious consequences for studies targeting these taxa, since, Hanuman langurs have been used extensively as a model system in various biomedical, ecological, behavioral, and evolutionary researches (Karanth et al. 2010). In addition, taxonomic status often dictates conservation priorities; thus this situation will also confound conservation efforts for Hanuman langurs.

To bring greater resolution in Hanuman langur taxonomy, current thesis attempted to map the congruence between some of the ecological, morphological, and demographical characters of Hanuman langurs of peninsular India. In doing so the thesis, ultimately aimed to correlate which of the existing classification scheme best explained the taxonomic position of these taxonomically challenged langurs. With this objective the study was conducted in peninsular India (8–21°N, 73–78°E), covering the states of Andhra Pradesh, Goa, Maharashtra, Karnataka, Kerala, and Tamilnadu in India, as well as some parts of northern Sri Lanka opportunistically. The study also included some Northern type Hanuman langurs as controls from parts of Gujarat, Madhya Pradesh, Chhattisgarh, and Orissa. As far as possible study included the type localities mentioned in various classification schemes.

The morphological study retrieved at least six distinct morphologically variable types (morphotypes) which could be identified in the field by using a combination of five diagnostic

characters. On the other hand, the species distribution modeling, based on maximum entropy (Maxent) algorithm was able to clearly demarcate the ecological niches of all of the six morphotypes from the morphological findings thereby observing little overlap between any two candidate species of interest. Demographical analysis mirrored the findings of ecological and morphological exercise with group size, adult female and infant numbers contributing to the overall variation amongst Hanuman langur morphotypes.

The thesis determined the approximate distributions of the morphotypes by plotting the sampling locations of each morphotype on a map using GIS software. One of the primary outcomes of the distributional study was that Northern type *S. entellus* ranges limit extended further south of Roonwal's borderline of Tapti- Godavari rivers. Current study recommended one population of Hanuman langurs in Palakkad district of Kerala state for a more systematic study based on the findings of morphological, ecological and demographical analysis.

Results from the current work indicated that peninsular Indian Hanuman langurs showed concordance to one of the previous classification scheme with respect to morphology, ecology and demographical characters. The study found concordances with some of the earliest classification schemes, but showed incongruence with recent classification schemes. Based on the consensus of the above results, the thesis, recommends that Hill's (Ceylon Journal of Science, Colombo 21:277-305, 1939) classification scheme should be used for future studies on Hanuman langurs.

OBJECTIVES

The specific objectives of the thesis were as follows:

1. How many morphologically variable Hanuman langurs are present in Peninsular India?
    - What diagnostic characters can be used to identify these morphologically variable types (morphotypes) of Hanuman langurs of Peninsular India?
2. What are the approximate distributional limits of the morphotypes?
    - Can we determine the southern limits of the distribution of Northern type (NT) Hanuman langurs in peninsular India?
3. What do we understand of the ecological requirements of Peninsular Indian Hanuman langurs through ecological niche modeling approach?
    - What are the predicted distributional boundaries of the morphotypes?
    - Is there a concordance in distributional boundaries between morphological and ecological niche modeling exercises?
4. Do variations in troop structure and compositions of Hanuman langur species substantiate the findings of niche modeling and morphological analyses?
5. Which of the existing classification scheme best fits the observed variations of Hanuman langurs in Peninsular India?

ORGANIZATION OF THE THESIS

Chapter 1: Introduces the general introduction to the problem of the theses followed by organizational history of leaf monkeys their characteristic features distinguishing them from macaques. This is followed by evolutionary history of the Asian colobines, radiation of south East Asian colobines and *Semnopithecus* in Asia; review on the taxonomic status of the genus *Semnopithecus.* This chapter concludes with the description of the study area.

Chapter 2: primarily reviews the literature extensively underlying the taxonomic status of Hanuman langurs in India and thus attempts to ascertain the number of morphologically recognizable units (morphotypes) of Hanuman langur in peninsular India and compares field observations with published classification schemes. The chapter also suggests the diagnostic characters for identifying Hanuman langurs along with approximate distributional boundaries.

Chapter 3: discusses the current range limits of Northern Type Hanuman langurs in peninsular India and reasons for observed change in the range limits.

Chapter 4: attempts to primarily understand ecological requirements of the various species of langurs in the present study through an ecological niche modeling approach. The chapter specifically looks at the ecological niches and distributional boundaries/limits of morphotypes described in chapter 2. The chapter concludes discussing the distinctive niches of various species in peninsular India, extent of overlapping boundaries between candidate species and their implications to delimitation of species boundaries.

Chapter 5: looks at the role of some important demographic variables in explaining the variations between species of Hanuman langurs of peninsular India. Variables such as group size, adult female and infant numbers explained overall significance between various species substantiating the findings of niche modeling and morphological analyses.

Chapter 5 is followed by references and appendices.

The thesis chapters are presented in the journal manuscript format containing introduction, objectives, materials and methods, results and discussion in that order. Chapter 2 which has been published in the August, 2011 issue International journal of primatology recommended one of the previous classification schemes to be consulted to undertake future studies on Hanuman langurs. Thus the chapter's 4 and 5 used Hill's (1939) classification schemes to designate names of the species and subspecies instead of "Morphotypes" to avoid further confusions pertaining to the nomenclature.

1. Introduction

"Species" being one of the fundamental units of biodiversity has been a great interest to taxonomists, evolutionary biologists, ecologists, and conservationists for various reasons (Harrison, 1998; W Kunz, 2001). Inspite of these obvious interests there is a little consensus on defining the term "Species" leading to many species concepts (about 24, Mayden, 1997) arriving at no single definition (Harrison, 1998; Mallet, 2001; de Queiroz, 1998). Thus the "species" still remains uncertain because of uncertainties (Alroy, 2002) regarding the species concept itself indicating that the classification of living organisms is by no means cut and dried.

Different systematists define "Species" within the framework of very different concepts (W Kunz, 2001). Species definitions footed on different properties lead to the recognition of different numbers and boundaries of species taxa (de Queiroz, 2006). Till date there has not been a single concept that incorporates "intrinsic reproductive isolation"(Mayr,1942; Dobzhansky,1970), "specific mate recognition or fertilization system"(Paterson, 1985; Masters et al. 1987), "phenetic differences"(Michener ,1970; Sokal and Crovello, 1970; Sneath and Sokal, 1973), "ecological distinctiveness"(Van Valen ,1976; Andersson 1990), "fixed character state differences"(Cracraft ,1983; Nixon and Wheeler , 1990), "monophyly"(Donoghue ,1985), "exclusive coalescence of alleles" (Baum and Shaw , 1995), "heterozygote deficits"(Mallet , 1995) etc. in defining "Species". Repeatedly there have been arguments that fundamental problem lies with the concepts itself thereby leading to inconsistent methods for recognizing species in practice (de Queiroz, 2005; Rojas, 1992; Hey, 2006). This riddle known to biologists as "species problem" is thus one of the most vexing problems of this century (Mayr, 1996). In their search for a possible solution to "the species problem" de Queiroz and Pigliucci offered some ray of hope by considering "species" as meta population lineages (2005; 2006; 2007) and family resemblance concepts (2003) respectively in order to resolve the confusions pertaining to species concepts. Regarding the methodologies for recognizing species there are some insights from Sites and Marshall, 2004 with respect to empirically delimiting species boundaries. However Sites and Marshall, 2004 methods are again reliant on the species concepts indicating their susceptibility to flaws.

As aforementioned "species problem" repeatedly is being discussed mostly in the light of incongruences between the phylogeny , taxonomy of taxa (Hey, 2001; Sites and Marshall, 2004) and their relevance in species identification for conservation (Isaac *et al.*, 2004). Some studies (Mallet, 2007; Cracraft, 1987; Baum, 2009) counting that of ICZN is of opinion that species concepts have their origin in taxonomy. But taxonomy solely based on specific traits often results in inadequate or misleading guides for phylogenetic distinctions at subspecies and species level (Avise, 1989; Steinberg et al, 2009). Scientific literature often defines a species complex as a group of closely related species, with no clear cut boundary between species or cryptic owing to their recent and usually still incomplete reproductive isolation.

Herein I attempt to address species complex issue taking Hanuman langurs as an example whose taxonomic status is hugely contested. Hanuman langurs are considered both to be single and multispecies in the literature so far (reviewed in chapter 2). Morphology-based classification schemes of Hanuman langurs (*Semnopithecus*) have not been successful in resolving their species/subspecies status (reviewed in chapter 2). The ecological and morphological variations in Hanuman langurs are quite high compared to any other primate taxa in India which could have contributed to the uncertainties with respect to their taxonomy and evolutionary history. Traditionally, morphological traits have been used to examine animal taxonomy from museum specimens since there have been consensus on morphological characters being less plastic than behavioral or ecological traits for reconstructing phylogeny and taxonomy (Atz, 1970; Wilson, 1975; Baroni Urbani, 1989). It has also been shown elsewhere that evolutionary history has an effect on traits such as ecological niche (Fleagle and Reed, 1999). Additionally Jolly (1993) observes that the degree of ecological niche separation among taxa may help to distinguish their evolutionary relationships since ecological divergence is often thought of as a characteristic of true biological species. Henceforth reasons mentioned above forms rationale for incorporating morphology, ecology, behavior in investigating taxonomic questions (Kamilar, 2006).

The purpose of this thesis work was to quantify morphological, ecological and demographical variations of Hanuman langurs of peninsular India to address their taxonomic status. In doing so, I have tested the congruence from morphological, ecological and demographical data to examine which of the existing classification schemes best explains the observed congruence.

Overview of the taxonomic position of Hanuman langur

The order primate constituting more than 300 species (Nadler et al, 2003) identifies two suborders namely the Strepsirrhini (wet-nosed primates) with 8 families and the Haplorrhini (dry-nosed primates) with 7 families (Nadler et al, 2003; Radhakrishna, 2004).

The Haplorrhini are distributed with four families in the Neotropics (Cebidae, Nyctipithecidae, Pitheciidae, and Atelidae), with two families in Asia (Tarsiidae and Hylobatidae), two families in Africa and Asia (Cercopithecidae and Hominidae). The Neotropic families are grouped in the Infraorder Platyrrhini (New World primates), whereas the Old World families are grouped in the Infraorder Catarrhini (Nadler et al, 2003).

The Catarrhine monkeys of the family Cercopithecidae are further divided into two extant subfamilies: Cercopithecinae and Colobinae. Cercopithecinae being monogastric often referred to as the cheek-pouched monkeys have varied diet patterns which commonly include the macaques, baboons, drills, mangabeys, and guenons. Colobinae are often referred to as leaf monkeys because of their predominantly specialized folivorous diet possessing many of the anatomical features related to their folivorous adaptation. It is well documented from the majority of the captive studies that colobines possess a specialized stomach. This specialized stomach is an adaptation of these predominantly leaf eating monkeys which allows the microbial fermentation indicated by the high number ($8X10^7$ to $4X10^8$ per gram dry matter) of cellulose digesting bacteria (Oates and Davies, 1994; Bauchop and Martucci, 1968; Nijboer and Clauss; Chivers, 1995). Other examples of leaf monkey's adaptation to folivorous diet lacking in Cercopithecines include an enlarged liver to processes the toxins, which many trees produce to protect mature leaves against predation. Likewise the salivary glands in contrast to cercopithecines are enlarged in colobines to assist the cellulose digestion. While molar cusps of the Cercopithecines are rounded and low cusped, leaf-monkeys possess high and pointed, molar cusps with long shear crests aiding them to finely mince leaves for digestion. Additionally, colobines lack cheek pouches, which in cercopithecines are used to keep food for a short time (Oates and Davies, 1994). A summary of morpho-anatomical features differentiating the Colobinae and the Cercopithecinae are listed in Table 1.1.

Conventionally, the colobines based on their region of distribution were subdivided into the African (*Colobus spp.*) and the Asian leaf monkeys (*Presbytis spp*, *Nasalis spp*, *Pygathrix spp. Rhinopithecus spp*.*Trachypithecus spp*.). However there have been contradictory phylogenetic trees of the colobines proposed in past. For example studies of Messier and Stewart (1997) tree based on mitochondrial DNA and the coding region of the lysozyme gene sequence clearly separated the African from the Asian colobines. Nijboer and Clauss ( ) in their review, draw attention to Caton's observations based on the anatomical fore stomach characteristic that while some "African *Colobus spp*. and the Asian *Semnopithecus*, *Trachypithecus* and *Presbytis* on the one hand all have a so-called tripartite forestomach that lacks a distinct *presaccus* , others such as African *Procolobus* and the Asian *Rhinopithecus*, *Pygatrix* and *Nasalis* on the other hand have a distinct *presaccus* at their forestomach, making this organ quadripartite" highlighting the degree of relatedness between African and Asian colobines. Nevertheless the Colobinae subfamily is supposedly represented by two major evolutionary radiations (*Oates et al.*, 1994; Groves 2001) one in Africa represented by *Colobus, Procolobus, Piliocolobus* (Groves, 2001) and the other in Asia represented by *Semnopithecus, Trachypithecus, Presbytis, Pygathrix, Rhinopithecus, Nasalis* and *Simias*.

Table 1.1 : Morpho-anatomical differences between Colobines and Cercopithecines (adapted from Delson, 1992 and Nadler et al, 2003)

Colobines	**Cercopithecines**
Generally known as "leaf monkeys"	Commonly known as "cheek-pouched monkeys"
Possess large multi chambered stomach for digesting leaves	Possess a simple stomach
Lack a cheek pouch for storing food	Possess a cheek pouch for storing food
Shows a high vaulted skull	Shows a low vaulted skull

Have a widely spaced orbits	Orbits are close together
Nasal bones short and broad (except Nasalis and Simias)	Nasal bones long and narrow
Molars have sharp high cusps	Molars have rounded low cusps
Deep jaw bone	Shallow jaw bone
Enlarged salivary glands	Small salivary glands
Enlarged liver	Small liver
Thumb absent or if present are short	Possess a well-developed thumbs
Long legs	Arms and legs of similar size
Tails usually very long	Both short and long tails seen

Overview of Evolutionary history of Asian Colobines from Fossil studies.

A synthesis of molecular data which consists of mitochondrial DNA datasets (Cytochrome-b and nuclear) and fossil data available for the old world monkeys suggests that the colobines which originated in Africa, dispersed into Asia from Africa around 10 million years ago (Stewart and Disotell, 1998). While Delson (1994) observes the split between Colobines and Cercopithecines occurred after 15 million years ago (mya) with colobines splitting geographically by 11 million years, Simons (1972) estimated that colobines probably originated in Africa over 12 mya and reached Asia via Europe via an emerging land bridge that connected Africa and the Arabian Peninsula in the late Miocene (Stewart and Disotell, 1998). Earliest fossil evidence for colobines dates back to the early Pliocene deposits of Eastern Europe and Middle East. Discovery of *Paracolobus* fossil in Kenya by Richard leakey and fossils from Siwalik hills of India by Lydekkar (1884) both belonging to late Pliocene period provides additional evidence for the sub family and split that occurred between Africa and Asian forms (Delson, 1994 and references therein). Thus some of these studies are indicative of the fact that colobines reached

Asia between 10-12 mya. Some of these data strongly suggest the reinforcement of existence of an African and Asian group (Xing et al, 2005; Disotell 2000).

Mesopithecus is believed to be the ancestral species from which the Asian colobines are likely to have evolved (Hrdy, 1977). *Mesopithecus* was a medium sized "Colobine" from late Miocene to the early and middle Pliocene deposits in Europe. *Mesopithecus* was known to possess two species differing in their chronological range and body size: *Mesopithecus pentelicus* WAGNER 1839 and *Mesopithecus monpessulanus* GERVAIS 1849. A third species *Mesopithecus delsoni* has been widely debated of its taxonomic status inspite of recent evidences (see Pradella and Rook, 2007 and references therein). There have been several reviews discussing the affinities of *Mesopithecus* to Africa and Asia. Simons (1972) study based on skulls and post cranial bones from Pliocene deposits in Greece opined that *Mesopithecus* showed a strong sexual dimorphism much similar to Asian colobines rather than African colobines. Pan et. al (2004) studies based on dental metrics and Merceron et al (2009) studies based on comparative dental micro wear analysis showed that *Mesopithecus* had strong affiliations with Asian colobines. Delson (1994) opined that *Mesopithecus* was most likely Eurasian in origin and not African. Many of the aforementioned studies also discussed the semi terrestrial/ woodland adaptations of *Mesopithecus*. Available *Mesopithecus* fossils, dating back to as old as 8.5 million years whose limb proportion and fossil findings described by Lydekker (1884) from the Siwalik Hills of India suggested the resemblance to the present day Indian langurs. Also noteworthy is that there have been no records of extinct colobines from Indo Pak region apart from the *Semnopithecus palaeindicus* by Lydekkar (1884) dated between 3.2 to 1.7 mya (Delson, 1994) though there have been some Pleistocene specimens of *Semnopithecus entellus* (Badam, 1979). All of the above studies thus points out as evidences for *Mesopithecus* representing as basal ancestry to all the present day Asian colobines. Pradella and Rook (2007) studies opined based on the remains from Villafranca d' Asti in Italy that *Mesopithecus* may have had their last occurrences in Europe citing "faunal turnover and a change of the palaeo environment" at the Early–Middle Villa franchian transition as reasons for their extinction.

Radiation of South East Asian colobines and *Semnopithecus* in Asia.

There have been several studies in recent years to explain the possibilities of further radiations of colobines in Indian sub-continent and South East Asia. Brandon-Jones (1996) is of the opinion that Pleistocene glaciations around 190,000 and 80,000 years Before Present (BP) must have had influenced in the extirpation of many species in Asia. He further adds that only species in moist warm refugia were successful in recolonizing during interglacial periods. According to the study *Semnopithecus entellus,* which was confined to refugia in south India, evolved from *S. vetulus* after the last glaciation (circa 80,000 years BP) and spread eastward and northwards across India continuing up to Nepal and Bhutan (Wangchuk, 2005).While *Semnopithecus* had its refugia in south India, *Trachypithecus* refugia was traced to south west China spreading out northwestwards through Thailand and Burma to India and as Wangchuk (2005) predicts, to Bhutan. Brandon-Jones (1996) writes that *Trachypithecus,* spread westward from Pleistocene Ice Age refuge in south China.

A Study by Karanth (2000) opined that, radiations of colobines in Asia are a result of major geological event namely, rising of Himalayas in the late Miocene caused by the collision of Indo-Australian tectonic plate with Eurasian plate. His PhD work based on molecular data showed colobines of Asia splitting into two major groups: langurs of Indian Subcontinent and leaf monkeys of South East Asia. He noted that Himalayas in the northern front and Bengal basin acted as major barriers that might have triggered the division of *Semnopithecus* and other Asian colobines (*Trachypithecus, Presbytis, Pygathrix, Rhinopithecus, Nasalis* and *Simias*) around 8 to 9 mya. The study observed that mitochondrial DNA genomes of *Trachypithecus and Semnopithecus* lineages diverged around 8.5 mya due to desiccation of the Tibetan plateau with *Semnopithecus* dispersing into the then wetter parts of Indian subcontinent. Further split between Sri Lankan and Indian langurs are likely to have occurred around 3.3 mya giving rise to Nilgiri langurs in south India along with Purple faced langurs in Sri Lanka. Also during the same time (3.3 mya) split between Hanuman langurs and Purple faced langurs happened in Sri Lanka. Another split might have happened around 2 to 3 mya between south Indian langurs and north Indian langurs in North and central India. This pattern now has additional support by Wangchuk (2005). The study however limited its explanations to only diversifications of *Semnopithecus* in Indian subcontinent.

Another study by Roos et. al (2011), proposed that , *Semnopithecus* was the first amongst all the Asian colobines to diverge, resulting in the langur paraphyly. Accordingly colobines reached East Asia from Africa via Eurasia most likely via a route north of the

Himalayas at the Hengduan Mountains in the border region of the present day Burma. It is at this Hengduan Mountains, Asian colobines diversified into a lineage comprising of *Trachypithecus, Presbytis, Pygathrix, Rhinopithecus, Nasalis* and *Simias* in South East Asia and *Semnopithecus*, in Indian subcontinent. Accordingly, the odd-nosed colobines (*Pygathrix, Rhinopithecus, Nasalis* and *Simias*) migrated to the south from China and expanded their range into Indochina and Sundaland with Nasalis and Simias further separating from each other around 1.1-1.9 mya. The study doesn't fail to mention the role of major rivers of South East Asia namely Mekong, Salween, Yangtze rivers of early Miocene as major barriers. The study points out that some areas of present day Burma, Bangladesh and India acted as the hybrid zone whereby *Semnopithecus and Trachypithecus* came into secondary contact and hybridized until ~2.6 mya supported by other studies as well (Osterholz et al, 2008; Karanth, 2010). So far these two studies apart from a study by Stewart and Disotell, (1998) and Jablonski (1992) provide us with comprehensive insights into the evolutionary history of colobine monkeys in Asia.

Semnopithecus **Desmarest, 1822**

Sem-no-pith`e-kus, (Semno-grave and pithecus-an ape, ape-like. Gr.,)

The generic level taxonomy of langurs and leaf monkeys based on morphology have been heavily contested for decades with very little success (refer Karanth *et al*. 2008). Traditionally the colobines of South and South East Asia based on neonatal coloration and cranial morphology were split into *Semnopithecus, Trachypithecus, Presbytis* [Pocock, 1935], and *Kasi* [Hill, 1934]. Much confusion existed until early years of twentieth century wherein all langurs were either called *Semnopithecus* [Hill, 1939; Pocock, 1939) *or Presbytis* (Roonwal, 1984; Napier and Napier, 1967) or both (Groves, 2001). A consensus has now been reached with ample evidences to segregate *Semnopithecus* (about two-thirds) from *Presbytis* into which it was formerly placed in (Brandon-Jones, 2004; Osterholz et al, 2008; Karanth et al, 2008; Karanth, 2010 and references therein). The Asian colobines according to the most recent classifications (Groves 2001; Brandon-Jones *et al*. 2004), comprise of five species groups: *Semnopithecus* (langurs), *Trachypithecus* (leaf monkeys), *Presbytis* (surili), *Rhinopithecus* and *Pygathrix* (snub-nosed monkeys), *Nasalis* (proboscis monkey), and *Simias* (pig-tailed monkey).

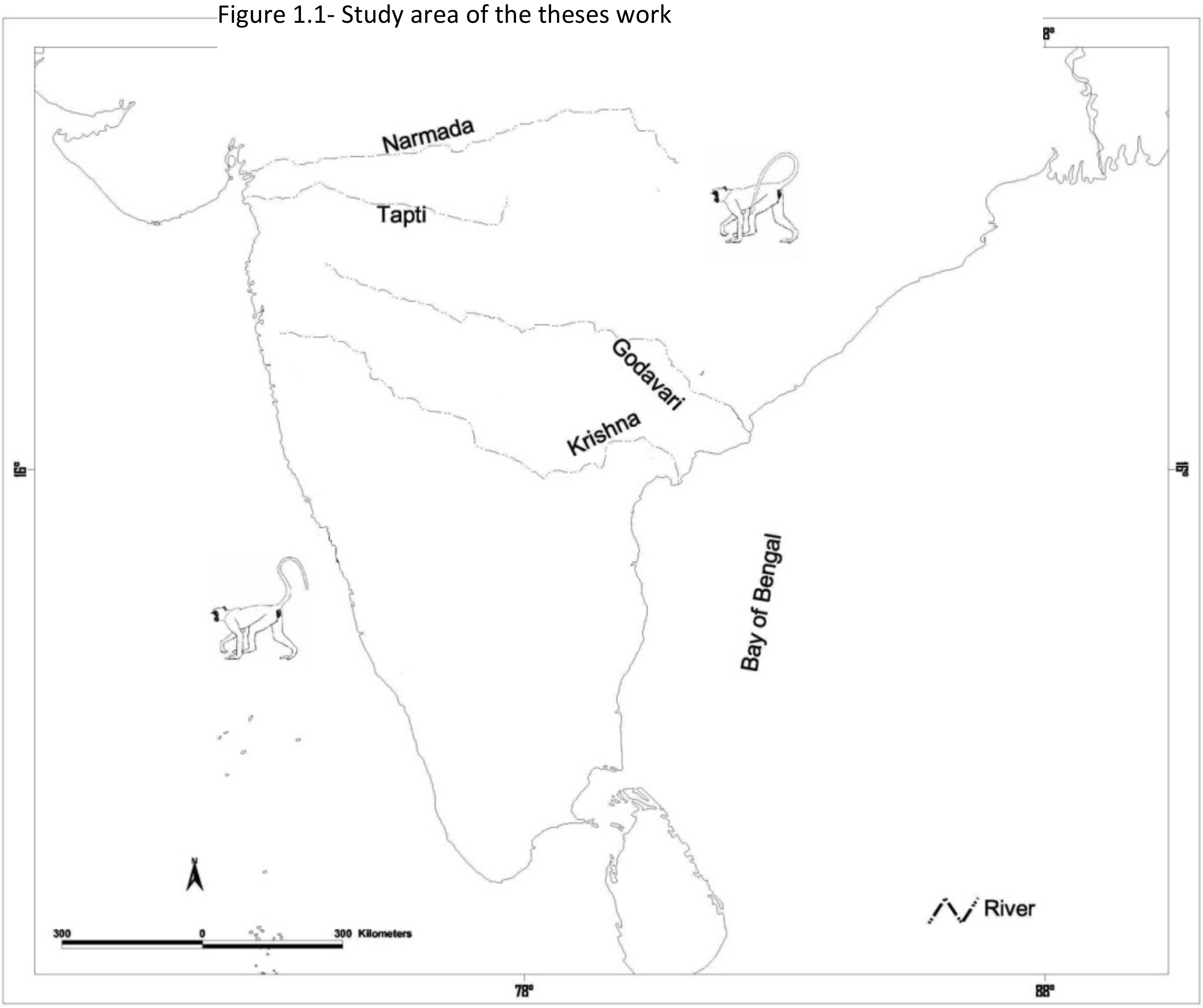
Colobines in South Asia particularly from Indian subcontinent are represented by two genera namely *Semnopithecus* and *Trachypithecus. Trachypithecus* consists of the langurs such as golden langur and capped langur found in the northeast states of India, Bhutan, and in northeast Bangladesh. Phayre's leaf monkey which is largely restricted to south East Asia is also reported in the Indian state of Tripura (Karanth *et al*. 2008; Karanth, 2010). *Semnopithecus* includes species like Hanuman langur, Nilgiri langur, and purple-faced langur. Phylogenetic analysis of langurs in Asia reveals that Hanuman langurs are closely related to Nilgiri (*Semnopithecus johnii*) and purple-faced langurs (*Semnopithecus* vetulus) (Karanth et al. 2008; Osterholz et al. 2008; Zhang and Ryder 1998), which are distributed in peninsular India and Sri Lanka respectively. Thus these 3 species of langurs are now placed in the genus *Semnopithecus*, distinct from leaf monkeys in the genera *Trachypithecus and Presbytis* (Brandon-Jones et al. 2003). Available molecular data on langurs suggest that Hanuman langurs are polyphyletic with respect to Nilgiri and purple-faced langurs (Karanth et al. 2008 and 2010; Osterholz et al. 2008)whereas Phayre's leaf monkeys along with other Southeast Asian leaf monkeys form another distinct clade of *Trachypithecus* spp. Furthermore Karanth *et al*. (2010) and Osterholz *et al*. 2008 argue that the Hanuman langurs should be tentatively split into three species namely Northern type (NT) Hanuman langurs from north India, Southern type (ST) Hanuman langurs from south India and Southern type (ST) Hanuman langur from Sri Lanka such that their taxonomy is consistent with their evolutionary relationships. On the other hand the phylogenetic position of capped and golden langurs remains ambiguous. Insights from molecular work so far suggest that they are closely related to each other but this group might have evolved through past hybridization between *Semnopithecus and Trachypithecus* (Roos et al, 2011; Karanth, 2010; Karanth, 2008).

Nadler et al (2003) makes an interesting observation regarding the confusions over the usage of "langur" in Asian colobines literature which traces back to Hindi word "langur" commonly used for the long-tailed monkeys (Oates *et al.,* 1994). They note the word "langur" has been used by various authors in both general and specific senses. Accordingly while some publications have used "langur" to include every Asian Colobinae others have limited the term to *Semnopithecus*, *Presbytis* and *Trachypithecus*. Herein the name Hanuman langur, has been adopted which is also referred to as Common langurs or Grey langurs by various others who have worked on langur taxonomy so far.

Study Area

I was primarily interested in Southern type (ST) Hanuman langurs, which are distributed south of the Tapti-Godavari rivers according to Roonwal (1979, 1984). ST Hanuman langurs were chosen because they exhibit higher levels of morphological variation than Northen type (NTs), as is apparent from more numbers of subspecies reported among Southern types in most classification schemes (Table 2.1). Therefore the survey was conducted in peninsular India (8–21°N, 73–78°E), with a total area of 635,780 km² covering the states of Andhra Pradesh, Goa, Maharashtra, Karnataka, Kerala, and Tamilnadu in India, as well as some parts of northern Sri Lanka opportunistically. The districts in these states were chosen based on past surveys (Kumara et al. 2010; Kumara and Singh 2004; Kurup 1981, 1984; Srinivasulu and Nagulu 2001; Baldwin et al. 1975) as well as forest department reports. The study also included some NTs as controls from parts of Gujarat, Madhya Pradesh, Chhattisgarh, and Orissa. As far as possible study included the type localities mentioned in various classification schemes.

Figure 1.1- Study area of the theses work



2. Taxonomic Implications of morphotype variation of Hanuman langurs in peninsular India

Introduction

Hanuman or common langurs (family Cercopithecidae, subfamily Colobinae) are the most widely distributed nonhuman primates in South Asia (Choudhury 2007; Napier and Napier 1967). They are dispersed throughout most of India and Sri Lanka (Ellerman and Morrison-Scott 1966; Oates et al. 1994), and are also established in parts of Pakistan (Minhas et al 2010), Nepal (Oates et al. 1994; Roonwal 1984), Bhutan (Wangchuk, 2005 ; Choudhury 2010), and Bangladesh (Choudhury 2007)(Figure 2.1).

They occur in a wide range of habitats from arid regions on the edge of the desert in Rajasthan to the rain forests of Western Ghats and at altitudes of 100–4270 m above mean sea level (msl) in the Himalayas (Bishop 1978; Hrdy 1977). Although Hanuman langurs are one of the most well-known, revered, and extensively studied nonhuman primates in India, the taxonomic status of this species have remained unresolved.

Hanuman langurs exhibit much morphological variation throughout their range, which is reflected in the multitude of classification schemes proposed to resolve its taxonomic status. Pocock (1928, 1939) conducted one of the earliest systematic reviews of Hanuman langur classification. He considered Hanuman langur as a single species, *Semnopithecus entellus*, with 14 subspecies including *S. e. schistaceus, S. e. entellus, S. e. ajax*, *S. e. achilles, S. e. hypoleucos, S. e. priam, S. e. dussumieri, S. e. thersites, S. e. achates, S. e. iulus, S. e. aeneas, S. e. priamellus, S. e. elissa, and S. e. anchises* (Pocock 1939 and Table 2.1). He also provided a detailed description of all subspecies and their approximate distributions.

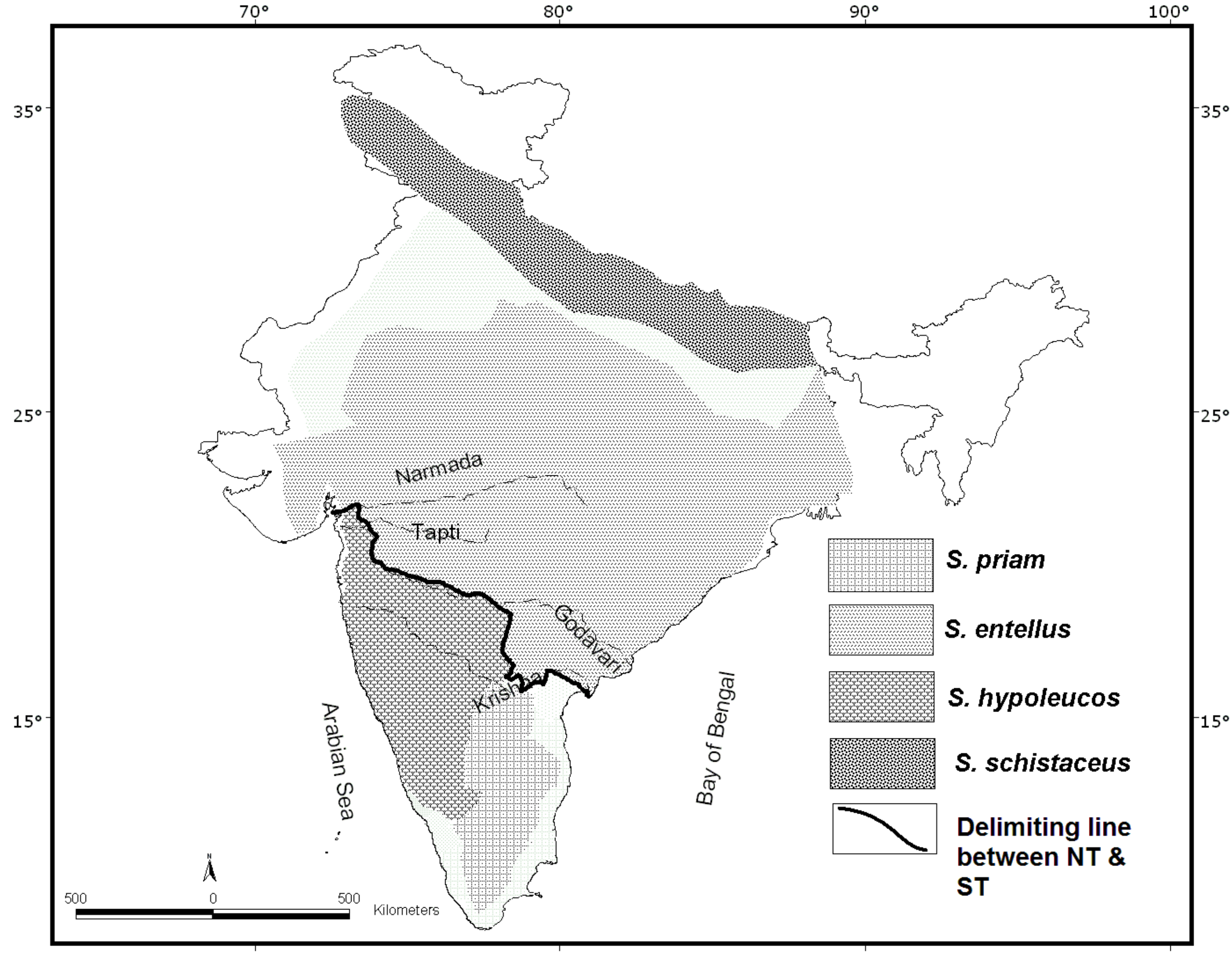


Figure 2.1 Present day distribution of Hanuman langurs in India based on Nag et al, 2011; Minhas et al ,2010; Choudhury,2010; Choudhury,2007; Sharma,2010.

Hill (1939), however, split the Hanuman langur into 4 species (*Semnopithecus schistaceus, S. entellus, S. hypoleucos, and S. priam*). He elevated Pocock's *Semnopithecus entellus entellus* to species level with no subspecies and placed the remaining subspecies in the other 3 species. Accordingly he placed the Himalayan subspecies *hector, schistaceus, achilles, ajax, and lanius* under *Semnopithecus schistaceus*. Similarly, he placed the subspecies from South India and Sri Lanka, *priam, thersites, and anchises* under *Semnopithecus priam, and hypoleucos, aeneas, elissa, iulus, dussumieri and achates* under *S. hypoleucos*.

Ellerman and Morrison-Scott (1966), Napier and Napier (1967), Roonwal and Mohnot (1977), and Roonwal (1984) followed these early classifications, all of which mirror Pocock (1928, 1939) with some changes (Table 2.1). *Semnopithecus* was subsumed into *Presbytis* and Hill's (1939) subspecies lanius was retained, but renamed lania. Thus, these classification schemes again considered the Hanuman langur as a single species but with 14–16 subspecies (Table 2.1). Roonwal (1979, 1984) classified the various subspecies of Hanuman langur into 2 broad groups: the Northern and Southern types based on tail carriage. The Northern type (NT) has a tail that loops forward toward the head and is distributed north of the Tapti-Godavari rivers. The Southern type (ST) has a tail that loops backward away from the head and is distributed south of these rivers in peninsular India and Sri Lanka (Roonwal, 1979, 1984 and Figure2.2). Hill (1938) was the first to report tail carriage variation among Hanuman langurs, reporting that *Semnopithecus entellus* exhibits NT tail carriage whereas S. *priam* has ST tail carriage.

Groves (2001) retained the genus name *Semnopithecus* and split the Hanuman langur into 7 species (*S. schistaceus, S. entellus, S. ajax, S. hector, S. hypoleucos, S. priam, S. dussumieri*), elevating 7 subspecies from earlier classification schemes to species level. He subsumed the remaining subspecies into these 7 species, with the exception of lania, which is no longer listed. IUCN follows this classification scheme.

Finally, Brandon-Jones (2004) split the Hanuman langur into 2 species, *Semnopithecus entellus and S. priam*, with 9 subspecies. Here, *Semnopithecus entellus* has 7 subspecies: *S. e. schistaceus, S. e. entellus, S. e. ajax, S. e. hector, S. e. achates, S. e. hypoleucos, and S. e. anchises* whereas *S. priam* has 2 subspecies: *S. p. priam and S. p. thersites.*

Thus most authors considered the Hanuman langur to be a single species, *Semnopithecus entellus (or Presbytis entellus),* but split this species into as many as 14 (Pocock 1928, 1939), 15 (Ellerman and Morrison-Scott 1966; Napier and Napier 1967; Roonwal 1984), and 16 (Roonwal and Mohnot 1977) subspecies. Other classification schemes have assigned the various populations of the Hanuman langur into 2 (Brandon-Jones 2004), 4 (Hill 1939), and 7 (Groves 2001) distinct species, each in turn consisting of multiple subspecies (Table 2.1). This multitude of classification schemes clearly indicates that the taxonomy of Hanuman langurs is in a flux.

Table 2.1 : Overview of the different classification schemes of Hanuman langurs proposed by various authors.

Pocock (1928)	Pocock (1939)	Hill (1939)	Roonwal (1977)	Roonwal (1984)*	Groves (2001)	B-Jones (2004)
Northern type						
Pi.e.schistaceus	*S.e.schistaceus*	*S.schistaceus*	*P.e.schistaceus*	*P.e.schistaceus*	*S.schistaceus*	*S.e.schistaceus*
Pi.e.entellus	*S.e.entellus*	*S.entellus*	*P.e.entellus*	*P.e.entellus*	*S.entellus*	*S.e.entellus*
Pi.e.ajax	*S.e.ajax*	*S.s.ajax*	*P.e.ajax*	*P.e.ajax*	*S.ajax*	*S.e.ajax*
Pi.e.achilles	*S.e.achilles*	*S.s.achilles*	*P.e.achilles*	*P.e.achilles*	-------	-------
Pi.e.lanius	-------	*S.s.lanius*	*P.e.lania*	*P.e.lania*	-------	-------
Pi.e.hector	-------	*S.s.hector*	-------	-------	*S.hector*	*S.e.hector*
-------	-------	-------	*P.e.anchises*	*P.e.anchises*	-------	*S.e.anchises*
-------	-------	-------	*P.e.shanicus*	-------	-------	-------
-------	-------	-------	-------	-------	-------	*S.e.achates*
Southern type						
Pi.e.achates	*S.e.achates*	*S.h.achates*	*P.e.achates*	*P.e.achates*	-------	-------
Pi.e.iulus	*S.e.iulus*	*S.h.iulus*	*P.e.iulus*	*P.e.iulus*	-------	-------

Pi.e.hypoleucos	*S.e.hypoleucos*	*S.h.hypoleucos*	*P.e.hypoleucos*	*P.e.hypoleucos*	*S.hypoleucos*	*S.e.hypoleucos*
Pi.e.aeneas	*S.e.aeneas*	*S.h.aeneas*	*P.e.aeneas*	*P.e.aeneas*	-------	-------
Pi.e.dussumieri	*S.e.dussumieri*	*S.h.dussumieri*	*P.e.dussumieri*	*P.e.dussumieri*	*S.dussumieri*	-------
Pi.e.pallipes	*S.e.priam*	*S.p.priam*	*P.e.priam*	*P.e.priam*	*S.priam*	*S.p.priam*
-------	*S.e.thersites*	*S.p.thersites*	*P.e.thersites*	*P.e.thersites*	-------	*S.p.thersites*
-------	*S.e.anchises*	*S.p.anchises*	-------	-------	-------	-------
Pi.e.priamellus	*S.e.priamellus*	-------	*P.e.priamellus*	*P.e.priamellus*	-------	-------
Pi.e.elissa	*S.e.elissa*	*S.h.elissa*	*P.e.elissa*	*P.e.elissa*	-------	-------

*** Also includes Ellerman and Morisson- Scott (1966), Napier and Napier (1967)**

Pi- *Pithecus*, S- *Semnopithecus*, P- *presbytis* , e- *entellus*, h- *hypoleucos*, p- *priam*

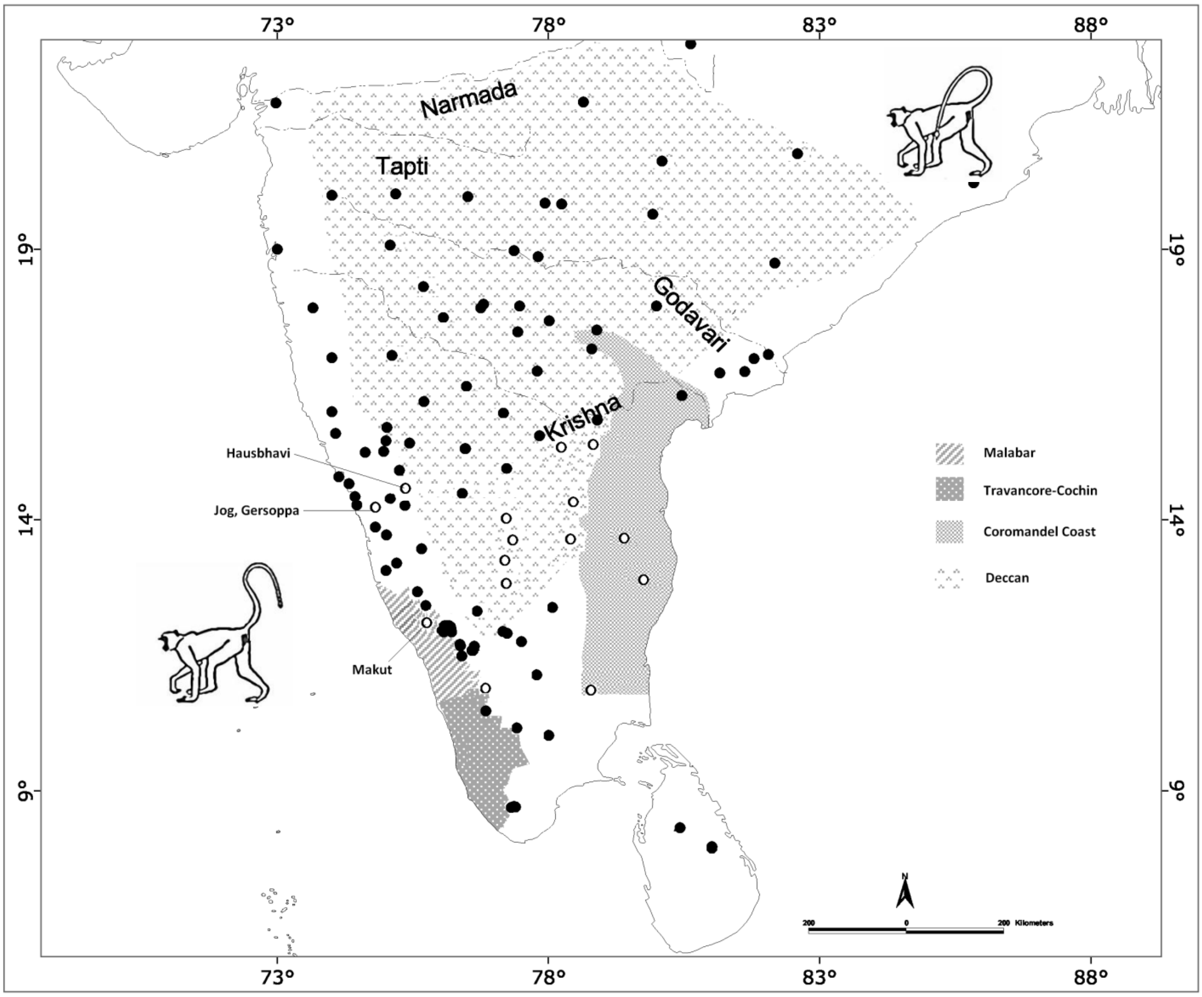


Figure 2.2 - shows the sampling locations of Hanuman langurs in peninsular India. Open circles represent sampling locations that were also type localities for various subspecies described by Pocock (1939).

Figure 2.2 includes *Semnopithecus entellus achates* (Hausbhavi), *S. e. iulus* (Gersoppa), *S. e. aeneas* (Makut), *S. e. priamellus* (Travancore-Cochin), *S. e. anchises* (Deccan), and *S. e. priam* (Coromandel). Also shown are the 2 broad groups among Hanuman langurs based on tail loop. The Northern type (NT) has a tail that loops forward toward the head and the Southern type (ST) has a tail that loops backward away from the head. The NT and ST are distributed north and south of the Tapti-Godavari rivers, respectively.

In this context, recent molecular studies of the langurs of the Indian subcontinent are important. These molecular phylogenetic studies based on nuclear and mitochondrial markers suggested that Hanuman langurs are closely related to Nilgiri (*Semnopithecus johnii*) and purple-faced langurs *(S. vetulus*: Karanth et al. 2008; Osterholz et al. 2008; Zhang and Ryder 1998), which are distributed in peninsular India and Sri Lanka respectively. Thus these 3 species are now placed in the genus *Semnopithecus*, distinct from leaf monkeys in the genera *Trachypithecus* and *Presbytis*. In addition, the mitochondrial tree in conjunction with nuclear markers did not support the monophyly of Hanuman langurs (Karanth et al. 2008, 2010; Osterholz et al. 2008). Instead Hanuman langurs were polyphyletic with respect to Nilgiri and purple-faced langurs. Accordingly, Karanth et al. (2010) recommended provisional splitting of Hanuman langurs into 3 species, such that the taxonomy is consistent with their evolutionary relationship. However, they did not attempt to designate species names because these studies were based on a limited sample. Nevertheless the molecular studies also suggest that Hanuman langurs consist of multiple species.

Thus there is much disagreement in the literature on the subspecies or species status of various populations of Hanuman langurs. This ambiguous taxonomic status has serious consequences for studies targeting these taxa. Hanuman langurs have been used extensively as a model system in various biomedical, ecological, behavioral, and evolutionary research (Karanth et al. 2010). In addition, taxonomic status often dictates conservation priorities; thus this situation will also confound conservation efforts for Hanuman langurs.

I believe that there are 3 reasons for the lack of resolution in Hanuman langur classification. 1) Classification schemes were largely based on coat color, which is often highly plastic. 2) They were informed opinions of taxonomists instead of being based on objective analysis of morphological characters using statistical tools. 3) In addition, they were inferred from reanalysis of existing museum specimens collected in the first half of the last century or reinterpretation of earlier work. Thus no new material from the field had been used in most of these studies, with the exception of Brandon-Jones (2004). This has resulted in an unfortunate dichotomy: Though there have been extensive field studies on behavioral and ecological aspects of Hanuman langurs, museum specimens have been the sole material for most taxonomic research. The validity of descriptions based merely on museum specimens over actual onsite observations has long been debated (Pennell 1934). In this regard, several authors advocate that field studies can complement the qualitative tools of descriptive taxonomy (Dunn 2003; Martin 2003; Wheeler 2004; Woodbury et al. 1956).

Objectives

To this end, I undertook a field study to document variation in external morphological characters among Hanuman langurs in South India and Sri Lanka. I subjected the color-independent characters to statistical analyses to identify distinct clusters or morphotypes and to address the following questions:

1. How many morphotypes of Hanuman langurs are present in South India and Sri Lanka?
2. What diagnostic characters can be used to identify these morphotypes?
3. What are the approximate distributional limits of these morphotypes?
4. Which classification scheme best fits the observed morphotypes from the field?

Materials and Methods

I prepared a comprehensive list of all probable species or subspecies for South India based on published taxonomic work (Table 2.1) and a list of all external morphological characters used to identify these species or subspecies. From this list I chose a total of 5 color-independent morphological characters for further study: presence or absence of crest, presence or absence of streak between the eye and the ear, Northern or Southern type tail carriage (Figure2.2), the extent of blackness (EOB) on the hand (Figure 2.3), and forms of tail carriage among the Southern type (Figure2.4). The Southern type has 2 forms of tail carriage (Roonwal 1979; 1984): TC1 appears like an inverted letter U, wherein the distal arm of the tail loop reaches the level of the back (distal and proximal arms of approximately same lengths) with the tail tip pointing straight downward (Figure 2.4B). TC2 appears like the letter S, wherein the distal arm of the tail loop is always shorter than the proximal arm with the tail tip pointing obliquely downwards (Figure 2.4C). I recorded tail carriage characters when the subject was walking and not when it was standing or running (as per Roonwal 1984).

I scored characters for ≥1 adult male or female per troop from the field as well as from photographs of individuals from various populations. I made observations using 8×50 binoculars and used a digital camera for photographs (Canon EOS 30D). In addition to the characters mentioned previously, I recorded pelage color for each troop studied, as well as troop size, troop count, troop range, and troop composition. For each location, I noted altitude, latitude, and longitude. I sought the assistance of volunteers to score the characters to minimize observer bias. I also keyed characters from photographs for central Indian and Sri Lankan langurs and included wild-caught individuals whose provenance could be clearly established.

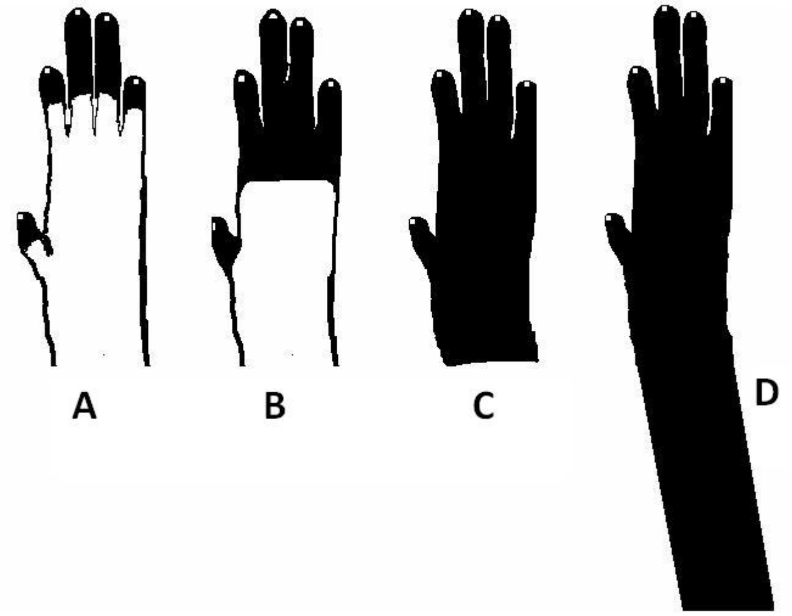


Figure 2.3 - Variation in the extent of blackness (EOB) of the manus of Hanuman langurs (A) EOB restricted to fingertips (B) EOB to knuckles (C) EOB to wrist (D) EOB to elbow (Modified from Pocock 1939)

Data Analyses

I coded binary characters as 1 for present and 0 for absent. For the extent of blackness and tail carriage characters I assigned a positive number (Table 2.3). I used this character matrix in PAUP (Swofford 2001) to determine the pairwise total distance (equivalent to Hamming's distance) between individuals. I used this pairwise distance to generate an unweighted paired group method with arithmetic mean (UPGMA) and neighbor-joining (NJ) trees in PAUP. I assigned clusters generated in these trees to various morphotypes. I determined the approximate distributions of these morphotypes by plotting the sampling locations of each

morphotype on a map via MapInfo Professional and DIVA-GIS (Hijmans et al. distributions with published classification schemes to determine the classification scheme that best fitted the field data.

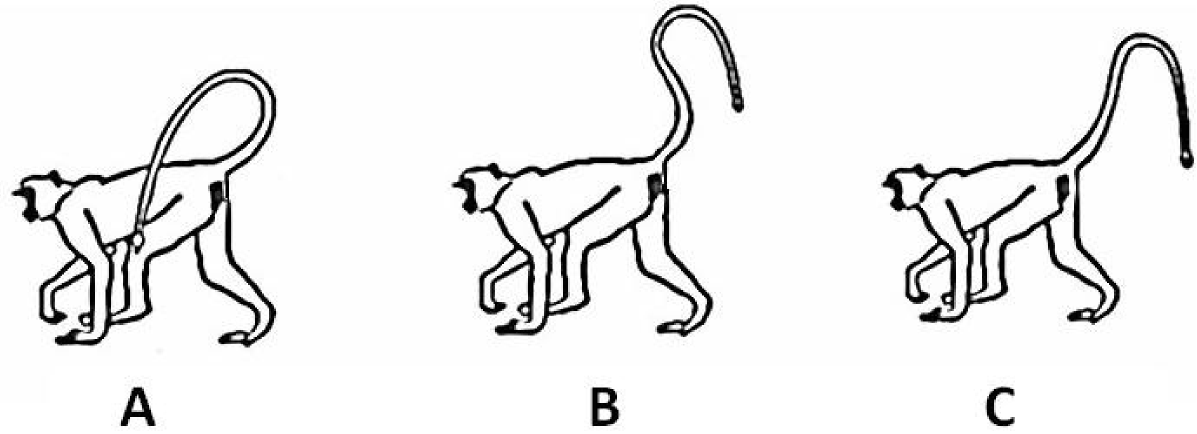


Figure 2.4 - Variation in tail carriage among Hanuman langurs. (a) Northern type. (b) Southern type with TC2 tail carriage. (c) Southern type with TC1 tail carriage (see text for details).

Table 2.2- Details of Hanuman langur locations sampled along with their coordinates for the Neigbour joining tree.

STATE	PLACE	CODE	LONGITUDE	LATITUDE	TYPE LOCALITIES † AND DISTRIBUTION AS PER POCOCK (1939)	MORPHOTYPE
ANDHRA PRADESH	NIZAMPUR	NZMPR	78.005	17.678		St1
ANDHRA PRADESH	EAST GODAVARI	EGOD	81.783	16.983		Nt
ANDHRA PRADESH	WEST GODAVARI	WGOD1	81.616	16.745		Nt
ANDHRA PRADESH	WARANGAL	WRNGL1	79.981	17.95		Nt
ANDHRA PRADESH	HORSELYHILLS (*Coromandel*)	HORSLY1	78.4	13.648	*S. e. priam*	St5
ANDHRA PRADESH	KADAPA (*Coromandel*)	KDP	78.466	14.366	*S. e. priam*	St5
ANDHRA PRADESH	NALGONDA	NLGND	78.788	17.157		Nt
ANDHRA PRADESH	MAHBUBNAGAR	MHBNGR	77.783	16.75		St1
ANDHRA PRADESH	TIRUPATHI (*Coromandel*)	TRPTI	79.416	13.65	*S. e. priam*	St5
ANDHRA PRADESH	KURNOOL (*Deccan*)	KRNL	78.220	15.31	*S. e. anchises*	St3
ANDHRA PRADESH	DIGUVAMETTA (*Deccan*)	D	78.809	15.392	*S. e. anchises*	St3
CHATTISGARH	GAUTAMPUR	GAUTMPR	75.04	23.01		Nt
GOA	BONDLA	GOA	74.066	15.605		St1
GUJRAT	BHARUCH	BHARUCH	72.966	21.7		?
JHARKHAND	PALAMAU	PALAMAU	84.6	23.416		Nt
KARNATAKA	HAMPI	HMP	76.457	15.318		St1
KARNATAKA	RAMNAGAR, HAMPI	RHMP	76.466	15.3335		St1
KARNATAKA	HAVERI	HVR	75.248	14.922		St1

KARNATAKA	BIDAR	BDR	77.463	17.956		St1
KARNATAKA	HONNAVAR	HNVR	74.46	14.269		St1
KARNATAKA	ANKOLA	ANK	74.317	14.674		St1
KARNATAKA	PAVAGADA (*Deccan*)	PVGD	77.219	14.107	*S. e. anchises*	St3
KARNATAKA	NAGARAHOLE	NGRH	76.083	12		St1
KARNATAKA	KUKKE SUBRAHMANYA	KKEF	75.574	12.667		St2
KARNATAKA	AGUMBE	AGMB	74.998	13.064		St2
KARNATAKA	KARKALA	KRKL	75.108	13.238		St2
KARNATAKA	MOODBIDRE	MDBD	74.993	13.069		St2
KARNATAKA	KUDREMUKHA	KDMK	75.195	13.199		St2
KARNATAKA	BANDIPUR	BND	76.624	11.663		St5
KARNATAKA	BILIGIRI RANGA TEMPLE	BRT	77.152	11.938		St5
KARNATAKA	BALLE	BALLE	76.212	11.925		St1
KARNATAKA	SUNKADAKATTE, NAGARAHOLE	NGRHSNK	76.194	11.976		St1
KARNATAKA	MAKUT	MAKUT	75.754	12.088	*S. e. aeneas* [†]	St2
KARNATAKA	THEERTHAHALLI	THRTLLI	75.011	13.718		St2
KARNATAKA	MUTHODI	MUTHDI	75.656	13.459		St2
KARNATAKA	JOGFALLS	JOGFALLS	74.808	14.224	*S. e.iulus* [†]	St1
KARNATAKA	HAUSBHAVI	HUSBHVI	75.383	14.553	*S. e. achates* [†]	St1
KARNATAKA	HALESORBA	HSORBA	75.078	14.392		St1
KARNATAKA	RANEBENNUR	RNEBENNR	75.668	14.624		St1
KARNATAKA	AMASEBAIL	AMSBL	74.949	13.612		St2

KARNATAKA	SHIKARIPURA	SHIKAPR	75.35	14.267		St1
KARNATAKA	MYSOREZOO	MYSZOO	76.67	12.299		St1
KERALA	TRIVANDRUM ZOO	TRIZOO	76.595	8.51		*St2*
KERALA	WALAYAR (*Cochin*)	WLYR	76.83	10.835	*S. e. priamellus*	St4
KERALA	MUTHANGA (*Malabar*)	MTHNGA	76.36	11.695		St4?
KERALA	TOLPETTY (*Malabar*)	TPTY	76.067	11.933		St1/St2?
KERALA	ARALAM (*Malabar*)	ARLM	75.681	12.003	*S. e. aeneas*	St2
KERALA	CHINNAR	CHNR	77.267	10.3		St5
MADHYA PRADESH	JABALPUR	JABALPUR	85.95	23.166		Nt
MADHYA PRADESH	KANHA	KANHA	85.616	22.283		Nt
MADHYA PRADESH	KANGERGHATI	KNGHRGHT	82.166	18.75		Nt
MAHARASHTRA	MATHERAN	MATHRN	73 .280	18 .999		St1
MAHARASHTRA	RADHANAGARI	RADHNGRI	73 .838	16 .359		St1
MAHARASHTRA	MAHABHALESHWAR	MHBLSWR	73.655	17.921		St1
MAHARASHTRA	LATHUR	LATHUR	76.749	17.922		St1
ORISSA	BHUVANESHWAR	BHUBNSWR	85.833	20.233		Nt
ORISSA	BAGRA	BAGRA	85.65	18.833		Nt
TAMIL NADU	THEPPAKAD	THPKD	76.601	11.591		St5
TAMIL NADU	KALAKKAD-MUNDANTHURAI	KMTR	77.383	8.7		St5
SRILANKA	ANURADHAPURA	ANRDPRA	80.396	8.334		St5
SRILANKA	POLONNARUWA	PLNRWA	81.008	7.936		St5

Table 2.3 - The 6 morphotypes of Hanuman langurs (*Semnopithecus*) reported from peninsular India and Sri Lanka, and their diagnostic characters. Also shown is the fit between the morphotypes observed in field and the various classification schemes

	Streak	**Crest**	**EOB**	**TL**	**TC**	**Pocock (1939)**	**Hill (1939)**	**Groves (2001)**	**B-Jones (2004)**
Nt	0	0	3	1	0	*S.e.entellus*	*S.entellus*	*S.entellus*	*S.e.entellus/* *S.e.achates/S.e.anchises*
St1	1	0	3	2	1	*S.e.achates* *S.e.iulus*	*S.h.achates* *S.h.iulus*	*S.dussumieiri*	*S.e.anchises*
St2	1	0	4	2	1	*S.e.hypoleucos* *S.e.aeneas*	*S.h.hypoleucos* *S.h.aeneas*	*S.hypoleucos*	*S.e.hypoleucos*
St3	0/1	0	2	2	2	*S.e.anchises*	*S.p.anchises*	*S.dussumieiri*	*S.e.achates*
St4	0	0	2	2	2	*S.e.priamellus*	-	*S.dussumieiri*	-
St5	0	1	1	2	2	*S.e.priam* *S.e.thersites*	*S.p.priam* *S.p.thersites*	*S.priam*	*S.p.priam* *S.p.thersites*

Streak and crest: present=1, absent=0.
EOB = extent of blackness on the hand, finger tips=1, to knuckles=2, to wrist=3, to the elbow=4; TL=tail loop, NT=1, ST=2; TC = tail carriage, TC1=1, TC2=2, absent=0.

Results

My survey included a total of 1523 individuals belonging to 107 troops observed at 102 locations in South India and Sri Lanka (Figure2.2). Troop size varied from 4 (Walayar, Muthanga, Nilambur in Kerala, and Makutta of Karnataka) to 106 (Kalamber, Nanded District of Maharashtra) individuals. I recorded Hanuman langurs from sea level in Gokarna and 2 m above msl at Honnavar in Karnataka to 1352 m above msl at Mahabaleshwar in Maharashtra. The majority (89) of the Hanuman langur troops were unimale, multifemale and the rest were multimale, multifemale (13) and all-male (2) troops. I was unable to determine troop composition for 3 troops. I also observed 7 captive individuals (1 from Saligrama, Kundapur; 3 from Trivandrum zoo; 2 from Mysore zoo; 1 from Pilikula Zoo, Mangalore).

I typed 94 adult individuals for the 5 color-independent morphological characters. I was unable to type adults for some troops because the subjects were very shy. The NJ dendrogram consisted of 6 distinct clusters (Figure2.5). These included NT Hanuman langur and 5 clusters among the ST Hanuman langurs. The clusters in the NJ tree did not change when I used other distance measures, such as average distance. I assigned these clusters to different morphotypes: Nt for NT Hanuman langur cluster and St1–5 for the 5 clusters among the ST Hanuman langurs. I found the same 6 clusters in the UPGMA tree (tree not shown). Table 2.3 summarizes the character states of the 6 morphotypes. Figure 2.6 shows their approximate distributions. Among the ST Hanuman langurs, morphotype St1 had the widest distribution and St4 was restricted to a very small area. Of the 6 morphotypes, Nt consisted exclusively of all northern tail loop individuals whereas other morphotypes (St1–5) consisted of southern tail loop individuals.

Morphotype St1 was crestless and often had a prominent streak (brownish to dark brownish band between the eye and the ear). In some populations the streak was not very

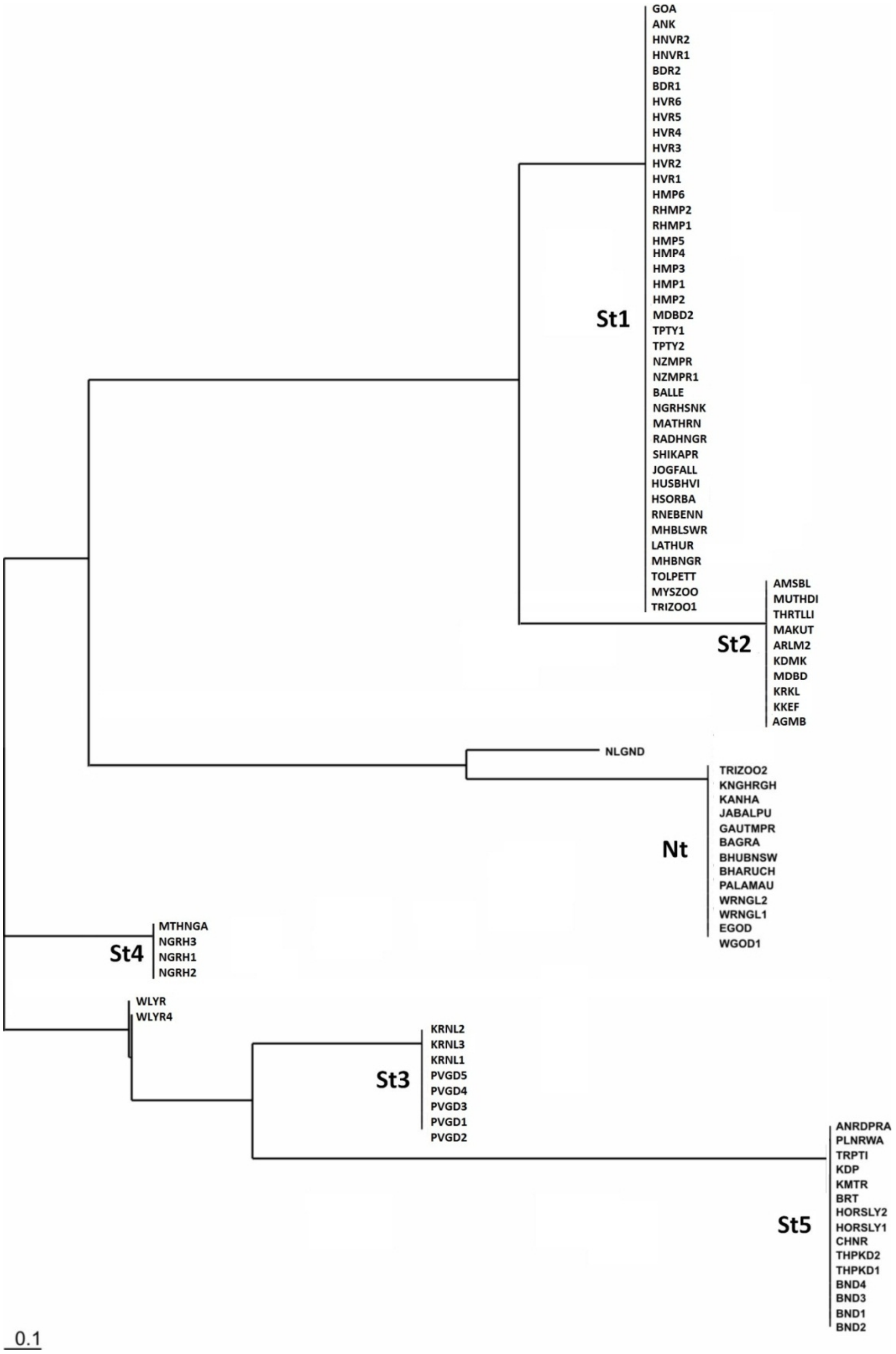


Figure 2.5- Neighbour-joining tree based on 5 color-independent morphological characters typed from 94 Hanuman langurs. St1–5 represents the 5 clusters (morphotypes) among the Southern type Hanuman langurs. Nt refers to Northern type Hanuman langur.

prominent and in a few cases it was completely absent. The EOB was up to the wrist (Figure2.3C). The dorsal and ventral sides of the body, limbs, and tail all had a brownish gray color and the paw was black. The coat color was generally darker in the wetter and humid areas (wet zone) and slightly dull in drier areas (dry zone) of peninsular India. The intensity of orange color on the belly and chest in adults was more prominent in wetter, coastal habitats and dull and paler in the drier regions. Nevertheless, the wet and dry zone populations all showed the TC1 form of ST tail carriage. Interestingly, some populations, e.g., from Nilambur in Kerala and Nagarahole in Karnataka, had all of the aforementioned characters except that the streak was absent. St1 had a very wide distribution ranging from Nagarahole in the South to Nashik in Maharashtra all along the coastal areas. Mahbubnagar and Medak of Andhra Pradesh formed the easternmost boundaries for this morphotype.

All the populations of St2 morphotype had a prominent dark brown streak and lacked a crest. The mane was dark brown to buff. The EOB on the hand extended to the elbow and sometimes up to the shoulder (Figure 2.3D). This EOB was one of theunique characters of St2 populations. The form of ST tail carriage observed was TC1, as in St1 populations. Some populations in the Brahmagiri range (Makutta, Aralam) possessed a mane suffused with orange along with dark brown hair. The coat color was much darker in all these populations vs that in St1 populations. The coat color was dark brown to black on the dorsal and ventral parts. The limbs and tail were black with a buff-colored tail tip. St2 populations ranged all along the wet evergreen and shola grassland habitats from as far north as Theertahalli in the Shimoga district of Karnataka to the end of the Brahmagiri range near Tolpetty in Kerala. St2 populations were abundant in Aralam in Kerala and Bhadra, Someshwara, Talacauvery, Pushpagiri wildlife sanctuaries, and Kudremukh National Park in Karnataka. Populations in and around Kutta and Tolpetty in the Karnataka and Kerala border, respectively, appeared to be intermediate forms of St1 and St2 morphotypes. In these individuals the EOB ranged from that of typical St1 to St2 types.

Individuals of morphotype St3 were usually streakless, but sometimes had a faint streak, and lacked a crest. They were paler in color than individuals of St1 morphotypes. The coloration on other parts of their body was very similar to St1 except that the EOB on the hand was restricted to the knuckles (Figure 2.3B). The form of ST tail carriage was TC2 (Figure 2.4B). These morphotypes were abundant in the Tumkur district (Pavgada, Devarayanadurga) of Karnataka, and the Ananthpur and Kurnool districts of Andhra Pradesh. Diguvametta in Andhra Pradesh formed the easternmost boundary of this morphotype.

Morphotype St4 lacked the streak as well as the crest. This morphotype had a pale sepia brown color on the dorsal side and mane was slightly buff in color. The contrast between mane and body was quite evident. The color of the tail resembled that of the dorsal area, with the tail tip being slightly buff colored. The form of tail carriage was the same as in St1 (TC1) and the EOB on the hand was restricted to the knuckles (Figure 2.3B), as in St3. I observed this morphotype in parts of Nagarahole in Karnataka and across the border in Muthanga in Kerala. Another population from Walayar in Kerala resembled St3 but I do not have NJ tree. The sample size of St4 morphotype was very small and further studies are required to confirm the validity of this morphotype and to establish their distributional range.

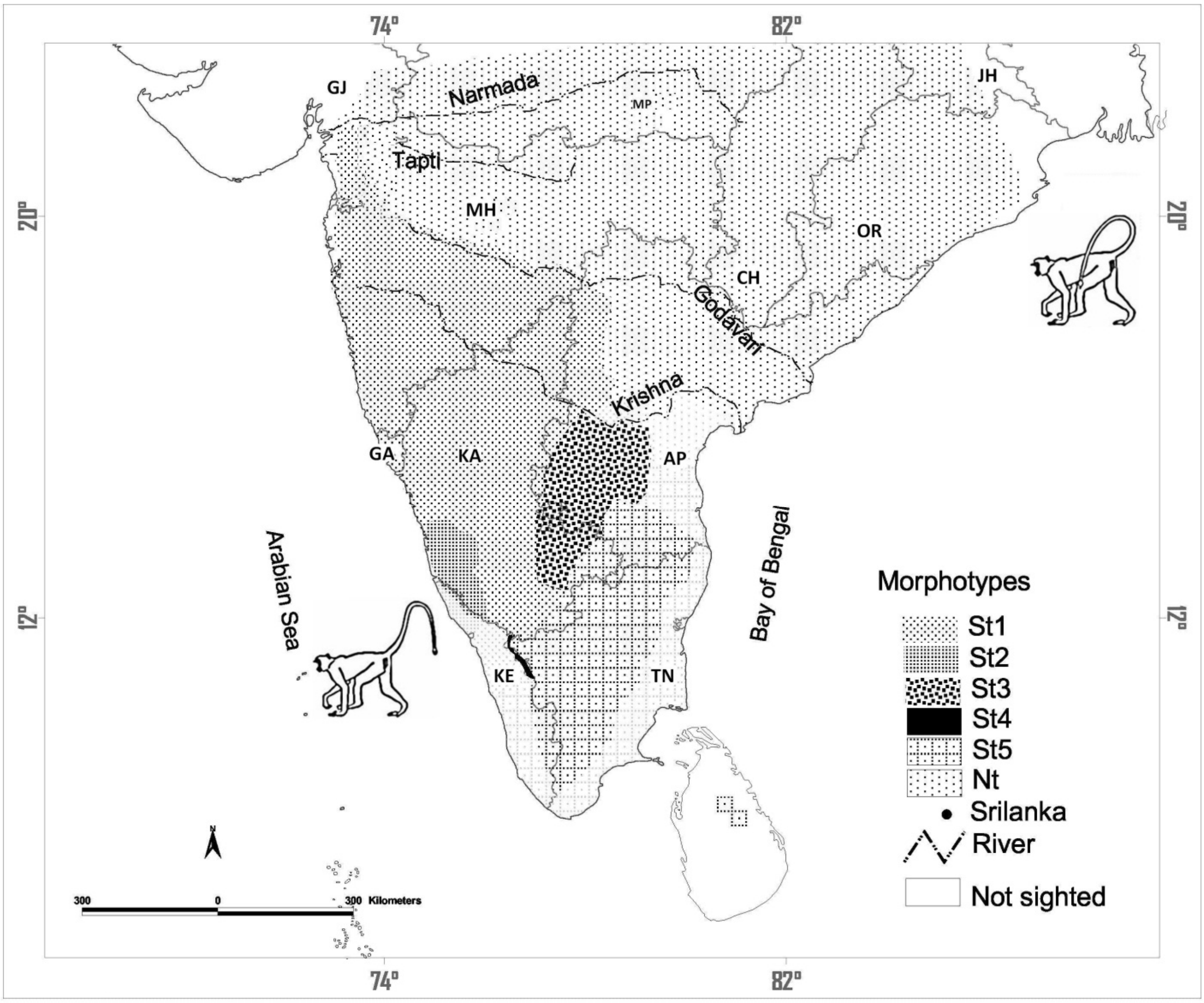


Figure 2.6 - Approximate distributions of Hanuman langur morphotypes in peninsular India.

In the figure 2.6, the state names are abbreviated as follows: GJ = Gujrat; MP = Madhya Pradesh; CH = Chattisgarh; OR = Orissa; KA =Karnataka; AP = Andhra Pradesh; KE = Kerala; TN = Tamil Nadu; GA = Goa; JH = Jharkhand. Faded areas represent locations where langurs were reported in the past but were not encountered in the survey

St5 was very distinct, with a prominent upstanding crest on the crown. These populations had no streak and the EOB of the hand was confined to the peripheries of the fingers (Figure2.3A). Pelage color was light grayish, and the limbs and the tail also had light grayish shade. The southern populations of this morphotype from Chinnar in Kerala, Kalakkad-Mundanthurai tiger reserve (KMTR) in Tamil Nadu and northern parts of Sri Lanka had a slightly darker pelage color vs. that of the northern populations from Kadapa and Tirupathi in Andhra Pradesh, Madumalai in Tamil Nadu and Bandipur in Karnataka. All the populations of this morphotype had TC2 tail carriage (Figure2.4B). The Cuddapah and Chittore districts of Andra Pradesh form the northern limits of the morphotype. I also observed them in Southern Karnataka along the banks of the Cauvery River, and in Biligiri Ranga temple and Bandipur tiger reserves. In Tamil Nadu they were confined to Western parts of the state along the Western Ghats. I have anecdotal evidences of this morphotype in Kerala south of Palakkad in Parambikulam, Thattekad, Idukki, Thekkady, Periyar tiger reserve, Achenkovil, Neyyar, and confirmed sightings from Chinnar. Kalakkad-Mundanthurai tiger reserve in Tamil Nadu forming the southernmost distribution of this morphotype in peninsular India. I also observed this morphotype in Anuradhapura and Polonnaruwa in northern Sri Lanka.

Populations exhibiting the NT tail carriage constituted the sixth morphotype (Nt) in peninsular India. These morphotypes were very similar to St1 except that they lacked the streak between the eye and the ear and exhibited the NT tail loop(Figure 2.4A). The Nt morphotype had the largest distribution range in peninsular India. They were distributed predominantly to the north of the Krishna River in the Nalgonda and Guntur districts of Andhra Pradesh and in northern and eastern Maharashtra. I also observed them in Gujrat, Madhya Pradesh, Chattisgarh, and Orissa.

Discussion

I describe 6 morphotypes of Hanuman langurs that could be identified in the fieldusing a combination of 5 diagnostic characters discussed in Hill (1938), Pocock (1928, 1939), and Roonwal (1979, 1984): the presence or absence of crest, presence or absence of streak, the EOB on the hand, the tail carriage (NT and ST), and form of tail carriage (TC1 and TC2). Most classification schemes for Hanuman langurs,including Ellerman and Morrison-Scott (1966), Napier and Napier (1967), Roonwal and Mohnot (1977), and Roonwal (1984), do not provide a detailed description of each subspecies or species and their approximate distributions; thus I am unable to compare them with the 6 morphotypes I report. Nevertheless, these classifications schemes, along with those of Hill (1939), Ire very similar to those of Pocock (1928, 1939; Table 2.1).

The field characters of the 6 morphotypes reported here match 9 of the subspecies described by Pocock (1939). St1 closely resembled his *Semnopithecus entellus achates* and S. e. *iulus*. Interestingly, the characters of the dry zone populations of St1 were similar to those of *Semnopithecus entellus achates*, whereas those from the wet zone resembled S. e. *iulus*. Pocock's *Semnopithecus entellus hypoleucos* and the darker coat colored S. e. aeneas were similar to morphotype St2. Morphotype St3 resembled the description for *Semnopithecus entellus anchises*. The description of the *Semnopithecus entellus priamellus* matched myobservations of morphotype St4 from Walayar in Kerala and Nagarahole in Karnataka roughly. This subspecies has been synonimized into *Semnopithecus priam* thersites (Brandon-Jones 2004; Hill 1939) or *S.* dussumieri (Groves 2001). Further work is required to confirm the validity of this morphotype and to determine its distribution. The characters described for *Semnopithecus entellus priam* and *S. e.* thersites were very similar to those I observed in morphotype St5. In morphotype St5 the southern populations from KMTR and Sri Lanka had darker coat color, as reported for *Semnopithecus entellus* thersites, whereas those from northern parts of the range had lighter coat color, as in S. e. *priam* (Pocock 1939). The distributions of these 5 morphotypes (Figure2.6) roughly corresponded to the distributions of the subspecies they resemble. Moreover, the type localities mentioned by Pocock for the aforementioned subspecies fall within the range of the various morphotypes (Table 2.2, Figure2.2). The Northern type morphotype, Nt, resembled Pocock's *Semnopithecus entellus entellus*. This was the only morphotype with NT tail carriage and was observed in the northern parts of peninsular India. Thus in my field survey I came across most of the subspecies reported by Pocock in South India. The 2 subspecies that I did not record are *Semnopithecus entellus* dussumieri and S. e. elissa. Given that Pocock's (1928) taxonomic review is one of the earliest and my field observations are largely concordant with his subsequent review (Pocock 1939), I use his subspecies names for the rest of the discussion.

Interestingly, in the NJ tree St1 (*iulus* and *achates*) and St2 (aeneas and *hypoleucos*) clustered together, corresponding to Hill's *Semnopithecus hypoleucos*. Similarly, the clustering of St3 (*anchises*) and St5 (*priam* and thersites) supports Hill's *Semnopithecus priam*. Hill also elevated the subspecies *Semnopithecus entellus entellus* (Nt morphotype in the NJ tree) to S. *entellus*. Recent molecular studies also support assigning species status to NT Hanuman langurs (Karanth et al. 2010). Thus the species assignments proposed by Hill (1939) appear to be consistent with current data.

In the NJ tree (Figure2.2), populations showing NT tail loop formed a cluster (Nt morphotype), but St morphotypes 1–5 did not fall in a separate ST cluster. Nevertheless, molecular data support the separation of NT populations of North India from ST populations of peninsular India (Karanth et al. 2010). The Tapti- Godavari rivers form the border between the Southern and Northern types. My field observations suggest that NTs have extended their range south of the River Godavari up to the River Krishna in the Guntur district of Andhra Pradesh (Figure2.6). I also came across troops showing both tail carriages. In Narasimha Jharna, North Karnataka, the majority of the individuals exhibited ST tail carriage but 2 males showed NT tail carriage, whereas in Lonar, Maharashtra most individuals had NT tail carriage but 5 individuals showed ST tail carriage. I also sighted 3 individuals exhibiting both ST and NT tail carriage in Lonar and Dharmabad, Maharashtra and in Aurangabad (Ellora caves), Buldhana and Nanded in Maharashtra, and Adilabad and Nalgonda in Andhra Pradesh. These populations in the transition zone often had characters that were intermediate between Nt and St1. Taken together these observations are indicative of a possible hybrid zone between Nt and St1 morphotypes.

Groves (2001) placed *achates, anchises, elissa, priamellus, and iulus* into a single species, *Semnopithecus dussumieri*, and assigned species status to *hypoleucos* and *priam*. However, my NJ tree did not cluster *achates, anchises, elissa, priamellus, and iulus*. Instead, *iulus, achates, and hypoleucos* clustered together (St1 and St2) whereas *anchises, priam, and thersites* (St3 and St5) formed another cluster. Hill (1939) was also doubtful of the existence of the *dussumieri* form. Nevertheless, the distributions and characters of Groves' *Semnopithecus hypoleucos, S. priam, and S. entellus* were consistent with my observations.

My field observations are largely incongruent with the distribution map in the classification scheme of Brandon-Jones (2004). For example, according to Brandon-Jones, the distribution of *Semnopithecus entellus anchises* extend from North Karnataka and Andhra Pradesh all the way into Northeastern Gujarat, whereas my observation suggests that *anchises* type (St3) was restricted only to a few districts of Andhra Pradesh and parts of Karnataka (Figure2.6). Likewise, I observed *achates* (dry zone St1) predominantly in drier parts of peninsular India, and the northernmost limits of this morphotype were in Maharashtra and Andra Pradesh, whereas Brandon-Jones shows it in much of North India along with parts of central peninsular India. It seems that Brandon-Jones has misclassified *entellus* type (Nt) as *anchises* (St3) and *achates* (dry zone St1) types, both of which have ST tail carriage. This is not surprising given that *achates* (dry zone St1) is quite similar to *entellus* type (Nt) with the exception of tail carriage and streak presence, and tail carriage can be observed only in the field. Brandon-Jones also shows *hypoleucos* (St2) as distributed as far north as Mahabaleshwar in Maharashtra, whereas my field observations suggest that their northern limit is further south in Karnataka. The Mahabaleshwar area harbors *iulus* (wet zone St1). Thus my study disagrees with Brandon-Jones (2004) with respect to the distributional range of *anchises* (St3), *achates* (St1), *hypoleucos* (St2), and *entellus* (Nt). However, my observations for *Semnopithecus priam priam* and S. p. thersites, i.e., morphotype St5, are comparable to the distribution maps in Brandon-Jones, with the caveat that I did not observe this morphotype in the coastal districts of Kerala and Tamil Nadu.

Pelage color was generally darker in the wetter and humid areas and slightly dull in drier areas of peninsular India. This trend was apparent along the east–west gradient in rainfall in peninsular India, with lighter forms in low rainfall areas in the east and darker forms in the high rainfall regions of the west. I also observed a north–south gradient in pelage color along the west coast and the Western Ghats that appears to be related to rainfall, with lighter forms in the north and darker forms in the south. Pocock (1939; p. 89) noted that there was a general darkening of pelage color when *entellus* was traced from plains of north southward into the wetter zone of the Western Ghats. Groves (2001) invoked Gloger's rule to explain the dark pelage color of *Semnopithecus hypoleucos*. Many primate species, including macaque (*Macaca*), patas (*Erythrocebus patas*), and vervets (*Chlorocebus pygerythrus*), show light and dark color variations that seem to be associated with habitat (Bradley and Mundy 2008). Taken together these observations suggest that pelage color might be plastic and probably should not be used to delimit morphotypes.

Brandon-Jones (2004) suggests that the presence of characters such as dark pelage color and the streak between the eye and the ear in some Hanuman langur populations were due to hybridization with Nilgiri langur (*Semnopithecus johnii*). My field observations do not support this hypothesis. During my surveys, I observed Hanuman and Nilgiri langur hybrids in KMTR and Top Slip (Anamalai hills), areas that formed the southwestern limits of St5 (*priam*) in peninsular India. In these areas the adjoining non hybridizing populations of St5 lacked the streak and did not have dark pelage color. Further north in the Nilgiri and Brahmagiri hills the distributions of Hanuman and Nilgiri langur overlap once again, but I recorded no hybrids. Interestingly, these areas are inhabited by St2 (*hypoleucos*), which had dark pelage color and a streak between the eye and the ear. Thus, I did not observe characters ascribed to hybridization in populations adjacent to hybrid zones but I did observe them in populations where no hybridization has been reported.

My field observations were largely consistent with those of Pocock (1939) and Hill (1939). The species status of the taxa described in these classification schemes needs to be tested using multiple lines of evidence that includes genetic, behavioral, and ecological data. However, the description and distribution of the Nt morphotype in my study as well as those from Karanth et al. (2010) matched the *entellus* type of Pocock (1939), Hill (1939), and Groves (2001). The Nt morphotype has NT tail carriage, lacks the streak between the eye and the ear, and is distributed north of the Tapti, Godavari, and Krishna rivers. Populations of Nt morphotype from as far apart as Jaipur in the west and Calcutta in the east harbored identical nuclear alleles and belonged to the same mitochondrial haplogroup (Karanth et al. 2010). Given that Nt is both morphologically, based on the NJ tree, and genetically (Karanth et al. 2010) distinct from St morphotype I recommend species status for this morphotype (*Semnopithecus* *entellus*), as in Hill (1939) and Groves (2001). Its northern boundary and relationship with the Himalayan types need to be ascertained. These observations render Brandon- Jones' (2004) delimitations of *Semnopithecus entellus entellus*, *S. e*. *anchises*, and *S. e.* achates untenable. More data, particularly molecular data, are needed to ascertain the species status of the St morphotypes.

Karnataka state harbored all the St Morphotypes (St1–5), followed by Kerala, which possessed 4 morphotypes (St1, 2, 4, and 5). These states could be targeted for a more rigorous study of ST Hanuman langurs. I observed 3 St morphotypes in Andhra Pradesh, whereas Tamil Nadu, Maharashtra, and Goa each had one. The Nilgiri biosphere reserve in the trijunction of Karnataka, Kerala and Tamil Nadu is of great importance because it harbors 4 St morphotypes (1, 2, 4, and 5). According to Pocock (1939), the distributions of aeneas, *priamellus*, and elissa also fall in this area. More intensive surveys are required in the Nilgiri biosphere reserve to confirm the presence of these morphotypes. The area encompassed by the Nilgiri biosphere reserve exhibits a high degree of variation in topography and habitat, and also shows high levels of diversity in other taxonomic groups (Daniels 1992, 1996; Easa and Shaji 1997), suggesting that this area might also have played an important role in the diversification of Hanuman langur St morphotypes.

Current Status of Various Morphotypes

St1 were the most widely distributed and appeared to be least threatened because St1 were found predominantly in human-dominated ecosystems and were often habituated to humans. However, I noted several instances of crop raiding by St1 populations, particularly in North Karnataka. This had led to human–langur conflict in these areas. Morphotypes St2, St3, and St4 appeared to be very shy, avoided proximity to humans, and had restricted distributions. I did not come across any populations of these morphotypes that were habituated to humans. Nevertheless, areas where these morphotypes were distributed were severely affected by various anthropogenic activities such as heavy vehicular movement, road constructions, hydroelectric projects, industries, and mining. The influence of these anthropogenic activities on morphotypes St2–4 is in urgent need of study.

The St5 morphotypes were also widely distributed but were confined predominantly to forested areas. Currently these populations did not appear to face any major threat. However, a handful of St5 populations were also habituated, mainly inside several protected areas of South India. In some cases these morphotypes were being fed junk foods such as salt biscuits, spicy chips, and bread by tourists, drivers of heavy motor vehicles, and local hotel owners. This trend of feeding langurs with junk food is worrisome because these monkeys are predominantly leaf-eaters.

I confirm previous reports of hunting (Kumara and Singh 2004; McCann 1933) of Hanuman and Nilgiri langurs for meat and therapeutic purposes by local people (tribal and nontribal) and migrant laborers. These cases were mostly restricted to the forested areas of Karnataka, Tamil Nadu, and Kerala. Habituated troops of morphotypes St1 and St5 were also more susceptible to road kills. I did not encounter morphotypes St3–5 in monoculture plantations of teak and eucalyptus within protected areas, suggesting that human modified landscapes were not suitable for these langurs.

Given increasing anthropogenic activities and their putative effect on langur survival, there is a pressing need to understand the biology, distribution, and status of the various morphotypes. Researchers should extend study of this kind to the NT Hanuman langurs of North India.

3. Range limits of Northern type *Semnopithecus entellus* (Dufresne, 1797) in peninsular India.

Introduction

Faunal range expansions being dynamic are of great relevance because they often indicate important changes in habitats usually due to the profound influence of human intervention, climate change or other environmental variables (Ohmart, 1994; Wehtje, 2003; Ehrlich et al, 1988; Oden et al, 2004). Variations in species distributions can alter important ecological interactions and thus range contractions or expansions may also have economic, management, and safety implications in wildlife management (Darimont et al, 2005). Here we report the range limits of one of the morphotypes of Hanuman langur (*Semnopithecus entellus*, Subfamily: Colobinae), which is one of the most widely distributed and common species of primate in India.

The Hanuman langur is a well-known, revered, and extensively studied non-human primate in India. Hanuman langurs have been documented for its habituation to humans and thus show a varied adaptation to urbanization (Sharma et al, 2011; Pirta et al, 1997; Chauhan and Pirta, 2010).They are dispersed throughout most of India and Sri Lanka (Oates *et al*. 1994; Ellerman and Morrison-Scott 1966) and are also found in parts of Pakistan, Nepal (Minhas et al 2010; Oates *et al*. 1994; Roonwal 1984), Bhutan and Bangladesh (Choudhury 2007). Hanuman langurs are well adapted to a wide range of habitats from arid regions of Rajasthan to the rainforests of the Western Ghats and altitudes from sea level (Nag et al., 2011) to 4270m above mean sea level in the Himalayas (Bishop 1978; Hrdy 1977).

Based on tail carriage, Roonwal (1979, 1984) identified two distinct morphotypes among Hanuman langur, namely Northern type (NT) and Southern type (ST). The NT has a tail that loops forward towards the head and is distributed north of the Tapti-Godavari rivers. The ST has a tail that loops backward away from the head and is distributed south of these rivers in peninsular India and Sri Lanka (Roonwal, 1979; 1984) (Fig. 1). These tail loop variations have been reported earlier by Hill (1938) and Rowell (1972). Nevertheless Roonwal (1984) for the first time gave the exact borderline (here after referred to as Roonwal's line) between the NT and ST which according to him runs along the Tapti-Godavari rivers (See Figure 3.1).

There have been several anecdotal evidences suggesting that the range of NT has extended beyond the Roonwal's line but no systematic study has been undertaken to confirm this scenario. Thus to fill this gap we attempted to map the southern limits of the distribution of NTs in peninsular India. Here we report new information that suggests the range limits of NTs in peninsular India and discuss the possible reasons and implications of these range extensional limits.

Methods

I conducted my survey in peninsular India in the states of Gujarat, Andhra Pradesh, Maharashtra and Karnataka such that states on either side of the borderline given by Roonwal (1984) were included. Every district along the borderline in each of the states mentioned above was intensively surveyed on foot along roads and trails between June to December 2009 for approximately six months. Surveys were also carried out in jeep and a two wheeler along major roads. All the surveys were carried out by the first author of this paper along with local field assistants provided by the respective state forest departments. In these districts langur troops were located based on information from past surveys (Kurup 1981, 1984; Roonwal 1979, 1984; Srinivasulu and Nagulu 2001) and also by conversing with the local people. On locating a troop the tail carriage information along with GPS location of the troop were recorded. Tail carriage characters were recorded when the animal was walking casually and not when it was standing or running (as per Roonwal 1984). Troops were typed as NT or ST when all members of the troop exhibited either northern or southern type tail carriage respectively. Whereas when both morphotypes were observed in the same troop (mixed troops) they were types as mostly NT (mNT) or mostly ST (mST) depending on the predominant tail carriage observed. Additionally tail carriage information for troops from adjoining state were also collated from published material (Srinivasulu and Nagulu 2001; Kumara and Singh 2004, Kumar *et al*. 2010; Nag et al,

2011) as well as information and photographs provided by other researchers in the field. The approximate distributions of these morphotypes were determined by plotting the sampling locations of each morphotype on a map using MapInfo Professional and DIVA-GIS software (Hijmans et al. 2004). On this map Roonwal's line was traced using MapInfo Professional software.

Results

Results from my survey are shown in Figure 3.1, wherein the locations of all NT and ST troops are given by black circles and rectangles respectively. Mixed troops are represented by open circles for mNT and open triangles for mST. The GPS locations of troops up to 200 km on either side of Roonwal's line are given in Table 3.1. As is apparent from Figure 3.1 there are up to ten troops to the south of Roonwal's line that consist of langurs with NT tail carriage. Among them two troops in the eastern parts of the range, south of river Krishna were NTs. Five troops were mNTs and three troops were mSTs. These results suggest that the southern limit of the NT morphotype is further south of Roonwal's line. Furthermore this "range extension" is more pronounced in the south-central and southeastern parts of the NT's distribution. For example according to Roonwal (1979; 1984) the southernmost limit of NTs along the east coast was Godavari delta north of river Krishna, whereas my observations indicate that they are distributed south of river Krishna in Guntur district of Andhra Pradesh (Figure3.1).

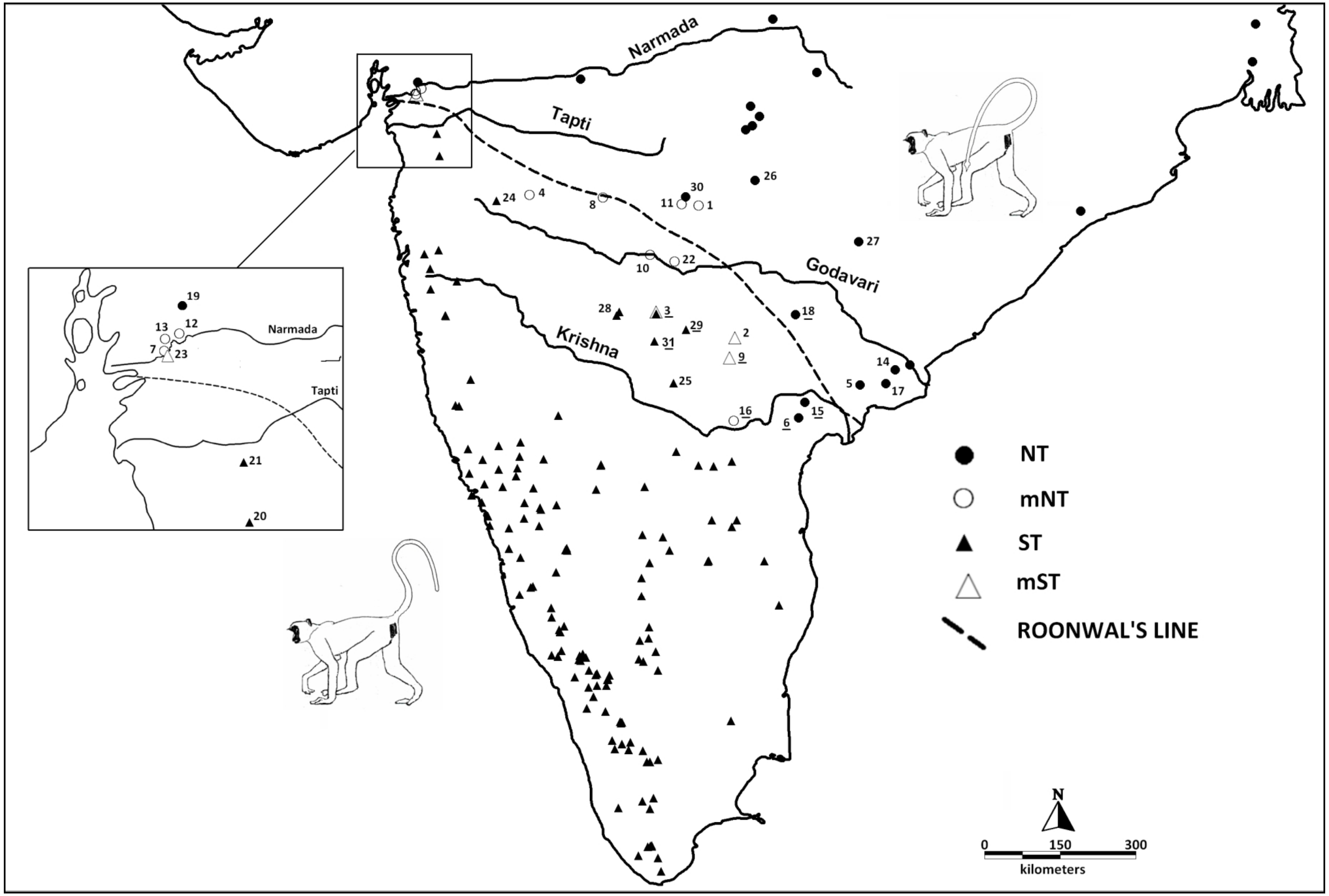


Figure 3.1 - Locations of troops up to 200km on either side of Roonwal's line and the tail type observed in these troops. Underlined numbers show locations of areas wherein human mediated translocations of langurs were reported.

However up to six troops to the north of Roonwal's line consisted of langurs with ST tail carriage, but these were predominantly mNT. Interestingly, these troops were largely restricted to the western end of Roonwal's line near the mouth of Tapti and Narmada rivers (See inset in Figure 3.1). In this part of Gujarat, Roonwal (1984) reported the northernmost populations of STs near Surat (bank of Tapti river) and southernmost populations of NT at Bharuch (bank of Narmada river). My field observations indicate that northernmost population of ST occurs 85km north of Surat, in and around Bharuch. Thus Narmada River in the northwest and Krishna River in the southeast form the borderline between the southern and northern types in peninsular India.

Discussion

Interestingly, there were twice as many troops (n=10) south of Roonwal's line with at least one NT individual than there were troops (n=6) north of this line with at least one ST individual. Moreover this change in the range of these morphotypes is more extensive in the case of NT, whereas in the STs it is largely confined to western end of Roonwal's line. Additionally in most of the mixed troops (n=14) the predominant tail type is NT (mNT=10, mST=4). Preliminary observations also suggest that these mixed troops represent a hybrid zone between NT and ST (Nag et. al, 2011). Taken together these patterns are indicative of introgression of NTs into the range of ST. occurs 85 km north of Surat in and around Bharuch. Thus Narmada river in the northwest and Krishna river in the southeast form the borderline between the southern and northern types in peninsular India.

There are three possible explanations for the incongruence between my observations and those of Roonwal (1984). The first possible scenario is that NTs were always distributed south of Roonwal's line but these areas were poorly /under sampled by Roonwal (1984). Thus my results might reflect the natural range of NTs. Alternately the results reported here might be indicative of range extension of NTs, in some parts, into areas where formerly STs were distributed.

Table 3.1 - The GPS locations of troops up to 200 km on either side of Roonwal's line and the tail type observed in these troops (NT, Northern type; mNT mostly Northern type; ST, Southern type; mST mostly Southern type)

Number	Place, District	State	Latitude	Longitude	Tail carriage type
1	Pipalgaon, Adilabad	Andhra Pradesh	19.838	78.238	mNT
2	Bhongir, Nalgonda	Andhra Pradesh	17.51	78.888	mST
3	Narasimha Jharna, Bidar	Karnataka	17.956	77.463	mST
4	Ellora caves, Aurangabad	Maharashtra	20.026	75.179	mNT
5	Eluru, West Godavari	Andhra Pradesh	16.717	81.150	NT
6	Kotapakonda, Guntur	Andhra Pradesh	16.142	80.039	NT
7	Kabirvad, Bharuch	Gujrat	21.76	73.14	mST
8	Lonar , Buldhana	Maharashtra	19.977	76.508	mNT
9	Wailpally, Nalgonda	Andhra Pradesh	17.158	78.788	mST
10	SavarKeda, Nanded	Maharashtra	18.976	77.362	mNT
11	Mahur, Nanded	Maharashtra	19.858	77.928	mNT
12	Nareshwar, Bharuch	Gujrat	21.87	73.23	mNT
13	Nikora, Bharuch	Gujrat	21.77	73.14	mNT
14	Rajamundry, East Godavari	Andhra Pradesh	16.983	81.783	NT
15	Sattenapalle, Guntur	Andhra Pradesh	16.415	80.153	NT
16	Srisailam, Kurnool	Andhra Pradesh	16.087	78.874	mST
17	Tanuku, West Godavari	Andhra Pradesh	16.745	81.616	NT

18	Pakhal dam, Warangal	Andhra Pradesh	17.95	79.988	NT
19	Baroda, Baroda	Gujrat	22.306	73.187	NT
20	Vansda national Park, Navsari	Gujrat	20.715	73.553	ST
21	Devalimadi mataji mandir, Surat	Gujrat	21.088	73.531	ST
22	Dharmabad, Nanded	Maharashtra-Andhra Pradesh	18.9	77.85	mNT
23	Rajpardi, Bharuch	Gujrat	21.77	73.221	mST
24	Anjaneri, Nashik	Maharashtra	19.913	74.59	ST
25	Koilkonda, Mahbubnagar	Andhra Pradesh	16.742	77.723	ST
26	Tadoba, Chandrapur	Maharashtra	20.266	79.163	NT
27	Indravati national park, Dantewada	Chattisgarh	19.233	81.011	NT
28	Kasar Sirsi, Latur	Maharashtra	17.95	76.746	ST
29	Kothlapur, Medak	Andhra Pradesh	17.675	77.951	ST
30	Mahur, Nanded	Maharashtra	19.847	77.923	NT
31	Sedam, Gulbarga	Karnataka	17.376	77.585	ST

This scenario is supported by the largely unidirectional introgression discussed above. Thirdly in parts of Andhra Pradesh and Karnataka the range extension of NTs might be due to human mediated translocations. Translocations of “problem langurs” were reported by forest department and local people around places like Guntur, Nalgonda, Warangal and Medakdistrictsof Andhra Pradesh, and Bidar and Gulbarga districts of Karnataka (Figure3.1). We have also observed two instances of translocations wherein NTs were caught around Guntur and later released into Srisailam forests.

Interestingly the range of NT Hanuman langur overlaps with that of Rhesus macaque (*Macaca mulatta*) in India and among Rhesus macaque’s too there have been reports of range extension. Here again the range extension is mostly into the northern parts of the state of Andra Pradesh in and around Srisailam (Kumar et al., 2011). These observations hint at a common underlying mechanism driving range extensions in these two sympatric primate species. Interestingly, Kumar et al. (2011) also invoke natural process as well as human introductions for range extension in Rhesus macaques. I believe that a detailed behavioral, ecological and genetic study of the hybrid zone between the two morphotypes of Hanuman langurs might help us better understand this pattern.

4. Analysis of niche variation within Hanuman langur species complex through ecological niche modeling.

Introduction

Information on faunal species biology and their distribution patterns plays a vital role in various applications in ecology, evolution and conservation biology (Karanth KK et al, 2010; Juvall and Wright, 1994). Fortunately in recent years due to the advancement in information technology, there has been a substantial usage of modeling approach such as species distribution models facilitating us to understand spatial patterns in biodiversity (Soberón and Peterson, 2004). A species distribution model (also known as ecological niche modeling) offers predictions of distributions "by relating abundance of species to environmental predictors" (Elith et al, 2006).In other words the objective of these models is to recreate species ecological requirements and anticipate geographic distributions of species in ecological space (Peterson, 2001). Needless to say these models can yield excellent results with the sound understanding of species ecology since species ecological characteristics is known to influence model performance (Hernandez et al, 2006; Araújo and Guisan, 2006). There have been wide debates regarding the uncertainties and reliability of these models with respect to different niche concepts, effective sampling designs, optimal sample size required for a reasonable prediction, optimal parameterization for effective projections of species habitats, model and algorithm selection criteria etc (reviewed in Araújo and Guisan, 2006; Hernandez et al, 2006; Pulliam, 2000; McPherson and Jetz 2007; Peterson, 2001; Soberón and Peterson, 2005; Anderson et al, 2003; Stockwell and Peterson, 2002; Elith et al, 2006). In the light of these reservations, authors have suggested that the reliability of these models and their predictions should be cautiously evaluated before suggesting any applicative measures such as conservation planning (McPherson and Jetz 2007; Araújo and Guisan, 2006). These models which largely employ empirical data are useful to characterize species ecological requirements (Austin and Meyers 1996; Luoto et al 2006; Diekotter et al 2006), understand distributions, biogeography and dispersal barriers (reviewed in Peterson 2001; Bauer and Peterson,2005), identify effects of climate change (Thuiller 2003; Guisan and Zimmermann,2000), forecast species invasions (Thuiller et al 2005), realize the effects of habitat alterations (Manel et al 2000), delimit species boundaries (Wiens and Graham 2005 ; Raxworthy et al 2007; Graham et al, 2004; Rissler and Apodaca, 2007), predict unknown populations and species (Kumara et al, 2009; Raxworthy et al, 2003).

Species distribution models are being utilized for a number of aforementioned reasons, and its application in the field of Primatology also seems to be slowly gaining momentum. Primates have known to play an important role in seed dispersal thereby helping to maintain and balance biodiversity (Ganesh and Davidar, 2001; Prasad et al, 2004; Punekar, 2002). A few handful of studies of primates have pitted time budget models against different model algorithms to assess the validity of different modeling approaches (Willems and Hill, 2009; Bettridge et al, 2010). However studies using primates as model systems largely assess the status and potential distributions for setting up conservation priorities (Thorn et al, 2009; Torres et al, 2010; Kumara et al,2009; Garcı´a et al, 2011; Martı´nez et al,2008; Boubli and Lima, 2009).

There have been fewer studies of species distributional modeling studies on Asian colobines to date (Karanth KK et al, 2010). Amongst the most widely distributed non-human primate in South Asia, Hanuman langurs or common langurs (Family: Cercopithecidae, Subfamily: Colobinae) are a common sight in most central and North Indian villages, towns, tourist areas, (Mathur and Manohar 1994; Chaudhuri et al. 2004; Rajpurohit et al. 2004, Bennett and Davies 1994; Southwick and Siddique, 1994). Hanuman langurs are exceptionally acclimatized to a wide range of habitats (Sugiyama 1976; Oppenheimer 1977; Bennett and Davies 1994; Yoshiba, 1967; Sugiyama, 1964; Kumara and Singh, 2004; Jathanna et al ,2003; Singh et al, 2000; Chellam, 1995; Ahsan and Khan,2006; Ross and Srivastava 1994; Newton,1992 , 1994; Sharma 2001; Mathur and Manohar, 1994,1986 and 1993; Mathur and Bhatnagar, 1993; Rahaman, 1973; Rajpurohit et al, 1994 ; Chhangani and Mohnot, 2004; Ramachandran and

Joseph, 2001; Bishop 1978; Sayers and Norconk 2008) from arid regions on the edge of the desert in Rajasthan to the rainforests of Western Ghats . They have been recorded at altitudes from 2m above mean sea level (msl) to 4270m above msl in the Himalayas (refer Chapter 2; Bishop 1978; Hrdy 1977). The rainfall in peninsular Indian Hanuman langur habitats is known to range between 10 cm annual precipitation to 740cm annual precipitation (Oppenheimer 1977; Yoshiba, 1967; Sugiyama, 1964; Kumara and Singh, 2004; Jathanna et al ,2003; Singh et al, 2000; Ramachandran and Joseph, 2001; Ahsan and Khan,2006; Ross and Srivastava, 1994; Newton,1992 , 1994 and 1986; Mathur and Bhatnagar, 1993; Rahaman, 1973; Rajpurohit et al, 1994; Chhangani and Mohnot, 2004; Punekar, 2002). Hanuman langurs are also known to show adaptation to strong seasonality from Himalayan habitats to extreme summer temperatures at Rajasthan (Sayers and Norconk 2008; Bishop 1979; Curtin 1982). Hanuman langur's diet includes leaves (both deciduous and evergreen) along with fruits, fruit buds and petioles (reviewed in Vogel 1977; Chalise 1994 and 1995; Sayers and Norconk 2008; Punekar, 2002; Sharma, 2001).However Hanuman langurs show a strong preference to mature leaves over young leaves (Koenig and Borries 2001).

Chapter 2 observed at least six morphotypes of Hanuman langurs in peninsular India by using a combination of five diagnostic morphological characters bringing in certain clarity about the identification of these langurs in peninsular India. Nevertheless majority of Hanuman langur studies in India and Sri Lanka have directed their attention to behavioral studies (Nag, unpublished) apart from a few selective studies on their foraging ecology (Sushma and Singh, 2006; Singh et al, 2010; Singh et al, 2000; Hladik, 1977; Sayers and Norconk 2008; Punekar, 2002; Sharma, 2001; Vasudev et al, 2008; Koenig et al, 1997; Newton, 1992; Sugiyama, 1976; Schuelke, 2001; Roy et al, 2010). Also there has been lack of a reliable data on the distributional aspects of various so called species/subspecies of Hanuman langurs of India with respect to ecological correlates. Accordingly there is strong requisite to understand the various ecological facets of Hanuman langurs given the fact they are used as model organisms for various biomedical, ecological, behavioral studies (Karanth, 2010 and references therein).

Thus the primary aim of the present study was

- To understand ecological requirements of the Hanuman langur species complex identified in the present study
- To explore potential distributional boundaries/limits of the Hanuman langur species complex of peninsular India and
- To substantiate the distinct species by their ecological requirements and distributional boundaries

Materials and Methods

Target species and occurrence data

The study obtained 196 occurrence records of seven *Semnopithecus* Hanuman langur morphotypes and one Nilgiri langur (*Semnopithecus johnii*) from previous field surveys (details of field surveys are given in chapter 2) and literature records (Kurup, 1984; B-Jones, 2004) representing the known distribution of the species (Table 2.2).In doing so the study strictly followed Hill's (1939) classification scheme to assign species for the morphotypes described in chapter 2. However for one population in Palakkad district study (for reasons described in chapter 2 and 4) retained the name *priamellus*.

Table 4.1 - Occurrence data points of Hanuman langur used in the present study.

Sl. No.	Species/Subspecies	Field survey data	Secondary data	Total
1	*S. hypoleucos* achates	32	8	40
2	*S. hypoleucos hypoleucos*	7	5	12
3	*S. priam anchises*	10	2	12
4	*S. priam priamellus?*	10	1	11
5	*S. priam*	22	13	35
6	*S. entellus*	21	24	45
7	*S. hypoleucos iulus*	26	4	30
8	*S. johnii*	6	5	11
Total occurrence points			**196**	

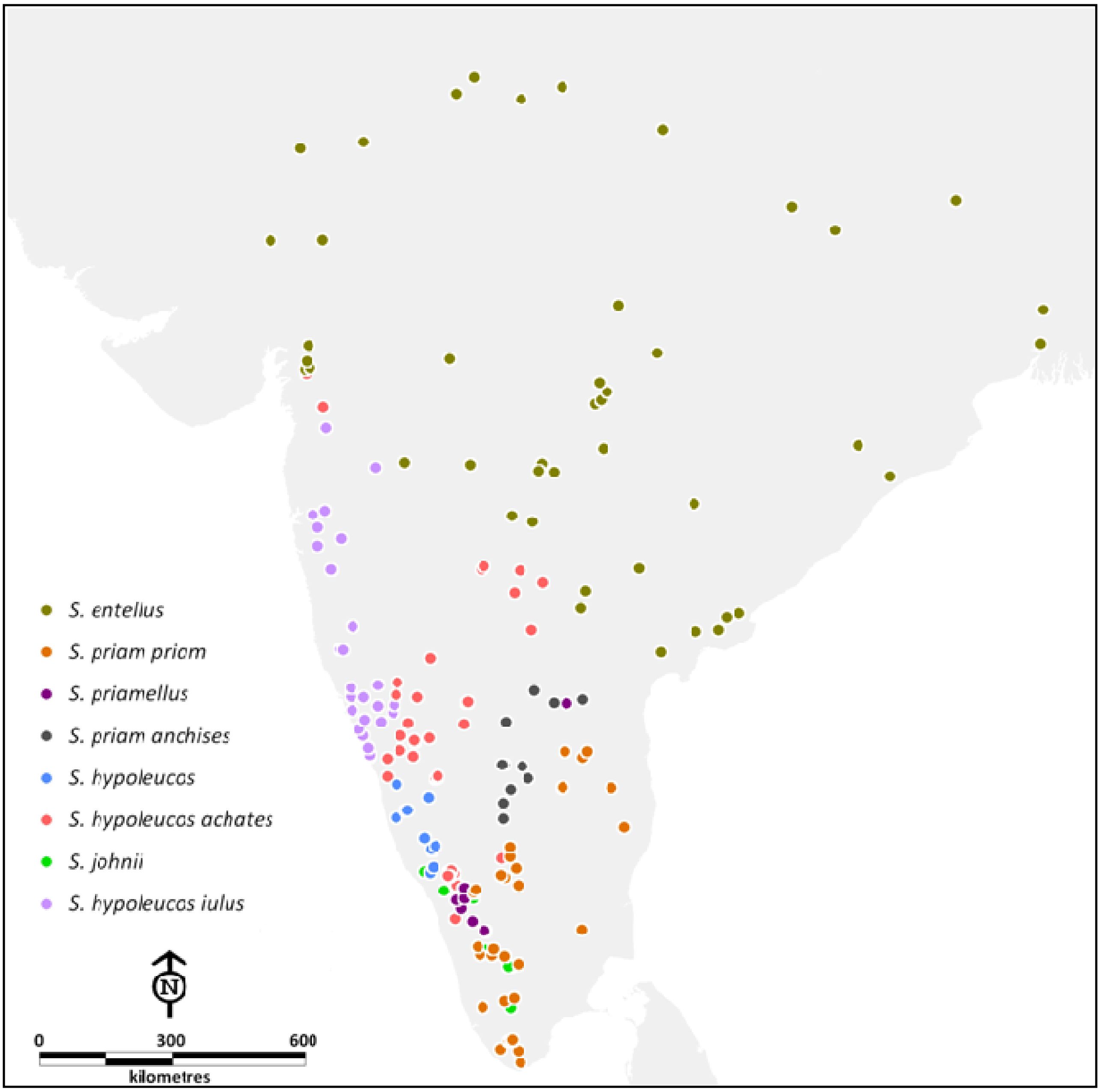


Figure 4.1 - Occurrence points of eight Hanuman langur species complex across peninsular India.

Environmental Coverage Variables

The study considered thirty seven environmental variables for modeling habitat distribution of various species of Hanuman langurs in peninsular India (Table 2.1). Of these thirty seven variables 19 were bioclimatic, 12 were vegetation and 6 were hydrological layers. The layers were related to precipitation, temperature, topography, and ecological bioregions (Table 4.2). **Study did not reduce the number of environmental layers, as the primary objective of the study is to understand the ecological drivers of the species, though there is a possibility of over estimation using more environmental variables and models can select irrelevant variables for modeling if very few environmental variables are selected (Elith and Leathwick, 2009).**

Bioclimatic layers

19 variables from Worldclim (http://www.worldclim.org), were downloaded which is a set of climate layers representing bioclimatic variables, derived from monthly temperature and rainfall recorded worldwide (Table 4.2. Hijmans and Graham 2006; Hijmans et al. 2005).

Table 4.2 - Derived bioclimatic, hydrological and vegetation layers used in the present study

Layer	Variable	Reference
Bioclimatic		
Bioclim1	Annual Mean Temperature (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim2	MeanDiurnalRange (Mean (period max-min)) (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim3	Isothermality (Bioclim2/Bioclim7) (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005

Bioclim4	Temperature Seasonality (SD*100)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim5	Max Temperature of Warmest month (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim6	Min Temperature of Coldest month (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim7	TemperatureAnnualRange (Bioclim5-Bioclim6)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim8	Mean Temperature of Wettest Quarter (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim9	Mean Temperature of Driest Quarter (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim10	Mean Temperature of Warmest Quarter (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim11	Mean Temperature of Coldest Quarter (°C*10)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim12	Annual Precipitation (mm)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim13	Precipitation of Wettest Period (mm)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim14	Precipitation of Driest Period (mm)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim15	Precipitation Seasonality	Worldclim (http://www.worldclim.org)

	(Coefficient of Variation)	Hijmans et al. 2005
Bioclim16	Precipitation of Wettest Quarter (mm)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim17	Precipitation of Driest Quarter (mm)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim18	Precipitation of Warmest Quarter (mm)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Bioclim19	Precipitation of Coldest Quarter (mm)	Worldclim (http://www.worldclim.org) Hijmans et al. 2005
Hydrological		
DEM	Digital Elevation model	USGS, EROS centre, Hydro1k for asia
Aspect	Direction of slope	USGS, EROS centre, Hydro1k for asia
Slope	Difference between two neighboring cells elevation	USGS, EROS centre, Hydro1k for asia
CTI	Composite Topographic Index (Wetness Index)	USGS, EROS centre, Hydro1k for asia
FA	Flow accumulation	USGS, EROS centre, Hydro1k for asia
FD	Flow direction	USGS, EROS centre, Hydro1k for asia
Vegetation		
January_2001		MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
February_2001		MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml

March_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
April_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
May_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
June_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
July_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
August_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
September_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
October_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
November_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml
December_2001	MODIS, Global Land Cover Facility, http://glcf.umiacs.umd.edu/index.shtml

Vegetation data

Study used enhanced vegetation index (EVI) as vegetation data. The EVI is an 'optimized' vegetation index that enhances the vegetation signal with improved sensitivity in high biomass regions and improved vegetation monitoring through a de-coupling of the canopy background signal and a reduction in atmosphere influences. The EVI is more responsive to canopy structural variations, canopy type, and canopy architecture. EVI has advantage over Normalized Difference Vegetation Index (NDVI) due to its ability to eliminate background and atmosphere noises and non-saturation. The true EVI value ranges from -1 to 1, however, the original data represented as multiples of 10000 in the present study.

Enhanced Vegetation Index (EVI) satellite data from the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) sensor were used. The dataset is monthly data (Jan-Dec) of the year 2001 with a spatial resolution of 1000 x 1000 m. The MODIS-EVI data were downloaded from the Global Land Cover Facility (GLCF; http://glcf.umiacs.umd.edu/index.shtml).

Hydrological data

HYDRO1k provides a standard suite of geo-referenced data sets at a spatial resolution of 1 km. This data set is aimed at providing hydrologic information on a continental scale. The raster data sets are the DEM (digital elevation model, also referred to as ‘elevation’), derived flow directions, flow accumulations, slope, aspect, and a compound topographic (wetness) index. The original data is converted to 8 bit values (value ranging from 0-255). HYDRO1k database was made using 30 arc-second digital elevation model at the EROS DataCenter in 1996, entitled GTOPO30.

Digital Elevation Model (DEM): DEM data from the HYDRO1k 1km spatial resolution, representing elevation of the region. Elevation range is separately given in Table 4.2, although not used.

Aspect: The aspect data set describes the direction of maximum rate of change in the elevations between each cell and its eight neighbors. It can essentially be thought of as the slope direction. It is measured in positive integer degrees from 0 to 360, measured clockwise from north. Aspects of cells of zero slope (flat areas) are assigned values of -1.

Flow Directions: The flow direction data layer defines the direction of flow from each cell in the DEM to its steepest down-slope neighbor. Values of flow direction vary from 1 to 255.

Flow Accumulations: The flow accumulation data layer defines the amount of upstream area draining into each cell. It is essentially a measure of the upstream catchment area. The flow direction layer is used to define which cells flow into the target cell. Since the cell size of the HYDRO1k data set is 1 km, the flow accumulation value translates directly into drainage areas in square kilometers. Values range from 0 at topographic highs to very large numbers (on the order of millions of cells) at the mouths of large rivers.

Slope: The slope data layer describes the maximum change in the elevations between each cell and its eight neighbors. The slope is expressed in integer degrees of slope between 0 and 90.

Compound Topographic Index: The Compound Topographic Index (CTI), commonly referred to as the Wetness Index, is a function of the upstream contributing area and the slope of the landscape. The CTI is calculated using the flow accumulation (FA) layer along with the slope as:

$CTI = \ln (FA / \tan (slope)$

In areas of no slope, a CTI value is obtained by substituting a slope of 0.001. This value is smaller than the smallest slope obtainable from a 1000 m data set with a 1 m vertical resolution.

Ecological Niche Modeling

To predict species geographical distribution study used a maximum entropy algorithm available in MAXENT (Phillips et al. 2004, 2006). Maxent is known to perform well in recent comparisons of methods (Araujo and Rahbek 2006; Elith et al, 2006) and have been widely used to delimit species boundaries (Smith and Donoghue 2010; Dupin et al 2011; Ross et al 2010; Reeves and Richards 2011). Maxent is a maximum entropy based machine learning program that estimates the probability distribution for a species occurrence based on environmental constraints (Phillips et al. 2006). MAXENT is designed to make predictions from presence-only data using background environmental of the study area of focus. In other words Maxent is designed to characterize probability distribution from incomplete information. Maxent is also advantageous since it uses both continuous and categorical variables (Baldwin, 2009) and the output is a continuous prediction. Maxent has been in wide use because of its effectiveness even with small sample sizes. Maxent thus became an appropriate choice for my data since I had small sample sizes with presence only data. However there have been very few drawbacks of Maxent approach such as model extrapolation or over fitting that have been discussed in the literature (Baldwin 2009).

A default setting of Maxent, was used except for random test percentage, set for 50% data and with 10 replicates. 196 data points were thoroughly checked for duplicate presence records. Regularization multiplier was 1 and maximum number of background points for sampling was kept at 10000. Study cross validated the replicates. Maximum iterations were 500, with $1*10^{-6}$ as convergence threshold.

50% of data were allocated for testing the model predictive performance and 50% for training the data set. Logistic modeling output was chosen that displays suitability values from 0 (unsuitable) to 1 (optimal). For extracting the range values of environmental variables, I considered values of >0.5 logistic output. Model validation was conducted by calculating area under the curve (AUC), which reflects the model's ability to distinguish between presence records and random background points. AUC values range from 0.5 (not different from a randomly selected predictive distribution) to 1 (with perfect predictive ability). Models having AUC values >0.9 are considered to have very good, >0.8 good and >0.7 useful discrimination abilities.

Jackknife test, which assesses a model based on its ability to predict the single locality that is excluded from the training dataset, is used. Thus Jackknife test provides information on the performance of each variable in the model in terms of how important each variable is at explaining the species distribution and how much unique information each variable provides.

Using ENMtools software, niche overlap was measured among species distribution. In niche overlap, Schoener's D (Schoener, 1968) and Relative Rank (Warren and Seifert, 2011) were measured. These metrics range from 0 (species without any niche overlap) to 1 (species with complete niche overlap/identical niches). In case D, the niche overlaps are calculated by taking the difference between species in suitability score at each grid cell, after suitablilities are standardized. Relative rank is an estimate of the probability that the relative ranking of any two patches of habitat is same for the two models, irrespective of the quantitative difference in suitability measures. A niche identity test, was performed to know whether ENMs generated from two or more species are more different than expected if they are drawn from the same underlying distribution and background similarity test, to know whether ENMs drawn from

Figure 4.2 - Maxent distribution modeling logistic output for four Hanuman langur species.

populations with partially or entirely non-overlapping distributions are any more different from one another than expected by chance (Warren et al, 2008).

Results

Species distribution

Based on maximum entropy modeling algorithm and using 37 environmental variables, study obtained eight different distribution maps corresponding to seven Hanuman langur species and one Nilgiri langur. Figure 4.2 and 4.3 shows the distribution maps with warmer colour indicating more suitable habitat to cooler colours indicating unsuitable habitats.

Extent of distribution of *Semnopithecus hypoleucos* achates

This species had a very wide projected distribution all along the eastern part of Western Ghats in the drier areas up to Pune, Maharashtra in the north with their limits extending up to dry deciduous forest patches of Tolpetty near Karnataka-Kerala border in the South. These species western and eastern limits were restricted up to moist patches of Jog falls, Karnataka and Adoni of Andhra Pradesh.

Extent of distribution of *Semnopithecus hypoleucos hypoleucos*

The species populations projected distribution ranged all along the lush wet evergreen and shola grassland habitats from as far as Anshi national park, Karnataka in the north all along the west coast to the places in and around Aralam wildlife sanctuary, Kannur district of Kerala in the south. Sakleshpur of Karnataka formed the easternmost stretch for this species.

Extent of distribution of *Semnopithecus priam anchises*

These species were predicted in the Sindhanur, Manvi places of North Karnataka upto Sathanur, Kanakapura, Karnataka in the south. Their distributions were predicted from Bhadravathi in the west up to the Giddalur forests of Eastern Ghats.

Extent of distribution of *Semnopithecus priam priamellus?*

This species was predicted mostly from Dandeli in the northern Karnataka up to Nagercoil, Tamil Nadu in the south with Kozhikode and Satymangalam forests forming the western and easternmost boundaries respectively.

Extent of distribution of *Semnopithecus priam*

The Chittore and Kadapa districts of Andra Pradesh form the northeastern limits of the species all along the banks of the Cauvery River in Biligiri Ranga temple and Bandipur tiger reserves of Southern Karnataka. In Tamil Nadu they were confined to Western parts of the state along the Western Ghats upto Gudalur up to Nagercoil district of Tamil Nadu encompassing Kalakkad-Mundanthurai tiger reserve in Southern Western Ghats formed the southernmost distribution of this species.

Extent of distribution of *Semnopithecus entellus*

These species were predicted predominantly as north as New Delhi followed by Jodhpur, Rajasthan in the northwest up to Krishna River in the Vijayawada, Nalgonda and Guntur districts of Andhra Pradesh in the south. Places in and around Akola of Maharashtra formed the south western boundaries. They were also predicted up to the coast of West Bengal in the east.

Extent of distribution of *Semnopithecus hypoleucos iulus*

The predicted distributions of this species extended from Tamhini ghats of Pune in the north upto places in and around Sulya, Karnataka in the south all along the west coast in these places. Sagara taluk of Shimoga district, Karnataka formed the easternmost boundary of this species.

Extent of distribution of *Semnopithecus johnii*

This evergreen habitat specialist species was predicted from places south of Vythiri of Wayanad district of Kerala in Northwest only along the Western Ghats gradients up to Nagercoil district of Tamil nadu in the south. Distributions of this species extended up to places like Pacchalur and Palani Hills Northern Slope West RF, Tamil Nadu in the east.

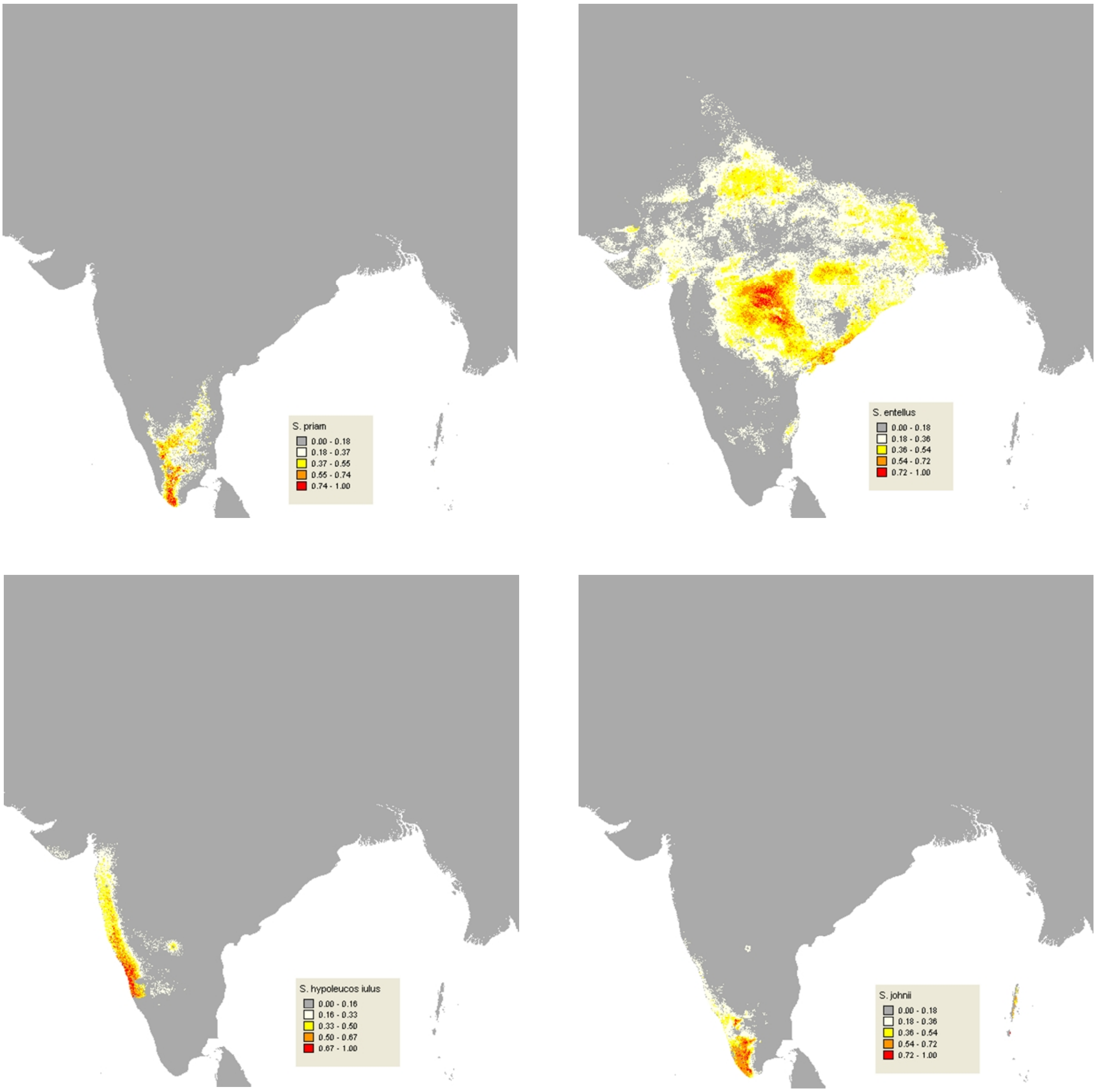


Figure 4.3 - Maxent distribution modeling logistic output for three Hanuman langur species and a Nilgiri langur.

Model prediction

Area of each species in predicted distribution is given in Table 4.3. Total area predicted is about 4038744sqkm. *Semnopithecus entellus* has the highest area under the prediction; *Semnopithecus entellus* is predicted to have about 2490641km^2, while it was least in *Semnopithecus hypoleucos hypoleucos* (80851). There was no statistical significance for number of data points to area predicted (r=0.65, p=0.81). The study converted the logistic model output to binomial, limiting the threshold value to 0.5, again *Semnopithecus entellus* predicting more and *Semnopithecus hypoleucos hypoleucos* predicting less. Converting the binomial output to percentage of total prediction, it was *Semnopithecus priam anchises* which had higher percentage of prediction and *S.entellus* was least.

Table 4.3- Area of each *Semnopithecus* species in predicted distribution

Species	Predicted area(Sq Km)	>0.5 probability	in %
***Semnopithecus hypoleucos* achates**	469151	32044	6.8
Semnopithecus hypoleucos hypoleucos	80851	9879	12.2
Semnopithecus priam anchises	278552	57822	20.8
Semnopithecus priam priamellus	127850	10070	7.9
Semnopithecus priam	217625	28006	12.9
Semnopithecus entellus	2490641	148331	6.0
Semnopithecus hypoleucos iulus	226550	26036	11.5
Semnopithecus johnii	147524	24596	16.7

Variable range and their importance

Based on the Maxent output, variable importance and permutation importance for each species are given in Table 4.5. As mentioned in the methods, objective of this study was to understand the ecological requirement of the species; study looked into all 37 environmental layers than reducing them. In addition to looking at percentage contribution of each variable, study also considered their permutation importance and jackknife test (Table 4.5).

***Semnopithecus hypoleucos achates*.**

Top four contributors were considered for deciding upon variables of importance and permutation importance. The four top variables of importance for this species were Bioclim3 (42.2%), Bioclim 14 (14.7%), Bioclim 19 (7.2%) and Bioclim 11 (4.1%). Likewise the top contributors for permutation importance were Bioclim 11 (48.9%), Bioclim 3 (10.2%), Bioclim 18 (6.3%) and Bioclim 4 (6.2%).

The jackknife variables of importance were Bioclim 4 (highest gain) and India aspect (lowest gain) respectively.

***Semnopithecus hypoleucos hypoleucos*.**

The four top variables of importance for this species were Bioclim19 (61.9%), Bioclim 3 (15.2%), May_EVI (8.2%) and Bioclim 4 (3.8%). Likewise the top contributors for permutation importance were Bioclim 4 (41.1%), Bioclim 3 (18.1%), May_EVI (17.6%) and Bioclim 11 (6.6%).

The jackknife variable of importance were Bioclim 19 (highest gain) and May EVI (lowest gain) respectively

***Semnopithecus priam anchises*.**

The four top variables of importance for this species were Bioclim 3 (48.9%), Bioclim 17 (17%), Bioclim 13 (8.2%) and Bioclim 16 (7%). Similarly the top contributors for permutation importance were Bioclim 3 (41.2%), Bioclim 6 (24.2%), Bioclim 13 (13.6%) and Bioclim 17 (9%).

The jackknife variables of importance were Bioclim 3(highest gain) and Bioclim 17(lowest gain) respectively.

***Semnopithecus priam priamellus*.**

The top variables of importance for this species were Bioclim 3 (42.2%), Bioclim 4 (13.4%), July_EVI (7.9%) and India_flow_direction (5.2%). Similarly the top contributors for permutation importance were Bioclim 3 (38.7%), Bioclim 4 (24.5%), Bioclim 9 (10.6%) and Bioclim 18 (9.7%).

The jackknife variables of importance were Bioclim 3(highest gain) and July EVI (lowest gain) respectively.

***Semnopithecus priam*.**

The top variables of importance for this species were Bioclim 19 (42.2%), Bioclim 3 (32.2%), Bioclim 15 (3.8%) andIndia slope (3.2%). As well the top contributors for permutation importance were Bioclim 4 (29.8%), Bioclim 3 (26.7%), Bioclim 19 (14.8%) and Bioclim 15 (9.8%).

The jackknife variables of importance were Bioclim 16 (highest gain) and Bioclim 18(lowest gain) respectively.

***Semnopithecus entellus*.**

The top variables of importance for this species were Bioclim 5 (20.5%), Bioclim 16 (20.2%), Bioclim 18 (11.2%) and Bioclim 10 (8.5%). Similarly the top contributors for permutation importance were Bioclim 18 (19.1%), Bioclim 1 (17.7%), Bioclim 16 (8.5%) and Bioclim 13 (7.3%).

The jackknife variables of importance were Bioclim 3(highest gain) and Bioclim 17(lowest gain) respectively.

***Semnopithecus hypoleucos iulus*.**

The top variables of importance for this species were Bioclim 13 (37.4%), Bioclim 3 (21.6%), Bioclim 14 (14.6%) and Bioclim 16 (6.7%). Similarly the top contributors for permutation importance were Bioclim 14 (45.9%), Bioclim 3 (27.8%), Bioclim 4 (16.5%) and Bioclim 15 (4.3%).

The jackknife variables of importance were Bioclim 13(highest gain) and Bioclim 14(lowest gain) respectively

***Semnopithecus johnii*.**

The top variables of importance for this species were Bioclim 3 (60.9%), Bioclim 4 (14.6%), Bioclim 14 (5.9%) and Bioclim 5(3.5%). Similarly the top contributors for permutation importance were Bioclim 3 (78.4%), Bioclim 4 (11.9%), Bioclim 5 (5.2%) and Bioclim 8 (1.7%).

The jackknife variables of importance were Bioclim 3(highest gain) and Bioclim 3 (lowest gain) respectively.

Table 4.4 - Range of Environmental variables in the predicted regions (suitability >0.5)

Variables	***S.h.achates***	***S.h.hypoleucos***	***S.p.priam***	***S.p.priamellus?***	***S.priam***	***S. entellus***	***S.h.iulus***	***S.johnii***
Bioclim1	197-291	170-277	216-292	195-291	130-288	232-290	201-276	122-278
Bioclim2	71-137	59-103	95-141	59-113	49-112	65-163	56-114	49-101
Bioclim3	44-67	52-67	48-67	54-67	49-67	37-52	51-67	56-67
Bioclim4	1051-3303	868-1987	1115-3287	857-2075	458-2956	2402-7214	1024-2404	458-1726
Bioclim5	289-403	256-357	316-402	252-371	194-387	322-432	291-360	190-344
Bioclim6	116-222	104-227	121-193	126-371	44-239	51-199	118-219	37-239
Bioclim7	111-270	90-186	160-269	90-204	75-207	146-358	99-212	75-168
Bioclim8	187-289	156-271	205-293	194-280	128-283	243-305	184-281	119-282
Bioclim9	200-285	177-285	218-278	191-280	125-289	155-307	203-274	117-281
Bioclim10	224-330	192-296	244-333	208-309	147-318	278-344	230-299	138-294
Bioclim11	181-266	155-267	195-256	183-267	118-266	137-248	180-263	109-267
Bioclim12	409-5471	1173-6016	382-935	638-5448	483-2837	295-1610	639-6083	859-4169
Bioclim13	102-1978	201-2198	96-217	135-1906	126-627	120-534	1454-2443	175-1491
Bioclim14	0-5	0-28	0-4	0-34	1-76	0-11	0	0-76

Bioclim15	73-165	61-157	77-106	50-148	36-107	80-160	95-159	36-135
Bioclim16	227-4330	473-4779	223-507	291-4298	262-1510	260-1296	382-4913	382-3352
Bioclim17	0-40	0-123	1-19	0-141	4-272	0-50	0-14	2-272
Bioclim18	48-512	97-930	48-220	74-583	88-588	47-492	47-1055	166-983
Bioclim19	0-3678	6-4086	6-136	6-3678	55-723	0-115	1-4739	74-2730
Aspect	0-255	0-255	0-255	0-255	0-255	0-255	0-255	0-255
Slope	0-255	0-255	0-255	0-255	0-255	0-255	0-255	0-255
CTI	0-255	0-255	0-255	0-255	0-255	0-255	0-255	0-255
DEM	0-255	0-255	0-255	0-255	0-255	0-255	0-255	0-255
FA	0-255	1-255	0-255	1-255	0-255	0-255	0-255	0-255
FD	1-128	1-128	1-128	1-64	1-241	1-241	1-128	1-241
EVI_1	-385 - 4874	1375-5678	-501-5046	1654-6356	545-6636	-942-6273	0-5521	1582-6595
EVI_2	-363-5582	539-6387	-643-6534	1632-6260	873-6197	0-6672	0-6322	1446-6292
EVI_3	-283-5244	453-5961	-361-5975	1543-5968	651-5946	-287-5982	0-5925	1340-5982
EVI_4	-96-6129	878-6319	294-6172	1581-6460	660-6441	-260-6195	0-6224	752-7106
EVI_5	-183-6598	1528-6606	705-5556	1487-6606	1053-6606	-296-6592	0-6561	884-6606

EVI_6	-539-7090	153-7027	881-6210	1364-7090	881-7092	-462-7070	0-7090	641-7092
EVI_7	251-7936	498-7812	-822-7049	1839-7936	956-7912	-1869-7840	0-7914	932-7932
EVI_8	170-8574	739-8626	-1448-7367	3437-8606	931-7758	-1794-8382	0-8683	432-8837
EVI_9	-152-7703	1366-7563	-1394-7653	2293-7637	917-7443	0-7702	0-7619	789-7730
EVI_10	-328-6780	1259-6290	-544-6645	1462-7062	855-7110	-371-6624	0-6167	775-7265
EVI_11	-615-5795	1781-6150	-615-6417	2036-6495	-479-6674	-385-6309	0-5926	1801-6685
EVI_12	107-5370	1273-6178	-666-5884	2155-6196	546-6334	-530-5498	0-5474	1726-6434
Elevation* (m)	2-1390	0-1810	126-1252	0-1442	7-2475	0-724	0-1355	0-2536

* DEM is used instead of Elevation layer in the Maxent analysis.

Table 4.5 - Variables of importance and permutation importance in predicted distribution of species.

Variables	***S.h.achates***	***S.h.hypoleucos***	***S.p.priam***	***S.p.priamellus?***	***S.priam***	***S. entellus***	***S.h.iulus***	***S.johnii***
Bioclim1	0.2	0	0	0	0.9	5.6	0.2	0.3
	0.1	0	0	0	0	17.7	0	0
Bioclim2	0.3	0	0	0	0	0.8	0.1	0
	0	0.1	0.6	0.1	0.1	1.5	0.3	0
Bioclim3	42.2	15.2	48.9	42.5	32.2	0.6	21.6	60.9
	10.2	18.1	41.2	38.7	26.7	0.9	27.8	78.4
Bioclim4	1.1	3.8	3.5	13.4	2.1	0.1	4	14.6
	6.2	41.1	0	24.5	29.8	0.2	16.5	11.9
Bioclim5	0.1	0	0	0	0.2	20.5	0	3.5
	0	1.7	0	0	1.6	4.8	0	5.2
Bioclim6	0.5	0	1.5	0.3	0	0	0.2	0
	2.2	0	24.2	0.1	0	0	0	0
Bioclim7	2	0	0.2	0	0.2	0.1	0	1.9
	0	0	0.4	0	0	0	0	0

Bioclim8	0.7	0.4	0	0	0.1	1	0.1	0.3
	2.1	1.6	0	0	0	4.4	0.1	1.7
Bioclim9	0.2	0	0.7	1.1	0.3	1.1	0.7	0
	0.5	0.8	0	10.6	0.2	0.9	0.1	0
Bioclim10	0.1	0	0	0	0	8.5	0	1.5
	0	0	0	0	0	1.5	0	0.9
Bioclim11	4.1	0.4	0	4.8	2.5	0.4	3.7	0
	48.9	6.6	0	4	0.6	0.1	0	0
Bioclim12	2.5	0.2	0.7	0	0.1	0.9	0.6	0
	6	1.5	0	0	0	1.4	0	0
Bioclim13	0	0.1	8.2	0	0.3	4.9	37.4	0
	0	0	13.6	0	3.5	7.3	0.1	0
Bioclim14	14.7	0.2	0.3	2.4	0.4	5.7	14.6	5.9
	4.3	0	0.1	0.3	1.3	3.8	45.9	0
Bioclim15	2.2	0.7	2.3	0.3	3.8	0.3	2.7	0.1
	1.5	0.7	1.6	1.6	9.8	0.3	4.3	0

Bioclim16	0.4	0	7	0.9	2.3	20.2	6.7	0
	0.2	0	0	0	0.9	8.5	0	0
Bioclim17	0.9	0.7	17	0.6	0.8	1.7	1.1	1.7
	0.4	0	9	0	0.8	2.3	3.6	0
Bioclim18	1.5	0	0.6	2.5	1.1	11.2	0.9	0.2
	6.3	0	2.3	9.7	1.1	19.1	0.3	0.4
Bioclim19	7.2	61.9	0.4	0	42.2	2.5	0.1	0.3
	2	2	0.3	0	14.8	6.2	0	0
Aspect	3.2	0.3	0.5	0.6	0.8	1.1	1.3	0.8
	0.4	0	0.1	0	0.9	1.2	0.5	0
Slope	3.4	0.1	0.7	2.8	3.2	1.6	0.3	0.4
	2.1	0	0	0.1	0.9	1.7	0	0
Cti	1	0	0	0	1.1	1.9	0	0.6
	1.3	0	0	0	3.5	3.5	0	0
Dem	2	0.3	1.3	0.2	0.8	1.7	1.9	0.2
	0.4	0.5	0.7	0	0.9	0.8	0.2	0

fl ac	1.4	0.1	1	0.2	0.6	0.9	0	0.5
	0.2	0	0.3	0	0.4	0.5	0	0
fl dir	0.8	2.7	0.5	5.2	1.1	0.5	0.2	0.2
	0.4	0.9	0.4	0.2	0.2	0.6	0	0
EVI_1	0	0.1	0.2	0	0.5	0.4	0	0.4
	0	0	0	0	0.1	0.5	0	0
EVI_2	0.1	0.8	0.2	0	0	1.7	0.1	0
	0.3	2.8	0.6	0	0	0.3	0	0
EVI_3	0.2	0.4	0	0	0.1	0.5	0.5	0.8
	0.1	0	0	0	0	0	0	0
EVI_4	0	0.1	0	0.2	0.1	0.1	0.1	1.3
	0	0.1	0	0	0	0	0	0
EVI_5	2.6	8.2	0	1.9	0.2	0.2	0	0
	0	17.6	0	0	0	0.3	0	0
EVI_6	1.7	2	1.6	0.5	0.3	0.5	0	0
	0.5	1.6	3.7	0	0.1	2.3	0	0

EVI_7	0.3	0.1	0	7.9	0.2	0.8	0.1	2.1
	0	0.2	0	1.6	0.1	1.3	0	1.3
EVI_8	1.8	0.1	0.5	3	0.2	0.3	0.2	0
	3	0.1	0.4	6.4	0.3	1	0.1	0
EVI_9	0.2	0	1.2	0.3	0.1	0.7	0.1	0.1
	0.3	0	0.5	0.2	0.1	1.2	0.1	0
EVI_10	0	0.5	0	0	0.1	0.1	0	0
	0	0	0	0	0.1	0.1	0	0
EVI_11	0.2	0.6	0.9	5	0.8	0.5	0	1
	0.2	1.5	0.2	0.1	1.2	2.2	0	0
EVI_12	0.1	0.1	0	3.2	0.3	0.5	0	0.2
	0.1	0.5	0	1.7	0	1.5	0	0

Model assessment and statistical analysis

Table 4.6 – Area Under Curve (AUC) values for various Hanuman langur species

Species	**AUC±SD**
Semnopithecus hypoleucos achates	0.926±0.071
Semnopithecus hypoleucos hypoleucos	0.971±0.057
Semnopithecus priam anchises	0.987±0.005
Semnopithecus priam priamellus?	0.984±0.011
Semnopithecus priam	0.988±0.004
Semnopithecus entellus	0.855±0.025
Semnopithecus hypoleucos iulus	0.988±0.004
Semnopithecus johnii	0.992±0.005

Although the model performances are very good, we looked into niche (distribution) overlaps between species to understand boundaries of each species. Study normalized the area of distribution (p>0.5) for each of the species and compared pairwise overlapping regions in their distribution. Figure 4.4 below illustrates the Bray-Curtis similarity in percentage overlap of regions between two species. Percentage overlap ranged from 0 to 21.14%, indicating that none of the species have significant overlap in their distribution. *Semnopithecus priam-Semnopithecus johnii* with 21.14% and *Semnopithecus hypoleucos hypoleucos- Semnopithecus hypoleucos iulus* with 19.43% are the only two pairs sharing less than 25% of their distribution with each other.

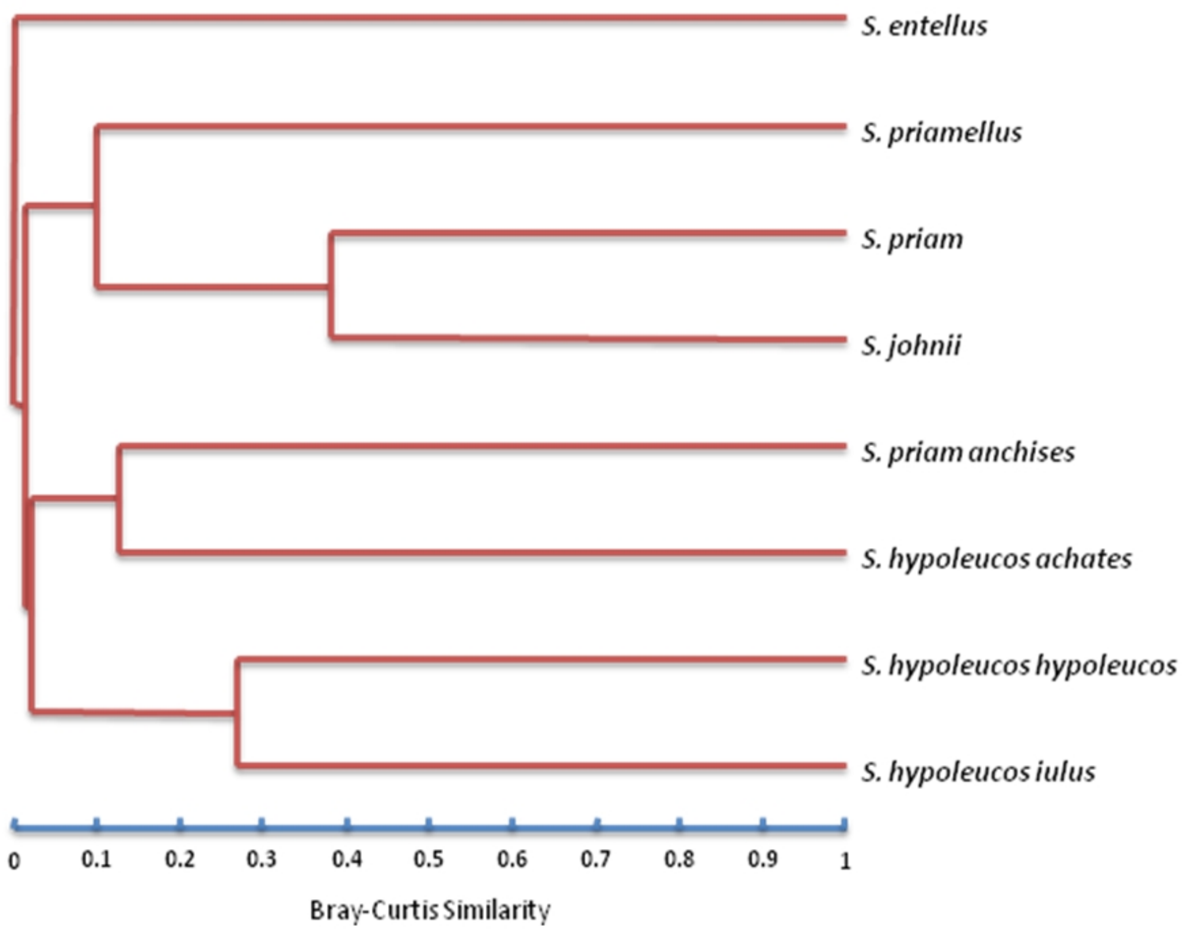


Figure 4.4 - Bray-Curtis similarity indexed overlap of regions between species of Hanuman langurs of peninsular India.

The minimally overlapping niches as shown in the dendrogram (*S. priam and S.johnii; S. hypoleuocs and S.h.iulus*) needs a statistical method to test the hypothesis of niche overlap and quantitatively measure the same. For which, study calculated three niche statistic, namely, Relative rank, I and D and tested niche conservatism for species with greater than 10% niche overlap.

Relative Rank Statistic (RR)

Table 4.7, provides RR statistic of niche overlap among various species of Hanuman langurs. This provides an estimate of probability that the relative ranking of any two patches of habitat is the same for the two models irrespective of quantitative difference in suitability estimates. According to RR values, habitats of *S.h.achates* and *S.h.hypoleucos*, *S.h.hypoleucos* and *S.h.hypoleucos*, *S.h.hypoleucos* and *S.p.priamellus*?, *S. johnii* and *S.priam* have higher (>=0.8) ranking, indicating they share similar kind of habitats with or without quantitative differences among the habitats. The remaining pair of species does not rank high among their habitats. As RR does not give quantitative differences between niches, study calculated D statistic.

Table 4.7- Relative ranking (RR) of similar habitat among the *Semnopithecus* species.

Species	*S.johnii*	*S.h.hypoleucos*	S.p.anchises	*S.p.priamellus*?	*S.priam*	*S.entellus*	S.h.iulus
S.h.achates	0.707	**0.835**	0.747	0.793	0.755	0.716	0.738
S.johnii		**0.819**	0.701	0.656	**0.800**	0.505	0.753
S.h.hypoleucos			0.719	**0.802**	0.798	0.644	0.705
S.p.anchises				0.664	0.682	0.662	0.775
S.p.priamellus?					0.730	0.795	0.584
S.priam						0.653	0.634
S.entellus							0.515

Study measured Schoener's (D) statistic for niche overlap as it very simple to calculate, used in many other studies and it permits direct comparison to traditional measures of niche similarity that focus on microhabitat (Warren et al., 2008). None of the niche overlap estimate using D statistic showed any significant niche overlap. In other words, it can be interpreted that all the *Semnopithecus* species have unique niches.

Table 4.8 - Niche overlap estimate D statistic.

Species	*S.johnii*	*S.h.hypoleucos*	S.p.anchises	*S.p.priamellus*?	*S.priam*	*S.entellus*	S.h.iulus
S.h.achates	0.247	0.311	0.497	0.340	0.241	0.239	0.457
S.h.hypoleucos		0.533	0.152	0.520	0.489	0.052	0.205
S.h.hypoleucos			0.172	0.530	0.243	0.139	0.358
S.p.anchises				0.200	0.250	0.154	0.288
S.p.priamellus?					0.398	0.166	0.227
S.priam						0.097	0.072
S.entellus							0.114

By considering spatial overlap and statistic measure of niche overlap, all *Semnopithecus* species of peninsular India have very unique niches and ecological variables to explain their distribution. However, physical overlap of *S.p.priam: S.johnii* and *S.h.hypoleucos: S.h.iulus* are 21.14% and 19.43% respectively, required an independent hypothesis testing using the distribution model. The identity test in the ENMtools is used to test whether ENMs generated from two or more species are more different than expected if they are drawn from the same underlying distribution (Warren et al., 2008). Identity test values between *S.p.priam and S.johnii*; *S.h.hypoleucos and S.h.iulus* are given in the histogram (Figure 4.5 and 4.6 respectively). Chi square (χ^2)test for the observed D value (through identity test) and expected D value (through niche overlap test) was 3.83, df=1, P>0.05, which did not statistically reject null hypothesis (Chi square table value was 3.84, df=1, p=0.05). However, Chi square test between *S.h.hypoleucos and S.h.iulus* was 52.02, df=1, p<0.001, indicating a clear rejection of null hypothesis and hence distinct niches between them.

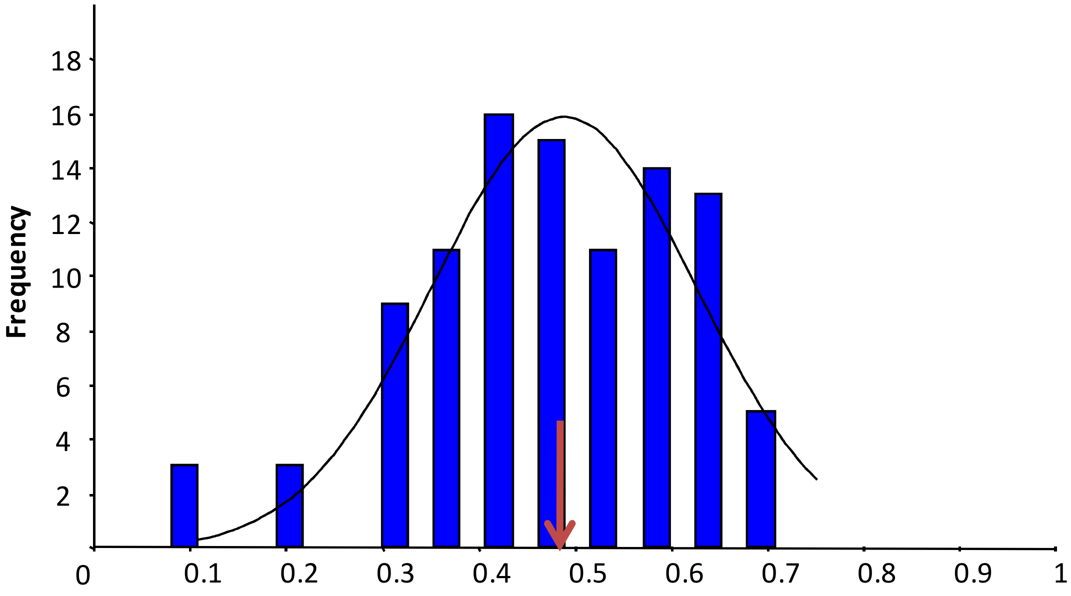


Figure 4.5 - Histogram of identity test D values between *S. johnii* and *S. priam* (D=0.487±0.137, 95% confidence value D=0.515). Red arrow indicates niche overlap statistic D value calculated using niche overlap (0.489).

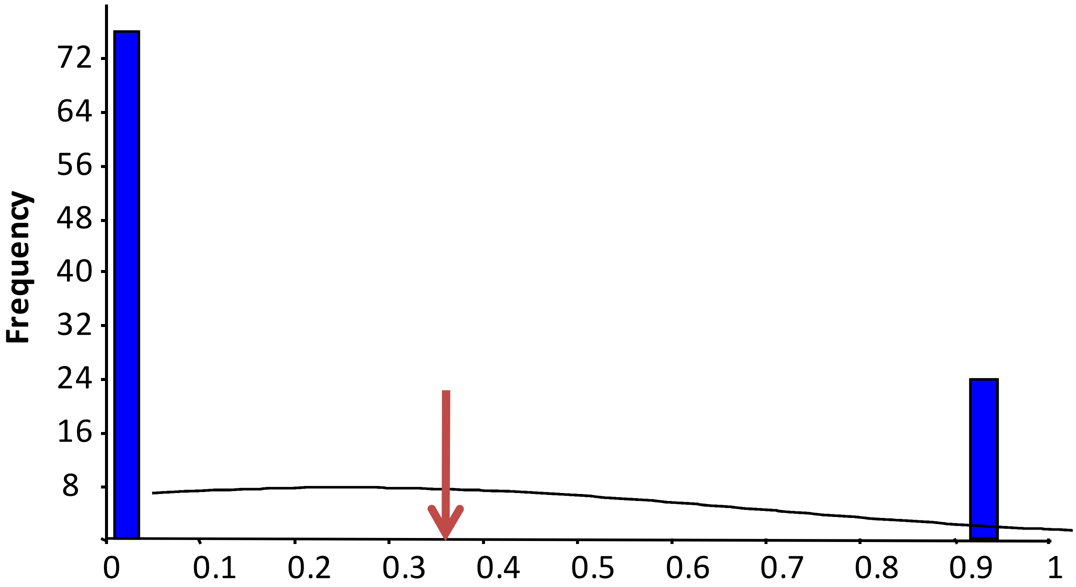


Figure 4.6 - Histogram of identity test D values between *S.h.hypoleucos* and *S.h.iulus* (D=0.254±0.421, 95% confidence value D=0.338). Red arrow indicates niche overlap statistic D value calculated using niche overlap (0.358).

Discussion

Species distribution modeling (SDM) based on maximum entropy (Maxent) algorithm explained distinct ecological niches of Hanuman langur species along with Nilgiri langur in peninsular India. It is to be recalled that according to Hill (1939) there are three species of Hanuman langurs in South India viz., *Semnopithecus entellus* having a northern tail carriage; *Semnopithecus hypoleucos* with three subspecies and *Semnopithecus priam* with two recognized subspecies. The seven distinct variations belonging to three species of Hanuman langurs have already been discussed in chapter 2 looking at morphological variations. In the present study, SDM clearly demarcated the ecological niches of various Hanuman langur species mentioned above, with higher AUC values in each of the distribution model. However, it required due support from ecological requirements of each of these species. The present study revealed such ecological niches and variables contributing to their distribution. At the outset the distributional areas of each of the Hanuman langur species from the niche modeling exercise established similarities in comparison with the morphological work. Also since the study aimed at understanding the ecological drivers of the so- called Hanuman langurs the present study employed 37 environmental layers instead of opting for a PCA which did not provide with satisfactory explanation of the variables of importance. Bioclim variables undoubtedly had the most contribution in determining the niche of a particular species followed by EVI and Hydrological layers (see table 4.5). Area under the curve (AUC) values for most of the candidate species were more than 0.9 thereby reflecting the robustness of the model. However the AUC value for *Semnopithecus entellus* was found to be at 0.85 which by definition is still a very good value. *Semnopithecus entellus* indeed had the widest distribution by far in peninsular India (table 4.6) thereby reflecting its huge adaptive nature to varying habitats.

Through this modeling exercise the study also looked at niche overlaps to understand the geographical boundaries of each of the Hanuman langur species and their subspecies in peninsular India. The model predicted that there were no significant overlaps between any two candidate species thereby ascertaining distinct ecological niches of Hanuman langurs of south India. In the present study, the ecological niches of *Semnopithecus johnii* and *Semnopithecus* *priam* were not resolved statistically (see table 4.8). Nilgiri langur (*S. johnii)* and *S. priam* both belong to Family: Cercopithecidae, and sub family: Colobinae. *S. johnii* is distributed in South India and is a well known distinct species of langurs wherein the individuals of species are easily distinguished by pelage color and vocalizations (Brandon-Jones, 2004; Hohmann, 1988 and 1991). There exists a primary difference with respect to black coat color of Nilgiri langurs in comparison to grey coat colored Hanuman langurs in South India. Also there exists a difference in calling patterns of Nilgiri langurs and Hanuman langurs (Hohmann, 1988 and 1991). *S. priam* with a prominent upstanding crest on the crown having a light grayish pelage color is distributed from Vempalli in Kadapa district of Andhra Pradesh to Kalakkad-Mundanthurai tiger reserve (KMTR) in Tamil Nadu. Northern parts of Sri Lanka have a slightly darker pelage color. The short phrased whooping loud calls of these species differ from that of *S. johnii* though both occupy the same habitat (Hohmann, 1988). While Nilgiri langurs are found in evergreen forests at higher elevations, *S.priam* are primarily found in deciduous forests.

The SDM predicted that *Semnopithecus priam* and *Semnopithecus johnii* shared 21.14% of niche. This prediction however in the light of my field observations should be cautiously viewed since these two colobines never shared their niches in majority of the localities. However there have been hybridizational events and associations occurring between these two distinct species in some parts of the Western Ghats since a long time (Chellam, 1995; Hohmann, 1989; Ramachandran et al, 2001). It is probable that model considered the localities where these two distinct species come together and thus might have predicted the overlap in niches. My personal observations of such associations have only been in the fringes of the forest where two habitats meet. Nevertheless such predictions hints at the limitations of SDM, that looking only from spatial variables may not provide complete niche separation of species. In such conditions, one must also look at other variables of species, viz., breeding behavior, feeding pattern, troop dynamics, and niche occupancy which can provide much deeper insight on realized niches of each species.

On the other hand the model also predicted niche overlaps between *Semnopithecus hypoleucos hypoleucos* and *S.h. iulus*. These two subspecies as per the model output shared 19.43% of their niche with each other. This is not surprising since both of these species were found in similar habitats during my field surveys. However *S.h.hypoleucos* always confined itself to wet evergreen habitat while *S.h. iulus* was found both in wet evergreen forests as well as habitats like moist to dry deciduos forests.

Another interesting output of the model is the support of a population of langurs known as Pocock's (1939) *priamellus* which are distributed north of Palakkad in the state of Kerala. These populations being morphologically different were distributed from Nilambur, Silent valley national park and Walayar during my field observations. These langurs which at present is either unrecognized or synonimised under *S.priam.* The SDM shows its niche as distinctive from all other with little overlap. Thus this population with reasonably good support from the present exercise should be considered to be a subspecies of *priam* for now. Interestingly Hill's classification scheme discussed *priam*ellus specimens as "doubtful" race in the light of the available evidence then. However he discussed *priam*ellus under *S. priam* giving enough reasons to be considered it as a subspecies of *S.priam*. However a detailed survey of this population should be undertaken which would give more clear distributional limits of this taxa.

Based on the ecological niches, many cryptic species or otherwise species complex similar to the present Hanuman langurs have been resolved in past (Hawks – Bosakowski et al., 1992; ants – Ross et al., 2010; beetles – Hawlitschek et al., 2011; plants – Smith and Donoghue, 2010, Reeves and Richards, 2011; salamanders – Rissler and Apodaca, 2007; Loris – Kumara et al., 2009). Based on the ecological niches of each species, I would like to put forth the classification which indicated such taxonomic units earlier (Hill, 1939) for future studies of this species. I also emphasize that, morphology, ecological niche and genetic data must complement each other to resolve the taxonomic identity of this taxonomically challenged primate of South India (Padial et al. 2010).

5. Variations in troop structure and composition among species of the Hanuman langur complex in peninsular India.

"...Averages are merely statistical abstractions: only the individuals of which the populations are composed have reality. The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (eidos) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real" - Mayr (1959, cited in Mayr 1963, pp. 4–5).

Introduction

Group structures have known to shape an animal's morphology and behaviour (Kappeler, 2000). Primates exhibit a striking range of grouping patterns and complex social behavior providing a platform to study various aspects of socioecology of faunal social systems. Primate social organization with respect to adult sex ratios in general show variations from being solitary to all male/ all-female groups, unimale or harem, multimale, age graded male groups, fission-fusion groups etc. (Kappeler, 2000; Eisenberg et al, 1972).Variation in troop compositions of primates is interesting since it has important consequences for social behaviour at several levels. For example a swap from unimale troopism to multi-male troopism has been explained in terms of mating system and reproductive strategies of both the sexes (Struhsaker, 2000). Besides, understanding and describing the demographic variances in non-human primates aids in development of credible models and also to develop effective conservation management plans. There have been several studies to explain and understand the variation in primate social structures. For example Andelman (1986) observed the adult sex ratios among multi-male cercopithecines were relatively invariant thereby challenging the notion that multi maleness is an adaptation to high predation pressure. Jeanne Altmann (1990) emphasized the importance of studying population sex ratios with respect to male reproductive strategies. Estimates of group size variability in a number of Cercopithecids have been provided in order to investigate differences in mean group size across species (Melnick and Pearl, 1987; van schaik and van Hooff, 1983).Crockett and Eisenberg (1987) cited interspecific difference among Alouatta species to the typical number of adult females. They invoked main factor limiting the number of adult females per troops to female reproductive competition.

Troop size and troop compositions in non-human primates are known to be a species specific trait (Carpenter, 1942).Also it's noteworthy that the size and composition of primate groups vary tremendously across species over a time scale (Kappeler, 2000).However Clutton-Brock and Harvey (1977) explained the nature of observed variation by studying the troop composition, troop sizes and other population parameters and argued that social organization was not entirely independent of taxonomic affiliation. Nevertheless demography and certain life history parameters in relation to ecological factors such as diet, habitat, and territoriality are largely invoked to explain the inter-specific variation amongst primate social organization (Clutton-Brock and Harvey, 1977; Eisenberg et al, 1972; Goodall 1986; Yamagiwa 1999).In addition to the species specific balance in numbers, it has been shown that behavioral attributes of a species also tend to be relatively constant, reflecting species specific adaptation (Eisenberg et al, 1972).Variability thus in group size and compositions has been linked to the stability of social groups (Poirier, 1969). Some of the above case studies clearly suggest that change and variability in troop structure and troop compositions are certain and the certainty has some implications both to theoretical and applied biology.

Since the first published report by Sugiyama (1965), Hanuman langurs have been the focal animal in studying various functional significance of their infanticidal behavior (Treves and Chapman 1996; Hrdy 1977; Borries 1997). Hanuman langur (Family: Cercopithecidae; Subfamily: Colobinae) are one of the highly studied non-human of primates in India which show extreme ecological adaptations and variable patterns of social organizations. Hanuman langurs live in one male bisexual groups (Unimale troops), multi-male bisexual groups, and temporary all-male groups with males being the dispersing individuals (Rajpurohit 1992; Newton 1994; Chhangani 2002; Newton and Dunbar 1994). Hanuman langurs are also known to show variations especially between different habitats (Mohnot and Srivastava 1992; Rajpurohit 1992; Srivastava and Dunbar 1996;Vogel, 1973; Eisenberg et al, 1972).For example

Vogel (1973) found significant differences in the acoustical repertoire of the Hanuman langurs of the two habitats and thus attributed the differences either to phylogenetic adaptations to different environmental conditions or to be related to special types of social organization in the two separate langur populations. However Sugiyama (1967) and Sugiyama and Parthasarathy (1978) observed that unimale Hanuman langur troop structures at Dharwad did not alter for a long period and opined that the maintenance of social structure for a long period is perhaps basic characteristic of the species itself. Thus Hanuman langur show extreme variations in both their size and composition. Nevertheless there have been very few studies regarding the troop structure and troop compositions of Hanuman langurs in peninsular India apart from Kurup (1984) survey in south India; Kumara et al (2010) survey in Karnataka and a few stray reports.

Interestingly majority of these surveys consider Hanuman langurs to be a single species and thus consider these demographic variations as intraspecific variation. However recent studies have clearly established that the Hanuman langurs constitute a species complex (Nag et al, 2011 and Karanth et al, 2010, and references therein). Thus the above studies need to be reinterpreted in the light of this alternate taxonomic scheme for the Hanuman langurs. Here I have used Hanuman langur classification proposed by Hill (1939) as recommended by Nag et al. (2011). The aim of this study was to find out if the various species of the Hanuman langur complex show significant differences in demographic variables.

Materials and Methods

The study was conducted between September 2007 and January 2011. Surveys were mostly opportunistic covering all states and their districts of peninsular India. Upon spotting the primate troop, sufficient time was devoted to collect data on details on location, habitat type, troop size, troop count, and troop composition. Group size was defined as total number of individuals found together in a specific group (within group data set) at the time of observation. Hrdy (1977) was followed for classifying troops as adult male, adult female, sub adults, juvenile, infants based on visible morphological characters. At any given time a troop was recorded as bisexual multimale troop if it contained more than one resident adult male with several adult females, juveniles and infants or as bisexual unimale troop if it contained only one full adult male with several adult females, juveniles and infants. All males living outside of a bisexual troops composing of several males irrespective of their age were recorded as all male group. Study could not be repeated since surveys were carried out in a large spatial area. Surveys were also conducted on foot along roads and trails mostly in the forested areas walking at an average speed of ~1km/h. Data was analyzed using PAST (Hammer et al, 2000)and Graph Pad Prism® trial software(GraphPad Prism version 5.04 for Windows, GraphPad Software, La Jolla California USA, www.graphpad.com).

Statistical analyses

The data set was tested for three species following Hill's (1939) classification schemes as suggested by Nag et al (2011) across peninsular India for the analysis. Only three all male bands (2 in Maharashtra state and one in Andhra Pradesh state of peninsular India) were encountered during the entire survey period. I was unable to determine the troop composition data for 9 troops. Troops, with incomplete data were not used in the analysis. Additionally since the identity of a population of langurs from Palakkad district of Kerala was unconfirmed I did not use them for the analysis. Variables such as troop size, adult female numbers, infant numbers used in the analysis were decided from a PCA plot. For each demographic variable, a one-way ANOVA followed non-parametric test (Mann- Whitney test) was performed to test for the differences between different species of langurs of south India. In case of overall significance, one-way ANOVA was followed by a post hoc comparison using a Bonferroni's test. The two-tailed (Wilcoxon) Mann-Whitney *U* non-parametric test was used to test whether the medians of two independent samples were different or not with the null hypothesis beingH_0: The two samples are taken from populations with equal medians. To estimate the proportion of variance explained by certain correlations, simple linear regression which analyzes the relationship between two variables, X and Y was used. All tests were considered significant at $p \leq 0.05$ with probability levels being two- tailed.

Results

Group size, adult female numbers and infant numbers turned out to be the strongest variables explaining 93.65 % variance in principal components analysis (PCA) for the present dataset. Thus we used these variables to test for significant differences and understand their role in troop composition amongst various species of Hanuman langurs. A one way ANOVA box plot showed the significant variations in means of group sizes ($F_{2, 100}=9.273$, $p<0.0001$) adult female numbers ($F_{2, 93}=10.83$, $p<0.0001$) and infant numbers$F_{2, 85}=6.379$, $p<0.0001$) of Hanuman langurs in peninsular India. In the box plot upper and lower whiskers (T) are the maximum and the minimum size values respectively that a troop exhibited in the present study. Horizontal thick lines inside the box plots are median values of respective Hanuman langur species in peninsular India. Note the difference in the upper (75 percentile) and the lower quartile (25 percentile) above and below the median values. While there was huge difference between maximum values and in upper quartile values for *priam* and *entellus*, there was very small difference between minimum values and lower quartile for *hypoleucos*.

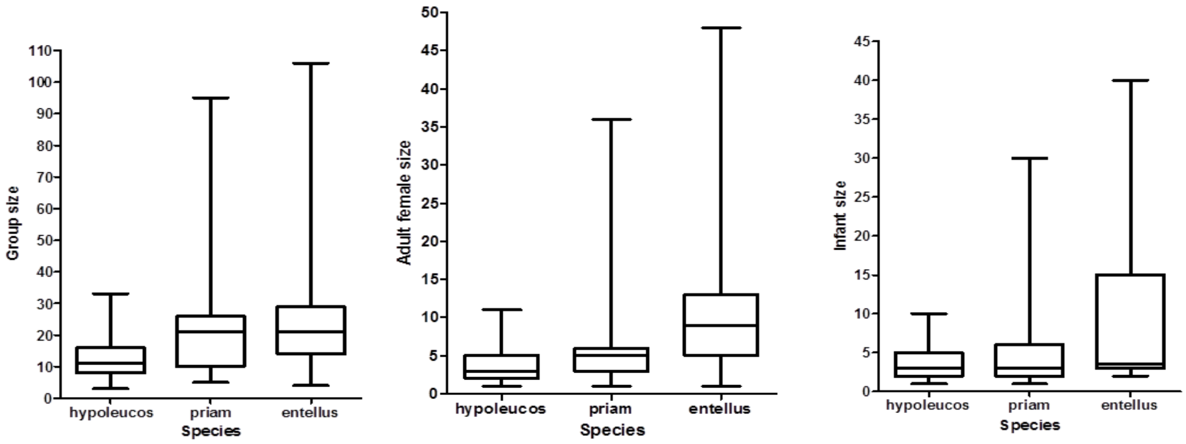


Figure 5.1 - One-way ANOVA box plot showing significant differences for various species of Hanuman langurs with respect to variables such as group size, adult female numbers and infant numbers.

Bonferroni's Multiple Comparison Test (One way ANOVA)

Bonferroni's Multiple Comparison test following a one-way ANOVA test showed that there was a significant difference in group size means between *hypoleucos* and *priam* as well as *hypoleucos* and *entellus* comparisons whereas there was no difference observed for *priam* and *entellus* group size means (Tables 5.1, 5.2 and 5.3).

Similarly there was significant difference in adult female number means between *hypoleucos* and *entellus* and *priam* and *entellus* comparisons. There was no significant difference observed for *hypoleucos* and *priam* comparisons dataset. Likewise Bonferroni's multiple comparison tests for testing means between the infant numbers showed significant difference for *hypoleucos* to *entellus* and *priam* to *entellus* comparisons while showed no significant difference at all for *hypoleucos* to *priam* comparison.

A Mann-Whitney test comparison across three species showed significant difference for *hypoleucos* to *priam* and *hypoleucos* to *entellus* datasets whereas failed to show difference for *priam* to *entellus* with respect to group size comparisons. While the test showed significant difference for all the three (*hypoleucos* to *priam*, *hypoleucos* to *entellus* and *priam* to *entellus*) comparisons with respect to adult female numbers it failed to show any difference in infant numbers for *hypoleucos* to *priam*, *hypoleucos* to *entellus* and *priam* to *entellus* comparisons.

Table 5.1-Bonferroni's Multiple Comparison Test and Mann-Whitney test results of Group size for three species of Hanuman langurs of South India.

MW test-→ **Bonferroni test ↓**	*hypoleucos*	*priam*	*entellus*
Hypoleucos		**	**
priam	**		**ns**
entellus	**	**ns**	

** Statistically significant   ns- not significant

Table 5.2 -: Bonferroni's Multiple Comparison Test and Mann-Whitney test results of Adult female numbers for three species of Hanuman langurs of South India.

MW test-→ **Bonferroni test ↓**	*hypoleucos*	*priam*	*entellus*
hypoleucos		**ns**	**
priam	**		**ns**
entellus	**	**	

** Statistically significant   ns- not significant

Table 5.3 -Bonferroni's Multiple Comparison Test and Mann-Whitney test results of infant numbers for three species of Hanuman langurs of South India.

MW test-→ **Bonferroni test ↓**	*hypoleucos*	*priam*	*entellus*
hypoleucos		**ns**	**
priam	**ns**		**
entellus	**ns**	**ns**	

** Statistically significant   ns- not significant

Table 5.4 -Group size data of Hanuman langur species of peninsular India

Taxon	Mean ± SD	Range	25 percentile	Median	75 percentile	Unimale troops(numbers)	Multimale troops(numbers)
S. hypoleucos	12.5 ± 6.7	3- 33	8	11	16	55	4
S. priam	22.3 ± 18.4	5- 95	10	21	26	9	7
S. entellus	28.1± 27.4	4- 106	14	21	29	10	1

Table 5.5 - Adult female and infant numbers of different species of Hanuman langurs of South India

Taxon	Adult female numbers	Infant numbers	Adult female numbers	Infant numbers	Adult female numbers	Infant numbers	Adult female numbers	Infant numbers	Adult female numbers	Infant numbers
	Mean ± SD		Range		25 percentile		Median		75 percentile	
S. hypoleucos	3.60 ± 2.3	3.6 ± 2.2	1 - 11	1 - 10	2	2	3	3	5	5
S. priam	6.3 ± 6.9	5.18 ± 5.9	1- 36	1- 30	3	2	5	3	6	6
S. entellus	12.3 ± 13.1	10.3 ± 13	1- 48	2- 40	5	3	9	3.5	13	15

Table 5.6- Different age–sex ratios of the Hanuman langur species of peninsular India. (M: F- Male to Female, F: J- female to juvenile, F: I- female to infant).

	Mean troop size	Mean Ratio (M:F) Unimale troops	Mean Ratio (M:F) Multimale troops	Mean Ratio (F:J) Unimale troops	Mean Ratio (F:J) Multimale troops	Mean Ratio (F: I) Unimale troops	Mean Ratio (F: I) Multimale troops
S. hypoleucos	12.57	1: 3.26	1: 1.36	1: 1.00	1: 1.33	1: 0.93	1: 1.26
S. priam	22.3913	1: 4.78	1: 2.05	1: 0.61	1: 0.73	1: 0.80	1: 0.76
S. entellus	10.375	1: 12.55	1: 2	1: 0.46	1:1	1: 0.76	1: 0.4

I used a simple linear regression analysis to understand the relative contribution the demographic variables such as group size, adult female numbers and infant numbers shaping the troop composition. The study thus found significant positive linear relationships (Tables 5.7, 5.8 and 5.9) between variables such as group size, adult females and infant numbers with good R square values for some species.

Table 5.7 - Relationships of group size (Y axis) and adult female numbers (X axis) between various species of Hanuman langurs of peninsular India

	Slope	**R square**	**P value**
hypoleucos	2.356 ± 0.2040	0.6861	< 0.0001
priam	2.483 ± 0.1949	0.8855	< 0.0001
entellus	2.086 ± 0.06822	0.9915	< 0.0001

Table 5.8 - Relationships of group size (Y axis) and infant numbers (X axis) between various species of Hanuman langurs of peninsular India

	Slope	**R square**	**P value**
hypoleucos	2.196 ± 0.2539	0.5719	< 0.0001
priam	2.795 ± 0.3181	0.7942	< 0.0001
entellus	2.203 ± 0.2332	0.9370	< 0.0001

Table 5.9 - Relationships of adult female numbers (X axis) with infant numbers (Y axis) between various species of Hanuman langurs of peninsular India

	Slope	**R square**	**P value**
hypoleucos	0.6339 ± 0.09582	0.4387	< 0.0001
priam	0.7951 ± 0.05956	0.8991	< 0.0001
entellus	0.8986 ± 0.07941	0.9552	< 0.0001

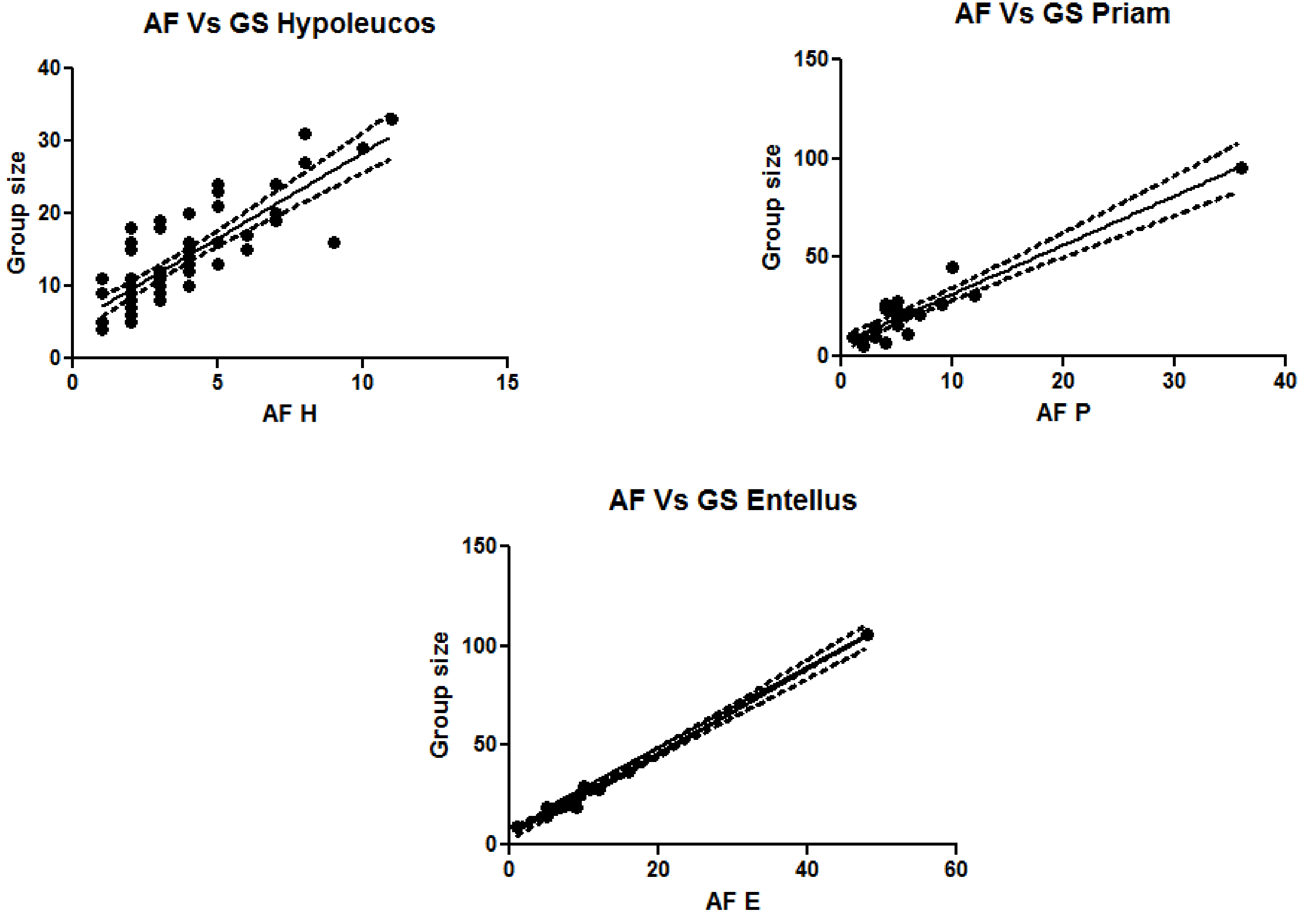


Figure 5.2 - Effect of Adult female numbers on group size of Hanuman langurs of peninsular India. Dotted lines are the 95% confidence intervals of the best fit values.

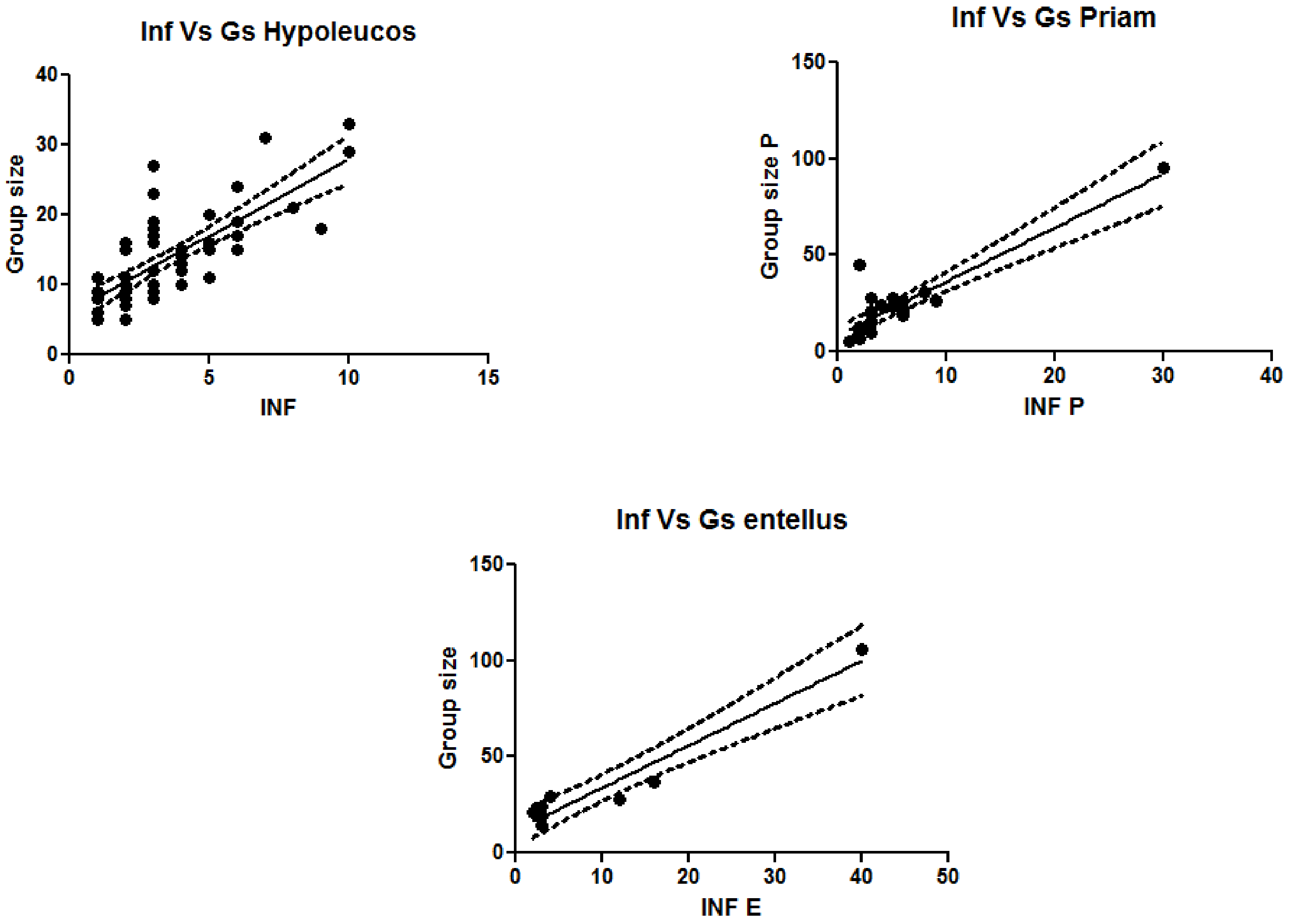


Figure 5.3- Effect of infant numbers on group size of various species of Hanuman langurs of peninsular India. Dotted lines are the 95% confidence intervals.

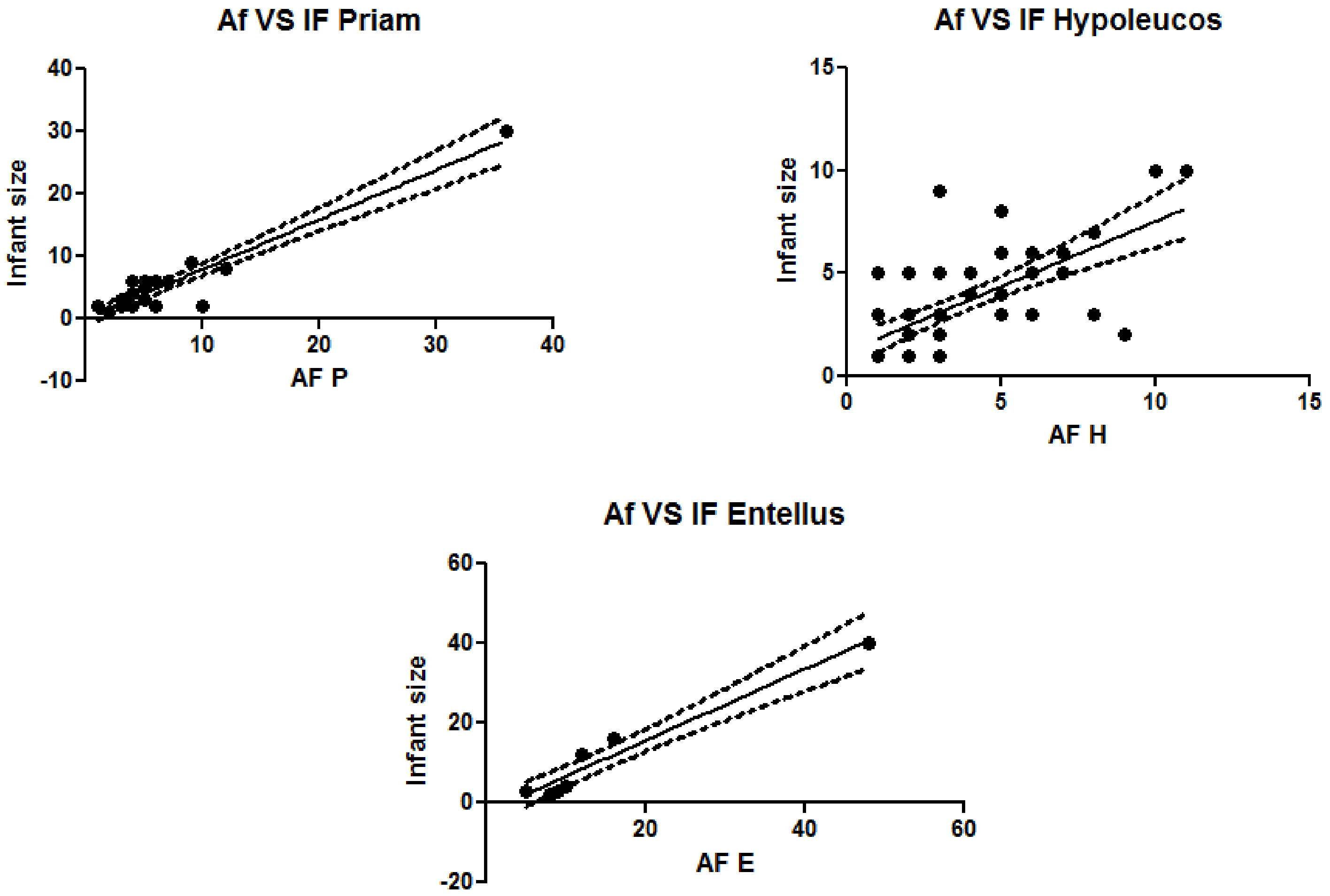


Figure 5.4 - Effect of adult female numbers on infant numbers of various species of Hanuman langurs of peninsular India. Dotted lines are the 95% confidence intervals.

Discussion

The present study suggests that indeed there happens to be an overall variation shown by various tests amongst different species of Hanuman langurs with respect to the various demographic variables (Figure 5.1).In total 78.9% unimale troops followed by 11 % multimale troops and 2% all male troops were observed during the study period. Variables such as group size, adult female numbers, and infant numbers in varying capacities did play some role in capturing variation across species of these Hanuman langurs (Tables 5.1-5.5). I followed Hill's (1939) classification schemes for the analysis of the dataset where south Indian langurs are grouped into 2 species namely *Semnopithecus hypoleucos* and *Semnopithecus priam.* I have also used *Semnopithecus entellus* from the same classification scheme to describe northern type langurs.

Hill's (1939) classification scheme further divides *S. hypoleucos* to various subspecies namely *S.h.*achates in the drier areas of Karnataka, Maharashtra and West Andhra Pradesh; *S.h.iulus* in the western Ghats ranges of Karnataka, Goa and Maharashtra ; *S.h.hypoleucos* in the wet evergreen forests of Karnataka ; *S.h.aeneas* in the wet evergreen forest of Karnataka and Kerala border. Largely *S hypoleucos* species groups ranged from a minimum of 3 to a maximum of 33 in the present study with a mean value of 12.57 (Table 5.3). Noteworthy are the values of quartile ranges of these species group which ranged from 8 -16. With a median value of 11 the group size varied from 16 (75 percentile value) to 33 at the upper end whereas the variation at lower end was negligible. This indicates that leaving out the extreme values, there is a higher probability of this species having a group size of 8-16 (Figure 5.1). Interestingly, values larger than 16 up to the maximum value of 33 were observed mostly in the places where anthropogenic pressures were high. Adult sex ratios varied from 3.26 females for every male in a unimale troop as against 4.62 and 4.94 observations of Sugiyama (1964) and Kumara et al (2010) from the Dharwad population. Adult sex ratios were 1.36 females per male in a multimale troop of this species across peninsular India. According to the relationship plots, there were significant relationships between the group size to adult female, group size to infants and adult females to infants (Figure 5.1). The slope values thus suggested that in this species, total group size of adult females could vary from 39.06% to 46.46% and total group size of infant numbers could vary from 40.83% to 51.49%. However the number of infants per female which predicts the female fitness was found to be little low with the values between 0.72- 0.53 infants per adult female for *S. hypoleucos*.

Noteworthy are the subspecies *Semnopithecus hypoleucos hypoleucos and Semnopithecus hypoleucos aeneas* which were confined to the wet evergreen forests of Western Ghats usually was found in very small group sizes. In the present survey, group sizes of this subspecies were higher in numbers in and around places often occupied by tourists. It is a common practice for primates to have a larger troop size as a strategy for protecting the troop members from the threats due to human presence. Otherwise these subspecies always remained arboreal, very shy, and elusive with an average of 10 members per troop (data not shown).The small troop sizes are also a characteristic feature of Nilgiri langurs (*Semnopithecus johnii)* who also inhabit wet evergreen forests of Western Ghats with mean group sizes up to 14 (Poirier, 1969; Tanaka, 1965; Sunderraj 2001; Hohmann, 1989). However because of the dense canopy in these evergreen forests and the very shy nature of the subspecies *Semnopithecus hypoleucos hypoleucos*, I, was not able to encounter these langurs inspite of the best efforts to trace them in the wet evergreen areas which had bearing on the overall sampling size. On the other hand amongst all other species in peninsular India, the arboreal subspecies *S.h.aeneas* always showed a uniform adaptation to a specific habitat (wet evergreen, semi evergreen) thus displayed a corresponding uniformity in their grouping tendencies. Also noteworthy is the fact that, I could not find a single instance of multimale troop structure in *S. h. hypoleucos* and *S.h.aeneas* during my entire study period. This seems to be consistent with the fact that highly arboreal primates do tend to have only unimale troop structure (Eisenberg et al, 1972). Likewise since the group size are less it can also be argued that the home range, predator pressure of this folivorous species should also be relatively less (van Schaik and van Hooff,1983) in comparison to their terrestrial counterparts. Conversely smaller group sizes of this species may also be a strategy to avoid hunting pressures (please refer van Schaik and van Hooff, 1983). Chapter 1 do notes such high hunting pressures in and around the habitats occupied by this species. Nevertheless it is too early to arrive at a conclusion and a long term study should give us more insights of their social structure.

Semnopithecus priam which is further divided into various subspecies such as *S.p.priam* along the Cauvery river banks of Karnataka and Tamil Nadu, south of Palakkad gap in Kerala and Tamil Nadu; *S.p.anchises* from north of Cuddapah to Srisailam all along the eastern Ghats. In general *S.priam* species groups ranged from a minimum of 5 to a maximum of 95 in the present study with a mean value of 22.39. With a median value of 21 the group size varied from 26 (75 percentile value) to 95 at the upper end whereas the variation at lower end was negligible. This also meant that there is a higher probability of *priam* species being sighted at a group size between the quartile ranges of 10 -26. Like *S. hypoleucos* troop size of *S.priam* larger than 26 were observed mostly in the places where anthropogenic pressures were high. There were 4.7 females for every male for unimale troops and 2 females per male in multimale troops. It can be observed from the regression plots that the relation between group size versus adult female, group size versus infant and adult female versus infant all were very significant for this *priam*. According to the relationship plots, there were significant relationships between the group size to adult female, group size to infants and adult females to infants. The relationship plots thus suggest that in this species, 37.45% to 43.85% of the group population will likely be adult females and 32.15% to 40.38% will be infants. However the number of infants per female which predicts the female fitness was found to be with the values between 0.73- 0.85.Additionally my field observation is suggestive of the trend that *S. priam* had higher tendencies of multimale troops in south India. Of the total S. *priam* troops I have come across, approximately 43% of them were multimale troops in south India. Interestingly anecdotal evidences seems to suggest that human presence seem to have much influence in determining multimaleness in these species at least in places like Tirupathi, Horsley Hills, , Cuddapah in the state of Andhra Pradesh and Kalakkad-Mundanthurai Tiger reserve, Theppakad of Tamilnadu. I however refrain from generalizing this pattern for this species in the light of few sample size.

Semnopithecus entellus groups ranged from a minimum of 4 at East Godavari district of Andhra Pradesh to a maximum of 106at Nanded district of Maharashtra in the present study with a mean value of 28.1. The values of quartile ranges of these species were between 14 -29. With a median value of 21 the group size varied from 29 (75 percentile value) to 106 at the upper end and from 14 to 4 at lower end. Adult sex ratios varied from 12.5 females per male in a unimale troop whereas it was 2 females per male in a multimale troop. Though it must be noted that this species showed huge variation, my sampling in this study was restricted to borderline areas between Tapti and Godavari rivers in peninsular India and henceforth cannot conclude on its group size trends for now. Besides several anecdotal evidences have also suggested such huge variation in the troop sizes of these species. However it seems that these species which were often sighted in drier habitats of peninsular India most often encompassed considerable individuals in their troops (Hrdy, 1977; Sugiyama, 1964). From the regression plots, the relation between group size to adult female, group size to infant and adult female to infant all were very significant for this species. Accordingly in a group, 46.59% to 49.55% will likely be adult females, 40.65% to 50.76% would be the infant counts. The positive relationship between infant numbers on adult female numbers has an important corollary to make in the light of infanticide. It shows that the numbers of infants necessarily has positive impact on the adult female numbers. It is a known fact that female fitness is limited by the number of offspring she rears (van Schaik and van Hoof, 1983). Going by the present dataset, the slope values for this species suggested positive female condition whose female to infant ratios were 0.82- 0.969. The present dataset for NT also seems to be consistent with the observations that all male troops are more likely to be formed where the female numbers are high (Grueter and van Schaik, 2009). Out of the 3 all male troops that were found, 2 belonged to the NT species and one belonged to *S. hypoleucos* all of which had high female numbers.

Interestingly in my field surveys I could locate one additional morphotype in south India which Hill (1939) did not assign species status. However other classification schemes (reviewed in chapter 1) identify this morphotype as *iulus*. This species was found only north of Palakkad gap in places like Walayar, Silent valley national park, and Nilambur. These groups yet to be confirmed ranged from a minimum of 4 to a maximum of 15 in the present study with a mean value of 9.09. The values of quartile ranges of these species which ranged from 4 -13 as of minimum and maximum numbers with a median value of 9 suggested a very low or no variation at all. The data did not show any significant variation at both quartile ends. It can be observed from the regression plots that the relation between group size versus adult female and adult female versus infant failed to show statistical significance while relation between group size versus infant showed significant result for this species . The relationship thus suggests that in these groups approximately 22.32% to 39.66% will likely be infants. More intensive surveys are warranted to get a better picture of this species.

Thus the present study showed that the three species of langurs exhibited significant difference in social structure which in turn might be adaptation to differing habitats . Variation in group size has been attributed to the variation in diet leading to formation of uni-male/multimale formation, male/female dispersal tendency (Treves and Chapman 1996, Koenig and Borries, 2001). It has been shown that group sizes amongst terrestrial species are larger than the arboreal ones (Clutton- Brock and Harvey, 1977; Wrangham, 1980). For example with a mean group size of 28.1, *S. entellus* showed significant variation from 4 to 106 in numbers in comparison to other species making them stand apart from the rest of langur populations in peninsular India. This observation of relatively large group size (Table 5.4) was also observed in *S. priam* in the present study. These species which were often terrestrial/semi terrestrial usually occupied drier habitats and human habitations. The relatively larger group size of these species on the other hand also may indicate their adaptation for a varied diet. Though there have been studies to demonstrate the ability of the Hanuman langurs to exploit abundant food source (having a more diverse diet) thereby reducing selectivity during periods of low food availability (Sushma and Singh, 2006; Roy et al, 2010; Hladik, 1977) all of the observations excepting Sugiyama (1964) come from wetter areas of peninsular India. Additionally, group sizing can also be influenced by human interventions. There have been studies to suggest that food provisioning might have strong implications on primate social structure (Sinha et al, 2005; Mathur and Manohar 1986). I have personally seen troop members of all the species in South India being provisioned by humans, which could have resulted in group sizes, being generally larger in comparison to the unprovisioned ones.

However it is noteworthy that present study considered tests as significant at $p \leq 0.05$ and any value slightly higher than 0.05 would be considered as not significant. Also the present study was a part of a molecular study conducted in the entire peninsular India; sampling was thus largely opportunistic surveys. As a result, observations of the present study thus might be little grosser and may be prone to some errors. Moreover since the demographic data required for a proper test is lacking for most of these species, many of socio-ecological hypotheses which could have explained the social structure of Hanuman langurs in south India is still warranted. Apart from the detailed long term studies in Dharwad by Sugiyama et al between 1960's-1970's and one study by Ross (1993) there have been absolutely no long term studies in the entire south India to the best of my knowledge. As Struhsaker (2008) rightly puts "It is imperative for both applied and theoretical science that we exert greater effort to incorporate in all studies and syntheses the variation that occurs within species and their populations over space and time". Thus there is strong need for a long term standardized data along with yearly surveys regarding demography to get a clearer picture of the social structure of Hanuman langurs of peninsular India.

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Appendices

A list of some food plants that Hanuman langurs foraged during the present study period.

Locality	Family	Genus/Species	Parts Eaten	Species (Hill, 1939)
Kadalekaalu Ganesha Temple,Hampi	Boraginaceae	*Cordia sp?*	Leaf	*Semnopithecus hypoleucos* achates
Kadalekaalu Ganesha Temple,Hampi	Molaceae	*Ficus religiosa*	Leaf	*Semnopithecus hypoleucos achates*
Hampi	Rumnaecease	*Ziziphus manritiana*	Leaf	*Semnopithecus hypoleucos achates*
Hampi	Euphorbiaceae	*Fluggea leucopyros*	Leaf	*Semnopithecus hypoleucos achates*
Hampi	Rubiaceae?	*?*	Leaf	*Semnopithecus hypoleucos achates*
Hampi	Rhamnaceae	*Ziziphus ocuoplea*	Leaf	*Semnopithecus hypoleucos achates*

Haveri	Apiaceae	*Pimpinella Sp*	Leaf	*Semnopithecus hypoleucos achates*
Haveri	Fabaceae	*Acacia Sp?*	Leaf	*Semnopithecus hypoleucos achates*
Haveri	Convolvulaceae	*Evolvulus alsinoides?*	Leaf	*Semnopithecus hypoleucos achates*
Haveri	Anacardiaceae	*Mangifera indica*	Leaf and fruit	*Semnopithecus hypoleucos achates*
Bondla w s ,Goa	Euphorbiaceae	*Mallotus stenanthus*	Leaf	*Semnopithecus hypoleucos iulus*
Bondla w s ,Goa	Poaceae	*Ochlandra thwatsii*	Leaf	*Semnopithecus hypoleucos iulus*
K.Rampura,Pavgada	Apocynaceae	*Wrightia tinctoria*	Leaf	*Semnopithecus priam anchises*
Soraba	Moraceae	*Artocarpus heterophyllus*	Leaf	*Semnopithecus hypoleucos achates*
Jog falls	Fabaceae	*Pongamia pinnata*	Leaf	*Semnopithecus hypoleucos iulus*
Haunsbhavi	Meliaceae	*Azadirachta indica*	Leaf	*Semnopithecus hypoleucos*

				achates
Honnvara	Anacardiaceae	*Mangifera indica*	Leaf	*Semnopithecus hypoleucos iulus*
Kollur	Loganiaceae	*Strychnos nox-vomica*	Fruit/leaf	*Semnopithecus hypoleucos iulus*
Jog falls	Fabaceae	*Pithecolobium saman*	Leaf	*Semnopithecus hypoleucos iulus*
Hampi	Muntunjiaceae	*Muntingia calabura*	Leaf	*Semnopithecus hypoleucos achates*
Hampi	Fabaceae	*Cassia alata*	Fruit	*Semnopithecus hypoleucos achates*
Ranebennur	Fabaceae	*Peltophorum ferrugineum*	Leaf	*Semnopithecus hypoleucos achates*
Shikaripur	Fabaceae	*Bauhinia variegata*	Leaf	*Semnopithecus hypoleucos achates*
Anshi	Lauraceae	*?*	Fruit	*Semnopithecus hypoleucos iulus*
Warangal	Fabaceae	*Acacia Sp?*	Leaf	*Semnopithecus entellus*
Madanapalli	Verbenaceae	*Lantana camara*	Leaf	*Semnopithecus priam priam*

Panhala , Kolhapur	Moraceae	*Ficus religiosa*	Leaf	*Semnopithecus hypoleucos achates*
Kapilatheertham, Chittoor	Bignoniaceae	*Millingtonia hortensis*	Leaf	*Semnopithecus priam priam*
Muthanga	Lythraceae	*Lagerstroemia microcarpa*	Leaf	*Semnopithecus priam priam*
Muthanga	Fabaceae	*Pterocarpus marsupium*	Leaves	*Semnopithecus priam priam*
Muthanga	Fabaceae	*Albizia lebbeck*	?	*Semnopithecus priam priam*
Bandipur	Fabaceae	*Butea monosperma*	Flower	*Semnopithecus priam priam*
Nhole	Combretaceae	*Terminalia sp*	Leaves	*Semnopithecus hypoleucos achates*
Devarayanadurga	Fabaceae	*Pithecolobium saman*	Flower	*Semnopithecus priam anchises*
Devarayanadurga	Fabaceae	*Albizia procera*	Fruit	*Semnopithecus priam anchises*
Muthanga	Litraceae	*Lagerstromia microcarpa*	Leaves	*Semnopithecus priam priam*
Panhala , Kolhapur	Sapotaceae	*Mimusops elengi*	Leaves	*Semnopithecus hypoleucos achates*

Panhala , Kolhapur	Magnoliaceae	*Michelia sps*	Leaves	*Semnopithecus hypoleucos achates*
Panhala , Kolhapur	Caesalpinieae	*Delonix regia*	Leaves	*Semnopithecus hypoleucos achates*
Bandigudde, Bhadravathy	Fabaceae	*Tamarindus indica*	Leaves	*Semnopithecus hypoleucos achates*

DATA SHEET FOR HANUMAN LANGURS

MALE / FEMALE

Name of the Observer

DATE: **TIME:** **PLACE:**

UNIMALE (um)/MULTIMALE (mm)/ALL MALE (al m):

Troop Size (in numbers):

Adjacent Troops (if any): **Distance :**

Troop count(in numbers)

A♂	A♀	AFI	UA	SA♂	SA♀	USA	Juveniles	Infants

Local name for langur(Kan/Tam/Tel/Mal):

Description of the animal
1. **Head** :
Crest/Crestless:
Whiskers present/Absent:
Head color (Ex: Blond, White Etc.,):
Color of the Mane:
Brow Fringe Present/Absent :
Fringe color:
2.Neck Color:
Nape Color:
3.Body Color:
Dorsal :
Chest:
Belly:
Loin :

Flank:

Anus/Rump:

4. Hand:

Forearm:

Shoulder color:

Palm color:

Wrist color:

Paw color:

Knuckles:

5. Legs :

Thigh Color outside: Inside:

Knee Color:

Shank Color:

Foot Color:

6. Tail loop(Diagram)

Tail color:

Tail tip color:

Ecological data

Diet(Food): Please collect the Samples(√)

Stem Inflorescence Leaves Flowers Fruits

Seeds Any others

Average height of foraging:

8. Vegetation type

9. Altitude (in mts):

10. Latitude : **Longitude:**

11. Distance from the water bodies:

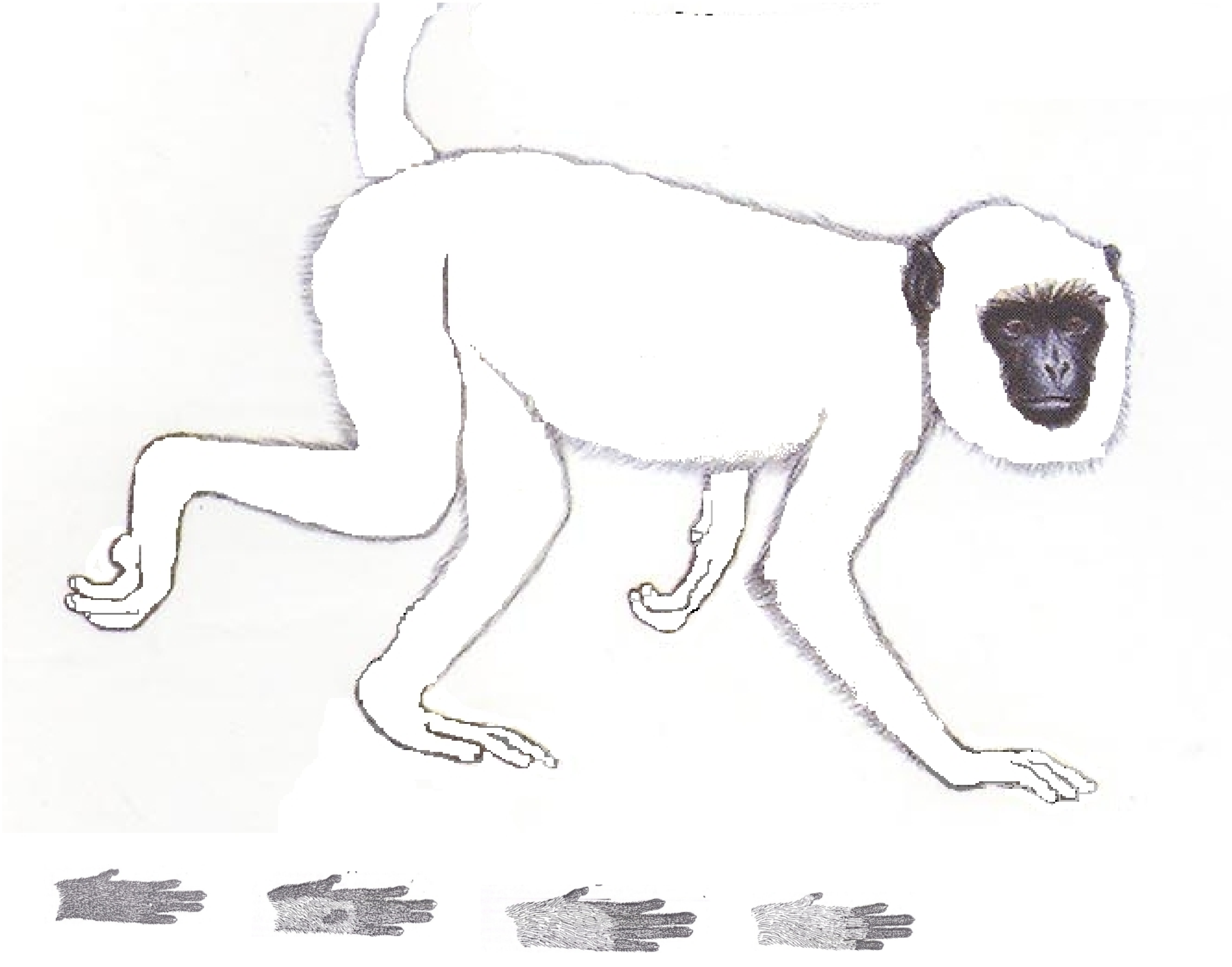
12. Nearest human habitat:

Habitat Pictures (√ or X)

Hair samples

Faecal samples

Picture Numbers :



Date: Place: Observer name:

Semnopithecus hypoleucos achates from Nagarahole National park, Karnataka. Pic courtesy: Talat Khalid

Semnopithecus hypoleucos iulus from Castle rock, Karnataka. Pic courtesy: K.Subramanian

Semnopithecus hypoleucos aeneas from Trivandrum Zoo

Semnopithecus priam priam from Bandipur national park, Karnataka

Pic courtesy : Ashok Kumar Mallick

Semnopithecus priam anchises from Kurnool, Andhra Pradesh

Semnopithecus priam thersites from Mundanthurai, Tamil Nadu

Pic courtesy : K.S.Sheshadri

Semnopithecus priam priamellus? from Walayar Deer park, Kerala

Pic courtesy: Achyuthan

Semnopithecus entellus from Palamu, Jharkhand

Pic courtesy: Azhivalagan